# Influence of Siphonophore Behavior upon Their Natural Diets: Evidence for Aggressive Mimicry

Abstract. *Collection by divers permitted determination of the natural diets of siphonophore species within 11 genera. Siphonophores that swim rapidly to spread their tentacles capture small prey, whereas those that swim very weakly capture much larger prey. Nematocyst batteries of two species of weak swimmers closely resemble copepods and fish larvae. Morphology, behavior, and diet suggest that these two species attract large prey by mimicking other zooplankton.*

Siphonophores, pelagic cnidarians of the class Hydrozoa, have been likened to spiders in capturing prey that bump into a nearly invisible sticky network (*1*). The tentacles of siphonophores form a three-dimensional web, armed with millions of nematocysts that inject toxin into the prey on contact. The diets of these nonvisual predators depend in part on prey behavior, including avoidance of the predators and the ability to escape if contacted (*2*). The diets of siphonophores must also depend on predator behaviors that counteract prey avoidance and escape. The types and sizes of prey captured by various siphonophores differ according to the swimming activity and gastrozooid size of the siphonophore species. In addition, two of the siphonophore species examined may attract large prey by the movements of tentacular structures that resemble small zooplankton, an indication of aggressive mimicry among zooplankton.

While scuba diving at depths of 0 to 25 m, I collected siphonophores in jars and immediately killed them in situ with formaldehyde solution. I examined ingested prey in the following numbers of colonies of these species: 60 *Bassia bassensis*, 53 *Nanomia bijuga*, 47 *Rosacea cymbiformis*, 14 *Agalma okeni*, 6 *Sulculeolaria quadrivalvis*, 3 *S. turgida*, and 11 *Diphyes dispar* from the Gulf of California (*3*); 6 *Athorybia rosacea*, 10 *S. chuni*, 3 *S. monoica*, 15 *Forskalia edwardsii*, and *F. tholoides* from both the Sargasso Sea (*4*) and the Gulf of California; 11 *Cordagalma cordiformis* and 2 *S. biloba* from the Sargasso Sea; and 13 *Sphaeronectes gracilis*, 7 *Diphyes dispar*, 5 *S. quadrivalvis*, and 2 *S. chuni* from the California current (*5*). Since species of *Sulculeolaria* and of *Forskalia* consumed similar prey, data are presented by genus. All gastrozooids ("stomachs") were dissected or mounted whole on microscope slides with cover slips for prey identification and measurement at magnifications of ×25 to ×100.

Differences in the diets of several siphonophore species corresponded to differences in their swimming patterns. Some species swim rapidly (strong swimmers), often in an arc or in spirals (*1*, *6*). These siphonophores drift between brief bouts of swimming that last 2 to 12 seconds and may be repeated up to 100 times per hour (*1*). Other species (weak swimmers), exhibit only subtle contractions or rotations to supplement water turbulence in spreading their tentacles.

The diets of strongly swimming siphonophores that have small gastrozooids consisted chiefly of small copepods (Fig. 1). In contrast, weakly swimming species that have larger gastrozooids captured a variety of relatively large prey. Regardless of swimming patterns, siphonophores that have large gastrozooids consumed large prey and, generally, a wide range of prey sizes. For example, *Nanomia*, a strong swimmer with large gastrozooids, consumed many large prey in addition to small prey. The distribution of prey sizes available in the environment, determined by plankton net tows (*7*), showed that 89 percent of available prey measured 1 mm or less, and 7 percent measured more than 4 mm (*8*). Thus the distributions of sizes of the ingested prey (Fig. 1) differed significantly (*9*) from that in the environment.

*Rosacea cymbiformis*, a weak swimmer, captured the widest variety of prey. Commonly consumed noncopepod prey measuring less than 4 mm included mollusk veliger larvae, crab zoea larvae, atlantid heteropods, and thecosome pteropods. Noncopepod prey larger than 4 mm included chaetognaths, fish larvae, crab megalopae, stomatopods, and juvenile shrimps. *Rhizophysa eysenhardti* is of special interest since it captured only fish larvae (*10*).

Siphonophores may affect the probability of encounters with different prey types by their swimming behavior. Strongly swimming siphonophores having numerous small gastrozooids captured small, common prey. These predators change locations, thus increasing their chances of encountering high-density patches of copepod prey. Weakly swimming siphonophores having fewer and larger gastrozooids captured relatively large, less common prey. Their in-

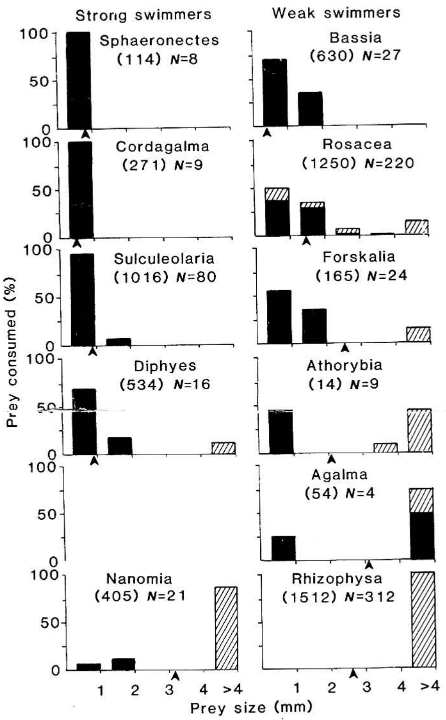


Fig. 1. Comparison of the sizes (measure of the greatest dimension, usually length) of natural prey captured by strongly and weakly swimming siphonophores. Gastrozooid length is indicated by an arrowhead under each horizontal axis. Copepod prey are indicated by black bars, noncopepod prey by diagonally shaded bars. Numbers of gastrozooids examined are in parentheses. Percentages are based on *N*, the number of measurable prey items.

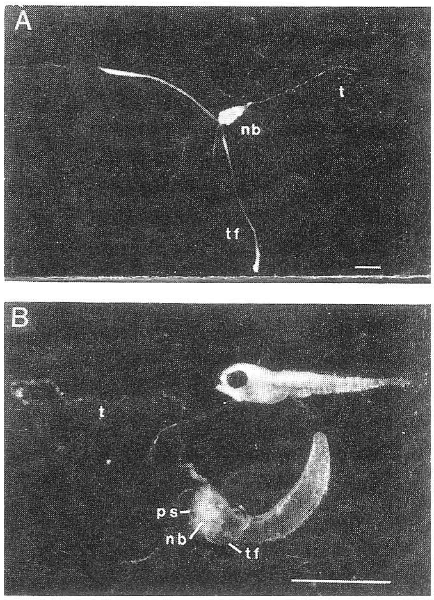


Fig. 2. (A) *Agalma okeni* nematocyst battery resembling a copepod. The terminal filaments (*tf*) appear similar to the antennae of a copepod. (B) Comparison of a fish larva (top) with a nematocyst battery from *Athorybia rosacea*. Two pigmented spots (*ps*) at the enlarged "head" resemble eyes, and two terminal filaments (*tf*) curl back in the position of pectoral fins; *t*, tentillum; *nb*, nematocyst battery. Scale bars, 1.0 mm.

activity could reduce avoidance by the more active noncopepods. Swimming to increase chance encounter with active uncommon prey would be energetically costly.

Two of the weakly swimming species may further enhance the capture of large prey by mimicking small zooplankton foods. Each siphonophore gastrozooid bears a tentacle with several branches (tentilla). In two of the three siphonophore suborders, each tentillum bears a complex, highly ordered battery of nematocysts (*11*), which fires explosively upon stretching of an elastic ligament that joins one or two terminal filaments to the battery. The coiled nematocyst batteries of *Agalma okeni* are red, with two terminal filaments projecting from one end. These structures resemble copepods with two long antennae (Fig. 2A). Laboratory observations of six specimens, which spread their tentacles in containers of seawater, showed that each tentillum contracts independently at variable intervals between 5 and 30 seconds. This motion resembles the darting swimming of a calanoid copepod. A specimen of *A. okeni* with two gastrozooids had 18 such "lures." *Agalma okeni* gastrozooids contained crab megalopa larvae (*1*), large copepods, and euphausiids, all of which eat copepods (*12*). This suggests that predators of copepods may be attracted by either visual or vibrational stimuli (*13*) to feed upon the nematocyst-packed lures, thus becoming prey for the siphonophore instead.

Some of the nematocyst batteries in *Athorybia rosacea* are elongated structures resembling small fish larvae (Fig. 2B). The tentilla of five specimens observed in the laboratory contracted rapidly two or three times, with a pause of a few seconds separating each bout. The resultant motions of the nematocyst battery are similar to the swimming or feeding movements of a larval fish. In a specimen of *A. rosacea* having two gastrozooids, nine of the nematocyst batteries resembled fish larvae. These were interspersed among 76 small oval batteries that resembled small copepods or nauplii. The *A. rosacea* gastrozooids contained fish larvae, chaetognaths, and a shrimp larva. Chaetognaths are known to consume fish larvae (*14*). This suggests that predators of fish larvae may be attracted to the fishlike nematocyst batteries. In addition, fish larvae may be attracted to school with the batteries that resemble other fish larvae.

The significance of the above results is threefold. (i) The methods enabled the determination of the natural diets of siphonophores. The few previous studies on other gelatinous planktonic carnivores have been limited to species that could be collected relatively undamaged in nets or at the surface (*2, 15, 16*). Ingestion of prey concentrated in nets can introduce artifacts in feeding studies (*17*). (ii) Differences in the diets of several siphonophore species showed a correlation with differences in their structure and behavior. (iii) This appears to be the first report of aggressive mimicry in zooplankton. Other animals which use lures to entice prey include angler fish (*18, 19*), bolus spiders (*18*), and fireflies (*20*).

Studies of the natural feeding of zooplankton species are necessary for understanding the ecology of pelagic communities.

JENNIFER E. PURCELL
*Department of Biological Sciences and Marine Science Institute, University of California, Santa Barbara 93106*

### References and Notes

1. D. C. Biggs, thesis, Woods Hole Oceanographic Institution (1976); *Mar. Behav. Physiol.* **4**, 261 (1977).
2. J. Hirota, *U.S. Fish Wildl. Serv. Fish. Bull.* **72**, 295 (1974).
3. 111°15′W, 25°45′N, July and August 1978.
4. R.V. *G. W. Pierce*, Woods Hole Oceanographic Institution cruise, 18 June to 16 July 1979.
5. Collections were made off Santa Catalina Island, November 1979, and off San Diego, R.V. *Severiana*, Scripps Institution of Oceanography cruise, May 1979, and R.V. *Lulu*, Woods Hole Oceanographic Institution cruise, September 1979.
6. G. O. Mackie and D. A. Boag, *Publ. Stn. Zool. Napoli* **33**, 178 (1963).
7. The percentages given are averages from nine tows in the Gulf of California (*3*). Five-minute horizontal tows were taken with a plankton net (0.75 m in diameter; 150-$\mu$m mesh). Zooplankton known to be prey for siphonophores were counted from subsamples. Presumably, the distribution of zooplankton sizes would be similar in the Sargasso Sea and in the California current.
8. These percentages probably underestimate small zooplankton that passed through the net. Chaetognaths comprised 33 percent of prey measuring more than 4 mm.
9. Small sample size prevented statistical testing for *Diphyes*, *Athorybia*, and *Agalma*. The percentage of available prey measuring less than 2 mm was compared to that consumed by each genus. All genera tested showed significant differences ($P < .001$), except *Forskalia*. Testing the equality of two percentages: R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, 1969), pp. 608–609.
10. J. E. Purcell, in preparation.
11. One nematocyst battery contains about 1700 nematocysts of four kinds [L. H. Hymen, *The Invertebrates* (McGraw-Hill, New York, 1940), vol. 1, p. 473].
12. M. V. Lebour, *J. Mar. Biol. Assoc. U.K.* **12**, 644 (1922); R. McDonald, *ibid.* **14**, 753 (1927); V. J. H. Hu, *Limnol. Oceanogr.* **23**, 296 (1978); J. D. Costlow, Jr., C. G. Bookhout, R. J. Monroe, *Physiol. Zool.* **39**, 81 (1966).
13. G. A. Horridge and P. S. Boulton, *Proc. R. Soc. London Ser. B* **168**, 413 (1967).
14. D. Kulhmann, *Ber. Dtsch. Wiss. Kommn. Meeresforsch.* **25**, 163 (1977).
15. M. D. Rowe, thesis, University of Hawaii (1971); J. P. Szyper, *Estuarine Coastal Mar. Sci.* **7**, 567 (1978); D. Feigenbaum, *Mar. Biol.* **54**, 75 (1979).
16. R. Bieri, *Pac. Sci.* **15**, 553 (1961); R. Bieri, *Publ. Seto Mar. Biol. Lab.* **17**, 305 (1970).
17. T. M. Lancraft and B. H. Robison, *U.S. Fish Wildl. Serv. Fish. Bull.*, in press.
18. W. Wickler, *Mimicry in Plants and Animals* (McGraw-Hill, New York, 1968).
19. T. W. Pietsch and D. B. Grobecker, *Science* **201**, 369 (1978).
20. J. E. Lloyd, *ibid.* **187**, 452 (1975).
21. I thank A. Alldredge, G. R. Harbison, J. King, P. Kremer, S. Liedle, V. McAlister, and J. Stretch for diving assistance, J. King for photography, and A. Alldredge, B. Robison, and J. King for aid in preparing the manuscript. Supported by NSF grant OCE 76-23534, and the International Women's Fishing Association. The Marine Science Institute of the University of California, Santa Barbara, provided field equipment; use of the Catalina Marine Science Center of the University of Southern California was generously provided; cruises aboard Woods Hole Oceanographic Institution vessels were made possible by G. R. Harbison and L. P. Madin.

23 January 1980; revised 20 March 1980