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Feeding ecology of *Rhizophysa eysenhardti*, a siphonophore predator of fish larvae[1]

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Abstract

Analysis of the gastrozooids (stomachs) of 646 colonies of the cystonect siphonophore *Rhizophysa eysenhardti* collected by hand in the Gulf of California showed that these specimens had fed only on fish larvae. Siphonophore density during bloom conditions averaged 0.038 ± 0.004 individuals·m^{-3} in an open-water channel, and 0.91 ± 0.55 in a shallow cove. Siphonophore feeding was greater in the cove where fish larvae were more abundant than in the channel, and during dawn and dusk in the cove when prey were more available. Gastrozooid analysis and behavioral experiments showed that siphonophores fed only in the light. Digestion of fish larvae required 3–7 h, increasing with prey size. Food was assimilated by the siphonophores with 72% efficiency. Each siphonophore was estimated to consume an average of 8.8 fish larvae during a day in the cove. The heavy predation on fish larvae by *R. eysenhardti* suggests that both fish mortality and siphonophore population growth may be strongly affected.

Few comprehensive field studies have been made of the types and quantities of prey consumed by carnivorous gelatinous zooplankton, because standard net-collection methods destroy most specimens. The few species studied to date have been those which can be collected relatively undamaged by nets, like the ctenophore *Pleurobrachia bachei* (Hirota 1974) and chaetognaths of the genus *Sagitta* (Pearre 1974; Szyper 1978; Feigenbaum 1979). Only preliminary data (Biggs 1977) exist on the field diets of siphonophores, which are colonial cnidarians of the class Hydrozoa. Short term laboratory experiments have led to speculation about field rates of siphonophore feeding (Biggs 1976*a*, *b*, 1977), growth (Biggs 1976*a*, *b*), and reproduction (Carre 1975), but it has not been possible to estimate the impact of siphonophore predation because of the absence of data on population abundance and in situ predation. "Bloom" conditions of the siphonophore *Nanomia cara* reported by Rogers et al. (1978) suggested a potential for rapid population growth given abundant prey.

A bloom of the cystonect siphonophore *Rhizophysa eysenhardti* Gegenbaur 1859 was observed in the Gulf of California in spring 1978 and persisted through July and August. I measured densities of this siphonophore during the bloom in an open-water channel and in a shallow cove where tides and wind conditions concentrated the plankton, and I examined natural feeding by *R. eysenhardti* with reference to prey availability, siphonophore diel activity, and digestion and assimilation of the prey.

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Materials and methods

I collected specimens of *R. eysenhardti* during July and August 1978 in hand-held jars while snorkeling in a shallow cove of Isla Danzante (111°15′W,

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25°45′N), a small island 5 km east of Puerto Escondido, Baja California Sur, and while SCUBA diving at depths of 5–15 m midway in the open channel between the island and the Baja Peninsula.

Feeding, digestion, and assimilation—Siphonophores were preserved in the channel by injecting Formalin immediately into the jar with a syringe during the SCUBA dive and in the cove within 15 min of collection. Gastrozooid (stomach) contents were not ejected during preservation. The proportions of gastrozooids containing prey and the digestive state of the prey were determined under 6–12× magnification.

Digestion rates of prey were determined from siphonophores that had just ingested fish larvae in the cove, or dead larvae placed near their gastrozooids. These specimens were collected individually and kept in 500-ml jars at ambient water temperature (23° ± 1°C). The fish larvae visible through the semitransparent gastrozooids were observed at hourly intervals and put into three categories: least digestion—eyes of larvae discrete; intermediate digestion—black eye pigment dispersed, much body tissue remaining; most digestion—eye pigment coalesced into an elongate rod, no body tissue apparent. The time until egestion of the consolidated waste was also determined. Some siphonophores were preserved at 30-min intervals after ingestion of a fish larva for comparison with field-preserved specimens.

Assimilation of the food was calculated according to the ratios of ash-free dry weight to dry weight in the ingested food and in the waste pellets (Conover 1966). This procedure assumes that none of the inorganic fraction of the food is assimilated. Although this assumption may introduce some error (Forster and Gabbott 1971; Cosper and Reeve 1975), separate determination of assimilation of the inorganic fraction was not possible under field conditions. Schooling fish larvae were captured in the cove with an insect net by divers. Standard length was measured to the nearest millimeter. The larvae then were swirled in distilled water, placed individually on preashed, preweighed aluminum foil squares in a desiccator, dried for 24 h in a 60°C oven, and weighed to the nearest 1 μg on a Cahn electrobalance. Specimens were then ashed 2–4 h in a 450°–500°C oven and reweighed.

Waste pellets egested from the siphonophore gastrozooids were drawn into a pipette from jars containing siphonophores, placed on preashed, preweighed aluminum foil squares, rinsed gently with distilled water, and stored in a desiccator. Dry and ash weights were determined as before.

Densities—Densities were determined by counting the number of siphonophores which passed through a 1-m-diam hoop with a flowmeter. In the cove, where bottom depths were 1.5–7 m, I made 16 measurements (avg vol sampled = 33.1 m^3) while snorkling at the surface. In the channel, 32 measurements were made (avg vol sampled = 33.6 m^3) at 5-m depth. All siphonophore densities were determined between 1000 and 1200 hours.

To determine the relative densities of fish larvae in the cove and in the channel between 1000 and 1200 hours, I used a 0.75-m-diam, 253-μm-mesh plankton net with flowmeter. I made one horizontal net tow at 5–10-m depth on each of 9 days immediately after a dive in the channel (avg vol sampled = 24 m^3). On four of those days, I made a tow at 3–5-m depth in the cove (avg vol sampled = 20 m^3). I preserved the samples immediately in Formalin and the fish larvae later were counted and identified to family.

I also determined the densities of fish larvae in the surface waters of the cove on 2 days in July 1979 at four times of day: after sunrise, but preceding direct sunlight; midday; late afternoon with direct sunlight; and just before sunset, but without direct sunlight. I made 5-min horizontal tows with a 0.5-m-diam, 70-μm-mesh plankton net at 3–5-m depth. I preserved the samples immediately, and all fish larvae were counted.

It should be emphasized that these measurements of fish larval density are

comparable only within each sampling set since the two sets were made in different years with different nets. The tows were made at high speeds (1–1.5 km·h^{-1}) for short times to minimize clogging and avoidance of the nets. Densities estimated from net tows should be considered approximate, particularly since fish larvae were seen schooling in the cove.

Diel feeding activity—In a laboratory aboard the RV *G. W. Pierce,* I observed the feeding behavior in the light and dark of seven specimens of *R. eysenhardti,* collected by divers at 15–25-m depth during the day in the Sargasso Sea during July 1979. Animals were kept in tall jars or 2-liter graduated cylinders at surface temperature (26°C). I determined whether the tentacles were contracted or extended at intervals of 1–4 h in the dark or under fluorescent light, during both day and night. The lighting conditions were changed several times during the 48-h observation period for each specimen. Specimens in the dark were observed for a few seconds by the reflected light from a flashlight with a red filter.

Results

Rhizophysa eysenhardti collected from the Gulf of California had from 1 to 28 gastrozooids (mean 7.2 ± 4.3). Large colonies were >1 m long. There were from 0 to 1.8 colonies·m^{-3} (0.91 ± 0.55) in the cove and from 0 to 0.1 (0.038 ± 0.004) in the channel, about 20 times fewer than in the cove. Densities of *N. cara* during bloom conditions ranged from 0.1 to 7–8 colonies·m^{-3} in the Gulf of Maine (Rogers et al. 1978). *Nanomia bijuga* in the deep scattering layer occurred in densities of 0.3 colonies·m^{-3} (Barham 1963). In contrast, the greatest density Biggs (1976*b*) observed for physonect siphonophores—the most abundant large siphonophores in the northern Sargasso Sea—was one colony per 4,300 m^3 (0.0002 per m^3). The densities of siphonophores in coastal areas can apparently be much higher than in oceanic areas.

Diel pattern of siphonophore feeding—Distended gastrozooids in colonies of *R. eysenhardti* contained fish larvae at varying degrees of digestion (Fig. 1A). Only a small proportion of gastrozooids contained intact or undigested prey. Most frequently, only a small black spot (consolidated waste) within the gastrozooid showed that a larva had been captured. No prey other than fish larvae were found in 646 colonies of *R. eysenhardti,* totaling 4,586 gastrozooids.

A total of 485 colonies (3,074 gastrozooids) were collected from a shallow cove throughout the day and into the night in 41 samples over a 2-month period. The data clearly show that the siphonophores did not consume prey equally at all times (Fig. 1A). There was little or no feeding before dawn or after dusk. The percentage of gastrozooids containing fish larvae increased rapidly after sunrise and decreased rapidly after sunset. Only recently caught larvae were found in the dawn samples, while at night only a few, highly digested larvae remained. Feeding was most intense in early morning and late afternoon, with most of the recently caught larvae in the gastrozooids at those times.

Fish larvae were abundant in the surface water of the cove at night (30.5·m^{-3}). Hence, their absence cannot explain the absence of siphonophore feeding before dawn and after dusk. At night, siphonophores held their tentacles contracted in loose spirals close to the main stem, not extended in a fishing position as during the day. Laboratory observations showed that the tentacles were extended only in the light (Table 1). Feeding behavior depended on light or dark conditions ($P \ll 0.005$), but not on time of day or night (test of independence in a multiway table: Sokal and Rohlf 1969). These data indicate that *R. eysenhardti* normally feeds between sunrise and sunset.

Effect of prey availability on siphonophore feeding—Since siphonophores kept their tentacles extended throughout the daylight hours, I thought that differences in the availability of fish larvae might explain the bimodal prey capture pattern (Fig. 1A). Plankton net tows in the surface waters of the cove at four times during the day collected markedly

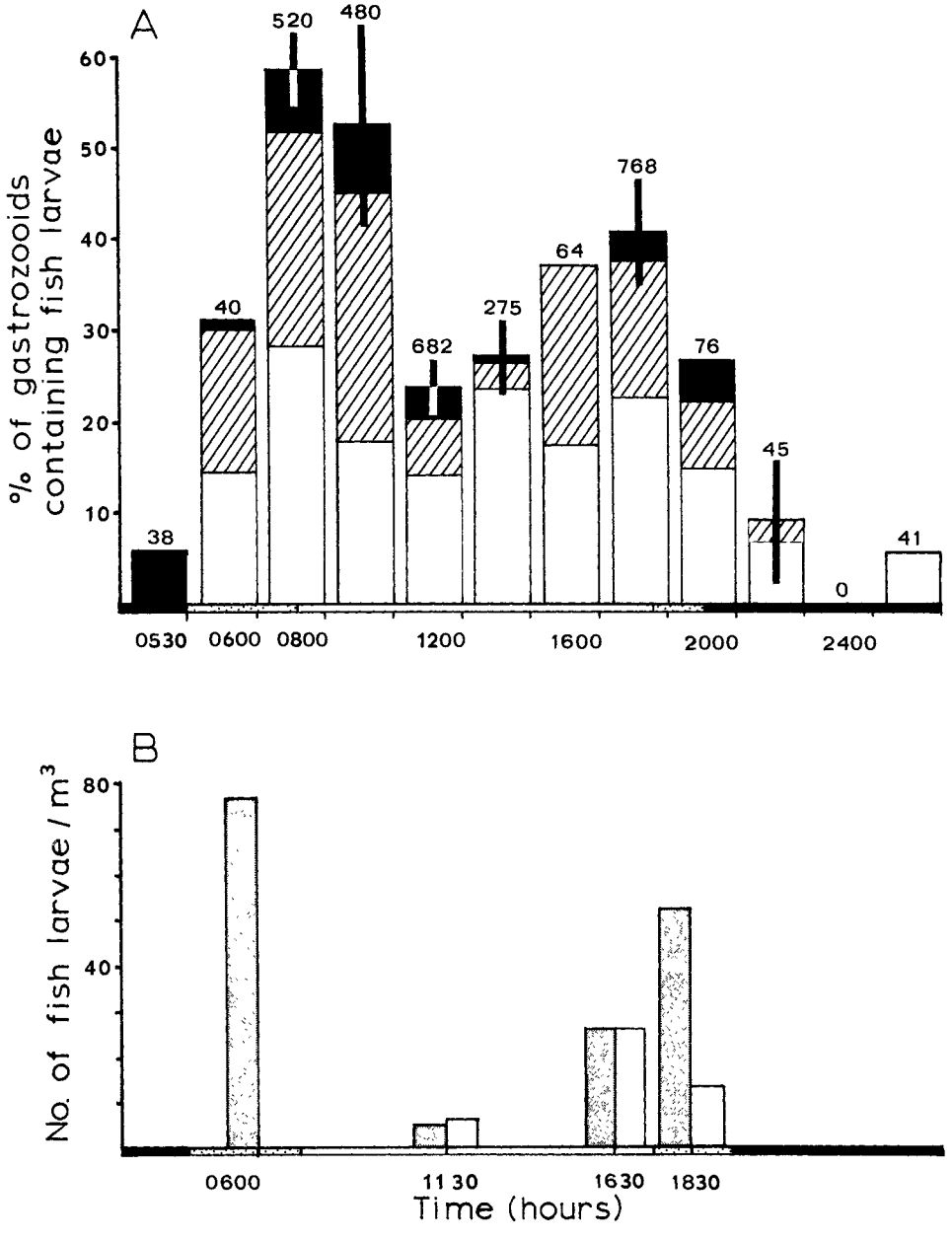

Fig. 1. Comparison of siphonophore predation and availability of fish larvae throughout the day in the cove. Shading beneath horizontal axes—darkness; stippling—reduced light due to shadow. A. Percentages of gastrozooids containing fish larvae. Data presented in 2-h intervals, except between 0500 and 0600 (0.5-h intervals) to show initiation of feeding at dawn. Proportions of recently caught (shaded), intermediate (hatched), and highly digested (open) prey are indicated. Number of gastrozooids examined shown above each bar. (SE marked with bars where samples were collected on four or more days.) B. Abundance of fish larvae in net tows taken at four times over each of 2 days (open bars—26 July; stippled bars—31 July 1979).

Table 1. Laboratory observations on tentacle extension of siphonophores exposed to periods of light and dark throughout day and night.

	Light		Dark	
	day	night	day	night
No. observations	36	19	24	21
No. extended	36	18	1	0

different numbers of fish larvae (Fig. 1B). The average abundance at each of the four sampling times showed a significant ($P < 0.05$) positive regression on the percentage of siphonophore gastrozooids containing prey at those times plus 1.5 h (to compensate for the residence time of fish larvae in the gastrozooids). The sampling does not firmly establish the daily pattern of larval fish abundance in the cove, but the results do suggest that the pattern of siphonophore feeding was influenced by the availability of the prey. Greater larval abundance corresponded to the periods of greater siphonophore feeding in early morning and late afternoon. The day–night vertical distributions of some pelagic fish larvae differ (Ahlstrom 1959; Russell 1976; Eldridge et al. 1978), and changes in their vertical movements and schooling behavior are related to light intensities and to dawn and dusk (Blaxter 1973; Smith et al. 1978; Shaw 1961). The pattern of daytime feeding by *R. eysenhardti* may thus be explained by the greater availability of fish larvae at low light intensities, when schools may disperse or the larvae may swim closer to the surface.

I also investigated the effect of prey availability on siphonophore feeding by comparing feeding in the channel and in the cove. *Rhizophysa* was collected between 0900 and 1200 hours in the channel on 19 days (161 colonies; 1,512 gastrozooids); the percentage of gastrozooids containing fish larvae was less than half that from cove samples during the same time period (Fig. 2). Digestion stages indicated that most of the fish larvae had been caught more than 2 h before the sampling at 0900. Siphonophores in both channel and cove captured more prey

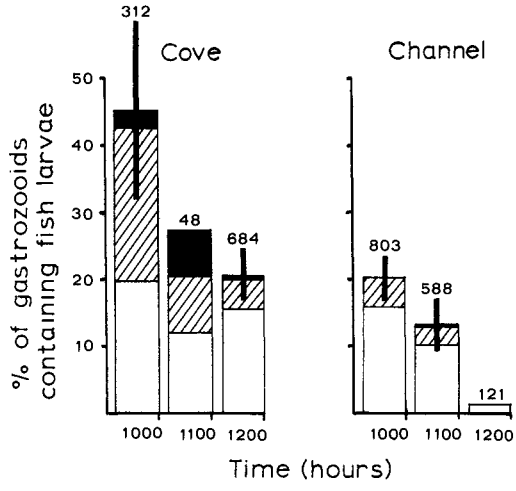

Fig. 2. Comparison of siphonophore predation from 0900–1200 hours in cove and in channel. Degrees of prey digestion and number of gastrozooids designated as in Fig. 1. (SE marked with bars when calculated on three or more samples.)

near dawn when larvae were likely to be more available.

The fish larvae in cove plankton tows were 15 times more abundant than in channel tows taken only minutes earlier (Table 2). Larvae of the same families of fish were present in both, but in very different proportions (Tables 2, 3). Mesopelagic fish constituted 75.6% of the channel larvae, but only 27.1% of those in the cove. Of the ingested fish larvae

Table 2. Mean abundances of families of fish larvae and siphonophores compared between cove and channel.

	Abundance (No. 100 m^{-3})	
	Cove	Channel
Mesopelagic fish		
Myctophidae	695	120
Gonostomatidae	12	4
Shallow-reef fish		
Sciaenidae	1,095	17
Serranidae	658	0
Gobiidae	95	11
Misc. fish	50	12
Total	2,605	164
Siphonophore		
Rhizophysa	91	4

Table 3. Percentages of types of fish larvae available (A), compared to percentages of types identified from siphonophore gastrozooids (G), from same depth stratum in cove and channel.

Fish type	Cove		Channel	
	A	G	A	G
Mesopelagic	27.2	17.5	75.6	85.7
Shallow-reef	68.9	77.5	17.1	0
Misc.	1.9	5.0	7.3	14.3
No. larvae		40.0		7.0

that could be identified, the percentages of types captured were similar to those available in both areas (Table 3). Differences between the numbers of mesopelagic, shallow-reef, and miscellaneous fish larvae captured and those expected from the percentages available were not significant (χ^2) in either areas.

Digestion and assimilation—The digestion of fish larvae by *R. eysenhardti* can take from 3 h for small prey (5 mm) to 7 h for large prey (15 mm). The duration of the three stages of digestion increased with prey size; fish larvae preserved in stage 1 (recently caught) were captured no more than 2 h earlier, while those preserved in stage 3 (highly digested) had been captured from 3 to 6 h earlier (Table 4).

The state of digestion of captured prey shows that the siphonophores contained only recently caught prey at dawn and only highly digested prey at night, and that most fish larvae were moderately or highly digested in midday samples (Fig. 1A). Feeding in the cove continued throughout the day. The decrease in the percentage of gastrozooids containing larval remains in morning channel samples indicates that most capture occurred before sampling at 0900 (Fig. 2). Only a few, highly digested prey remained in gastrozooids by 1200, implying a maximum digestion time of 6–7 h, which agrees with experimental results.

Table 5 gives the mean values of dry weights and ash-free dry weights for fish larvae of three size classes, and for waste egested from *R. eysenhardti*. The ratios of ash-free dry weight to dry weight were averaged for 46 waste pellets, and for 15 fish larvae (4–15-mm standard length). Ingested prey was assimilated with 72% efficiency by *R. eysenhardti*. This value is comparable to assimilation efficiencies measured for other carnivorous zooplankton: the ctenophore *Mnemiopsis*, 52–75% (Reeve et al. 1978), the pteropod *Clione*, >90% (Conover and Lalli 1974), and the chaetognath *Sagitta*, 80% (Cosper and Reeve 1975).

Discussion

Rhizophysa eysenhardti fed only on larval fish; some selective mechanism apparently excluded crustacean prey of comparable size and activity. Other species of siphonophores that consumed fish larvae also consumed crustacean prey (Purcell 1980). Such differential capture of prey could be due to various characteristics of the nematocysts and tentacle structure. More nematocysts of *R. eysenhardti* may be chemically stimulated by contact with the mucus that covers fish larvae than by contact with a crustacean exoskeleton. The toxins in the nematocysts of *R. eysenhardti* may be more effective against vertebrate prey than against invertebrates. The injection

Table 4. Siphonophore digestion rates for three size classes of fish larvae. Digestion stages 1, 2, and 3 correspond to those shown graphically in Figs. 1, 2 (recently caught, intermediate, and highly digested). Times of each digestion stage and of egestion indicate mean number of hours since ingestion of prey ±SD. Number of replicates shown in parentheses.

Size of larva (mm)	Hours from ingestion to digestion stage			
	1	2	3	egested
4–7	1.0 (3)	2.0 (4)	3.1±1.0 (6)	3.6±1.5 (15)
8–12	1.0 (1)	2.3±0.9 (19)	5.0 (1)	4.0±1.0 (26)
13–15	2.0 (3)	3.0±1.5 (7)	5.8±1.7 (8)	5.1±1.7 (3)

Table 5. Dry weights (mg), ash-free dry weights (mg), and calculated caloric values of three size classes of fish larvae, and of waste egested from siphonophores. Percentage of intact fish larvae of each size found in gastrozooids also included (N = 40). Number of replicates shown in parentheses.

Size of larva (mm)	Dry wt	Ash-free dry wt	Avg cal per larva	% of consumed larvae
4–7	0.40±0.23 (7)	0.34±0.13 (5)	2.0	40
8–12	3.24±1.10 (14)	2.88±1.75 (6)	16.5	50
13–15	6.15±1.45 (6)	5.53±1.18 (4)	31.3	10
Waste	0.34±0.25 (58)	0.13±0.08 (48)		

of extracts from *Physalia* nematocysts killed both fish and crabs (Lane and Dodge 1958); however, those results cannot eliminate the possibility of a different action of siphonophore-injected doses of toxin on small fish and on planktonic crustaceans. The tentacles of siphonophores in the suborder Cystonectae lack the stretch-receptive nematocyst battery complexes with several nematocyst types which are present in the suborders Calycophoreae and Physonectae. Lacking these nematocyst complexes, the tentacles of cystonect siphonophores may require strong stretching by prey for nematocyst discharge, making them insensitive to small prey. The nematocysts in the tentacles of *R. eysenhardti* appear to be of a single type, similar to the isorhizas described for *Physalia* by Totton (1960). These nematocysts may not be effective in entangling crustacean prey or in penetrating the exoskeleton of crustaceans. I saw specimens of *R. eysenhardti* being pulled through the water attached by their tentacles to large, swimming copepods. Prey removed from the gastrozooids of *Rhizophysa filiformis* included not only fish but alcyopid polychaetes (Biggs 1977), which have a thin exoskeleton that might be more easily penetrated than that of a crustacean.

Gastrozooids of *R. eysenhardti*, *R. filiformis*, and *Bathyphysa sibogae* from the Sargasso Sea all contained fish larvae (pers. obs.). Although there are no comprehensive data on the diet of *Physalia physalis*, observations have been made on its capture and digestion of fish (Wilson 1947). This limited information on four of the five recognized species (Totton 1965) in three genera suggests that siphonophores of the suborder Cystonectae may be primarily predators on fish and fish larvae.

My observations showed that *R. eysenhardti* feeds only during daylight, but the fish larval prey are at least as abundant in surface waters at night as during the day (e.g. Ahlstrom 1959). Exclusively daytime feeding in *R. eysenhardti* may have evolved in response to the large numbers of vertically migrating mesopelagic fish and crustaceans in the surface waters at night. Retraction of the siphonophores' tentacles during darkness would prevent their entangling potentially destructive prey that they could not capture and ingest.

Although *R. eysenhardti* captured more prey when prey availability was greater, siphonophore feeding in the cove was only twice that in the channel but larval abundance was 15 times greater. The feeding rate of tentaculate predators may be limited by the handling time of prey items, as suggested by evidence for ctenophores (Reeve et al. 1978). Complete ingestion of fish larvae (5–15-mm standard length) by five undisturbed *R. eysenhardti* took 8 min. Tentacles without fish larvae remained extended. Gastrozooids containing fish larvae ingested additional larvae, but no more than three were found within any gastrozooid. Feeding in these siphonophores may be limited by both prey handling time and space within the gastrozooids.

Rhizophysa eysenhardti was found in extremely high densities in shoreline areas that harbored large numbers of fish larvae. To estimate the daily siphonophore predation on fish larvae in the

cove, I added the average number of fish larvae in each siphonophore at hourly intervals during the continuous sampling period 0500–2200 hours and divided this by a standard digestion time (3.9 h) calculated from the mean digestion times for each of three sizes of fish larvae, multiplied by the proportion of each size class found in the diet (Table 5). The result, that 8.8 fish larvae were consumed per siphonophore per day in the cove, multiplied by the average siphonophore density measured in the cove ($0.91 \cdot m^{-3}$) and divided by the number of fish larvae in the cove ($28.3 \cdot m^{-3}$, avg for 11 tows), shows that 28.3% of the fish larvae could be consumed each day by *R. eysenhardti* in the surface waters of the cove.

The variability in siphonophore densities and the difficulty of accurately assessing larval fish numbers make such estimates uncertain. Siphonophore densities in the cove fluctuated over the day and between days. Densities of siphonophores were $>1 \cdot m^{-3}$ on 20 days during July and August. Even greater siphonophore predation on fish larvae could be expected during the earlier months of the bloom. The accurate assessment of the numbers of larval fish was difficult due to schooling and to the lack of information on their vertical distribution and movement in and out of the cove. The actual number of fish larvae present may be closer to the maximum number sampled than to the average number used in the calculations. I cannot estimate the siphonophore impact on larval fish populations in the open-water channel because I have no data on siphonophore feeding during much of the day, on larval abundances over the day, and on vertical distributions of both fish larvae and siphonophores.

The reproduction and population growth of siphonophores may be greatly enhanced when they can feed in high prey densities along the shoreline. The mean respiration of nine recently fed colonies of *R. eysenhardti* from the California Current, each having six or seven gastrozooids, was measured at 32 ± 13 μg of O_2 per hour per colony at 13°C (P. Kremer pers. comm.). The energy requirements of *R. eysenhardti* can be calculated from these data, assuming an oxycaloric equivalent of 5 $cal \cdot ml^{-1}$ of oxygen consumed (Parsons and Takahashi 1977). A colony of average size (6–7 gastrozooids) would require 2.7 $cal \cdot d^{-1}$ at 13°C for maintenance. At the higher temperatures in the Gulf of California (21°–23°C), a colony would require 5.4 $cal \cdot d^{-1}$, assuming a Q_{10} of 2. The caloric values of fish larvae (Table 5) were estimated according to the conversion of Osteichthyes of 5,086 $cal \cdot g$ dry wt^{-1} (Cummins and Wuycheck 1971). The caloric value of one medium fish larva (16.5 cal) multiplied by 72% assimilation gives 11.9 cal gained by the siphonophore. Thus even one fish larva far exceeds a siphonophore's metabolic needs, and considerable excess energy would be available for growth and reproduction, especially to siphonophores feeding in the cove. The extent of siphonophore mortality on the shore is not known.

These calculations are meant only to demonstrate the huge population growth potential of siphonophores with low metabolic rates that consume prey of high caloric value. Feeding along shorelines may contribute significantly to the formation of blooms of *R. eysenhardti*. Predation by *R. eysenhardti* probably has only a sporadic impact on the populations of fish larvae. Unfortunately, no data exist on the frequency, extent, or duration of blooms of this siphonophore. It was common in early spring off Santa Barbara, California, in 1978 and 1979 (pers. obs.). Extensive blooms of long duration, such as that in the Gulf of California in 1978, probably occur only periodically, but may have devastating effects on recruitment of that year-class of fish.

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