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A review of cnidarians and ctenophores feeding on competitors in the plankton

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Abstract

Predation among pelagic cnidarians and ctenophores is reviewed. The diets of semaeostome scyphomedusae and hydromedusae commonly include other gelatinous zooplanktivores. However, few species of siphonophores and ctenophores are known to consume other gelatinous species. Most of these species can be said to exhibit intraguild predation, since they consume species that potentially compete with them for food. In addition, some hydromedusan and ctenophore species may consume other gelatinous zooplanktivores exclusively. Characteristics of cnidarians and ctenophores as predators and as prey of other gelatinous species are discussed.

Introduction

Gelatinous zooplankton often seems to lack obvious predators. However, many species are eaten by other gelatinous species. Only a few studies have focused on such interactions. Greve (1971, 1981) has discussed the dynamics of ctenophore populations that resulted from predation in *Pleurobrachia pileus* by *Beroe gracilis*. Predation of the scyphomedusan *Chrysaora quinquecirrha* on the ctenophore *Mnemiopsis leidyi* apparently affected zoo- and phytoplankton populations in Chesapeake Bay (Feigenbaum & Kelly, 1984). Strand & Hamner (1988) described the foraging behavior of the scyphomedusan *Phacellophora camtschatica* on *Aurelia aurita*. Arai & Jacobs (1980) found that several species of hydromedusae and one scyphomedusan fed on medusae and ctenophores in the laboratory.

Intraguild predation is defined as 'the eating of species that use similar, often limiting resources, and are thus potential competitors' (Polis *et al.*, 1989). Herein, I review predation by scyphomedusae, hydromedusae, siphonophores and ctenophores on other species in these taxa. Many species exhibit intraguild predation. The major prey of most species is crustacean zooplankton (e.g., Purcell, 1981, 1990; Alvariño, 1985). In most cases, the extent of dietary overlap between gelatinous predator and prey is unknown. Some species may eat only other gelatinous zooplanktivores, and therefore are not intraguild predators.

Intraguild predation by gelatinous zooplankton

There are reports of predation among many species of scyphomedusae, hydromedusae, siphonophores and ctenophores (summarized in Tables 1–2). Even so, dietary information on pelagic species is limited.

Scyphomedusae

Intraguild predation occurs frequently in semaeostome scyphomedusae (Table 2). However, few instances of predation by scyphomedusae on

Table 1. Species consumed by other gelatinous zooplankton (see Table 2).

Scyphomedusae
- a. *Aurelia aurita* (Linnaeus)
- b. *Chrysaora melanaster* Brandt

Hydromedusae
- a. *Aegina citrea* Eschscholtz
- b. *Aequorea victoria* (Murbach & Shearer)
- c. *Aglantha digitale* (O. F. Müller)
- d. *Amphinema dinema* (Péron & Lesueur)
- e. *Bougainvillia* spp.
- f. *Catablema* spp.
- g. *Clytia gregaria* (A. Agassiz); *C. hemisphaerica* (Linnaeus)
- h. *Cosmetira pilosella* Forbes
- i. *Eperetmus typus* Bigelow
- j. *Euphysa japonica* (Maas)
- k. *Eutima gracilis* (Forbes & Goodsir)
- l. *Eutonina indicans* (Romanes)
- m. *Hybocodon prolifer* L. Agassiz
- n. *Laodicea undulata* (Forbes & Goodsir)
- o. *Leukartiara* spp.
- p. *Liriope tetraphylla* (Chamiso & Eysenhardt)
- q. *Melicertum octocostatum* (M. Sars)
- r. *Mitrocoma cellularia* (A. Agassiz)
- s. *Mitrocomella polydiademata* (Romanes)
- t. *Nemopsis bachei* L. Agassiz
- u. *Obelia* spp.
- v. *Proboscidactyla flavicirrata* Brandt
- w. *Rathkea octopunctata* (M. Sars)
- x. *Sarsia tubulosa* (M. Sars); *S. princeps* (Haeckel)
- y. *Staurophora* sp.
- z. *Tiaropsis multicirrata* (M. Sars)

Siphonophores
- a. *Chelophyes appendiculata* (Eschscholtz)
- b. *Dimophyes arctica* (Chun)
- c. *Muggiaea atlantica* Cunningham
- d. *Nanomia cara* A. Agassiz
- e. *Physophora hydrostatica* Forskål
- f. *Rhizophysa eysenhardti* Gegenbaur

Ctenophores
- a. *Bolinopsis infundibulum* (O. F. Müller); *B. vitrea* L. Agassiz
- b. *Beroe cucumis* Fabricius; *B. ovata* Bosc
- c. *Cestum veneris* Lesueur
- d. *Eurhamphaea vexilligera* Gegenbaur
- e. *Leucothea multicornis* (Quoy & Gaimard)
- f. *Mnemiopsis leidyi* A. Agassiz; *M. mccradyi* Mayer
- g. *Ocyropsis crystallina* (Rang); *O. maculata* (Rang)
- h. *Pleurobrachia bachei* A. Agassiz; *P. pileus* (Fabricius)

other scyphomedusae have been reported. The ephyrae of *Aurelia aurita* were eaten by adult *A. aurita* and *Chrysaora hysoscella*, and adult *A. aurita* were eaten by *Cyanea capillata*, *Drymonema dalmatinum* and *Phacellophora camtschatica*. Strand & Hamner (1988) found that larger *P. camtschatica* caught more and larger medusae. Several species of hydromedusae and ctenophores were consumed by scyphomedusae (Table 2). Fancett (1988) found that hydromedusae constituted 9% of the prey items of *C. capillata*. *Rathkea octopunctata* and *Obelia* sp. constituted as much as 83% of the prey of *A. aurita* during March and April (B.K. Sullivan, pers. comm.). Siphonophores were also eaten but the species were often not identified. No scyphomedusan is known to feed exclusively on gelatinous zooplankton.

Hydromedusae

Intraguild predation appears to be widespread in hydromedusae (Table 2). Hydromedusae were the most frequently reported intraguild prey of other hydromedusae. Gelatinous zooplankton constituted 10.5% of the prey in gut contents of *Aequorea victoria* during March to June in British Columbia (Purcell, in press). *Rathkea octopunctata* averaged 7.3% of the prey of *Tiaropsis multicirrata* (see Zelickman *et al.*, 1969). Although dietary evidence is limited, no prey other than soft bodied zooplankton have been reported from *Stomotoca atra*, and the narcomedusan *Solmissus* sp. contained only hydromedusae (Table 2). Purcell & Mills (1988) suggested that all species of narcomedusae may consume exclusively gelatinous zooplankton.

Siphonophores

Predation on ctenophores and other cnidarians is not common among siphonophores (Table 2). *Apolemia uvaria* is the only siphonophore shown to eat gelatinous zooplankton frequently. Purcell (1981) found that hydromedusae and ctenophores each constituted 1% of its prey. No siphonophore is known to eat only other gelatinous zooplankton.

Ctenophores

A few species of ctenophore consume other ctenophores or cnidarians in addition to other zooplankton (Table 2). In addition to those species, ctenophores in the genus *Beroe* are widely known to consume other ctenophore species

Table 2. Intraguild predation by scyphomedusae and hydromedusae. Table 1 gives the prey species identifications by letters.

Predators	Prey				References
	Scypho-medusae	Hydro-medusae	Siphono-phores	Cteno-phores	
Scyphomedusae					
Aurelia aurita	– – – –	g,u	[1]	[1]	Delap, 1907 [2]
	– – – –	g,w	– – – –	– – – –	Lebour, 1923 [2]
	– – – –	e,u,w,x	– – – –	a,b	Loginova & Perzova, 1967
	– – – –	g,x	– – – –	h	Arai & Jacobs, 1980 [2]
	a	[1]	– – – –	– – – –	Möller, 1980
	– – – –	u,w,x	– – – –	a	Alvariño, 1985 [2]
Chrysaora sp.	– – – –	o	[1]	b	Delap, 1901 [2]
C. hysoscella (Linnaeus)	a	d,g,h,u	– – – –	[1]	Lebour, 1923 [2]
C. melanaster	– – – –	1	– – – –	– – – –	Hamner, 1983
C. quinquecirrha (Desor)	– – – –	– – – –	– – – –	f	Phillips *et al.*, 1969
	– – – –	– – – –	– – – –	b,f	Miller, 1974
	– – – –	t	– – – –	f	Purcell, unpubl.
Cyanea sp.	u	– – – –	– – – –	– – – –	Littleford, 1939
	– – – –	t,w,x	– – – –	– – – –	Brewer, 1989
Cyanea capillata (Linnaeus)	a [2]	r [2],w [2] y,z	e	a,b	Plotnikova, 1961
	– – – –	– – – –	– – – –	f	Cargo & Schultz, 1967
	a	– – – –	– – – –	– – – –	Loginova & Perzova, 1967
	– – – –	u	– – – –	[1]	Alvariño, 1985 [2]
	b	b,j,x	– – – –	– – – –	Hamner, 1983
	– – – –	[1]	– – – –	– – – –	Fancett, 1988
	– – – –	t	– – – –	f	Purcell, unpubl.
C. lamarcki Péron & Lesueur	– – – –	g,h,m n,u	– – – –	a,b,h	Delap, 1905 [2]
Drymonema dalmatinum Haeckel	a	– – – –	– – – –	[1]	Larson, 1987a
Pelagia noctiluca Forskål	[1]	u	[1]	[1]	Delap, 1907 [2]
	– – – –	[1]	[1]	[1]	Larson, 1987b
Phacellophora camschatica Brandt	a	f	– – – –	a,h	Strand & Hamner, 1988
	– – – –	l,v	d	h	Purcell, 1990
Hydromedusae					
Aequorea sp.	– – – –	– – – –	– – – –	h	Lebour, 1923
	– – – –	– – – –	– – – –	a	Hamner *et al.*, 1975
	– – – –	– – – –	– – – –	d,g	Harbison *et al.*, 1978
A. victoria	a	g,x	– – – –	h	Arai, 1980 [2]
	a	c,g,j,l,r s,u,v,w,x	b,c,d	h	Purcell, in press
	a	g,j,r,u,x	– – – –	h	Arai & Jacobs, 1980 [2]

Table 2. (Continued).

Predators	Prey				References
	Scypho-medusae	Hydro-medusae	Siphono-phores	Cteno-phores	
Amphinema dinema (Péron & Lesueur)	----	k,u	----	----	Lebour, 1922 [2]
Catablema spp.	----	c,g,j,l	----	----	Hamner, 1983
Clytia hemisphaerica	----	k,u,w	c	----	Lebour, 1922, 1923
Cosmetira pilosella	----	----	----	h	Lebour, 1922, 1923
Eutima gracilis	----	u	----	----	Lebour, 1923
Eutonina indicans	a	x	----	h	Arai & Jacobs, 1980 [2]
Gonionemus vertens A. Agassiz	----	1	1	1	Fraser, 1969 [2]
Leuckartiara octona (Fleming)	----	1	1	1	Fraser, 1969 [2]
	----	----	d	----	Alvariño, 1985 [2]
L. nobilis Hartlaub	----	c,x	----	----	Fraser, 1969 [2]
Melicertum octocostatum	----	y	----	----	Fraser, 1969 [2]
Obelia sp.	----	----	----	1	Lebour, 1922 [2]
Orchistoma sp.	----	----	e	----	Biggs, 1976
Solmissus sp. [3]	----	g	----	----	Purcell & Mills, 1988
Staurophora sp.	----	1	1	1	Fraser, 1969 [2]
Stomotoca atra [3]	----	u	----	----	Hyman, 1940
A. Agassiz	a	b,e,g,i l,r,v,x	----	h	Arai & Jacobs, 1980 [2]
	----	e,g,q,y	----	----	Hamner, 1983
	----	1	----	----	Larson, 1987b
	----	u	----	----	Purcell & Mills, 1988
Tiaropsis multicirrata	----	----	----	a [2]	Plotnikova, 1961
	----	w	----	----	Zelickman *et al.*, 1969
	----	j,x	----	----	Alvariño, 1985 [2]
Siphonophores					
Apolemia uvaria Lesueur	----	1	----	h	Purcell, 1981
Rosacea cymbiformis Chiaje	----	----	f	----	Purcell, 1981
Ctenophores					
Beroe sp. [3]	----	----	----	h	Hirota, 1974
Beroe cucumis [3]	----	----	----	a,h	Lebour, 1923
	----	----	----	a	Greve, 1971
	----	----	----	a,d,g	Swanberg, 1974

Table 2. (Continued).

Predators	Prey				References
	Scypho-medusae	Hydro-medusae	Siphono-phores	Cteno-phores	
B. ovata [3]	----	----	----	f	Nelson, 1925
	----	----	----	h	Horridge, 1965
	----	----	----	f	Miller, 1974
	----	----	----	a,c,e,g	Swanberg, 1974
B. gracilis Künne	----	----	----	h	Hamond & Williams, 1977
Haeckelia rubra [3] (Kölliker)	----	a	----	----	Mills & Miller, 1984
H. beehleri (Mayer)[3]	----	----	a	----	Harbison, 1984
Hormiphora palmata Chun	----	x	----	----	Alvariño, 1985
Ocyropsis maculata	----	----	----	b	Harbison *et al.*, 1978
Pleurobrachia sp.	----	----	----	[1]	Alvariño, 1985

[1] observed but not identified
[2] laboratory observations, all others from gut contents or field observations.
[3] may consume only gelatinous zooplankton

(Table 2). Other zooplankters also are reported from the diets (Alvariño, 1985) but these may be from their ctenophore prey. Additionally, species of *Haeckelia* may eat only gelatinous zooplankton (Harbison, 1984) (Table 2).

Other phyla

In addition to pelagic cnidarians and ctenophores, other zooplankton predators are potential intraguild prey of gelatinous zooplanktivores. Chaetognaths were listed as prey of the scyphomedusae *Aurelia aurita* (by Alvariño, 1985), *Chrysaora* sp. (by Delap, 1901), *C. hysoscella* (by Lebour, 1923) and *Pelagia noctiluca* (by Larson, 1987b). The only case of intraguild predation reported in a non-semaeostome medusa was the feeding of *Rhizostoma octopus* (L.) on chaetognaths (Alvariño, 1985). Chaetognaths have been reported in the diets of several hydromedusae: *Aphinema dinema* and *Bougainvillia superciliaris* (L. Agassiz) (see Alvariño, 1985), and *Eutonia gracilis*, *Hybocodon prolifer*, *Clytia hemisphaerica* and *Proboscidactyla stellata* Uchida (see Lebour, 1923). Several species of siphonophore contained chaetognaths *in situ* (*Apolemia uvaria*, *Athorybia rosacea* (Forskål), *Forskalia* spp., *Nanomia bijuga* (delle Chiaje), *Rosacea cymbiformis*, *Sulculeolaria* spp. (see Purcell, 1981), and *Physalia physalis* (L.) (see Purcell, 1984)). Alvariño (1985) and Hirota (1974) reported the ctenophores *Pleurobrachia* spp. feeding on chaetognaths.

Pelagic cnidarians and ctenophores have been thought to compete with larval fish for food. Fish larvae are eaten by many such species (Alvariño, 1985; Purcell, 1985; Bailey & Houde, 1989), and are possible intraguild prey of these predators. Purcell (1990) and Purcell & Grover (1990) found that of 11 hydromedusans, the diets of only 3 species (*Aglantha digitale*, *Obelia* sp., *Proboscidactyla flavicirrata*) overlapped greatly with the diet of first-feeding herring larvae. They concluded that gelatinous predators could not have reduced the microzooplankton prey of the larvae, except in one location, and that competition for food probably did not occur.

Gelatinous zooplankton as prey

Gelatinous zooplanktivores may be favourable prey for several reasons. First, gelatinous zooplankton would encounter tentaculate predators with increased frequency due to their large size relative to other zooplankton. Second, they may be easier to catch than crustacean zooplankton, because they lack an exoskeleton, and because they may lack effective escape responses. However, behavior sequences presumably for escape have been reported from *Aglantha digitale*, *Proboscidactyla flavicirrata*, and *Aurelia aurita* (by Donaldson *et al.*, 1980; Spencer, 1975; and Strand & Hamner, 1988, respectively). Third, gelatinous zooplankton may also be easy to digest because most of their tissue is in thin layers external to the mesoglea.

There are also disadvantages of having gelatinous zooplanktivores as prey. First, the predators must be large enough to consume the large gelatinous prey. Second, all cnidarian species and ctenophores of the genus *Haeckelia* possess nematocysts that could injure predators and deter ingestion. Third, gelatinous species usually occur in low densities compared with crustacean zooplankton. The few species that consume only gelatinous zooplankton may be able to locate their prey, as *Beroe* spp. (Swanberg, 1974). Fourth, their weight-specific carbon content can be $<25\%$ that of crustacean zooplankton. However, this may be compensated for by the large size of gelatinous species relative to crustaceans.

Gelatinous zooplankton as predators

Several species of semaeostome scyphomedusae and hydromedusae are known to eat other species of gelatinous competitors: however, intraguild predation is less common by siphonophores and ctenophores. Such differences among these groups may be due to differences in morphology and mechanisms of prey capture. Species that eat gelatinous zooplankton usually have large gastric areas that can engulf large prey. Some hydrozoan species have unusual nematocysts of a single type that may penetrate soft-bodied prey, but may be unable to penetrate or adhere to crustacean exoskeleton (Purcell & Mills, 1988). In contrast to the predators of gelatinous species, most siphonophores and ctenophores have small gastric areas. Most siphonophore nematocysts and ctenophore colloblasts are adhesive and may be best suited to capturing hard-bodied prey (Purcell & Mills, 1988). In addition, siphonophores and tentacle-bearing ctenophores remain still in the water with their tentacles spread rather than swimming while fishing. This may lessen the chance of encounter with gelatinous species that occur in low densities or that swim little.

In contrast to other organisms in which intraguild predation has been considered (Polis *et al.*, 1989) most pelagic cnidarians and ctenophores do not actively attack prey organisms, but instead rely on prey coming into contact with their feeding surfaces. Therefore, predation on gelatinous competitors may seem to be entirely fortuitous. However, their large size, and species differences in nematocysts types and diets (Purcell & Mills, 1988) suggest that some pressures have led to the evolution of intraguild predation by some gelatinous zooplankton.

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