Swimming Sea Cucumbers (Echinodermata: Holothuroidea): A Survey, with Analysis of Swimming Behavior in Four Bathyal Species

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ABSTRACT

Miller, John E., and David L. Pawson. Swimming Sea Cucumbers (Echinodermata: Holothuroidea): A Survey, with Analysis of Swimming Behavior in Four Bathyal Species. *Smithsonian Contributions to the Marine Sciences*, number 35, 18 pages, 4 figures, 1990.—New information on swimming behavior of four species of deep-sea holothurians has been obtained using the research submersibles *Johnson-Sea-Link* (Harbor Branch Oceanographic Institution) and *Pisces V* (University of Hawaii, HURL Program). *Hansenothuria benti* Miller and Pawson and *Enypniastes eximia* Theel were studied off the Bahama Islands, *Paelopatides retifer* Fisher off the Hawaiian Islands, and *Pelagothuria natatrix* Ludwig off the Galapagos Islands. Video recordings were made of swimming behavior, and individuals of all species were collected at the time of observation. Four contrasting life modes are represented: *H. benti* lives and feeds on the seafloor, but when disturbed it can swim vigorously for several minutes by rapidly flexing the anterior and posterior ends of the body into S curves. *Enypniastes eximia* swims almost continuously, briefly settling to the seafloor to ingest surface sediments. The bulbous body is propelled upwards by rhythmic pulsation of a webbed anterodorsal veil; stability during swimming is maintained by counteractive flexing of posterolateral veils. *Paelopatides retifer* lives on or near the seafloor and has been found up to 300 meters above the seafloor. The swimming behavior of this species combines locomotory movements of the two preceding species. An anterior veil pulsates, and the posterior half of the body flexes into S curves. *Pelagothuria natatrix* is truly pelagic, floating or drifting near the seafloor or high in the water column. Swimming is effected by infrequent and irregular pulsation of an enormous anterior veil. There is no evidence to suggest that *P. natatrix* descends to feed on the seafloor.

Published data on the approximately 25 known species of swimming holothurians are summarized. Probable reasons for swimming behavior are discussed. Swimming appears to be most useful in predator avoidance, escape from physical hazards, locomotion, seeking out suitable substrata for feeding, and dispersal of juveniles or adults.

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Introduction

Holothurians have long been known to comprise an important component of the deep-sea fauna (Théel, 1882). In extensive areas they comprise up to 95% of the megafaunal biomass, and they are abundant even at hadal depths (Heezen and Hollister, 1971). The numerous epibenthic species are mobile, and they are capable of ingesting and reworking copious quantities of surface sediments; accordingly, the holothurians are important reworkers of soft bottom habitats.

The ability of some sea cucumber species to leave the seabed and venture upwards into the water column has been documented numerous times over the 120 years since the first report (Sars, 1867) of swimming in *Bathyplotes natans* Sars. Although at least six shallow-water species have been reported to swim, the true natatorial acrobats among the class Holothuroidea are deep-sea species of the orders Aspidochirotida and Elasipodida. Approximately 20 species in the families Synallactidae, Psychropotidae, Elpidiidae, and Pelagothuriidae have been captured or observed near the bottom or at depths several hundred to several thousand meters above the seafloor. A few deep-sea species have even been found in surface waters.

Species that are capable of active swimming movements are also the dominant megafaunal element at some localities in the bathyal-abyssal zone. In general, holothurians that can swim descend to the seabed to feed, and some species can transport surface sediments for considerable distances, both horizontally and vertically, from the source area (Billett et al., 1985; Billett, 1986).

Several bathyal and abyssal species possess conspicuous external features that appear to be morphological adaptations for swimming, but they have not yet been captured or observed in the water column. Pawson (1976) suggested that as many as one-half of the approximately 110 species in the order Elasipodida might be capable of swimming activity.

In past studies, very few species of deep-sea holothurians had been observed to swim. Pérês (1965), reporting on observations from the submersible *Archimede* in the Puerto Rico Trench, mentioned a *Benthodytes*-like species swimming, and Barnes et al. (1976) recorded the swimming behavior of *Peniagone diaphana* from the submersibles *Turtle* and *Seacliff* off Southern California. Pawson (1976, 1982) provided several anecdotal notes on swimming in abyssal species from *Alvin* dives in the Tongue of the Ocean, Bahamas, and on the continental slope off the eastern USA. Otsuka (1987) reported his observations on swimming in *Enypniastes eximia* from the submersible *Shinkai 2000* in the Suruga Trough, Japan. Additional information on deep-water swimmers has been compiled through chance collections in plankton nets (Hansen, 1975; Billett et al., 1985) and through deep-sea photography (Ohta, 1983, 1985). Recently, Pawson and Foell (1986) based the description of a new benthopelagic species, *Peniagone leander*, solely on remotely collected photographs and videotapes of the holothurian.

With advances in the technology of manned submersibles over the past 10–12 years, it is now possible to observe and record in situ the swimming behavior of bathyal and abyssal

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holothurians. In this paper, we describe the swimming activity of four deep-sea species, *Hansenothuria benti* Miller and Pawson, *Enypniastes eximia* Théel, *Paelopatides retifer* Fisher, and *Pelagothuria natatrix* Ludwig, as analyzed through video tapes made during submersible dives. In addition, a survey of published accounts of swimming holothurians is included.

ACKNOWLEDGMENTS.—We thank our colleagues in the Bahama Islands submersible project, Gordon Hendler (Los Angeles County Museum of Natural History) and Porter M. Kier (retired; formerly of National Museum of Natural History, Smithsonian Institution) for their many contributions to the swimming holothurian study over the past five years. Numerous other researchers generously supplied us with information and data. Video footage, photographs, or specimens of holothurians were kindly provided by the following individuals: R. Appeldoorn, B. Cutress (University of Puerto Rico): E. Armstrong, L. Cameron, R. Harbison, S. Pomponi, C. Young, M. Youngbluth (Harbor Branch Oceanographic Institution—HBOI); A. Carey (Oregon State University); I. MacDonald (Texas A&M University); W. Nelson (National Marine Fisheries Service, Mississippi). Funds to conduct submersible dives were granted through the following organizations (principal investigators in parentheses): HBOI (R. Harbison, J. Miller, S. Pomponi, C. Young); National Cancer Institute (S. Pomponi); National Oceanic and Atmospheric Administration/National Undersea Research Program (R. Appeldoorn, L. Cameron, I. MacDonald, W. Nelson, C. Young, M. Youngbluth); National Science Foundation (L. Cameron, R. Harbison, C. Young); Smithsonian Institution (J. Miller, D. Pawson).

We are grateful to the crews of the *Johnson-Sea-Link* submersibles (JSL) and the research vessels *Johnson, Seward Johnson,* and *Edwin Link* for their dedicated efforts on our behalf. Constructive comments by G. Hendler (Los Angeles County Museum of Natural History) and S.D. Cairns (National Museum of Natural History, Smithsonian Institution) greatly improved the text. Photographic assistance in construction of figures was provided by T. Smoyer (HBOI). This paper is HBOI Contribution No. 715 and Smithsonian Institution Marine Station at Link Port Contribution No. 248. Contribution No. 15—Studies on bathyal echinoderms of the Bahama Islands, J. Miller (HBOI) Principal Investigator.

Methods

In situ observations, still and video photography, and collection of live specimens of *Hansenothuria benti, Enypniastes eximia,* and *Pelagothuria natatrix* were accomplished using the research submersibles *Johnson-Sea-Link I* and *II*. The JSL submersibles permit four occupants to work at depths to 914 m for 6–8 hrs in a 24-hour period. An externally mounted, Marine Optical Systems color video camera (MOS 3000-Z) and a Sony (BVU-50) 3/4″ video recorder were used to tape swimming sequences. Seafloor photographs (Figure 1*a,c,d*) were made using a repackaged Benthos camera system (Model 372) with an 85 mm Olympus lens and a 200-watt-second strobe (Model 383) with a modified reflector for telephoto photography. To assure proper subject framing and camera-to-subject distance, a helium-neon laser aiming system (HBOI, see Caimi and Tusting, 1987) was used in conjunction with the camera system. Additional information on the JSL submersibles can be found in Askew (1984).

Data on swimming in *Paelopatides retifer,* including still photographs, videotapes, and a preserved specimen, were obtained during dives of the *Pisces V,* sponsored by NOAA's Hawaiian Undersea Research Laboratory (HURL) program at the University of Hawaii.

Video recordings of behavioral sequences in all four species investigated were analyzed by direct observation of the video signal produced through a Sony video cassette deck (U-Matic VO-5800) capable of slow-motion and still-frame sequencing and equipped with a real-time clock. A Polaroid Freeze-Frame Video Image Recorder (Polaroid Corp.) was used to transfer swimming movements recorded on videotape to a 35 mm film format (Figures 1*e–g,* 2–4).

The use of brand names in this publication is for descriptive purposes only and does not constitute endorsement by the Smithsonian Institution.

Voucher material of species studied during this research have been deposited at the Indian River Coastal Zone Museum, HBOI, or the National Museum of Natural History, Smithsonian Institution.

Morphology and Classification

Many bathyal and abyssal holothurians in the orders Elasipodida and Aspidochirotida possess conspicuous external features that appear to be morphological adaptations to swimming. Hansen and Madsen (1956) and Billett (1986) discuss swimming abilities of holothurians. Pawson (1976) suggested that as many as one-half of the approximately 110 species in the order Elasipodida have morphological features that might enable them to swim, although so far only about 10 species have been captured or observed in the water column. The species that have frequently been observed to swim share some characteristics, the most conspicuous of which are veils (Figure 1*c–g*) or brims (Figure 2) that assist in swimming activities by flapping or undulating, providing some upward lift to the animal. A veil (or velum) is usually located on the anterior dorsal surface of the body, and consists of a series of enlarged and inflatable podia joined by a continuous or discontinuous web (Figure 1*d–e*). There may be from 2 to more than 20 podia in this anterodorsal veil. Brims are extensions of the ventrolateral radii, comprising podia joined by webs. Brims may be of constant width along each side of the body, or they may vary in width, being widest towards the anterior and posterior ends of the body.

Species that swim for the longest periods of time have very fragile bodies and translucent or transparent body walls, and

they are more or less neutrally buoyant. Most swimming species, when captured by conventional dredges and trawls, are reduced to unrecognizable gelatinous lumps when they are removed from the collection gear. The calcite skeletons are usually reduced or absent in swimming forms; a notable exception is *Psychropotes hyalinus* Pawson, which has an armor of ossicles. Swimming movements usually involve contraction of the radial longitudinal muscles; some species, particularly in the aspidochirote family Synallactidae, possess very well-developed radial muscles.

Of the six extant orders of holothurians, only three, Elasipodida, Aspidochirotida and Apodida, include species that are capable of active swimming movements. Only in the order Elasipodida have some attempts have been made (as noted below) to refer swimming species to special taxonomic categories.

Östergren (1938) noted that most species in the Family Psychropotidae and some synallactids such as genus *Paelopatides* are darker in color ventrally than dorsally. He suggested that the differing colors may conceal swimming animals from predators above and below. Hansen (1975) cited the case of the known swimmer *Galatheathuria aspera*, which is dark all over, and our investigations do not lend support to Östergren's intriguing suggestion.

Ludwig (1894) erected the family Pelagothuriidae to include his newly discovered *Pelagothuria natatrix*. Ostergren (1907) erected the family Enypniastidae for *Enypniastes eximia* Théel. Herouard (1923) erected the family Cyclionidae and included *Enypniastes* and *Euriplastes* Koehler and Vaney, 1905 (= *Enypniastes*) in a subsection "Reptantia" and *Pelagothuria* in a subsection "Natantia." Ekman (1926) discussed the assignment of swimming holothurians to new families by previous authors. Heding (1950) diagnosed a new order Pelagothurioida, equal to the order Elasipodida, and included two families, Pelagothuriidae Ludwig, 1894, and Planktothuriidae Heding, 1950. Billett et al. (1985) agreed in principle with Heding's classification, but they favored lower taxonomic levels, with the order Pelagothurioida reduced to family Pelagothuriidae and included within the order Elasipodida. The family currently includes two genera, *Pelagothuria* and *Enypniastes;* in these, the tentacles are connected directly to the water vascular ring canal, whereas in other Elasipodida they are connected to the radial water vessels.

Behavioral Categories

For purposes of convenience, we assign the swimming species to three broad behavioral categories:

Pelagic species spend their entire lives swimming and drifting in the water column, feeding on resuspended sediments or on the rain of detrital material from shallower depths. At present, only the pelagothuriid elasipod *Pelagothuria natatrix* (Ludwig) is known with certainty to fall into this category.

Benthopelagic species swim for much of their lives, but depend on seafloor sediments for sustenance. This category includes not only adults that spend abbreviated periods feeding on the seafloor (e.g., *Enypniastes eximia* Théel, *Peniagone diaphana* (Théel)), but also typically benthic species that spend extended periods in the water column only as juveniles (e.g., *Benthodytes typica* Théel).

Facultative swimmers are benthic for the most part; these species are able to swim, but usually swimming is an escape response to a physical disturbance. It appears that some synaptid species with swimming abilities swim in response to environmental cues (see p. 5). Many deep-sea species and all of the shallow-water swimming species fall into this category.

Survey of Published Records

In the following survey, an attempt is made to list published records of swimming activity for all swimming species. Under each species the only references cited, apart from the original description, are those that refer to swimming behavior. For complete synonymies, relevant systematic literature should be consulted.

Order ELASIPODIDA

Family PELAGOTHURIIDAE Heding, 1950

Pelagothuria natatrix Ludwig, 1894. Pelagic.—Ludwig, 1894, central East Pacific, 596-3298 m.—Chun, 1900 [as *P. ludwigi*, a synonym of *P. natatrix* according to Heding, 1950], equatorial Atlantic, 200 m.—Clark, 1920, northeast of Marquesas Islands, Galapagos Islands, tropical East Pacific, from surface to 4433 m. Incorrect record: Lemche et al., 1976, South New Hebrides Trench, 6758-6776 m, on seafloor [these organisms are cnidarians, not holothurians; see page 14 herein].

Enypniastes eximia Théel, 1882. Benthopelagic.—Sluiter, 1901 [as *Enypniastes ecalcarea*], Ceram, Indonesia, 567 m, noted to have "large eggs."—Koehler and Vaney, 1905 [as *Euriplastes obscura*], west of the Andaman Islands, 3245 m.—Herouard, 1906 [as *Pelagothuria bouvieri*], central North Atlantic, pelagic.—Koehler and Vaney, 1910 [as *Enypniastes (?) decipiens*], northern Indian Ocean.—Mitsukuri, 1912, Suruga Bay, Japan, 1080-1350 m.—Ohshima, 1915, Japan, 369-427 m, eggs 3.0-3.5 mm in diameter.—Gilchrist, 1920 [as *Planktothuria diaphana*], off South Africa, depth unknown.—Heding, 1940 [as *Euriplastes atlanticus*], North Atlantic.—Hansen and Madsen, 1956 [as *Enypniastes globosa*], South China Sea, 3400-3800 m [bottom at 4390 m].—Pawson, 1976, West Atlantic, 5689 m; 1982, West Atlantic, 1938-2141 m, swimming, and feeding on seafloor.—Ohta, 1983, Suruga Bay, Japan, abundant in 1200-1700 m;

1985, Suruga Bay and Sagami Bay, Japan, 516-1600 m, description of swimming behavior.—Billett et al.,1985 [as *Enypniastes diaphana*], northeast Atlantic, 995-4980 m bottom depth, specimens captured from 0-3000 m above seafloor.—Otsuka, 1987, Suruga Trough, Japan.

Family ELPIDIIDAE Théel, 1879

Peniagone leander Pawson and Foell, 1986. Benthopelagic.—Pawson and Foell, 1986, central East Pacific, 4000-5000 m.

Peniagone diaphana (Théel, 1882). Benthopelagic.—Herouard, 1923 [as *Scotoanassa translucida*], North Atlantic, from four pelagic stations (see Hansen, 1975) at depths of 0-4900 m.—Hansen, 1975, noted that specimens from Herouard's (1923) pelagic stations show "ability to lead a pelagic life . . . ."—Pawson, 1976 [as *Scotoanassa translucida*], western North Atlantic, 2450 m, 3-4 m above seafloor.—Barnes et al., 1976, off California, 1900-2100 m, in immense numbers.—Sibuet, 1977, Bay of Biscay, France.—Billett et al., 1985, North Atlantic, 1500-4780 m depth, specimens collected 0-1500 m above seabed, concluded that individuals feed on seafloor.—Gage et al., 1985, Northeast Atlantic, 4810 m; most abundant holothurian below 4,000 m in Bay of Biscay.

Family PSYCHROPOTIDAE Théel, 1882

Psychropotes longicauda Théel, 1882. Benthopelagic only as juvenile.—Mortensen, 1927, speculated that "The long tail probably is a swimming apparatus"; his suggestion apparently true for juveniles of this species, but not for adults.—Belyaev and Vinogradov, 1969 [as *Nectothuria translucida* new genus, new species; Hansen (1975) believed this to be juvenile of *Psychropotes longicauda*, but Billett et al. (1985) suggested that it may be juvenile of another *Psychropotes* species].—Billett et al., 1985, Northeast Atlantic, 7 of 8 juveniles captured occurred greater than 500 m above seafloor, at depths of 3470 to 4008 m.

Psychropotes depressa (Théel, 1882). Facultative swimmer.—Arrhenius, 1963, seafloor photographs of swimming specimens near seafloor at 1930 m off Baja California [identified as possibly *P. depressa* by Hansen (1975)].—Pawson, 1976 [as *Euphronides* sp.], West Atlantic in 2450 and 2477 m; when disturbed, specimens leapt from seafloor, moving forwards and upwards by slow flexing of body in vertical plane, similar to swimming of *Bathyplotes natans* M. Sars.—Billett et al., 1985, North Atlantic, juveniles swimming at depth of 1000-1500 m, 2500-3000 m above seafloor.

Psychropotes hyalinus Pawson, 1985. Facultative swimmer.—Pawson, 1985, single specimen captured in trap set 5 m above seafloor at depth of 5891 m, North Pacific, north of Hawaii.

Benthodytes typica Théel, 1882. Benthopelagic only as juvenile.—Grieg, 1921, North Atlantic, at depth of 1400 m, 1600 m above seafloor.—Billett et al., 1985, East Atlantic off Ghana, at depth of 1205-1300 m, 3400 m above seafloor.

Benthodytes sordida (Théel, 1882). Benthopelagic only as juvenile.—Billett et al., 1985 [as *B. lingua* R. Perrier, 1896], North Atlantic, at depth of 3485-3515 m, 575-605 m above seafloor [referred to *B. sordida* by Tyler and Billett, 1987].

Benthodytes sanguinolenta Théel, 1882. Facultative swimmer.—Pérês, 1965, observed *Benthodytes*-type holothurians swimming in Puerto Rico Trench, at depth of 3100 m.—Heezen and Hollister, 1971:84, showed photographs of probably *B. sanguinolenta*, with one end of body raised off of seafloor; commented on swimming possibilities.—Pawson, 1976 [as "probably *B. typica* Théel"], numerous photographs of West Atlantic specimens with one end of body raised off of seafloor.—Pawson, 1982, swimming of several specimens studied from submersible *Alvin* in West Atlantic at depth of 1938-2141 m; noted S-shaped body posture; swimming movements similar to those described by Pawson (1976) for *Psychropotes depressa* (Théel).

Order ASPIDOCHIROTIDA

Family SYNALLACTIDAE Ludwig, 1894

Galatheathuria aspera Hansen and Madsen, 1956. Benthopelagic.—Hansen and Madsen, 1956, South China Sea, seafloor depth 4390 m, specimen collected at 3400-3800 m depth.

Scotothuria herringi Hansen, 1978. Benthopelagic.—Hansen, 1978, Northeast Atlantic, 100-3000 m above seafloor; swims by lateral undulations; suggests that *Dendrothuria* Koehler and Vaney, 1905, and *Pseudothuria* Koehler and Vaney, 1905, also pelagic, for they resemble *Scotothuria*.—Billett et al., 1985, Northeast Atlantic, 1250-4980 m depth; specimens collected from 0-3900 m above seafloor; also off Kenya (*Galathea* collection) on seafloor in 3960 m, and equatorial Atlantic (Swedish Deep-Sea Expedition) [possible synonym of *Dendrothuria similis* Koehler and Vaney, 1905].

Bathyplotes natans M. Sars, 1867. Facultative swimmer.—Sars, 1867, observed swimming movements—flexing of body in the vertical plane—in North Atlantic specimens.—Ohta, 1983, noted that species often photographed on seafloor in 400-700 m in Suruga Bay, Japan, but seldom trawled; individuals probably swam up and away when "bow wave" of trawl was detected, or they were passively pushed aside by bow wave.

Hansenothuria benti Miller and Pawson (1989). Facultative swimmer.—Miller and Pawson (1989, and herein), West Atlantic, 363-904 m.

Paelopatides gigantea (Verrill, 1884). Facultative swimmer.—Grassle et al., 1975, observed to be neutrally buoyant; specimen observed swimming "with a 'flip-flop' motion over the bottom . . ." at depth of 1800 m in West Atlantic.—Pawson, 1976 [as *Paelopatides* sp.], seafloor photograph shows swimming in this species off Bahama Islands; swimming achieved by sinusoidal undulation of lateral brim.

Paelopatides grisea R. Perrier, 1902. Facultative swimmer.—Billett et al., 1985, photographs of specimens on seafloor in Northeast Atlantic indicate that this species swims in similar manner to *P. gigantea;* Billett et al. suggest that these two species are synonymous.

Paelopatides retifer Fisher, 1907. Facultative swimmer.—Miller and Pawson, herein, Hawaiian Islands, 405–1900 m.

Paelopatides confundens Théel, 1886. Facultative swimmer.—Miller and Pawson herein, off northern California, 500–1000 m above seafloor in 4200–4300 m depth.

Paelopatides species. Facultative swimmer.—Gage et al., 1985; Northeast Atlantic, 1942–1949 m; large specimen photographed on seabed from trawl, but not captured by trawl.

Kareniella gracilis Heding, 1940. Facultative swimmer.—Miller and Pawson, herein [B. Cutress, personal communication]; Puerto Rico, 544 m; videotaped leaping off seabed and swimming by flexing body in S-curves.

Family STICHOPODIDAE Haeckel, 1896

Astichopus multifidus (Sluiter, 1910). Facultative swimmer.—Glynn, 1965; when disturbed, Puerto Rican specimens made active "bounding" movements [undulating in vertical plane], but almost always remained in contact with substratum; observed on one occasion to leave seafloor and "swim."

Parastichopus californicus (Stimpson, 1857). Facultative swimmer.—Margolin, 1976; when contacted by some species of seastars, Californian specimens vigorously swim for short distances by undulating bodies in vertical plane.

Order APODIDA

Family SYNAPTIDAE Ostergren, 1898

"Synaptids." Facultative swimmers.—Clark, 1907; young synaptids ". . . up to 2 cm in length, are sometimes found floating, if not swimming, in the water."

Leptosynapta inhaerens (Müller, 1776). Facultative swimmer.—Costello, 1946; specimens swimming at night near surface at Woods Hole, Massachusetts; when swimming, specimens expanded, filled with seawater, intestines empty; swimming movements involved flexing of body into U-shape.

Leptosynapta albicans (Selenka, 1867). Facultative swimmer.—Glynn, 1965, observed specimens swimming at night near the surface in Monterey Bay, California; swimming movements sinusoidal undulations.

Labidoplax dubia (Semper, 1868). Facultative swimmer.—Hoshiai, 1963, observed young specimens swimming near surface, at night, off Asamushi, Japan; like *Leptosynapta inhaerens,* specimens were expanded, with empty intestines; swimming movements involve sinusoidal undulations.

Results

Hansenothuria benti Miller and Pawson, 1989

FIGURES 1*a*, 2

MATERIAL EXAMINED, HABITAT, AND IN SITU OBSERVATIONS.—Specimens of *H. benti* were first encountered south of Great Abaco Island, Bahamas, during Dive No. JSL-II-808, 9 April 1984. One individual was photographed, videotaped, and collected at 700 m, and two others were collected at 699 m and 683 m. The specimens were found on a 40 degree slope, which was covered with a thick layer of fine sediment and *Halimeda* sp. flakes. None of the specimens made any attempt to swim while being collected, but after being placed in a holding bucket, all three swam in the bucket by rolling and arching their bodies. This behavior continued for at least two hours. Members of the Division of Biomedical Marine Research, HBOI, during a dive (JSL-I-1649, 13 August 1985) off Crooked Island, Bahamas, videotaped a specimen of *H. benti* swimming a few meters off the bottom at a depth of 791 m. The swimming behavior was taped for two minutes. Commentary on the video described other specimens in the vicinity, swimming and "resting" on a 45 degree slope covered with fine silt, loose rocks, and boulders. L. Cameron (HBOI) collected several specimens of *H. benti* from a sandy bottom (JSL-I-1705, 10 November 1985) at depths of 691–762 m off San Salvador Island, Bahamas. He noted that the specimens would leave the bottom and swim in the water column with rapid S-undulations when disturbed by the manipulator arm of the submersible. During dives aboard JSL in the Bahamas, 1987–1988, the present authors and their colleagues encountered several additional specimens of *H. benti* at depths of 639–904 m. These specimens were found on shallow to steep (20–60 degree) slopes with a moderate to thin layer of fine, silty sand.

DESCRIPTION OF LIVING INDIVIDUALS.—*Hansenothuria benti* is a holothurian of moderate size, ranging in length from 10 to 23 cm. The ventral surface is a flattened sole with minute tube feet; dorsally the body wall is vaulted, with steep sloping margins (Figure 1*a*). The ventrolateral margin is a brim composed of webbed podia. The brim is widest along the anterior and posterior ends of the body, where it aids in active swimming movements. The anterior end is high and bluntly rounded; the posterior end is abruptly tapered into a low short

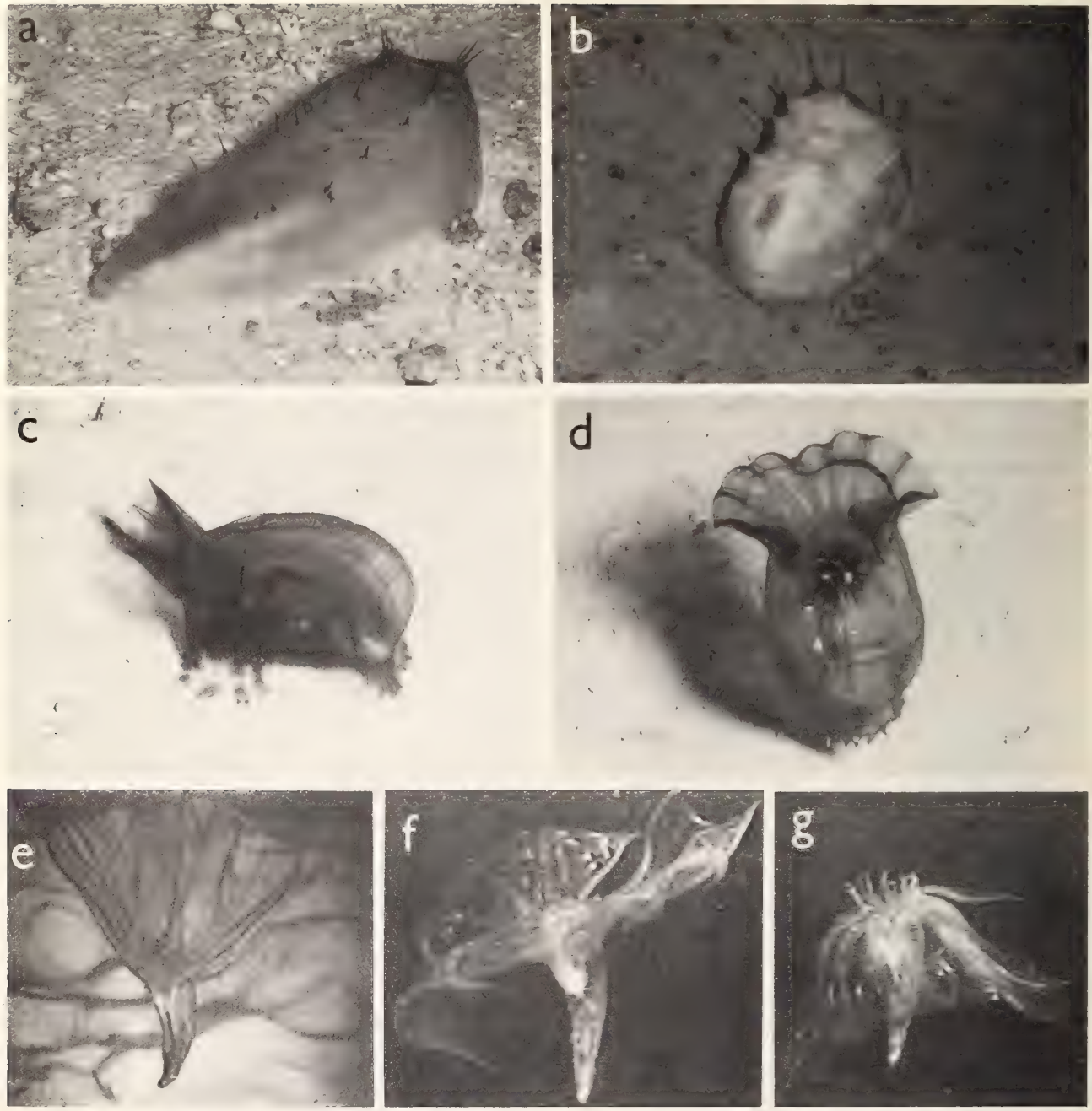

FIGURE 1.—In situ photographs of swimming holothurians discussed herein: *a, Hansenothuria benti* Miller and Pawson, photographed in French Bay, San Salvador, Bahama Islands, 23°55.05′N, 74°31.67′W, at 694 m; *b, Paelopatides retifer* Fisher, photographed off Kailua-Kona, Hawaii, at 1060 m (photo credit C. Young, L. Cameron, HBOI); *c,d, Enypniastes eximia* Theel, photographed in Northwest Providence Channel off Stirrup Cay, Berry Islands, Bahama Islands, 26°01.72′N, 78°04.94′W, 902–910 m; *e–g, Pelagothuria natatrix* Ludwig, photographs transferred from videotape recorded off Isla San Cristobal, Galapagos Islands, at 542 m (video credit E. Armstrong, HBOI).

"tail." The two dorsal radii each carry a row of slender, erect, hair-like papillae with pointed tips. In each row there are 10–31 papillae, nearly regularly spaced along the length of the body. Between the rows of papillae, the mid-dorsal interradius forms a distinct, shallow trough. Though relatively thick, the body wall is transparent to translucent, and portions of the sediment-filled intestine are usually visible through it. The body is a pale purplish blue with gray or black dorsal papillae.

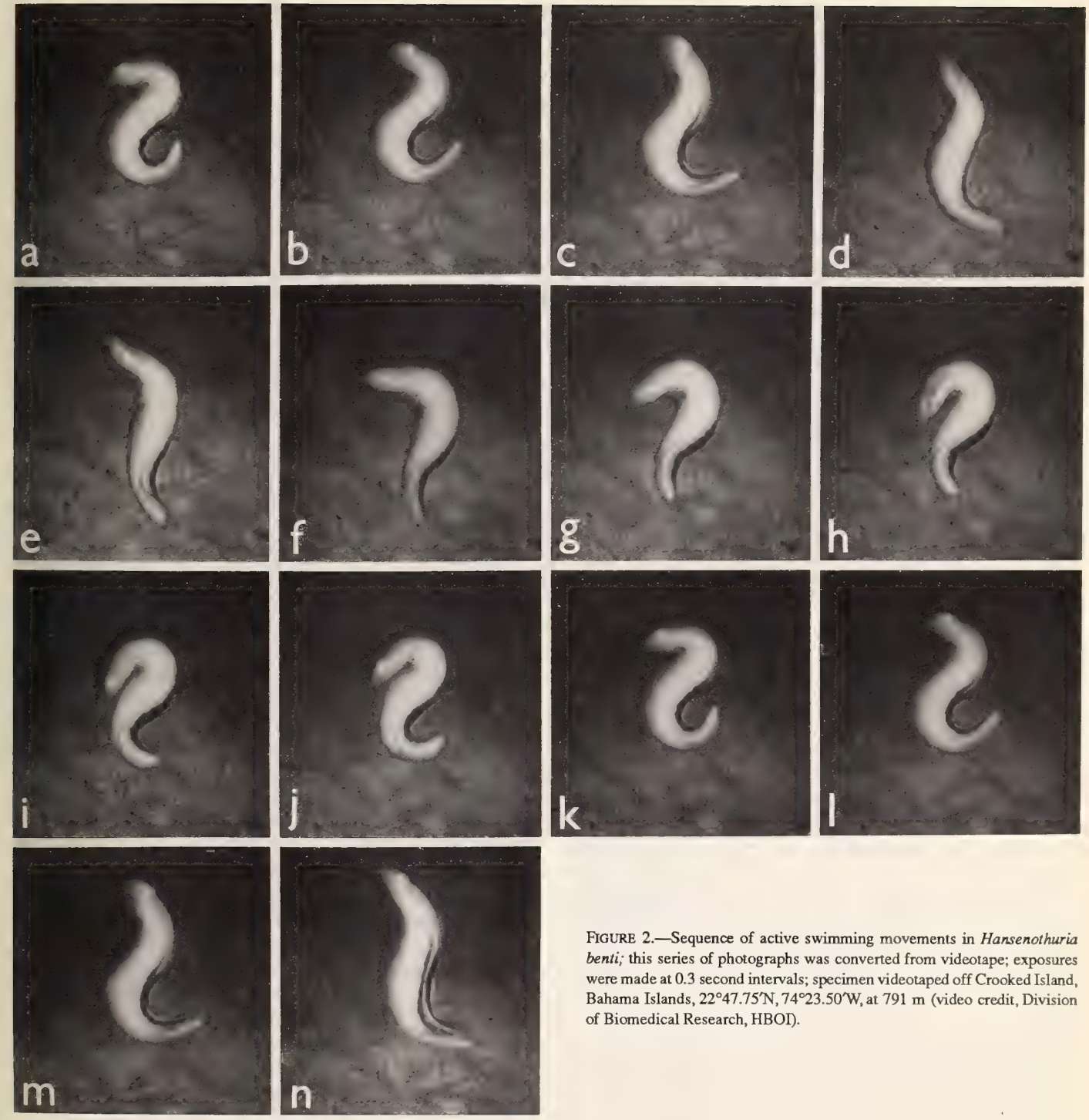

FIGURE 2.—Sequence of active swimming movements in *Hansenothuria benti;* this series of photographs was converted from videotape; exposures were made at 0.3 second intervals; specimen videotaped off Crooked Island, Bahama Islands, 22°47.75′N, 74°23.50′W, at 791 m (video credit, Division of Biomedical Research, HBOI).

For a detailed description of *H. benti,* see Miller and Pawson (1989).

SWIMMING BEHAVIOR.—A powerful and active swimmer, *H. benti* has been found to swim only in response to disturbance. Observers in submersibles have not seen individuals that were swimming when first encountered. Video records of this species confirm that it can maintain active swimming movements for at least two minutes, and individuals held in collection containers have remained above the bottom of the containers for two hours or more.

When provoked, *H. benti* pushes rapidly off the seafloor, propelling itself upward with rapid flexing of the anterior and posterior portions of its body. One specimen defecated after completing several swimming strokes, at which point the sea

cucumber was approximately 3 m above the seafloor.

This species achieves vertical lift through the power strokes of the anterior and posterior ends of the body. The power strokes are staggered; the posterior power stroke begins as the anterior recovery stroke is being completed. Likewise, at the completion of the anterior power stroke, the posterior recovery stroke is nearing completion. There is no glide period between these complementary power strokes.

At the beginning of a swimming cycle, the anterior end of the body is arched over the dorsal surface at a right angle to the anterior-posterior axis, while the posterior one-third of the body is strongly curled ventrally in the shape of a hook or C (Figure 2*a*). Modified webbed podia, arising laterally from the posterior body wall to form a conspicuous brim, function like oar blades by increasing the surface area of the "tail." The posterior power stroke precedes the anterior power stroke and is initiated by a rapid downward thrust of the posterior end (Figure 2*a–f*) brought about by contraction of the dorsal longitudinal muscles. Initiation of the anterior power stroke occurs one second after initiation of the posterior power stroke. At the onset of the anterior power stroke, the anterior end is slightly arched dorsally, and the posterior end, which is nearing the completion of its power stroke, is arched ventrally (Figure 2*d*). In this posture, the animal assumes a reversed S-shape. A transparent veil of webbed podia completely surrounds the anterior end of the body. As the dorsal longitudinal muscles contract to curl the anterior end dorsally, the veil is expanded and held erect; the power stroke progresses until the anterior end contacts the mid-dorsal surface (Figure 2*i*).

Staggering of the power strokes provides initial lift through (1) the posterior stroke (averaging 1.0 sec), combined lift through (2) a brief period of overlap of anterior and posterior power strokes (each averaging 0.7 sec), and final lift through (3) completion of the anterior stroke (averaging 1.0 sec). Thus, anterior and posterior power strokes are of approximately equal duration, each averaging 1.7 sec. Each coordinated power stroke serves to move the animal obliquely (diagonally) through the water column a distance approximately equal to one-half of its body length. As the holothurian ascends, it rotates slowly around its anterior-posterior axis, completing one 360 degree rotation in 20 anterior and posterior power strokes.

Both the anterior and posterior recovery strokes are effected by contraction of the ventral longitudinal muscles. At the onset of the posterior recovery stroke, the holothurian is mid-way through the anterior power stroke. In this configuration, the holothurian resembles an upside-down and reversed L, with the anterior end set at a right angle to the anterior-posterior axis, and the posterior end almost in line with the axis (Figure 2*f*). In contrast, as the anterior recovery stroke is initiated, the holothurian is mid-way through the posterior recovery stroke. At this point in the swimming cycle, the anterior end is fully folded dorsally to meet the mid-dorsal body wall, and the posterior end is curled nearly 90 degrees to the anterior-posterior axis (Figure 2*i*). As both recovery strokes begin, the webbed podia of the posterior and anterior brims are passively appressed to the body wall by water resistance. Duration of the anterior and posterior recovery strokes equals the duration of the individual power strokes, which is 1.7 sec each. Thus, a total cycle (power stroke plus recovery stroke) for the posterior or the anterior end takes approximately 3.3 sec. However, because the anterior power stroke is delayed by 1 sec beyond initiation of the posterior power stroke, the total time for the holothurian to complete both power and recovery strokes equals 4.3 sec. The series of photographs in Figure 2 illustrates a complete swimming cycle at 0.3 sec intervals, from initiation of the posterior power stroke to completion of the anterior recovery stroke.

Only one individual videotaped during swimming was observed to slow the swimming cycle. The cycle slowed approximately 2 minutes after swimming commenced; soon afterwards active swimming movements ceased, and the specimen assumed a horizontal posture. Thereafter, it started passively rotating in a clockwise direction while slowly descending towards the seabed.

DISTRIBUTION.—*Hansenothuria benti* is known only from the Bahama Islands at depths of 639–904 m, and from St. Vincent in the Lesser Antilles at depths of 363–447 m. Bahamas specimens collected to date with the JSL submersibles have been found off Great Abaco, Egg Island, Andros Island, Black Rock, San Salvador, New Providence, Plana Cays and Crooked Island. This species probably occurs on bathyal slopes along many islands of the Greater and Lesser Antilles.

COMMENTS.—*Hansenothuria benti* can be relatively common at a given locality, but individuals are usually widely scattered and solitary. Despite its rather sturdy appearance in situ, *H. benti* is fragile, and captured specimens seldom arrive at the surface intact. Usually during the ascent from the seafloor to the surface, specimens will slough off (autotomize) epidermal and dermal layers of bodywall. This self-mutilation may be a response to increased temperature, decreased pressure and/or increased light intensity. Following collection, the specimens are well protected in Plexiglas containers; autotomy does not appear to begin until the submersible is ascending to the surface.

Paelopatides retifer Fisher, 1907

FIGURES 1*b*, 3

MATERIAL EXAMINED, HABITAT, AND IN SITU OBSERVATIONS.—During a submersible dive in *Pisces V* (Dive No. P5-047, February 1988) to investigate mid-water organisms off Oahu, Hawaiian Islands, M. Youngbluth (HBOI) encountered a specimen of *Paelopatides retifer* at 800 m depth. The specimen was floating in an almost horizontal posture approximately 300 m above the seabed. As the submersible moved closer to videotape the specimen, it rotated to a vertical position and began actively swimming. Additional specimens

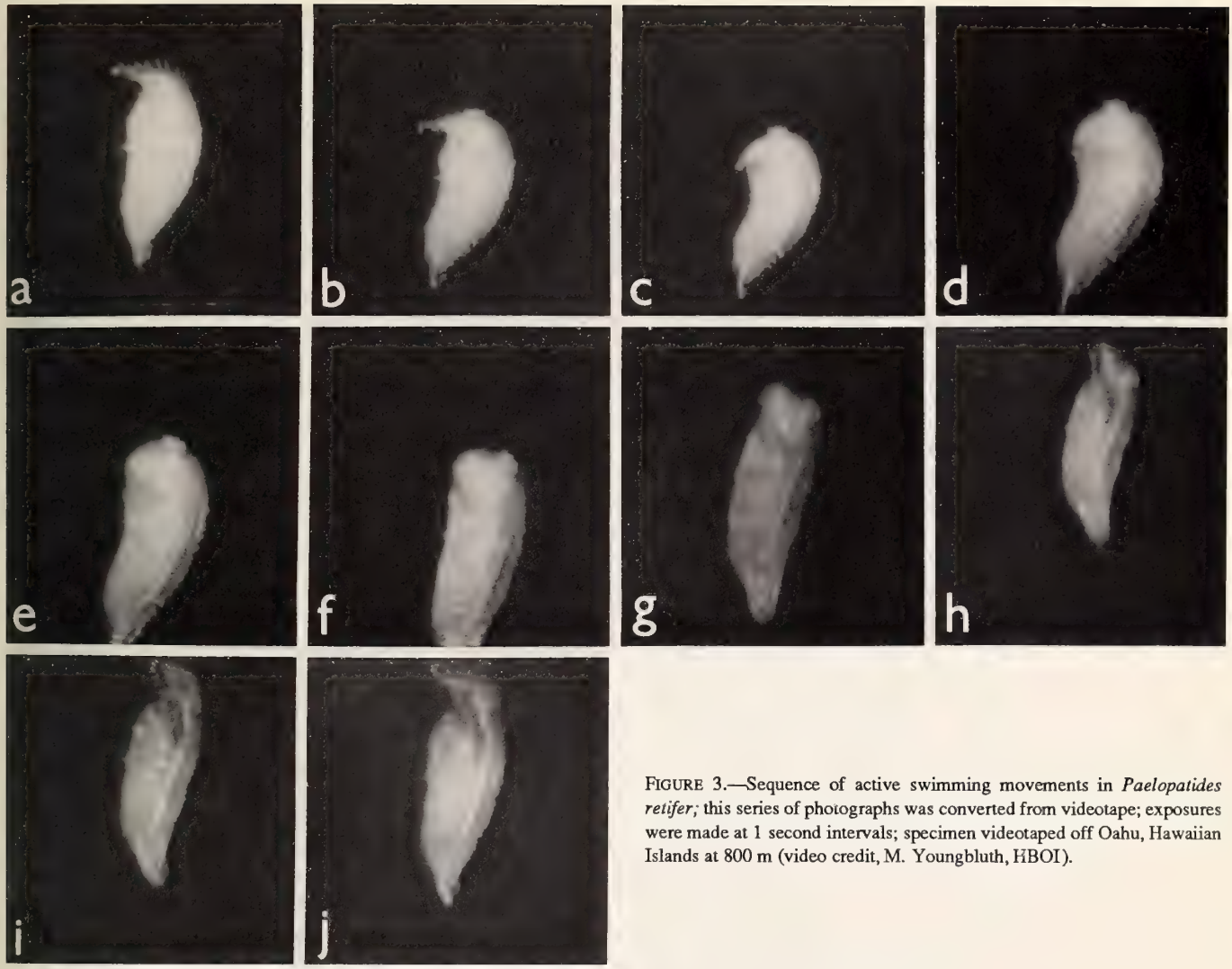

FIGURE 3.—Sequence of active swimming movements in *Paelopatides retifer;* this series of photographs was converted from videotape; exposures were made at 1 second intervals; specimen videotaped off Oahu, Hawaiian Islands at 800 m (video credit, M. Youngbluth, HBOI).

of this species were observed, photographed, and videotaped by C. Young and L. Cameron (HBOI) using *Pisces V* (Dive Nos. P5-081, P5-082; July 1988) off Kailua-Kona, Hawaiian Islands, at depths of 1060–1900 m. Specimens observed during these latter dives were feeding on the seabed. One individual actively swam upwards after being prodded with the submersible's manipulator arm. The substrate where the holothurians were observed on Dive No. P5-081 consisted of a shallow slope with occasional basalt outcrops, covered with silty sediment.

DESCRIPTION OF LIVING INDIVIDUALS.—This species reaches a length of approximately 20–25 cm. The flattened ventral surface is elliptical in outline. At the anterior and posterior ends, the ventrolateral margins are composed of webbed podia forming a distinct brim; the anterior brim is twice as wide as the posterior. The body is arched, with high, steeply sloping sides. Along each dorsal radius is a row of 4–6 almost evenly spaced papillae (Figure 1*b*). The papillae are long and slender and supported on large, prominent, conical bases. In the middorsal interradius, the body wall is slightly convex, forming a low but distinct rounded ridge. The anus is conspicuous, situated high on the posterior end of the body. The bodywall colors are various hues of purple.

SWIMMING BEHAVIOR.—*Paelopatides retifer* is a slow swimmer that appears to combine swimming movements used by both *Hansenothuria benti* (p. 5) and *Enypniastes eximia* (p. 10), that is, flexing of the posterior portion of the body and rhythmic pulsation of the anterior brim. The holothurian assumes a vertical posture for swimming. A videotape record of this species shows that it can sustain active swimming movements for more than 20 minutes.

Depending upon the amount of sediment in the intestine, *P. retifer* appears to be neutrally buoyant or slightly negatively buoyant. The single individual videotaped in the water column often drifted motionless while maintaining a constant depth, and specimens on the seafloor were swept away by the bow wave of the approaching submersible.

Swimming is initiated by contraction of the dorsal longitudinal muscles, which simultaneously pull the anterior and posterior ends dorsally. As the anterior end curls backwards, the anterior brim or veil is extended and held erect while sweeping toward the dorsal surface. At the onset of the anterior power stroke the mouth is in its normal ventral position (Figure 3*a*). However, when the anterior power stroke is complete, the mouth, with partially extended tentacles, points directly upwards in line with the anterior-posterior axis (Figure 3*d*). In this posture, the anterior veil is fully appressed to the anterior and dorsal body wall. The anterior brim is longer than the posterior brim, and twice as wide. Accordingly, the anterior brim contributes the majority of lift to the swimming holothurian. The duration of the anterior power stroke is approximately 3.5 sec.

The anterior recovery stroke is effected by contraction of the ventral longitudinal muscles, which return the anterior end to its normal position, with the mouth oriented ventrally. Throughout the anterior recovery stroke (Figure 3*e–i*), the brim remains partially appressed to the body, probably forced backwards by water flowing over the animal. Even as the anterior power stroke is initiated, the distal half of the brim lags behind the proximal half, and the entire brim is not fully inflated until 0.5–1.0 sec after the power stroke begins. The duration of the anterior recovery stroke is greater than the anterior power stroke, lasting approximately 5.5 sec. A complete anterior cycle, from initiation of the power stroke to completion of the recovery stroke, takes 9.0 sec.

The action of the posterior brim appears to contribute very little to swimming in this species. During the posterior power stroke, the posterior brim is pulled dorsally 12–15 degrees beyond vertical (Figure 3*d*), and at the completion of the posterior recovery stroke, the brim, curled slightly ventrally, is positioned just 5 degrees beyond vertical (Plate 3*j*). In other words, the posterior brim describes a maximum arc of only 20 degrees during its complete cycle of approximately 9.0 sec duration.

DISTRIBUTION.—*Paelopatides retifer* is known from the Hawaiian Islands at depths of 405–1900 m. The only other report of this species is the original description by Fisher (1907) of material collected by the *Albatross* off the islands of Molokai, Bird (Mokumanu), Kauai, Hawaii, and Niihau.

COMMENTS.—According to C. Young and L. Cameron of HBOI (personal communication), one individual of this species defecated soon after swimming off the seabed. The distinctive annulated fecal strand deposited on the seabed was similar to numerous other fecal strands scattered on the seabed. This same variety of fecal strand was frequently noted on both dives when *P. retifer* was encountered, and on another dive (P5-080) when no specimens were seen. Therefore, it is possible that fairly large numbers of *P. retifer* occur around the Hawaiian Islands.

This species, like *Enypniastes eximia*, may spend the majority of its life in the water column. Because we lack empirical data to support this hypothesis, *P. retifer* has been listed as a facultative swimmer in the survey (page 5). Other species of *Paelopatides*, for example *P. grisea* and *P. gigantea* from the Atlantic Ocean, have been reported as swimmers (Pawson, 1976; Billett et al., 1985), but the swimming movements, undulation of lateral brims, are so inefficient that these congeners appear to be capable of ascending only a few meters above the seafloor. In contrast, another Pacific Ocean species, *P. confundens* Théel can venture great distances from the seafloor. A. Carey (Oregon State University) collected a specimen of this species off the northern California coast in a midwater net trawling 500–1000 m above the seabed, which lay at a depth of 4200–4300 m.

Enypniastes eximia Théel, 1882

FIGURES 1*c,d*, 4

MATERIAL EXAMINED, HABITAT, AND IN SITU OBSERVATIONS.—*Enypniastes eximia* was first videotaped and collected at 717 m on 7 April 1984 during Dive JSL-I-804 off Sandy point, Great Abaco Island, Bahamas. The specimen was taped for 12.3 minutes while actively swimming approximately 2.5–5.0 m above the seabed. Several other individuals were noted in the vicinity. Another individual was observed briefly at 622 m (Dive JSL-II-820) off Nassau, New Providence Island, 17 April 1984, swimming a few meters above the seabed. Additional video records of *E. eximia* were made during three dives in *Johnson-Sea-Link* off the Bahama Islands: JSL-II-1495, 17 October 1987, off Stirrup Cay, Berry Islands, 900–910 m; JSL-I-2267 and JSL-I-2268, 15 September 1988, off Crooked Island, 873–900 m. On each of these latter dives, numerous individuals were observed feeding on the sediment or swimming within several meters of the seabed. Interestingly, the number of individuals encountered decreased dramatically at depths shallower than 900 m, and none were noted in depths of less than 873 m. All *E. eximia* were found on or above gently sloping bottoms covered with a thick layer of silty sand up to 30 cm or more in depth.

Information on the behavior of *E. eximia* found off Puerto Rico and in the Gulf of Mexico was made available through R. Appeldoorn (University of Puerto Rico) and W. Nelson (National Marine Fisheries Service, Mississippi) (JSL-II-1178, 12 October 1985, off La Parguera at 731 m), and I. MacDonald (Texas A&M University) (JSL-I-2066, 17 June 1987, 716 m, Green Canyon Lease Site No. 272) respectively.

DESCRIPTION OF LIVING INDIVIDUALS.—This species has a distinctive bulbous, barrel-shaped body and a large anterior webbed veil incorporating up to 12 conical podia (Figure 1*d*). There are 2 rectangular posterolateral veils composed of 10–15 webbed podia. Individuals examined during this study ranged from 6 to 20 cm in length, and Ohta (1985) reported that some specimens can reach a length of 25 cm. *Enypniastes eximia* is transparent; internal structures, especially the sediment-filled coiled intestine, are readily visible through the body wall. The

coloration of the integument varies with body size; small individuals are pale pink and large adults are dark brown-red to crimson.

FEEDING AND SWIMMING BEHAVIOR.—As noted by previous investigators (Pawson, 1976, 1982; Billett et al., 1985; Ohta, 1985), few individuals of this species were encountered on the seabed; only two were videotaped landing on the seabed, and two taking off. Apparently, *E. eximia* descends to the seabed only to feed; non-feeding individuals were not observed on the seabed.

When approaching the seabed to land, *E. eximia* reverses the action of its anterior veil by holding the veil erect over the anterior end and gently undulating the veil margin to thrust the animal downwards. The undulations are waves initiated at the ventral margins of the veil and passing dorsally until the tips of the component podia meet above the anterior end of the body. During descent, the posterolateral veils are erected, with the pointed tips of the component podia slightly curled ventrally. When contact is made with the seabed, the tips of these podia are firmly planted into the soft substratum and the animal "weathervanes" in the current until the anterior end of the body is facing downcurrent. At the same time, the podia of the anterior veil curl ventrally, causing the veil to collapse. Once the animal is secured on the seabed, the anterior veil remains pointed anteriorly (Ohta, 1985) or it is held erect above the dorsal and lateral surfaces (Figure 1*c*).

Within seconds of touchdown, the bifurcate tentacles of the holothurian extend and begin rapidly grasping small parcels of sediment and transferring them to the mouth. We found no evidence to suggest that *E. eximia* was selectively feeding on sediment; particles of sediment were observed falling from the tentacles as they were moved towards the mouth, and during take-off, sediment continued to fall from the tentacles as they were retracted. Although the movement of the tentacles during feeding is very rapid compared to most shallow-water sediment-ingesting holothurians (personal observations), it is unlikely that *E. eximia* could fill its entire intestine during a single visit to the seafloor; of those individuals observed to be feeding, none remained on the seafloor for more than 64 sec. During feeding, movement across the bottom is accomplished by one or a combination of the following methods. In still water, *E. eximia* gently undulates the ventrolateral margins of the anterior veil, thus "rowing" itself forward. When a current exists, the tentacles pull the animal downcurrent. Also, in this situation, the anterior veil acts as a sail, and the curled podia of the posterolateral veils act as brakes; they may be released from the sediment to allow forward movement or set in the sediment to slow or stop the animal's progress. Forward movement is also effected by pulling with the tentacles and pushing with individual podia of the lateral veils. All of these methods of benthic locomotion except the first ("rowing") were hypothesized by Ohta (1985).

A take-off involves action of the anterior and posterior veils, which are simultaneously thrust ventrally by a strong contraction of the ventral longitudinal musculature. This action rapidly propels the holothurian upwards and backwards, into the current. Once clear of the seabed, *E. eximia* quickly retracts the tentacles and then immediately reverses the stroke of the anterior veil to propel itself upwards and downcurrent (Figure 1*d*). One individual videotaped soon after leaving the bottom kept its tentacles fully extended, with the mouth agape for several minutes, while the tentacles waved and curled towards the mouth. This was not feeding activity; rather, it appeared to be aberrant behavior caused by the intense video lights illuminating the animal.

After leaving the seabed, *E. eximia* tends to remain erect in the water column, with the anterior-posterior axis vertical (Figure 1*d*). In this orientation, the coiled portion of the sediment-filled intestine is situated in the posterior half of the body, and may act as ballast, keeping the holothurian upright. When not actually swimming, *E. eximia* has been observed to either maintain a constant altitude above the bottom, or slowly sink; the rate of sinking is apparently dependent upon the amount of sediment in the intestine.

Ascent in the water column is effected by the anterior veil, which is pulled posteriorly to meet the anterodorsal surface of the body (Figure 4*a–e*) by contraction of the ventral longitudinal muscles. The water pushed posteriorly by the anterior veil induces a sympathetic wave along the dorsal body wall. This wave disappears near the posterior end of the body. Both lateral veils move in unison as they are pulled dorsally by their component podia (Figure 4*a–e*). The anterior 4–5 podia bend sequentially to initiate the movement, while the more posterior feet appear to be passively flexed by the action of the veil. Lift is effected by the anterior veil; the lateral veils work in unison to offset the disorienting effect of the anterior veil, and keep the animal in its preferred vertical orientation.

In its recovery stroke, the anterior veil is pulled inwards towards the body and upwards, by curling of the component podia (Figure 4*f–k*). During this recovery phase the animal glides upwards. Once the veil is extended by straightening of the podia, the power stroke is initiated again. The recovery stroke of the lateral veils is effected by the anteriormost 4–5 component podia, which pull the veils ventrally until they are perpendicular to the lateral body wall (Figure 4*k*).

A complete cycle for the anterior veil (power stroke and recovery stroke) takes an average of 8.7 sec. The lateral veils initiate their power stroke approximately 1.0 sec before the anterior veil, completing a full cycle in 7.5 sec. Thus, the cycles for the anterior and lateral veils are precisely coordinated.

Some swimming specimens appeared to be disturbed by the submersible's lights or bow wave and slowed or stopped the stroke cycle. One individual began swimming upwards with very irregular movements, altered its strokes to descend, then reversed course once more to ascend with regular strokes as described above.

DISTRIBUTION.—*Enypniastes eximia* is cosmopolitan at depths of 516–5689 m. Swimming specimens observed from

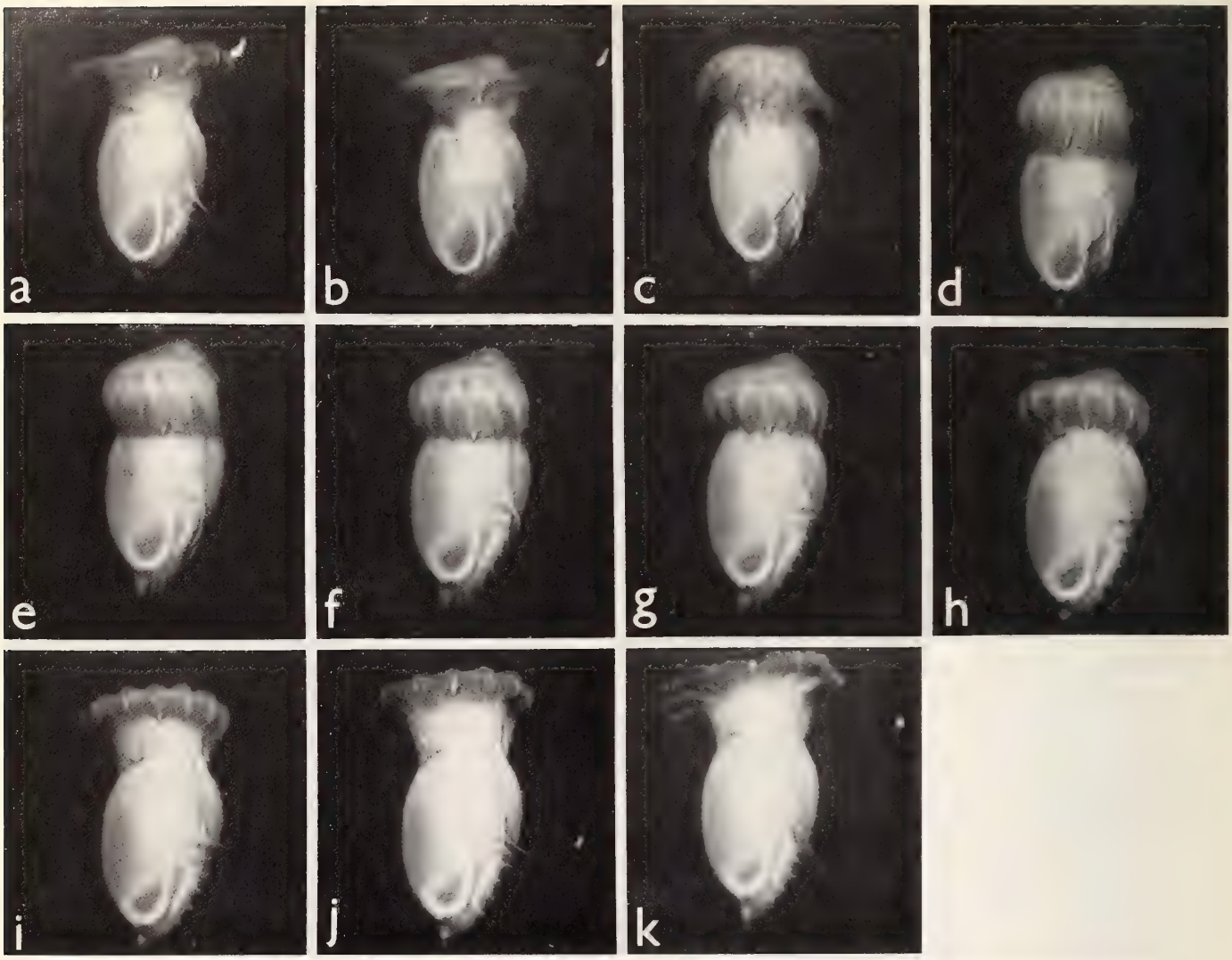

FIGURE 4.—Sequence of active swimming movements in *Enypniastes eximia;* this series of photographs was converted from videotape; exposures were made at 1 second intervals; specimen videotaped off Great Abaco Island, Bahama Islands, at 717 m.

submersibles or in seafloor photographs have always been found within a few meters of the seabed. Our observations confirm this finding. In contrast, Billett et al. (1985) have collected juvenile specimens as much as 3000 m above the seabed, and the same species has been reported (as *Pelagothuria bouvieri*) at the surface (Herouard, 1923).

COMMENTS.—Through an excellent analysis of seafloor and near-seafloor photographs taken in Suruga and Sagami Bays, Japan, Ohta (1985) proposed a behavioral sequence for swimming in *E. eximia.* Our results, based on real-time observations and video recordings, support most of his findings; some differences noted are discussed below.

Ohta (1985) suggested that *E. eximia* rises from the seafloor by lifting its anterior end and stroking upwards with metachronal fanning of the posterior webbed podia. In contrast, we found that *E. eximia* leaves the seafloor after a strong contraction of the ventral longitudinal muscles, which rapidly pulls the anterior and posterior veils ventrally, thus thrusting the holothurian upwards and backwards.

Ohta (1985) noted that during swimming, *E. eximia* ascended obliquely; we observed some individuals rising obliquely when detectable currents were present; at localities with little or no current, *E. eximia* ascended vertically. Pawson (1982) also found *E. eximia* ascending vertically in the Tongue of the Ocean, Bahamas.

In the opinion of Ohta, vertical propulsion during ascent was accomplished by the power strokes of both the anterior and posterolateral veils. He also assumed that the power stroke of the anterior veil proceeded while the posterior veils were in their recovery stroke and vice versa. Our findings show that instead of contributing to lift through metachronal fanning, the posterolateral veils act as opposed rudders, countering rota-

tional forces about the anterior-posterior axis. In addition, the power and recovery strokes of the anterior and posterior veils occur concurrently, and not in opposition, as supposed by Ohta.

Ohta suggested that movement of the anterior veil during the recovery stroke proceeded in a radial or undulatory manner by serial curling of the component podia around the veil. However, we observed a coordinated simultaneous ventral curling of the podia, pulling the veil anteriorly to the level of the mouth.

According to Ohta, *E. eximia* can hover or hang in the water by "gentle undulation of the anterior velum" and a "gentle metachronal fanning wave generated in the anterior part of the posterior webs." We have encountered numerous specimens drifting in the water column while maintaining a constant altitude, but in no case have we observed a gentle fanning of the veils. It appears to us that *E. eximia* can regulate its buoyancy, perhaps by unloading ballast through defecation. Ohta posited that *E. eximia* descends in a "free fall," by extending the anterior veil anteriorly and sinking to the seafloor. We have observed some individuals sinking slowly, but none held the anterior veil anteriorly. Specimens would swim downwards to the seafloor by extending the anterior veil anteriorly and rhythmically undulating the veil.

Finally, Ohta states that "when the holothurian walks on the bottom, the antero-dorsal velum is fully expanded forward." In contrast, we have observed feeding individuals with anterior veils held erect and the component podia slightly curled posteriorly into the current. The ability of the holothurian to keep the anterior veil erect is most likely a function of current velocity; undoubtedly it would be difficult for *E. eximia* to maintain position on the seafloor in a strong current if the anterior veil were held erect.

Pelagothuria natatrix Ludwig, 1894

FIGURE 1*e–g*

MATERIAL EXAMINED AND HABITAT.—A single individual of this species and a short videotape of its swimming behavior were loaned to us by S. Pomponi and E. Armstrong (HBOI). The specimen was encountered and collected within a few meters of the seabed at a depth of 542 m off Isla San Cristobal, Galapagos Islands (JSL-I-1919, 17 November 1986). The seabed at the dive site was a 5 degree slope covered with mud.

DESCRIPTION OF LIVING INDIVIDUALS.—*Pelagothuria natatrix* is perhaps the most bizarre holothurian species in existence. Its shape is more reminiscent of a medusa (Figure 1*e–g*), and it bears no obvious resemblance to most sea cucumbers. The anterior end of the slender, conical body supports an enormous, umbrella-like veil. The veil, composed of 12–16 large webbed podia, is almost continuous, the web being absent only from the ventral radius. With the veil fully extended anteriorly, the total length of the specimen collected was 16 cm (veil 10 cm; body 6 cm). The (usually) 15 tentacles, approximately 2 cm in length, surround the terminal mouth; they are bifurcate at their tips and non-retractile. The body wall is transparent and pigmented a pale violet or pink. Within the body cavity the slender intestine is evident, and the dense yellow to white gonad is clearly visible when ripe.

FEEDING AND SWIMMING BEHAVIOR.—After careful review of the video record of this species, one might best characterize *Pelagothuria natatrix* as a drifter instead of a swimmer. Although the holothurian is quite capable of active swimming movements, it appears to spend a great deal of time "hanging" vertically in the water column. In this neutrally buoyant posture, *P. natatrix* resembles an umbrella turned inside out by a gusting wind (Figure 1*e*). It seems possible that the holothurian uses its veil to collect or concentrate the rain of detritus from shallower depths, or superficial sediments that have been resuspended. Video footage clearly shows movement of the tentacles when surrounded by the conical veil.

Due to inadequate illumination of the specimen while recording, the video tape of this species was not of sufficient quality to produce a full series of still photographs depicting swimming behavior. However, the three photographs in Figure 1 illustrate the basic postures observed during drifting (Figure 1*e*) and swimming (Figure 1*f,g*) activities. Swimming movements appear to occur irregularly and infrequently, and they are performed at a much slower rate than in the three preceding species. A complete stroke cycle takes approximately 27 sec.

In altering its posture from drifting (feeding?) activity to swimming activity, *P. natatrix* slowly curls the component podia of the veil towards the mouth. When this inward curl has reduced the veil to approximately one-half of its fully erect height, the curling of the podia is reversed to an outward direction. In this posture, the veil forms a ventrally cupped collar around the anterior end, just above the level of the mouth (Figure 1*f*). As the power stroke progresses, the entire veil is pulled posteriorly by the podia, which remain curled until the margin of the veil reaches the level of the posterior end of the body (Figure 1*g*). By this time, the animal has started to rise upwards as a result of the thrust created by the veil. As the forward motion continues in a glide, the flow of water over the veil causes it to collapse, causing the distal tips of the podia to make contact below the posterior end of the body. Because the veil does not completely encircle the anterior end, the thrust created is not equal around the body, and the holothurian tends to ascend obliquely, with the ventral surface facing downwards. The recovery stroke is accomplished by a coordinated inward curling of the podia; this returns the veil to its cupped posture slightly above the anterior end of the body.

Because of their attachment to the base of the podia in the veil, the tentacles are pulled upwards and outwards when the veil is thrust posteriorly in the power stroke. Conversely, as the recovery stroke progresses, the tentacles are moved inward and downward toward the mouth. The fully extended tentacles can be seen arising from the bases of the veil podia in Figure 1*g*. During the power stroke, while the tentacles are pulled outwards, the mouth is gaping, and it is assumed that some ingestion of food occurs at this time.

DISTRIBUTION.—Ludwig (1894) reported on more than 34

specimens of *Pelagothuria natatrix* collected by the *Albatross* between the Gulf of Panama and the Galapagos Islands at depths of 605–3350 m. He also reported that the species was found in surface waters off the west coast of Panama. Chun (1900) reported this species (as *Pelagothuria ludwigi*) from the Indian Ocean, near the Seychelles, depth "pelagic." Heding (1950) reduced *P. ludwigi* to synonymy with *P. natatrix*.

COMMENTS.—Both Herouard (1923) and Heding (1950) reported that the veil of *P. natatrix* is not webbed in the midventral radius. Hansen and Madsen (1956) confirmed that the greatly enlarged laterodorsal veil is comparable to that found in many benthic elasipods, and that "...hitherto published figures of *Pelagothuria* are artistic reconstructions...."

To date, *Pelagothuria natatrix* is the only known truly pelagic holothurian. Previous reports on the intestine contents of this species (Chun, 1900) provide no evidence that this species derives its nourishment from the seafloor. Our examination of the specimen at hand confirms this finding; the intestine contents are unidentifiable fragments of particulate matter, and some pteropod shells and tintinnid tests. There is no unequivocal evidence of benthic organisms or sediment.

Lemche et al. (1976) suggest that *P. natatrix* descends to the seafloor to feed, and they support this contention with two seafloor photographs (their plate 20*c,d*) illustrating an invertebrate species perched on a rocky substratum at hadal depths in the New Hebrides Trench. Although Lemche et al. believe the organisms in the photographs to be specimens of *P. natatrix*, we suggest that the animals in these photographs, as well as the supposed brisingid asteroids in their Plate 17*c–e* are actually deep-sea cnidarians, probably actiniarians. The "veil" in the specimens illustrated by Lemche et al. shows "podia" of greatly varying length, a trait not observed by us in either *Pelagothuria* or *Enypniastes*. We believe that these holothurians cannot strongly expand or contract the webbed podia comprising the anterodorsal veil. The photographs show no evidence, on the animal itself or in the shadow on the rocky substratum, of the presence of the fragile web between the podia. After reviewing the behavior of *P. natatrix* on videotape, we suspect that this species is incapable of inverting itself to feed on the seafloor, as stated by Lemche et al. (p. 289).

Discussion

Despite the growing body of information on the adaptations of deep-sea holothurians, we can as yet only speculate upon the significance of swimming in some species. The contrasting swimming patterns, four of which are described in this paper, provide further complications. Several working hypotheses have been proposed to account for swimming ability, and we discuss some of these here.

PREDATOR AVOIDANCE.—Margolin (1976) determined experimentally that the common eastern Pacific aspidochirote *Parastichopus californicus* will consistently flee, and may vigorously swim, when contacted by sea stars. The swimming behavior of *Hansenothuria benti* and *Paelopatides retifer* may play a similar role in predator avoidance. *Hansenothuria benti* was observed to swim only when stimulated, for example by being prodded with the submersible's manipulator arm. An individual of *P. retifer* feeding on the seabed was provoked to swim by physical contact with the submersible (C. Young, L. Cameron, personal communication). The ability of both of these species to swim actively for several minutes would be of value in escaping potential benthic or bottom-feeding predators. Likewise, the brevity of the feeding period on the seabed of *Enypniastes eximia* (see below) might play a role in predator avoidance.

ESCAPE PHYSICAL HAZARDS.—The ability to leave the seafloor and maintain an altitude above the substratum for several minutes could also allow swimming species to escape burial by sediment slumping or turbidity currents. Throughout the Bahama Islands, the steep bathyal slopes are generally covered by a thin sediment veneer. Areas of instability were obvious during our submersible dives, and small rivulets of sediment were often observed flowing downwards along the limestone faces of steeper slopes.

Based upon our observations of the amount of perturbation required to elicit a swimming response in *Hansenothuria benti*, the bow wave created by an approaching sediment flow would be sufficient stimulus to evoke a swimming response in this species. Alternatively, as *H. benti* is nearly neutrally buoyant, the bow wave of an approaching flow could provide the lift necessary to carry the animal above the source of disturbance, whence it could swim upwards and away from the area.

Heezen et al. (1955) suggested that turbidity currents may be responsible for mass burial of benthic organisms inhabiting the abyssal seafloor. Ohta (1983) found that *Enypniastes eximia* was abundant at a locality where "turbidity currents and/or slumping causes depauperation of nonmotile benthic organisms." He further suggested that the success of *E. eximia* in areas of unstable sediments could be attributed to the holothurian's ability to remain above the seafloor by actively swimming for extended periods of time (Ohta, 1985). In the Tongue of the Ocean, Bahamas, this highly mobile species was most common in canyon-like areas where slumping had recently occurred (Pawson, 1982).

ACTIVE AND PASSIVE DISPERSAL.—The efficient use of limited energy reserves may be an important consideration for deep-sea holothurians that subsist on nutrient-poor sediments. For some species, swimming or drifting as a means of dispersal may require expenditure of a minimal amount of energy. We have observed specimens of *E. eximia* being passively carried along in near-bottom currents. In this species, and probably also in *P. retifer*, horizontal displacement is more a function of prevailing currents than active swimming movements.

The ability of some holothurians to enter the pelagic realm, even temporarily, may provide an efficient means of long-distance dispersal. This method is obviously employed in the

case of species that reside on the seafloor as adults but as juveniles can be found several hundred to several thousand meters above the seafloor (Hansen, 1975; Billett et al., 1985; see also survey on page 3 of this paper). It also seems likely that the commonly occurring large, yolky eggs of elasipodans are buoyant and are dispersed by ocean currents. Hansen (1975) states "the eggs in all families of Elasipoda are so large that possible pelagic larvae are likely to be independent of the plankton for food intake—thus serving only the dispersal of the species."

Hansen (1975) suggested that the similarity between abyssal holothurian faunas of the North Atlantic and southwestern Pacific may be attributed to pelagic transport of young stages by deep-sea currents. At least three elasipodan species common to both of these regions have been collected in mid-water trawls as juveniles (Hansen, 1975).

Ohta (1985) posited that swimming activity in *Enypniastes eximia* and *Pelagothuria natatrix* is an important long-distance dispersal mechanism. His speculation was based upon published records indicating that these species lack pelagic larvae, and are supposedly viviparous. However, evidence for viviparity in *E. eximia* (Ohshima, 1915; Gilchrist, 1920) and *P. natatrix* (Heding, 1940) is, at best, equivocal. Ohshima (1915) reported large egg sizes (up to 3.5 mm diameter) in *E. eximia*. Hansen (1975) and Tyler and Billett (1987) have shown that very large eggs are common among elasipodans. Such large eggs do not provide any proof of viviparity, but they suggest that development may be entirely lecithotrophic. Large eggs, with high content of lipids, and probably buoyant, could be dispersed by currents. Young and Cameron (1987) and Cameron et al. (1988) provide clear evidence that large lecithotrophic eggs of two echinothuriid sea urchin species from bathyal depths are positively buoyant in both in vitro and in situ experiments.

In spite of attempts by several authors to split *Enypniastes* into more than one species (see Heding, 1950; Hansen and Madsen, 1956; Billett et al., 1985), examination of the literature and of material at hand indicates that the genus is monotypic and cosmopolitan in distribution. As stated above (page 14), horizontal distribution in *E. eximia* is dependent largely upon current flow; undoubtedly, oceanic current patterns play a major role in the widespread geographic distribution of this and other deep-sea holothurian species.

TRACKING EPHEMERAL FOOD SUPPLIES.—Deep-sea holothurians may seek desirable substrata, as evidenced by movement of epibenthic species towards sources of high organic input. For example, numerous specimens of *Scotoplanes* sp. were photographed moving towards a decaying fish on the seabed (Pawson, 1976). In a later paper, Pawson (1982) showed that short tracks and trails on the seabed are produced by swimming holothurians that land on the seabed, feed for a short time, and then move away, perhaps in search of more suitable sediments. *Benthodytes sanguinolenta* was observed to make such short tracks. Recent studies by Ohta (1985), Pawson and Foell (1986), and this paper confirm that *Enypniastes eximia* and swimming *Peniagone* species have a short resident time on the seafloor. Sibuet (1985) found a significant correlation between holothurian abundance and organic carbon flux, percent organic carbon in the sediment and terrigenous matter at 4000 m in the tropical Atlantic off French Guiana.

INCREASE EFFICIENCY OF DISSOLVED OXYGEN UPTAKE.—Elasipodan holothurians usually possess unique external structures such as brims or veils of webbed podia, elongate sails, enormous podia (see Théel, 1882; Hansen, 1975), but they lack respiratory trees, which shallow water aspidochirotes and dendrochirotes use for gas exchange. Although no empirical data exist to suggest that these modified structures serve as sites of dissolved oxygen uptake, they might indeed play an important role in gas exchange in these animals that seem to lack specialized respiratory organs. It has been shown, or suggested, that the tube feet of echinoderms aid in respiration (see reviews in Hyman, 1955; Nichols, 1969; Lawrence, 1987). If the modified webbed podia of elasipodans are involved in respiration, perhaps exaggerated movement of these structures during swimming activity improves respiratory efficiency.

INCREASE EFFICIENCY OF DISSOLVED ORGANIC MATTER (DOM) UPTAKE.—The uptake through the bodywall of DOM (parenteral absorption) may be of considerable importance to epibenthic organisms feeding on seafloor sediments with low organic content. Considerable evidence has been presented for epidermal absorption of DOM by echinoderms (Smith et al., 1981; Ferguson, 1982; Bamford, 1982; Feral, 1985; Clements et al., 1988) and other marine invertebrates (Southward and Southward, 1970; Manahan and Crisp, 1982; Manahan, 1983, and others). Again, empirical data for deep-sea holothurians are lacking, but if indeed DOM contributes to nutritional requirements in these animals, then an increase in surface area of the body wall should be advantageous. The extreme in modified body wall structures appears to be reached in swimming elasipods, especially pelagothuriids; possibly these animals are best equipped to use dissolved organics.

In conclusion, active swimming movements in deep-sea holothurians may serve a variety of functions, as suggested above. Whatever the reasons might be, such behavior can have significant and wide-ranging ecological effects on benthic and pelagic areas in many parts of the world's oceans. The conventional view of one-way transport of particulate matter, and ultimately, energy, downwards to the seafloor from the waters above requires modification in light of the evidence that swimming holothurians with intestines full of seafloor sediment can transport this material upwards for hundreds or even thousands of meters. The ability of swimming holothurians to transport large quantities of sediment, perhaps for great horizontal distances from a source area, offers endless complexities for organizations that are seeking suitable deep-sea sites of "low biological activity" for dumping of wastes, especially radioactive wastes!

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