

FIRST RECORDS OF A GIANT PELAGIC
TUNICATE, *BATHOCHORDAEUS CHARON*
(UROCHORDATA, LARVACEA), FROM
THE EASTERN PACIFIC OCEAN, WITH
NOTES ON ITS BIOLOGY

Recent studies (Hamner et al. 1975; Alldredge 1972, 1976a; Silver et al. 1978) have demonstrated the importance of gelatinous macroplankton and their mucous secretions in planktonic communities as sources of particulate organic carbon and surface habitat in an otherwise homogeneous environment. Pelagic tunicates of the Class Larvacea appear to be especially important members of this assemblage because they periodically secrete and release numerous external, mucous, feeding structures or "houses." In midwater trawling off southern California we obtained several specimens of a unique, giant larvacean, *Bathochordaeus charon* Chun 1900. This species may be a major source of suspended organic aggregates, or "marine snow" (Silver et al. 1978), as well as a major consumer of living and detrital particulate organic carbon in mesopelagic regions. Only eight specimens of this unusual tunicate, whose trunk may reach 25 mm long, have been reported. The present material increases the number of known intact specimens to 13 and represents a major extension of the range of the monotypic genus.

History of *Bathochordaeus charon* Collections

Collection data for all known specimens are given in Table 1. *Bathochordaeus charon* was first described as a new genus and species by Chun

(1900:519-521) on the basis of two gigantic specimens taken in 1898 in the southeastern Atlantic Ocean by the German Deep Sea Expedition, aboard the *Valdivia*. Lohmann (1914) described these specimens in greater detail and assigned them to the Oikopleuridae. He later (1931) described two additional, smaller animals taken in 1899 in the Indian Ocean during the same expedition. Garstang (1936, 1937) collected two small specimens off Bermuda, which he described as a new species, *B. stygius*, because of minor differences from the original descriptions. Fenaux (1966) synonymized the two species and Garstang (1937) himself believed the differences lay mainly in misinterpretations of morphology by Chun (1900) and Lohmann (1914, 1931). A single specimen was listed, without description, from the German Atlantic Expedition on the *Meteor* (1925-27) (Lohmann and Hentschel 1939). Thompson's (1948) report of a single small specimen from eastern Australia was the first record of the genus from the Pacific Ocean.

These eight specimens were the only reliable records prior to this report. Tokioka (1960) obtained five large (to 20 mm long) isolated larvacean tails from collections of the Shellback (lat. 13° N, long. 99° W) and EQUAPAC (lat. 8° S, long. 164° E) expeditions of the Scripps Institution of Oceanography. Tokioka tentatively assigned these to *Bathochordaeus charon* on the basis of their length; however, all conform in size with *Megalocercus* sp., another large larvacean which also was taken on these expeditions, and only one of the tails had the characteristic shape of *B. charon*. Thus the affinity of Tokioka's (1960) material cannot be established with certainty and only one of his specimens is included in Table 1.

TABLE 1.—Collection and size data for known specimens of the pelagic tunicate *Bathochordaeus charon*. The specimen of Tokioka is only tentatively assigned to this species (see text).

Specimen number	Date of collection	Depth of tow (m)	Location		Trunk (mm)		Tail (mm)		Reference
			Lat.	Long.	Length	Width	Length	Width	
1	21 Oct. 1898	0-2,500	31°00' S	8°00' E	25	19	70	30	Chun 1900; Lohmann 1914, 1931
2	21 Oct. 1898	0-2,500	31°00' S	8°00' E	25	19	70	30	Chun 1900; Lohmann 1914, 1931
3	9 Mar. 1899	0-2,000	4°34' S	53°43' E	5	—	18	—	Lohmann 1931
4	10 Mar. 1899	0-2,000	4°38' S	51°17' E	1	—	4	—	Lohmann 1931
5	25 Mar. 1927	50-100	15°04' N	44°39' W	—	—	—	—	Lohmann and Hentschel 1939
6	Mar. 1935	0-300	32°50' N	64°50' W	6	5	20	6	Garstang 1936, 1937
7	Mar. 1935	0-300	32°50' N	64°50' W	4	3	14	5	Garstang 1936, 1937
8	Feb. 1940	8-200	33°55' S	151°10' E	3	—	8	—	Thompson 1948
9	—	—	—	—	12	11	30	11	This report
10	29 June 1976	0-500	33°15' N	118°25' W	12	14	47	15	This report
11	20 Sept. 1977	0-300	33°37' N	118°19' W	—	—	34	8	This report (tail only)
12	8 Oct. 1977	0-480	33°41' N	118°25' W	16	11	47	9	This report
13	8 Oct. 1977	0-200	33°41' N	118°25' W	15	14	34	11	This report
14	8 Oct. 1977	0-200	33°41' N	118°25' W	12	11	25	11	This report
15?	18 June 1952	0-300	15°32' N	99°50' W	—	—	20	8	Tokioka 1960 (tail only)

Materials and Methods

Five of the six new specimens (Table 1) were collected in Isaacs-Kidd midwater trawls from about 500 m to the surface, aboard the RV *Nautilus* of the Southern California Ocean Studies Consortium and the RV *Velero IV* of the Allan Hancock Foundation, University of Southern California in 1976-77 off the coast of southern California. Collection data are lacking for specimen number 9.

Bathochordaeus charon reaches a trunk length of at least 25 mm, yet most previously collected specimens were considerably smaller. Even large animals are difficult to sort from samples until one is trained to recognize the unusual body form (Figures 1, 2). I have found it useful to dilute the entire fresh sample into one or more large (20-50 l), glass aquaria and examine it with transmitted light. The mucous house, typical of larvaceans of the family Oikopleuridae (and presumably of

gigantic proportions in this species), has never been collected intact in a plankton tow. Turbulence in the net probably causes its disintegration, as is true of many other mucous structures (Hamner et al. 1975; Silver et al. 1978). The animal itself is virtually transparent and is often of delicate consistency. The large trunk is frequently separated from the tail or is otherwise damaged.

Results

Description of *Bathochordaeus charon*

The present specimens (Table 1, Figure 1) conform generally to published accounts of *B. charon*, detailed descriptions of which were given by Chun (1900), Lohmann (1931), Garstang (1937, as *B. stygius*), and Thompson (1948). Final confirmation must await careful morphological study of the new material.

The conspicuous feature of this species is its

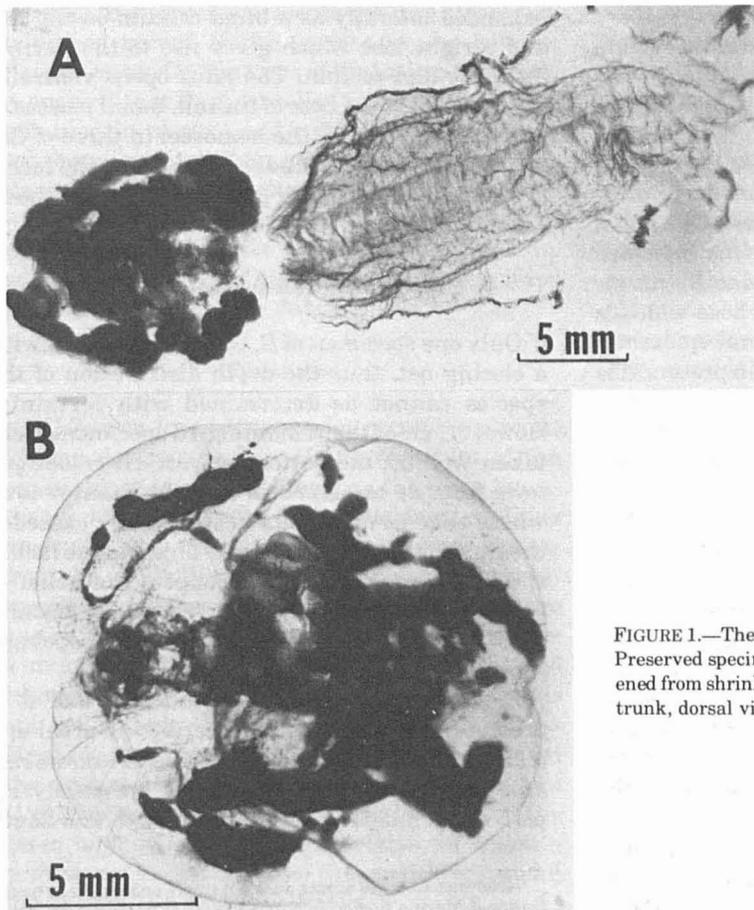


FIGURE 1.—The pelagic tunicate *Bathochordaeus charon*. A. Preserved specimen, trunk and tail, dorsal view. Tail is shortened from shrinkage during fixation. B. Preserved specimen, trunk, dorsal view.

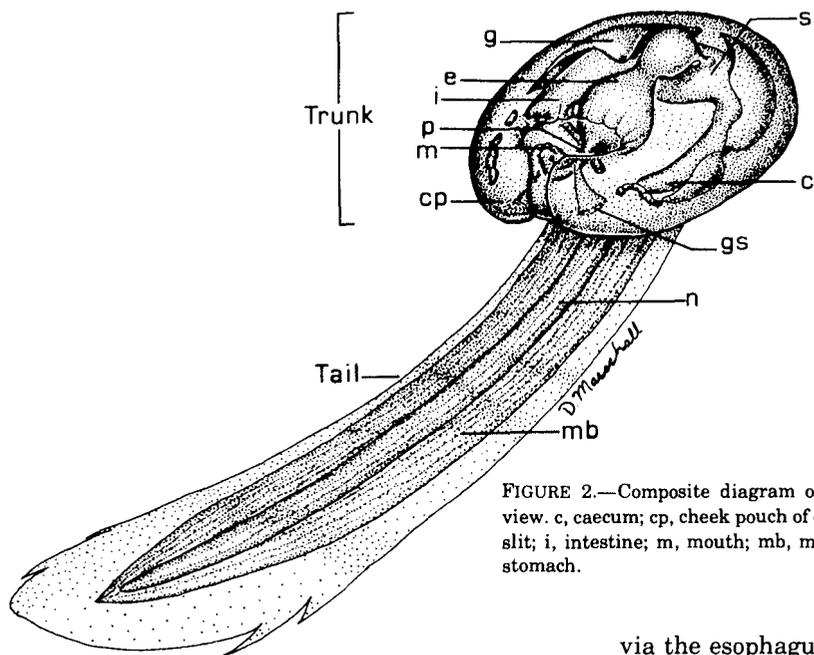


FIGURE 2.—Composite diagram of *Bathochordaeus charon*, anterolateral view. c, caecum; cp, cheek pouch of epidermis; e, esophagus; g, gonad; gs, gill slit; i, intestine; m, mouth; mb, muscle band; n, notochord; p, pharynx; s, stomach.

great size relative to other larvaceans, whose adult trunk lengths are usually <5 mm. The present specimens are the largest collected since Chun's (1900) first two giants (Table 1). The ratio of tail length to trunk length ranges from 2.1 to 3.9, but damage to the tail and shrinkage after fixation make these figures unreliable. The mean ratio of 3.0 for all 12 intact specimens indicates that, in contrast to other Oikopleuridae, *B. charon* has a relatively short, broad tail whose width is about one-third its length. The lateral epidermal fin is usually torn or absent, but when present it is widest distally, unique in the Oikopleuridae. The notochord is clearly visible as the central axis of the tail, sandwiched between the two broad muscle bands.

In contrast to other Oikopleuridae, the trunk is strongly compressed dorsoventrally and is nearly as broad as long (Figure 2). The epidermis is thin and often diaphanous, and it protrudes on either side of the oral region as a pair of "cheek" pouches. The mouth, unique in its dorsal and subterminal position, lies atop a low buccal cone and leads into the short, narrow pharynx. The long, spindle-shaped openings of the two stigmata (gill slits) arise from the floor of the pharynx just behind the level of the dorsal mouth and ventral endostyle. The gut, the only conspicuous internal structure, is light brown in Formalin¹-preserved material and lies free in the body cavity. The pharynx opens

via the esophagus into the large stomach that is expanded laterally as a blind caecum on the left and a right lobe which gives rise to the narrow intestine and rectum. The anus opens ventrally just anterior to the base of the tail. Small masses of gonadal tissue lie in the hemocoel in three of the specimens. In mature individuals the gonad forms a U-shaped mass which protrudes into the cheek pouches.

Distribution of *Bathochordaeus charon*

Only one specimen of *B. charon* was taken with a closing net, thus the depth distribution of the species cannot be determined with certainty. However, all of the remaining 13 specimens were taken well off the bottom in vertical or oblique tows from at least 200 m or in horizontal tows whose time at maximum depth greatly exceeded the time for hauling in the net. This and the lack of specimens in surface tows support the belief of Chun (1900), Lohmann (1931), and Garstang (1937) that *B. charon* is a deep-living, mesopelagic species.

Few specimens have been collected and it is premature to conclusively describe the areal distribution of *B. charon* on the basis of known records (Figure 3). Since the eight previously reported specimens came from the North and South

¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

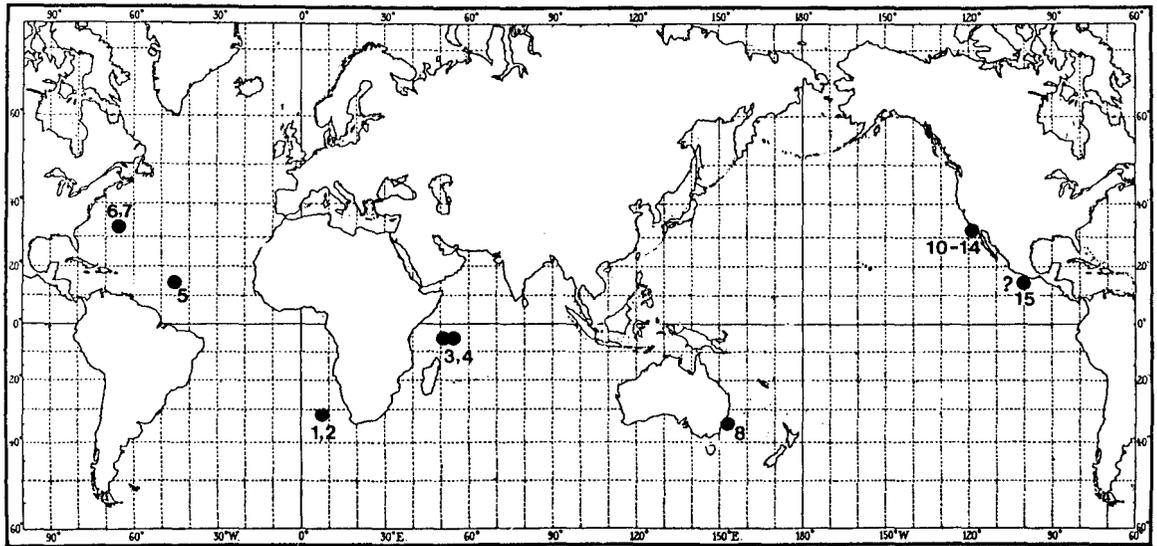


FIGURE 3.—Known collection sites of *Bathochordaeus charon*. Numbers correspond to specimen number listed in Table 1.

Atlantic, Indian, and southwestern Pacific Oceans, this report represents the first clearly established record of the species in the eastern Pacific Ocean. On the basis of the known material, it appears that *B. charon* has a circumglobal distribution in tropical and subtropical oceanic waters between lat. 35° N and 35° S. Forneris (1957) classified it as a "eurythermic thermophile," but such a characterization seems unwarranted, as it was based on only eight specimens obtained from widely separated localities and without associated physical oceanographic data.

Discussion

All known larvacean species secrete a mucous feeding device, the house. The structure of the house varies considerably among the three larvacean families, but in the Oikopleuridae it contains mucous filters which remove particulate matter from the water. Periodically, when the filters become clogged, the animal abandons the old house and within a few minutes produces a new one from a mucous rudiment secreted while in the old house. The type of house produced by *B. charon* is not yet known. Chun (1900) believed it was as large as a pumpkin and that it completely enclosed the animal, as in other Oikopleuridae. Lohmann (1931) believed that the house was probably of the "nose bag" type, as in Fritillariidae, in which a mucous net is cast out from the buccal region and the animal is free in the water.

Barham (1969) observed spherical, mucous structures, at least 25 to 50 cm in diameter, from deep submersibles off San Diego, Calif., at about 200 m. Inside some of these structures, the swimming motions of a large, tadpolelike animal were visible. The structure and size of these "busted balloons" leave little doubt that they were occupied and abandoned larvacean houses, very likely those of *B. charon*. Because the houses have not been collected in nets, Barham's account represents the only observation of them. Studies of photographs from such in situ observations and of the secretory apparatus of the animals themselves may elucidate the structure of the house of *B. charon*.

Bathochordaeus charon is considered to be rare because of sparse records obtained since its discovery in 1900. However, current evidence indicates that the animals and their houses may be relatively common, comparable with other species of similar, large size, at least at certain depths, locations, or times. Barham² estimated the densities of presumed giant larvacean houses off Cape Corrientes, Mexico, to be on the order of 1 to 3/m³ within narrow layers near the thermocline, between about 50 and 300 m. At least six of the known specimens occurred in pairs in the same plankton sample. Thus, despite their large size,

²Eric G. Barham, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. March 1978.

they may be difficult to collect because of a vertically stratified distribution or they may remain unrecognized in midwater plankton samples because of their fragility, transparency, and deviation from typical larvacean structure.

Epipelagic larvacean relatives of *B. charon* filter feed on nanoplankton, especially cells $<10\ \mu\text{m}$ (Lohmann 1899; Alldredge 1975). The muscular tail pumps water through the house and permits the concentration of suspended particles from larger volumes of water than would be possible using ciliary currents alone. Since food is selected only on the basis of size, detritus may constitute a significant fraction of the food in some locations (Gerber and Marshall 1974).

In waters below the euphotic zone, particulate organic carbon is scarce, generally present at levels from 10 to $10^2\ \mu\text{g C/l}$, compared with roughly 10^2 to $10^3\ \mu\text{g C/l}$ in the euphotic zone (Holm-Hansen et al. 1966; Hobson 1967; Menzel 1967). Most of the particulate carbon below 200 m contains little or no chlorophyll (Holm-Hansen et al. 1966) and is composed mainly of detritus. However, Fournier (1971) and others have reported the presence of living, pigmented cells ("olive-green cells," or OGC's) averaging $3.5\ \mu\text{m}$ in diameter in virtually all waters sampled deeper than about 50 m in the Atlantic and Pacific Oceans. These cells reach their maximum density of about $10^5/\text{l}$ at 300 to 500 m and may contribute up to about $1\ \mu\text{g C/l}$, or up to 10% of the total particulate organic carbon in aphotic marine environments. Fournier (1971) suggested that copepods are not likely to be major consumers of OGC's because of their limited abilities to filter such small particles at low concentrations and that pelagic tunicates, which filter water through mucous sheets, may be better suited to utilize such particles. Fournier (1973) demonstrated that the gut contents of colonies of the pelagic tunicate, *Pyrosoma*, from below the euphotic zone consisted mainly of OGC's. If *B. charon* is indeed a resident of midwaters, as suggested above, and if it, like its epipelagic relatives, filters particles <10 to $20\ \mu\text{m}$ in size, then it may be a major consumer of OGC's as well as detritus. The localized occurrence of dense layers of *B. charon* indicated by the in situ observations of Barham (1969) may depend on the presence of peak concentrations of OGC's between 200 and 1,000 m, as observed by Fournier (1971). Alternatively, the filter meshes of the house of *B. charon* may be larger than those of smaller, epipelagic larvaceans and the food may then consist largely

of slow zooplankton. Knowledge of house structure and analyses of gut contents of additional specimens may clarify the role of *B. charon* in mesopelagic food webs.

Bathochordaeus charon may contribute large amounts of mucus to the water column in the form of its discarded houses. *Oikopleura dioica* secretes and discards four to six houses per day (Paffenhöfer 1973). Such occupied and empty houses are sources of particulate food and surface habitat for microorganisms in planktonic ecosystems (Alldredge 1972, 1976a) and, along with other organic aggregates, may serve as a barrier to the downward flux of particulate matter and substances adhered or adsorbed to them (Silver et al. 1978). Moreover, such "marine snow" provides a trophic link between large consumers and nanoplankton, protozoa, and microcrustaceans, allowing the former to tap an otherwise unavailable food source (Hamner et al. 1975). Larvaceans and their houses are known prey for fish and planktonic invertebrates (Alldredge 1976a, b; Bailey et al. 1975; Hobson 1974; Hobson and Chess 1976).

Bathochordaeus charon produces large mucous structures, although the size and frequency of production of the houses is not known. The rate of turnover of houses is probably less than in *O. dioica* because of lower temperatures and lower concentrations of particulates which could clog the house filters. Other Oikopleuridae produce houses which are roughly 5 to 15 times the trunk length (Alldredge 1975). If this ratio holds for *B. charon*, then a 25 mm individual would produce a house about 10 to 40 cm in diameter, comparable with in situ estimates (Barham 1969). If *B. charon* is concentrated in layers just above the thermocline, as suggested by in situ observations (Barham see footnote 2), then its houses may form a major component of mesopelagic marine snow.

Note Added in Proof

I am grateful to A. Bückmann and H. Kapp for calling my attention to their paper (Untersuchungen am Zooplankton von der Atlantischen Kuppenfahrt der „Meteor“, März bis Juli 1967, published 1973 in „Meteor“ Forschungsergebnisse, Reihe D, No. 13:11-36) in which they described and illustrated two additional specimens, referred to as *B. stygius*. The specimens were taken April 1967 in the North Atlantic (lat. $30^{\circ}18' \text{N}$, long. $29^{\circ}20' \text{W}$) between 100 m and the surface.

One specimen was 6.1 mm trunk length and the other was not measurable. The authors provided a valuable discussion of the taxonomic problems of the genus and suggested that *B. stygius* should be applied at least to all known juvenile specimens.

Acknowledgments

Thanks to Eric Barham for sharing his unpublished observations and for critically reading the manuscript; to Janie Layton, Suzanne Latauska, Robert Freligh, and Michael Schadt for technical assistance; and to Theodore Pietsch, Laurie Stuart, Jay Quast, and an anonymous reviewer for commenting on the manuscript. This work was supported in part by a grant-in-aid from the Office of Graduate Studies and Research, California State University, Long Beach.

Literature Cited

- ALLDREDGE, A. L.
1972. Abandoned larvacean houses: A unique food source in the pelagic environment. *Science* (Wash., D.C.) 177:885-887.
1975. Quantitative natural history and ecology of appendicularians and discarded appendicularian houses. Ph.D. Thesis, Univ. of California, Davis, 149 p.
1976a. Discarded appendicularian houses as sources of food, surface habitats, and particulate organic matter in planktonic environments. *Limnol. Oceanogr.* 21:14-23.
1976b. Field behavior and adaptive strategies of appendicularians (Chordata: Tunicata). *Mar. Biol.* (Berl.) 38:29-39.
- BAILEY, J. E., B. L. WING, AND C. R. MATTSON.
1975. Zooplankton abundance and feeding habits of fry of pink salmon, *Oncorhynchus gorbusha*, and chum salmon, *Oncorhynchus keta*, in Traitors Cove, Alaska, with speculations on the carrying capacity of the area. *Fish. Bull.*, U.S. 73:846-861.
- BARHAM, E. G.
1969. A window in the sea. *Oceans Mag.* 1(1):54-60.
- CHUN, C.
1900. Aus den Tiefen des Weltmeeres. *Gustav Fischer*, Jena, p. 519-521 (2d ed., 1903, p. 554-557).
- FENAUX, R.
1966. Synonymie et distribution géographique des Appendiculaires. *Bull. Inst. Oceanogr.* (Monaco) 66(1363), 23 p.
- FORNERIS, L.
1957. The geographical distribution of the Copelata. *An. Acad. Bras. Cienc.* 29:273-284.
- FOURNIER, R. O.
1971. Studies on pigmented microorganisms from aphotic marine environments. II. North Atlantic distribution. *Limnol. Oceanogr.* 16:952-961.
1973. Studies on pigmented microorganisms from aphotic marine environments. III. Evidence of apparent utilization by benthic and pelagic tunicata. *Limnol. Oceanogr.* 18:38-43.
- GARSTANG, W.
1936. On a new Appendicularian, *Bathochordaeus* sp., from Bermuda, with a revision of the genus. (Abstract.) *Proc. Linn. Soc. Lond.* 148:131-132.
1937. On the anatomy and relations of the Appendicularian *Bathochordaeus*, based on a new species from Bermuda (*B. stygius*, sp. n.). *J. Linn. Soc. Lond. Zool.* 40:283-303.
- GERBER, R. P., AND N. MARSHALL.
1974. Ingestion of detritus by the lagoon pelagic community at Eniwetak Atoll. *Limnol. Oceanogr.* 19:815-824.
- HAMNER, W. M., L. P. MADIN, A. L. ALLDREDGE, R. W. GILMER, AND P. P. HAMNER.
1975. Underwater observations of gelatinous zooplankton: Sampling problems, feeding biology, and behavior. *Limnol. Oceanogr.* 20:907-917.
- HOBSON, E. S.
1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fish. Bull.*, U.S. 72:915-1031.
- HOBSON, E. S., AND J. R. CHESS.
1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. *Fish. Bull.*, U.S. 74:567-598.
- HOBSON, L.
1967. The seasonal and vertical distribution of suspended particulate matter in an area of the Northeast Pacific Ocean. *Limnol. Oceanogr.* 12:642-649.
- HOLM-HANSEN, O., J. D. H. STRICKLAND, AND P. M. WILLIAMS.
1966. A detailed analysis of biologically important substances in a profile off southern California. *Limnol. Oceanogr.* 11:548-561.
- LOHMANN, H.
1899. Das Gehäuse der Appendicularien, sein Bau, seine Funktion und Entstehung. *Schr. Naturwiss. Ver. Schleswig-Holstein* 11:347-406.
1914. Die Appendicularien der VALDIVIA Expedition. *Verh. Dtsch. Zool. Ges.* 24:157-192.
1931. Die Appendicularien der Deutschen Tiefsee-Expedition. *Wiss. Ergeb. Dtsch. Tiefsee-Exped.* 21:1-158.
- LOHMANN, H., AND E. HENTSCHEL.
1939. Die Appendicularien im Südatlantischen Ozean. *Wiss. Ergeb. Dtsch. Atl. Exped.* 13:153-243.
- MENZEL, D. W.
1967. Particulate organic carbon in the deep sea. *Deep-Sea Res.* 14:229-238.
- SILVER, M. W., A. L. SHANKS, AND J. D. TRENT.
1978. Marine snow: Microplankton habitat and source of small-scale patchiness in pelagic populations. *Science* (Wash., D.C.) 201:371-373.
- THOMPSON, H.
1948. Pelagic Tunicates of Australia. *Commonw. Council. Sci. Ind. Res., Aust.*, 196 p.
- TOKIOKA, T.
1960. Studies on the distribution of appendicularians and some thaliaceans of the North Pacific, with some morphological notes. *Publ. Seto Mar. Biol. Lab.* 8(2):129-221.

CHARLES P. GALT

Biology Department
California State University
Long Beach, CA 90840