FEEDING BEHAVIOR OF TENTACULATE PREDATORS: IN SITU OBSERVATIONS AND A CONCEPTUAL MODEL

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ABSTRACT

The recent focus on behavior of individual zooplankters has led to several models describing predatory encounters; in this paper a general model is extended to gelatinous zooplankton that catch prey with tentacles. Because of their large size and fragility, these organisms are best observed *in situ* by divers. Observations on the feeding behavior of several medusae, siphonophores, and ctenophores are reported, along with information on diet composition and measurements of tentacle size, spacing, and deployment pattern made from photographs or videotapes. From these data two additional parameters affecting the probability of prey capture can be estimated. The "encounter zone" is the space around the predator in which the tentacles may be found, and the "tentacle density" is the fraction of that space actually filled with tentacles. These spatial parameters, and others relating to predator size, prey swimming speed and pattern, prey size and type, and nematocyst characteristics are incorporated into a conceptual model of prey selection and capture by tentaculate feeders.

In the last decade, new techniques have shifted the focus of research in zooplankton behavior from observation of large scale phenomena like schooling and diel migration to the detailed study of behavior of individual zooplankters (Alcaraz et al., 1980). The attention of zooplankton biologists has been redirected to single animals and their repertoire of activities. Instead of inferring behavior of individuals from the observed properties of populations, it becomes possible to explain and predict characteristics of populations from the observed behavior of individuals.

Data on the sensory capabilities and related behavior of predators have made possible models of predatory encounters between individual organisms. Gerritsen and Strickler (1977) developed a mathematical model based on freshwater zooplankton, which expressed the rate of predation by an invertebrate predator on similar-sized prey as a function of several physical and behavioral parameters. Their model discussed the role of the "encounter radius," the distance at which a predator could detect and respond to prey, and the relative swimming speeds of predator and prey in determining encounter frequencies. Giguere et al. (1982) subsequently modified the basic model to accommodate a stationary "ambush" predator with a cylindrical encounter field around it. The predators in these models are "raptors" (Greene, 1985), which detect the prey mechanically, and then make active, directed attacks toward them.

Many marine zooplankton predators are entangling predators (Greene, 1985). Such non-visual organisms as radiolaria, foraminifera, medusae, siphonophores and ctenophores catch prey without an organism-level response or active chase by entangling them in pseudopodia or tentacles. There are important functional differences between these predators and the active raptors. Encounter radii are defined by the limits of the tentacles, not the sensory range. The size of the encounter region may vary as tentacles are expanded and contracted, and the probability of capture within it may depend on several morphological and behavioral factors. Variations of the encounter model have been applied to some of these predators. Caron and Bé (1984) used a simple version to predict capture of copepods by pelagic forams. The encounter radius of the predator was equal

to the length of the foram's spines, and it was assumed that 100% of prey contacting the spines were caught. Encounters were generated only by movement of the prey, since the forams don't swim or make active responses. Greene et al. (1986) suggested a similar model to describe prey capture by the ctenophore *Pleurobrachia*, in which encounter rate depends on the density of the prey and its swimming speed. They assumed that the size and behavior of the predator did not affect differential encounter rates with different prey.

Here I consider mechanisms of feeding in several medusae, siphonophores and ctenophores, reporting in situ observations and measurements of morphological and behavioral factors that appear to affect encounters with prey. These include the sizes of the predators, the size, spacing and arrangement of their tentacles, and aspects of their feeding and escape behavior. Also included are data on the kinds of prey eaten, based on direct observations, gut contents studies, or reports in the literature. In an attempt to extend a model of encounter between predator and prey to this diverse group of macroplanktonic, tentaculate predators, I define and estimate the values of two additional spatial parameters: the "encounter zone" around the predator in which prey are likely to be caught, and the "tentacle density" within these zones. The roles of the spatial, behavioral and physiological parameters considered are summarized in a conceptual model of prey encounter and selection by tentaculate predators.

Most of these gelatinous animals are large or fragile, and do not display normal feeding behavior in captivity. My data are therefore taken from in situ observations of undisturbed animals in the open ocean. There are disadvantages to this approach—the difficulty of controlling variables, of manipulating behavior or replicating observations, as well as logistic problems of spending time underwater. The important advantage, however, is the ability to observe normal behavior, often seeing things that cannot otherwise be seen, and determining spatial relationships that might be unnaturally cramped in confinement.

The species included here are those which I have had an opportunity to observe. They do not represent all tentaculate predators, but illustrate a fairly wide range of sizes, tentacle morphologies, and diets. Other discussions of functional morphology, locomotion, and feeding of medusae can be found in Arai and Jacobs (1980), Larson (1979; 1985), Mills (1981) and Mills and Miller (1984). Swimming, fishing and feeding behavior of siphonophores is reported by Mackie and Boag (1963), Biggs (1977), Purcell (1980; 1981; 1984; 1985), and Mackie et al. (1987). Additional data on functional morphology, and feeding behavior of ctenophores can be found in several papers, including Anderson (1974), Swanberg (1974), Harbison et al. (1978), Greene et al. (1986), Hamner et al. (1975; 1987), and Mills (1987).

MATERIALS AND METHODS

The general techniques of blue-water diving have been described by Hamner (1975) and Heine (1986). In situ behavioral studies of zooplankton also require means of recording images and observations, and making simple measurements in space and time. Information on shape, size, color, orientation and activity of organisms was recorded on film or videotape. In some cases reference objects of known size were placed in the field of view to permit measurement of absolute size. Often however, such placement would disturb the animal, so that only relative proportions could be obtained from the images. Sizes and distances too large to be covered in the field of view of a camera were sometimes measured directly by divers, using tape measures, measuring sticks or the tether lines (10 m long). Still larger distances were estimated visually, with reference to nearby objects (e.g., other divers) of known size.

The relative dimensions of animals and their parts were measured directly from projected slides or enlarged prints. For video images, measurements were made directly off the monitor by tracing onto

Table 1. Dimensions of bodies and tentacles for medusae, siphonophores and ctenophores. Body size is bell diameter for medusae, stem length for siphonophores and oral–aboral height for ctenophores (except *Cestum* = length). Tentacle and tentilla lengths are relative to body sizes listed

Species	Body size (cm)	Tentacle number	Tentilla number	Tentacle length (cm)	Tentilla length (cm)	Tentacle diameter (mm)	Tentilla diameter (mm)	Tentacle spacing (cm)
Medusae								
Calycopsis typa	3	80	—	15	—	0.10	—	1
Stomotoca pterophylla	3	2	—	120	—	0.04	—	100
Aequorea macrodactyla	10	40	—	500	—	0.07	—	10
Laodicea undulata	3	300	—	6	—	0.03	—	0.01
Dichotomia cannoides	1	50	—	15	—	0.02	—	0.1
Liriope tetraphylla	3	4	—	75	—	0.05	—	10
Solmundella bitentaculata	1	2	—	3	—	0.50	—	1
Aeginopsis laurentii	3	4	—	6	—	0.50	—	1
Solmaris spp.	1	20	—	1.5	—	0.02	—	0.1
Pelagia noctiluca	10	8	—	300	—	0.10	—	100
Siphonophores								
Forskalia spp.	60	60	3,000	48	2.0	0.10	0.02	10
Sulculeolaria spp.	80	400	24,000	32	0.5	0.10	0.02	0.1
Ctenophores								
Mertensia ovum	4	2	2,000	60	8.0	0.04	0.02	0.1
Callianira bialata	5	2	1,000	55	7.5	0.04	0.02	1
Hormiphora spp.	5	2	200	500	0.5	0.07	0.42	10
Lampea pancerina	5	2	100	500	0.5	0.05	0.02	100
Leucothea multicornis	12	—	500	—	—	—	—	—
Cestum veneris	80	—	3,000	—	4.0	—	—	0.01

clear acetate, or from prints of single video frames. Measurements were made from several individuals when possible, although suitable photographs or videotapes were often available only for single individuals. The lengths of tentacles, tentilla (tentacle side branches), or other structures were expressed as multiples of bell diameter in medusae, of stomodeal height in ctenophores and of stem length in siphonophores.

These body dimensions are known for most species, allowing estimates of the absolute lengths of the tentacles. Length of very long tentacles was estimated in situ. Numbers of tentacles were determined from photographs, videotapes or literature data and are approximate in most cases. Total numbers of tentilla were estimated by counting the tentilla on a section of tentacle and multiplying by the length and number of the tentacles. Diameter of tentacles and tentilla were measured from photographs wherever possible, scaled to other parts of the body and expressed in mm. In some cases, these dimensions were taken from literature reports or estimated by comparison with other organisms. Swimming speeds, and the time taken for such actions as setting and retracting tentacles or handling prey, were measured directly in situ or taken from videotapes.

RESULTS

Observations on feeding and swimming behavior are arranged here by taxonomic group. These examples represent the major groups of tentaculate predators, and reference is made to other species with similar behavior but for which detailed observations are lacking. Except for literature reports, data on prey types are from direct observations of prey capture in the field, or from recognizable gut contents in diver-collected specimens. Figure 1 illustrates several common patterns of tentacle deployment seen in medusae, siphonophores and ctenophores. The "encounter zones" around the animals (discussed below) are outlined with dotted lines, the dimensions of bodies or tentacles used to calculate the volume of these zones are indicated on the Figure, and the formulae used are given in the legend.

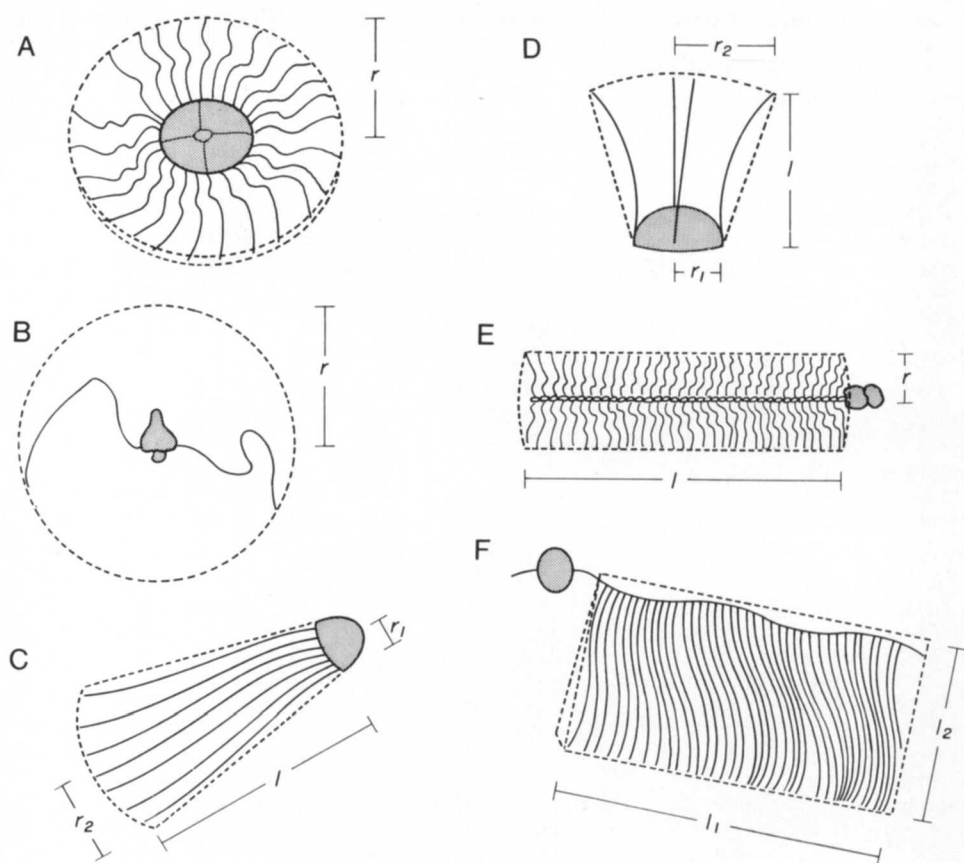Body sizes, number and length of tentacles and tentilla, and tentacle spacing

Figure 1.   Patterns of tentacle deployment seen in medusae, siphonophores and ctenophores. A. Tentacles radiate from the body, filling a disk-shaped space. Volumes of encounter zones of this shape are calculated as cylinders ($V = \pi r^2 h$) where r = the tentacle extension + half the body diameter and h = a nominal thickness of 1 cm. B. tentacles are somewhere within a sphere around the body, the volume of which is calculated by $V = 4/3\pi r^3$, where r = average tentacle extension. C. Tentacles stream behind the body, filling a truncated cone. The volume is given by $V = 1/3\pi L(r_1^2 + r_2^2 + r_1 r_2)$; r_1 = half the body diameter, r_2 = half the maximum spread of the tentacles, L = the tentacle extension. D. Tentacles are held ahead of the body in a cylinder or truncated cone. Volume is calculated as in C or E. E. Tentacles radiate from a long stem, filling a cylindrical space. The volume is calculated as $V = \pi r^2 L$, where r = the average tentacle extension and L = the stem length. F. Tentacles or tentilla form a nearly flat curtain. Some siphonophores may have encounter zones of this shape, with L_1 = the stem length and L_2 = the tentacle length. The body surface zone of *Cestum veneris* is of this shape also. Encounter zones for cydippid ctenophores with this tentacle pattern are considered to be spherical, calculated as in B.

for most of the species described below are given in Table 1. For medusae, body size is the bell diameter, for siphonophores it is the total stem length, and for ctenophores the oral-aboral height (except *Cestum,* which is total width). Sizes in Table 1 are for the particular specimens observed, and are typical adult values. Siphonophores increase in length as they grow; the specimens listed here are fairly large ones. Lengths of tentacles and tentilla are for animals of the given body sizes. Tentacle spacing is the average distance between adjacent tentacles (or tentilla), as measured from photographs or estimated in situ. The spacing varies with distance from the body and movement of the animal or water, so values in

Table 1 are given only to orders of magnitude, for comparison among the different predators.

Medusae

Anthomedusae

Calycopsis typa. —This species has a firm, globular bell and numerous thick, hollow tentacles with bulbous tips. When fishing, the tentacles are held out radially in a disk-shaped volume about 3 times as wide as the bell (Fig. 1A). The distance between adjacent tentacles is a few millimeters at the bell and a few centimeters at the distal ends. The medusa pulses only a few times per minute, holding the tentacles quite still in either a horizontal or vertical plane. When disturbed, it swims away, pulling the tentacles behind it and contracting them over a period of about a minute. I have not observed prey capture, and have no gut contents data for *C. typa.* The spacing and stoutness of the tentacles and the nematocyst-studded bulbs at their tips suggest that this species catches large prey.

Stomotoca pterophylla. —This species has only two tentacles, which may be 40 to 50 times the bell diameter when extended. *S. pterophylla* and its congener, *S. atra,* prey on other medusae (Arai and Jacobs, 1980; Larson, 1982; Purcell and Mills, 1988). I have seen it eat *Linuche unguiculata* which were bigger than it was, as well as the smaller *Dichotomia cannoides. S. pterophylla* fishes by "long-lining"; it hangs motionless in the water, with the two tentacles stretched around it. The tentacles lie in a large spherical zone around the medusa, but occupy only a tiny fraction of its volume (Fig. 1B). Encounter depends on the prey swimming into a tentacle. The tentacles then contract, bringing the prey up against the crenulated lips, which engulf it over a period of about half an hour. Arai and Jacobs (1980) found that *S. atra* in a small container would eat any medusae offered it, and *Amphinema,* a related, smaller species with two tentacles, also eats other medusae (Lebour, 1922). Mills (1981) describes an up-and-down swimming pattern in *S. atra* which allows it to fish its tentacles through more water. Several other species in the same family (Pandeidae) also take gelatinous prey. *Eutiara mayeri* appears to specialize on ctenophores; I have seen it eating *Bolinopsis vitrea, Eurhamphaea vexilligera* and *Cestum veneris. Catablema nodulosa* eats gelatinous animals (Purcell and Mills, 1988) and *C. vesicaria* appears to prey on narco-medusae (Madin, unpubl.).

Leptomedusae

Aequorea macrodactyla. —Species of *Aequorea* are large, lenticular medusae with numerous radial canals and tentacles. *Aequorea macrodactyla* swims almost continuously, trailing tentacles behind it for a length 50 times the bell diameter or more. The related species *Rhacostoma atlanticum* and *Orchistoma pileus* have a similar fishing behavior. The tentacles form a truncated cone, larger at the distal ends where they are spread out (Fig. 1C). The distance between the tentacles at the bell margin is about one centimeter in *A. macrodactyla,* but tens of centimeters over the rest of the tentacle length. Prey that get stuck on one or more tentacles may be towed around for a while before the tentacles retract sufficiently to bring the prey to the mouth. The mouth has numerous lips and can open wide, enabling it to engulf large gelatinous animals. Once in the gastrovascular cavity, the prey shrink rapidly and are digested within an hour or two. Hyperiid amphipods ingested along with their gelatinous hosts are not killed or digested in the stomach of *Aequorea. Brachyscelus,* the amphipod parasitic on *A. macrodactyla,* commonly

lives in its gastrocoel. I have observed *A. macrodactyla* to prey on a variety of planktonic organisms—salps, ctenophores, thecosome pteropods, foraminifera, and medusae, including other *Aequorea.* Arai and Jacobs (1980) found that *A. victoria* ate a variety of other medusae in laboratory encounters.

Laodicea undulata. —This small species is very thin and flat, with hundreds of fine tentacles arranged radially around the bell (Fig. 1A, Table 1). *Laodicea* appears to behave the same during day and night. I have no information on the kinds of prey taken; most specimens seen had empty stomachs. The size and number of the tentacles suggest that the prey are small; Lebour (1923) reported that they catch copepods and larval fish.

Dichotomia cannoides. —This small leptomedusa has a conical bell, with up to 50 evenly spaced marginal tentacles. These are alternately long and short; the long ones coil into helices when contracted and extend to about ten times the bell diameter when relaxed (Table 1). *D. cannoides* is usually seen fishing at night, although tentacles are sometimes extended during the day. The medusa hangs motionless in the water, often upside down, with the tentacles radiating in a disk or cone (Fig. 1A, C). Distance between the tentacles ia a few millimeters at most. The prey are probably small crustacea, but I have no data on gut contents for this species. *Dichotomia* contain algal cells in their tissue, but the contribution of these algae to the nutrition of the medusa is not known.

Trachymedusae

Liriope tetraphylla. —This widely distributed species has a long, prehensile gastric peduncle with the stomach at the end. The 4 main tentacles extend up to 25 times the bell diameter (Table 1); four smaller, solid tentacles are not extensile. I have seen *Liriope* fishing mainly at night. It hangs motionless, mouth downwards, with the tentacles occupying a small fraction of a spherical volume around it. Prey that I have seen caught or found in the guts include small heteropods (*Firoloida*), appendicularians, crustacean larvae and juvenile fish. The closely related *Geryonia proboscidalis* is similar in form and behavior, but is larger and has 6 main tentacles. Its prey include salps, alciopid polychaetes and juvenile fish.

Narcomedusae

Solmundella bitentaculata. —This common mesopelagic species is the smallest medusa in the family Aeginidae, with a bell diameter of about 1 cm. Its two solid tentacles are about 3 times as long as the bell diameter (Table 1). In narcomedusae, the tentacles do not contract, but can curl up near the bell. They are held aborally ahead of the medusa as it swims (Fig. 1D), occupying a cylindrical or conical volume extending three bell diameters in front of the animal. I have no data on its prey. The size and arrangement of the two tentacles suggests a specialization for relatively large prey; other narcomedusae are known to eat gelatinous animals (Mills and Miller, 1984; Purcell and Mills, 1988).

Aeginopsis laurentii. —This mesopelagic species is similar to *Solmundella,* but somewhat larger and with 4 tentacles. They are also held out over the bell, forming a cone ahead of the medusa. Based on relatively few observations from submersibles, these medusae appear to swim and fish like *Solmundella*; there are no data on natural prey.

Solmaris spp.—The genus includes several small, epipelagic and mesopelagic species. The bell is quite flat and transparent, with 10 to about 30 tentacles (Table

1). Tentacles are held aborally, forming a rather broad cone (Fig. 1D), or radially (Fig. 1A). *Solmaris* remains motionless most of the time, swimming in short bursts when disturbed. I have never seen prey in the gut, but would speculate that species of *Solmaris* catch small, motile animals like copepods.

Scyphomedusae

Pelagia noctiluca.—P. noctiluca is the most cosmopolitan of the semaeostome medusae, occurring in all temperate and tropical oceans. The bell diameter ranges up to 15 cm. and the eight tentacles extend to about 30 times this dimension. *Pelagia* swims smoothly and continuously, trailing the tentacles behind in graceful arcs (Fig. 1C). The spacing between tentacles ranges from centimeters at the bell to tens of centimeters at the distal ends (Table 1). Once caught, prey are slowly pulled up to the oral arms, which engulf them and convey them into the gastrocoel. Prey items I have seen include salps, doliolids, lobate ctenophores, medusae, thecosome and pseudothecosome pteropods, foraminifera, chaetognaths and fish. Larson (1987) found additionally siphonophores, polychaetes, copepods, ostracods, isopods, amphipods and fish eggs. When feeding on salps, *Pelagia* catch entire chains and ingest dozens of salps at a time. Hyperiid amphipods ingested along with salps roam unharmed in the gastrocoel, as do the amphipods which are specific symbionts of *Pelagia*. On at least two occasions, I have collected *P. noctiluca* with gooseneck barnacles growing out of their stomachs.

Siphonophores

Physonectae

*Agalma okeni.—*Small *A. okeni* (to 5 cm) are found in surface waters during the day, but extend the tentacles and feed only at night (Biggs, 1977; Purcell, 1981). I have seen larger ones (to 20 cm stem length) near the surface only after dark; they apparently migrate vertically. *A. okeni* commonly hangs motionless in the water, with the stem held horizontally or at an angle. The tentacles extend several times the length of the stem, usually hanging down in a curtain (Fig. 1F). The siphonophore is extremely sensitive to light; it contracts the tentacles and swims rapidly away, usually horizontally, when a diver's light falls on it. Because of this behavior, I have not been able to make measurements of *A. okeni* for Table 1.

Forskalia spp.—Specimens of *F. edwardsii* and *F. tholoides* range from a few centimeters to nearly a meter in stem length. The siphosome occupies most of the length of the stem, and can contract to about half its full length. In the fishing posture, tentacles, bearing numerous fine tentilla, radiate in all directions from the siphosome, densely filling a roughly cylindrical volume (Fig. 1E). When fishing, *Forskalia* spp. remain motionless, usually in a horizontal position. Individual tentacles contract and relax, creating a "casting" effect, noted also by Mackie and Boag (1963). It is difficult to judge how long this stationary position is normally held, because the proximity of a diver probably disturbs the siphonophore prematurely. When disturbed, *Forskalia* spp. pull in the tentacles within a few seconds and swim off. The stem rotates as the animal swims, partially winding the tentacles up and hastening their full contraction. In large individuals disturbance also causes release of small clouds of reddish brown fluid from the palpons (see also Totton, 1965), and sometimes breaking off of some tentacles. The diet of *Forskalia* spp. has been reported to include copepods, amphipods, chaetognaths, molluscs, fish and fish eggs (Biggs, 1977; Purcell, 1981; 1985).

Calycophorae

Sulculeolaria spp.—These are large species, with total stem lengths reaching a meter. There are 7 to 9 recognized species of *Sulculeolaria* (Carré, 1979) which differ in details not obvious to divers. Most of the specimens we have seen are probably *S. quadrivalvis,* or *S. monoica* (Biggs, 1977). Below the two nectophores, the siphosome consists of numerous stem groups bearing tentacles with fine tentilla. The tentacles are only millimeters apart; extended, they form a dense curtain hanging down from the stem or radiating in a cylinder around it (Fig. 1E, F; Table 1).

When disturbed, *Sulculeolaria* contracts the tentacles within approximately 5 seconds and swims off at about 30 cm s^{-1}. To reset the tentacles into fishing position, the siphonophore executes a "veronica" movement (Mackie and Boag, 1963; Biggs, 1977). From swimming in a relatively straight line during escape, the animal begins to describe an open helix, relaxing the tentacles as it goes, so that they extend radially from the stem (see Fig. 1 in Purcell, 1984). The tentacles are so closely spaced that initially they form a broad helical band. As the stem straightens out at the end of the "veronica," the tentacles fill a cylindrical volume having a radius about 40% of the stem length. I have also seen *Sulculeolaria* with the stem horizontal and the tentacles hanging in a 2-dimensional curtain below it. Probably the tentacles are initially spread by the "veronica" behavior, and then drift into other patterns if the animal is not disturbed. Purcell (1981) found that copepods were the nearly exclusive prey of 5 species of *Sulculeolaria*.

Ctenophores

Cydippida

Callianira bialata.—This is a large species, up to 5 cm long. The tentacles extend to about 10 times the body length, and bear hundreds of identical tentilla (Table 1) which hang in dense curtains (Fig. 1F). Like most other cydippids, *C. bialata* hangs motionless in the water with the tentacles and tentilla relaxed around it. If disturbed, the tentacles are retracted in about 3 seconds, and the animal swims away at approximately 3 body lengths s^{-1}. Small *C. bialata* (1–3 cm) were seen during the day, but larger ones (to 5 cm) were most often seen at night, suggesting that older individuals may vertically migrate. Large animals seen at night often swam down when disturbed. *C. bialata* prey on fairly large animals, including hyperiid amphipods (Madin et al., in prep.).

Mertensia ovum.—This boreal species is similar in size and behavior to *Callianira,* but its two tentacles possess about twice as many finer and longer tentilla. Spaced about 1 mm apart, they form dense curtains below the main tentacles (Fig. 1F, Table 1). *M. ovum* were observed (G. Dietzmann, pers. comm.) most often oriented mouth up. Prey caught on the tentacles were ingested by contraction of the tentacle and rotation of the body to bring the end of the tentacle over the mouth, guided by the deep longitudinal grooves down the side of the body. Only the tentacle with prey would contract, while the ctenophore continued fishing with the other one. These ctenophores seemed quite sensitive to the presence of divers, and would contract the tentacles and swim away when approached within a few feet. From a fishing position, the ctenophore begins its escape with a short burst of aborally directed swimming, then turns about 180° and swims away in the oral direction while contracting the tentacles. The maneuver is accompanied by release of a cloud of luminescent particles. The diet of specimens collected from the subarctic Atlantic near Greenland consisted almost entirely of copepods.

Hormiphora spp.—This genus of fairly large cydippids contains several poorly defined species. Most have unusually shaped tentilla on the tentacles. These are widely spaced, and may resemble clubs, paddles or many-fingered hands. They are closely covered with colloblasts, which are absent from the shaft of the main tentacle. The tentacles are extremely extensile, stretching out two or three meters on either side of the motionless animal. The feeding technique of *Hormiphora* is similar to that of *Stomotoca*; it extends two very long tentacles (Table 1), and catches relatively large organisms which swim into them. The large tentilla of *Hormiphora* can apply hundreds of colloblasts quickly to large prey, including heteropods, nudibranchs and fish (Madin et al., in prep.).

Lampea pancerina.—*Lampea* is a large cydippid with a voluminous stomodeum and extensile mouth. Although I have not been able to measure them in situ, I estimate the two tentacles are at least one hundred times as long as the body, with relatively few short, simple tentilla. *L. pancerina* is a specific predator of salps (Harbison et al., 1978), often catching and eating prey much larger than itself. It uses a "long-lining" technique, waiting for a salp to swim into the extended tentacles. Since the salp usually swims more strongly than the *Lampea,* the ctenophore is towed along while it contracts the tentacles, pulling itself mouth-first onto the surface of the prey. On contact, it spreads the edges of the mouth widely, either engulfing the salp or spreading its stomodeum over it.

   Lampea of all sizes prey on salps. Small ones act like parasites, burrowing into the test of the salp as they eat, and remaining attached to the prey for long periods. Larger ctenophores, sometimes several at once, attach to the surface of the prey, completing ingestion in a day or so. The largest *L. pancerina* can catch entire chains of salps, up to a meter long, swallowing them one after another over a period of hours. The *Lampea* that I have seen preyed mainly on *Salpa cylindrica,* and to a lesser extent on other species of *Salpa* and other genera (Harbison et al., 1978; Madin et al., in prep.).

Lobata

Leucothea multicornis.—This is one of the largest ctenophores, attaining an oral-aboral length of about 15 cm, and a width across the open lobes of nearly 30 cm. Its feeding behavior has been described by Harbison et al. (1978) and Hamner et al. (1987). *L. multicornis* feeds while swimming slowly in the oral direction with the lobes spread open. The inner surface of the oral lobes and the lower body are covered with fine tentilla extending from the main tentacle shafts. Long, sinuous auricles writhe rhythmically in the open space between the lobes. Their function is not entirely clear; they do not appear to contribute to swimming, which is accomplished with the comb rows, but may help to spread the lobes after they have been folded (Harbison et al., 1978). My observations suggest also that their motion may startle copepods swimming nearby, causing them to dart into the nearby lobe (see also Hamner et al., 1987). Once prey contacts the lobe surface, the affected quadrant of the lobe rolls up over it, ensuring that it gets stuck on the tentilla which extend over the inner lobe surface. The prey is pulled into the oral groove by contraction of these tentilla, and then conveyed by cilia to the mouth. The prey of *Leucothea* consists mostly of copepods (Madin et al., in prep). Hamner et al. (1987) have described a patch-foraging behavior of *Leucothea* in waters off the California coast, which appears to increase their feeding efficiency.

   The body of *Leucothea* is covered with extensile papillae, which have colloblasts on their tips, and extend toward mechanical stimuli. Horridge (1965) reported that *Leucothea* could stun copepods with them. I have never observed any such

use of the papillae for catching prey, and it is not clear how prey stunned by them could be transferred to the mouth. The papillae may be defensive mechanisms, perhaps against parasitic amphipods or polychaetes (Harbison et al., 1977).

Leucothea spp. also have a pair of long tentacles which trail aborally for tens of centimeters. They do not catch prey, but appear to act as "alarms," that alert the ctenophore to predators approaching it from behind. If gently touched, these tentacles contract, and simultaneously the ctenophore folds its oral lobes and begins swimming rapidly forward. This escape behavior also occurs if the body is touched, but the trailing tentacles produce a quicker and more stereotypic response. A similar reaction is seen in the lobate *Eurhamphaea vexilligera* when its aboral filaments are touched (Harbison et al., 1978).

Cestida

Cestum veneris. — The "Venus' Girdle," and its close relative *Velamen parallelum,* share a unique morphology. The body is up to a meter in length (actually width); its flat sides are covered with fine tentilla extending from the main tentacle shafts which lie in a groove along the oral edge of the body (Table 1). The animal moves through the water propelled by comb rows on its aboral edge. Small prey which contact the sides of the ctenophore stick to one or more tentilla, which pull it into the oral groove for transport by cilia to the stomodeum (Harbison et al., 1978). The prey are mainly small copepods and nauplii (Madin et al., in prep.). This feeding behavior continues until the ctenophore is disturbed, whereupon it contracts the tentilla and swims by a sinusoidal undulation of its body, moving away at 90° to its previous course. Wriggling behavior is often seen when divers are nearby, but is probably infrequent in undisturbed ctenophores. The smaller *Velamen parallelum* feeds and swims similarly (Stretch, 1982).

DISCUSSION

Spatial and Behavioral Parameters of Prey Capture by Tentaculate Predators. — I have included a range of taxonomic and functional groups in the preceding descriptions to illustrate the variety of morphological and behavioral characteristics that affect prey capture, selection, and handling by tentaculate animals. Morphological differences among the species are illustrated in Figure 1 and Table 1. To develop further comparisons among species or functional types, I present in Table 2 two additional parameters derived from the morphological characteristics: the "encounter zone" and the "tentacle density." These will be considered in the context of a general scheme for feeding interactions by tentaculate predators.

I use the term "encounter zone" to mean the space into which the predator's tentacles can extend when it is fishing. Prey will encounter tentacles only within this zone, but are not necessarily caught whenever they enter it. By analogy with the "encounter radius" of Gerritsen and Strickler (1977), the encounter zone of a tentaculate predator describes the spatial limit of the predator's effect on its surroundings. For most medusae, siphonophores and cydippid ctenophores the encounter zone is a three dimensional volume (Fig. 1A–E), the size of which is determined by the extension of the tentacles. It is harder to define for lobate and cestid ctenophores, which catch prey on their body surface. For lobates, I have calculated a cylindrical volume enclosed by the lobes, as prey within this space are at risk of contacting the lobes and being caught. For cestids, I use only the two dimensional surface of the body since the tentilla covering it are the only mechanism of capture, and must be directly contacted by the prey.

I have estimated the volumes or areas of the encounter zones by approximating

Table 2. Calculated tentacular length and volume, encounter zone volume, and tentacle density. Encounter zone volumes and tentacle densities have been rounded off. See Fig. 1 for illustrations and formulae, notes for relative dimensions used

Species	Encounter zone shape (notes)	Tentacular length (m)	Tentacular volume (cm³)	Encounter zone volume (cm³)	Tentacle density (ppm)
Medusae					
Calycopsis typa	disk (1)	12.0	0.0942	850	110.2000
Stomotoca pterophylla	sphere (2)	2.4	0.0033	900,000	0.0036
Aequorea macrodactyla	cone (3)	200.0	0.7697	1,500,000	0.5300
Laodicea undulata	disk (1)	18.0	0.0088	175	50.0000
Dichotomia cannoides	cone (4)	7.5	0.0019	50	36.8000
Liriope tetraphylla	sphere (2)	3.0	0.0052	220,000	0.0230
Solmundella bitentaculata	cylinder (5)	0.1	0.0118	2	5,000.0000
Aeginopsis laurentii	cone (6)	0.2	0.0471	100	476.2000
Solmaris spp.	cone (7)	0.3	0.0001	2	40.0000
Pelagia noctiluca	cone (8)	24.0	0.1794	870,000	0.2100
Siphonophores					
Forskalia spp.	cylinder (9)	88.2	0.2400	434,000	0.5600
Sulculeolaria spp.	cylinder (9)	243.2	1.0400	257,000	4.1000
Ctenophores					
Mertensia ovum	sphere (2)	161.2	0.0403	113,000	0.3600
Callianira bialata	sphere (2)	76.1	0.0204	87,000	0.2300
Hormiphora spp.	sphere (10)	11.0	0.1713	65,500,000	0.0026
Lampea pancerina	sphere (10)	10.5	0.0164	65,500,000	0.0002
Leucothea multicornis	cylinder (11)	—	—	2,000	—
Cestum veneris	body (12)	—	—	640	—

Notes: (1) r = tentacle length + bell diameter/2; (2) r = tentacle length/2; (3) r_1 = bell diameter/2, r_2 = 10r_1, L = 100r_1; (4) r_1 = bell diameter/2, r_2 = 3r^1, L = 20r_1; (5) r_1 = bell diameter/2, L = tentacle length; (6) r_1 = bell diameter/2, r_2 = 2r_1, L = 4r_1; (7) r_1 = bell diameter/2, r_2 = 1.5r_1, L = 1.5r_1; (8) r_1 = bell diameter/2, r_2 = 10r_1, L = 60r_1; (9) r = tentacle length, L = stem length; (10) r = tentacle length; (11) r = distance between lobes/2, L = height of lobes; (12) body surface calculated as $L_1 \cdot L_2 \cdot 2$, L_1 = length, L_2 = height.

them to regular geometric solids or surfaces whose dimensions are set by the measured body and tentacle sizes. Formulae used to calculate the volume of the encounter zones are given in the legend to Figure 1, and the calculated values are given in Table 2. These values assume the predator to be stationary; the effect of a cruising predator on encounter zones is discussed below.

Clearly, the encounter zone volumes arrived at in this way are not precise values. Moreover, the shapes and sizes given here for particular species are derived from observations of a few individuals, and are not invariably characteristic. They illustrate a range into which most tentaculate predators will fall, and can be used for comparisons among different morphological types. For example, a spherical encounter zone is assumed for *Stomotoca, Liriope, Callianira, Mertensia, Hormiphora* and *Lampea,* which have few tentacles and do not hold them in any particular way. The radius of the sphere is determined by the average extension of the tentacles from the body, which may not be the same as their length. In the *Stomotoca, Liriope, Callianira* and *Mertensia* I observed, the tentacles were not stretched straight, so the radius used for encounter zones in Table 2 is half the total tentacle length. *Hormiphora and Lampea* have huge encounter zones because their long tentacles were seen to be stretched. These spherical volumes are perhaps analogous to the orbits of electrons in the atom—there is a certain probability that tentacles will be present at any given point in the sphere, but their location cannot be specified at any moment in time. Encounter zones are delineated better for medusae with numerous tentacles in a conical or radial pattern, like *Laodicea,*

Dichotomia or *Aeginopsis,* for siphonophores with tentacles arranged uniformly along the stem, and for lobate ctenophores.

The encounter zone will vary with swimming activity of the predator. For stationary, ambush predators (Greene, 1985), the zone stays in one place, perhaps collapsing and expanding as the animal withdraws and resets its tentacles. Many medusae, nearly all siphonophores, and the cydippid ctenophores appear to be ambush entanglers. The examples in this paper are *Calycopsis, Stomotoca, Laodicea, Dichotomia, Liriope, Solmaris, Agalma, Forskalia, Sulculeolaria, Callianira, Mertensia, Hormiphora* and *Lampea.* Some medusae and the lobate and cestid ctenophores are cruising predators, moving slowly and constantly while fishing, with the tentacles held in front, trailing behind, or covering their body surface. Cruisers described here include *Aequorea, Solmundella, Aeginura, Pelagia, Leucothea* and *Cestum.* For these predators, the encounter zone is "instantaneously" stationary to an individual prey animal, but from the point of view of a population of prey it moves, stretching over time into a long cylinder traversed by the swimming predator.

The probability of actual capture within this volume will depend, in part, on how densely filled the zone is with tentacles. Other authors (Mackie and Boag, 1963; Biggs, 1977; Mills, 1981) have summed the total length of all the tentacles, as an indication of the quantity of "fishing line" available. For comparison I have included total tentacular lengths, estimated by multiplying the average tentacle/tentilla lengths by their number, in Table 2. However, this linear measure does not adequately describe the three-dimensional disposition of tentacles around the predator, and I prefer here to compare the density or concentration of tentacles within the encounter zone. The "tentacle density" given in Table 2 is simply the fraction of the capture zone that is filled with tentacles. I have estimated it by calculating the volume of all the tentacles and tentilla, and expressing this as a fraction of the encounter zone volume in parts per million. Like the encounter zones, this is an approximate calculation, intended to facilitate comparison of predation impact by a wide range of organisms. Values for tentacular volume are generated by calculating the volume of a tentacle and/or tentillum as a uniform cylinder, and multiplying by the total numbers of each. Tentacular volumes and tentacle densities were not calculated for *Leucothea multicornis* and *Cestum veneris.* In *Leucothea* and other lobates, tentilla do not occupy the encounter zone between the lobes, but cover the inner lobe surfaces, all of which react to prey (Harbison et al., 1978), making the tentacle density effectively 100%. In *Cestum* the encounter zone is two dimensional, and covered with tentilla spaced about 0.01 cm apart (Table 1).

A General Model of Tentaculate Predation. — Based on her observations of feeding behavior in hydromedusae, Mills (1981) suggested seven morphological and behavioral factors that appeared to influence their feeding efficiency. In this discussion, I propose a conceptual scheme for predatory interactions by tentaculate feeders, incorporating some of the variables listed by Mills (1981) and Larson (1987), as well as others not explicitly included in previous formulations. The model is general and non-mathematical, to encompass the range of morphology, behavior and prey types seen among the thousands of species of tentaculate predators in the marine plankton. The relative importance of these variables will differ in different situations. Once the functional morphology involved is understood, simplifying assumptions can be made, and appropriate mathematical models developed for particular predator-prey interactions.

This model is limited to short term spatial and behavioral parameters of pred-

ator-prey encounters. It does not consider larger scale strategies for optimizing feeding such as ontogenetic or diel migration, nor intermediate scale behavior such as localization of prey patches (Swanberg, 1974; Hamner et al., 1987), or allocation of swimming and fishing time (Biggs, 1977; Mills, 1981; Hamner, 1985; Hamner et al., 1987). Clearly, a comprehensive description of predation would include these other scales, but the data for gelatinous predators are far too sparse to attempt that now.

Figure 2 illustrates the relationships among these variables in diagrammatic form. The predatory interaction is divided into four sequential events—encounter, capture and/or selection, ingestion, and digestion. These are arranged in four horizontal rows, while parameters of predator and prey which act at the level of each event are arranged under the two columns labeled spatial and behavioral/physiological.

The interaction begins with encounter. The model assumes that medusae, siphonophores and ctenophores do not use sensory means to orient toward individual prey, although they may be able to locate or recognize patches of prey (Swanberg, 1974; Greene et al., 1986; Hamner et al., 1987). Over short time periods the encounter zone of a predator is defined by the dimensions and arrangement of its tentacles, and its swimming behavior. The degree of tentacle extension in some medusae, siphonophores and ctenophores is reported to vary with the hunger of the animal (Biggs, 1977; Reeve and Walter, 1978; Mills, 1981). This probably will affect the size of the encounter zone for all tentaculate predators. The probability that prey enter the encounter zone will also be related to their swimming speed and behavior, and of course their abundance (Gerritsen and Strickler, 1977; Greene et al., 1986).

Within the encounter zone, the likelihood that various prey types will be caught depends on the interaction of tentacle density, tentacle spacing, prey size, type and behavior, and properties of the nematocysts or colloblasts on the tentacles (Fig. 2). The spacing of the tentacles or tentilla, a function of both morphology and behavior, sets rough limits on prey size. Frequently, predators with fine, dense tentacles catch small animals, and those with large, widely spaced tentacles catch large ones (Biggs, 1977; Harbison et al., 1978; Mills, 1981; but see Mills, 1987). In Table 2, *Laodicea undulata, Dichotomia cannoides* and *Solmaris* spp. have high tentacle densities and close tentacle spacings within small encounter volumes; I would predict that they catch small prey. *Solmundella bitentaculata* and *Aeginopsis laurentii* also have high tentacle density in a small zone, but the tentacles are few and the spacing wider; these medusae prey on larger, gelatinous animals (Purcell and Mills, 1988), increasing their likelihood of encounter with those sparser prey by cruising. *Aequorea* and *Pelagia* have very large encounter zones, low tentacle densities, and wide tentacle spacing. Their prey are mainly large, and they too increase encounters over time by cruising.

A more sophisticated aspect of tentacle morphology is the apparent development of "lures" on the tentilla of some siphonophores (Purcell, 1980) which may act as mimics or decoys to bring visually oriented prey close to the nematocysts. Although not yet widely documented, such mechanisms could have significant effects on prey selection and capture within the encounter zone.

The speed and pattern of prey swimming are probably significant factors both for encounter with tentacles and capture by them. Higher prey swimming speeds increase encounters in the models for *Pleurobrachia* (Greene et al., 1986) and forams (Caron and Bé, 1984) by increasing the rate of entry into the encounter zones. Anderson (1974) found fast swimming copepods more vulnerable to ambush, cydippid ctenophores and slow swimmers more vulnerable to cruising,
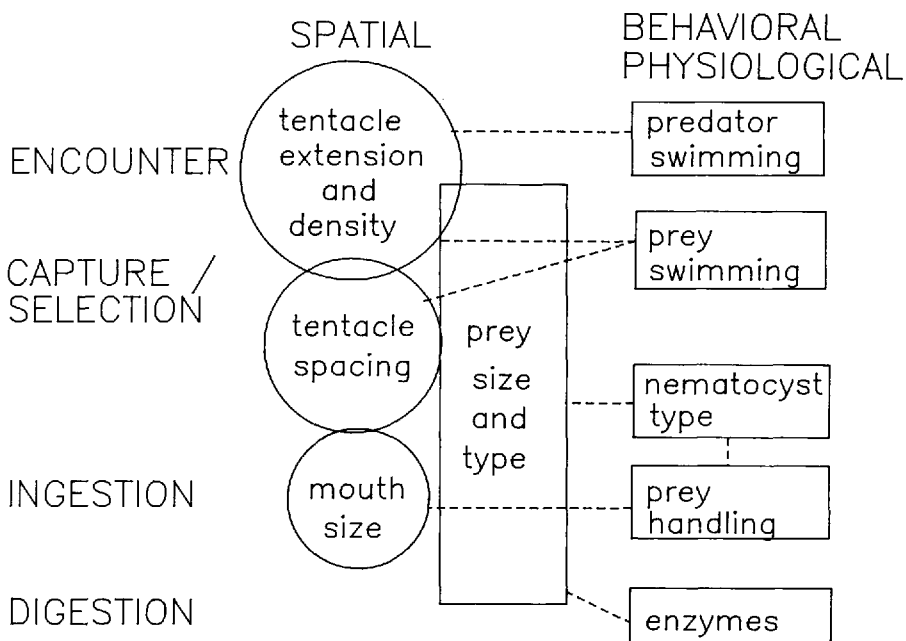
Figure 2. Conceptual model of spatial and behavioral/physiological parameters affecting encounter, capture and selection, ingestion, and digestion of prey by tentaculate predators. See text for further explanation.

lobate species. Within the relatively large and empty encounter zones discussed here, prey swimming can have several effects. Prey that dart and pause, swim in circles, or meander spend more time in the zone, with greater risk, than those that swim straight through. Swimming prey must impact the tentacles hard enough to trigger discharge of nematocysts and stimulate contraction of the tentacle, but if very fast or strong may be able to free themselves, or even break off tentacles.

Tentaculate predators are themselves potential prey, and must distinguish between contacts with their food and their predators. Strong stimulation of the tentacles can cause them to escape rather than capture. The threshold appears to be low in *Mertensia,* disturbed by a diver 3 feet away, and high in *Hormiphora* or *Lampea,* which are tugged about considerably by their prey. Escape responses are less obvious in cruising medusae like *Aequorea* or *Pelagia,* but lobate and cestid ctenophores have escape maneuvers that are very distinct from cruising. The lobates are especially sensitive to stimulation at the aboral, non-feeding, end. In *Leucothea* the separation of feeding and escape behavior includes use of the trailing primary tentacles as sensors. In *Eurhamphaea,* aboral sensory filaments and luminescent ink are components of an escape behavior unrelated to feeding.

The type of nematocyst on the tentacles is important at this stage of prey capture or selection. Purcell (1984) and Purcell and Mills (1988) have examined the relationship between nematocyst types of siphonophores and hydromedusae and their prey. In general, predators that catch crustaceans have nematocysts which entangle or adhere to the exoskeleton. Those that catch soft bodied prey like fish or gelatinous plankters have penetrating nematocysts which harpoon and poison the animal. The colloblasts of ctenophores all function similarly, and seem to stick to both crustacean and soft bodied prey. They are rather uniformly spaced

on the tentacles and tentilla of ctenophores which catch small prey, but concentrated in specialized tentilla in *Hormiphora,* which catches large crustacean and gelatinous prey (Madin et al., in prep.).

Upper limits on prey size may be set by the strength of the tentacles, their ability to maneuver prey to the mouth, or simply the size of the mouth. Animals usually eat things smaller than they are, but predators with extensile mouths and guts like *Beroe, Lampea* or *Aequorea,* can ingest animals as large as themselves, and cystonect siphonophores can use many gonozooids to digest prey much bigger than any single mouth.

The final stage of a successful predatory encounter is digestion of the prey. Since tentaculate predators don't chew their food, digestion depends on the action of enzymes. Some crustaceans appear to be quite resistant to digestion. I have seen zoea larvae ingested by the lobate ctenophore *Mnemiopsis leidyi* simply crawl out of the stomodeum and swim away. Hyperiid amphipods associated with hydro- and scyphomedusae live inside the gastrocoels without ill effect, although other hyperiid species are sometimes found as prey of siphonophores and ctenophores (Harbison et al., 1977). Symbiotic hyperiids may actually change hosts by having the old host eaten by a new one.

Applications and Implications.—The model of tentaculate predation and selectivity presented here does not describe or predict predatory interactions in a quantitative fashion. The purpose of the scheme is instead to identify those parameters which are likely to affect such interactions, and describe some of the ways in which they operate. For any particular case, the role of each of these parameters would need to be determined and the most important ones quantified to generate a predictive model.

Techniques for collecting data for specific predation models need to be appropriate to the fragility and sensitivity to disturbance of most tentaculate predators. It is evident from the in situ observations reported here, and the estimates of encounter zone size, that many tentaculate predators require large volumes of water, free from artificial boundaries, to behave normally. The natural feeding situation may require more space than the encounter zones alone for periodic swimming or escape behavior. Underwater observations usually don't affect normal behavior, but they can be difficult to quantify; new techniques like stereoscopic photography and video imaging promise to improve the resolution and information content of in situ data collection (Klimley and Brown, 1983; Hamner et al., 1988). Observations and experiments in tanks or aquaria are much easier to quantify and replicate but risk altering feeding behavior. Limited space could either depress feeding rates by restricting feeding activity, or enhance them by altering normal avenues of prey escape. Even ambush predators that sit still while feeding may be continually stimulated into escape responses by contact with container walls. Behavioral and feeding experiments in aquaria should be designed to accommodate at least a reasonable encounter zone for the predator. Very large tanks have been successfully used for behavioral studies of gelatinous and crustacean plankton (Balch et al., 1978; Mills, 1981; 1983; Price, 1987), and are a practical approach for tentaculate predators which tolerate captivity.

LITERATURE CITED

Alcaraz, M., G.-A. Paffenhöfer and J. R. Strickler. 1980. Catching the algae: a first account of visual observations on filter feeding calanoids. American Society of Limnology and Oceanography Special Symposium. W. C. Kerfoot, ed. 241–248.

Anderson, E. 1974. Trophic interactions among ctenophores and copepods in St. Margaret's Bay, Nova Scotia. Ph.D. Thesis, Dalhousie University. 85 pp.

Arai, M. N. and J. R. Jacobs. 1980. Interspecific predation of common Strait of Georgia planktonic coelenterates: laboratory evidence. Can. J. Fish. Aquat. Sci. 37: 120–123.

Balch, N., C. M. Boyd and M. M. Mullin. 1978. Large-scale tower tank systems. Rapp. et Proc.— Verb. Cons. Int. Explor. Mer 173: 13–21.

Biggs, D. C. 1977. Field studies of fishing, feeding and digestion in siphonophores. Mar. Behav. Physiol. 4: 261–274.

Caron, D. A. and A. W. H. Bé. 1984. Predicted and observed feeding rates of the spinose planktonic foraminifer *Globigerinoides sacculifer*. Bull. Mar. Sci. 35: 1–10.

Carré, C. 1979. Sur le genre *Sulculeolaria* Blainville, 1834 (Siphonophora, Calycophorae, Diphyidae). Ann. Inst. Oceanogr. Paris 55: 27–48.

Gerritsen, J. and J. R. Strickler. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. J. Fish. Res. Board Can. 34: 73–82.

Giguere, L. A., A. Delage, L. M. Dill and J. Gerritsen. 1982. Predicting encounter rates for zooplankton: a model assuming a cylindrical encounter field. Can. J. Fish. Aquat. Sci. 39: 237–242.

Greene, C. H. 1985. Planktivore functional groups and patterns of prey selection in pelagic communities. J. Plankton Res. 7: 35–40.

———, M. R. Landry and B. C. Monger. 1986. Foraging behavior and prey selection by the ambush entangling predator *Pleurobrachia bachei*. Ecology 67: 1493–1501.

Hamner, W. M. 1975. Underwater observations of blue-water plankton: logistics, techniques and safety procedures for divers at sea. Limnol. Oceanogr. 20: 1045–1051.

———. 1985. The importance of ethology for investigations of marine zooplankton. Bull. Mar. Sci. 37: 414–424.

———, L. P. Madin, A. L. Alldredge, R. Gilmer and P. Hamner. 1975. Underwater observations of gelatinous zooplankton: sampling problems, feeding biology and behavior. Limnol. Oceanogr. 20: 907–917.

———, C. T. Prewitt and E. Kristof. 1988. Quantitative analysis of the abundance, swimming behavior, and interactions of midwater organisms *in* Global venting, midwater, benthic ecological processes. Nat. Undersea Res. Prog., Res. Rpt. 88-4. No pagination.

———, S. W. Strand, G. I. Matsumoto and P. P. Hamner. 1987. Ethological observations on foraging behavior of the ctenophore *Leucothea* sp. in the open sea. Limnol. Oceanogr. 32: 645–652.

Harbison, G. R., D. C. Biggs and L. P. Madin. 1977. The associations of Amphipoda Hyperiidea with gelatinous zooplankton. II. Associations with Cnidaria, Ctenophora, and Radiolaria. Deep-Sea Res. 24: 465–488.

———, L. P. Madin and N. R. Swanberg. 1978. On the natural history and distribution of oceanic ctenophores. Deep-Sea Res. 25: 233–256.

Heine, J. N. 1986. Blue water diving guidelines. Calif. Sea Grant College Program La Jolla. 46 pp.

Horridge, G. A. 1965. Non-motile sensory cilia and neuromuscular functions in a ctenophore independent effector organ. Proc. Roy. Soc. London, B 162: 335–350.

Klimley, A. P. and S. T. Brown. 1983. Stereophotography for the field biologist: Measurement of lengths and three-dimensional positions of free-swimming sharks. Mar. Biol. 74: 175–185.

Larson, R. J. 1979. Feeding in coronate medusae (Class Scyphozoa, Order Coronatae). Mar. Behav. Physiol. 6: 123–129.

———. 1982. Life history of the Hydromedusa *Stomotoca pterophylla* Haeckel and its ichthyoparasitic hydroid. Pages 433–439 *in* K. Rutzler and I. G. Macintyre, eds. The Atlantic Barrier Reef ecosystem at Carrie Bow Cay, Belize, 1: Structure and communities. Smithsonian Contr. to Marine Sciences. Smithsonian Institution, Washington, D.C.

———. 1985. Trophic ecology of gelatinous predators (Cnidaria and Ctenophora) in Saanich Inlet, Vancouver Is., B.C., Canada. Ph.D. Thesis, University of Victoria, Canada, 253 pp.

———. 1987. A note on the feeding, growth and reproduction of the epipelagic scyphomedusa *Pelagia noctiluca* (Forskal). Biol. Oceanogr. 4: 447–454.

Lebour, M. 1922. The food of plankton organisms. J. Mar. Biol. Assoc. U.K. 12: 644–677.
———. 1923. The food of plankton organisms. II. J. Mar. Biol. Assoc. U.K. 13: 70–92.
Mackie, G. O. and D. A. Boag. 1963. Fishing, feeding and digestion in siphonophores. Pubbl. Stazione Zoologica Napoli 33: 178–196.
———, P. R. Pugh and J. E. Purcell. 1987. Siphonophore biology. Adv. Mar. Biol. 24: 98–263.
Mills, C. E. 1981. Diversity of swimming behaviors in hydromedusae as related to feeding and utilization of space. Mar. Biol. 64: 185–189.
———. 1983. Vertical migration and diel activity patterns of hydromedusae: studies in a large tank. J. Plankton Res. 5: 619–635.
———. 1987. Revised classification of the genus *Euplokamis* Chun, 1880 (Ctenophora: Cydippida: Euplokamidae n. fam.) with a description of the new species *Euplokamis dunlapae*. Can. J. Zool. 65: 2661–2668.
——— and R. L. Miller. 1984. Ingestion of a medusa (*Aegina citrea*) by the nematocyst-containing ctenophore *Haeckelia rubra* (formerly *Euchlora rubra*); phylogenetic implications. Mar. Biol. 78: 215–221.
Price, H. J. 1987. Swimming behavior of krill relative to algal patches in a mesocosm: a video analysis [Abst.]. Eos 68: 1732.
Purcell, J. E. 1980. Influence of siphonophore behavior upon their natural diets: evidence for aggressive mimicry. Science 209: 1045–1047.
———. 1981. Dietary composition and diel feeding patterns of epipelagic siphonophores. Mar. Biol. 65: 83–90.
———. 1984. The functions of nematocysts in prey capture by epipelagic siphonophores (Coelenterata, Hydrozoa). Biol. Bull. 166: 310–327.
———. 1985. Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. Bull. Mar. Sci. 37: 739–755.
——— and C. E. Mills. 1988. The correlation between nematocyst types and diets in pelagic hydrozoa. *In* D. A. Hessinger and H. Lenhoff, eds. The Biology of Nematocysts. Academic Press, New York.
Reeve, M. R. and M. A. Walter. 1978. Nutritional ecology of ctenophores—A review of recent research. Adv. Mar. Biol. 15: 249–287.
Stretch, J. J. 1982. Observations on the abundance and feeding behavior of the cestid ctenophore. *Velamen parallelum*. Bull. Mar. Sci. 32: 796–799.
Swanberg, N. R. 1974. The feeding behavior of *Beroe ovata*. Mar. Biol. 24: 69–76.
Totton, A. K. 1965. A synopsis of the Siphonophora. British Museum (Natural History) London, 230 pp.