Selective Predation and Caloric Consumption by the Siphonophore *Rosacea cymbiformis* in Nature

J. E. Purcell*

Department of Biological Sciences and the Marine Science Institute, University of California at Santa Barbara;
Santa Barbara, California 93106, USA

Abstract

Individuals of the siphonophore *Rosacea cymbiformis* (Chiaje, 1822) were collected in surface waters of the Gulf of California during July/August 1978, off Southern California during May 1980, and in the Sargasso Sea during July 1979. Specimens were preserved within 30 min after capture, and the ingested prey in the gastrozooids were examined microscopically and identified to the closest practical taxon. Most gastrozooids (50 to 84%) contained recognizable prey organisms. The prey were primarily copepods, but crab zoeae, pelagic molluscs, juvenile shrimps and mysids were also commonly eaten. There were significant differences between the sizes and types of prey organisms that had been ingested and that were available in the environment of the siphonophores. Electivity indices for the prey demonstrated that the large and/or active prey were selected. The feeding selectivity exhibited by the siphonophores probably depends upon speed and diameter of the prey, which affect the frequency of contact with the siphonopore tentacles. Behavioral observations suggest that *R. cymbiformis* feeds primarily in the light. Digestion experiments indicate that most prey remain in the gastrozooids for 8 h or more before egestion. The caloric values of common prey types were derived from their length to dry weight regressions. The caloric consumption of *R. cymbiformis* during the 4 to 6 h feeding period following sunrise was estimated to be from 0.109 to 0.365 cal per gastrozooid; the daily caloric consumption was projected to be at least 2.4 to 8.2 times that required to balance metabolism.

Introduction

Prey selection, and its role in competition and resource partitioning, has received considerable attention from ecologists working in terrestrial, freshwater, and marine environments. In planktonic communities, the influence of prey size on selective predation has been examined for: larvae of *Chaoborus* sp. (Swift and Fedorenko, 1975; Lewis, 1977), mysids (Cooper and Goldman, 1980), copepods (Kerfoot, 1977; Landry, 1978; Li and Li, 1979), chaetognaths (Pearre, 1974; Feigenbaum, 1979), heteropods (Seapy, 1980), ctenophores (Anderson, 1974; Hirota, 1974), and siphonophores (Purcell, 1980, 1981). Evidence from these studies shows that prey size alone is not sufficient to explain the observed selectivity by predators. Some of these studies implicate other prey characteristics, including shape, armor, locomotion, and escape responses, as important determinants of selective feeding. Characteristics of the predators including locomotion (Gerritsen and Strickler, 1977) and morphology, can also determine which prey are captured.

Prey selection by siphonophores has only recently been studied in detail (Purcell, 1980, 1981). Siphonophores, which are pelagic, colonial cnidarians, are non-visual predators and cannot actively seize prey. They drift in the water and paralyze prey which come into contact with the nematocyst-laden tentacles. Many siphonophore species swim in arcs or spirals to spread their tentacles in a three-dimensional array; in contrast, the siphonophore *Rosacea cymbiformis* (Chiaje, 1822) does not swim to deploy its tentacles, which hang in a two-dimensional curtain beneath the horizontally oriented chain of zooids. Such species differences in behavior and tentacle array apparently influence the size and type of prey captured (Purcell, 1980). Little dietary data existed for siphonophores until recently, since the colonies fragment when collected by nets. Collection by SCUBA divers enabled Biggs (1977a) to make preliminary observations on prey captured by

* Present address: Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, USA

siphonophores. More extensive dietary analyses have revealed marked differences between species and strong selectivity of prey (Purcell, 1980, 1981).

The following study presents a dietary analysis of *Rosacea cymbiformis*, with emphasis on feeding selectivity and the possible effect of prey activity on feeding in this siphonophore. This study also describes diel periodicity of feeding behavior and digestion of prey. Additional objectives were to estimate the daily prey and caloric consumption of *R. cymbiformis* based on the quantities of each prey type consumed *in situ*: first, to compare this with the data of Biggs (1977b) on the metabolic requirements of the same siphonophore species; and second, to determine whether the siphonophores significantly influence prey populations. While the present study on *R. cymbiformis* does not present a complete carbon budget, natural dietary data are utilized to estimate the number of calories available for growth and reproduction after metabolic demands have been met. Estimates of the predation impact of the siphonophores upon their prey populations are made by combining prey consumption data with information on predator and prey population densities.

Materials and Methods

Specimens of the siphonophore *Rosacea cymbiformis* (Chiaje, 1822) were collected in the Gulf of California during July and August 1978. Siphonophores were collected and preserved with formalin in hand-held jars during SCUBA dives at 5 to 15 m depth in the 5 km wide channel between the Baja Peninsula and a small island (Isla Danzante, 111 ° 15 °W; 25 ° 45'N). Additional specimens were captured at depths of 1 to 3 m in a shallow cove of the island and were preserved within 15 min of collection. All collections were made between 09.00 and 11.00 hrs. Other specimens, used only to compare the number of prey captured by *R. cymbiformis* in different environments, were collected at depths of 10 to 20 m in the California Current 83 km off San Diego, California, in May, 1978 and in the Sargasso Sea during mid-June to mid-July, 1979. These siphonophores were preserved aboard ship 20 to 30 min following collection. Gastrozooid ("stomach") contents were not egested upon preservation.

Predation and Selectivity

All gastrozooids were dissected, and prey remains identified and measured at 25x - 400x magnification according to cephalothorax or carapace length (crustaceans), total length (chaetognaths), standard length (fish larvae), or longest dimension (molluscs). Total lengths of juvenile shrimps and crab zoea larvae are included in Fig. 4 for comparison with other studies. Cephalothorax length, which was used in this study,

measured 70 to 80% of total length in copepods, depending on the species. Certain copepod species could be identified accurately by their brightly colored appendages, even in advanced stages of digestion. Of these, *Labidocera acutifrons* and *Pontellopsis lubbochi* could not be distinguished when highly digested, and so are considered together.

Natural densities of zooplankton commonly consumed by *Rosacea cymbiformis* were determined using a 0.75 m Diam, 250 μm mesh plankton net with flow meter. One horizontal net tow was made at 5 to 10 m depth immediately following siphonophore collection off Southern California, but no tows were made in the Sargasso Sea. One horizontal net tow at a speed of approximately 2 km h^{-1} was made at 5 to 10 m depth on each of 9 d between 09.00 and 11.00 hrs in the channel in the Gulf of California (average volume sampled = 24 m^3). The samples were preserved in formalin, and then subsampled using a Folsom plankton splitter. Electivity indices were calculated for the different prey types in the Gulf of California according to Chesson (1978). Feeding "selectivity" and "preference" indicate here that prey types were not consumed in proportion to their measured abundances, and no active choice of prey by the siphonophore is implied.

Prey Swimming Rates

The swimming rates of some common prey organisms were measured to examine the importance of prey swimming speed to siphonophore prey capture. Zooplankton were collected in short, vertical tows from the California Current off Santa Catalina Island in April and May, 1980. Individual calanoid copepods of 4 size classes, and zoea larvae of brachyuran crabs were pipetted into a narrow aquarium (30 x 30 x 10 cm) or into petri dishes (9 cm in diameter, 1.5 cm deep). The swimming rates at 13° C ± 1 C° were determined by tracing their paths during 60 s trials. The distances in paths travelled without interference from surfaces were measured by retracing the paths with a map wheel calibrated in centimeters.

Siphonophore Diel Feeding Activity

Observations on siphonophore feeding activity in the light and in the dark were made in a shipboard laboratory on 10 specimens of *Rosacea cymbiformis* collected by divers at 15 to 25 m depth during the day in the Sargasso Sea during July, 1979. Specimens were maintained in 4 liter containers at surface water temperatures of 26°C. Observations on tentacle extension during a 48 h period were made at intervals of 1 to 4 h either in the dark or under fluorescent light. Light and dark conditions were alternated several times during the 2 d observation period for each specimen. Siphonophores in the dark were observed for a few seconds in the reflected light of a flashlight with a red filter to minimize disturbance by light.

Table 1. *Rosacea cymbiformis*. Comparison of prey-capture frequency by siphono-phores in surface waters of different environments: in a shallow cove and in an open-water channel in the Gulf of California during July/August 1978, in the California Current during May 1978, and in the Sargasso Sea during July 1979. A maximum of 7% of the gastrozooids contained unidentifiable prey remains

| | Gulf of California | | California Current | Sargasso Sea |
	Cove	Channel		
No. of gastrozooids examined	171	1 250	57	56
% of gastrozooids with prey	83.6	50.4	78.9	50.0
% of copepods in diet	41.4	75.4	100.0	88.0
Average no. of prey in a gastrozooid	1.3	0.6	0.8	0.7
Total *in situ* prey density (no. m^{-3})	1 695.0	1 495.8	5 613.5	no data

Digestion

The crustacean prey items within the gastrozooids were classified into the following categories: least digestion (appendages intact, most body tissue apparent); intermediate digestion (appendages often disarticulated, much body tissue cleared from the exoskeleton); greatest digestion (appendages and often body segments disarticulated, little or no body tissue apparent). Chaetognaths were classified similarly, according to the amount of body tissue.

Digestion experiments were conducted in the Gulf of California to estimate the length of time between prey capture by the siphonophore and fixation of gut contents. Small specimens of *Rosacea cymbiformis* were maintained after collection in 500 ml jars at ambient water temperature of 23 °C ± 1 C° for 5 h, at which time no prey were visible in the gastrozooids. These siphono-phores were then fed for 15 min on freshly-collected unsorted zooplankton. After feeding, the siphonophores were maintained as before in seawater without prey, and some siphonophores were preserved at 15 min intervals over the next 4.5 h. The degrees of digestion of the prey from these experiments were determined as explained above. One specimen having 50 gastrozooids was maintained at 24°C in constant light and without food aboard ship in the Sargasso Sea in June, 1980. Prey remains egested from the gastrozooids were pipetted from the container floor and counted at intervals over the 18 h following collection of the siphonophore to estimate the time required to clear gastrozooids of natural prey (which presumably had been consumed throughout 9 h after sunrise).

Caloric Consumption

Individual zooplankters from one formalin-preserved tow sample from the Gulf of California were measured, dipped in distilled water, and placed individually or in groups on pre-ashed, pre-weighed aluminum foil squares. Specimens were dried 24 h in a 60°C oven and weighed

to the nearest 1 μg on a Cahn electrobalance. Estimated caloric values of prey were related to dry weight according to published values for copepods (Comita et al. 1966) and the pteropod *Clione limacina* (Conover and Lalli, 1974). The caloric values of copepods and other prey types were estimated according to a formula (Platt et al., 1969) relating the percentage of carbon per mg dry weight (Beers, 1966) to caloric content of zooplankton. Table 6 summarizes these literature values relating dry weight to carbon and to caloric content.

Results

Specimens of *Rosacea cymbiformis* collected in the California Current and in the Sargasso Sea were budding colonies with two nectophores (swimming bells). Specimens collected in the Gulf of California were fragments without nectophores (with two exceptions), having 5 to 171 cormidia (mean 32.5 ± SD 38.4), which are repeating units in a linear array, each containing 1 gastrozooid, reproductive zooids, and a gelatinous bract for floatation. Such fragments extended several centimeters to over 1 m in length. Since gastrozooids are the functional units in feeding, data are presented on a per gastrozooid basis. The data refer to siphonophores and prey collected from the Gulf of California unless specifically indicated otherwise.

Predation and Selectivity

A high proportion of the 1 534 *Rosacea cymbiformis* gastrozooids which were examined contained food (Table 1). Approximately 80% of the gastrozooids of specimens collected in the cove environment in the Gulf of California and in the temperate California Current contained prey, while only 50% of the gastrozooids contained prey in the open channel environment in the Gulf of California and in the semi-tropical waters of the Sargasso Sea. The percentages of *R. cymbiformis* gastrozooids with prey were much greater than the 5 to 20%

Table 2. *Rosacea cymbiformis.* Prey availability, prey consumed, and calculated electivity indices in cove and in channel in the Gulf of California. Electivity values lie between 0 and 1. Values greater than α indicate positive selection (+), and those less than α indicate negative selection (−). Prey density averaged 1695 prey m^{-3} in the cove and 1495 m^{-3} in the channel. Percentages of "prey consumed" were based upon a total of 226 prey in the cove and 688 prey in the channel. "Other copepods" include: calanoids (*Acrocalanus longicornis, Centropages furcatus, Eucalanus attenuatus, Labidocera acuta, Paracalanus parvus, Scolecithrix danae, Temora discaudata*), cyclopoids (*Coryacaeus catus, Coryaceus* sp., *Farranula gibbula, Oithona plumifera*), and an harpacticoid (*Clytemnestra rostrata*)

Prey	Cove				Channel		
	Size (mm)	Prey available (%)	Prey consumed (%)	Electivity $\alpha = .083$	Prey available (%)	Prey consumed (%)	Electivity, $\alpha = .083$
Copepods							
Labidocera acutifrons +							
Pontelopsis lubbochi	2.0 − 4.0	0.05	0.44	.084 +	0.35	0.07	.001 −
Candacia curta	1.0 − 3.0	0.04	0.88	.211 +	0.06	4.54	.442 +
Onacea venusta	0.5 − 0.6	0.13	0	.000 −	1.84	0.64	.002 −
Onacea media	0.5 − 0.6	0.22	1.32	.058 −	0.99	1.86	.011 −
Other copepods	0.5 − 5.0	87.33	38.50	.004 −	84.86	68.34	.005 −
Total copepods		87.77	41.14		87.10	75.45	
Chaetognaths, *Sagitta enflata*	5.0 − 20.0	4.30	3.54	.008 −	6.36	5.74	.005 −
Pteropods, *Creseis* sp.	1.2 − 3.3	0.001	0	.000 −	0.60	2.32	.023 −
Heteropods, *Atlanta* sp.	1.0 − 2.0	0.02	0.89	.426 +	0.08	4.30	.314 +
Clam veligers	0.3 − 0.4	1.61	0.44	.003 −	3.58	1.22	.002 −
Gastropod veligers	0.2 − 0.4	1.07	1.76	.016 −	1.32	4.64	.021 −
Crab zoea larvae	0.4 − 1.0	2.60	47.76	.176 +	0.11	2.18	.116 +
Juvenile shrimp	0.8 − 1.6	0	0		0.35	3.54	.059 −
Mysids	1.0	2.54	4.42	.017 −	0	0	
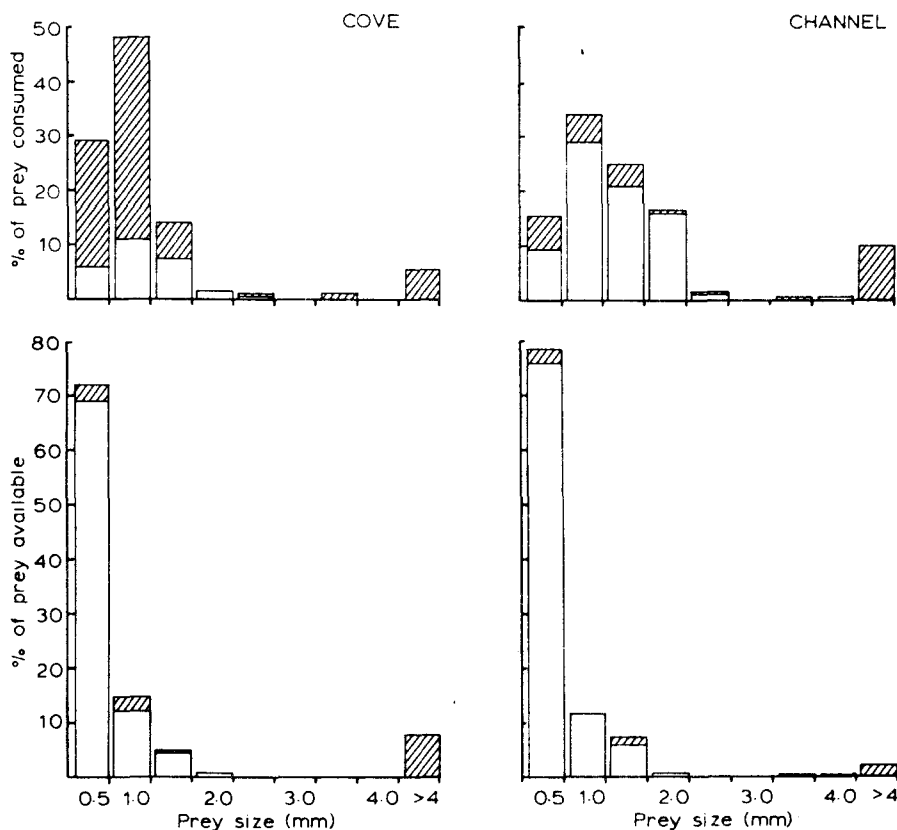
Fig. 1. Size distributions of prey available and prey consumed by *Rosacea cymbiformis* in both the cove and the channel of the Gulf of California. Open areas of bars represent copepods, hatched areas represent known prey other than copepods. Each bar covers a 0.49 mm size interval

Table 3. *Rosacea cymbiformis*. Prey availability, prey consumed by siphonophores and calculated electivity indices for copepods of 4 size groups and crab zoea larvae. For explanation of electivity values see legend to Table 2

Copepod length (mm)	Cove			Channel		
	Prey available (%)	Prey consumed (%)	Electivity, $q = .200$	Prey available (%)	Prey consumed (%)	Electivity, $q = .200$
$\leqslant 0.5$	69.77	9.40	.005 −	70.16	9.3	.004 −
0.6 − 1.0	12.35	17.04	.049 −	10.36	28.42	.064 −
1.1 − 1.5	5.18	11.75	.081 −	5.54	21.06	.089 −
> 1.5	0.49	2.94	.213 +	1.04	16.67	.377 +
Crab zoea larvae	2.60	47.76	.652 +	0.11	2.18	.466 +

generally found in other siphonophore species examined from the same environments (Purcell, 1980). Each gastrozooid with ingested food contained from 1 to 4 prey organisms.

Copepods were the most numerous prey in the diet of *Rosacea cymbiformis* (Tables 1 and 2). Copepod species from the Gulf of California identified from gastrozooid contents are listed in Table 2. *R. cymbiformis* consumed a wide variety of zooplankton in addition to copepods, commonly chaetognaths (*Sagitta enflata*), thecosome pteropods (*Creseis* sp.), heteropods (*Atlanta* sp.), mollusc veliger larvae, crab zoea larvae, juvenile shrimp, and mysids (Table 2). Prey found infrequently in the gastrozooids included crab megalopa larvae (0.8 to 1.0 mm), fish larvae (1.0 to 3.0 mm), cladocerans (0.4 mm), barnacle cyprid larvae (0.5 to 0.6 mm), hyperiid amphipods (0.8 mm), anomuran zoea larvae (2.0 mm), ostracods (0.8 to 1.2 mm), caridean mysis (0.8 · to 1.2 mm) and zoea larvae (0.2 mm), stomatopod larvae (1.6mm), polychaetes (1.0 mm), the sergestid *Leucifer* sp., and the siphonophore *Rhizophysa eysenhardti*. Only 5 to 7% of the gastrozooids contained unidentifiable tissue without any exoskeleton or hard structures.

Fig. 1 illustrates that the size distribution of prey consumed by *Rosacea cymbiformis* differed from that of prey available in the cove (P < 0.05, Friedman's method for randomized blocks, Sokal and Rohlf, 1969). Very small zooplankton were consumed less frequently than their availability would suggest, while larger zooplankton were consumed more frequently. The percentage of non-copepod prey consumed was significantly greater than the percentage available in the cove (P ≪ 0.001) and in the channel (P < 0.01, test comparing two percentages: Sokal and Rohlf, 1969).

The percentages of the several types of common prey consumed by *Rosacea cymbiformis* and the percentages of these zooplankters available in the environment were calculated for the cove and channel sites in the Gulf of California (Table 2). Differences in availability (average no. m^{-3}) of the various prey types between the cove and channel were not statistically significant (pair-wise *t*-test: Sokal and Rohlf, 1969). The availability of total copepods in the cove and channel was 87.77 and 87.10% of the total available prey, respectively; copepod densities

in the cove and channel were 1 487.7 and 1 302.8 m^3, respectively. The striking difference in the percentage contribution of copepods to the diet (41% in the cove versus 75% in the channel) was due to the large percentage of crab zoea larvae consumed in the cove (48%). The availability of zoeae was 23.6 times greater in the cove. The consumption of zoeae was proportionately greater, being 21.9 times that in the channel.

The numbers of each of the several prey types consumed were significantly different from the numbers expected based on availability (x^2 test, P ≪ 0.005) in both the cove and the channel. Electivity was negative for the small prey (small copepods *Onacea* spp. and veligers), but generally positive for the large prey (large copepod species *Labidocera acutifrons* + *Pontellopsis lubbochi* and *Candacia curta*, and heteropods) (Table 2). Crab zoea larvae, highly-preferred prey, have a large diameter and must swim continuously to prevent sinking. Electivity was negative for chaetognaths, which were the longest prey but which have narrow diameters and remain nearly motionless in the water. Shoaling and/or greater escape or avoidance abilities of juvenile shrimp and mysids could explain the observed negative selection, which was unexpected since both are large and active. Electivity indices were also calculated for 4 size groups of copepods and for crab zoea larvae (Table 3). Electivity increased with increasing copepod length, and was greatest for crab zoea larvae.

Prey Swimming Rates

The preceding dietary data indicate that *Rosacea cymbiformis* prefers large, active prey. In the "Discussion", swimming speed and body diameter of the prey are predicted to be important in determining how frequently prey organisms would contact a siphonophore tentacle. Table 4 summarizes the parameters examined in determining the importance of prey speed and size to siphonophore prey capture. Swimming speed increased with increasing size in 4 size groups of copepods, and was also high for crab zoea larvae. Diameter increased with length in copepods, and was greatest in crab zoea larvae. A measure of preference was calculated according

Table 4. *Rosacea cymbiformis*. Predicted preference of prey based on prey swimming speed and diameter. Swimming speeds are means ± SD; number of measurements are in parentheses. "Relative predicted preference" = swimming speed multiplied by diameter, and is presented as a proportion of the greatest value

	Copepod length (mm)				Crab zoeae
	< 0.5	0.6 – 1.0	1.1 – 1.5	> 1.5	
Swimming speed (cm s⁻¹)	0.15 ± 0.06 (20)	0.20 ± 0.09 (28)	0.28 ± 0.13 (26)	0.32 ± 0.20 (26)	0.28 ± 0.12 (29)
Diameter (mm)	0.2	0.3	0.6	0.7	0.8
Relative predicted preference	0.132	0.257	0.752	1	0.985
Ranking of predicted preference	5	4	3	1	2
Ranking of observed preference (from Table 3)	5	4	3	2	1

Table 5. *Rosacea cymbiformis*. Diel feeding behavior, monitored by state of contraction versus extension of tentacles. Observations were made in light and in darkness, at all times of day and night, in the laboratory

	State of tentacles		Total no. of observations
	Expanded	Contracted	
Light			
Day	71	5	76
Night	57	9	66
Dark			
Day	16	41	57
Night	15	31	46
			245
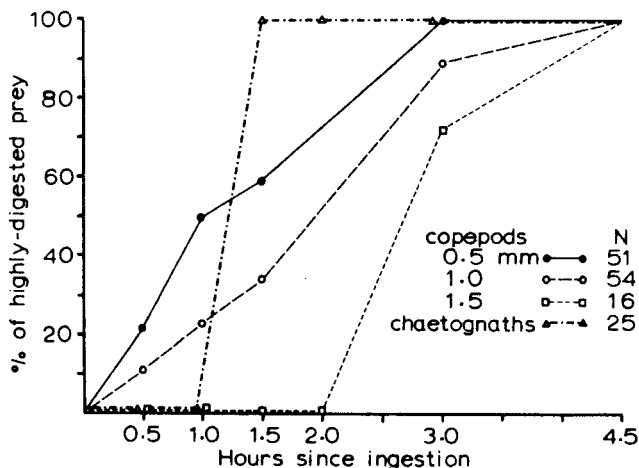
to the prediction that the frequency of contact with a siphonophore tentacle would increase with increasing prey speed and diameter. The ranking of the calculated relative preferences of the prey corresponds to the ranking of the observed preferences from field data. Thus, prey swimming speed and diameter appear to be important in the feeding selectivity demonstrated in *R. cymbiformis*.

Siphonophore Diel Feeding Activity

Laboratory observations of the state of tentacle extension of *Rosacea cymbiformis* were made to determine whether feeding periodicity was exhibited. Siphonophore tentacles were extended in the light, but were generally contracted in the dark (Table 5). Tentacle extension was related only to the presence or absence of light (P ≪ 0.005) and not to the time of day (test of independence in a multiway table: Sokal and Rohlf, 1969). Contracted siphonophore tentacles extended during 1.5 min after the lights were turned on. Contraction of the tentacles upon the change from light to dark conditions was not as rapid. The intensity of light required for the changes in behavior was not investigated. These results suggest that *R. cymbiformis* feeds during daylight hours.

Digestion

Results from the digestion experiments indicate that digestion was more rapid for small copepods than for large ones (Fig. 2). Much digestion of the prey occurred rapidly. Copepods 0.5 mm in cephalothorax length reached a highly-digested state in an average of 2 h, and those 1.0 to 1.5 mm in length, in 3 h. Chaetognaths appeared to be highly digested after 1 h. Siphonophores collected in the cove contained nearly twice the percen-

Fig. 2. *Rosacea cymbiformis*. Results from digestion experiment, showing percentage of highly-digested prey removed from gastrozooids over 4.5 h since prey were ingested. Copepods of 4 size groups and chaetognaths are presented. N: total number of each prey type removed
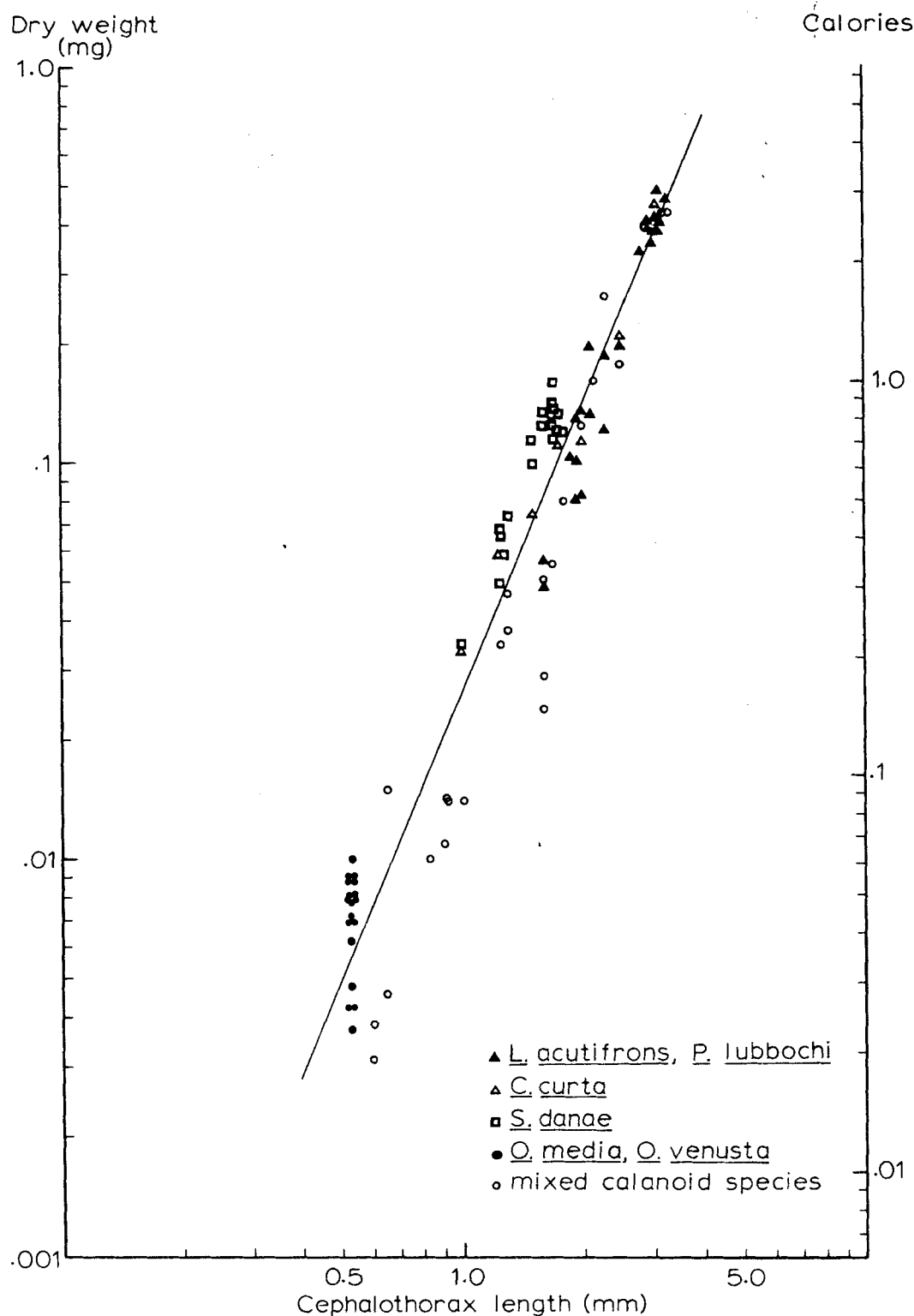
Fig. 3. Cephalothorax length to dry weight relationship measured for several copepod species consumed by *Rosacea cymbiformis* in Gulf of California. Correlation coefficient = 0.96 (P ≪ 0.01). Calculated regression line: log y = log 0.0265 + 2.413 log x. Caloric relationship to dry weight was calculated according to values in Table 6. Copepod species as are detailed in Table 2

Table 6. Percentage carbon and caloric values used in establishing relationships between caloric value, dry weight, and size (Figs. 3 and 4) of major prey types consumed by *Rosacea cymbiformis* in Gulf of California

Prey type	Carbon (% dry wt)[a]	Calories per g dry wt
Copepods	41.6	6 096.2[b]
Calanus finmarchicus	–	6 097.6 ± 1 196.5[c]
Euphausiids, mysids	40.7	5 959.4[b]
Other crustaceans	36.9	5 381.8[b]
Chaetognaths	28.3	4 074.6[b]
Pteropods	–	4 133.9[d]

[a] Average values from Beers (1966)

[b] Calculation based on percentage carbon method of Platt et al. (1969)

[c] Averaged for males and females from Table 1 in Comita et al. (1966)

[d] From Conover and Lalli's (1974) data for small specimens

Table 7. *Rosacea cymbiformis.* Caloric consumption in 4 to 6 h after sunrise in Gulf of California. Calories were estimated from lengths of consumed prey according to regressions in Figs. 3 and 4. Unidentified and unmeasurable prey were not included in calculations

	Cove	Channel
Average calories per gastrozooid	0.365	0.109
% copepod calories of total	34.78	65.75
% of total prey included in calculations	88.97	83.63

tage of copepods showing little digestion (32%) compared with siphonophores in the channel (19%), suggesting that many copepods were captured very recently within the cove. Prey may remain within the gastrozooids in a highly digested condition for a long time, as suggested by the large proportion (42 to 65%) of highly digested prey found in gastrozooids preserved *in situ*. In observations of egestion of prey consumed *in situ* (which had been consumed up to 9 h earlier) in the Sargasso Sea, 60% of the gastrozooids with food were cleared 4.5 h after the siphonophore was collected, 81% were cleared after 7.5 h, and 100% were cleared after 18 h. Egestion of *Artemia* sp. nauplii required 8 to 24 h (Biggs, 1977a). These results suggest that even small prey probably remain in the gastrozooids for 8 h or more.

Caloric Consumption

Fig. 3 shows the cephalothorax length to dry weight relationship determined for several species of copepods

over the size range utilized as food by *Rosacea cymbiformis*. Caloric value was related to dry weight according to information from other sources (Table 6). The length to dry weight relationships were also determined for common prey types other than copepods (Fig. 4), and caloric values estimated similarly. Caloric values determined from .the dry weights of preserved zooplankters may be as much as 30% too low, due to the decrease in dry weight over time after preservation (Durbin and Durbin, 1978). From sizes measured for individual prey removed from *R. cymbiformis* gastrozooids, the approximate caloric values for 84 to 89% of the consumed prey could be derived from the calculated regressions in Figs. 3 and 4.

The average number of calories consumed by each siphonophore gastrozooid collected between 09.00 and 11.00 hrs was 0.365 cal in the cove and 0.109 cal in the channel (Table 7). Three times more calories were consumed in the cove than in the channel, and the proportion of copepod-derived calories was only half that of the channel specimens (Table 7).

Evidence suggested that *Rosacea cymbiformis* does not feed during the night (Table 5). Therefore, the prey found in siphonophores collected between 09.00 and 11.00 hrs had evidently been captured within the 4 to 6 h period following sunrise (at 05.30 hrs). Digestion and gut clearance rates suggested that prey were captured that same day, and that little would have been egested during that 4 to 6 h period. During the 15 h between sunrise and sunset, the siphonophores might consume approximately three times the amount found in specimens collected in the morning, if one assumes equal prey availability and equal ingestion at all times. A 72% food assimilation efficiency was assumed for *R. cymbiformis*, since food was assimilated by the siphonophore *Rhizophysa eysenhardti* with 72% efficiency (Purcell, 1981); this value is also consistent with assimilation efficiencies determined for other gelatinous predators (e.g. see Reeve et al., 1978).

Based on the preceding information, daily caloric consumption for each cormidium which contains one gastrozooid of *Rosacea cymbiformis* can be estimated to range from 0.235 cal d^{-1} in the channel to 0.788 cal d^{-1} in the cove. Biggs (1977b) found the respiration rates of *R. cymbiformis* at 26 °C to be 8 μl O_2 h^{-1} mg^{-1} protein, with an average of 0.10 ± 0.02 mg protein in each cormidium (Biggs, personal communication). The calculated daily caloric requirements for each siphonophore cormidium would be 0.096 cal d^{-1} (assuming an oxycaloric equivalent of 5 cal ml^{-1} O_2 consumed; Parsons et al., 1977). The caloric consumption of *R. cymbiformis* in the Gulf of California appears to be from 2.4 times to 8.2 times that required to balance metabolism.

Discussion

Dietary analyses for tentaculate ctenophores (*Pleurobrachia pileus*, Anderson, 1974; *P. bachei*, Hirota, 1974)
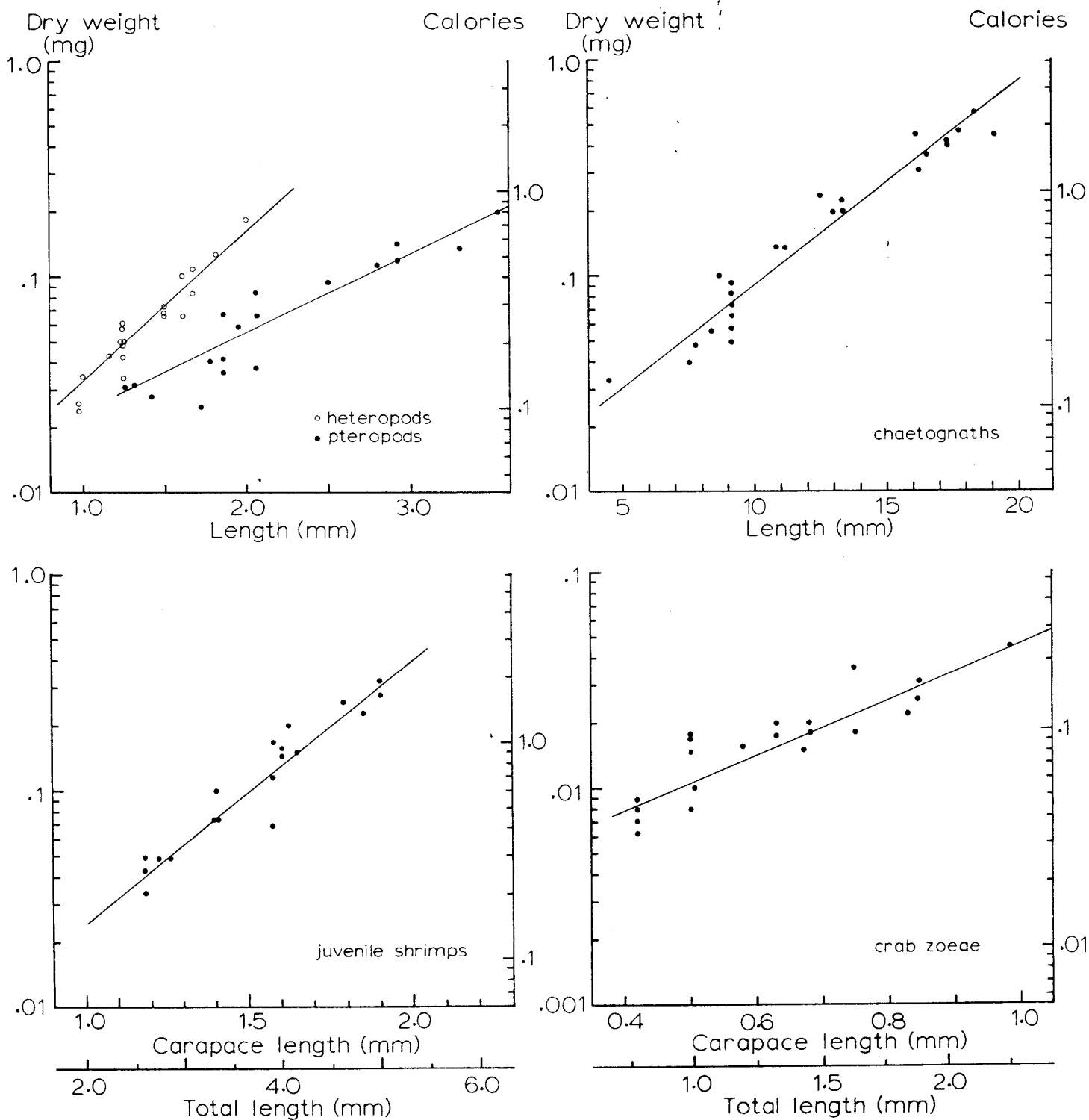
Fig. 4. Length to dry weight relationships measured for non-copepod zooplankton consumed by *Rosacea cymbiformis* in Gulf of California. Correlation coefficients and regression lines = heteropods, 0.97 (P ≪ 0.01), log *y* = 0.69 *x* −2.17; pteropods, 0.86 (P <0.01), log *y* = 0.38 *x* −2.0; chaetognaths, 0.97, (P ≪ 0.01), log *y* = 0.09 *x* −1.95; juvenile shrimps, 0.94 (P ≪ 0.01), *y* = 1.12 *x* −2.70; crab zoeae, 0.86 (P ≪ 0.01), log *y* = 1.24 *x* − 2.58. Caloric to dry weight relationships were calculated according to values in Table 6

and siphonophores (Purcell, 1980, 1981, and present study) show that these gelatinous zooplankters exhibit selectivity in predation. The fact is especially intriguing, since these predators depend on locomotion of the prey for predator-prey encounters. While characteristics of both predator and prey influence prey capture, prey characteristics have been emphasized here. Morphological traits of the predators, suggested in the preceding references, which may determine the prey captured, include: spacing of the tentacles or tentacle branches; tensile strength of the tentacles; and "stickiness" of the tentacles (specifically, adherence properties of the colloblasts of ctenophores, and penetration, entangling, and toxic properties of the nematocysts of cnidarians). Swimming patterns and arrangement of the extended tentacles of the predators may also affect the types of prey captured. Hirota (1974) observed 3 distinct patterns of tentacle spreading in *P. bachei*. Some siphonophores display active swimming to spread their tentacles in a three-dimensional array, while others do not (e.g. *Rosacea cymbiformis*). This first group consumes almost exclusively small copepods, while the second group consumes many large prey in addition to copepods (Purcell, 1980).

Diel feeding behavior of the predator could strongly influence the types and quantities of prey captured, since prey populations may change drastically through diel vertical migration. *Rosacea cymbiformis* extends its tentacles primarily during periods of light, as does another siphonophore, *Rhizophysa eysenhardti*, which consumed only fish larvae in the Gulf of California (Purcell, 1981). The proposed explanation for nocturnal contraction of tentacles in *Rhizophysa eysenhardti* — that a colony may suffer damage from large, vertically-migrating fish and crustaceans if these are caught in the tentacles at night — may be advanced for *Rosacea cymbiformis* as well.

Characteristics of the prey that could influence their capture by pelagic tentaculate predators include: size, protection by the exoskeleton or shell; ability to avoid contact with the tentacles; escape responses if contacted; and particularly swimming activity. The present paper assumes that the faster copepods swim, the greater the probability that they will contact siphonophore tentacles. The speeds of 4 species of copepods swimming in normal feeding patterns (Anderson, 1974) agree well with those measured here for corresponding copepod sizes, although maximal copepod swimming speeds, which have been measured in relation to vertical migration and energy expenditure (e.g. Vlymen, 1970; Enright, 1977), are considerably faster.

Electivity indices measured for prey consumed by siphonophores increased with increasing swimming speed and body diameter of the prey. Moreover, swimming patterns that could affect encounter probabilities also differed among prey types. Small copepods (chiefly grazers) swam in tight circles, and medium-sized copepods (omnivores and grazers) swam in larger circles or in "hop-and-sink" patterns. Such swimming patterns restrict these copepods to small volumes of water. Large copepods (omnivores and predators) swam in very wide circles, as did crab zoea larvae, a pattern presumably exposing such zooplankters to large volumes of water necessary for locating their food and increasing the chance of encountering a siphonophore. Anderson (1974) found that copepods having higher horizontal velocities and less recursive paths were more likely to be caught by the tentaculate ctenophore *Pleurobrachia pileus*.

The siphonophore *Rosacea cymbiformis* may be considered to be a biological filter, with more or less parallel rows of vertical tentacles. Tentacles project from the main stem at intervals of 7 to 21 mm (Biggs, 1977a), a spacing much greater than prey diameter. The chance of direct interception of a particle (prey) upon a fiber (tentacle) of given size would depend only upon the diameter of that particle (Rubenstein and Koehl, 1977). The frequency of particle encounter with the fiber would depend upon the number of particles passing by the filter — related to the speed of the medium, in the case of a stationary filter, or related to the speed of the particles, as in the case of *R. cymbiformis* which moves along the medium. Thus, larger, faster prey would encounter a siphonophore tentacle most frequently (assuming large and small prey to be equal in abundance) since greater speed increases the number of passes near a tentacle, and greater diameter increases the chance of hitting that tentacle.

The diet of *Rosacea cymbiformis* contained a greater proportion of large prey than would be expected from availability. Copepod swimming speed was shown to increase with increasing size. A very simple index (prey diameter times prey speed) of prey interception by a siphonophore tentacle was proposed. The ranking of prey preference indices predicted in this way corresponded to the ranking of prey electivity indices calculated from gut contents, thus indicating that prey swimming activity is an important determinant in the feeding "selectivity" observed in *R. cymbiformis*. Other prey characteristics, such as exoskeleton thickness and escape responses, probably also influence prey capture by siphonophores, and predator behaviors may be important as well. For example, when a large prey encounters a tentacle of *R. cymbiformis*, the siphonophore contracts that localized stem region, bringing several tentacles near the struggling prey. This behavior may be most effective in preventing escape by large zooplankton.

The ingestion rate of gelatinous predators in response to different prey levels has been investigated in the laboratory (e.g. Reeve *et al.*, 1978; Kremer, 1979). Quantification of the diet of *Rosacea cymbiformis* and of prey availability enabled comparison of feeding at different *in situ* prey densities. Crab zoea larvae (highly-preferred prey) were 20 times more abundant in the cove than in the channel of the Gulf of California, and siphonophores consumed 20 times more crab zoea larvae in the cove. *R. cymbiformis* experienced greatly different prey densities in the Gulf of California channel and off Southern California and more gastrozooids

contained food where prey densities were higher, but the difference in feeding was not directly proportional to the difference in prey density. Ingestion by tentaculate ctenophores increased linearly with prey concentration over two orders of magnitude, but reached a critical prey concentration beyond which ingestion increased no further (Reeve et al., 1978). Perhaps the high prey density measured off Southern California exceeded an analagous critical food concentration for R. cymbiformis.

Digestion rate experiments showed that the speed of digestion varied with copepod size and prey type (chaetognaths versus copepods). However, more extensive digestion experiments are necessary to show gastrozooid clearance rates for each prey type. Digestion of atlantid heteropods, pteropods, veligers, and decapod larvae might be very slow due to external shells and thick exoskeletons. Cyclopoid copepods remained intact longer than calanoid copepods, thus decreasing the apparent digestion rate of cyclopoids. Prey remaining longer in the gastrozooids for digestion would thus appear to be consumed in greater numbers than rapidly-digested prey, thus affecting consumption rate and selectivity determinations, unless differences in digestion rates were considered. This problem should not have affected the presented dietary composition for Rosacea cymbiformis, since siphonophore collections for gut contents were made after initiation of feeding at sunrise and before egestion of prey would occur.

Determination of prey ingestion and selectivity by Rosacea cymbiformis required making the following assumptions: (1) The siphonophores fed only during daylight; behavioral observations in the laboratory were consistent with this assumption. (2) No prey were left in the gastrozooids from the preceding day; digestion experiments suggest that nearly all prey should have been egested in the 10.5 h between dusk and dawn. (3) No prey were egested between sunrise (when siphonophore feeding is assumed to commence) and the time when the siphonophores were preserved; siphonophores were collected 4 to 6 h following sunrise, and digestion experiments suggest that prey remain in the gastrozooids for more than 6 h. (4) Plankton net tows accurately reflected the abundances of prey in situ and net avoidance by large zooplankton was not significant.

Calculation of daily predation and caloric intake of Rosacea cymbiformis required the assumption that siphonophore predation was constant throughout their feeding period. This assumption is unavoidable since data on the diurnal variation of siphonophore feeding are not available. Siphonophore feeding was shown to differ with prey density. If prey densities differed over the day, so would the rate of prey capture. An additional problem in the caloric calculations arises from the use of preserved zooplankton to derive length versus dry weight regressions. Preservation may have lowered dry weights by up to 30% without decreasing prey length (Durbin and Durbin, 1978). Although the exact effects of preservation upon the length-dry weight relationships derived for prey of R. cymbiformis are not known, the values compare well with measurements on unpreserved copepod specimens (Comita et al., 1966; Durbin and Durbin, 1978) and on preserved copepods (Feigenbaum, 1979). Comparison of the length-dry weight regression for chaetognaths (Sagitta enflata) with that in Feigenbaum (1979) showed close correspondence for small specimens, but an increasing deviation with increasing length, possibly because of disproportionately greater shrinkage of large specimens with preservation.

Approximation was also necessary in the conversion for dry weight to calories. Caloric values measured by Shuskina and Sokolova (1972) on formalin-preserved zooplankton and on unpreserved specimens by Musayeva and Sokolova (1979) are considerably lower than values calculated in this study and as measured for unpreserved copepods by Comita et al. (1966). The caloric consumption calculated in this study for Rosacea cymbiformis probably underestimates the true values, since (1) only 89% of the consumed prey could be measured and were included in the calculations, and (2) dry weights may have been reduced due to preservation of the available prey. Nevertheless, values of caloric consumption presented here are believed to be reasonable estimates.

Food utilization and predation impact of some gelatinous predators have been investigated recently. Hirota (1974) calculated the carbon ingested from gut contents in the ctenophore Pleurobrachia bachei, but used ingestion rates measured in the laboratory to calculate a carbon budget (Hirota, 1972). Other investigators have used laboratory ingestion rates to calculate carbon budgets for the ctenophores Mnemiopsis mccradyi and P. bachei (Reeve et al., 1978), and also to estimate the predation impact of M. leidyi (Miller, 1970; Kremer, 1976). Respiration measurements have been used to extrapolate ingestion rates and predation impact for the ctenophore M. leidyi (Miller, 1970), and the chaetognath Sagitta elegans (Sameoto, 1972). Biggs (1976) used respiration and short-term growth in the siphonophore Agalma okeni to calculate the caloric intake necessary to balance metabolism. Szyper (1978) and Feigenbaum (1979) quantified in situ predation by the chaetognath Sagitta enflata, and Szyper estimated a population impact based on field densities of chaetognaths and their copepod prey.

The present study on in situ prey consumption by the siphonophore Rosacea cymbiformis in the Gulf of California allowed calculation of daily predation rates, caloric consumption, and predation impact on zooplankton populations. This siphonophore species was estimated to consume 2.4 to 8.2 times the number of calories required to balance metabolism. According to these estimates, 41 to 88% of the calories assimilated could be available for growth and reproduction. No information is available on growth or reproductive rates of this siphonophore. Chains of R. cymbiformis were encountered by divers at densities of from 1 siphonophore colony in 10 m^3 to densities less than 1 in 125 m^3. With prey densities of 1 500 m^{-3}, it seems unlikely that siphonophores at the observed densities would affect prey populations significantly. The largest copepods, which comprised 1.04% of the prey available,

averaged densities of 15.6 m^{-3} in the channel. An average-sized colony of R. cymbiformis (32 gastrozooids) can be estimated to consume 8.8 of the largest copepods each day, if one uses the assumptions discussed previously. Similarly, 80.6 of the smallest copepods, having densities which averaged 1 049.4 m^{-3}, would be consumed daily. At the observed siphonophore densities, even populations of the preferred prey probably would not be significantly reduced.

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