With best wishes,
Doug

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Field Studies of Fishing, Feeding, and Digestion in Siphonophores†

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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. The fishing posture of a siphonophore is determined by its flotation and by the contractility of its stem; fishing postures can be similar in siphonophores which are unrelated generically. Tentacle length in colonies with 2–3 mg body protein can total 4.5 meters. Variations in the morphology of tentacles 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. By extrapolating from laboratory feeding experiments with small siphonophores it is suggested that colonies with 50–150 feeding polyps could eat several hundred individuals within minutes if they encountered aggregations of small zooplankton.

INTRODUCTION

Siphonophores are a group of planktonic coelenterates which occur throughout open-ocean regions of the world. These colonial hydrozoans commonly have 5–150 feeding polyps, each armed with a contractile fishing tentacle bearing batteries of nematocysts. Siphonophores like *Nanomia cara* with a colony length of 11 cm can have a total tentacle length of 5.4 m (Mackie and Boag, 1963), while individual tentacles of others, like *Physalia physalis*, can extend over 6 m (Wilson, 1947).

Carnivores like these, with several meters of branched, stinging tentacles, are probably important predators in oceanic ecosystems. Because they are quite

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fragile and fragment when captured in nets, however, little is known about their diet or feeding biology. To study their fishing and feeding behavior with minimum disturbance, I observed siphonophores *in situ* while SCUBA diving in the open-ocean. This paper will present some morphological bases for siphonophore fishing behavior and will speculate on their impact as predators upon different size classes of zooplankton.

METHODS†

During 1973–75, I and others at the Woods Hole Oceanographic Institution made 171 SCUBA dives in the upper 30 m of the western North Atlantic Ocean to study gelatinous zooplankton. We followed the procedures for open-ocean diving described by Hamner (1975). Each diver was connected by a pulley-operated 10-m tether line to a plumb line drifting beneath a motorized rubber raft. The raft was launched from an oceanographic research vessel, which kept in radio contact. Most dives were made during the day, when visibility often exceeded 30 m. Surface temperatures ranged from 17–29°C.

Siphonophores, like most non-visual gelatinous zooplankton, seemed undisturbed by divers unless in close contact. Dimensions and configurations of their fishing tentacles were estimated from underwater photographs of colonies relaxed in fishing posture taken by a 35 mm Nikonos camera fitted with a 1:3 extension tube and synchronized with electronic flash.

Swimming 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 (e.g., Hamner, 1975). After measuring swimming speeds in undisturbed colonies, I estimated their escape speeds by gentle prodding of the stem or tentacles.

Siphonophores collected with swollen feeding polyps were dissected. Frequently, portions of large prey had been digested or lost, and most were too fragmented to be identified to species (see Table III). 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^{-1}. After they had captured a number of nauplii, the siphonophores were transferred to finger bowls of clean water. The nauplii had been fed on a suspension of carmine particles and had red guts. Since feeding polyps and stem are transparent, the carmine content of a colony could be observed to follow the time course of digestion. Feeding rates at high densities of prey were estimated by adding 100 *Artemia* nauplii liter^{-1} and

†See Totton (1965) for taxonomic authorities.

counting the number ingested by a single feeding polyp in a ten-minute period.

OBSERVATIONS

The fishing cycle

Feeding behavior of siphonophores of the Suborders Calycophorae and Physonectae can be partitioned into a fishing phase and a swimming phase. While fishing, these siphonophores floated motionless in the water with stem and tentacles relaxed. If no prey encountered their tentacles or when the fishing configuration compacted by sinking of the colony, they contracted and withdrew tentacles and stem to become streamlined. Simultaneously, they began swimming and then moved to an adjacent place to relax their fishing networks.

An active calycophore like *Chelophyes appendiculata* repeated the fishing 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 relaxed. During the swimming interval, siphonophores swam 1–16 cm sec^{-1} (Table I). *Chelophyes appendiculata* and *Sulculeolaria monoica* used only their anterior nectophore to propel them between settings of the tentacles, while *Diphyes dispar* used only the posterior nectophore. Physonectae, unless escaping capture, swam by asynchronous contractions of their nectophores.

Several siphonophores modified their swimming behavior when provided with *Artemia* nauplii in the laboratory. For example, *S. monoica*, *Stephanophyes superba*, and *Rosacea cymbiformis* swam for shorter times and remained

TABLE I

Approximate swimming speeds (cm sec^{-1}) of siphonophores, measured *in situ* by SCUBA divers

Species	Number measured	Undisturbed swimming speed	Escape speed
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

relaxed in fishing posture 2–3 times longer between swimming periods. Such orthokinetic behavior (Fraenkel and Gunn, 1940), if not a laboratory artifact, should allow siphonophores to remain among aggregations of prey.

Fishing postures

The fishing posture of a siphonophore is determined by its flotation and by the contractility of its stem. Fishing postures can be similar in siphonophores which are unrelated generically and most fall into four broad groups.

The first group has short, noncontractile stems and tentacles that are long in relation to colony length. These are Physonectae like *Athorybia rosacea*, *Physophora hydrostatica*, and *Agalma okeni*. The buoyant pneumatophore (gas float) of *A. rosacea* and *P. hydrostatica* kept these species upright, so the tentacles hung directly downward (Figure 1). Both species have short, curvilinear stems, 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*, so its slight lift did not constrain colonies to orient vertically. Colonies of *A. okeni* were usually inclined 15–40° from the vertical, and the inclined posture allowed tentacles to extend without entanglement (Figure 2A). Since the stem of *A. okeni* was linear and noncontractile, its tentacles hung coplanar. However, by alternate contraction of its biserial rows of swimming bells, *A. okeni* could rotate about the axis created by its stem and allow drag to extend its tentacles in a radial configuration (Figure 2B). Since

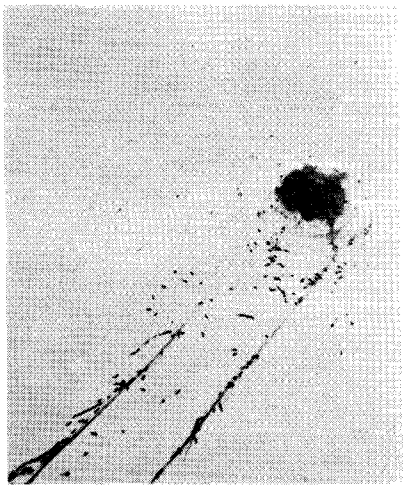

FIGURE 1 *Athorybia rosacea*, a physonect siphonophore with a non-contractile, curvilinear stem. The long tentacles extend directly below the colony to enclose a cylinder of water. Photographed *in situ*.

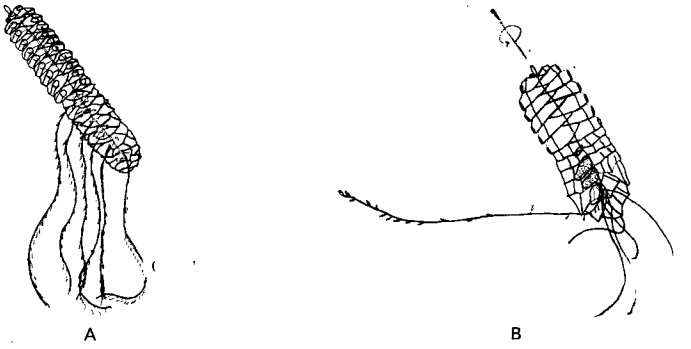

FIGURE 2 *Agalma okeni*, a physonect siphonophore with a non-contractile, linear stem. (A) Colony is inclined, which allows the tentacles to extend ventrally without entanglement. Redrawn from Chun (1897). (B) After counterclockwise rotation, which allowed tentacles to extend centripetally. Five unbranched palpon tentacles are visible. Drawn from an *in situ* photograph.

A. okeni did not rotate while swimming between fishing sites, rotation probably represents fishing behavior modified to allow the tentacles to cover a maximum volume of water.

The second group of siphonophores has longer, flexible stems which are somewhat contractile. This group includes both Physonectae, like *Agalma elegans*, and Calycophorae, like *Stephanophyes superba*. The stem of *A. elegans* has a large surface area of long, thin bracts which are neutrally buoyant; it is often supported in arcs (Figure 3). The tentacles, when relaxed, hang ventrally from the arched stem and lie in more than a single plane. Each of the 10–24 stem groups of *S. superba* has both a gelatinous bract and a nectophore; *in situ* the surface area of these gelatinous individuals frequently supported the flexible stem in a horizontal arc. The tentacles, when relaxed, hung downward to enclose a shallow cylinder of water (Figure 4).

The third group of siphonophores has stems which are quite long and contractile. This includes Cystonectae of the Family Rhizophysidae, as well as Calycophorae like species of *Rosacea*, *Sulculeolaria*, *Chelophyes*, 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 III), and local turbulence drifted the delicate, thread-like tentacles in all directions.

Rosacea cymbiformis fished extended in "long-line" posture (Figure 5). Intermittant contractions and subsequent relaxations of individual tentacles did not cause the expanded stem to contract, though if I contacted several

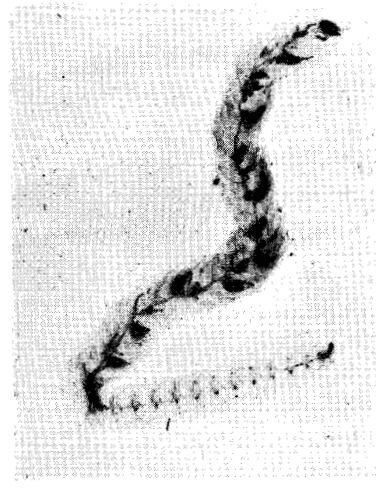

FIGURE 3 *Agalma elegans*, a physonect siphonophore with a flexible stem. The stem has drifted to lie in arcs above the nectosome. Photographed in an aquarium by L. P. Madin.

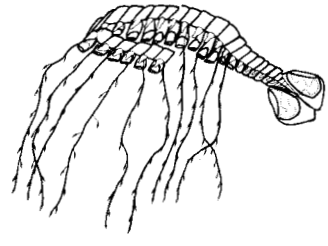

FIGURE 4 *Stephanophyes superba*, a calycophore siphonophore with a flexible stem. The stem lies in a horizontal arc, which allows tentacles to surround a cylinder of water. Drawn from an *in situ* photograph.

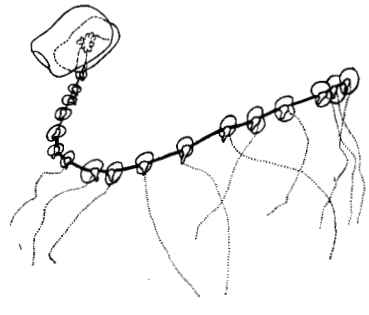

FIGURE 5 *Rosacea cymbiformis*, a calycophore siphonophore with a contractile stem. The stem is partially relaxed in a "long-line" configuration. Drawn from an *in situ* photograph.

TABLE II

Approximate dimensions of stem, tentacles, and lateral branches of tentacles (tentilla) of siphonophores relaxed 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	*Rosac_a 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

tentacles simultaneously colonies frequently "crumpled" by synchronous contractions of stem and tentacles.

Sulculeolaria monoica and *S. quadrivalvis* set their tentacles in a "veronica" movement (named after the bull fighter's 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 the relaxing, then elongating posterior appendages caused the anterior part of the stem to arch round in a series of spirals. The relaxed tentacles then spread centripetally from the stem, which remained as a helix of 2–3 turns (Figure 6). Colonies of *S. quadrivalvis* had even longer stems which came to rest in less regular arcs (Figure 7).

The fourth group is composed of Physonectae of the genus *Forskalia*. Feeding polyps of *F. edwardsi* and *F. tholoides*, rather than arranged linearly along the stem, extended from it on long pedicles like spokes of a wheel (Figure 8). 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 had 5 feeding polyps. Each of the tentacles had about 32 lateral branches. In a relaxed tentacle, these were spaced at 10-mm intervals (Table II), and combined the 5 tentacles extended

1.6 meters. The lateral branches, each 4-mm long, combined added another 0.6 m, to total 2.2 m of fishing line per colony. In addition, each palpon had a fine, thread-like tentacle.

By comparison, a siphonophore like *F. edwardsi* or *F. tholoides* with 15 feeding polyps had 15 tentacles, each with an average of 15 lateral branches

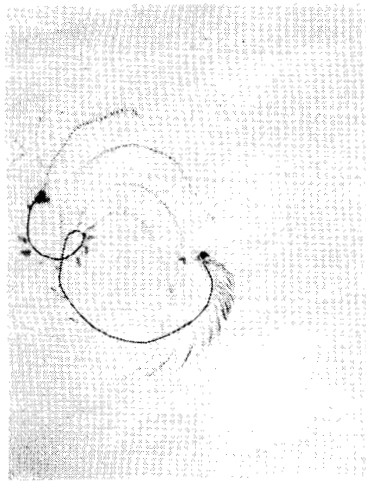

FIGURE 6 *Sulculeolaria monoica*, a calycophore siphonophore with a contractile stem. Photographed *in situ*, showing helical configuration of the stem.

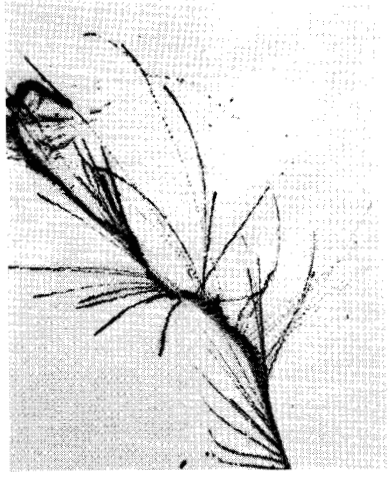

FIGURE 7 *Sulculeolaria quadrivalvis*, a long-stem relative of *S. monoica* (Figure 6). Photographed *in situ* immediately after relaxing stem and tentacles in fishing posture.

FIGURE 8 *Forskalia edwardsi*, a physonect siphonophore with feeding polyps attached to the stem on pedicles. Tentacles extend radially. Photographed *in situ* by L. P. Madin.

(Table II). When partially-relaxed, the lateral branches were spaced at 5-mm intervals and combined the tentacles extended 1.1 m. The lateral branches, with terminal filaments 15-mm long (Table II), combined added about 3.4 m to total 4.5 m of fishing line per colony. Although the biomass of a colony of *Forskalia* with 15 feeding polyps is about 2–3 mg protein, which is half that of a colony of *A. okeni* with 28 nectophores and 5 feeding polyps, its length of fishing line is over two times longer.

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

Types of prey captured by siphonophores

Siphonophores have enormous 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" apparatus to erupt when

TABLE III

Prey removed from feeding polyps of siphonophores

Siphonophore	Prey
Suborder Calycophorae	
Rosacea cymbiformis	copepods (*Corycaeus*, *Candacia* spp.), gastropod veliger
Sulculeolaria monoica	copepods (*Candacia* sp.)
Stephanophyes superba	euphausiids (7–10 mm overall length), copepods (*Candacia* sp.)
Suborder Physonectae, Group 1 (tentilla with a single terminal filament)	
Nanomia bijuga	mysid (17 mm overall length)
Forskalia edwardsi; F. tholoides	stomatopod larvae, small fish (6–7 mm overall length), hyperiid amphipods (*Anchylomera blossevillei*, *Hemityphis rapax*), copepods (*Candacia* sp.), polychaetes, atlantid heteropod (2 mm shell diameter)
Suborder Physonectae, Group 2 (tentilla with paired terminal filaments and a median ampoulla)	
Agalma okeni; A. elegans	hyperiid amphipods (*Parathemisto* sp.), megalops larvae
Athorybia rosacea	small fish (6–9 mm overall length), sergestid (*Lucifer typis*), hyperiid amphipods, copepods (*Candacia*, *Corycaeus* spp.), polychaetes
Suborder Cystonectae	
Rhizophysa filiformis	small fish (5–10 mm overall length) alcyopid polychaetes

stretched and bring hundreds of nematocysts instantly to bear on prey (see Korotneff, 1884; Chun, 1897). 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^{-1} in the laboratory, although they ate larger prey as well (Table III). A colony of *C. cordiformis* with three fishing polyps captured and ingested 30 *Artemia* nauplii within 10 minutes; one polyp in this colony ingested 13 nauplii.

The long terminal filaments of *F. edwardsi* and *F. tholoides* were "sticky" and 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 *S. 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 of nematocysts to erupt.

Tentilla of *Agalma okeni*, *A. elegans*, *A. clausi*, and *Athorybia rosacea* are completely encapsulated in an involucrum and terminate in a pair of filaments and a bulbous ampoulla. Unlike species of *Forskalia*, the terminal filaments of species of *Agalma* and *A. rosacea* had to be stretched several millimeters before the tentillar nematocyst battery erupted; tentillar batteries never discharged in collecting jars. Though colonies of *A. okeni* and *A. elegans* captured copepods (*Acartia* sp. and *Pleuromamma* sp.) and shrimp (*Leander* sp.) in the laboratory, their tentillar batteries were not used in feeding. In the field, species of *Agalma* and *A. rosacea* ate zooplankton ranging in size from copepods to sergestids, as well as small fish (Table III). In surface waters, it is highly likely that *A. okeni* feeds mostly at night, as tentacles were contracted in 93 of 114 colonies observed *in situ* during the day but were extended in all seven colonies observed at night.

Artemia nauplii were eaten by pre-reproductive colonies of *A. okeni*, but apparently they are too small to be sensed as prey by *A. rosacea* or by large colonies of *A. okeni* and *A. elegans*, even in the dark at densities of 100 nauplii liter^{-1}. In the laboratory, 14 of 20 colonies of *A. okeni*, *A. elegans*, and *A. rosacea* did not ingest any nauplii in 150 minutes; five ingested three or less, and one colony of *A. okeni* ingested four nauplii. Although nauplii were struggling on them, most tentacles did not contract to allow feeding polyps to eat the trapped nauplii.

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

Laboratory studies of digestion

A small colony of *A. okeni* which captured four carmine-dyed *Artemia* nauplii egested the carmine and unassimilated fraction within 2–3 hours at 24–26°C. Most other species required similar times for digestion of nauplii, though *R. cymbiformis* sometimes required 8–24 hours before egestion was complete. Digestion of larger prey required more time. Three colonies of *A. okeni* which had captured megalops larvae waited 7–18 hours before they disgorged the undigested remains, and their feeding polyps were swollen for 18–48 hours.

Several feeding polyps commonly assist in the digestion of large prey. For example, a colony of *R. filiformis* with 18 polyps ate a 30-mm fish (*Fundulus* sp.) in the laboratory. Initially, one polyp 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 polyps then encountered the fish and everted to cover an additional 20% of its surface. 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 digested; its caudal surfaces were eroded and mucus-covered.

When prey were small enough to be ingested entirely within a single polyp, 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 mucus and exoskeleton.

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 the 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.

A swimming interval which lasted about ten seconds and swimming speeds which averaged less than 16 cm sec^{-1} (Table I) 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 capture as rapidly 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* (overall length of both nectophores 50–60 mm) swim so weakly that they rarely exceed speeds of 3–5 cm sec^{-1} (Table I).

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 stems 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^{-1} (Table I). A cold-water congener, *N. cara*, moved off in laboratory aquaria at 20–30 cm sec^{-1} 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^{-1} (Berrill, 1930; Mackie, 1964). These latter velocities should be 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 the siphonophores that I observed in the laboratory, have some of the highest rates of respiration and excretion (Biggs, 1977). Conversely, *R. cymbiformis*, which required the longest time to digest *Artemia* nauplii, has a very low rate of respiration and excretion (Biggs, 1977). Mackie and Boag (1963) reported that *N. cara* egested carmine particles 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 polyp immediately upon digestion of the outer surfaces. While I did not encounter *N. cara* in the tropical and subtropical North Atlantic Ocean, I expect that this species would require longer than 25 minutes to digest live 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. copepods 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 until their 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 can ingest 13 or more small zooplankton in ten minutes, a single colony feeding at high densities of microzooplankton should be able to rapidly graze several hundred individuals.

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