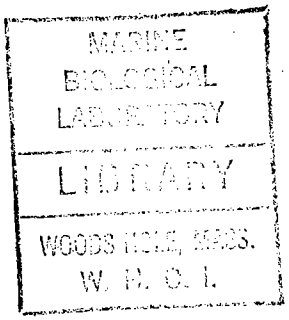
NUTRITIONAL ECOLOGY OF AGALMA OKENI AND OTHER SIPHONOPHORES FROM THE EPIPELAGIC WESTERN NORTH ATLANTIC OCEAN



by

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(1972)

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Nutritional Ecology of Agalma okeni and Other Siphonophores from the Epipelagic Western North Atlantic Ocean

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ABSTRACT

The feeding and fishing behavior of siphonophores in their natural environment was observed by SCUBA diving at 171 stations in warm-water areas of the Western North Atlantic Ocean. Calycophorae and Physonectae showed a two-phase cycle of fishing and swimming. The fishing posture of a siphonophore is determined by its floatation and by the contractility of its stem; fishing postures can be similar in siphonophores which are unrelated generically. Total tentacle length in colonies with 2 - 3 mg body protein can extend 4.5 meters.

Variations in the morphology of tentilla reflect differences in the kinds of prey which can be captured. Dissection of feeding polyps revealed that most siphonophores could eat copepods, amphipods, polychaetes, pteropods, heteropods, veliger larvae, sergestids, mysids, euphausiids, and small fish, though laboratory experiments showed that not all could eat nauplii. Species which could capture Artemia nauplii usually required 2 - 4 hours to digest them, while large prey took 7 - 18 hours to be digested. Since a single feeding polyp of species which captured nauplii could ingest more than one per minute, colonies with 20 - 150 feeding polyps may be able to eat several hundred individuals within minutes if they encounter aggregations of small zooplankton.

Agalma okeni was the most common siphonophore encountered by divers. Colonies of A. okeni maintained in the laboratory on a diet of Artemia nauplii, copepods, or shrimp budded an additional feeding polyp and 1 - 2 pairs of nectophores about every two days. Energetic calculations suggest that small and medium-size colonies incorporate 48% and 33%, respectively, of ingestion into production. A small colony of A. okeni with six nectophores probably requires 2.8 - 5.0 calories to balance daily rates of oxygen consumption and growth; a

medium-size colony with 14 nectophores probably requires 5.8 - 9.2 calories. Extrapolating from short-term increases in size in the laboratory, the generation time of A. okeni in tropical and subtropical regions is likely 2 1/2 - 4 weeks.

Respiration of siphonophores at 26 ± 3°C ranged from 2 - 86 µl O_2/mg protein-hr, and ammonia excretion ranged from 0.1 - 3.3 µg NH_4^+/mg protein-hr. The cystonects Rhizophysa filiformis and Bathyphysa sibogae had low rates of respiration and excretion, while calycophores of the genus Sulculeolaria had the highest rates. For most siphonophores, ratios of oxygen consumed to ammonia-nitrogen excreted ranged from 16 - 36 and suggest that both protein and lipid are important metabolites.

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PREFACE AND ACKNOWLEDGMENTS

Siphonophores are a group of gelatinous, oceanic zooplankton which taxonomists rarely see alive and which have never been studied in their natural environment. Many of these colonial animals are incredibly beautiful combinations of sculptured, gelatinous swimming bells and delicate bracts. There are three suborders, the Physonectae, Cystonectae, and Calycophorae, in which over 140 species are now recognized.

Physonectae have an apical gas-filled float, or pneumatophore, often followed by a series of swimming bells, called nectophores, which are commonly arranged in biserial rows along the nectosome. Below the nectosome is the siphosome with its gastrozooids, palpons, gonophores, and clusters of bracts. Each gastrozooid and palpon has a tentacle. The tentacles of gastrozooids often have numerous lateral branches, or tentilla, bearing terminal batteries of nematocysts. Figure 1 illustrates the organization of a colony of Agalma elegans. It is shown in life in Figure 5. Calycophorae lack a pneumatophore and most have only one or two nectophores. Rosacea cymbiformis, Stephanophyes superba, and Sulculeolaria quadrivalvis are representative Calycophorae (Figures 6 and 8). Cystonectae have no gelatinous individuals and the pneumatophore is greatly enlarged. Bathyphysa sibogae (figured in Appendix 3) is a member of this group, as is Physalia physalis, the Portuguese Man-of-War. For a discussion of siphonophore taxonomy and phylogeny, see Garstang (1946) and Totton (1965).

Figure 1. Colony of Agalma elegans, illustrating the principal parts of a siphonophore.

Pn : Pneumatophore

N : Nectophore

Gz-4 : Gastrozooid # 4

Br : Bract

Gz-3 : Gastrozooid # 3

Go ♀ : Female gonophore

Go ♂ : Male gonophore

Gz-2 : Gastrozooid # 2

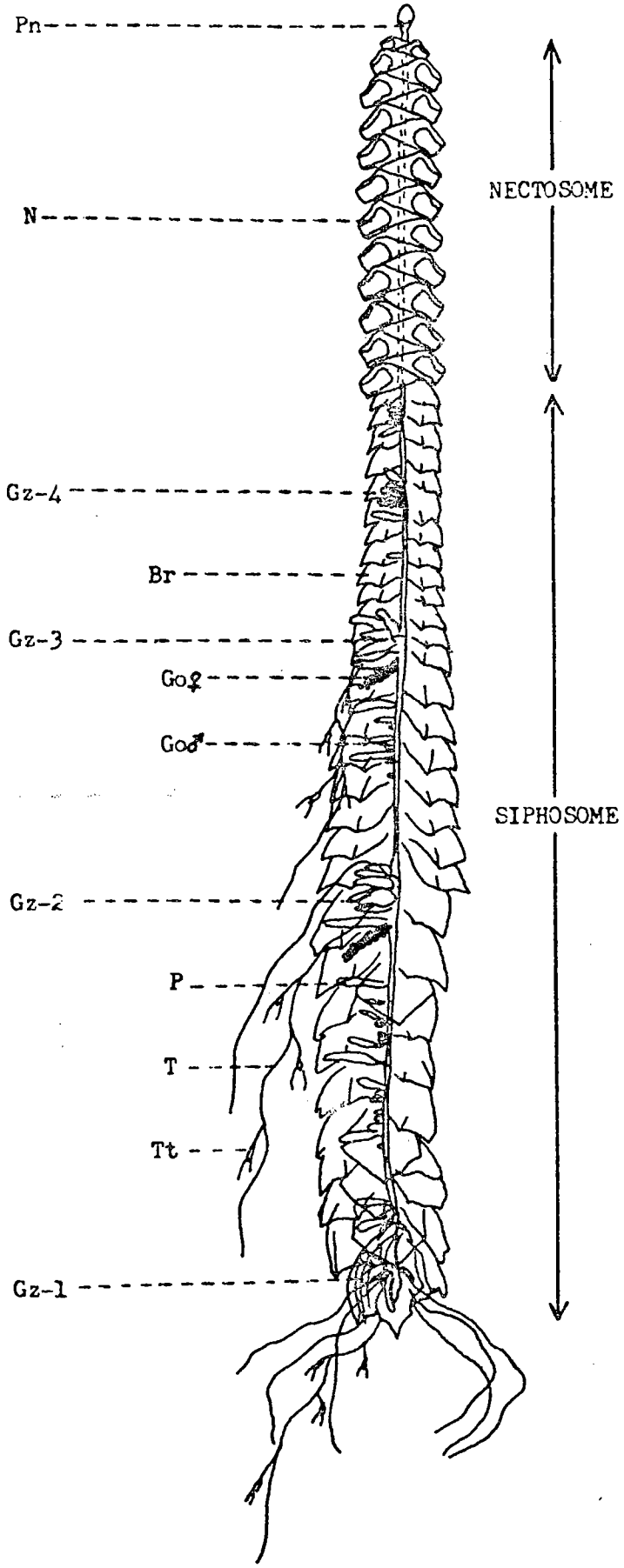
P : Palpon

T : Tentacle

Tt : Tentillum

Gz-1 : Gastrozooid # 1

(Redrawn from Totton, 1954)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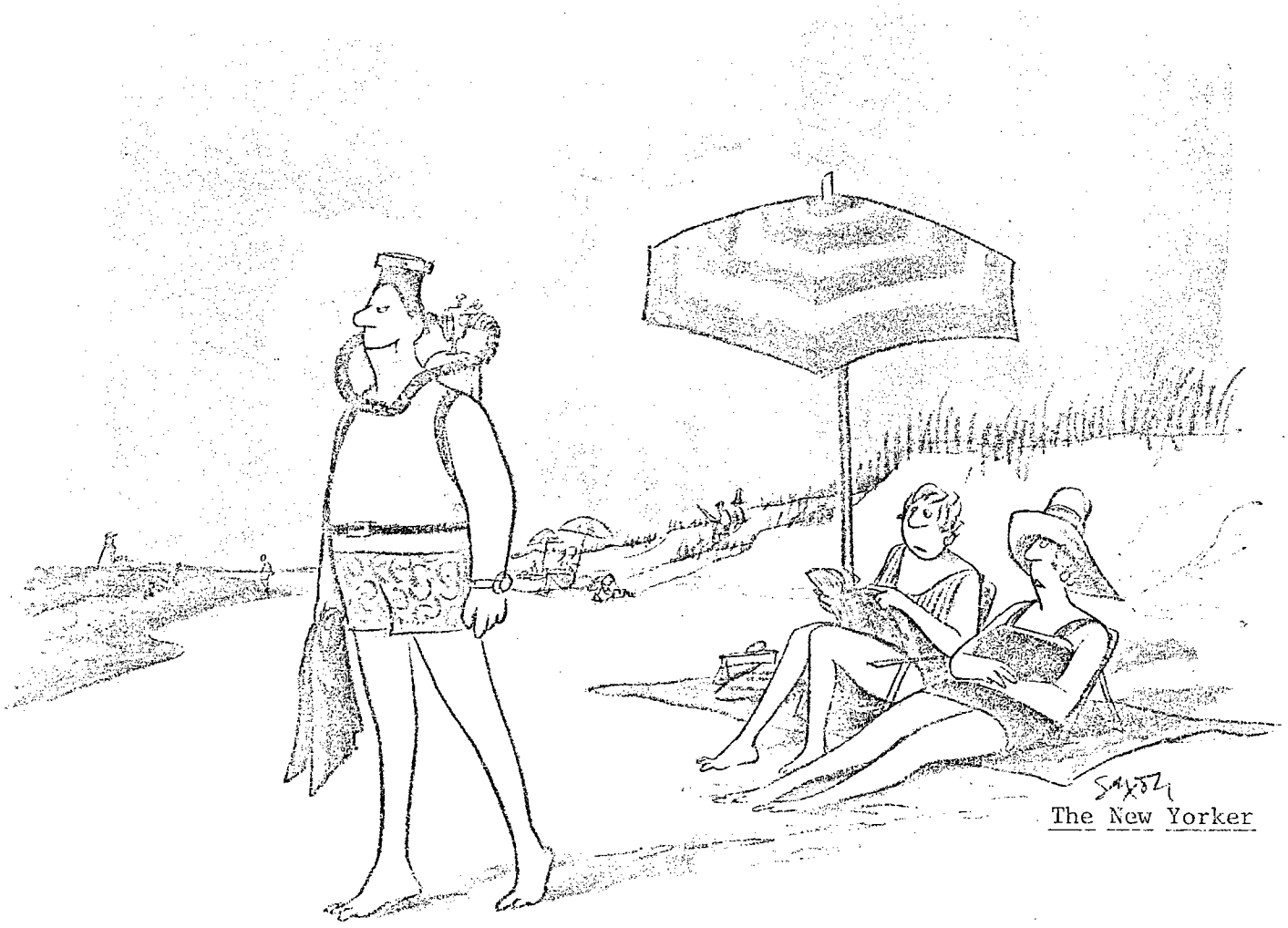
This dissertation summarizes the results of a 26-month program of field studies on aspects of the nutritional ecology of siphonophores. It is divided into four parts, which consider the distribution, feeding biology, oxygen consumption and ammonia excretion, growth and reproduction of siphonophores. In situ observations and simple experiments performed while SCUBA diving contribute to and unify these four sections.

I am especially grateful to my thesis supervisors, John Teal and Richard Harbison, who introduced me to siphonophores, dived with me, and offered constructive comments during all phases of this research. I would also like to thank the other members of my thesis committee, Vaughan Bowen, Fred Grassle, Ned Holt, and Peter Wiebe, who provided me some of their ship time (V.B., P.W.) and were available for provocative discussions. Larry Madin, Ron Gilmer, and Neil Swanberg also dived with me throughout most of these studies, and I benefited from their expertise on other groups of gelatinous zooplankton.

During this research, I was supported by predoctoral fellowships from the National Science Foundation and the Woods Hole Oceanographic Institution, and in part by NSF Grants GA-39976 and GA-21715. I am indebted to Burr Steinbach and Adair Feldman, Directors of the Harbor Branch Foundation Laboratory, for providing laboratory space and ship time to Richard Harbison and me during 1973-1974 research in the Florida Current. I would also like to thank David Mook and Ross Wilcox, who dived with us in Florida.

Most especially, I would like to thank my wife Joanne for her toleration of my enthusiasm for open-ocean diving during 14 cruises which contributed to this research, and dedicate this dissertation to her:



"My rival is the sea."

Part 1. Distribution of Siphonophores in the upper 30 m of the North Atlantic Ocean.

INTRODUCTION

Siphonophores have intrigued marine naturalists since the time of Captain James Cook's first voyage of discovery (Parkinson, 1768, in Totton, 1954). A few Calycophorae may be indicator species for neritic water masses (e.g., Russell, 1934; Fraser, 1967), and pleustonic species like Physalia physalis, the Portuguese Man-of-War, are occasionally blown or carried by currents close inshore (e.g., Totton and Mackie, 1960; Kennedy, 1972). Most, though, are exclusively creatures of the open ocean.

Siphonophores occur from the surface to bathypelagic depths in excess of 4391 m (Lens and van Riemsdijk, 1908). Many species are cosmopolites of tropical and subtropical Atlantic, Pacific, and Indian Oceans (Margulis, 1972), while a few are restricted to Arctic and Antarctic seas (Moser, 1925; Stepanyants, 1963). Despite their cosmopolitan distribution, however, quantitative zoogeographic information is largely unavailable.

Conventional sampling of populations of Cystonectae with nets cannot provide unbiased presence-absence data, since all those of the Family Rhizophysidae adhere to fabric. As these are delicate and easily fragmented, most specimens captured in plankton nets probably do not remain in recognizable condition. Almost all Physonectae, as well, fragment when captured in trawls or plankton nets. Because siphonophores grow by budding, the nectophores and

bracts of a single physonect colony are present in a wide range of sizes. Unless the siphosome or pneumatophore remains as a recognizable entity, it is impossible to determine whether the gelatinous components represent one or several colonies.

It is only for some of the Calycophorae that estimates of population size are feasible by enumeration of plankton collections. Most calycophores, especially those of the Families Diphyidae and Abylidae, have only one superior nectophore and one inferior nectophore per colony. The superior nectophore is morphologically distinct from the inferior; often either can be used for specific identification and enumeration. However, calycophores have fragile stems which, when extended in fishing posture, may stretch several meters (see Part 2). Since most plankton nets used for quantitative sampling are 1 m or less in diameter, they seldom collect the entire colony of large Calycophorae. Unless the plankton net snags the extreme anterior ends of these siphonophores, estimates of population numbers (derived from counts of the anterior nectophores) will represent minimum population values.

In summary, difficulties in quantitatively sampling populations of large, fragile colonial animals like siphonophores arise both from the general characteristics of present samplers and from the small volume of water which they routinely sample (usually, 200 - 500 m^3). However, SCUBA divers can see an enormous volume of water,

thanks to excellent visibility in open-ocean surface water. By noting the species of siphonophores encountered in situ, divers can record qualitative zoogeographic data by direct observation. If the volume of water searched per dive is known or approximated, divers can provide estimates of population density, as well.

METHODS

During 1973 - 1975, I (with others) made 171 SCUBA dives in the upper 30 m of the North Atlantic Ocean (Figure 2 and Appendix 1). We followed logistics and safety procedures for open-ocean diving described by Hamner (1975). In this mode of diving, each diver was connected by a pulley-operated 10-meter tether to a plumb line drifting beneath a motorized rubber raft. The raft was launched from an oceanographic research vessel, which kept in radio contact. Surface temperatures ranged from 17 - 29°C (Appendix 1), and visibility during the day was usually in excess of 30 meters.

Seven dives were made at night: three in the Northern Sargasso Sea, three in the Southern Sargasso Sea, and one in the tropical Atlantic. At night, divers remained in the upper 10 meters, within an area of illumination provided by a one-meter square semi-submerged array of nine automobile headlamps.

On dives during KNORR Cruise 53, pellets of fluorescein dye were dropped at intervals from the rubber raft. I marked the time

in which the plume of dye drifted the 10-meter length of my tether and was able to approximate my drift in relation to the water. On any dive, I spent most of my time looking up from depth so that siphonophores and other gelatinous plankton were silhouetted above me. Since many species of Physonectae are large and have pigmented stem groups, they were readily visible at least 10 meters away. I estimate that, on any dive, the other divers and I were able to locate and collect in jars most or all of the physonect siphonophores in half a cylinder of radius 10-meters and length equal to that of our drift (see Table 2).

RESULTS

Although there is morphological variability within species, especially between juvenile and mature colonies, I collected seven specimens of Athorybia Eschscholtz, 1825 which are different from previously described species synonomized by Totton (1954) as Athorybia rosacea. I will refer to these as Athorybia sp. A (Table 1). Similarly, I collected three specimens of Rosacea sensu Bigelow, 1911 which cannot be attributed to previously described species (P. R. Pugh, personal communication); I will refer to them as Rosacea sp. A (Table 1).

Figure 2. SCUBA Stations, September 1973 - November 1975. Zoogeographic regions and provinces are those proposed by Backus, et al., in prep .

LEGEND:

North Atlantic Temperate Region

1 = Slope Water

North Atlantic Subtropical Region

2 = Northern Sargasso Sea

3 = Southern Sargasso Sea

4 = Northern North African Subtropical Sea

5 = Southern North African Subtropical Sea

Atlantic Tropical Region

6 = Straits of Florida (Florida Current)

7 = Caribbean Sea

8 = Lesser Antillean Province

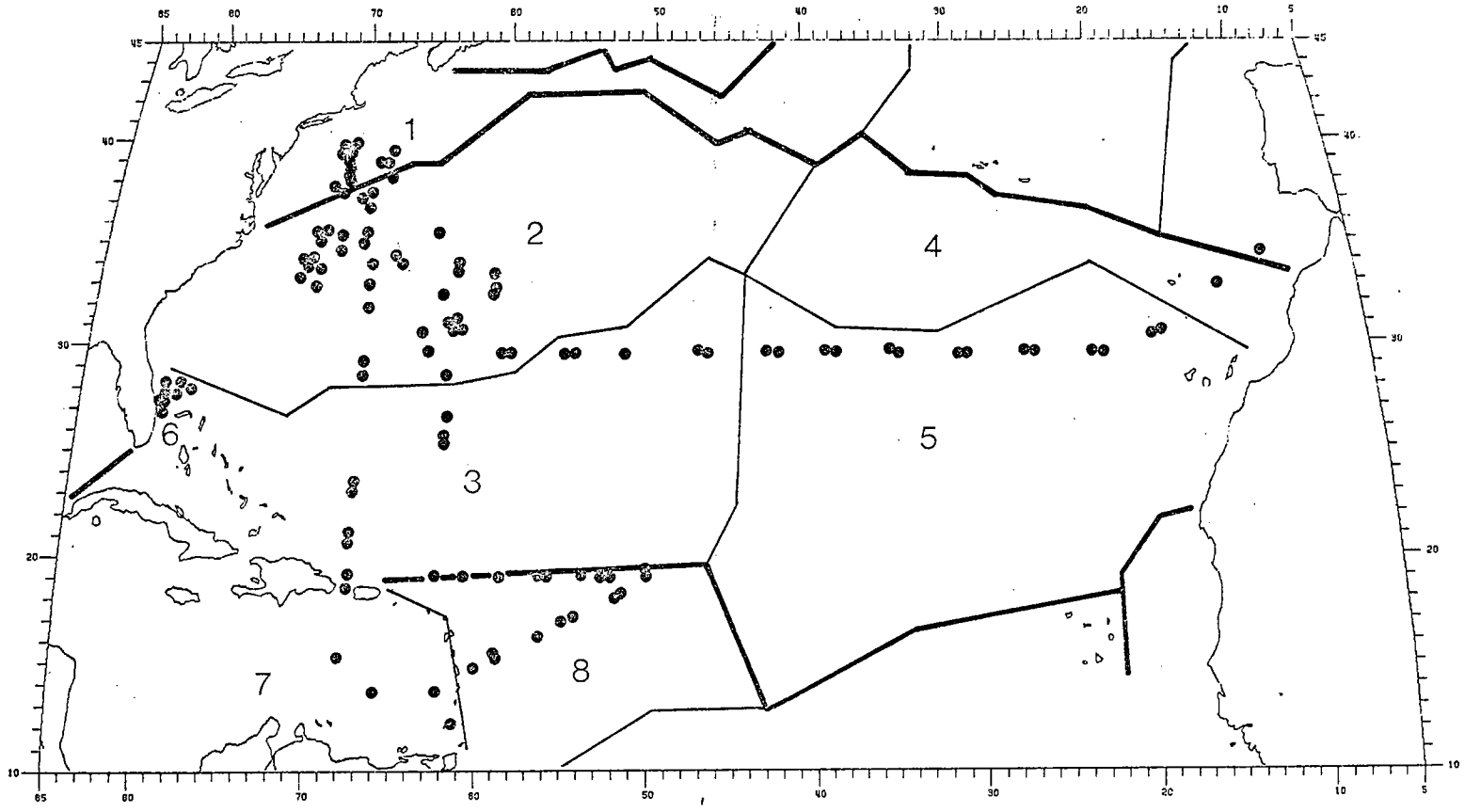

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Table 1 gives the relative abundance of 21 species of siphonophores collected by divers. I was unable to distinguish between Forskalia edwardsi and F. tholoides during collections made prior to August, 1974, so I have totaled these species together. Calycophorae other than species of Stephanophyes, Rosacea, and Sulculeolaria were sometimes present but were small, transparent, and often overlooked. For this reason, I have not listed occurrences of Diphyes dispar Chamisso and Eysenhardt, 1821, Chelophyes appendiculata (Eschscholtz, 1829), and Hippopodius hippopus (Forskal, 1775), as well as species of Abyla, Abylopsis, Lensia, and miscellaneous Calycophorae reproductive stages (eudoxids).

Bathyphysa sibogae, Sulculeolaria chuni, Athorybia sp. A, and Rosacea sp. A were collected only in the subtropical North Atlantic Ocean. Agalma clausi was collected only in the tropical Atlantic Ocean. The rest of the species were found in both tropical and subtropical regions. Only six species were found in slope water.

Halistemma rubrum, Apolemia uvaria, and Sulculeolaria biloba were present in surface waters only at night (Table 1) and probably migrated there from daytime depths below 30 meters. Very large specimens of Forskalia tholoides (station 316) and Agalma okeni (station 318) were also seen at night in surface waters.

Table 1. List of siphonophores encountered by SCUBA divers in seven zoogeographic provinces of the North Atlantic Ocean (provinces according to Backus, et al., in prep). Calycophorae other than *Stephanophyes*, *Rosacea*, and *Sulculeolaria* spp. were ignored.

LEGEND:

- \- = species absent
- \+ = less than one colony per dive
- ++ = one or more colonies per dive
- * = Does not include a mass aggregation of *N. bijuga* at stations 286 - 288.

Species	Total Number	Slope Water (day)	Northern Sargasso Sea (day)	Northern Sargasso Sea (night)	Southern Sargasso Sea (day)	Southern Sargasso Sea (night)	Southern North African Subtropical (day)	Florida Current (day)	Caribbean Sea (day)	Lesser Antillean (day)	Lesser Antillean (night)
Agalma okeni Eschscholtz, 1825	121	++	+	+	-	+	-	++	+	+	-
Agalma elegans (Sars, 1846) Fewkes, 1880	23	++	+	-	-	-	-	-	-	+	+
Agalma clausi Bedot, 1888	5	-	-	-	-	-	-	+	+	+	+
Nanomia bijuga (Chiaje, 1841)	28*	-	+	+	-	-	-	+*	-	+	+
Halistemma rubrum (Vogt, 1852)	1	-	-	+	-	-	-	-	-	-	-
Cordagalma cordiformis Totton, 1932	20	-	+	-	+	-	+	+	+	+	-
Physophora hydrostatica Forskal, 1775	2	-	+	-	-	-	-	-	-	+	-
Apolemia uvaria (Lesueur, 1811)	2	-	-	+	-	+	-	-	-	-	-
Forskalia edwardsi Kolliker, 1853; *Forskalia tholoides* Haeckel, 1888	97	+	++	+	+	+	-	+	+	++	+
Athorybia rosacea (Forskal, 1775)	24	+	+	-	+	-	+	+	+	+	-
Athorybia sp. A	7	-	+	-	+	-	+	-	-	-	-
Bathyphysa sibogae Lens and van Riemsdijk, 1903	14	-	+	-	-	-	-	-	-	-	-
Rhizophysa filiformis (Forskal, 1775)	25	+	+	-	+	-	-	+	+	+	-
Stephanophyes superba Chun, 1888	55	-	+	-	+	+	+	+	+	+	+
Rosacea cymbiformis (Chiaje, 1822)	58	-	+	-	+	-	-	+	+	++	-
Rosacea sp. A	3	-	+	-	-	-	-	-	-	-	-
Sulculeolaria quadrivalvis Blainville, 1834	24	+	+	-	+	-	+	+	+	+	-
Sulculeolaria monoica (Chun, 1888)	16	-	+	+	+	+	-	+	-	-	+
Sulculeolaria chuni (Lens and van Riemsdijk, 1908)	9	-	+	-	+	-	+	-	-	-	-
Sulculeolaria biloba (Sars, 1846)	5	-	-	+	-	+	-	-	-	-	-

Agalma okeni was the most common siphonophore in surface waters during the day (Table 1). Forty-six per cent of all specimens of A. okeni were collected in the Florida Current. Physonectae, including A. okeni, were seen on 85 of 164 dives made during the day. Table 2 presents estimates of their abundance made in situ on 15 dives during KNORR Cruise 53. Physonectae seemed more abundant at night in both the Northern and Southern Sargasso Sea, although I have no estimates of volume of water searched at night. During a period in early May, 1974 (stations 286 - 288 in Appendix 1) hundreds of Nanomia bijuga were present in the Florida Current close inshore off Fort Pierce, Florida. I estimate that there was more than one colony of N. bijuga per cubic meter at Capron Shoal (station 287), where water was less than 10 meters deep.

DISCUSSION

One can average the data from all fifteen stations in Table 2 and estimate that during the day there is one physonect siphonophore per 15,000 m^3 in the upper 30 meters of the Western North Atlantic. In the upper 110 meters of the California Current, Physonectae are present at densities less than one per 2,000 m^3 (Alvarino, 1967). Some species of Calycophorae may be locally several orders of magnitude more abundant than Physonectae (e.g., Bigelow and Sears, 1937; Alvarino, 1967; Lewis and Fish, 1969) and at times comprise over 50% of the macroplankton (Boucher and Thiriot, 1972).

Table 2. Population density of Physonectae during the day in the upper 30 meters of the Western North Atlantic Ocean, determined in situ by SCUBA divers. Data are from KNORR Cruise 53 (see Appendix 1 for additional station information).

	STATION NUMBER	DIVE TIME (minutes)	METERS DRIFTED	VOLUME SEARCHED (m^3)	NUMBER OF SIPHS	VOLUME (m^3) per SIPH
Northern Sargasso Sea along edge of Gulf Stream	417	30	150	24,000	3	7,900
	426	30	63	9,800	1	9,800
Northern Sargasso Sea proper	418	35	230	37,000	0	>37,000
	419	30	120	19,000	1	19,000
Northern Sargasso Sea outer edges of cold core eddy D	420	25	110	17,000	2	8,500
	421	30	78	12,000	1	12,000
Northern Sargasso Sea near center of cold core eddy D	422	27	54	8,500	2	4,300
	423	25	250	39,000	0	>39,000
	424	25	130	20,000	0	>20,000
	425	30	87	13,000	2	6,500
Gulf Stream eddy on Continental Slope	427	20	140	22,000	2	11,000
	428	20	170	26,000	2	13,000
	429	22	550	76,000	10	7,600
	430	25	370	59,000	6	9,800
	431	17	170	27,000	1	27,000

Zoogeographic Distribution

Pugh (1975) has enumerated a series of oblique (1 - 100 m) plankton tows along an Atlantic transect at 32°N, from 16°W to 60°W. He found 66 species of siphonophores, of which the 19 most abundant were Calycophorae. Thirteen of these 19 species differed in abundance between the North African Subtropical provinces and the Sargasso Sea, though none were restricted to either of the two areas.

On a SCUBA diving transect of the North Atlantic at 30°N (Figure 2), I encountered few siphonophores in the North African Subtropical provinces. When present in the upper 30 meters, they were the same species I found in the Sargasso Sea. However, the three species of Calycophorae I collected common to both areas (Table 1) were rare in Pugh's (1975) net tows. Species Pugh found common in the North African Subtropical area which would have been large enough for divers to see, like Ceratocymba sagittata and Rosacea sp., were not seen by us on our 16 dives there. Apparently, they are either very patchy in space in time or live deeper than 30 meters in this region.

Rarity

Several siphonophores once considered rare are relatively common in North Atlantic surface waters. The cystonect siphonophore

Bathyphysa sibogae is neither rare nor obligately bathypelagic (Biggs and Harbison, 1976). Young colonies of Stephanophyes superba, which have two apposed apical nectophores with a single bifurcation of the somatocyst in each, are sometimes locally abundant in surface waters (Table 1). The limited number of specimens of S. superba known to systematists (P. R. Pugh, personal communication) probably reflects their extreme fragility. The nectophores of Cordagalma cordiformis, which is probably the smallest physonect siphonophore, were described 45 years ago (Totton, 1932), but the colony has only recently been described adequately (Carré, 1968). Since its gelatinous components are fragile and extremely small, they may have been mistaken for immature forms of related genera by previous systematists.

Vertical Distribution of Physonectae

Bathyscaphe dives in the San Diego Trough revealed a close spatial relation between physonect siphonophores and the deep scattering layer as recorded by precision depth recording echosounders (Barham, 1963, 1966). The siphonophores looked like species of Nanomia and were tentatively identified as N. bijuga (Barham, 1963). It is apparent from my SCUBA collections (Table 1), though, that N. bijuga and nine other physonects are not restricted to deep-scattering layers. In fact, Pugh's (1974)

enumeration of siphonophores in plankton collections made with opening-closing nets off Fuerteventura in the Canary Islands suggests that Physonectae have a wide vertical distribution. Bradbury, et al. (1970), who sampled scattering layers in the equatorial Indian Ocean, also found Physonectae distributed throughout the upper 500 meters both day and night.

My own observations indicate that temperature may influence the distribution of congeneric species of Agalma. Agalma okeni is basically a warm-water species, while A. elegans is sometimes abundant in temperate and boreal waters (Alvarino, 1971). SCUBA stations where both species co-occurred usually showed small-scale temperature heterogeneity. In June, 1975, slope water stations 388 - 396 frequently had water at a depth of 5 - 17 meters which was 0.5 - 1.2°C warmer than that at the surface or below 17 meters. Agalma okeni was most abundant in these warm lenses, while A. elegans was restricted to colder water below 17 meters. Temperatures at 30 meters were 16 - 20°C at these stations. In August, 1975, A. elegans was also collected in slope water. Temperatures at depth of collection were 20 - 23°C. Divers captured A. elegans on only two occasions outside the continental slope. One specimen was collected during the day at station 425 in the Northern Sargasso Sea, where the temperature

was 23.1°C. The other was captured at night at station 351 in the Lesser Antillean province, where the surface temperature was 25.9°C.

SUMMARY

1. I observed and collected 21 species of siphonophores (small Calycophorae excluded) on SCUBA dives in the upper 30 meters of warm-water areas of the North Atlantic Ocean.

2. Physonectae were seen on 85 of the 164 dives made during the day. One of these, Agalma okeni, was the most common siphonophore encountered by divers.

3. Apolemia uvaria, Halistemma rubrum, and Sulculeolaria biloba were seen only at night.

4. Bathyphysa sibogae, Sulculeolaria chuni, and two previously undescribed species of Athorybia and Rosacea were collected only in the subtropical North Atlantic Ocean; Agalma clausi was collected only in the tropical Atlantic Ocean. The rest of the species were found in both tropical and subtropical regions. Only six of 19 species of siphonophores seen by divers in the daytime were found in slope water.

5. The population density of Physonectae in the upper 30 meters of the Northern Sargasso Sea is about one colony per 15,000 m^3 during the day.

Part 2. Fishing, Feeding, and Digestion in Siphonophores.

INTRODUCTION

Each stem group of siphonophore colonies is armed with a contractile fishing tentacle bearing batteries of nematocysts. Tentacles of Physalia physalis can extend 10 meters and paralyze and kill fish 6 - 10 cm long within an hour (Bigelow, 1891; Wilson, 1947). Colonies of Nanomia cara with a stem length of only 11 cm may have a total tentacle length of 5.4 meters (Mackie and Boag, 1963).

I believe that carnivores like these, with several meters of branched, stinging tentacles, are important predators in oceanic ecosystems. However, the fishing behavior of siphonophores has never been studied in their natural environment, and the diet of siphonophores living under field conditions is unknown. Although digestion time in Nanomia cara has been approximated in the laboratory (Mackie and Boag, 1963), nothing is known about rates of feeding on naturally-occurring zooplankton.

To study the fishing and feeding behavior of siphonophores, I observed them in situ in the open ocean while SCUBA diving. These non-visual animals seemed undisturbed by divers unless in close proximity. I will show some morphological bases for their fishing behavior and will speculate on predation by siphonophores upon different size-classes of zooplankton.

METHODS

Dimensions and configurations of siphonophore fishing tentacles were estimated from underwater photographs of colonies extended in fishing posture. Siphonophores were photographed with a 35 mm Nikonos camera fitted with a 1:3 extension tube and synchronized with electronic flash.

Swim speeds were estimated by marking points along the path of a swimming colony with fluorescein dye and then measuring distances between them with a meter stick. Times when dye was released were recorded on an underwater cassette tape recorder (see Hamner, 1975). I estimated escape speeds after gently prodding the stem or tentacles.

Siphonophores collected with swollen feeding polyps were dissected. Frequently, portions of larger prey had been digested or lost, and many were too fragmented to be identified to species (Table 5). For laboratory studies of digestion, siphonophores were released into 3.8 liter cylindrical aquaria and were allowed to feed for 5 - 10 minutes on stage-2 Artemia nauplii at densities of 100/liter. The nauplii had fed previously on a suspension of carmine particles and had easily visible red guts. After they had captured a number of nauplii, siphonophores were transferred to finger bowls of clean water. Since feeding polyps and stem are transparent, the carmine content of a colony was monitored to follow the time

course of digestion. Colonies were observed hourly for three hours, and at less frequent intervals thereafter. When more than one nauplius was ingested, I recorded the observation interval when carmine was first voided into the wash dish as the time egestion began.

Feeding rates at high densities of prey were estimated by adding 100 Artemia nauplii per liter and counting the number ingested by a single feeding polyp in a 10-minute period. To study feeding on naturally-occurring zooplankton, copepods (Acartia sp. and Pleuromamma sp.) and hyperiid amphipods (Parathemisto sp.) were collected with a 505 μm mesh plankton net. They were provided to siphonophores in 3.8 liter aquaria at densities of 4 - 24 per liter. After 12 hours, the siphonophore was removed and the number of zooplankton remaining was determined by filtering the contents of each aquarium through Gelman Type A glass fiber filters. I selected Forskalia tholoides and Agalma okeni, which infrequently collide with aquarium surfaces, for most of the 12-hour feeding experiments, but also studied the larger, faster physonect Agalma elegans. In all feeding experiments, aquaria were kept in the dark so that prey would be distributed homogeneously.

OBSERVATIONS

The Fishing Cycle

Calycophorae and Physonectae had a two-phase cycle of fishing and swimming. While fishing, they floated motionless in the water with tentacles extended. If no prey encountered their tentacles or when the fishing configuration dissolved by sinking of the colony, siphonophores withdrew the tentacles and contracted the stem to become streamlined. Simultaneously, they began swimming and then moved to an adjacent place to fish.

An active calycophore like Chelophyes appendiculata repeated the cycle about 100 times per hour in the field, while physonects repeated it less than a dozen times per hour. Periods of swimming lasted 2 - 12 seconds and were short in relation to the time during which the network of fishing tentacles was extended. During the swimming interval, siphonophores swam 1 - 16 cm/sec (Table 3). Chelophyes appendiculata and Sulculeolaria monoica used only their anterior nectophore to propell them between settings of the tentacles, while Diphyes dispar used only the posterior nectophore. Physonectae, unless escaping from stimuli, swam by asynchronous contractions of their nectophores.

When provided with Artemia nauplii in the laboratory, several siphonophores modified their swimming behavior. Sulculeolaria monoica

Table 3. Approximate swimming speeds (cm/sec) of siphonophores, measured in situ by SCUBA divers.

SPECIES	NUMBER MEASURED	UNDISTURBED SWIM SPEED	ESCAPING FROM STIMULI
Agalma okeni	27	2 - 5	10 - 13
Nanomia bijuga	2	-	25
Physophora hydrostatica	1	7	-
Forskalia edwardsi; F. tholoides	10	1 - 3	2 - 5
Stephanophyes superba	3	10 - 15	-
Rosacea cymbiformis	5	1 - 3	3
Sulculeolaria monoica	5	2 - 5	12 - 16
Chelophyes appendiculata	6	7 - 16	23
Diphyes dispar	3	1 - 3	5 - 10

Stephanophyes superba, and Rosacea cymbiformis reduced the duration of periods of swimming activity observed in situ and remained extended in fishing posture 2 - 3 times longer between activity periods. If this form of orthokinesis (Fraenkel and Gunn, 1940) is not a laboratory artifact, it might allow siphonophores to remain among aggregations of prey.

Fishing Postures

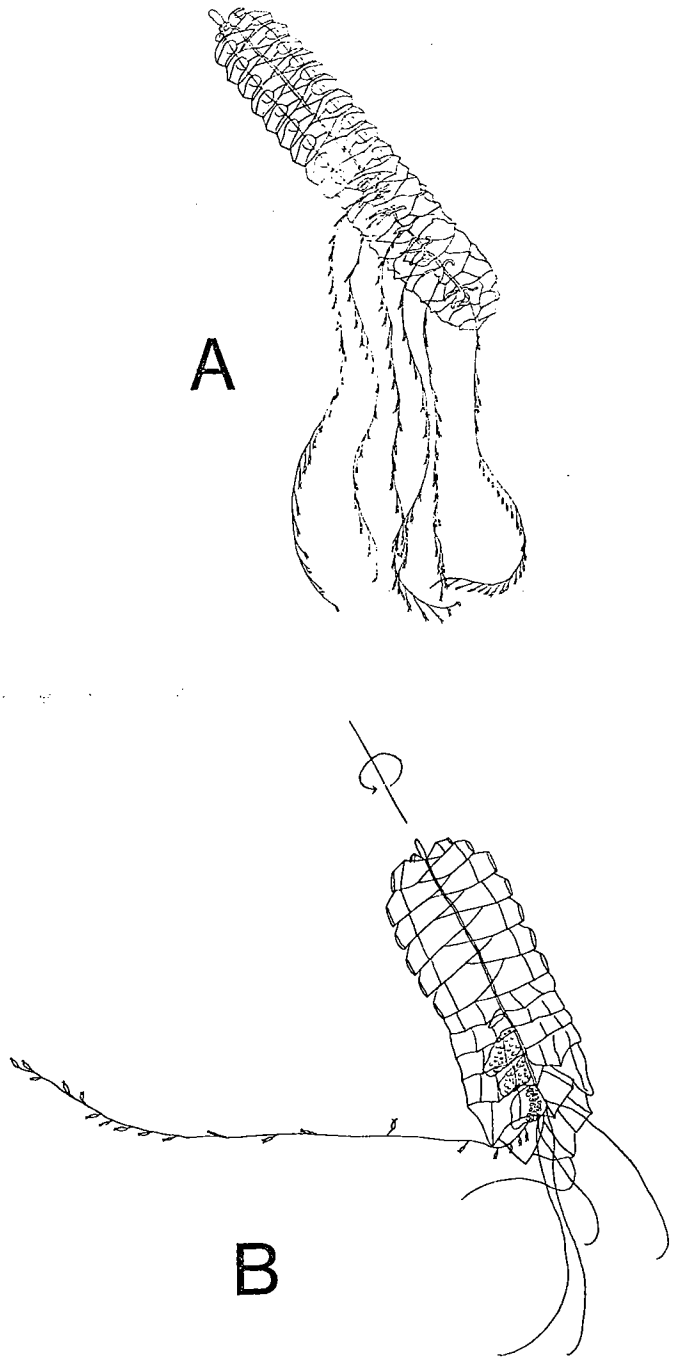
The fishing posture of a siphonophore is determined by its floatation and by the contractility of its stem. The network of fishing tentacles in siphonophores which may belong to different families yet which have similar stem dimensions often appears quite similar. I would like to describe four broad groups of siphonophores with related fishing postures.

The first, a group of Physonectae with short, noncontractile stems, includes Athorybia rosacea, Physophora hydrostatica, and Agalma okeni. All have tentacles that are long in relation to siphosome length (see dimensions of A. okeni in Table 4). In A. rosacea and P. hydrostatica, buoyancy of the pneumatophore kept it upright, and 1 - 7 tentacles hung directly downward (Figure 3). Both species have short, curvilinear siphosomes, and their tentacles enclosed a narrow cylinder of water.

The pneumatophore of A. okeni is smaller than that of either A. rosacea or P. hydrostatica, and its slight lift did not constrain

Figure 3. Athorybia rosacea, a physonect siphonophore with a non-contractile, curvilinear stem. The long tentacles extend directly below the colony to enclose a cylinder of water. Photographed in situ.

Figure 4. Agalma okeni, a physonect siphonophore with a non-contractile, linear stem. (A) Colony is inclined, which allows the tentacles to extend ventrally without entanglement. Redrawn from Chun (1897). (B) After counterclockwise rotation, which allowed tentacles to extend centripetally. Five unbranched palpon tentacles are visible. Drawn from in situ photograph.


A
B

colonies of A. okeni to orient vertically. In situ, colonies of A. okeni were usually inclined 15 - 40° from the vertical. Since the siphosome of A. okeni is linear and noncontractile, its tentacles hung coplanar; the inclined posture allowed tentacles to extend without entanglement (Figure 4 A). However, A. okeni could rotate about the axis created by its stem, and so allow drag to extend its tentacles in a radial configuration (Figure 4 B). Alternate contraction of its nectophores, arranged in two biserial rows, created rotation. Agalma okeni did not rotate while swimming, so rotation is probably a modification of fishing behavior which allows the tentacles to cover a larger volume of water.

A second group of siphonophores has flexible stems which are somewhat contractile. This group includes Agalma elegans and Stephanophyes superba.

The siphosome of A. elegans is 1 - 2 times longer than the nectosome. The stem has a large surface area of long, thin bracts which are neutrally buoyant, and it is often supported in arcs (Figure 5). The tentacles, hanging ventrally from the arched stem, lie in more than a single plane. Each of the 10 - 24 stem groups of S. superba has both a gelatinous bract and a special nectophore; in situ the surface area of these gelatinous individuals frequently supported the flexible stem in a horizontal arc. Tentacles hung downward to enclose a shallow cylinder of water (Figure 6A).

Figure 5. Agalma elegans, a physonect siphonophore with a flexible stem. The stem has drifted to lie in arcs above the nectosome. Photographed in an aquarium by L. P. Madin.

A third group of siphonophores has stems which are both long and contractile. This includes Cystonectae of the Family Rhizophysidae, as well as Calycophorae like species of Rosacea, Chelophyes, Sulculeolaria, and Diphyes.

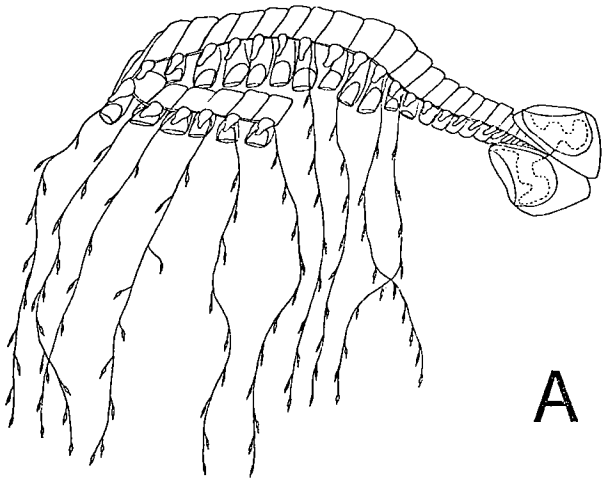
Cystonectae have no gelatinous appendages, and the stem usually hung vertically beneath the enlarged apical pneumatophore. In situ, colonies of Rhizophysa filiformis and Bathyphysa sibogae extended several meters (Table 4), and local turbulence drifted the delicate, thread-like tentacles in all directions.

Rosacea cymbiformis fished extended in "long-line" posture (Figure 6 B). Intermittant contractions and subsequent relaxations of individual tentacles did not cause the expanded stem to contract, although colonies whose tentacles I touched often "crumpled" by contraction of stem and tentacles.

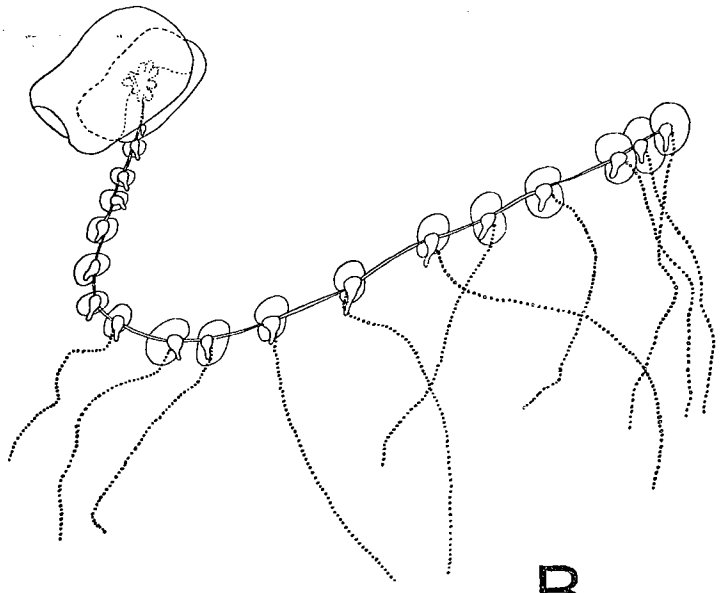
Sulculeolaria monoica and S. quadrivalvis set their tentacles in a "veronica" movement (named after the bull-fighters pass it resembles) like that described for Muggiaea atlantica by Mackie and Boag (1963). The stem of S. monoica is longer than that of M. atlantica and drag created by relaxing, elongating posterior appendages caused the anterior part of the stem to arch round in a series of spirals. The tentacles then spread centripetally from the stem, which remained as a helix of 2 - 3 turns (Figure 7). Colonies of S. quadrivalvis had even longer stems which came to rest in less regular arcs (Figure 8).

Figure 6. (A) Stephanophyes superba, a calycophore siphonophore with a flexible stem. The stem lies in a horizontal arc, which allows tentacles to surround a cylinder of water. Drawn from in situ photograph.

(B) Rosacea cymbiformis, a calycophore siphonophore with a contractile stem. The stem is partially extended in a "long-line" configuration. Drawn from in situ photograph.



A



B

Figure 7. Sulculeolaria monoica, a calycophore siphonophore with a contractile stem. Photographed in situ, showing helical configuration of the stem.

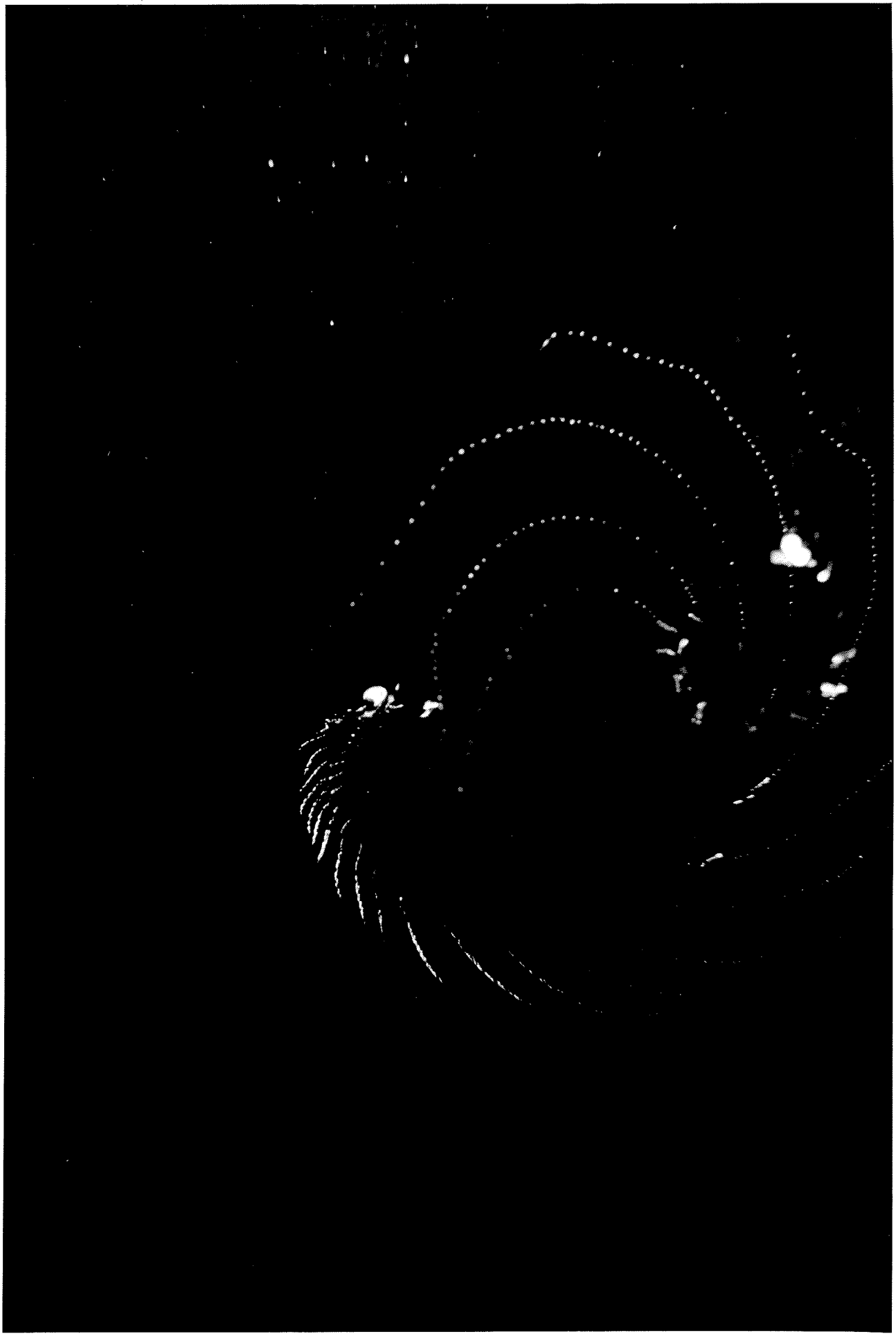


Figure 8. Sulculeolaria quadrivalvis, a long-stem relative of S. monoica (Figure 7). Photographed in situ immediately after extending stem and tentacles in fishing posture.

Figure 9. Forskalia edwardsi, a physonect siphonophore with gastrozooids attached to the stem on pedicles. Tentacles extend radially. Photographed in situ by L. P. Madin.

The fourth group is made up of species of Forskalia. Small colonies had stubby, poorly contractile stems, yet their fishing networks were not restricted to planar configurations. Feeding polyps, rather than arranged linearly along the stem, extended out from it on long pedicles, rather like spokes of a wheel (Figure 9). Small colonies had an almost radial symmetry and tentacles enclosed a cylindrical or spherical volume. The orientation of the colony was not restricted by the minute pneumatophore, and I observed five colonies hanging "upside-down" in the water, with siphosome upright and nectosome below.

Dimensions of Fishing Tentacles

A colony of A. okeni with 28 nectophores has 5 gastrozooids and about 160 tentilla (Figure 10). If its five fishing tentacles are maximally extended, tentilla are spaced at 10-mm intervals (Table 4), and combined the tentacles extend 1.6 meters. Tentilla 4-mm long combined extend 0.6 meters, so the total fishing line of A. okeni extends 2.2 meters. In addition, each palpon has a fine, thread-like tentacle.

A colony of Forskalia edwardsi or F. tholoides with 15 gastrozooids has 15 tentacles, each with an average of 15 tentilla (Table 4). If tentilla are spaced at 5-mm intervals in a partially-extended configuration, combined the tentacles stretch 1.1 meters. Tentilla

Figure 10. Number of tentilla (combined total for all tentacles) in Agalma okeni of different sizes.

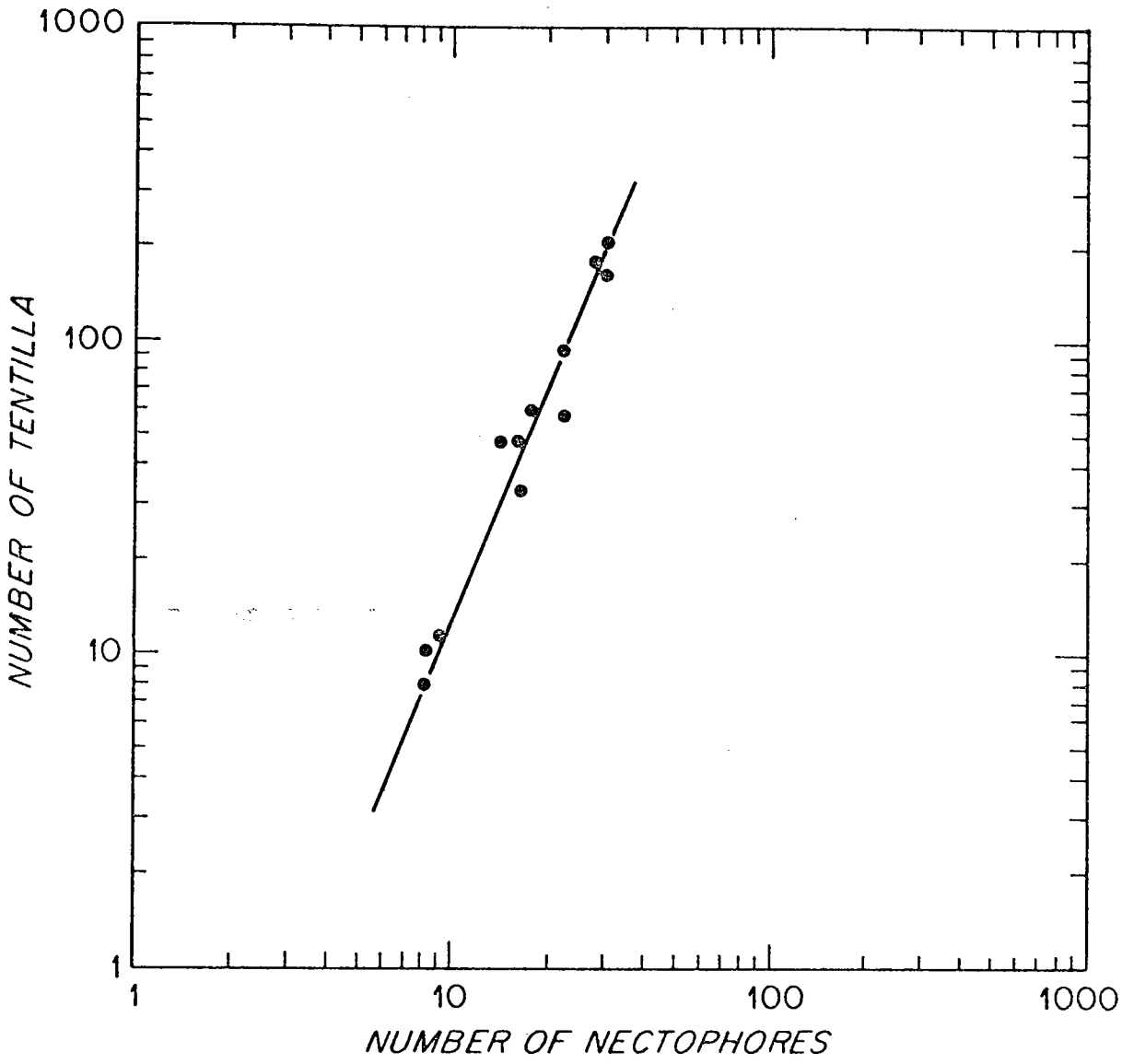

1000
100
10
1
NUMBER OF TENTILLA
1
10
100
1000
NUMBER OF NECTOPHORES

Table 4. Approximate dimensions of stem, tentacles, and tentilla in siphonophores extended in fishing posture.

NUMBER MEASURED	SPECIES	NUMBER OF STEM GROUPS	DISTANCE (mm) BETWEEN STEM GROUPS	NUMBER OF TENTILLA PER TENTACLE	LENGTH (mm) OF TENTACLE BETWEEN TENTILLA	LENGTH (mm) OF EACH TENTILLUM
5	*Agalma okeni*	1 - 6	1 - 4	20 - 50	3 - 10	2 - 5
5	*Agalma elegans*	3 - 17	6 - 30	20 - 30	3 - 10	2 - 5
5	*Stephanophyes superba*	10 - 28	3 - 15	9 - 15	7 - 19	2 - 5
5	*Rhizophysa filiformis*	5 - 25	50 - 200	50 - 150	2 - 7	2 - 5
5	*Rosacea cymbiformis*	10 - 100	7 - 21	30 - 55	2 - 5	5 - 7
5	*Sulculeolaria monoica*; *S. quadrivalvis*	20 - 150	2 - 5	30 - 40	1 - 5	5 - 7
5	*Forskalia edwardsi*; *F. tholoides*	8 - 50	5 - 15	10 - 20	5 - 11	15 - 25

have long terminal filaments (Table 4); combined these represent at least 3.4 meters, to total 4.5 meters of fishing line per colony. Although the biomass of a colony of Forskalia with 15 gastrozooids is about 2 - 3 mg protein, or half that of a colony of A. okeni with 28 nectophores and 5 gastrozooids, its length of fishing line is over two times longer.

Satiation can limit the length of tentacles fished. Colonies of F. edwardsi and F. tholoides encountered in situ which had recently eaten several or large prey (Table 5) did not have their tentacles maximally extended. Intratentillar distances were less than 5 mm, and one colony had withdrawn its tentacles entirely. In the laboratory, as well, colonies of Forskalia and A. okeni which had fed on copepods had intratentillar spacings of 3 mm or less.

Types of Prey Captured by Siphonophores

Siphonophores have large concentrations of nematocysts in complex batteries located distally on each tentillum. Calycophorae have a band packed with parallel arched rows of nematocysts (the cnidoband) which is folded in half and ends in a terminal filament. Physonectae have a coiled cnidoband which can end in more than one terminal filament.

Both Calycophorae and Physonectae have elastic ligaments attached to the cnidoband which trigger the "spring-loaded" tentillar

battery to erupt when stretched and bring hundreds of nematocysts instantly to bear on prey. Cystonectae do not have an exploding ligament-cnidoband system, though tentilla terminate in clusters of large nematocysts (Totton, 1965; Biggs and Harbison, 1976).

Tentacle morphology seems to reflect fishing ability and determines prey selectivity. Tentillar batteries of Forskalia edwardsi, F. tholoides, Nanomia bijuga, Cordagalma cordiformis, Rosacea cymbiformis, Stephanophyes superba, and Sulculeolaria monoica terminate in single, long filaments. All of these species ingested Artemia nauplii at densities of 100/liter in the laboratory, although they ate larger prey as well (Table 5). A colony of C. cordiformis with three gastrozooids captured and ingested 30 Artemia nauplii within 10 minutes; one gastrozooid in this colony ingested 13 nauplii.

The long terminal filaments of F. edwardsi and F. tholoides were "sticky" and very sensitive to stretch. I observed that copepods entangled in them caused the tentillar batteries of nematocysts to erupt, as Chun (1891) described and figured for Stephanophyes superba feeding on copepods. The terminal filaments of species of Forskalia were sufficiently sensitive that 2 - 3 hours of contact with surfaces in a collecting jar caused several terminal batteries to erupt.

Tentilla of Agalma okeni, A. elegans, A. clausi, and Athorybia rosacea terminate in a pair of filaments and a bulbous ampoulla. The cnidoband is encapsulated in an involucrum. Unlike species of Forskalia, the terminal filaments of species of Agalma and Athorybia rosacea had to be stretched several millimeters before the tentillar nematocyst battery erupted; tentillar batteries never discharged in collecting jars. Though colonies of Agalma okeni and A. elegans captured copepods (Acartia and Pleuromamma spp.) and shrimp (Leander sp.) in the laboratory, tentillar batteries were not used in feeding. In the field, species of Agalma and Athorybia rosacea ate zooplankton ranging in size from copepods to sergestids, as well as small fish (Table 5). In surface waters, it is highly likely that Agalma okeni feeds mostly at night, as tentacles were contracted in over 90 of 114 colonies observed in situ during the day but were extended in the seven colonies observed at night.

Artemia nauplii were eaten by pre-reproductive colonies of Agalma okeni, but apparently they are too small to be sensed as prey by Athorybia rosacea or by large colonies of Agalma okeni and A. elegans, even in the dark at densities of 100 nauplii per liter. In the laboratory, 14 of 20 colonies of Agalma okeni, A. elegans, and Athorybia rosacea did not ingest any nauplii in 2 1/2 hours; five ingested three or less, and one colony of Agalma okeni ingested four nauplii. Although nauplii were struggling on them, the tentacles did not contract to allow gastrozooids to eat the trapped nauplii.

Table 5. Survey of prey removed from feeding polyps of siphonophores.

STATION NUMBER	SIPHONOPHORE	PREY
Suborder Calycophorae		
350	*Rosacea cymbiformis*	*Corycaeus*, *Candacia* spp. (copepods)
417	*Rosacea cymbiformis*	gastropod veliger; copepods
381	*Stephanophyes superba*	3 euphausiids (7-10 mm overall length)
384	*Sulculeolaria monoica*	*Candacia ethiopica*
Suborder Physonectae (tentilla with single terminal filament)		
289	*Nanomia bijuga*	mysid
327	*Forskalia* sp.	atlantid heteropod (1.5 mm)
345	*Forskalia* sp.	fish (7 mm)
349	*Forskalia* sp.	fish (6 mm)
419	*Forskalia* sp.	polychaete
417	*Forskalia edwardsi*	*Candacia* sp.
430	*Forskalia edwardsi*	*Candacia* sp.
406	*Forskalia tholoides*	stomatopod larva
430	*Forskalia tholoides*	*Candacia* sp.
316	*Forskalia tholoides*	*Anchylomera blossevillei*; *Hemityphis rapax* (hyperiid amphipods)
Suborder Physonectae (tentilla with paired terminal filaments and ampoulla)		
285	*Agalma okeni*	hyperiid amphipod
297	*Agalma okeni*	megalops larva
390	*Agalma okeni*	megalops larva
398	*Agalma okeni*	megalops larva
411	*Agalma elegans*	*Parathemisto* sp. (hyperiid amphipod)
411	*Agalma elegans*	*Parathemisto* sp.
321	*Athorybia rosacea*	2 fish (7 mm and 9 mm)
350	*Athorybia rosacea*	*Lucifer typis* (sergestid)
373	*Athorybia rosacea*	5 *Corycaeus* sp.; fish (6 mm)
417	*Athorybia rosacea*	*Candacia* sp.; polychaete
421	*Athorybia rosacea*	hyperiid amphipod
Suborder Cystonectae		
321	*Rhizophysa filiformis*	alcyopid polychaete; fish (5 mm)

Cystonectae may be able to eat only large zooplankton or nekton. Two colonies of Bathyphysa sibogae did not feed on either Artemia nauplii or copepods (Acartia sp.) in the laboratory, and a colony of Rhizophysa filiformis captured only a Sargassum shrimp (Leander sp.) when provided with Artemia nauplii, copepods, and shrimp in laboratory aquaria.

Rates of Feeding on Naturally-Occurring Zooplankton

Forskalia tholoides consistently captured more copepods in 12 hours than did A. okeni (Table 5). Agalma elegans captured intermediate numbers of copepods. However, except for a colony of A. okeni with only one gastrozooid which did not capture any copepods, large siphonophores did not capture more zooplankton than small individuals of the same species. Since small colonies had fewer or shorter tentacles than large colonies, large siphonophores were probably inhibited from extending their fishing network to dimensions observed in the field (Table 4), perhaps by more frequent contact with aquarium surfaces.

Laboratory Studies of Digestion

A colony of A. okeni which captured four Artemia nauplii egested carmine and unassimilated portions within 2 - 3 hours (Table 6). Most other species required similar times for digestion

Table 6. Ingestion rates of siphonophores feeding on copepods and hyperiid amphipods in the laboratory.

Size (mg protein)	Number of Feeding Polyps	Number of Zooplankton per liter	Number of Zooplankton Captured per Feeding polyp	Per Cent of Zooplankton Captured in 12 hours
Forskalia tholoides, feeding on *Acartia* sp.				
2	9	5	1.0	45
2	11	6	1.3	67
0.2	4	12	5.5	49
2	10	12	3.2	70
2	12	11	2.0	60
2	9	19	3.8	49
2	8	27	6.0	48
Agalma okeni, feeding on *Acartia* sp. and **Parathemisto* sp.				
0.7	1	8	0	0
2.8	2	*7	1.5	12
6.0	3	6	1.7	24
8.8	4	8	1.3	17
4.5	3	11	3.0	20
9.8	4	11	1.8	17
3.1	2	16	3.0	10
3.8	3	16	2.3	12
9.8	4	16	1.8	12
3.8	2	20	5.0	14
3.0	3	28	4.3	13
6.0	4	28	2.3	9
7.6	4	27	2.3	9
Agalma elegans, feeding on *Pleuromamma* sp.				
19.0	15	5	0.5	35
6.4	7	13	1.0	14
6.4	7	13	2.3	32
14.0	12	22	2.4	41

of nauplii, though R. cymbiformis sometimes required 8 - 24 hours before egestion was complete. Digestion of large prey required more time. Three colonies of A. okeni which captured large crustaceans waited 7 - 18 hours before they disgorged the undigested remains (Table 6). Their palpons and gastrozooids remained swollen for 18 - 48 hours.

If prey is large, several gastrozooids assist in its digestion. For example, a colony of R. filiformis with 18 gastrozooids ate a 30 mm fish (Fundulus sp.) in the laboratory. Initially, one gastrozooid contacted the fish and within five minutes began to envelop the caudal area. When maximally everted, this polyp covered the posterior third of the fish. Two additional gastrozooids then encountered the fish and everted to cover an additional 20% of its area. The R. filiformis may have been too small to ingest the entire fish and dropped it after 10 - 12 hours. By this time, the siphonophore had become distended and translucent. About 20% of the fish seemed to be digested; its caudal surfaces were eroded and amorphous with mucus.

When prey were small enough to be ingested entirely within a single gastrozooid, they were more completely digested. The remains of a 15 mm Sargassum shrimp (Leander sp.), when egested by A. okeni between 12 - 18 hours after capture, was a 10 mm bolus of uncompacted

Table 7. Time course of egestion in siphonophores maintained in the laboratory.

SPECIES	PREY	OBSERVATION INTERVAL (HOURS) WHEN EGESTION BEGAN	OBSERVATION INTERVAL (HOURS) WHEN EGESTION COMPLETE
Agalma okeni	crab megalops	-	8 - 9
Agalma okeni	*Leander* sp.	-	7 - 18
Agalma okeni	*Leander* sp.	-	12 - 18
Agalma okeni	*Artemia* sp.	2 - 3	3 - 4
Forskalia sp.	polychaete	-	2 - 3
Forskalia sp.	hyperiid amphipod	-	5 - 8
Forskalia sp.	*Artemia* nauplii	1 - 2	2 - 3
Forskalia sp.	*Artemia* nauplii	2 - 3	3 - 4
Forskalia sp.	*Artemia* nauplii	2 - 3	2 - 3
Forskalia sp.	*Artemia* nauplii	3 - 6	3 - 6
Rosacea cymbiformis	*Artemia* nauplii	3 - 6	(no observations)
Rosacea cymbiformis	*Artemia* nauplii	6 - 12	(no observations)
Rosacea cymbiformis	*Artemia* nauplii	6 - 10	10 - 24
Rosacea cymbiformis	*Artemia* nauplii	6 - 16	(no observations)
Rosacea cymbiformis	*Artemia* nauplii	10 - 12	(no observations)
Rosacea cymbiformis	*Artemia* nauplii	8 - 10	(no observations)
Rosacea cymbiformis	*Artemia* nauplii	6 - 8	8 - 18
Stephanophyes superba	*Artemia* nauplii	4 - 6	4 - 6
Stephanophyes superba	*Artemia* nauplii	3 - 4	4 - 5
Stephanophyes superba	*Artemia* nauplii	2 - 3	6 - 8
Sulculeolaria quadrivalvis	*Artemia* nauplii	1 - 2	2 - 3
Sulculeolaria chuni	*Artemia* nauplii	1 - 2	3 - 4
Sulculeolaria chuni	*Artemia* nauplii	2 - 3	3 - 4
Sulculeolaria	*Artemia* nauplii	1 - 2	2 - 3
Diphyes dispar	*Artemia* nauplii	2 - 3	3 - 4
Diphyes dispar	*Artemia* nauplii	2 - 3	3 - 4
Diphyes dispar	*Artemia* nauplii	2 - 3	3 - 4

mucus and exoskeleton. Material egested by siphonophores is not bound in a peritrophic membrane and fragmented when I tried to collect it quantitatively.

DISCUSSION

The siphonophore cycle of swimming and then lying in wait for prey is well-suited to life in an oligotrophic environment. It allows siphonophores to concentrate food from a large volume of water while reducing energy expended searching actively for prey. One might imagine orb-weaving spiders, which extend a network of prey-ensnaring lines and then wait for prey to approach or drift into them, as terrestrial analogs. However, siphonophores are not restricted from moving about and cover a larger volume than can spiders, whose webs are anchored in one location. Moreover, the buoyancy of the fluid environment of siphonophores does not restrict their "webs" to planar configurations.

A swimming interval which lasted 12 seconds or less and swimming speeds which averaged less than 16 cm/sec (page 23) caused most siphonophores to progress less than two meters before again setting their network of fishing tentacles. This behavior seems to imply a feeding adjustment to scales of zooplankton patchiness much smaller than the scales of 10^1 - 10^3 meters currently visualized by biological oceanographers.

When the stem has been retracted, Calycophorae like Chelophyes appendiculata and species of Sulculeolaria are well streamlined and can escape from stimuli as fast as larvaceans and heteropods (see Hamner, et al., 1975). However, Calycophorae with flabby nectophores or very long stems, like Rosacea cymbiformis and large specimens of Diphyes dispar (50 - 60 mm overall length of both nectophores) swim so weakly that they rarely exceed speeds of 3 - 5 cm/sec (Table 3).

The architecture of some Physonectae makes them inefficient swimmers. For example, the radial arrangement of nectophores in the genus Forskalia restricts rapid forward movement. The fastest Physonectae have two biserial rows of nectophores and siphosomes of narrow diameter. Colonies of Nanomia bijuga with 28 nectophores and 13 stem groups, when jostled by divers, escaped at speeds exceeding 25 cm/sec (Table 3). A cold-water congener, N. cara, moved off in laboratory aquaria at 20 - 30 cm/sec through synchronous contraction of its nectophores (Mackie, 1964). Contraction of N. cara's nectophores in sustained swimming was asynchronous, and sustained speeds averaged only 8 - 10 cm/sec (Berrill, 1930; Mackie, 1964). The latter velocities are theoretically sufficient, though, to permit individuals of Nanomia to keep pace with a migrating deep scattering layer.

Siphonophore digestion times correspond to metabolic rates approximated from their oxygen consumption and nitrogenous excretion. Species of Sulculeolaria, which had the fastest digestion of siphonophores I observed in the laboratory, have some of the highest rates of respiration and excretion (see Part 3). Conversely, Rosacea cymbiformis, which required the longest time to digest Artemia nauplii, has a very low rate of respiration and excretion (Part 3). Mackie and Boag (1963) reported that Nanomia cara egested carmine within 25 minutes after it had eaten a piece of carmine-dyed crab muscle. However, most of the carmine was apparently adhering to the surface of the muscle and was probably released into the gastric cavity of the feeding polyp immediately upon digestion of the outer surfaces. While I did not encounter N. cara in the tropical and subtropical North Atlantic, I expect (on the basis of Table 6), that this species would require longer than 25 minutes to digest living prey.

The range of siphonophore digestion times I measured includes those reported for other gelatinous zooplankton. Swim-collected heteropods Cardiopoda placenta and Pterotrachea coronata required 4.5 - 7 hours, and 6 - 8 hours, respectively, between ingestion and defecation (Hamner, et al., 1975). The ctenophore Bolinopsis infundibulum digested stage-5 Calanus sp. within one hour; Beroe cucumis, preying on B. infundibulum, digested it within 3 - 3.5 hours (Kamshilov, 1960; Fraser, 1962).

Laboratory experiments with Cordagalma cordiformis suggest that siphonophores able to eat small zooplankton could glut themselves on dense aggregations of microzooplankton until tentacle-spreading behavior became limited by satiation. Feeding polyps of most siphonophores are larger than those of C. cordiformis. If, like C. cordiformis, feeding polyps of long-stem forms like Rosacea cymbiformis or Sulculeolaria quadrivalvis can ingest 13 or more small zooplankton in ten minutes, a single colony feeding at high densities of microzooplankton might be able to rapidly ingest several hundred individuals.

SUMMARY

1. Calycophorae and Physonectae observed in situ by SCUBA divers showed a two-phase cycle of fishing and swimming. An active calycophore like Chelophyes appendiculata repeated the cycle 100 times per hour in the field, while physonects repeated it less than a dozen times per hour. During the swimming interval, swim speeds ranged from 1 - 16 cm/sec.
2. The fishing posture of a siphonophore is determined primarily by its floatation and by the contractility of its stem; fishing postures can be similar in siphonophores which are unrelated.
3. The total length of tentacles in colonies with only 2 - 3 mg body protein can extend 4.5 meters.
4. Variations in the morphology of tentilla reflect differences in the kinds of prey which can be captured. Dissection of feeding polyps revealed that most siphonophores could eat copepods, amphipods, polychaetes, pteropods, heteropods, veliger larvae, sergestids, mysids, euphausiids, and small fish, though laboratory experiments showed that not all could eat nauplii. Cystonectae can probably eat only large zooplankton and nekton.
5. Siphonophores able to capture Artemia nauplii usually required 2 - 4 hours to digest them. Large prey took 7 - 18 hours to be digested.

Part 3. Oxygen Consumption and Ammonia Excretion

INTRODUCTION

Most of the macrozooplankton encountered on daytime SCUBA dives in the upper 30 m of the Western North Atlantic Ocean are gelatinous, transparent forms (see Gilmer, 1972; Madin, 1974; Swanberg, 1974; Harbison and Gilmer, 1976). Besides siphonophores, gelatinous zooplankton include medusae, ctenophores, thaliaceans, pseudothecosome pteropods, and several heteropods. Despite their widespread occurrence in open-ocean regions, there is little quantitative information on the energy requirements of gelatinous animals. Measurements of respiration or excretion for gelatinous zooplankton are mostly limited to nearshore ctenophores (e.g., Williams and Baptist, 1966; Hirota, 1972) and medusae (Kruger, 1968). There are a few respiration measurements on open-ocean gelatinous animals (e.g., Rajagopal, 1962; Nival, et al., 1972; Gilmer, 1974), but simultaneous measurements of respiration and excretion have been reported for only a dozen species (Mayzaud and Dallot, 1973; Ikeda, 1974).

Because of their fragility, siphonophores and other gelatinous animals make poor subjects for classical laboratory respiration and excretion measurements. Turbulence, abrasion, or prolonged contact with surfaces causes ctenophores and siphonophores to fragment and can cause salps to shed their tests. Previous

investigators have collected gelatinous animals with nets and held them without food in small laboratory aquaria for up to 2 days before measuring oxygen consumption or ammonia excretion. Although neritic species might survive this treatment, it will cause most open-ocean forms to become moribund.

To minimize damage to them, I collected oceanic gelatinous zooplankton individually in hand-held jars while SCUBA diving and measured oxygen and subsampled ammonia in the jars within 6 hours of collection. I made measurements of respiration and excretion on over 220 siphonophores. The results indicate that interspecific differences in metabolism are related to differences in their morphology and ecology.

I am grateful to G. Woodwell for allowing me to use his laboratory for Kjeldahl analyses and thank J. McCarthy for use of his Bausch and Lomb 710 spectrophotometer on CHAIN Cruise 122. R. Gilmer performed the carbon-hydrogen-nitrogen (CHN) analyses on Agalma okeni, using a Perkin-Elmer model 240 CHN analyzer.

METHODS

SCUBA divers collected gelatinous plankton in 130 - 980 ml glass jars fitted with screw-top plastic lids with polypropylene liners. Before collecting a specimen, divers flushed the open jars by shaking them vigorously. Care was taken not to damage siphono-

phores by direct contact with the divers. Siphonophores were usually allowed to swim into the jars, in order to minimize shearing turbulence and also obtain the entire fishing network.

At most stations where siphonophores were collected, temperature in the upper 30 m was 23 - 29°C (see Appendix 1). Colonies in their collecting jars were incubated aboard ship in a flowing sea water bath at surface temperature for 1 - 6 hours after enclosure. Oxygen consumption and ammonia excretion were estimated by difference from control jars of sea water collected simultaneously. The tension of dissolved oxygen in each jar was measured with a polarographic oxygen electrode (Kanwisher, 1959) connected to a portable, battery-powered amplifier which allowed oxygen to be measured with a precision of $\pm$ 0.035 ml/liter at 4.800 ml O_2/liter. The amplifier was designed and constructed at W.H.O.I. by K. Lawson. Oxygen electrodes were calibrated by Winkler titration (Strickland and Parsons, 1972) or standardized against oxygen-saturated surface water.

Laboratory experiments were performed to investigate the effect of short-term changes in temperature on oxygen consumption. After measuring the oxygen consumption of two colonies of Forskalia edwardsi by the method outlined above, I placed them and five other colonies of Forskalia in a water bath 5°C below in situ collection temperature for one hour. All were then transferred gently into new jars of water at this temperature, sealed, and incubated for 1 - 6

hours. Oxygen consumption was measured by difference from jars of water enclosed simultaneously.

For determination of ammonia, 100 ml of water was decanted from each collecting jar and filtered under low vacuum (10 - 12 psi) through Gelman Type A glass fiber filters. The filtrate was immediately fixed with phenol (Deggobis, 1973) and refrigerated. Ammonia was determined in duplicate by the phenol-hypochlorite method (Solorzano, 1969) within 1 - 2 weeks. There was no measurable change in ammonia concentration in fixed, refrigerated samples during this time. I used 50% less sodium nitroprusside than specified by Solorzano (1969) and allowed color to develop in the dark at room temperature. Color development was complete in two hours, and serial dilutions of an NH_4Cl standard gave a linear photometric response from 0 - 15 µg-at NH_4^+ per liter. Others (Dal Pont, et al., 1974; Liddicoat, et al., 1975) have suggested similar modifications in the nitroprusside reagent and in development time. At sea, using a 5-cm pathlength in a Bausch and Lomb model 710 spectrophotometer, precision was equal to that ashore: $\pm$ 0.1 µg-at NH_4^+/liter at 3.0 µg-at NH_4^+/ liter.

In ten instances, additional water samples were decanted, filtered, and frozen for determination of total dissolved nitrogenous excretion by Kjeldahl digestion ashore. Within one month of collection, samples were thawed and ammonia determined again to

calculate per cent loss of ammonia during storage. Replicate 25 ml aliquots of the remainder of each sample were then digested for 2 hours by 5 ml of concentrated H_2SO_4, deionized water, and a 5% $CuSO_4$ solution mixed 50:50:5 by volume. After reconstitution to 25 ml with deionized water and titration to pH 5.4, ammonia was measured by the phenol-hypochlorite method outlined above. Total dissolved nitrogenous excretion, as NH_4^+ equivalents, was calculated and corrected for ammonia lost during storage. Addition of NH_4Cl to digestion mixture blanks showed a linear photometric response from 0 - 10 µg-at NH_4^+/liter, though blank absorbance was about 0.810 at 640 nm (10-cm pathlength). Precision of the phenol-hypochlorite analyses of the digestate was $\pm$ 0.2 µg-at NH_4^+/liter at 3.0 µg-at NH_4^+/liter.

Incubation times for oxygen consumption and ammonia excretion experiments were chosen to correspond to the size of a siphonophore relative to the size of its collecting jar. Ammonia in control jars of sea water was less than 0.4 µg-at NH_4^+/liter. Six hours was sufficient for the smallest siphonophores to produce a measurable change in both ammonia and oxygen. I disregarded incubations in which oxygen tension fell to less than 70% of saturation.

Experimental animals were frozen on Gelman Type A glass fiber filters. Within 1 - 6 months after freezing, they were homogenized individually in 1.0 N NaOH for protein analysis by the Lowry method

(Lowry, et al., 1951). Freeze-dried bovine serum albumin (BSA) was the reference standard.

All measurements were standardized to protein, rather than dry weight, since the organic fraction of siphonophores is only 3% - 16% of their dry weight (Beers, 1966). Previous investigators have found that protein is the major organic fraction in zooplankton (Reeve, et al., 1970; Ikeda, 1972; Mayzaud and Martin, 1975). For purposes of comparison, carbon-hydrogen-nitrogen analyses were also performed on colonies of Agalma okeni.

RESULTS

There was no measurable change in oxygen or ammonia in replicate control jars of sea water after a six-hour incubation at ambient temperature. Moreover, when a siphonophore was placed in unfiltered sea water and ammonia measured hourly for four hours, cumulative ammonia excretion showed a linear relationship with time. These results suggest that there was minimum growth of micro-organisms in the collecting jars.

Neither oxygen consumption nor ammonia excretion had a negative correlation with jar size or incubation time, suggesting that siphonophores did not respond to capture with rapid, short-term increases in metabolism. However, the mobility of very active forms like Nanomia bijuga and species of Sulculeolaria may be

inhibited in jars of 130 - 980 ml volume. Apart from these species, rates of oxygen consumption and ammonia excretion measured by in situ collection and continuing shipboard incubation at environmental temperature probably reflect rates which undisturbed colonies show in their natural environment.

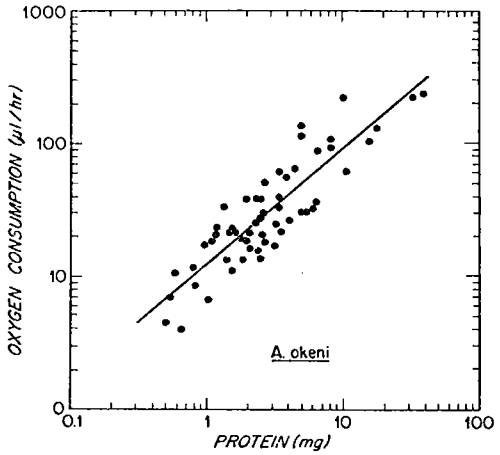
Regression equations expressing oxygen consumption and ammonia excretion as power functions of body protein were calculated for nine of the more abundant siphonophores (Tables 8 and 9, and Figures 11 and 12). I have grouped two species of Forskalia because I was unable to distinguish between them. I have more arbitrarily grouped other species in Tables 8 and 9 for which individual data are limited but which had similar rates of respiration and ammonia excretion (Table 10). The average coefficient of determination ($r^2 \pm s$) in the nine groups was $0.81 \pm .10$ for oxygen consumption and $0.77 \pm .11$ for ammonia excretion. All coefficients of determination were highly significant statistically ($P < 0.001$).

Respiration of siphonophores ranged from 2 - 86 μl O_2/mg protein-hr, and excretion from 0.1 - 3.3 μg NH_4^+/mg protein-hr (Table 10). Colonies of smaller size had higher rates of respiration and excretion than those of larger animals. Ratios of respiration at environmental temperatures to respiration at temperatures 5°C lower varied from 1.3 - 5.0, with a tendency for the lower ratios to occur at higher environmental temperatures (Table 11).

Table 8 and Figure 11:

Oxygen consumption at 26 $\pm$ 3°C of some of the more abundant tropical and subtropical siphonophores, estimated by linear regression: log y = a + b (log x); where y = oxygen consumption (μl O_2/hr); x = body protein (mg); a $\pm$ s and b $\pm$ s = regression coefficients $\pm$ standard errors; s_{yx} = standard error of the estimate (of y on x); r^2 = coefficient of determination.

Species	n	a ± s	b ± s	s_{yx}	r^2
Siphonophora: Physonectae					
Agalma okeni	58	1.07 ± .04	0.87 ± .06	0.20	0.77
Nanomia bijuga	19	1.36 ± .02	0.70 ± .04	0.08	0.93
Forskalia edwardsi; *F. tholoides*	20	1.26 ± .03	0.90 ± .06	0.13	0.94
Athorybia rosacea; *Athorybia* sp. A	13	1.51 ± .15	0.34 ± .06	0.12	0.81
Siphonophora: Cystonectae					
Rhizophysa filiformis; *Bathyphysa sibogae*	13	0.80 ± .16	0.87 ± .15	0.18	0.72
Siphonophora: Calycophorae					
Rosacea cymbiformis	13	0.75 ± .08	1.24 ± .19	0.19	0.79
Diphyes dispar	17	1.08 ± .15	0.65 ± .06	0.18	0.88
Sulculeolaria quadrivalvis	10	1.61 ± .08	0.79 ± .15	0.18	0.78
Sulculeolaria monoica	9	1.41 ± .08	0.77 ± .23	0.22	0.61


OXYGEN CONSUMPTION (µl/hr)
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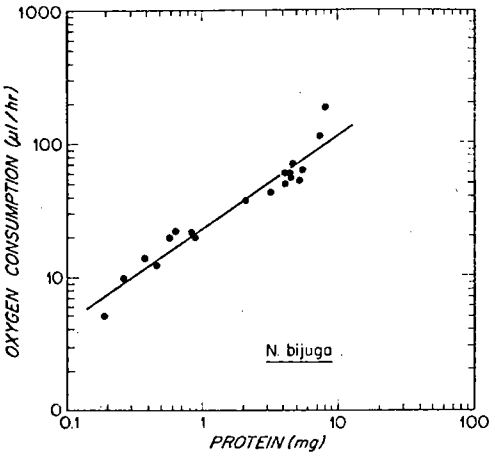
100
10
0
0.1
1
10
100
PROTEIN (mg)
A. okeni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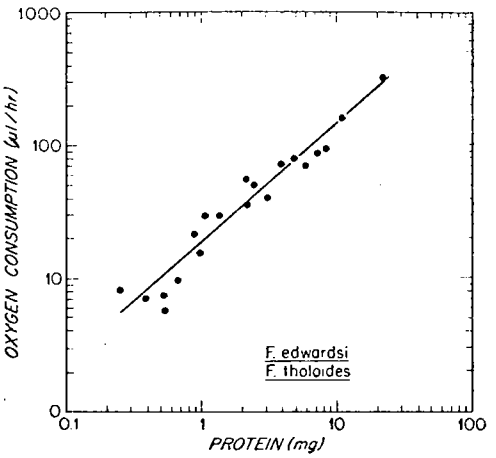
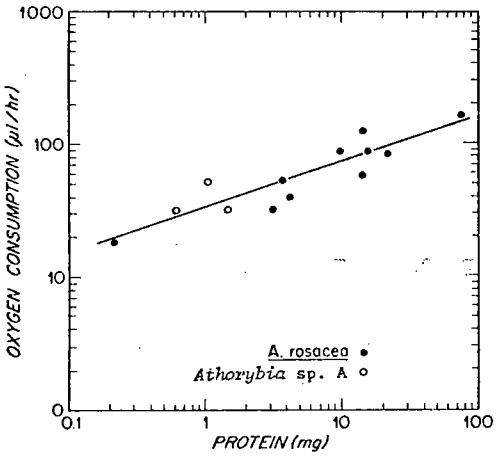
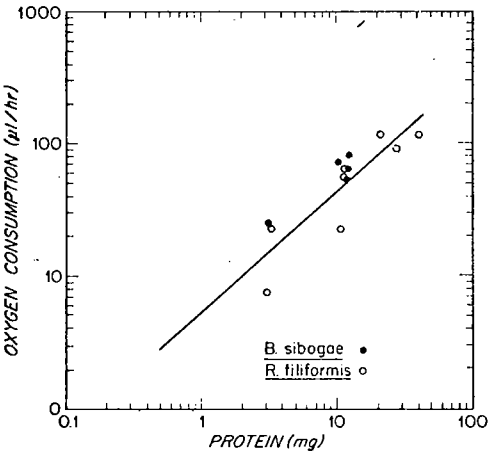
0.1
1
10
100
PROTEIN (mg)
N. bijuga


OXYGEN CONSUMPTION (µl/hr)
1000
100
10
0
0.1
1
10
100
PROTEIN (mg)
F. edwardsi
F. tholoides


OXYGEN CONSUMPTION (µl/hr)
1000
100
10
0
0.1
1
10
100
PROTEIN (mg)
A. rosacea
Athorybia sp. A


OXYGEN CONSUMPTION (µl/hr)
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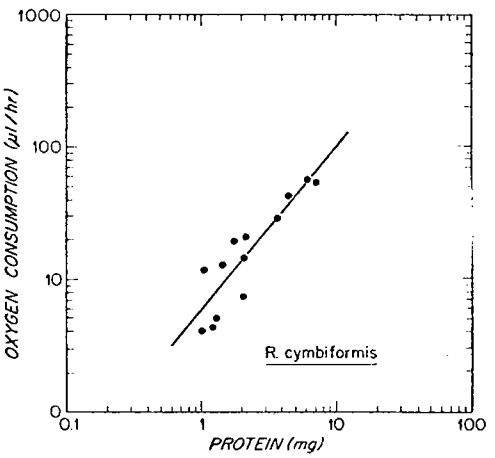
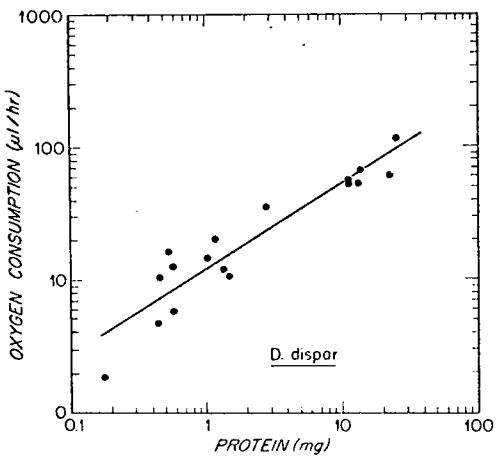
10
0
0.1
1
10
100
PROTEIN (mg)
B. sibogae
R. filiformis


OXYGEN CONSUMPTION (µl/hr)
1000
100
10
0
0.1
1
10
100
PROTEIN (mg)
R. cymbiformis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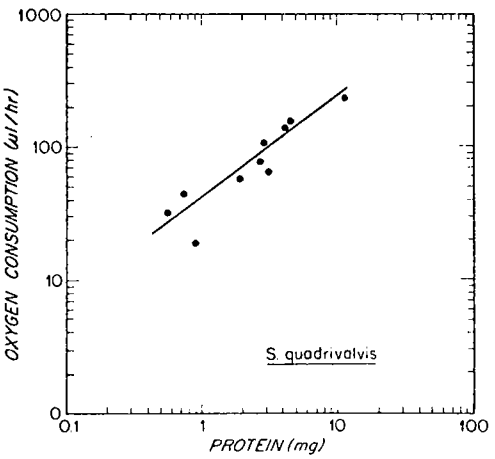
100
10
0
0.1
1
10
100
PROTEIN (mg)
D. dispar


OXYGEN CONSUMPTION (µl/hr)
1000
100
10
0
0.1
1
10
100
PROTEIN (mg)
S. quadrivalvis

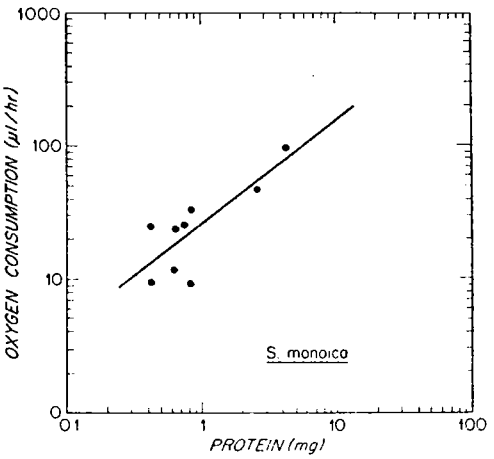
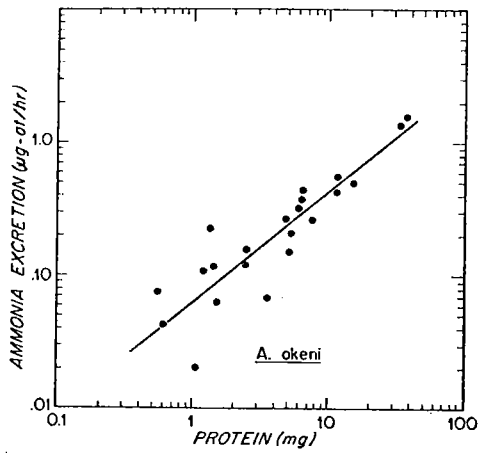
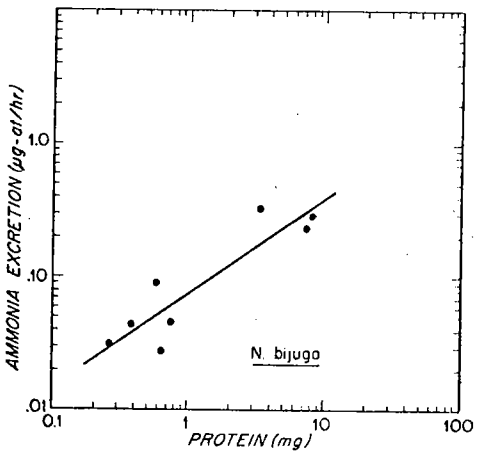

OXYGEN CONSUMPTION (µl/hr)
1000
100
10
0
0.1
1
10
100
PROTEIN (mg)
S. monoica

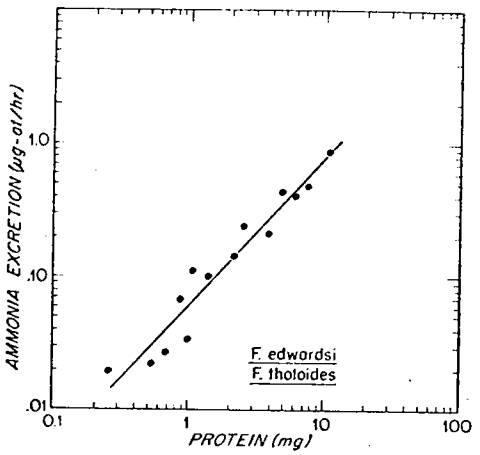
Table 9 and Figure 12:

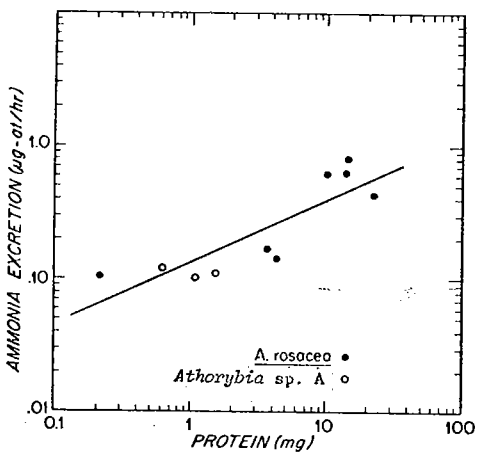
Ammonia excretion at 26 $\pm$ 3°C of some of the more abundant tropical and subtropical siphonophores, estimated by linear regression: log y = a + b (log x); where y = ammonia excretion (µg-at NH_4^+/hr); x = body protein (mg); a $\pm$ s and b $\pm$ s = regression coefficients $\pm$ standard errors; s_{yx} = standard error of the estimate (of y on x); r^2 = coefficient of determination.

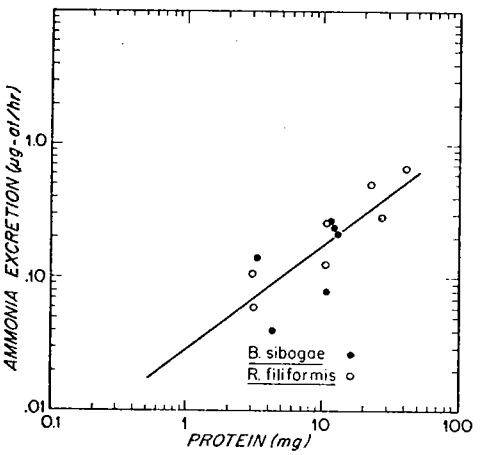
Species	n	a ± s	b ± s	s_{yx}	r^2
Siphonophora: Physonectae					
Agalma okeni	22	-1.21 ± .07	0.82 ± .10	0.23	0.79
Nanomia bijuga	8	-1.13 ± .07	0.71 ± .14	0.21	0.82
Forskalia edwardsi; *F. tholoides*	14	-1.20 ± .04	1.10 ± .08	0.15	0.93
Athorybia rosacea; *Athorybia* sp. A	11	-0.88 ± .08	0.48 ± .09	0.19	0.77
Siphonophora: Cystonectae					
Rhizophysa filiformis; *Bathyphysa sibogae*	13	-1.55 ± .18	0.80 ± .17	0.22	0.66
Siphonophora: Calycophorae					
Rosacea cymbiformis	13	-1.43 ± .08	0.95 ± .19	0.20	0.71
Diphyes dispar	10	-1.39 ± .08	0.68 ± .09	0.18	0.88
Sulculeolaria quadrivalvis	10	-0.91 ± .13	0.84 ± .25	0.27	0.59
Sulculeolaria monoica	8	-1.13 ± .10	1.35 ± .30	0.27	0.77


AMMONIA EXCRETION (µg-at/hr)
1.0
.10
.01
0.1
1
10
100
PROTEIN (mg)
A. okeni


AMMONIA EXCRETION (µg-at/hr)
1.0
.10
.01
0.1
1
10
100
PROTEIN (mg)
N. bijuga


AMMONIA EXCRETION (µg-at/hr)
1.0
.10
.01
0.1
1
10
100
PROTEIN (mg)
F. edwardsi
F. tholoides


AMMONIA EXCRETION (µg-at/hr)
1.0
.10
.01
0.1
1
10
100
PROTEIN (mg)
A. rosacea
Athorybia sp. A


AMMONIA EXCRETION (µg-at/hr)
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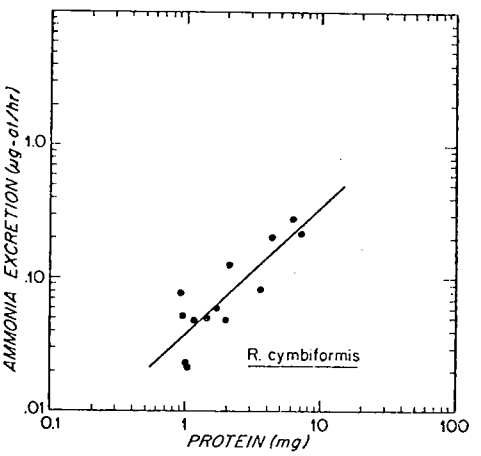
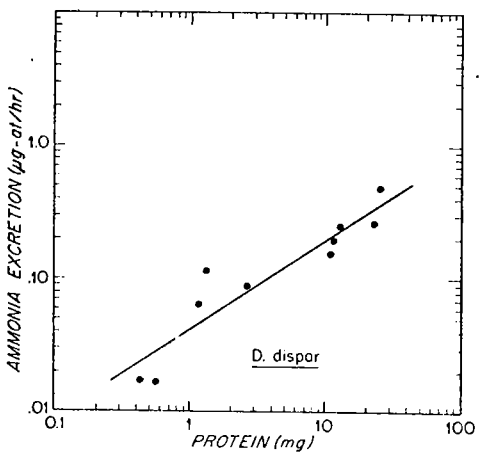
.10
.01
0.1
1
10
100
PROTEIN (mg)
B. sibogae
R. filiformis


AMMONIA EXCRETION (µg-at/hr)
1.0
.10
.01
0.1
1
10
100
PROTEIN (mg)
R. cymbiformis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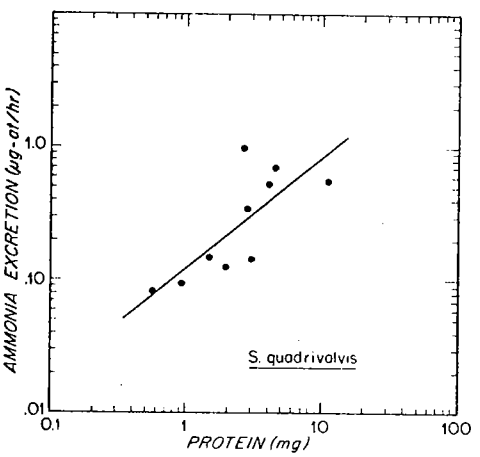
.01
0.1
1
10
100
PROTEIN (mg)
D. dispar


AMMONIA EXCRETION (µg-at/hr)
1.0
.10
.01
0.1
1
10
100
PROTEIN (mg)
S. quadrivalvis

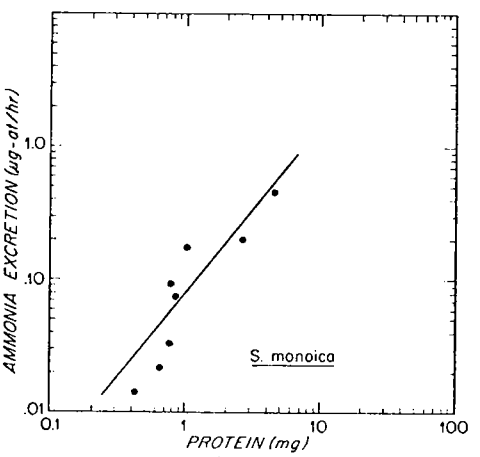

AMMONIA EXCRETION (µg-at/hr)
1.0
.10
.01
0.1
1
10
100
PROTEIN (mg)
S. monoica

Table 10. Respiration (µl O_2/mg protein-hr), excretion (µg NH_4^+/mg protein-hr), and O:NH_4^+ ratio for siphonophores, of three different sizes.

	Weight-Specific Oxygen Consumption (µl/mg-hr) 0.1-1.0 mg N Mean ± S	1.1-10.0 mg N Mean ± S	10.1-100 mg N Mean ± S	Weight-Specific Ammonia Excretion (µg/mg-hr) 0.1-1.0 mg N Mean ± S	1.1-10.0 mg N Mean ± S	10.1-100 mg N Mean ± S	O:NH_4^+ Ratio all sizes N Mean ± S
Suborder Physonectae							
Agalma okeni	(7) 12 ± 3.9	(46) 12 ± 5.5	(5) 6 ± 0.8	(3) 1.3 ± 0.8	(15) 1.0 ± 0.6	(4) 0.6 ± 0.1	(22) 19 ± 7.8
Agalma elegans	(4) 39 ± 12.7	(3) 16 ± 2.5	-	-	-	-	-
Cordagalma cordiformis	(6) 27 ± 4.0	-	-	(4) 2.5 ± 0.7	-	-	(4) 16 ± 1.9
Nanomia bijuga	(8) 31 ± 5.1	(11) 14 ± 3.3	-	(5) 1.6 ± 0.7	(3) 1.0 ± 0.5	-	(7) 38 ± 20.5
Forskalia edwardsi; F. tholoides	(8) 20 ± 7.1	(10) 17 ± 4.7	(2) 15 ± 0.1	(6) 1.1 ± 0.5	(8) 1.3 ± 0.2	-	(14) 25 ± 8.0
Athorybia rosacea	(1) 86.2	(4) 11 ± 2.3	(5) 5 ± 2.3	(1) 0.9	(3) 0.8 ± 0.2	(4) 0.7 ± 0.2	(8) 17 ± 14.1
Athorybia sp.	(3) 40 ± 13.7	-	-	(1) 3.3	(2) 1.5 ± 0.1	-	(3) 22 ± 3.6
Suborder Cystonectae							
Bathyphysa sibogae	-	(1) 6.9	(4) 6 ± 0.9	-	(2) 0.5 ± 0.3	(4) 0.3 ± 0.1	(5) 20 ± 8.1
Rhizophysa filiformis	-	(2) 5 ± 2.5	(6) 4 ± 1.4	-	(2) 0.3 ± 0.1	(5) 0.3 ± 0.1	(5) 23 ± 7.6
Suborder Calycophorae							
Stephanophyes superba	(4) 22 ± 3.2	(13) 14 ± 6.3	-	(2) 1.8 ± 0.4	(4) 1.1 ± 0.6	-	(6) 22 ± 8.1
Rosacea cymbiformis	(2) 8 ± 3.6	(11) 8 ± 2.5	-	(4) 0.8 ± 0.4	(9) 0.6 ± 0.3	-	(11) 23 ± 10.3
Diphyes dispar	(7) 17 ± 7.4	(4) 12 ± 3.8	(6) 4 ± 0.9	(2) 0.6 ± 0.1	(3) 1.0 ± 0.4	(5) 0.3 ± 0.1	(10) 25 ± 7.4
Sulculeolaria quadrivalvis	(3) 45 ± 17.1	(6) 36 ± 13.9	(1) 21.3	(2) 2.1 ± 0.3	(7) 2.4 ± 1.7	(1) 0.8	(9) 29 ± 9.8
Sulculeolaria monoica	(7) 32 ± 15.1	(2) 21 ± 2.3	-	(6) 1.5 ± 0.9	(2) 1.6 ± 0.3	-	(7) 36 ± 21.0
Sulculeolaria chuni	(4) 75 ± 25.2	-	-	(4) 2.7 ± 1.0	-	-	(4) 50 ± 23.9
Sulculeolaria biloba	-	(2) 13 ± 0.5	-	-	(2) 1.2 ± 0.2	-	(2) 17 ± 2.3
Abyla sp.	-	(3) 5 ± 0.5	-	-	(3) 0.5 ± 0.2	-	(3) 17 ± 5.5
Chelophyes appendiculata	-	(5) 8 ± 3.3	-	-	(3) 0.5 ± 0.2	-	(3) 26 ± 9.5
Hippopodius hippopus	(1) 17.3	(1) 3.5	-	-	-	-	-
eudoxid phase, *Diphyes dispar*	(2) 78 ± 20.2	-	-	(2) 1.4 ± 0.7	-	-	(2) 121 ± 78.7
eudoxid phase, *Ceratocymba sp.*	(1) 75.6	(1) 2.3	-	(1) 0.8	(1) 0.1	-	(2) 88 ± 52.9

Table 11. A comparison of respiration (μl O_2/mg protein-hr) of Forskalia tholoides and F. edwardsi at ambient temperature and at 5°C below ambient temperature.

SPECIES	SIZE (mg protein)	TEMPERATURE (°C) ambient	expmntl	RESPIRATION ambient(R_0)	expmntl(R_1)	RATIO R_0/R_1
Forskalia tholoides	0.48	25.5	20.5	20.0*	15.2	1.3
Forskalia tholoides	3.23	25.5	20.5	16.1*	8.1	2.0
Forskalia tholoides	3.15	22.0	17.0	16.0*	5.7	2.8
Forskalia edwardsi	6.33	22.0	17.0	14.1	3.7	3.8
Forskalia edwardsi	10.66	22.0	17.0	18.1	4.1	4.4
Forskalia tholoides	6.38	21.0	16.0	14.9*	3.2	4.7
Forskalia edwardsi	7.77	21.0	16.0	14.6*	2.9	5.0

*Oxygen consumption calculated from Table 8.

Table 12. Nitrogenous excretion in some tropical and subtropical siphonophores.

SPECIES	SIZE (mg protein)	AMMONIA EXCRETION ($\mu g\ NH_4^+$/hr)	TOTAL NITROGENOUS EXCRETION ($\mu g\ NH_4^+$ equivalents/hr)	$\frac{NH_4^+}{\text{TOTAL N}}$
Agalma okeni	1.3	0.4 ± 0.1	0.5 ± 0.2	0.80
Agalma okeni	2.4	1.5 ± 0.1	2.2 ± 0.2	0.68
Agalma okeni	2.5	2.6 ± 0.1	4.7	0.56
Agalma okeni	8.6	3.7 ± 0.1	5.0 ± 0.2	0.74
Agalma okeni	8.6	5.9	5.9	1.00
Agalma okeni	8.6	4.4 ± 0.2	7.7 ± 0.1	0.58
Agalma okeni	8.6	11.7 ± 0.1	13.2 ± 0.6	0.89
Agalma okeni	10.1	8.2 ± 0.2	23.6 ± 3.9	0.35
Rosacea cymbiformis	2.8	3.5 ± 0.1	4.8	0.73
Stephanophyes superba	1.4	1.9 ± 0.4	3.5	0.56

In eight specimens of A. okeni, ranging in size from 1.3 - 10.1 mg protein, ammonia excretion averaged 69% of total nitrogenous excretion (Table 12). Measurements on single colonies suggest that Rosacea cymbiformis and Stephanophyes superba may also be primarily ammonotelic (Table 12). This is the case for most planktonic invertebrates (Corner and Cowey, 1968; Jawed, 1973; Mayzaud and Dallot, 1973).

In A. okeni, total body carbon, C (by CHN analysis), and body protein, P (by Lowry analysis), can be related by the following equation:

$$\log C = 0.894 (\log P) - 0.137$$

Smaller colonies had a higher C:P ratio than large colonies.

DISCUSSION

Rates of oxygen consumption reported for siphonophores taken from nets and held for 1 - 2 days in the laboratory without feeding (Nival, et al., 1972; Ikeda, 1974) were consistently lower than most rates determined in the present study. Since stresses of collection, maintenance in laboratory aquaria, and transfer to respirometer vessels may damage these very delicate animals, extrapolation of previous estimates of oxygen consumption to field populations of siphonophores is unrealistic. Although estimates of respiration and excretion in the present study are not free from bias which may

be induced by confinement, colonies were collected in situ in the ocean which minimized damage to them.

Temperature Acclimation

Although most respiration measurements were made on siphonophores collected at temperatures from 23 - 29°C, those acclimated to lower habitat temperatures had similar rates of oxygen consumption. Species of Forskalia which had 1 - 10 mg protein respired 17 ± 4.7 µl O_2/mg protein-hr at 23 - 29°C (Table 10). Four additional colonies (not included in Table 10), ranging in size from 3.15 mg protein to 8.21 mg protein but collected in surface waters of 21 ± 1°C showed equivalent respiration (20 ± 9.1 µl O_2/mg protein-hr). This implies that species of Forskalia can acclimate metabolically to a temperature range of at least 9°C.

Short-term exposures to temperatures only 5°C lower than ambient, though, caused twofold to fivefold reductions in oxygen consumption (Table 11). Temperature changes of this magnitude could influence the metabolism of diel migrators. If some siphonophores feed at night in surface waters and then migrate through the thermocline to their daytime depths, they could conserve energy (McLaren, 1963), providing increases in respiration due to swimming activity and increased hydrostatic pressure are less than the decrease induced by temperature (e.g., Teal and Carey, 1967).

Interspecific Differences

The value b (Tables 8 and 9) is the exponent in the relation between metabolic rate and size; if metabolism is directly proportional to weight (mg protein), b = 1. Actually, b was usually less than 1.0 (Tables 8 and 9), and in most species was not significantly different statistically (t-test; $P < 0.05$) from Hemmingsen's (1960) index of 0.73. Variation in the rate at which metabolism changes with size may reflect differences in dietary or reproductive state. Behavioral and ecological differences between groups of siphonophores also contribute to differences in metabolism.

For example, cyctonect siphonophores had lower respiration and excretion rates than physonect siphonophores (Table 10). Since cystonects lack swimming bells and are only able to writhe about in the water and rise or sink by release or secretion of gas, it is reasonable that they have lower metabolic rates. Within the Physonectae, respiration and excretion rates were somewhat lower in species like Athorybia rosacea and Agalma okeni, which are slow swimmers and largely inactive.

Calycophorae are highly variable in form, and the range of respiration and excretion rates in this group was correspondingly broad. Slow-swimming inactive species like Hippopodius hippopus and Abyla sp. had the lowest rates. Rosacea cymbiformis had lower

respiration and excretion than a faster and more active confamilial like Stephanophyes superba.

I have measured oxygen consumption and ammonia excretion in other groups of gelatinous zooplankton by the same methods (Biggs, in prep). Specimens of cydippid and cestid ctenophores, hydromedusae, and the scyphomedusa Aurelia sp. had relatively low rates of respiration and excretion (6 - 13 µl O_2/mg protein-hr, and 0.2 - 1.1 µg NH_4^+/mg protein-hr for animals with 1 - 10 mg protein). More active, muscular carnivores of the same size, like Pelagia noctiluca, Ocyropsis maculata, and Pterotrachea hippocampus, as well as most herbivores, had higher rates (16 - 36 µl O_2/mg protein-hr, and 0.7 - 2.9 µg NH_4^+/mg protein-hr).

Nutrient Cycling

Over large areas of the oligotrophic central gyre of the North Atlantic Ocean, concentrations of ammonia in the upper 100 m are less than 0.8 µg-at/liter (Goering, et al., 1964). Most medium to large siphonophores have more than 5 mg body protein and excrete ammonia at rates exceeding 0.3 µg-at/hr (from Table 9). Ammonia may be a preferred nitrogenous source for phytoplankton and microbial populations (Corner and Davies, 1971), and ammonia released by zooplankton has been proposed as a significant nitrogenous input in areas of the Pacific Ocean off Peru (Walsh and Dugdale, 1971) and Washington (Jawed, 1973). Since, by per cent displacement

volume in plankton tows, siphonophores are one of the ten major taxonomic groups of zooplankton in the upper 200 m of the Sargasso Sea (Grice and Hart, 1962), they and other zooplankton may be important in regenerating nutrients there.

$O:NH_4^+$ Ratios and Nutrition

Ratios of oxygen atoms consumed to ammonia nitrogen atoms excreted by siphonophores are in accord with those reported for many non-gelatinous species. For example, in tropical, subtropical, and temperate planktonic crustacea, most $O:NH_4^+$ ratios ranged between 8 and 24 (Harris, 1959; Conover and Corner, 1968; Ikeda, 1974). Lipid and protein are probably both important metabolites. Protein is about 16% N and requires 1.04 liters of oxygen for complete combustion of one gram (Ikeda, 1974). If ammonia was the end-product of nitrogen metabolism, the metabolic $O:NH_4^+$ ratio for protein catabolism would be about 8. Oxidation of equivalent weights of protein and lipid requires 2.02 liters of oxygen for complete combustion of one gram and yields an $O:NH_4^+$ ratio of about 24 (Ikeda, 1974), which is in agreement with most of the $O:NH_4^+$ ratios I measured for siphonophores (Table 10).

The very high $O:NH_4^+$ ratios measured in four Calycophorae eudoxids (Table 10) may reflect a large amount of non-protein catabolism in these tiny reproductive forms. In fact, some eudoxids

do not seem to feed after being released from the siphonophore colony, and therefore may subsist on carbohydrate or lipid reserves for their relatively brief existence.

In general, mean $O:NH_4^+$ ratios in subtropical gelatinous herbivores were higher than those measured in siphonophores and medusae, ranging from 18 for the aggregate generation of Salpa maxima to 89 for pteropods like Corolla spectabilis (Biggs, in prep). The extremely low O:N ratios reported for salps and other macroplankton from areas of the Mediterranean Sea (Mayzaud and Dallot, 1973) may reflect damages incurred in collection. Animals collected from plankton nets (300 μm mesh) and from IKMT hauls may have experienced significant abrasion arising from the filtering characteristics of these samplers. After being held for 12 hours in the laboratory, some or all may have been moribund, and either catabolized or leaked unnaturally high levels of nitrogen compounds.

SUMMARY

1. Siphonophores were individually collected in jars by SCUBA divers and their rates of oxygen consumption and ammonia excretion were estimated by difference from control jars of sea water enclosed simultaneously.

2. Respiration at 26±3°C ranged from 2 - 86 µl O_2/mg protein-hr, and ammonia excretion ranged from 0.1 - 3.3 µg NH_4^+/mg protein-hr. Colonies of small size had higher rates of respiration and excretion than those of larger colonies.

3. Although most respiration measurements were made on siphonophores collected at temperatures of 23 - 29°C, those acclimated to lower habitat temperatures had similar rates of oxygen consumption. Short-term exposures to temperatures only 5°C lower than ambient, however, caused twofold to fivefold reductions in respiration.

4. Ratios of oxygen consumed to ammonia-nitrogen excreted for most species ranged from 16 - 36 and suggest that both protein and lipid are important metabolites.

5. Rates of oxygen consumption measured by me in hand-collected siphonophores are higher than most rates reported by previous investigators. I suggest that most siphonophores which were taken from nets and held for 1 - 2 days in the laboratory without feeding were moribund, and that their respiration was certainly not representative of populations living in the natural environment.

Part 4. Growth and Reproduction of *Agalma okeni*

INTRODUCTION

Siphonophores increase in size by budding. Nectosome and siphosome are unable to replace lost gelatinous parts, though, except by budding new ones apically (e.g., Moser, 1925; Mackie and Boag, 1963). When unprotected areas are exposed by loss of nectophores and bracts, the stem rotates and contracts to close them and maintain bilateral symmetry (Mackie, 1964). When the stem, in regions outside proximal zones of budding, fragments or is severed surgically, it seems unable to regenerate additional parts.

Because regenerative ability is so limited, reproduction is probably obligately sexual. Most colonies are hermaphroditic and have an alternation of male and female gonophores (Totton, 1965). Since siphosome budding occurs at the base of the nectosome, gonophores which are most ripe are those farthest from the anterior end of the colony. In Physonectae, gonophores are budded multiplely from the bases of palpons associated with each stem group. Eggs and sperm may be released free into the water, as in species of Nanomia (Totton, 1965), or ripe gonophores may be shed from the stem to swim weakly under their own power, as I have observed in species of Agalma. As gonophores mature, some Calycophorae release their distal stem groups as free-swimming units known as eudoxids.

Despite the ubiquity of siphonophores in oceanic regions, their productivity is difficult to measure quantitatively. In

theory, secondary production can be estimated by following size-frequency changes in natural populations, or by measuring growth and reproduction of species in laboratory culture. Although there are theoretical and practical difficulties in sampling a single population of oceanic plankton through time, populations of some gelatinous zooplankton may be amenable to size-frequency analysis when they occur in swarms (Heron, 1972). Populations of most siphonophores, though, are too disperse and too fragile to be accurately sampled with nets (see Part 1). Because of their colonial organization, they are especially ill-suited to analysis by size-frequency distribution. Although neritic ctenophores can be maintained in laboratory culture (Greve, 1970; Hirota, 1972; Baker and Reeve, 1974), none of the oceanic jellies have been successfully cultured through an entire reproductive cycle.

Although there are difficulties in evaluating the effects of laboratory confinement, it is possible to measure short-term growth of siphonophores. Mackie and Boag (1963) were able to keep carefully-collected colonies of Nanomia cara at 12-14°C in large-volume flow-though aquaria for up to 36 days. Approximately every three days, colonies under culture were fed particles of fresh crab meat or small crustaceans. Mackie and Boag found that small colonies of N. cara would live and grow on this diet.

Agalma okeni, the most common tropical and subtropical relative of N. cara, is smaller and generally less active in

aquaria. I was able to maintain sexually-immature colonies for up to five days aboard ship by allowing them to feed on high densities of Artemia nauplii or on species of the copepods Acartia and Pleuromamma. During this time, most colonies budded new individuals along both nectosome and siphosome.

METHODS

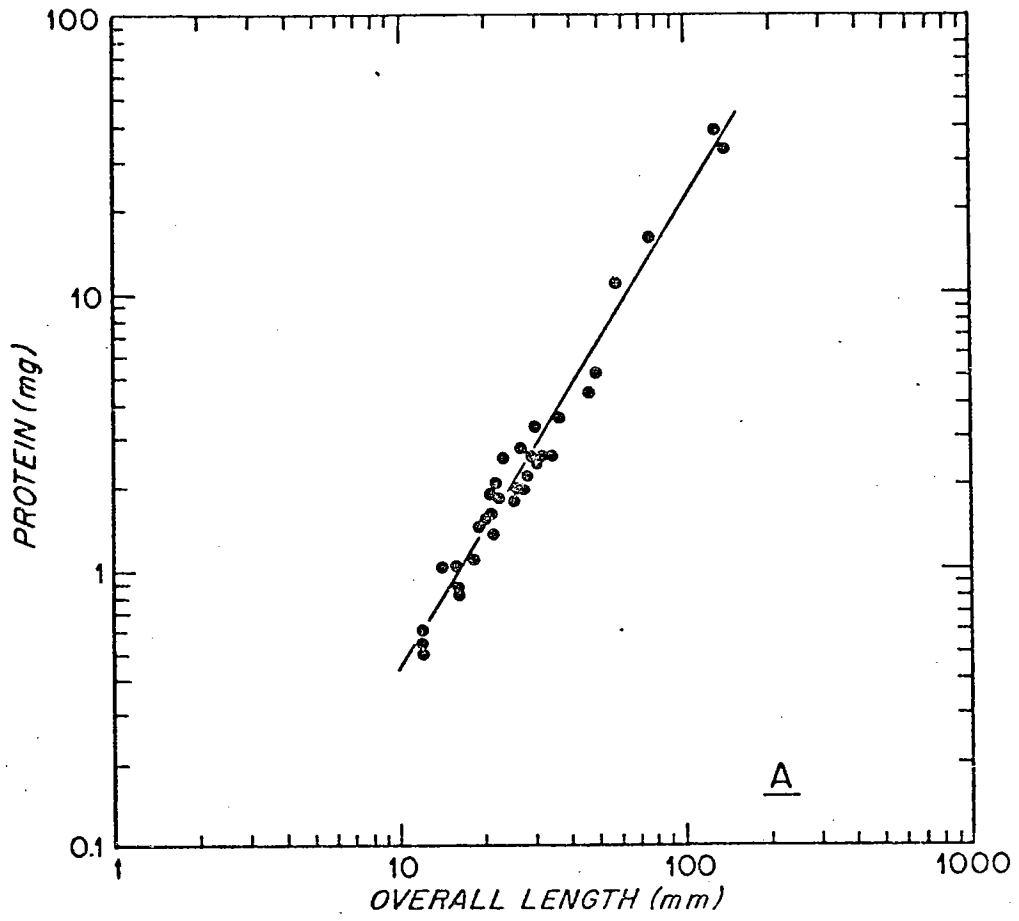
Colonies of A. okeni were individually collected by SCUBA divers and released into 3.8-liter and 20-liter cylindrical aquaria. Laboratory temperatures ranged from 24 - 26°C. Colonies were maintained in the dark. Those in 3.8-liter aquaria were provided with Artemia nauplii at densities greater than 100 per liter. Copepods were added to colonies in 20-liter aquaria at densities of 20 or more per liter. By maneuvering struggling Sargassum shrimp (Leander tenuicornis) against the fishing tentacles, I allowed three colonies to capture and ingest shrimp 10 - 20 mm long. I changed the water and added new prey every second day.

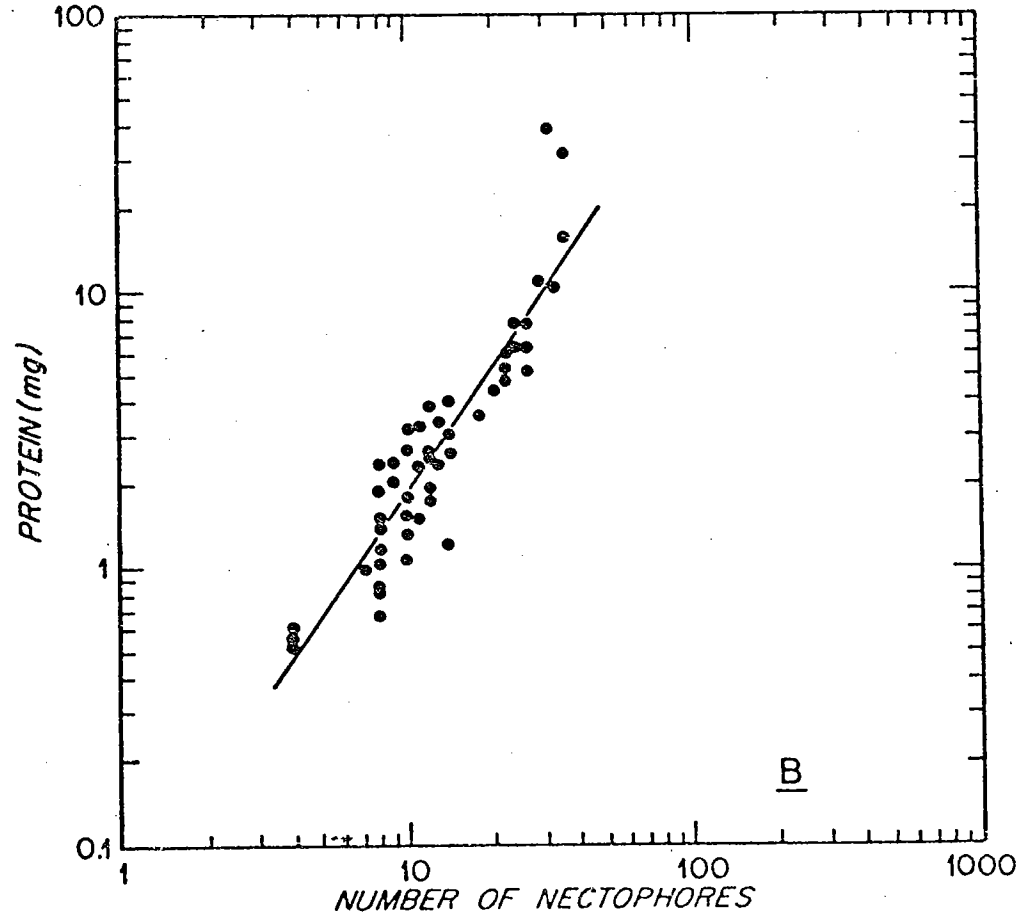
I estimated growth rates by counting the increase in number of nectophores and stem groups in 12 colonies of A. okeni in captivity for 1 - 4 days. As colonies of A. okeni grow, individual nectophores increase in size (Table 13), though at any time all except 2 - 4 apical nectophores (buds) are roughly equivalent. Carefully hand-collected colonies having the same number of nectophores are similar in size (Figures 13 A and B), and colony biomass can be estimated

Table 13. Nectosome size in Agalma okeni.

OVERALL LENGTH OF COLONY (mm)	NUMBER OF NECTOPHORES (other than buds)	DIMENSIONS OF NECTOPHORES (mm)	PROTEIN (mg) per NECTOPHORE
49	24	7 x 7	0.05
59	22	8 x 8	0.06
59	30	9 x 9	0.06
--	--	10 x 8	0.11
65	25	12 x 10	0.11
86	32	13 x 13	0.17
140	36	13 x 13	--

Figure 13. Protein content of colonies of Agalma okeni as a function of overall length (A) and number of nectophores (B).


100
10
1
0.1
PROTEIN (mg)
A
1
10
100
1000
OVERALL LENGTH (mm)


100
10
1
0.1
PROTEIN (mg)
B
1
10
100
1000
NUMBER OF NECTOPHORES

from either the number of nectophores or from overall colony size. The mean difference in size between colonies with 2 and 3 pairs of nectophores is 480 μg protein, while colonies with 6 and 7 pairs of nectophores differ by about 600 μg protein (Figure 13 B).

RESULTS

Despite varying diets, most colonies of A. okeni added 1 - 2 pairs of nectophores within 1 1/2 - 2 1/2 days and five colonies maintained for 2 additional days added 2 - 3 pairs of nectophores (Table 14). All colonies maintained for longer than 1 1/2 days budded a new gastrozooid and tentacle, in addition to nectosome growth. Small colonies with 1 or 2 pairs of nectophores roughly doubled their protein biomass in two days, while large colonies with 4 - 6 pairs of nectophores added 33 - 36% more protein (Table 14).

The steady increase in size shown by carefully-maintained colonies was offset somewhat by accidental loss of gelatinous parts. Although the effects of laboratory confinement are difficult to assess, the faculty for autotomy is so well developed in most Physonectae and Calycophorae that shedding of nectophores and bracts probably occurs in situ as well as in the laboratory.

Colonies of A. okeni first show well-developed gonophores at about the 14 ± 2 nectophore stage (32 ± 4 mm overall colony length). Pre-reproductive colonies have nectophores with a single

Table 14. Increase in size of colonies of Agalma okeni maintained for 1 - 4 days in the laboratory.

(A = after 1 ± 1/2 days; B = after 2 ± 1/2 days;

C = after 4 ± 1/2 days)

INITIAL SIZE NECTOPHORES PLUS BUDS	*PROTEIN (mg)	DIET	NECTOPHORES + BUDS ADDED A	B	C	FINAL SIZE *PROTEIN (mg)
1+0	0.1	nauplii	-	2+1	-	0.3
3+1	0.5	nauplii; shrimp	-	3	5+1	1.6
4+1	0.6	nauplii; shrimp	-	-	5+1	1.9
5+0	0.7	nauplii	-	2+1	-	1.1
6+0	0.9	nauplii	0+2	-	-	1.1
6+1	1.1	copepods	-	4+2	6+2	3.5
6+1	1.1	nauplii	-	4+1	-	2.1
7+0	1.1	nauplii	1	-	-	1.3
7+0	1.1	nauplii	1+1	-	-	1.4
8+0	1.4	nauplii	-	1+2	-	1.9
10+1	2.1	copepods	1+1	-	5	3.5
13+0	2.5	nauplii; shrimp	-	2+2	-	3.5

*Calculated from Figure 13.

vertical lateral ridge (1-r variety), while nectophores budded by colonies larger than the 16 ± 2 nectophore stage have two vertical lateral ridges (2-r variety). The more distal nectophores in colonies of A. okeni with 14 - 18 nectophores may be 1-r forms, while those more proximal are all 2-r. I never encountered a colony of totally 1-r morphology which was larger than the 14-nectophore stage, and none of these were sexually mature. Thus, the genus Crystallomia Dana, 1858 which was established for 1-r forms of Agalmidae is invalid, since it is but a growth phase of A. okeni.

DISCUSSION

I can now estimate the energy requirements of colonies of A. okeni. A small colony with three pairs of nectophores has about 1.0 mg of protein (Figure 13 B) and consumes about 12 µl O_2/hr (Table 8). Assuming an oxycaloric equivalent of 4.9 calories per ml, 3.5 calories would be consumed in respiration during a 2 1/2 day period.

The caloric value of a Candacia sp. copepod is about 0.5 calories (estimated from Shushkina and Sokolova, 1972). If assimilation by siphonophores ranges between 70 - 90% of ingestion, a colony with 1.0 mg protein would have to ingest 8 - 10 such copepods in 2 1/2 days to balance its metabolism. Assimilation efficiencies of 70 - 90% are not unrealistic for aquatic carnivores (Welsh, 1968); values of 80% and 88% have been reported for

Sagitta hispida (Cosper and Reeve, 1975) and Euphausia pacifica (Lasker, 1966), respectively.

If siphonophores living under natural conditions can increase in size at rates suggested by short-term laboratory growth experiments, a colony of A. okeni with 3 pairs of nectophores could grow to the 8 or 10 nectophore stage in 2 1/2 days. This corresponds to an increase in size of about 480 - 900 μg protein (Figure 13 B). Since the caloric value of protein is about 5.5 kilocalories per gram (Morowitz, 1968), this increase in size represents 2.6 - 5.3 calories. Additional consumption of 6 - 15 copepods of Candacia size should support this increase in size, for a total ingestion of 14 - 25 copepods over a 2 1/2 day period. A colony of A. okeni initially 3 times larger, with 3.0 mg protein and 14 nectophores, would have to consume 29 - 46 copepods of similar size to balance its respiratory energy losses and increase in size at a similar rate.

The preceding calculations suggest that growth in siphonophores like A. okeni may be quite efficient. In fish and euphausiids the greatest fraction of ingestion goes to support respiration (Table 15). Physonect siphonophores able to grow to a colony size two pairs of nectophores larger in 2 1/2 days should have a higher ratio of growth to respiration, or more like chaetognaths in overall production efficiency (Table 15).

Table 15. A comparison of production, respiration, and egestion estimated for Agalma okeni with other marine carnivores. Production and respiration of A. okeni were calculated from caloric equivalents; an assimilation efficiency of 80% was assumed (see text).

SPECIES	PRODUCTION	RESPIRATION	EGESTION	SOURCE
Agalma okeni				
3.0 mg protein	33%	47%	20%	
1.0 mg protein	48%	32%	20%	
carnivorous fish	20%	60%	20%	Welsh (1968)
Euphausia pacifica	29%	59%	12%	Lasker (1966)
Sagitta elegans	35%	37%	28%	calculated from Sameoto (1972)

In colonies of Agalmidae, female gonophores have 1 - 4 eggs which measure about 0.7 mm in diameter (Totton, 1965). When fertilized in the laboratory at 14°C, eggs of Agalmidae require about 2 - 3 weeks to develop to the postlarva (Carré, 1969, 1971, 1973). In tropical and subtropical environments, development is probably more rapid and might proceed in 1 - 2 weeks. Extrapolating from laboratory growth rates I measured at 25°C, a colony might grow from the postlarva to the 14-nectophore stage in 1 1/2 - 2 weeks. This suggests that the generation time of Agalmidae living in tropical and subtropical oceanic regions may be between 2 1/2 - 4 weeks. Among Calycophorae, times for larval development are similar (Carré, 1967), although many species must grow to large size before gonophores become ripe. Other gelatinous carnivores have generation times of 3 - 4 weeks (Hirota, 1972; Baker and Reeve, 1974), as do tropical and subtropical chaetognaths (Reeve and Walter, 1972).

SUMMARY

1. Colonies of Agalma okeni maintained in the laboratory on a diet of Artemia nauplii, copepods, or shrimp budded an additional feeding polyp and 1 - 2 pairs of nectophores about every two days.
2. Agalma okeni became reproductive at the 14 ± 2 nectophore stage, when it measured 32 ± 4 mm overall length.
3. Energetic calculations suggest that small and medium-size colonies of A. okeni incorporate 48% and 33%, respectively, of ingestion into production.
4. A small colony of A. okeni with six nectophores probably requires 2.8 - 5.0 calories to balance daily rates of oxygen consumption and growth. A medium-size colony with fourteen nectophores probably requires 5.8 - 9.2 calories.
5. Generation time of A. okeni in tropical and subtropical regions is probably 2 1/2 - 4 weeks.

GENERAL DISCUSSION: FOOD LIMITATION, PREDATION PRESSURE, AND MASS AGGREGATIONS

The preceeding respiration and production data permit a comparison of the nutritional requirements of siphonophores of the Family Agalmidae with the availability of food in the environment. In the upper 30 meters of the Sargasso Sea, Agalmidae are present at densities of less than one colony per 15,000 m^3 (from Part 1). The average numerical abundance of calanoid copepods in semi-monthly plankton collections from the upper 500 meters of the Sargasso Sea exceeds $100/m^3$ (Deevey, 1971). Even if only 10% of these occur in the upper 30 meters and a high percentage of those which encounter siphonophores escape capture, I suggest that Agalmidae are unlikely to be food-limited here. Total tentacle length of most Agalmidae extends over 2 meters, and in situ observations suggest that colonies may fish several cubic meters daily (from Part 2). Moreover, since they are not restricted to feeding on copepod-size prey, Agalmidae like A. okeni could capture a euphausiid or mysid less than an inch long (with 5 mg body protein) and extract enough energy for 1 - 2 weeks maintenance or to increase in size to within the range of reproductive capacity.

In situ observations suggest that hyperiid amphipods, fish, and other gelatinous carnivores like medusae and heteropods are predators of siphonophores. Every common species of siphonophore

which I encountered in subtropical surface waters has been collected with hyperiid amphipods (Table 16). Although the nature of these associations are not completely understood, many are quite specific and at least four genera of hyperiids eat parts of their siphonophore hosts (Harbison, et al., in prep). Larval hyperiids of the Family Pronoidae encyst in gelatinous parts of physonect colonies and molt through at least three developmental stages there. Since the radial canals of nectophores and bracts communicate with the gastrovascular cavity of the siphonophore, a colony may provide pre-digested food for these endoparasitic juveniles. Multiple infestations of juveniles in siphonophores are common, and often more than one juvenile is present in the same nectophore or bract.

Several gelatinous zooplankton prey on siphonophores (Table 17). About 20% of all Pterotrachea coronata collected in the Florida Current had been feeding on physonect siphonophores (Hamner, et al., 1975). In fact, heteropods were able to digest gelatinous parts of siphonophores in 6 - 8 hours (Hamner, et al., 1975). A transparent pelagic polychaete, which swallowed a colony of the small siphonophore Eudoxoides spiralis (Table 17), digested it completely in 7 1/2 hours. The stem was digested in less than 3 hours.

Juveniles of at least seven species of fish associate with Physalia physalis and may bite off pieces of this siphonophore (Mansueti, 1963). While diving, I twice collected juvenile fish

Table 16. Associations of hyperiid amphipods with siphonophores.

SPECIES	GENERA IN ASSOCIATION
Suborder Physonectae	
Agalma okeni	*Thyropus*; *Eupronoe* (encysted juveniles)
Agalma elegans	*Scina*; *Tryphana*; *Amphithyrus*; *Eupronoe*
Agalma clausi	*Paralycaea*; *Tetrathyrus*; *Eupronoe* (encysted juveniles)
Cordagalma cordiformis	juveniles (specimen lost)
Nanomia bijuga	*Tetrathyrus*; *Paralycaea*
Forskalia edwardsi; *F. tholoides*	*Thyropus*; *Eupronoe* (encysted juveniles)
Physophora hydrostatica	*Platyscelus*
Athorybia rosacea	*Thyropus*; *Eupronoe* (encysted juveniles)
Athorybia sp. A	*Thyropus*
Suborder Cystonectae	
Rhizophysa filiformis	*Thyropus*
Bathyphysa sibogae	*Schizoscelus*; *Thyropus*
Suborder Calycophorae	
Stephanophyes superba	*Thyropus*
Rosacea cymbiformis	*Sympronoe*; *Paraphronima*
Diphyes dispar	*Thyropus*; *Lycaeopsis*
Sulculeolaria quadrivalvis	*Paralycaea*
Sulculeolaria monoica	*Paralycaea*
Sulculeolaria chuni	*Paralycaea*
Abyla sp.	*Thyropus*
Abylopsis tetragona	*Phronima*
Chelophyes appendiculata	*Amphithyrus*

living among the tentacles of colonies of Forskalia tholoides (stations 299 and 428). Pigmentation of these juveniles mimicked the reds and browns of this siphonophore. Phyllosome larvae of stomatopods also accompany some gelatinous carnivores (Shojima, 1963), and I collected two from the nectosome of colonies of A. okeni and Diphyes dispar (stations 396 and 428).

Larger fish, as well, may feed on siphonophores and other gelatinous zooplankton (Hamner, et al., 1975). In a one-cubic-meter tank on board ship, I have observed oceanic filefish (Family Monacanthidae) feeding on colonies of Agalma elegans. The filefish approached this siphonophore as soon as I had dipped a colony into the aquarium, and rapidly bit off every pigmented stem group. After a few moments, a fish bit off the pigmented pneumatophore, but discarded it almost immediately. The filefish had no interest in the gelatinous remainder of the colony.

Agalma okeni may be subject to similar predation. I twice found colonies missing portions of the stem. A large colony with 34 nectophores (station 297) had only the first three stem groups and 15 mm of siphosome. At station 392, a colony of A. okeni with five stem groups had only ten nectophores. The entire apical portion of the colony, including the pneumatophore and nectosomal budding zone, was missing and presumably had been bitten away.

Gelatinous carnivores may sometimes occur in enormous abundance. Along the Atlantic Coast of the United States, populations of scyphomedusae often bloom in May and June, followed in July - September by

Table 17. Zooplankton predators of siphonophores (Hyperiidae are listed separately in Table 16).

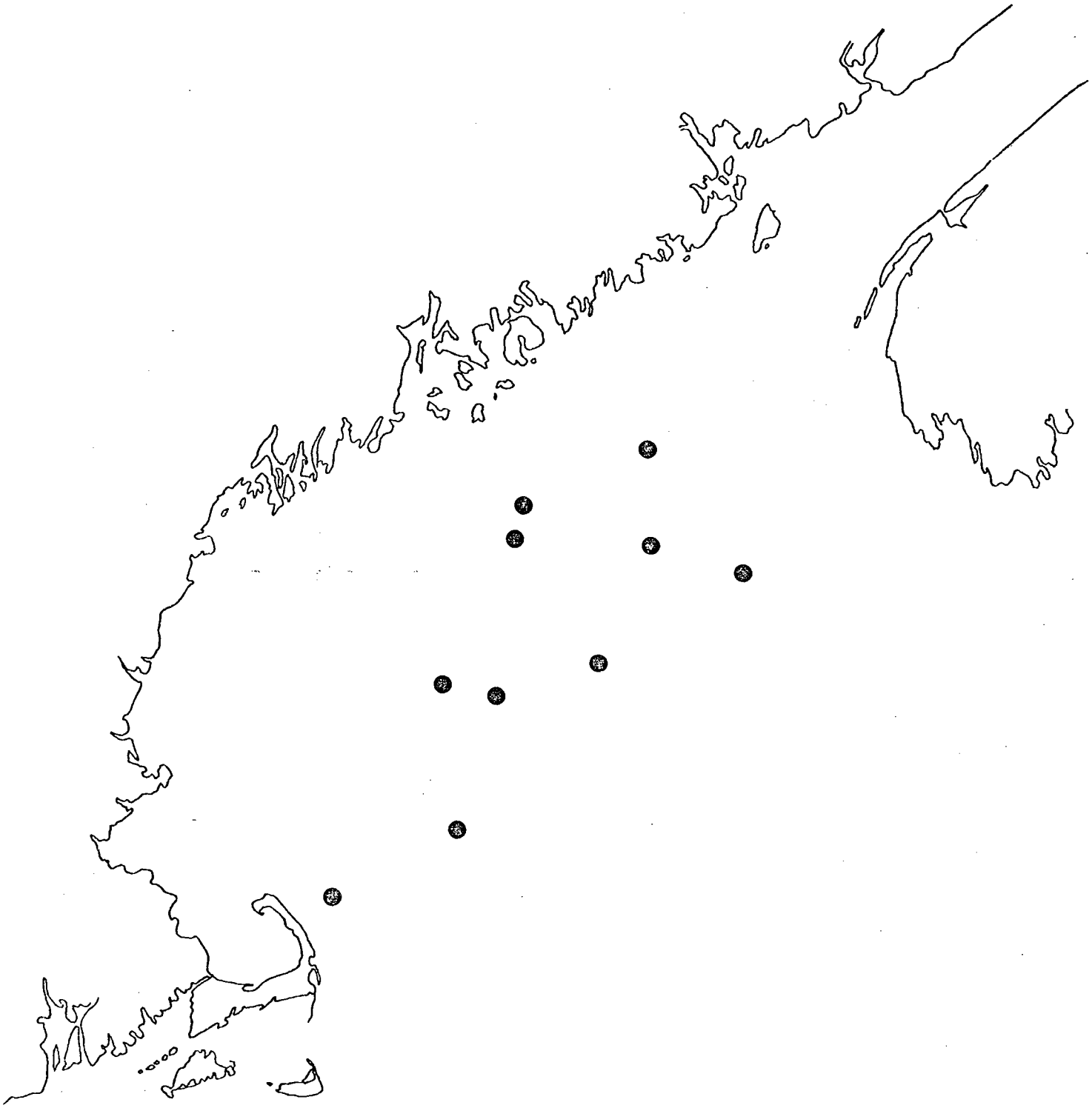
SIPHONOPHORE	PREDATOR	SOURCE
Nanomia bijuga	Cephalopyge trematoides	Sentz-Bracconot & Carré (1966)
Nanomia bijuga	nudibranch	station 302
Abyla sp., eudoxid	Ocyropsis maculata (50 mm)	station 303
Chelophyes appendiculata	Ocyropsis crystallina (40 mm)	station 284
Chelophyes appendiculata	Ocyropsis crystallina (40 mm)	station 347
Abylopsis eschscholtzi	leptomedusa	station 304
Physophora hydrostatica	Orchistoma sp.	L.P. Madin (communication)
Eudoxoides spiralis	polychaete	station 419
(physonect siphonophores)	Pterotrachea coronata	Hamner, et al. (1975)
Physalia physalis	Ianthina prolongata Lepas ansifera Glaucus atlanticus Fiona pinnata	Bieri (1966)

a large standing crop of Mnemiopsis ctenophores (see Miller and Williams, 1972). Mass aggregations of oceanic species have also been reported (Zelickman, 1969). I encountered a swarm of thousands of Nanomia bijuga off Fort Pierce, Florida (stations 286 - 288), coincident with a bloom of the salp Thalia democratica. Nanomia bijuga has been reported in enormous numbers off the coast of Ireland, and on one occasion there were large numbers of this species in an estuary of the English Channel (Berrill, 1930).

Apparently, large aggregations of a related species, N. cara, were present in October and November, 1975, in the Gulf of Maine. At some locations (Figure 14), colonies were so abundant that trawls set by the U.S. National Marine Fisheries Service and by commerical fishermen were littered with pieces of this species (F. Lux, personal communication). The cause of the aggregation of N. cara has not been determined. It is conceivable that widespread reproduction of N. cara occurred earlier in the fall and local patterns of circulation aided in concentrating and maintaining the aggregation. While siphonophores of the genus Nanomia are the only ones known to occur in aggregations of vast dimensions, orthokinetic modifications of the fishing-prey search cycle (page 26) could perhaps generate local aggregations of siphonophores with a patch size corresponding to that of their zooplankton prey.

In conclusion, siphonophores seem able to capture a wide variety of prey, despite differences in prey size and abundance.

Figure 14. Stations where aggregations of Nanomia cara were encountered by U.S. National Marine Fisheries Service bottom trawl survey in the Gulf of Maine, 7 October - 18 November, 1975.



Although standing stocks of siphonophores are low, high growth efficiency and 2 1/2 - 4 week generation times suggest that Agalma okeni and other epipelagic siphonophores are well adapted to oceanic life and probably function as important predators in most warm-water open-ocean areas of the world.

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Appendix 1. SCUBA stations, September 1973 - November 1975

Ship Code:

KN = KNORR

A2 = ATLANTIS-II

CH = CHAIN

GS = GOSNOLD

JO = JOHNSON

HB = Harbor Branch Foundation Laboratory motorboats

Date Code:

Year-Month-Day

BLUE WATER PLANKTON STATION LIST: THESIS

TABLE OF STATIONS

STATION	SHIP	CRUISE	LAT.	LONG.	DATE	COLLECT. TIME	SURF. SALIN.	SURF. TEMP.
BWP 259	KN	33	39 46N	69 51W	73* IX *14	1545*1630	•	•
BWP 260	KN	33	35 19N	63 43W	73* IX *16	1430*1457	•	•
BWP 261	KN	33	33 34N	62 16W	73* IX *17	1030*1104	•	•
BWP 262	KN	33	33 40N	6* 16W	73* IX *17	1415*1457	•	•
BWP 263	KN	33	33 21N	59 50W	73* IX *18	1430*1504	•	•
BWP 264	KN	33	32 21N	59 51W	73* IX *19	1201*1253	•	•
BWP 265	KN	33	32 35N	59 43W	73* IX *20	1000*1058	•	•
BWP 266	KN	33	32 20N	63 6W	73* IX *21	900* 950	•	•
BWP 267	KN	33	32 18N	63 0W	73* IX *21	1530*1620	•	•
BWP 268	KN	33	32 32N	59 48W	73* IX *23	1000*1055	•	•
BWP 269	HB	0	27 25N	80 0W	73* X *31	945*1115	•	27*4
BWP 270	HB	0	27 25N	80 0W	73* XI * 2	1030*1245	•	•
BWP 271	HB	0	27 12N	80 0W	73* XI * 3	0* 0	•	•
BWP 272	HB	0	27 25N	80 5W	73* XI * 6	1300*1320	•	•
BWP 273	GS	208	28 11N	78 49W	73* XI *14	928*1030	•	27*5
BWP 274	GS	208	28 7N	79 46W	73* XI *14	1355*1512	•	27*6
BWP 275	GS	208	27 44N	79 47W	73* XI *15	930*1012	•	•
BWP 276	GS	208	27 46N	79 44W	73* XI *15	1330*1445	•	•
BWP 277	GS	210	27 25N	79 52W	73* XI *26	1520*1630	•	27*2
BWP 278	GS	210	27 28N	79 45W	73* XI *27	1015*1110	•	27*4
BWP 279	GS	212	27 34N	79 49W	73*XII * 6	1249*1352	•	26*7
BWP 280	GS	212	27 40N	79 43W	73*XII * 6	1507*1614	•	26*5
BWP 281	GS	215	27 34N	79 40W	74* I * 7	1517*1631	•	26*0
BWP 282	GS	215	27 53N	78 8W	74* I * 8	1243*1347	•	26*0
BWP 283	GS	215	27 37N	79 8W	74* I * 9	1034*1107	•	25*6
BWP 284	GS	215	27 39N	79 29W	74* I * 9	1423*1534	•	25*6
BWP 285	GS	215	26 53N	79 42W	74* I *10	1043*1143	•	25*7
BWP 286	HB	0	27 25N	80 13W	74* V * 5	935*1130	•	•
BWP 287	HB	0	27 25N	80 10W	74* V * 9	0* 0	•	•
BWP 288	HB	0	27 24N	80 12W	74* V *10	1015*1100	•	•
BWP 289	HB	0	27 25N	80 13W	74* V *21	0* 0	•	•
BWP 290	HB	0	27 25N	80 13W	74* VI *11	955*1015	•	•
BWP 291	GS	238	27 25N	79 57W	74* VI *12	1430*1440	•	29*3
BWP 292	GS	238	27 17N	79 45W	74* VI *13	1006*1056	•	•
BWP 293	GS	238	27 23N	79 38W	74* VI *13	1410*1448	•	•
BWP 294	GS	238	27 34N	79 55W	74* VI *14	1220*1315	•	•
BWP 295	JN	0	26 45N	79 55W	74*VII *16	1405*1440	•	28*3
BWP 296	JN	0	26 45N	79 55W	74*VII *17	1110*1130	•	•
BWP 297	JN	0	26 45N	79 55W	74*VII *17	1547*1613	•	•
BWP 298	JN	0	26 45N	79 55W	74*VII *18	1131*1150	•	•
BWP 299	JN	0	26 45N	79 55W	74*VII *19	1058*1128	•	•
BWP 300	JN	0	26 45N	79 55W	74*VII *20	1130*1215	•	•
BWP 301	JN	0	26 45N	79 55W	74*VII *22	0* 0	•	•
BWP 302	JN	0	26 45N	79 55W	74*VII *23	1411*1432	•	•

BLUE WATER PLANKTON STATION LIST: THESIS

TABLE OF STATIONS

STATION	SHIP	CRUISE	LAT.	LONG.	DATE	COLLECT. TIME		SURF. SALIN.	SURF. TEMP.
BWP 303	A2	84	13 40N	62 21W	74-VIII- 8	1011-1051		34.57	27.6
BWP 304	A2	84	13 39N	65 55W	74-VIII- 9	956-1016		34.60	27.6
BWP 305	A2	84	15 13N	68 5W	74-VIII-10	1124-1146		34.71	28.3
BWP 306	A2	84	16 29N	67 45W	74-VIII-11	947-1022		36.00	28.5
BWP 307	A2	84	19 4N	67 45W	74-VIII-11	1544-1613		36.00	28.5
BWP 308	A2	84	20 38N	67 46W	74-VIII-12	1013-1049		36.33	28.5
BWP 309	A2	84	21 3N	67 44W	74-VIII-12	1549-1625		36.33	28.5
BWP 310	A2	84	23 1N	67 42W	74-VIII-13	1045-1122		36.34	28.5
BWP 311	A2	84	23 28N	67 42W	74-VIII-13	1510-1618		36.34	28.5
BWP 312	A2	84	28 31N	67 38W	74-VIII-15	1004-1034		36.08	28.8
BWP 313	A2	84	29 10N	67 41W	74-VIII-15	1510-1636		36.08	28.8
BWP 314	A2	84	31 40N	67 43W	74-VIII-16	1105-1145		36.26	28.8
BWP 315	A2	84	31 41N	67 43W	74-VIII-16	1515-1545		36.26	28.8
BWP 316	A2	84	31 42N	67 41W	74-VIII-16	2009-2103	*	36.26	28.8
BWP 317	A2	84	32 46N	67 48W	74-VIII-17	1034-1103		36.23	28.8
BWP 318	A2	84	33 54N	67 48W	74-VIII-17	2320-2359	*	36.23	28.8
BWP 319	A2	84	34 52N	68 30W	74-VIII-18	1000-1030		35.40	26.7
BWP 320	A2	84	36 37N	68 23W	74-VIII-20	1315-1430		35.93	27.4
BWP 321	A2	84	37 39N	70 52W	74-VIII-21	1400-1503		•	24.3
BWP 322	A2	85	31 8N	60 10W	74- IX -27	1615-1655		•	28.5
BWP 323	A2	85	30 39N	62 17W	74- IX -27	2010-2017	*	•	•
BWP 324	A2	85	26 30N	62 18W	74- IX -28	2038-2131	*	•	29.0
BWP 325	A2	85	25 29N	62 21W	74- IX -29	1044-1123		•	28.5
BWP 326	A2	85	25 16N	62 20W	74- X - 1	1552-1629		•	28.5
BWP 327	A2	85	25 16N	62 21W	74- X - 1	2035-2057	*	•	•
BWP 328	A2	85	25 16N	62 25W	74- X - 2	1507-1538		•	•
BWP 329	A2	85	25 27N	62 27W	74- X - 2	2000-2033	*	•	•
BWP 330	A2	85	25 31N	62 30W	74- X - 3	1555-1638		•	27.7
BWP 331	A2	85	29 37N	63 45W	74- X - 4	1645-1655		•	27.7
BWP 332	A2	85	30 32N	64 11W	74- X - 7	1516-1539		•	27.3
BWP 333	A2	86	18 59N	62 32W	75- I -30	1430-1505		35.38	25.3
BWP 334	A2	86	19 0N	60 48W	75- I -31	1323-1343		35.71	24.9
BWP 335	A2	86	18 58N	58 41W	75- II - 1	957-1024		35.71	24.7
BWP 336	A2	86	19 1N	56 16W	75- II - 2	1016-1033		36.69	24.7
BWP 337	A2	86	19 0N	55 50W	75- II - 2	1450-1516		36.69	24.7
BWP 338	A2	86	18 59N	53 47W	75- II - 3	1340-1407		37.05	24.5
BWP 339	A2	86	18 58N	52 28W	75- II - 4	1310-1350		36.65	24.4
BWP 340	A2	86	18 56N	52 9W	75- II - 4	1625-1733		37.05	24.5
BWP 341	A2	86	19 2N	50 1W	75- II - 5	1013-1046		36.52	24.4
BWP 342	A2	86	19 22N	50 0W	75- II - 5	1515-1555		•	•
BWP 343	A2	86	19 11N	51 22W	75- II - 6	1005-1035		36.86	24.3
BWP 344	A2	86	19 0N	51 48W	75- II - 6	1410-1441		36.26	23.1
BWP 345	A2	86	17 59N	54 15W	75- II - 7	1005-1044		35.38	25.2
BWP 346	A2	86	17 53N	54 53W	75- II - 7	1515-1554		34.71	24.9

* night dive

BLUE WATER PLANKTON STATION LIST: THESIS

TABLE OF STATIONS

STATION	SHIP	CRUISE	LAT.	LONG.	DATE	COLLECT. TIME	SURF. SALIN.	SURF. TEMP.
BWP 347	A2	86	16 11N	56 13W	75- II - 8	1005-1040	35.88	24.4
BWP 348	A2	86	16 12N	56 15W	75- II - 8	1439-1512	35.88	24.4
BWP 349	A2	86	15 17N	58 50W	75- II - 9	1040-1105	35.41	25.9
BWP 350	A2	86	15 17N	58 50W	75- II - 9	1425-1507	35.41	•
BWP 351	A2	86	15 22N	58 56W	75- II - 9	1945-2025 *	35.41	25.9
BWP 352	A2	86	14 44N	60 1W	75- II -10	1005-1045	35.79	25.5
BWP 353	A2	86	14 44N	60 1W	75- II -10	1415-1452	35.79	25.5
BWP 354	A2	86	12 9N	61 21W	75- II -11	1400-1433	35.68	25.5
BWP 355	CH	122	34 16N	10 47W	75- V -24	1503-1533	36.48	17.0
BWP 356	CH	122	32 41N	13 53W	75- V -25	934-1003	36.65	18.4
BWP 357	CH	122	30 33N	17 56W	75- V -26	921- 955	36.71	19.0
BWP 358	CH	122	30 20N	18 30W	75- V -26	1445-1515	•	19.7
BWP 359	CH	122	29 29N	21 42W	75- V -27	913- 930	37.00	20.0
BWP 360	CH	122	29 29N	22 27W	75- V -27	1450-1512	•	21.0
BWP 361	CH	122	29 30N	26 4W	75- V -28	927- 952	36.79	21.3
BWP 362	CH	122	29 33N	26 31W	75- V -28	1417-1432	•	22.1
BWP 363	CH	122	29 28N	30 13W	75- V -29	900- 921	36.74	21.8
BWP 364	CH	122	29 28N	30 13W	75- V -29	957-1030	36.74	21.8
BWP 365	CH	122	29 26N	30 37W	75- V -29	1443-1513	•	23.0
BWP 366	CH	122	29 28N	34 20W	75- V -30	910- 940	36.75	23.2
BWP 367	CH	122	29 31N	34 53W	75- V -30	1501-1530	•	23.6
BWP 368	CH	122	29 30N	38 26W	75- V -31	900- 940	36.83	23.2
BWP 369	CH	122	29 33N	39 0W	75- V -31	1542-1612	•	23.2
BWP 370	CH	122	29 29N	42 3W	75- VI - 1	910- 940	36.70	23.5
BWP 371	CH	122	29 31N	42 47W	75- VI - 1	1515-1547	•	23.0
BWP 372	CH	122	29 30N	46 22W	75- VI - 2	915- 945	36.83	23.4
BWP 373	CH	122	29 31N	46 50W	75- VI - 2	1415-1450	•	•
BWP 374	CH	122	29 28N	51 25W	75- VI - 3	1530-1605	36.74	23.8
BWP 375	CH	122	29 30N	54 30W	75- VI - 4	932-1002	36.86	24.0
BWP 376	CH	122	29 27N	55 4W	75- VI - 4	1430-1500	•	24.2
BWP 377	CH	122	29 30N	58 27W	75- VI - 5	845- 917	36.61	25.1
BWP 378	CH	122	29 30N	58 59W	75- VI - 5	1350-1420	•	24.5
BWP 379	CH	122	29 29N	59 9W	75- VI - 5	1615-1642	•	24.3
BWP 380	CH	122	30 38N	61 43W	75- VI - 6	855- 930	36.47	24.1
BWP 381	CH	122	31 1N	62 25W	75- VI - 6	1540-1610	•	24.0
BWP 382	CH	123	34 15N	66 21W	75- VI -13	933-1001	•	22.7
BWP 383	CH	123	34 16N	66 24W	75- VI -13	1447-1509	•	22.7
BWP 384	CH	123	33 52N	65 51W	75- VI -14	1432-1507	36.44	22.9
BWP 385	CH	123	33 54N	65 54W	75- VI -15	1130-1150	35.44	23.4
BWP 386	CH	123	37 19N	68 20W	75- VI -17	918- 953	36.52	26.8
BWP 387	CH	123	37 18N	68 26W	75- VI -17	1520-1535	36.52	27.0
BWP 388	CH	123	39 47N	70 11W	75- VI -18	1435-1505	35.93	21.3
BWP 389	CH	123	38 42N	70 12W	75- VI -19	900- 930	35.93	20.2
BWP 390	CH	123	39 23N	70 3W	75- VI -22	900- 924	35.98	20.7

*night dive

BLUE WATER PLANKTON STATION LIST: THESIS

TABLE OF STATIONS

STATION	SHIP	CRUISE	LAT.	LONG.	DATE	COLLECT. TIME	SURF. SALIN.	SURF. TEMP.
BWP 391	CH	123	39 40N	70 37W	75* VI *22	1650-1720	35.73	21.6
BWP 392	CH	123	39 40N	70 37W	75* VI *23	906- 930	35.59	21.2
BWP 393	CH	125	39 19N	70 15W	75*VII *31	1426-1453	•	24.7
BWP 394	CH	125	38 26N	69 57W	75*VIII- 1	1047-1122	•	23.6
BWP 395	CH	125	38 25N	69 58N	75*VIII- 1	1423-1448	•	23.8
BWP 396	CH	125	38 28N	70 0W	75*VIII- 2	1020-1050	•	23.8
BWP 397	CH	125	37 7N	68 55W	75*VIII- 4	1045-1110	•	26.2
BWP 398	CH	125	35 21N	68 18W	75*VIII- 5	1302-1332	•	26.6
BWP 399	CH	125	35 16N	69 58W	75*VIII- 6	1415-1450	•	26.0
BWP 400	CH	125	34 31N	69 54W	75*VIII- 8	1025-1050	•	25.4
BWP 401	CH	125	34 32N	69 51W	75*VIII- 8	1542-1913	•	25.4
BWP 402	CH	125	34 28N	69 57W	75*VIII-10	1113-1143	•	25.5
BWP 403	CH	125	34 30N	69 54W	75*VIII-10	1618-1653	•	25.5
BWP 404	CH	125	34 9N	71 33W	75*VIII-11	1052-1116	•	27.4
BWP 405	CH	125	34 11N	71 38W	75*VIII-11	1514-1549	•	27.4
BWP 406	CH	125	34 9N	71 37W	75*VIII-12	1109-1139	•	27.4
BWP 407	CH	125	34 8N	71 38W	75*VIII-12	1537-1618	•	27.4
BWP 408	CH	125	34 56N	71 13W	75*VIII-13	1537-1603	•	•
BWP 409	CH	125	37 22N	70 11W	75*VIII-14	1021-1043	•	•
BWP 410	CH	125	38 0N	70 3W	75*VIII-14	1530-1600	•	25.3
BWP 411	CH	125	38 10N	70 5W	75*VIII-15	1410-1430	•	25.2
BWP 412	CH	125	38 20N	70 5W	75*VIII-15	1022-1046	•	25.3
BWP 413	CH	125	39 5N	70 6W	75*VIII-16	1517-1542	•	24.8
BWP 414	CH	125	39 11N	70 11W	75*VIII-17	1115-1140	•	24.9
BWP 417	KN	53	35 32N	70 58W	75* XI *16	932-1002	•	24.4
BWP 418	KN	53	32 45N	71 11W	75* XI *17	1045-1120	36.46	23.8
BWP 419	KN	53	32 43N	71 9W	75* XI *18	1046-1116	36.60	23.8
BWP 420	KN	53	33 39N	71 3W	75* XI *19	1540-1605	36.30	23.1
BWP 421	KN	53	33 13N	72 17W	75* XI *20	840- 910	36.30	23.2
BWP 422	KN	53	33 55N	71 46W	75* XI *20	1533-1600	36.30	23.4
BWP 423	KN	53	33 49N	71 54W	75* XI *21	1230-1255	36.30	23.3
BWP 424	KN	53	33 55N	71 59W	75* XI *22	1530-1555	36.32	23.3
BWP 425	KN	53	34 1N	71 53W	75* XI *23	959-1029	36.40	23.1
BWP 426	KN	53	35 27N	71 34W	75* XI *25	1057-1127	•	22.7
BWP 427	KN	53	36 7N	67 10W	75* XI *26	1540-1600	35.50	25.5
BWP 428	KN	53	36 55N	67 44W	75* XI *27	945-1005	35.50	22.0
BWP 429	KN	53	36 55N	67 46W	75* XI *28	815- 840	35.60	13.6
BWP 430	KN	53	36 55N	67 59W	75* XI *28	1434-1459	35.30	21.2
BWP 431	KN	53	39 26N	67 17W	75* XI *29	935- 955	35.90	20.0

Appendix 2. Carbon monoxide composition of float gas in the siphonophores Rhizophysa filiformis, Bathyphysa sibogae, and Athorybia rosacea.

ABSTRACT: Carbon monoxide averaged 83% of the float gas in Cystonectae and Physonectae siphonophores collected by SCUBA divers in the Western North Atlantic Ocean. Concentrations of 80 - 90% CO are characteristic of non-pleustonic siphonophores.

Wittenberg (1958) announced that carbon monoxide (CO) comprised one to five per cent of the float gas in colonies of the surface-living siphonophore Physalia physalis (Suborder Cystonectae). More recent studies with freshly-collected colonies of P. physalis reported higher percentages of CO, though CO was variable and seldom made up more than 35% of the total float gas (e.g., Copeland, 1968). Pickwell and his colleagues (see Pickwell, 1970, for review) found higher concentrations of CO in float gas of siphonophores of the Suborder Physonectae. They reported that 80 - 90% of the float gas was CO in colonies of Nanomia bijuga collected in midwater trawls, and that less than four per cent of recently secreted gas was O_2 and CO_2.

I analyzed the float gas composition of 10 colonies of Rhizophysa filiformis and Bathyphysa sibogae (Suborder Cystonectae) and two colonies of Athorybia rosacea (Suborder Physonectae). Siphonophores were collected individually in jars by SCUBA divers in the Western North Atlantic Ocean on ATLANTIS-II Cruise 86, CHAIN Cruises 122 and 125, and KNORR Cruise 53. All analyses were carried out within one to two hours of collection. Gas was withdrawn by suction from the pneumatophore of living colonies into a syringe of acid-citrate solution. The bubble of gas was transferred into a Scholander 0.0284-cc Gas Analyzer, and carbon dioxide

and oxygen were analyzed sequentially by the microgasometric method of Scholander, et al. (1955). Carbon monoxide was absorbed with a solution of cuprous chloride in ammonium chloride (Wittenberg, 1960). Nitrogen was not assayed, but is part of the residual gas remaining after absorption of CO_2, O_2, and CO,

I found consistently high concentrations of CO in siphonophore float gas. In the twelve colonies I collected which had floats large enough to provide at least 2.6 mm^3 of gas for analysis, carbon monoxide averaged 83% of the float gas (Table A). The variable and low concentrations of CO reported in pleustonic species like Physalia physalis (whose large float remains above the air-sea interface) probably reflect diffusive exchanges with atmospheric gases.

References

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Wittenberg, J. B. 1960. The source of carbon monoxide in the float of the Portuguese Man-of-War, Physalia physalis L. J. Exp. Biol. 37: 698-705.

Table A. Composition of float gas in siphonophores collected by SCUBA divers in the Western North Atlantic Ocean.

Volume Analyzed (mm^3)	CO_2	O_2	CO	residual
Rhizophysa filiformis				
21.9	2%	3%	85%	10%
22.6	1%	3%	87%	9%
22.2	2%	3%	86%	9%
4.4	-	7%	83%	10%
9.5	1%	7%	78%	14%
7.1	2%	2%	86%	10%
8.5	-	8%	72%	20%
			mean: 82%	
Bathyphysa sibogae				
2.6	-	5%	84%	11%
4.5	-	6%	85%	9%
3.8	-	4%	89%	7%
Athorybia rosacea				
2.8	-	5%	85%	10%
3.1	-	5%	79%	16%
			grand mean: 83%	

Appendix 3. The siphonophore Bathyphysa sibogae Lens and van Riemsdijk, 1908 in the Sargasso Sea, with notes on its natural history.

THE SIPHONOPHORE *BATHYPHYSA SIBOGAE* LENS AND VAN RIEMSDIJK, 1908, IN THE SARGASSO SEA, WITH NOTES ON ITS NATURAL HISTORY

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THE SIPHONOPHORE *BATHYPHYSA SIBOGAE* LENS AND VAN RIEMSDIJK, 1908, IN THE SARGASSO SEA, WITH NOTES ON ITS NATURAL HISTORY

D. C. Biggs and G. R. Harbison

ABSTRACT

Eleven specimens of *Bathyphysa sibogae* Lens and van Riemsdijk, 1908 (Siphonophorae: Cystonectae) were collected by SCUBA divers in the upper 30 m of the Sargasso Sea. The appearance and behavior of the living animal are described for the first time. The larger gastrozooids are attached to the stem by pedicles, and their tentacles have tricornate tentilla. The hyperiid amphipod, *Schizoscelus ornatus* Claus, 1879 seems to be preferentially associated with this siphonophore.

Bathyphysa sibogae Lens and van Riemsdijk, 1908 (Siphonophorae: Cystonectae) is known only from two specimens found in preserved collections of the SIBOGA Expedition (Lens and van Riemsdijk, 1908). Both came from trawls to 2080 m deep near the Celebes Islands. This paper reports the occurrence of *B. sibogae* in the Western North Atlantic Ocean.

We observed and collected 11 specimens of *B. sibogae* while SCUBA diving in the upper 30 m of the western Sargasso Sea during R/V ATLANTIS-II Cruises 84 and 85 (Table 1). Since this siphonophore is considered a rare species, we will describe its morphology and provide some information on aspects of its natural history.

Description of the Species

The most prominent features of a colony of *B. sibogae* are the pneumatophore (apical gas-filled float) and series of gastrozooids (feeding polyps) which are arranged along one side of the highly contractile stem (Fig. 1). The living colony appears colorless except for a cap of red-violet pigment around the apical pore of the pneumatophore. The pneumatophore is bluntly fusiform in shape and while alive measured 4.0×1.0 mm. Small hypocystic villae are located at the base of the reflective gas-filled pneumatosaccus. The small gastrozooids are transparent, while large gastrozooids have opaque patches of nematocysts in the ectoderm.

Several forms of gastrozooids occur along the stem. Gastrozooids closest to the apical float are flattened dorso-ventrally and have ptera (lateral aliform ridges which distinguish the genus *Bathyphysa* from *Rhizophysa*). Gastrozooids #18-22 also have ptera, but each has a small basal tentacle bud as well. The tentacle is more pronounced in gastrozooids #23-25, and ptera are absent. Gastrozooids #23-25 are each attached to the stem by pedicles.

The specimens we observed and collected are much smaller than the two described by Lens and van Riemsdijk (1908). In 4% formalin buffered with sodium borate, the colony illustrated in Figure 1 is only 25 mm long. The remainder of the stem (not illustrated in Fig. 1) is complexly contracted and has six gastrozooids with well-developed tentacles and pedicles. The largest gastrozooids are 5-10 mm long and are attached to the stem by pedicles 3 mm long (Fig. 2). Each of these large gastrozooids has a tentacle with 35-40 tentilla. The tentacles produce a sharp stinging sensation when touched. The largest tentilla (those most distal) are segmented and measure about 0.1 mm in diameter. They are faint pink in color and each ends in a swelling 0.2-0.3 mm long with two lateral projections (Fig. 3). A smaller terminal projection represents the developing central filament (Lens and van Riemsdijk, 1908, Fig. 164).

Gonodendra are located midway along the

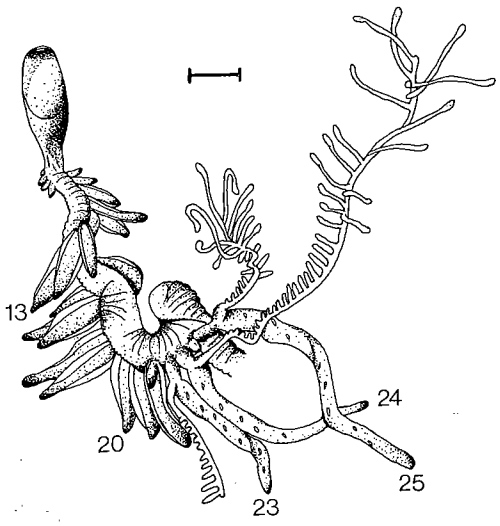

Figure 1. Upper part of a colony of *Bathyphysa sibogae* from the Sargasso Sea, showing the pneumatophore at the apical end of the colony, the first 25 gastrozooids and the tentacles of gastrozooids 23, 24, and 25. Gastrozooids 13, 20, 23, 24, and 25 are numbered in the figure. Pedicles are visible at the bases of gastrozooids 23, 24, and 25. Scale line 1 mm.

stem between two gastrozooids and their early developmental stages closely resemble those of *B. conifera* (Leloup, 1936, Fig. 6). The largest gonodendrum from the animals we collected measured 1.3 × 0.8 mm (including gonostyle) and bore 14 colorless lateral buds. Each bud was a grapelike swelling which measured about 0.3 × 0.1 mm (Fig. 4). The lack of differentiation of the gonophore buds and the small size of the animals we collected both suggest that all were juvenile, sexually-immature colonies.

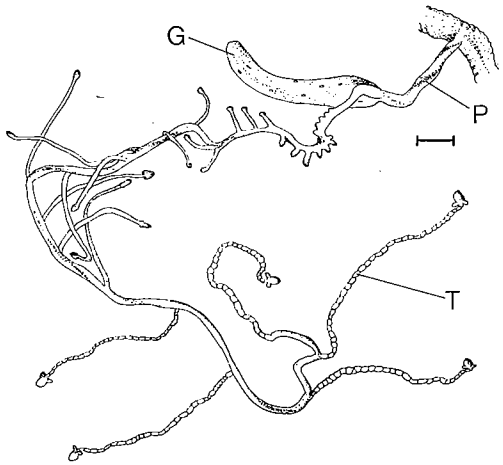

Figure 2. Older gastrozooid (G) of *Bathyphysa sibogae*, showing pedicle (P) and form of the tentilla (T). Scale line 1 mm.

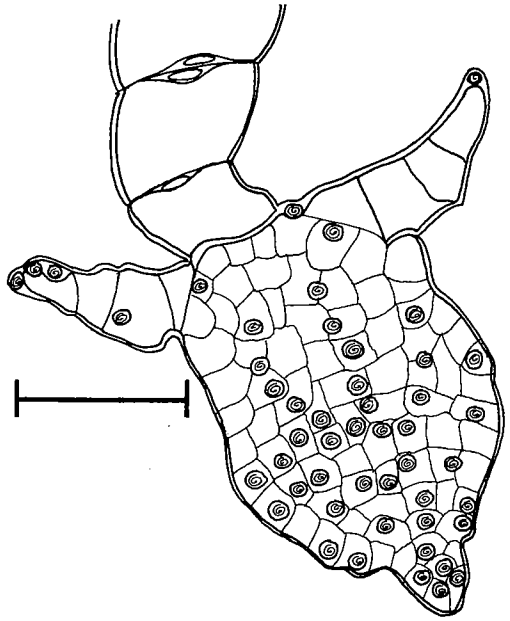

Figure 3. Tentillum of *Bathyphysa sibogae*, showing the arrangement of the nematocysts. Scale line 0.1 mm.

Notes on the Natural History of *B. SIBOGAE*

An undisturbed living colony of *B. sibogae* hangs vertically in the water with the stem often extending more than 300 mm below the pneumatophore. In this fishing posture, the longer tentacles may trail an additional 60 mm and the pedicles may extend up to 10-15 mm in length. The colony can contract to about one-tenth of its extended length through a series of longitudinal contractions of stem and tentacles which cause the stem to spiral dextrally.

Bathyphysa sibogae does not swim by contraction of the ptera of younger gastro-

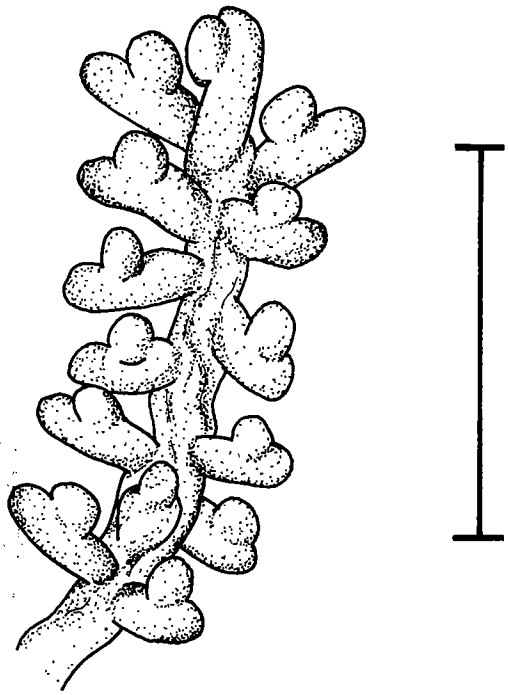

Figure 4. Developing gonodendrum of *Bathyphysa sibogae*. Scale line 1 mm.

zooids, as suggested by Lens and van Riemsdijk (1908). It can only writhe about in the water by repeated contraction and relaxation of the stem as does *Rhizophysa filiformis* Forskal, 1775 (Totton, 1965). Gastrozooids with ptera are no more prehensile than the larger, tentaculate gastrozooids, which is contrary to Fewkes' (1884) suggestion. Our observations of living colonies of *B. sibogae* suggest that the ptera may function primarily to retard the sinking of the colony. In colonies of *B. sibogae* extending in fishing posture, the smaller gastrozooids are oriented at right angles to the stem.

The hyperiid amphipod, *Schizoscelus ornatus* Claus, 1879 seems to be preferentially associated with *B. sibogae* (Table 1). Of the eleven colonies of *B. sibogae* we collected, five had *S. ornatus* associated with them, and one had a mature *Thyropus edwardsii* (Claus, 1879). The rest had no amphipods. We have collected *S. ornatus* only with *B. sibogae*, while we have found *T. edwardsii* with other species of siphonophores.

Table 1. Stations where *Bathyphysa sibogae* was collected

Date	Time	Position	Surface Temp.	Numbers of *B. sibogae*	Number and Kind of Associated Amphipods
15 August 1974	1000	28°31′N, 67°38′W	28.8°C	1	1 *Schizoscelus ornatus* (4.3 mm female)
				3	no amphipods
	1540	29°10′N, 67°41′W	28.8°C	1	1 *Schizoscelus ornatus* (5.4 mm mature female)
				1	1 *Schizoscelus ornatus* (4.7 mm female)
16 August 1974	1100	31°40′N, 67°43′W	28.8°C	1	1 *Thyropus edwardsii* (6.2 mm mature male)
	1515	31°41′N, 67°43′W	28.8°C	1	4 *Schizoscelus ornatus* (4.3 mm mature male) (3.5 mm male) (3.4 mm male) (4.4 mm female)
				1	no amphipods
3 October 1974	1600	28°31′N, 62°30′W	27.7°C	1	no amphipods
4 October 1974	1700	29°37′N, 63°45′W	27.7°C	1	1 *Schizoscelus ornatus* (3.5 mm female)

Our field and aquarium observations indicate that *S. ornatus* moves about freely on the pneumatophore and the smaller gastrozooids but avoids the gastrozooids with tentacles. If the amphipod's freedom of movement is restricted, as when it is enclosed in a jar with its host, it can be captured and quickly ingested.

Discussion

Both of Lens and van Riemsdijk's type specimens of *B. sibogae* were badly fragmented. The smaller of the two apparently had no gastrozooids with mature tentilla (Lens and van Riemsdijk, 1908, Fig. 148), suggesting that it may have been the apical part of a much larger colony. Only two gastrozooids with tentacles remained on the stem of the second, but these seemed to be attached by long filamentous pedicles (Lens and van Riemsdijk, 1908, Fig. 160).

Leloup (1936) was unable to discern the presence of pedicles when he reexamined the type material. He published a figure of an isolated gastrozooid from *B. sibogae* and identified the basal filament as a tentacle (Leloup, 1936, Fig. 9). Accordingly, Leloup abandoned previous classification schemes based on the presence or absence of pedicles and grouped all previously described Cystonectae material with ptera and simple tentacles as *Bathyphysa conifera* (Leloup, 1936). Leloup retained *B. sibogae* as a second distinct species because it had tentilla.

Our specimens clearly have pedicles, and suggest that Leloup's synonomy may not be appropriate. If other species of *Bathyphysa* exist (e.g., *B. abyssorum* Studer, 1878; *B. japonica* Kawamura, 1954), *B. sibogae* may be distinguished by two anatomical features: (1) The tentacles have tentilla (terminating in an ampulla and two lateral filaments); (2) Pedicles are present at the basal end of the larger gastrozooids.

The different morphological forms of gastrozooids which occur sequentially along the stem of *B. sibogae* probably represent stages in gastrozooid development. During growth of Cystonectae siphonophores, gastrozooids produced in the budding region at the base of the pneumatophore become progressively situated towards the posterior part of the stem. Gastrozooids with ptera are found adjacent to this budding zone. These are probably juvenile gastrozooids unable to capture and ingest prey. Later, they develop by differential growth into the larger pediculate, tentaculate gastrozooids. Gastrozooids #18-23 (Fig. 1) represent stages in this transformation process. Shortly after the formation of a tentacle bud (gastrozooids #18-22), the basal region of the gastrozooid seems to elongate and differentiate into the pedicle. The ptera disappear and simultaneously the tentacle and pedicle become well-developed (gastrozooids #23-25).

Siphonophores of the genus *Bathyphysa* have been considered to be deep-living organisms, since most specimens collected came from deep trawls or were removed from hydrowire or cable being retrieved from casts deeper than 1000 m (Leloup, 1936; Totton, 1965). Records of *B. conifera* from the Atlantic Ocean have a distributional range extending from at least 47°53′N to 24°24′S (Leloup, 1936). *Bathyphysa* has also been collected from the equatorial Pacific Ocean (Lens and van Riemsdijk, 1908) and off the east coast of Japan (Kawamura, 1954). However, many specimens of each of the three other genera of Cystonectae siphonophores (Totton, 1965) have been obtained from surface tows. Both *Physalia* and *Epibulia* float on the surface (Alvarino, 1972), while *Rhizophysa* is frequently present in the epipelagic zone (Bigelow and Sears, 1937; Pugh, 1974).

The fact that we have collected 11 specimens of *B. sibogae* implies that this species is not rare and may even be abundant in the upper water layers. Though it is difficult to understand why *B. sibogae* has not been reported since its original description, it is perhaps significant that all Cystonectae siphonophores of the Family Rhizophysidae adhere to fabric. Since they are delicate and easily fragmented as well, most specimens

captured in plankton nets probably never reach the cod-end in recognizable condition.

The specimen of *B. sibogae* described in this paper has been placed in the Museum of Comparative Zoology at Harvard University.

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