Dietary Composition and Diel Feeding Patterns of Epipelagic Siphonophores

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Abstract

Prey consumption patterns are described for 24 species of epipelagic siphonophores studied during 1977–1980 in the Gulf of California, off Southern California, in the Sargasso Sea, and in Friday Harbor, Washington. Of the species, 7 were studied by day and at night, 15 were studied only by day, and 2 were studied only at night. Each of the 3 suborders of siphonophores had a characteristic diet. Siphonophores in the suborder Cystonectae, which had large gastrozooids, fed primarily on fish larvae. Species in the suborder Physonectae, which generally had few, large gastrozooids, consumed some small copepods, but consumed mainly large copepods and a variety of large, non-copepod prey. Species in the suborder Calycophorae, which generally had many small gastrozooids, fed mainly on small copepods, and also on other small prey organisms. The maximum size of prey tended to be correlated with gastrozooid length for all the siphonophores studied. For a given siphonophore species, the number of ingested prey was greatest at localities where prey organisms were most abundant in the surrounding seawater. For siphonophore species collected both day and night, there was a tendency for more prey to be consumed at night. Behavioral observations in the laboratory indicated that of 7 siphonophore species tested, 2 fed only in the light, and another fed only in the dark.

Introduction

Few studies have examined natural predation by gelatinous marine zooplankton. Qualitative information exists for oceanic ctenophores (Harbison et al., 1978, in situ and laboratory observations), scyphomedusae (Larson, 1978, gut contents), and siphonophores (Biggs, 1977, gut con-

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tents). Quantitative analyses of natural diet composition have been made for several species of the chaetognath genus Sagitta (e.g. Pearre, 1973, 1974; Szyper, 1978; Feigenbaum, 1979), for ctenophores in the genus Pleurobrachia (Anderson, 1974, P. pileus; Hirota, 1974, P. bachei), for heteropods (Seapy, 1980, Carinaria cristata), for surface-dwelling chondrophores (Bieri, 1961, Velella lata; Bieri, 1970, Porpita sp.), and for siphonophores (Purcell, 1980, 1981a, b). For species within each of these taxa, there are striking differences in the types and sizes of prey consumed.

Several of these quantitative studies have examined diel differences in predation. Chaetognaths generally consume more prey at night (e.g. Pearre, 1973; Szyper, 1978), although Feigenbaum (1979) found no such pattern. Anderson (1974) and Hirota (1974) saw no diel differences in predation by ctenophores, which are non-visual predators. In contrast, heteropods consumed more during the day, presumably since they locate prey visually (Seapy, 1980). Siphonophores, which are non-visual predators, appear to have different patterns: Agalma okeni feeds only at night (Biggs, 1977), and Rhizophysa eysenhardti and Rosacea cymbiformis feed only during daylight (Purcell, 1981a and b, respectively). The preceding results show that neither continuous nor indiscriminate feeding can be assumed in ecological studies of these zooplankton predators.

The order Siphonophora is a group of morphologically diverse species of colonial, pelagic cnidarians. Siphonophores can be very abundant in the plankton (see Pugh, 1974), and can even outnumber all other gelatinous predators and chaetognaths in some environments (Purcell, unpublished data). Some species of siphonophores swim vigorously to spread their tentacles in a 3-dimensional array, while others rely mostly on water motion or gravity for tentacle extension. Prey which come into contact with the extended, nematocyst-laden tentacles are captured as the siphonophores drift in the water. The ecology of siphonophores and other gelatinous predators is

poorly understood. This is largely due to the fragility of these animals, most of which are damaged or destroyed when collected by nets, thus preventing even accurate determinations of their abundances. Herein I survey the prey consumed by 24 siphonphore species *in situ*, primarily during the day, and present laboratory evidence that feeding in some of these species is related to light conditions.

Materials and Methods

Prey Consumption

Siphonophores were collected in hand-held jars by SCUBA divers during 1977–1980 in 4 geographic locations. Most specimens examined for consumed prey were preserved immediately *in situ* by injecting formalin into the jars. Some specimens were preserved aboard ship within 30 min of collection. These methods eliminated the possibility of feeding during collection in a net, and minimized the loss of prey due to digestion following collection. Gastrozooid contents were not egested upon preservation. Table 1 gives the location and details of each expedition during which siphonophores were collected for gut analyses.

Large gastrozooids ("stomachs") of the siphonophores were dissected, and the contents were identified and measured using an optical micrometer at 25 to 400× magnification. Small gastrozooids were mounted on microscope slides with cover slips, and their contents could be identified and measured at 100 to 400× through the semi-transparent tissue. Prey were measured according to cephalothorax length (70 to 80% of total length, for copepods), standard length (fish larvae), or longest dimen-

sion (all other crustaceans, molluscs, salps). Chaetognaths, which were 5 to 20 mm in length, were unmeasurable when digested and therefore were not included in the range of prey lengths. Siphonophore gastrozooids without food were measured at 12 to 100× magnification. These gastrozooid lengths are probably minimum estimates, due to contraction and shrinkage upon preservation of the siphonophores.

Plankton net tows were made to assess relative prey abundances in the locations where siphonophores were collected. Details of this sampling are presented in Table 2.

Light-Related Feeding Patterns

Siphonophores were collected by SCUBA divers with jars in the Sargasso Sea during June and July, 1979. Specimens were kept in 25° to 26°C seawater in 1- to 4-liter containers. Observations on the state of tentacle extension were made at intervals of 1 to 4 h in the dark, and under fluorescent light. Light and dark conditions were alternated several times during the 2 d continuous observation period for each specimen. Observations were made during the dark periods for only a few seconds, using indirect light from a flashlight fitted with a red filter to minimize disturbance.

Results

Prey Consumption

Siphonophores of the suborder Cystonectae, which had large gastrozooids, all had consumed fish larvae (Table 3).

Table 1. Locations and details of collections of siphonophores used in analysis of prey consumption. Species collected at locations where many species were found are listed in Table 3. Location abbreviations are those used throughout paper

Location and (abbreviation)	Date (mo/yr)	Time (hrs)	Depth (m)	Temperature (°C)	Species
Gulf of California (GC)					
near Loreto, Baja California (111°15′W; 25°34′N)	7/1977	08.00	5 – 20	21 – 23	*Apolemia uvaria*
	7 – 8/1978	09.00 – 11.00	5 – 20	21 – 23	see Table 3
Southern California (SC)					
(a) 80 km off San Diego					*Rosacea cymbiformis*
(b) 160 km off San Diego	5/1978	10.00 – 14.00	5 – 20	15 – 16	*Diphyes dispar*
(c) 320 km off San Diego					*Sulculeolaria chuni, S. quadrivalvis*
San Clemente Basin	9/1979		surface	16 – 17	*Diphyes dispar*
Santa Catalina Island	4 – 5/1980	08.00 – 11.00	10 – 15	14 – 15	*Sphaeronectes gracilis*
		03.00	surface		*Apolemia uvaria*
Sargasso Sea (SS)	6 – 7/1979	10.00 – 11.30	15 – 25	25 – 28	see Table 3
		15.00 – 16.30			
	6/1980	22.30 – 23.00	3 – 5	26	see Table 3
Friday Harbor, Washington (FH)	10/1980	day, night	surface	8 – 10	*Muggiaea atlantica*

Table 2. Locations and details of plankton net tows which accompanied sampling of siphonophores for assessment of prey consumption (Tables 1 and 3). Sampling protocol at each location and percentages of abundant zooplankton types known to be prey of siphonophores are given. p = prey types present in small numbers; n = not quantified. Numbers of "Mean total prey" refer to listed prey types only

Location	Date (mo/yr)	Time (hrs)	Tow (orientation, depth)	Net (diameter, mesh)	No. of tows	Mean total prey (No. m^{-3})	Mean % of prey available									
							Copepods	Amphipods	Decapod larvae	Ostracods	Shrimp	Chaetognaths	Fish	Molluscs	Gelatinous zooplankton	Miscellaneous
GC	7–8/1978	09.00–11.00	Horizontal, 10 m	0.75 m, 253 μm	9	1 695	87.1	p	0.1	p	0.4	6.4	0.1	5.6	p	p
SC	5/1978(a)[a]	10.00–14.00	Horizontal, 10 m	0.75 m, 253 μm	1	5 614	99.4	p	p	p	0.3	0.3	p	p	p	p
	(b)				1	2 752	85.0	p	p	p	0.2	0.8	p	p	p	14.0
	(c)				1	243	92.3	p	p	p	p	4.5	p	p	p	3.1
	4–5/1980	08.00–11.00	Vertical, 0–35 m	0.75 m, 235 μm	7	288	96.2	p	p	p	p	3.8	p	p	p	p
		03.00	Vertical, 0–35 m	0.75 m, 253 μm	2	338	98.9	p	p	p	p	0.9	p	p	0.2	p
SS	7/1960[b]	day, night	Oblique, 0–200 m	0.75 m, 230 μm	12	108	96.2	p	p	n	0.4	3.4	n	0.1	p	p
	7/1961[c]	day	Oblique, 0–500 m	1.0 m, 203 μm	3	257	68.1	n	n	6.7	n	3.0	n	n	6.7	n
	6/1980	23.00	Horizontal, 15 m	1.0 m, 342 μm	1	42	77.8	p	p	18.6	2.2	p	p	p	p	p
FH	10/1980	day	Horizontal, surface	0.5 m, 150 μm	5	10 022	99	p	p	p	p	p	p	p	p	p
		night	Horizontal, surface	0.5 m, 150 μm	8	8 557	99	p	p	p	p	p	p	p	p	p

[a] Areas (a) (b) (c) are described in Table I
[b] Grice and Hart (1962): means from "Atlantis" cruise, Stations LL and NN
[c] Deevey (1971): average from July tows

Gastrozooids of *Rhizophysa eysenhardti* contained only fish larvae in the Gulf of California. While gastrozooid contents of the other cystonect species were not examined extensively, all specimens of *Bathyphysa sibogae* and *R. filiformis* also contained larval fish remains. Biggs (1977) reported that *R. filiformis* consumed alcyopid polychaetes as well as fish.

Siphonophores of the suborder Physonectae which had large gastrozooids consumed a variety of prey organisms, with copepods comprising from 14 to 91% of their prey. Other commonly consumed prey were often among the largest zooplankters available, such as juvenile shrimp and euphausiids, chaetognaths, and fish larvae.

In the suborder Calycophorae, copepods constituted more than 66% of the daytime diets of all siphonophore species in this group. Several calycophores consumed copepods exclusively. Ostracods constituted important portions of the diets of some calycophores, but only in nighttime samples. Most calycophores had small gastrozooids and had consumed only small zooplankton.

Prey items not identified in Table 3 included the following: *Apolemia uvaria* contained barnacle cyprid and nauplius larvae, cladocerans, atlantid heteropods, salps, ctenophores, hydromedusae; *Athorybia rosacea* contained caridean mysis; *Nanomia bijuga* contained a barnacle nauplius; *Diphyes dispar* contained a gastropod veliger; *Rosacea cymbiformis* contained crab zoeae and megalopa larvae, stomatopod larvae, caridean zoea and mysis larvae, anomuran larvae, barnacle cyprids, cladocerans, polychaetes, clam and gastropod veligers, pteropods, atlantid heteropods; and *Sulculeolaria quadrivalvis* contained an anomuran zoea, cladocerans, clam and gastropod veligers.

Some of the siphonophore species had diets in which the most abundant prey types comprised only a small fraction of the prey available in the environment; this relationship emerges from a comparison of dietary data (Table 3) and prey availability data (Table 2). *Rhizophysa eysenhardti* consumed exclusively fish larvae, which constituted only 0.1% of available prey in the Gulf of California. Possible mechanisms for this marked selectivity are discussed by Purcell (1981a). Shrimp formed a large proportion of the diets of *Agalma elegans* and *Nanomia bijuga* relative to the small portion (0.4 and 2.2% of the prey available in the Gulf of California and the Sargasso Sea, respectively). Specimens of *Hippopodius hippopus* were collected on three different nights, yet all specimens had consumed only ostracods, which comprised 18.6% of the available prey.

Table 3. Dietary information for siphonophores. D = day; N = night. Further collection details in Table 1. Percentages of gastrozooids with prey were calculated by (No. of prey/No. of gastrozooids) × 100. Gastrozooid lengths and prey lengths, which include specimens examined from all locations, can be compared for each species of siphonophore. p = prey present in small numbers; n = not quantified; a = prey absent. Further prey items are identified in "Results – Prey Consumption" B indicates prey types reported by Biggs (1977). Species of the genus *Forskalia*, *F. edwardsi* and *F. tholoides*, were not distinguished, and so are presented together

Siphonophores (suborders, species)	Location	Time of collection	No. of colonies	Total No. of gastrozooids	% of gastrozooids with prey	Gastrozooid length (mm)	Prey length (mm)	Copepods	Amphipods	Decapod larvae	Ostracods	Shrimp	Chaetognaths	Fish	Molluscs	Gelatinous zooplankton	Miscellanous or unidentified
Cystonetae																	
Bathyphysa sibogae	SS	D	6	n	n	n	n	n	n	n	n	n	n	p	n	n	n
Rhizophysa eysenhardti	GC	D	312	1 512	11.7	2.5	3.0 – 15.0	a	a	a	a	a	a	100	a	a	a
	SS	D	7	n	n			n	n	n	n	n	n	p	n	n	n
R. filiformis	SS	D	5	n	n	n	n	n	n	n	n	n	n	p	n	n	n
Physonectae																	
Agalma elegans	GC	D	14	41	4.6	2.3	5.0	a	a	a	a	100	a	a	a	a	a
	SS	N	7	107	15.9			35.3	B	a	a	47.1	a	17.6	a	a	a
A. okeni	GC	D	14	54	6.2	3.3	2.9	75.0	a	a	a	25.0	a	a	a	a	a
	SS	N	1	6	16.7			a	B	a	a	a	a	100	a	a	a
Apolemia uvaria	GC	D	1	100	15.0	10.0	0.2 – 11.7	a	a	a	a	73.3	20.0	a	6.7	p	a
	SC	N	1	98	82.6			14.0	a	2.0	a	0.7	62.0	0.7	a	13.3	7.3
Athorybia rosacea	GC	D	2	6	50.0	2.2	0.4 – 5.0	33.3	a	33.3	a	a	33.3	a	a	a	a
	SS	D	3	8	112.5			44.4	B	a	a	B	a	55.6	a	a	B
Cordagalma cordiformis	SS	D	11	271	5.2	0.6	0.4	90.9	a	a	7.1	a	a	a	a	a	a
Forskalia spp.	GC	D	5	81	14.8	2.5	0.4 – 1.4	58.3	6.7	25.0	a	a	16.6	a	a	a	a
	SS	D	5	84	17.9			79.9	B	6.7	a	B	a	B	6.7	a	B
Nanomia bijuga	GC	D	53	405	15.0	3.0	0.6 – 5.0	25.0	a	4.0	a	16.0	20.0	a	a	a	a
Calycophorae																	
Abyla schmidti	SS	N	1	n	n	4.2	0.8	100	a	a	a	a	a	a	a	a	a
A. trigona	SS	D	2	10	40.0	2.5	1.0 – 1.4	100	a	a	a	a	a	a	a	a	a
Bassia bassensis	GC	D	60	630	8.2	0.4	0.4 – 1.2	100	a	a	a	a	a	a	a	a	a
Chelophyes appendiculata	SS	D	4	84	4.8	0.4	0.2 – 0.8	100	a	a	a	a	a	a	a	a	a
	SS	N	10	114	7.0			62.5	a	a	37.5	a	a	a	a	a	a
Diphyes dispar	GC	D	11	205	12.8	0.9	0.4 – 0.9	88.0	4.0	a	a	4.0	a	a	4.0	a	a
	SC	D	5	183	28.8			96.7	a	a	a	a	a	a	a	a	3.3
	SC	D	11	211	29.9			100.0	a	a	a	a	a	a	a	a	a
	SS	D	2	108	4.6			80.0	a	a	20.0	a	a	a	a	a	a
	SS	N	1	27	11.1			33.3	a	a	66.7	a	a	a	a	a	a
Hippopodius hippopus	SS	N	5	100	94.0	3.3	0.4 – 1.4	a	a	a	100	a	a	a	a	a	a
Muggiaea atlantica	FH	D	33	786	2.0	0.5	0.1 – 1.0	100	a	a	a	a	a	a	a	a	a
	FH	N	84	1 818	6.9			100	a	a	a	a	a	a	a	a	a
Rosacea cymbiformis	GC	D	> 40	1 250	50.4	3.2	0.3 – 5.5	75.4	p	3.0	p	3.5	5.7	p	12.5	a	p
	SC	D	1	57	78.9			100	a	a	a	a	a	a	a	a	a
	SS	D	3	56	50.0			88.0	a	a	a	4.8	4.8	2.4	a	a	a
Sphaeronectes gracilis	SC	D	52	1 614	7.0	0.8	0.1 – 0.9	100	a	a	a	a	a	a	a	a	a
Sulculeolaria biloba	SS	D	2	28	n	n	0.3	100	a	a	a	a	a	a	a	a	a
S. chuni	SS	D	7	113	5.3	1.2	0.2 – 0.8	100	a	a	a	a	a	a	a	a	a
	GC	D	3	196	17.8			100	a	a	a	a	a	a	a	a	a
S. monoica	SS	D	2	36	8.3	0.9	n	100	a	a	a	a	a	a	a	a	a
	GC	D	2	33	3.0			100	a	a	a	a	a	a	a	a	a
S. quadrivalvis	GC	D	6	437	17.4	0.8	0.2 – 0.6	100	a	a	a	a	a	a	a	a	a
	SC	D	5	781	3.5			96.3	a	a	a	a	a	a	a	a	3.7
	SS	N	5	161	37.9	`	0.2 – 2.5	62.4	9.8	a	a	a	1.6	1.6	3.3	a	21.3
S. turgida	GC	D	3	61	9.8	n	0.2 – 0.5	66.7	a	a	a	a	33.3	a	a	a	a

Apolemia uvaria off Southern California at night consumed mostly chaetognaths (62.0%) and gelatinous zooplankton including salps (11.3%), ctenophores (1.0%) and hydromedusae (1.0%). Plankton tows taken at that time contained 0.9% chaetognaths, no salps, 0.02% ctenophores, and 0.1% hydromedusae. In contrast, the diet of *A. uvaria* collected during the day in the Gulf of California was composed mostly of shrimp (73.3%) and chaetognaths (20.0%). Some gelatinous zooplankton were also present in these gastrozooids, but were too well digested to quantify. These dietary differences probably reflect differences in prey availability in the two locations, not differences in selectivity by the siphonophores. *A. uvaria* was the only siphonophore examined that had consumed conspicuous quantities of other gelatinous zooplankton.

The predominance of copepods in the diets of calycophore siphonophores (Table 3) is not surprising since copepods composed more than 85% of the zooplankton in all daytime plankton tows (Table 2). Several of the calycophore species consumed copepods to the exclusion of other available prey organisms. *Hippopodius hippopus* and *Rosacea cymbiformis* had larger gastrozooids than the other calycophores. A dietary analysis revealed that *R. cymbiformis* consumed a greater proportion of large, noncopepod prey than would be expected based on prey availability alone (Purcell, 1981b). Specimens of *H. hippopus* had consumed only ostracods.

The size of empty gastrozooids of the various species of siphonophores was related to the size of prey captured (Table 3). As gastrozooid length increased, the maximum prey size increased ($P=0.015$, Kendall rank correlation, Sokal and Rohlf, 1969). Siphonophores having many, small gastrozooids (most calycophores and one physonect, *Cordagalma cordiformis*) consumed copepods almost to the exclusion of other prey. Siphonophores having large, and usually fewer gastrozooids (cystonects, most physonects, and the calycophores *Hippopodius hippopus* and *Rosacea cymbiformis*) consumed many large, non-copepod prey. The physonects appear to be capable of consuming prey over a wide range of sizes.

Daytime feeding was compared for species which were collected in more than one location. In most cases, these comparisons revealed that a greater percentage of gastrozooids contained prey (Table 3) in environments where prey densities (Table 2) were higher. No daytime plankton tows were made in the Sargasso Sea in the present study, so data from other sources are presented for comparison in Table 2. For *Diphyes dispar*, both feeding and prey density were greatest off Southern California, next greatest in the Gulf of California, and least in the Sargasso Sea (abbreviated SC > GC > SS). For *Rosacea cymbiformis*, the percentage of gastrozooids with prey followed the pattern SC > GC = SS, while the prey density was SC > GC > SS. The specimens from the Sargasso Sea were collected later in the day, and therefore could have fed for a longer period after dawn when *R. cymbiformis* begins feeding (see following section: "Light-Related Feeding Patterns"). Feeding of *Sulculeolaria chuni*, as well as prey density,

were greater in the Gulf of California than in the Sargasso Sea. Similarly, more prey were found in gastrozooids of *S. quadrivalvis* in the Gulf of California, where prey densities were higher, than in the California Current. *Athorybia rosacea* and *Forskalia* spp. were the only species for which the number of prey found in gastrozooids did not parallel prey densities in the Gulf of California and the Sargasso Sea, but few of these siphonophores were examined. Generally, the data support the intuitive conclusion that the higher the environmental prey densities, the more the siphonophores fed.

The available dietary data are not extensive for nighttime samples (Table 3). For species where day and night comparisons of feeding can be made, the data suggest that feeding may have been greater at night. Of species collected both day and night in the same location, *Chelophyes appendiculata* contained somewhat more prey at night than during the day (7.0 vs 4.0% of the gastrozooids contained prey, respectively), as did *Diphyes dispar* (11.1 vs 4.6%) and *Muggiaea atlantica* (6.9 vs 2.0%). Specimens of other siphonophore species were collected from different locations during the day than at night, and therefore cannot be directly compared. However, specimens collected at night (*Agalma elegans, A. okeni, Apolemia uvaria, Sulculeolaria quadrivalvis*) contained more prey than specimens collected during the day (Table 3), even though plankton densities were greater at the daytime sampling locations than at nighttime locations (Table 2). Evidence from the present study (see following section: "Light-Related Feeding Patterns") and from Biggs (1977) indicates that *Agalma okeni* feeds only at night; therefore, gastrozooid contents in daytime samples probably were remnants from feeding during the previous night.

Light-Related Feeding Patterns

Laboratory observations were made on siphonophores in water free of food to determine whether feeding behavior was independent of light and dark conditions. It was assumed that extended tentacles indicated readiness to feed, and conversely, that contracted tentacles indicated indisposition to feed. Table 4 lists the percentages of observations when tentacles were extended for 7 species of siphonophores. The numbers of observations for each species in the four experimental conditions (light-during-day, light-during-night, dark-during-day, dark-during-night) were compared in tests of independence in a 3-way table, with *a priori* tests of partitions (Sokal and Rohlf, 1969). The results of these tests (Table 4) were very clear for 3 species of siphonophores. *Rhizophysa eysenhardti* extended its tentacles in the light ($P \ll 0.005$), regardless of the time of day. These data corroborate *in situ* nighttime behavioral observations and results from gut analysis indicating that no food was captured at night (Purcell, 1981a). *Agalma okeni* extended its tentacles in the dark ($P \ll 0.005$), regardless of the time of day. These results

Table 4. Results of laboratory observations on feeding activity of siphonophores (determined by extended versus contracted state of the tentacles). Observations were made in the light and in the dark, during day and night. Percentages of observations when tentacles were extended (indicating readiness to feed) is followed by number of observations in parentheses. Total percentages compare light to dark and day to night. Statistical probabilities, P, were calculated in tests of independence. NS indicates not significant ($P > 0.05$)

Siphonophore species	No. of speci-mens	% of observations when tentacles were extended								
		Light day	Light night	Dark day	Dark night	Totals				
						Light – Dark	P		Day – Night	P
Bathyphysa sibogae	6	89.5 (19)	94.7 (19)	75.0 (12)	73.3 (15)	92.1 – 74.1	$P = 0.048$		82.2 – 84.0	NS
Rhizophysa eysenhardti	7	100 (36)	94.7 (19)	4.2 (24)	0 (21)	98.2 – 2.2	$P \ll 0.005$		52.1 – 47.4	NS
R. filiformis	5	100 (4)	100 (2)	0 (1)	50.0 (4)	100.0 – 40.0	$P = 0.011$		50.0 – 75.0	NS
Agalma okeni	36	19.1 (152)	22.5 (11)	66.3 (95)	81.4 (70)	20.5 – 72.7	$P \ll 0.005$		42.7 – 52.0	NS
Athorybia rosacea	13	65.5 (29)	90.5 (21)	50.0 (22)	66.7 (18)	76.0 – 57.5	NS		57.8 – 78.6	$P = 0.037$
Forskalia spp.	21	78.1 (32)	100 (18)	86.6 (26)	66.7 (21)	86.0 – 76.6	$P = 0.025$		81.4 – 83.4	NS
Rosacea cymbiformis	10	93.4 (76)	86.4 (66)	21.1 (57)	32.6 (46)	90.1 – 30.1	$P \ll 0.005$		60.8 – 59.5	NS

corroborate *in situ* observations that *A. okeni* tentacles were contracted in the daytime, but not at night (Biggs, 1977; Purcell, personal observations). *Rosacea cymbiformis* extended its tentacles in the light ($P \ll 0.005$), regardless of the time of day. Specimens extended their tentacles within 1.5 min when conditions were changed from dark to light, but required more time to contract when switched from light to dark.

The other 4 siphonophore species did not show clear behavioral differences in light and in dark conditions. *Bathyphysa sibogae*, *Rhizophysa filiformis*, and *Forskalia* spp. had tentacles extended significantly more often in the light (0.048, $P = 0.011$, and 0.025, respectively). *Athorybia rosacea* extended its tentacles somewhat more at night ($P = 0.037$). The results show, however, that *B. sibogae*, *A. rosacea*, and *Forskalia* spp. frequently had tentacles extended in both light and dark conditions. The numbers of observations for *R. filiformis* were very small. It is impossible to extrapolate with confidence to *in situ* behavior of these 4 species based on the present laboratory results. The results suggest that feeding activity may be enhanced in light conditions for *B. sibogae* and *Forskalia* spp., and during the night for *A. rosacea*. Neither the effects of different light intensities nor the presence of prey upon tentacle extension were investigated.

Discussion

Interesting generalizations can be drawn from the survey of prey consumption by siphonophores. A characteristic diet was observed for each suborder. Cystonect siphonophores fed upon fish larvae, physonects consumed many large types of zooplankton in addition to copepods, and most calycophores fed principally upon copepods. Siphonophores in the suborders Cystonectae and Physonectae generally had large gastrozooids, while calycophores generally had small gastrozooids. Siphonophore species having small gastrozooids (most calycophores and the physonect *Cordagalma cordiformis*) usually had many

gastrozooids per colony (> 20), consumed small prey (primarily copepods), and had low percentages of gastrozooids containing prey. In contrast, siphonophores having large gastrozooids (cystonects, most physonects, and the calycophores *Rosacea cymbiformis* and *Hippopodius hippopus*) usually had few gastrozooids (< 20), consumed many large, non-copepod prey, and had high percentages of gastrozooids containing prey. Larger prey requires more time for digestion (Biggs, 1977; Purcell, 1981b); hence siphonophores consuming larger prey would retain each item longer, which would be reflected in those siphonophores having a greater proportion of gastrozooids containing prey.

Many of the siphonophore species did not consume prey types in proportion to prey availability in the environment. This "selectivity" can be discussed in terms of the preceding generalizations. Siphonophores with many, small gastrozooids have closely-spaced tentacles and branches (tentilla) that are spread in a 3-dimensional net by the swimming activity of the siphonophore. Siphonophores with large gastrozooids often have fewer and/or more widely spaced tentacles, and do not exhibit rapid swimming to spread their tentacles. The tentacle array is probably an important determinant of the size of prey captured. Small, common prey are more likely to encounter the tentacle strands of small siphonophores with closely-spaced tentacles and tentilla forming a fine network. Widely-spaced tentacles covering a large volume of water are more suited to the capture of large, less common prey types.

A range of degrees of these characteristics for the two artificial groups of siphonophores described here can explain the distribution of prey sizes captured by the different siphonophore species. Siphonophores with small gastrozooids can be ranked as follows, beginning with the species with the smallest gastrozooids and the strongest swimming ability: *Chelophyes appendiculata*, *Muggiaea atlantica*, *Cordagalma cordiformis*, *Sulculeolaria* spp., *Diphyes dispar*, *Sphaeronectes gracilis*, *Bassia bassensis*, and *Abyla* spp. These species (less true for *B. bassensis* and *Abyla* spp.) cover a broad area with a fine network of

tentacles. Sizes of captured prey also increased approximately according to this ranking.

The group of siphonophores having large gastrozooids included only one species (*Nanomia bijuga*) which swims rapidly to spread its tentacles. The other, weakly-swimming species, form the following gradient of body plans from species with short stems and 3-dimensional tentacle arrays, to species with very long stems and widely-spaced tentacles in a more 2-dimensional array: *Athorybia rosacea, Hippopodius hippopus, Forskalia* spp., *Agalma okeni, A. elegans, Rosacea cymbiformis,* and *Apolemia uvaria.* The cystonect siphonophores do not swim, since they lack swimming bells, and they have widely-spaced tentacles spread in 3 dimensions. The siphonophore species with large gastrozooids and widely-spaced tentacles all consumed large, non-copepod prey. The size of captured prey increased roughly according to this ranking, with siphonophores having widely-spaced tentacles capturing prey of larger sizes. In addition, some of these species may enhance capture of large, low-density prey by attracting them with "lures" that resemble other zooplankton (Purcell, 1980).

Analysis of gastrozooid contents suggested that siphonophore species feeding both day and night consumed more prey at night. The data presented here for prey availability in the environment are not extensive, but are included to show the considerable differences between the locations sampled. Evidence in the literature for greater zooplankton abundance in surface waters at night due to vertical migration is overwhelming (e.g. Longhurst, 1976). Ortner (1977) gives the night:day ratio of biomass in the upper 200 m of the Sargasso Sea in August as 1.78 to 1.84. Therefore, greater densities of prey would be available to the siphonophores in the surface waters at night. Greater siphonophore feeding would be expected at night since results from this and other studies (Purcell, 1981 a, b) show that siphonophore feeding is enhanced at greater prey densities.

Factors in addition to greater prey density could also enhance zooplankton capture by siphonophores at night. Prey size and prey swimming speed were shown to be important in influencing prey encounter with siphonophore tentacles (Purcell, 1981 b). Larger zooplankton are more common in deeper waters by day (e.g. Deevey and Brooks, 1971), but often migrate to surface waters at night, thereby increasing the proportion of large available prey. Additional evidence indicates that feeding by some planktonic crustaceans is greater at night. For example, strongly migrating euphausiids fed primarily at night in surface waters (Rogers, 1975, *Euphausia* sp.; Sameoto, 1980, *Thysanoessa* spp.). Greater feeding at night by copepods was found (Wimpenny, 1938; Mackas and Bohrer, 1976), even without vertical migration (Petipa, 1958; Hayward, 1980). Such evidence suggests that the zooplankton prey of siphonophores may be more active at night. Thus larger, more active prey may be more available at night, thereby increasing the chances of prey encounter with extended siphonophore tentacles.

Laboratory observations indicated that three species of siphonophores showed feeding periodicity mediated by light and dark conditions. *Rhizophysa eysenhardti* and *Rosacea cymbiformis* extended their tentacles in the light, while *Agalma okeni* extended its tentacles in the dark. Further observations on the effects of different light intensities and wavelengths, in combination with data on the depth ranges of these siphonophores are necessary to determine the proportion of each diel period when feeding would occur. Unfortunately, only limited information exists on the diel vertical distributions of these species. *Rosacea cymbiformis* is believed to occur primarily below 100 m, and *A. okeni* has been collected from less than 100 to 600 m (Pugh, 1974). All three species have been collected extensively within the upper 30 m during the day by SCUBA divers (present study; and Biggs, 1977). *Agalma elegans, A. okeni, Nanomia bijuga, Chelophyes appendiculata, Hippopodius hippopus,* and *Sulculeolaria quadrivalvis* were collected during the night near the surface by divers in the Sargasso Sea in 1980. None of these species were observed within SCUBA depth range during the day at the same stations, suggesting a daytime descent.

Explanations of diel feeding periodicity in these three species of siphonophores are purely speculative at this time. *Agalma okeni,* which appears to be a nocturnal feeder, may benefit energetically by not feeding during the day, and feeding instead at night when more large prey are available. Any energetic advantage to the diurnal feeder *Rosacea cymbiformis* is difficult to imagine; however, fish larvae, which are visual predators, may be more active, and therefore more available, during the day when the siphonophore *Rhizophysa eysenhardti* feeds upon them. *Rhizophysa eysenhardti* and *Rosacea cymbiformis* could conceivably sustain damage if they were to entangle large vertically-migrating fish and crustaceans in surface waters at night; hence, it may be advantageous for these siphonophores to keep their tentacles contracted in the dark.

The differences among the co-occurring epipelagic species of siphonophores would tend to separate them ecologically. Some species consumed very small prey, while others consumed large prey, and even specific types of prey. The observed diel differences in feeding behavior would separate some species temporally. Of course, many other species, unreachable by SCUBA, are separated spatially by depth. Such differences tend to reduce overlap in prey utilization by the numerous species of siphonophores.

Whereas extensive effort has been devoted to the study of feeding by planktonic marine and freshwater crustaceans (primarily herbivores), relatively little attention has been paid to feeding by gelatinous marine zooplankton. The following non-crustacean zooplankton are abundant consumers in some marine environments; salps (Heron, 1972 a, b; Madin, 1974); larvaceans (Alldredge, 1981), ctenophores (Miller, 1970; Hirota, 1974; Kremer, 1979), chaetognaths (Szyper, 1978; Feigenbaum, 1979), and siphonophores (Rogers *et al.,* 1978; Purcell, 1981a). As

data accumulate on feeding by these organisms, a more complete understanding of the trophic interactions in the pelagic marine environment will develop. Data on *in situ* feeding, such as those in the present study, can be applied to abundance data for predators and prey organisms to estimate predation upon zooplankton populations and the relative importances of the various predators.

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