THE CORRELATION BETWEEN NEMATOCYST TYPES AND DIETS IN PELAGIC HYDROZOA[1]

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SUMMARY

Among the pelagic hydrozoans, which include the siphonophores, hydromedusae, and velellids (chondrophores), members of some taxonomic subgroups exclusively or primarily consume soft-bodied prey, while others primarily consume hard-bodied (crustacean) prey. The dietary differences are related to the types of nematocysts in the tentacles of these hydrozoans. The predators of crustaceans are the calycophore and physonect siphonophores, Anthomedusae (except the family Pandeidae), Limnomedusae, and Trachymedusae. These groups possess 2 to 5 types of nematocysts, including rhopalonemes (acrophores, anacrophores, and desmonemes) which adhere to and entangle prey, and stenoteles, microbasic euryteles, or microbasic mastigophores, which can penetrate crustacean exoskeleton. Adhesion of nematocyst

tubules to prey surfaces appears to be important in capture of crustaceans by hydrozoans. Predators of soft-bodied plankton include the cystonect siphon-ophores, Apolemia uvaria (Physonectae), pandeid Anthomedusae, Lepto-medusae, and Narcomedusae. Their cnidoms usually contain one type or one predominant type of nematocyst, primarily isorhizas, mastigophores, or other types often unique to them, that penetrate the soft prey tissues, but they lack surface-adhering nematocyst types.

Herein, we briefly review earlier work on the diets and nematocysts of the Siphonophora, and present new data on the diets and nematocysts of the diverse hydromedusan species from the Strait of Georgia region, Northeast Pacific.

I. INTRODUCTION

Within the class Hydrozoa, the orders Siphonophora, Chondrophora [now considered to be the Family Velellidae in the Anthomedusae (Bouillon, 1985)], Narcomedusae, and Trachymedusae are holoplanktonic, and many species in the orders Anthomedusae, Leptomedusae, and Limnomedusae have a pelagic medusa stage. The life cycle for medusae in the new order Laingio-medusae (Bouillon, 1978) is not known. The colonial siphonophores and velellids (chondrophores) do not swim while their tentacles are extended to capture prey. Hydromedusae exhibit a diversity of swimming and feeding behaviors (Mills, 1981) and may either fish while they swim, or separate these two activities (Mills, in prep.). For feeding, all of these hydrozoans depend on interception of prey by their nematocyst-laden tentacles. The nematocysts in the tentacles are directly responsible for prey capture, and differences in cnidoms could be expected to result in dietary differences.

Among the cnidarian classes, the greatest number of nematocyst types are found in the class Hydrozoa; 23 of the 30 described types of cnidae occur, and 17 types are unique to this class (reviewed by Mariscal, 1974). Numerous papers describe the cnidoms of many species in this class. Recent reviews, cited below, compile many of these earlier data, and we refer readers to references therein. Cnidoms are very similar among species in each of the siphonophore suborders (Purcell, 1984a; Mackie et al., in press), and in the hydromedusan orders (Bouillon, 1985), with a few exceptions. We limit our present analysis to nematocysts in the tentacles because of their direct relation-ship to prey capture.

Until recently, little information existed on the diets of pelagic hydro-zoans. The natural diets of 25 epipelagic siphonophore species were quantified by Purcell (1981a, b, 1984b). The diets of several hydromedusa species recently have been quantified by Larson (1985) in Saanich Inlet, Vancouver Island, British Columbia, Canada, and by Purcell (unpubl.) in Friday Harbor, Washington and southeastern Vancouver Island. Alvariño (1985) summarized prey captured by numerous siphonophore and medusa species, but virtually all data cited therein were from observations of feeding made in the laboratory. In the present paper, we restrict our analysis to species for which natural diets have been determined, to avoid possible laboratory artifacts.

Only a few studies have examined the effects of nematocysts on prey organisms. Toppe (1909), Ewer (1947), and Tardent and Holstein (1982) studied nematocysts of hydra and found that prey were penetrated by stenoteles and were entangled by desmonemes. Ewer (1947) further noted that the "atrichous" and holotrichous isorhizas of hydra did not discharge on crustacean prey, but were used in locomotion and defense, respectively. Although some discharge of the holotrichous isorhizas was seen against soft-bodied prey organisms, hydra gave no feeding response, and the interaction was interpreted to be defensive.

Purcell (1984a), using scanning electron microscopy to examine the discharged nematocysts of numerous siphonophore species, defined two feeding groups of siphonophores. Species in the suborder Cystonectae eat soft-bodied prey and have only isorhiza nematocysts; physonect and calyco-phoran siphonophores primarily eat copepods and have 4-5 nematocyst types, including rhopalonemes and stenoteles, organized in batteries. New dietary and nematocyst data presented herein suggest that a parallel situation exists in hydromedusae. Species that primarily eat soft-bodied prey have one type of nematocyst that predominates (usually isorhizas or mastigophores), while most species that eat crustaceans have a mixture of desmonemes and stenoteles. Pelagic hydrozoans that feed on crustaceans have some nematocyst types with tubules specialized to adhere to the hard prey surfaces, while species that feed on soft-bodied prey have nematocyst tubules that penetrate prey.

II. MATERIALS AND METHODS

Hydromedusae used for dietary analyses during April, 1982 [data cited as Purcell, unpubl. (1982)] and for all nematocyst measurements were collected individually from the docks at the Friday Harbor Laboratories, Washington, USA. Specimens for gut analyses were preserved immediately in 5% formalin. Specimens also were collected using a 0.75 m diameter, 333 μm mesh plankton net in 0.5-3 min tows at 0-5 m depth in Kulleet Bay, on southeast Vancouver Island, British Columbia, Canada during March-June, 1983, April, 1985, or April, 1986 and immediately preserved [cited Purcell, unpubl. (1983), unpubl. (1985), unpubl. (1986)]. Prey were removed from the jellyfish manubria and identified using 8-50x magnification with a dissecting microscope.

Nematocysts in the tentacles of hydromedusae were examined and photo-graphed using a compound microscope. Whole tentacles were placed on a slide along with sea water and $MgCl_2$. When each tentacle was relaxed, a drop of 5% formalin was added to the preparation to prevent ciliary and muscular movement, and a coverslip supported by small plasticene feet was applied. Measurements of undischarged nematocysts were made at 1000x and represent the range of sizes from at least 10 randomly selected nematocysts of each type.

Scanning electron microscopy (SEM) was used to examine nematocyst adhesion and penetration into prey. Medusae were allowed to capture cope-pods, ctenophores, or other species of medusae in the laboratory, and these prey were quickly retrieved with forceps from the tentacles. In some cases,

TABLE I. Nematocyst types and range of dimensions (μm) in the tentacles of siphonophores (from Purcell, 1984a). Ratios represent the number of species having those nematocyst types / number of species examined in each group

	Rhopalonemes	Stenoteles	Microbasic mastigophores	Anisorhizas	Isorhizas
Calycophorae	12/12 3.0 x 1.5 - 23.0 x 3.0	----	12/12 36.0 x 7.0 - 153.0 x 15.0	12/12 * 12.0 x 2.0 - 54.0 x 12.5	11/12 7.0 x 5.0 - 25.0 x 12.5
Physonectae	7/8 3.0 x 4.5 - 17.5 x 10.0	4-5/8 22.5 x 12.5 - 109.0 x 29.0	2-3/8 112.5 x 20.0 - 180.0 x 28.0	8/8 * 22.6 x 6.0 - 72.5 x 12.5	P
Cystonectae	----	----	----	----	4/4 10.0 x 10.0 - 32.5 x 32.5

* numerically predominant
P present

prey held in forceps were brushed along the tentacles of medusae. The prey specimens were fixed overnight in 5% formalin in sea water and were postfixed for one hour in 2% osmium tetroxide (OsO_4) in distilled water. Specimens were dehydrated in a series of 35%, 50%, 70%, and 95% ethanol, followed by two 5-minute rinses in 1, 2 dimethoxypropane. The specimens were critical-point dried using CO_2, mounted on stubs with double-stick tape or silver paint, and sputter-coated with gold-palladium. The observations were made using a JEOL JSM-35 scanning electron microscope, operated at 15 KV.

III. RESULTS

A. Siphonophores

Data on the nematocysts of siphonophores from Purcell (1984a) are summarized in Table I. The calycophoran and physonect (except Apolemia spp.) siphonophores have one highly-organized nematocyst battery on each of the side branches (tentilla) of the tentacles. In calycophorans, the straight cnidoband contains from 50 homotrichous anisorhizas in small species to 2,000 in large species. At the free end of the battery are found a few isorhizas, and a terminal filament containing small rhopalonemes. At the attached end of the battery are 4 to 30 microbasic mastigophores that are 2 to 4 times longer than the anisorhizas.

In physonects, the coiled cnidoband contains from 150 homotrichous anisorhizas in small species to 20,500 in large species. Along the edge of the cnidoband are 4 to 120 stenoteles or microbasic mastigophores that, again, are much larger than the anisorhizas. The 1 or 2 terminal filaments contain small rhopalonemes.

The nematocysts of cystonect siphonophores are not organized into batteries, but may occur in bands or clusters. Only homotrichous and atrichous isorhizas are found.

Data on the natural diets of siphonophores in Table II were calculated from published data (see Table 3 in Purcell, 1981a and Table 1 in Purcell, 1984b) by adding all percentages of a given prey type among species in a suborder, and then expressing the total for each prey type as a percentage of the summed totals. The compiled data show that 97.3% of the prey of the calycophorans examined were crustaceans, primarily copepods. The diets of physonects consisted mostly of crustaceans (69.3%), including large copepods and larvae of benthic crustaceans, and also included some soft-bodied prey. The diets of cystonect siphonophores exclusively consisted of soft-bodied prey, of which fish larvae predominated (91-100%).

Thus, calycophore and physonect siphonophores have similar cnidoms and similar diets, while cystonects are dramatically different in both respects.

Purcell (1984a) used SEM to examine prey after they were captured by siphonophores but before the prey were ingested. Prey (copepods and chaetognaths) captured by calycophorans and physonects were wrapped and entangled in nematocyst tubules which adhered to the prey surfaces. Nema-

TABLE II. In situ dietary data for siphonophores, as percent of prey items in gut contents (from Purcell, 1981a,b, 1984b)

	Copepods	Decapod larvae	Cladocerans	Amphipods	Shrimp	Ostracods	Molluscs	Chaetognaths	Fish larvae	Gelat. zoopl.	No. of prey/ No. of siphs. examined
Calycophorae	87.5	0.1	P	0.5	0.5	8.7	0.7	1.8	0.2	---	>1,484/360
Physonectae	39.7	6.2	P	0.6	22.8	P	1.1	13.2	15.2	1.2	233/117
Cystonectae	---	---	---	---	---	---	4.1	4.9	91.0 - 100.0	---	>2,174/370

P, present

tocyst penetration of the prey was seen only twice. In one case, stenoteles of Nanomia bijuga seemed to have penetrated at the cephalothorax/abdominal joint of a copepod, and in the other case, stenoteles of Forskalia edwardsi penetrated a chaetognath. Cystonect isorhizas penetrated fish larvae, but were not seen to adhere to or penetrate a shrimp (Leander sp.).

Thus, the siphonophores examined appeared to capture small crustacean prey primarily by entangling them in nematocyst tubules. Previously only stenoteles (Toppe, 1909; Tardent and Holstein, 1982) and microbasic mastigophores (Godknecht, 1985) have been shown to penetrate crustacean exoskeleton. In siphonophores, these nematocysts capable of penetration are far outnumbered (20 to 200 times) by other nematocyst types. Few stenoteles were seen penetrating prey of siphonophores, and no microbasic mastigophores had penetrated the prey. Cystonect nematocysts seem unsuitable for adhesion to prey and unable to penetrate crustaceans, perhaps limiting cystonect siphonophores to soft-bodied prey.

B. Hydromedusae

In Table III, we present new data on the sizes and types of tentacle nematocysts from the hydromedusa species for which we have dietary data, primarily from nearshore waters of Washington State and southern British Columbia. We also include data from Bouillon (1985) who has summarized all nematocyst types known to be present in each of the families of hydromedusae.

Among the Anthomedusae, most species have a combination of desmonemes along with either stenoteles or microbasic euryteles, except species in the family Pandeidae, which lack desmonemes, and have either microbasic euryteles or mastigophores. Bouillon (1980) identified the nematocysts of Indo-Pacific Stomotoca atra as microbasic euryteles, but specimens from the Northeast Pacific examined by Mills (unpubl.) contained microbasic mastigophores (Fig. 1I, 2C, 2D).

The only local species of the Limnomedusae for which we have dietary information, Proboscidactyla flavicirrata, has desmonemes and macrobasic mastigophores. Rees (1979) identified the latter type as macrobasic euryteles, rather than macrobasic mastigophores, in P. flavicirrata. Aglantha digitale, the only local Trachymedusa, has stenoteles and microbasic euryteles [variations in these are discussed in Russell (1940)].

The nematocysts in the tentacles of the Leptomedusae predominantly consist of basitrichous and "atrichous" isorhizas and some microbasic mastigophores. Identification of these small (<15 μm) nematocysts has been difficult using light microscopy, and designations of certain types vary by the author's choice of descriptive names. This appears to be the case for basitrichous isorhizas, microbasic mastigophores, and less often, microbasic euryteles. Russell (1939) identified the nematocysts of Aequorea spp. as basitrichous isorhizas, rather than microbasic mastigophores as we denote them in Table III, and "atrichous" isorhizas. Kubota (1976, 1981) found both microbasic mastigophores and basitrichous isorhizas in tentacles of Obelia sp. medusae (but not both in one specimen). We found only microbasic mastigo-

TABLE III. Nematocyst types and ranges of undischarged dimensions (μm) in the tentacles of hydromedusae (ratios following family names represent the number of species having those nematocysts / number of species examined)

	Desmonemes	Stenoteles	Microbasic euryteles	Microbasic mastigophores	Isorhizas	References
Anthomedusae						
Fam. Corynidae	**12/13**	**13/13**	**0-1/13**	----	**2/13**	Bouillon, 1985
Sarsia eximia	9.5-12.0 x 4.0-5.5	9.5-16.0 x 6.5-10.0	----	----	---	Russell, 1938
Sarsia tubulosa	10.8-12.0 x 5.6-6.4	14.0-16.0 x 10.4-12.0	----	----	---	Mills, unpubl.
Fam. Rathkeidae	**1/1**	----	**1/1**	----	---	Bouillon, 1985
Rathkea octopunctata	3.0-5.0 x 2.0-3.0	---	6.0-10.5 x 2.5-4.0	----	---	Russell, 1938
Fam. Bougainvilliidae	**11/11**	----	**11/11**	----	---	Bouillon, 1985
Bougainvillia principis	4.8-5.2 x 2.4-3.2	----	6.4-7.2 x 3.6-4.0	----	---	Mills, unpubl.
Fam. Pandeidae	**1-2/15**	----	**14-15/15**	**3-4/15**	**1/15**	Bouillon, 1985
Catablema nodulosa	----	12.0-14.4 x 8.0-9.6	8.8-9.6 x 3.6-4.0	----	---	Mills, unpubl.
Stomotoca atra	----	----	----	8.4-9.6 x 2.4-3.2	---	Mills, unpubl.
Fam. Tubulariidae	**6/6**	**6/6**	**4-5/6**	**0-2/6**	**5/6**	Bouillon, 1985
Hybocodon prolifer	P	P	P	----	---	Bouillon, 1974
Fam. Polyorchidae	**4/4**	**4/4**	**0-1/4**	----	---	Bouillon, 1985
Polyorchis penicillatus	12.0-14.5 x 6.0-7.0	15.5-20.5 x 10.0-13.5	----	----	---	Mackie & Mackie, 1963
Fam. Velellidae	----	**2/2**	**1/2 (macro.)**	----	**2/2**	Bouillon, 1985
Velella velella	----	18.0-21.0 x 14.0-16.0 13.0-15.0 x 10.0-11.0	---- (P, macrobasic) +	----	8-9 x 4.5	Russell, 1939

TABLE III (continued)

	Desmonemes	Stenoteles	Microbasic euryteles	Microbasic mastigophores	Isorhizas	References
Limnomedusae						
Fam. Proboscidactylidae	**4/4**	---	**2/4**	**4/4 (macro.)**	----	Bouillon, 1985
Proboscidactyla flavicirrata	5.0-7.0 x 4.0-6.0	---	---	8.0-12.0 x 5.0-7.2 (macrobasic)	----	Hand, 1954; Mills, unpubl.
Trachymedusae						
Fam. Rhopalonematidae	----	**4-5/5**	**3-5/5**	----	**01-/5**	Bouillon, 1985
Aglantha digitale	----	11.6-12.0 x 11.2-12.0	8.8-9.6 x 5.6	---	----	Russell, 1940; Mills, unpubl.
Leptomedusae						
Fam. Aequoriidae	----	---	---	**0-3/5**	**5/5 ***	Bouillon, 1985
Aequorea victoria	----	---	---	14.4-16.8 x 3.2 ▵	22.4-24.4 x 11.6-12.0	Mills, unpubl.
Fam. Campanulariidae	----	----	---	**7/7**	**6/7 ***	Bouillon, 1985
Obelia sp.	----	----	---	6.8-8.0 x 2.0-2.4 ▵	----	Mills, unpubl.
Phialidium gregarium	----	----	---	9.6-11.2 x 2.4-2.8 ▵	----	Mills, unpubl.
Fam. Mitrocomidae	----	----	---	**1/4**	**4/4 ***	Bouillon, 1985
Mitrocomella polydiademata	----	----	---	8.8-10.0 x 2.4 ▵	12.0-14.4 x 4.8-5.6	Mills, unpubl.
Mitrocoma cellularia	----	----	---	12.0-14.8 x 3.6-4.2 ▵	----	Mills, unpubl.
Fam. Eutimidae	----	----	---	**5-6/9**	**7/9 ***	Bouillon, 1985
Eutonina indicans	----	----	---	9.2-10.8 x 2.4-2.6 ▵	----	Mills, unpubl.

TABLE III (continued)

	Desmonemes	Stenoteles	Microbasic euryteles	Microbasic mastigophores	Isorhizas	References
Narcomedusae						
Fam. Aeginidae	----	----	----	--	2/2 °	Bouillon, 1985
Aegina	----	----	----	--	16.8-20.0 °	Mills, unpubl.
citrea					6.4-8.4 °	
Fam. Cuninidae	----	----	----	--	3/3 °	Bouillon, 1985
Solmissus	----	----	----	--	22.5-25.5 °	Mills, unpubl.
albescens					8.4-9.6 °	
Solmissus	----	----	----	--	21.0-23.0 °	Mackie &
marshalli					7.0-9.0 °	Mackie, 1963

P present
+ from Bouillon, 1974
* numerically predominant
Δ identified as basitrichous isorhizas in other species of same genera by other authors
° spherical apotrichous isorhizas

phores in <u>Obelia</u> sp. medusa tentacles, in agreement with Östman (1982). Species of <u>Phialidium</u> other than <u>P. gregarium</u> were found to have atrichous or homotrichous isorhizas in addition to microbasic mastigophores (Russell, 1938; Kubota 1978; Östman, 1979).

The Narcomedusae all have only apotrichous isorhizas, usually in two sizes (Mills and Miller, 1984; Bouillon, 1985; Mills, pers. obs.) (Table III, Fig. 1J).

Dietary data show that the anthomedusan species that we have examined primarily consumed crustaceans (75-100%). In addition to the prey types listed in Table IV, the diet of <u>Polyorchis penicillatus</u> contained 14.8% epibenthic crustaceans (gammarid and caprellid amphipods, cumaceans) and 28.7% soft-bodied benthic prey (polychaetes) (Arkett, 1984). Species in the family Pandeidae may primarily eat soft-bodied prey (jellyfish), but few quantitative dietary data are available. We report <u>in situ</u> observations of pandeids repeatedly feeding on other hydromedusae: <u>Stomotoca atra</u> consuming <u>Phialidium gregarium</u> (Mills, Purcell, pers. obs.), and <u>Catablema nodulosa</u> consuming <u>Mitrocomella polydiademata</u> (Mills, pers. obs.).

The limnomedusa <u>Proboscidactyla flavicirrata</u> consumed mostly veligers and tintinnids. Small specimens of the trachymedusa <u>Aglantha digitale</u> consumed large copepods, and tintinnids (Purcell, pers. obs.).

The leptomedusae examined mostly consumed soft-bodied prey, especially larvaceans and invertebrate eggs (euphausiid and copepod). The data of McCormick (1969) for <u>Phialidium gregarium</u> in Yaquina Bay, Oregon, contrast markedly with the data from Purcell (unpubl., 1982) and Larson (1980, 1985) for <u>P. gregarium</u> in the Strait of Georgia region (Table IV). The cause of this discrepancy is not obvious, but raises the point that available prey, and hence the medusa diets, will differ both with location and date. In addition to the prey listed in Table IV, <u>Aequorea victoria</u> also consumed polychaetes <u>in situ</u> (Larson, 1980; Purcell, Mills, pers. obs.). One specimen of <u>Eutonina indicans</u> contained numerous <u>Hybocodon prolifer</u> hydromedusae (Mills, pers. obs.). Data in Zelickman <u>et al.</u> (1969) indicate that the medusa <u>Tiaropsis multicirrata</u> contained 85.5% crustaceans, 5.4% veligers, 1.8% tintinnids, and 7.3% hydromedusae. No data on the nematocysts of <u>T. multicirrata</u> are available.

Narcomedusae may consume exclusively gelatinous zooplankton, but few data exist: one specimen of <u>Aegina citrea</u> at Friday Harbor contained a <u>Mitrocomella polydiademata</u> medusa, <u>Solmissus albescens</u> in the Mediterranean contained <u>Cavalinia</u> pteropods, and a specimen of <u>S. marshalli</u> at Friday Harbor contained a <u>Euphysa</u> medusa (Mills, unpubl.).

In summary, of the species that we examined, the hydromedusae that eat hard-bodied prey include the Anthomedusae (except the family Pandeidae), and probably most Limnomedusae and Trachymedusae. These medusae usually have desmonemes, which adhere to prey, and either stenoteles, which can penetrate crustaceans and soft-bodied prey, or microbasic euryteles, which may serve the same purpose. The hydromedusae that primarily eat soft-bodied prey include the Leptomedusae and pandeid Anthomedusae, having microbasic mastigophores, euryteles, or basitrichous isorhizas, and the Narcomedusae, having apotrichous isorhizas.

TABLE IV. In situ dietary data for hydromedusae, as percent of prey items in gut contents (see additional data in text)

	Cope-pods	Copepod nauplii	Barnacle larvae	Crab zoeas	Clado-cerans	Veligers	Larva-ceans	Invert. eggs	Tintin-nids	Fish larvae	Gelat. zoopl.	No. of prey/ No. medusae	References
Anthomedusae													
Sarsia eximia	89.7	7.7	----	----	2.6	----	----	----	----	----	----	39/37	McCormick, 1969
Sarsia princeps	39	18	4	----	----	<1	<1	39	<1	----	----	299/11	Larson, 1985
Sarsia tubulosa	13.0	2.5	83.9	----	0.3	----	----	----	----	0.3	----	360/26	Purcell, unpubl.(1982)
	61.9	3.2	31.7	----	----	----	----	3.2	----	----	----	63/54	Purcell, unpubl.(1985)
Rathkea octopunctata	----	----	62.5	----	----	----	25.0	----	----	12.5	----	8/8 *	Purcell, unpubl.(1986)
Bougainvillia principis	1.2	2.4	94.0	0.6	----	----	1.2	0.6	----	----	----	168/15 *	Purcell, unpubl.(1982)
Catablema nodulosa	1.1	----	44.4	----	----	----	33.3	----	----	----	11.1	9/8 *	Purcell, unpubl.(1982)
Stomotoca atra	----	----	----	----	----	----	----	----	----	----	M *	---	Hyman, 1940
Hybocodon prolifer	68.4	5.2	21.0	----	----	----	----	----	5.2	----	----	19/12 *	Purcell, unpubl.(1982)
Polyorchis penicillatus	P	7.3	38.0	7.3	----	3.9	----	----	----	----	----	>771/>180	Arkett, 1984
	55.2	1.7	0.3	1.7	0.7	----	0.7	39.7 (1 medusa)	----	----	----	299/11	McCormick, 1969
Velella velella	3.0	----	0.5	1.5	1.0	----	11.0	78.0	----	3.5 (eggs)	----	? /38	Bieri, 1961

(continued)

TABLE IV (continued)

	Cope-pods	Copepod nauplii	Barnacle larvae	Crab zoeas	Clado-cerans	Veligers	Larva-ceans	Invert. eggs	Tintin-nids	Fish larvae	Gelat. zoopl.	No. of prey/ No. medusae	References
Limnomedusae													
Proboscidactyla flavicirrata	<1	1	<1	----	----	67	2	3	25	----	----	259/81	Larson, 1985
	----	----	----	----	----	25	----	----	75	----	----	4/3 *	Purcell, unpubl.(1982)
	57.1	----	----	14.3	----	28.6	----	----	----	----	----	7/3	McCormick, 1969
	----	1.0	1.0	----	----	27.7	----	1.0	69.3	----	----	101/32	Purcell, unpubl.(1985)
Trachymedusae													
Aglantha digitale	5	1	<1	----	----	<1	<1	94	<1	----	----	503/283	Larson, 1985
	100	----	----	----	----	----	----	----	----	----	----	23/6 *	Purcell, unpubl.(1982)
	7.4	3.7	----	----	----	----	----	----	88.9	----	----	27/3 *	Purcell, unpubl.(1985)
	10.0	10.0	----	----	----	----	----	20.0	60.0	----	----	12/6 *	Purcell, unpubl.(1986)
Leptomedusae													
Aequorea victoria	----	----	----	----	----	----	----	----	----	----	93.8	32/307	Larson, unpubl.(1980)
	6.6	P	2.3	1.4	----	----	71.1	P	P	5.0	12.4	16,297/521	Purcell, unpubl.(1983)
Obelia sp.	----	----	----	----	----	----	----	----	100	----	----	3/3 *	Purcell, unpubl.(1986)

(continued)

TABLE IV (continued)

	Cope-pods	Copepod nauplii	Barnacle larvae	Crab zoeas	Clado-cerans	Veligers	Larva-ceans	Invert. eggs	Tintin-nids	Fish larvae	Gelat. zoopl.	No. of prey/ No. medusae	References
Phialidium gregarium	79.9	0.5	1.6	0.5	3.1	0.5	6.8	7.3	----	----	----	192/61	McCormick, 1969
	16.3	----	1.0	----	8.2	1.0	15.3	45.9	5.1	6.1 (eggs)	----	98/155	Larson, unpubl.(1980)
Phialidium spp.	<1	<3	<1	----	----	<1	2	83	<1	----	----	4985/768	Larson, 1985
	1.8	----	----	1.8	----	----	36.4	54.6	----	1.8	----	55/24 *	Purcell, unpubl.(1982)
Mitrocomella polydiademata	2	4	<1	----	----	<1	19	75	<1	----	----	98/23	Larson, 1985
	2.3	----	2.3	----	----	----	95.4	----	----	M	----	44/18 *	Purcell, unpubl.(1982)
Mitrocoma cellularia	<1	2	<1	----	----	<1	<1	98	<1	M	M	65/14	Larson, 1985
	3.1	----	----	----	----	----	55.4	38.5	----	----	3.0	65/17	Purcell, unpubl.(1982)
Eutonina indicans	1.4	1.4	2.1	0.5	----	----	3.2	89.5	----	0.1	1.0	630/28	Purcell, unpubl.(1982)
Narcomedusae													
Aegina citrea	----	----	----	----	----	----	----	----	----	----	M	1 obs. *	Mills, unpubl.
Solmissus albescens	----	----	----	----	----	----	----	----	----	----	M	10 obs. *	Mills, unpubl.
Solmissus marshalli	----	----	----	----	----	----	----	----	----	----	M	1 obs. *	Mills, unpubl.

* many more specimens were examined that contained no food

M, present (Mills, unpubl.)

The distributions of nematocysts along the tentacles of ten species of hydromedusae are shown in Figure 1. Among species that mostly capture hard-bodied prey, Sarsia tubulosa and Proboscidactyla flavicirrata (Fig. 1A, 1C) have the nematocysts of their tentacles grouped into raised clusters containing two types of nematocysts. This arrangement may be especially effective in capturing crustaceans with complex surfaces. Aglantha digitale does not have raised clusters of nematocysts on its tentacles, and it eats some non-crustacean prey (Table IV).

Species of hydromedusae that eat primarily soft-bodied prey generally have nematocysts of only one type, or one predominant type (Table III). The nematocysts may be scattered regularly along the length of the tentacle (Fig. 1E, 1H), or arranged in a pattern (Fig. 1G, 1I), but rarely occur in raised clusters. Aequorea victoria is unusual in having one nematocyst type on the exumbrellar side of the tentacles, and another type on the subumbrellar side (Fig. 1G). Tentacles without raised nematocyst clusters may be most effective in contacting the broad uniform surfaces of soft-bodied prey.

Tentacles with raised clusters of nematocysts occur throughout the Capitata, which constitutes about half of the Anthomedusae (super-families Tubularioidea, Corynoidea, Zancleopsoidea, Zancleoidea, and Velelloidea) (Bouillon, 1985). Anthomedusae in the Filifera (super-families Pandeoidea, Bougainvillioidea, Rathkeoidea, Hydractinioidea, and Moeridioidea) usually do not have raised nematocyst clusters (except most of the Moeridioidea and incidental species in the other groups). Most, if not all, Limnomedusae have raised nematocyst clusters, frequently in the form of rings, on their tentacles. Leptomedusae, Narcomedusae, Trachymedusae (except the Geryonidae), and Laingiomedusae, have relatively even tentacle surfaces. Their nematocysts may be uniformly distributed, or concentrated along one side of the tentacle or near the tentacle tip.

Examination of the surfaces of prey captured by the anthomedusa Sarsia tubulosa showed some stenoteles to penetrate copepod exoskeleton and others, failing to penetrate, instead wrapping around prey surfaces (Fig. 2A). Although both desmonemes and stenoteles occur together in raised clusters, only desmonemes are found wrapped around the setae of the copepods, and stenoteles are found penetrating larger surfaces (Fig. 2A, 2B). The microbasic mastigophores of the anthomedusa Stomotoca atra, which we believe eats soft-bodied prey (medusae) primarily, were able to penetrate both crustacean exoskeleton (euphausiid larva) and soft-bodied prey (hydromedusa Phialidium gregarium), and also adhered to exoskeleton (Fig. 2C, 2D). Unfortunately, no prey were found in our systematic gut analyses of S. atra. Another pandeid anthomedusa, Catablema nodulosa, consumed crustaceans as well as soft-bodied prey in the field (Table IV). The microbasic mastigophores of the leptomedusa Phialidium gregarium also penetrated and adhered to copepods (Fig. 2E, 2F), even though most gut analyses showed crustaceans to comprise only a small part of its diet in nature (Table IV).

IV. DISCUSSION

The pelagic hydrozoans fall into two groups, 1) those that primarily eat hard-bodied prey, and 2) those that primarily eat soft-bodied prey (Table V). Species in the first group have rhopalonemes (desmonemes, acrophores, anacrophores), which adhere to the surfaces of hard-bodied prey. Species that eat larger crustaceans (epibenthic species, decapod larvae, shrimps, large copepods) usually have stenoteles (Anthomedusae, physonect siphonophores). Other crustacean-eating species have microbasic euryteles (Anthomedusae) or microbasic mastigophores (calycophoran siphonophores) in addition to rhopalonemes.

In species that primarily eat soft-bodied prey, usually only one type of nematocyst occurs, or one is predominant, and they lack adhesive rhopalonemes. The cystonect siphonophores are the clearest example of this group, having only atrichous or homotrichous isorhizas and eating only soft-bodied prey. Most Leptomedusae have either homotrichous isorhizas or microbasic mastigophores (or basitrichous isorhizas). Their diets include some small crustaceans in addition to soft-bodied prey.

Other species that eat soft-bodied prey have nematocyst types unique to them. The Narcomedusae probably eat only gelatinous zooplankton and have apotrichous isorhizas. These nematocysts presumably penetrate soft-bodied prey, and the large spines on the distal two-thirds of the tubule may aid in anchoring them in soft prey tissues. The physonect Apolemia uvaria has only birhopaloides, which are like isorhizas, but with two small swellings along the tubule. Unlike other physonect siphonophores, the diet of A. uvaria includes many soft-bodied prey (salps, ctenophores, hydromedusae, and chaetognaths; total 20-75.3%), as well as crustaceans (16.7-73.3%).

Species feeding on other medusae do not seem to narcotize or kill these prey upon capture. Prey medusae contract when they are first contacted, but they resume pulsations of the swimming bell during ingestion. In contrast, copepods or fish larvae become quiescent soon after contact with a tentacle and do not subsequently resume movement .

Purcell (1984a) found that the size of copepods eaten by siphonophores increased with increasing size and numbers of nematocysts in the batteries. Comparison of the nematocysts of siphonophores and hydromedusae shows

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Fig. 1. Interference contrast micrographs of nematocysts in the tentacles of ten species of hydromedusae. Letters in parentheses following species names indicate Order (a = Anthomedusae, le = Leptomedusae, li = Limnomedusae, n = Narcomedusae, t = Trachymedusae) and predominant prey type (c = crustacean, s = soft-bodied). A. Sarsia tubulosa (a, c). B. Aglantha digitale (t, c). C. Proboscidactyla flavicirrata (li, c). D. Phialidium gregarium (le, s). E. Eutonina indicans (le, s). F. Obelia sp. (le, s). G. Aequorea victoria (le, s). H. Mitrocoma cellularia (le, s). I. Stomotoca atra (a, s). J. Aegina citrea (n, s). Scale bar = 10 μm for all species.
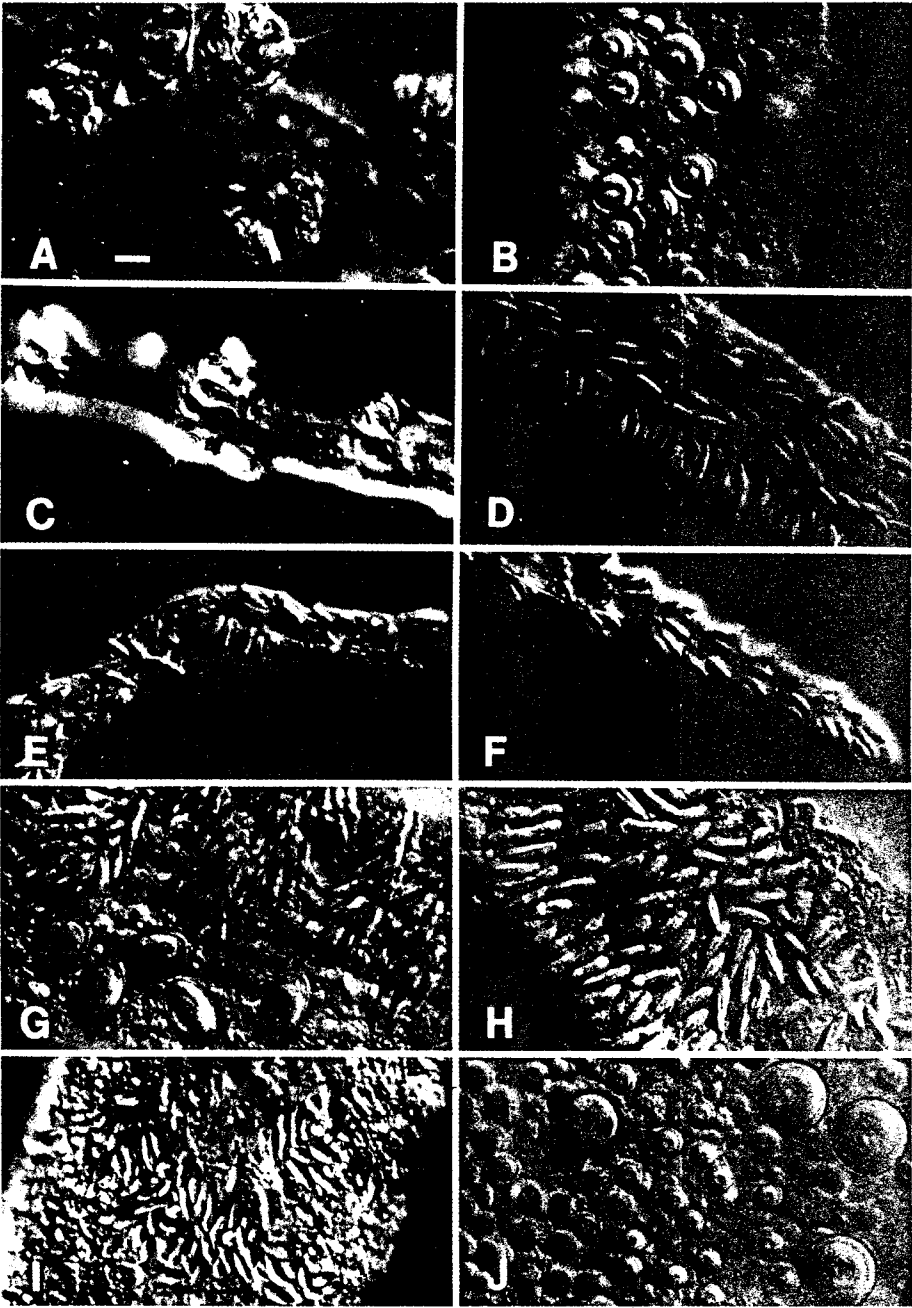
Figure 1

that rhopalonemes and isorhizas in the two groups are of similar size. However, stenoteles and microbasic mastigophores of siphonophores are much larger than those of hydromedusae. We estimate the volumes of these nematocysts as in Purcell (1984a) from the formula for the volume of an elipsoid, $4\pi ab^2$, where a = length/2 and b = diameter/2. Stenoteles ranged in volume from 1.84 -17.22 µl in siphonophores, but only 0.21-1.96 µl in hydromedusae, nearly a 9-fold difference. Microbasic mastigophores ranged in volume from 0.68-73.85 µl in siphonophores, but only 0.014-0.090 µl in hydromedusae; 48- to 820-fold differences. Presumably, large nematocysts could contain longer tubules and more venom, and might potentially be more effective in prey capture than small nematocysts.

These differences in nematocyst volume are not reflected in the sizes of copepods captured. Lengths of copepods removed from hydromedusae in the Strait of Georgia region were as follow: Sarsia spp., 1.3 ± 0.7 mm, n = 46; Hybocodon prolifer, 1.0 ± 0.3, n = 12; Aglantha digitale, 1.0 ± 0.5, n = 16; Mitrocoma cellularia, Phialidium gregarium, and Eutonina indicans combined, 0.6 ± 0.2, n = 9; Aequorea victoria, 1.2 ± 0.8, n = 200 (Purcell, unpubl.). Copepods captured by siphonophores ranged in mean cephalothorax length from 0.36 mm to 1.97 mm (Purcell, 1984a). The siphonophore species most common in the Strait of Georgia region, Muggiaea atlantica, consumed copepods 0.36 mm in mean length, substantially smaller than those consumed by the local hydromedusae, even though its nematocysts were generally larger in size [microbasic mastigophores 36 x 6 µm, anisorhizas 15 x 4 µm, rhopalonemes 6 x 4 µm and 6 x 2 µm (Purcell, 1984a)]. We suggest that prey capture primarily by nematocyst adhesion, as in siphonophores, may require larger nematocysts than prey capture that also involves nematocyst penetration, as in hydromedusae.

Fairly consistent trends in cnidom and diet occur among the hydro-medusan orders, but the distinctions are not as clear as in the Siphonophora. The nematocysts of medusae that feed on soft-bodied prey (many of which also eat some hard-bodied prey) do penetrate crustacean exoskeleton. There-fore medusae are not limited to soft-bodied prey because of an inability to penetrate crustaceans. An alternative explanation is that soft-bodied feeders lack the adhesive nematocysts that enable ready capture of crustaceans.

Fig. 2. Scanning electron micrographs of hydromedusan nematocysts on prey. A. Stenoteles from Sarsia tubulosa penetrating and adhering to copepod exoskeleon; scale bar = 20 µm. B. Desmonemes from S. tubulosa wrapping around copepod setae; scale bar = 10 µm. C. Microbasic mastigo-phores from Stomotoca atra penetrating and adhering to crustacean (larval euphausiid) exoskeleton; scale bar = 10 µm. D. Microbasic mastigophores from S. atra penetrating exumbrella of the hydromedusa Phialidium gregarium; scale bar = 5 µm. E. Microbasic mastigophores from P. gregarium penetrating and adhering to copepod exoskeleton; scale bar = 10 µm. F. Microbasic mastigophores from P. gregarium adhering to copepod setae; scale bar = 10 µm.
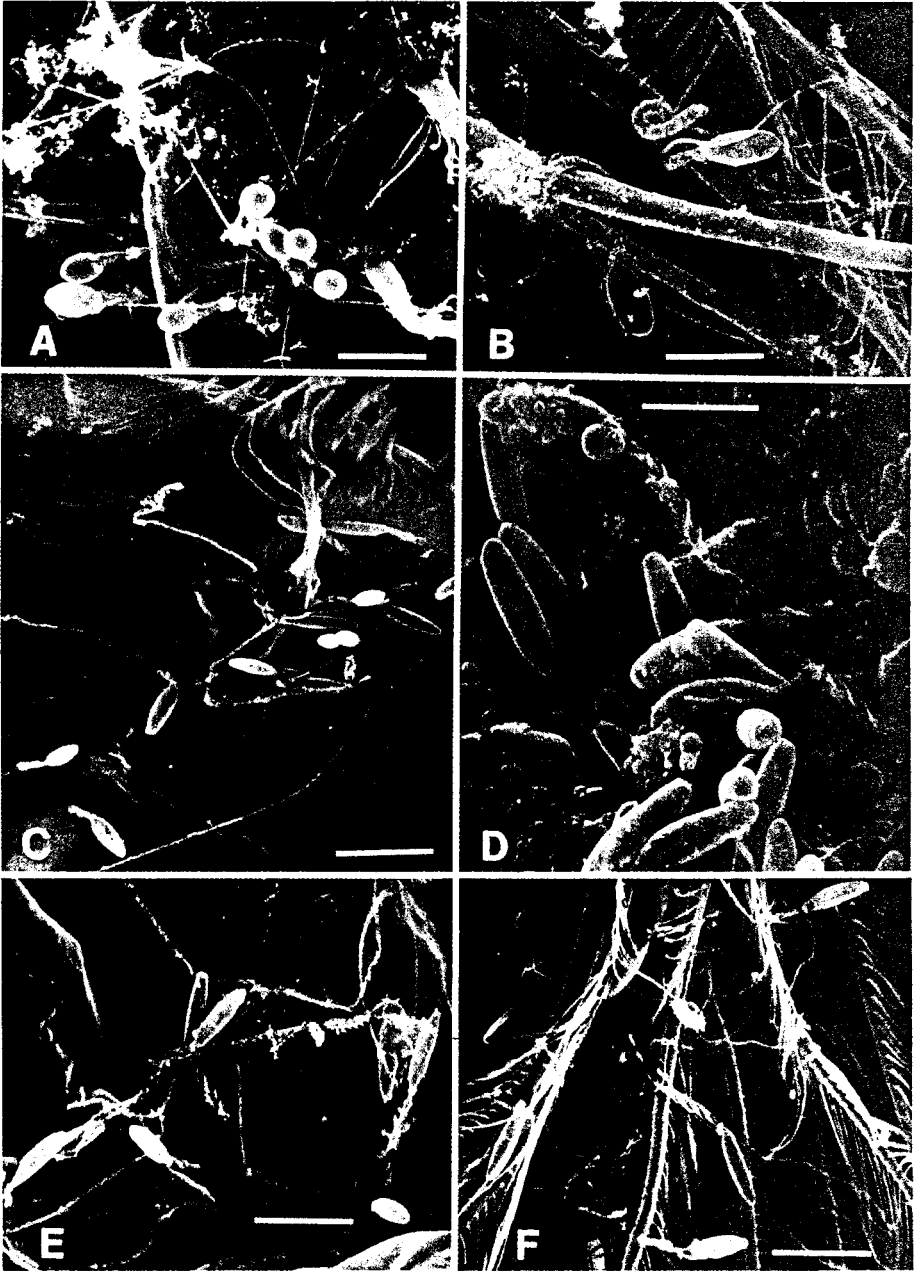
Figure 2

TABLE V. Pelagic hydrozoans grouped according to predominant prey type (soft-bodied or crustacean)

Soft-bodied prey		Crustacean prey	
Predator	Predominant nematocyst types	Predator	Predominant nematocyst types
Cystonect siphonophores	isorhizas	Calycophore and physonect siphonophores	rhopalonemes microbasic mastigophores or stenoteles anisorhizas *
Apolemia uvaria (Physonectae)	birhopaloides		
Family Pandeidae (Anthomedusae)	microbasic euryteles	Anthomedusae	desmonemes stenoteles or euryteles
Leptomedusae	microbasic mastigophores isorhizas *	Limnomedusae	desmonemes microbasic euryteles or macrobasic mastigophores
Narcomedusae	apotrichous isorhizas	Trachymedusae	stenoteles or microbasic euryteles

* numerically predominant

Some surface adhesion of nematocyst tubules that failed to penetrate crustaceans was seen in the hydromedusae, but the amount of adhesion was far less than was seen in calycophoran and physonect siphonophores, which discharged thousands of nematocysts with heavily-spined tubules onto prey. The predators of crustaceans all have adhesive rhopalonemes, which are lacking in the predators of soft-bodied plankton. We conclude that adhesion is very important in the capture of crustacean prey.

Differences in the types of nematocysts present probably do not completely explain the dietary differences that exist among the Hydrozoa. It is possible that differences may exist in the stimuli necessary to discharge the nematocysts. Additionally, feeding behaviors differ among hydrozoans, particularly in the hydromedusae, and these may affect the types of prey captured. Morphological differences among species and in ontogeny also are great, and undoubtedly influence prey capture. Diets will change with location and time, due to variation in prey availability. We stress that most of the dietary data presented here are from specimens of many species collected concurrently, and that true differences in diet exist among pelagic hydrozoan species.

V. CONCLUSIONS

There are consistent trends in nematocyst types and in diets among the orders of hydromedusae and among the suborders of siphonophores. Species that mostly eat crustaceans generally have rhopalonemes and other nematocyst types that adhere to the prey surfaces, and stenoteles that can penetrate the prey exoskeleton. Species that mostly eat soft-bodied prey lack adhesive rhopaloneme nematocysts, and usually have a simple cnidom of one or two nematocyst types, both of which penetrate soft-bodied organisms. Surface adhesion of the nematocyst tubules, and the entanglement of prey is critical in the capture of crustaceans, but adhesion may be ineffective in the capture of soft-bodied organisms.

ACKNOWLEDGMENTS

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