Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems

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Medusae, siphonophores, and ctenophores are planktivorous predators operating at higher trophic levels in marine ecosystems of a wide range of productivity. It has been hypothesized that high-productivity ecosystems such as areas of upwelling tend towards food chains dominated by larger phytoplankton, large copepods, and ultimately many species of fish rather than gelatinous predators; ecosystems with lower productivity are characterized by small flagellate phytoplankton, small copepods, and ultimately numerous medusae and ctenophores. Evidence is provided that medusae, siphonophores, and ctenophores are actually important predators in both sorts of planktonic ecosystems, although uneven reporting in the literature may be cause for underestimates of the importance of these carnivores in some systems. As world fisheries begin to experience serious declines, it is relevant to recognize that the carnivorous "jellyfishes" are ubiquitous and are thus opportunistically positioned to utilize secondary production that is ordinarily consumed by fish.

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Introduction

Parsons and Greve (1977, 1979) suggested that high productivity or upwelling ecosystems tend towards food chains dominated by larger phytoplankton, accompanied by the production of large copepods, and many species of fish, whereas low productivity or convergent ecosystems, on the other hand, are characterized by small flagellate phytoplankton, with the production of small copepods, and eventually large numbers of medusae and ctenophores. Only the endpoints of this hypothesis, the progression through food chains dominated ultimately either by fishes or jellyfishes, will be discussed here. I hope to convince the reader that in fact, medusae, siphonophores, and ctenophores (referred to inclusively as jellyfishes) are present nearly to the same extent in upwelling systems as in regions of low productivity. By accidents of weather, ship locations, and home residence locations of scientists who study these animals, the numerical abundance and importance of the planktonic carnivorous jellyfishes has been overlooked on a global scale.

Observations from blue-water diving and manned submersibles

When the dual food chain hypothesis was originally proposed (Greve and Parsons, 1977), it was partially supported by the work of Greve (1971, 1972), who showed through field and laboratory observations that the tentaculate ctenophore *Pleurobrachia pileus* grew best in rather low concentrations of small species of copepods. Large copepods were shown to be detrimental in different ways to both adult and larval *P. pileus*, as large copepods can escape being eaten, often tearing the tentacles of larger ctenophores in the process, and they sometimes even prey on larval ctenophores. Parsons (1979), in further support of jellyfish being an endpoint in low productivity waters, cited the important role of gelatinous zooplankton in areas such as the Sargasso Sea as portrayed by direct observation in the new technology of blue-water diving.

A series of papers in the late 1970s reporting observations of the fragile gelatinous zooplankton by SCUBA divers (Hamner, 1975; Hammer *et al.*, 1975; Harbison *et al.*, 1977, 1978; and others) reminded many

Table 1. A comparison of the diversity of medusae, siphono-
phores, and ctenophores collected on submersible cruises using
the "Johnson-Sea-Link I" and "II" in two locations. Studies
were of approximately equal duration in water columns of
nearly the same depth.

	High productivity	Low productivity
	North Atlantic off New England	Alboran Sea Mediterranean
	23 dives 800 m bottom	26 dives 700–800 m bottom
Hydromedusae	10	9
Siphonophores	13	13
Scyphomedusae	6	3
Ctenophores	9	11

oceanographers about the existence and putative
importance of the gelatinous macrozooplankton. Most
of the blue-water SCUBA diving in the 1970s and early
1980s occurred in the Caribbean and Sargasso Seas, and
thus Parsons and perhaps others concluded that
gelatinous zooplankton was most plentiful and most
important in oligotrophic waters. In fact, the locations
of these dives had more to do with the logistics of blue-
water diving than with the expected presence or absence
of gelatinous zooplankton. Blue-water diving at nearly
any location in the world would yield the same sorts of
fragile epipelagic planktonic jellyfish in substantial
numbers (G. R. Harbison and L. P. Madin, pers.
comm.). For example, during the past 15 years there has
been an ongoing program of blue-water diving off Santa
Barbara, California, by faculty and students at the
University of California. These dives, often in upwelling
conditions (in direct contrast to the oligotrophic and
stable water masses of the Sargasso Sea) have revealed
similar taxa, often with even the same cosmopolitan
epipelagic species (S. H. D. Haddock, pers. comm.), as
were described in the early blue-water diving papers
from the Sargasso Sea and Caribbean.

Comparable submersible studies of the water column
also reveal similar numbers of species of jellyfish in high
and low productivity regions of the ocean. Table 1
summarizes findings from three submersible cruises, two
in the NW Atlantic off Massachusetts (August–
September 1986 and August 1987) and one in the
Alboran Sea (Mediterranean) off the coast of Morocco
(April 1991), in which the same taxonomic specialists
working on medusae (R. J. Larson and C. E. Mills),
siphonophores (P. R. Pugh), and ctenophores (G. R.
Harbison) participated. In each location, specimens
were collected on approximately the same number of
dives in a water column of nearly the same depth.
Species diversity of the three groups of gelatinous
carnivores was remarkably similar between the two

locations. The total numbers of jellyfishes were much
greater off New England than in the Alboran Sea,
reflecting the greater numbers of all categories of
zooplankton at that location. The key to discovering
similarities in jellyfish diversity between these two sites
was the inclusion of specialists interested in all three
groups in both scientific parties. Although only a small
number of jellyfish species are recognized by most
oceanographers, a similarly diverse group of medusae,
siphonophores, and ctenophores is present in most parts
of the open ocean; but it is rare for oceanographic
expeditions to have anyone on board interested in
working with these animals.

Jellyfishes and radical ecological change

The most graphic example to date of a highly productive
ecosystem, that has converted from supporting a
number of valuable commercial fisheries to having few
fishes and high numbers of jellyfishes, is the Black Sea
and its adjacent Sea of Azov. The Black Sea has a
history over the past several decades of increased
pollution and eutrophication, coupled with a number
of unfortunate introductions of alien marine inverte-
brates that have done much to change the ecology of
both benthos and the water column (Zaitsev, 1992).
There were 26 commercial fishes in the Black Sea in the
1960s; disappearance of most of the large predatory
fishes led to an increase in small predatory fishes over
the next decades, so that by the 1980s only five
commercial fishes were left (Zaitsev, 1992), and nearly
all of the zooplankton production was going into these
planktivorous fishes (Studenikina et al., 1991).

The ctenophore Mnemiopsis leidyi, accidentally in-
troduced from the eastern seaboard of America to the
Black Sea in 1982, and entering the Sea of Azov a few
years later, has now succeeded in nearly completely
replacing the planktivorous fishes in the Sea of Azov as
the terminal zooplankton consumer, and is also very
important in the ecosystem of the entire Black Sea basin
(Shushkina and Musayeva, 1990; Studenikina et al.,
1991; Harbison and Volovik, 1995). Although a number
of investigations in the USA have been devoted to the
study of Mnemiopsis leidyi in its native environment,
where it may be very abundant in bays in the
summertime, it is unlikely that oceanographers really
understood the importance of this lobate ctenophore,
nor could anyone have predicted the general collapse of
the fishing industries in the Sea of Azov, and to a lesser
extent, the Black Sea, brought about by its arrival there.

Another potentially alarming situation is portended
by large numbers of the siphonophore Nanomia cara
observed in the Gulf of Maine in August 1992 (C. H.
Greene, pers. comm.) and September 1993 (by the
author participating on a cruise with C. H. Greene).
While using the manned submersible "Johnson-Sea-

Link I" to search for copepods and euphausiids in 300 m deep Wilkinson Basin, we found instead large numbers of *N. cara*. These siphonophores, which varied in length from about 20 to 50 cm, were located only in the lower half of the water column by day, but migrated up and were throughout the entire water column at night. My estimates of distances between *N. cara* colonies, on the 18 September 1993 dusk submersible dive, when the animals were still in the process of vertically migrating, indicated fairly uniform densities of about 0.2 m^{-3} in the upper 50 m, densities varying patchily from 1 to 10 m^{-3} between 50 and 250 m, and densities up to 50–100 m^{-3} individuals from 250 m to the bottom at 270 m. In addition to *N. cara*, three species of ctenophores (*Pleurobrachia pileus, Euplokamis dunlapae*, and *Bolinopsis infundibulum*) and a hydromedusa (*Aglantha digitale*) were also very numerous, and taken as a group, also spanned the entire water column. A similar aggregation of *N. cara* was reported by Rogers *et al.* (1978) in the same part of the Gulf of Maine, persisting at least from autumn 1975 through June 1976 and with estimated densities up to 7 m^{-3} as observed by manned submersible.

We do not know if the 1975–1976 and 1992–1993 *Nanomia* siphonophore blooms in the Gulf of Maine are regular cyclical events or if they are highly unusual, and we do not know the full duration of either episode. Other submersible observations in canyons south of Woods Hole, Massachusetts, have revealed *Nanomia cara* to be a normal and common member of the nearby NW Atlantic deep water community (Larson *et al.*, 1988). The extraordinary numbers of *N. cara* seen on submersible dives in 1992 and 1993 indicate that gelatinous predators must be a driving force in the water column ecology during such blooms.

With the general collapse of NW Atlantic fisheries from over-harvesting, it will be difficult to determine the effect of the recent *Nanomia cara* bloom on the pelagic Gulf of Maine ecosystem. A few interesting correlations can be made for the 1975–1976 *Nanomia* bloom, by looking back at records of fish recruitment in the area during those years. Myers *et al.* (1990) report that the 1975 and 1976 year classes of haddock and herring had average to good recruitment, but that yellowtail flounder, silver hake, redfish, and cod had unusually poor recruitment in those years. At present, we cannot determine whether the siphonophore was responsible for these poor fish recruitments. The diet of *N. cara* in the Gulf of Maine has yet to be investigated, but a similar species, *N. bijuga*, has been reported to feed primarily on copepods, chaetognaths, and shrimp in the Gulf of California (Purcell, 1981a) and primarily on *Euphausia pacifica* in Monterey Bay, California (B. H. Robison, pers. comm.) (Table 3).

Greve (1994) reported an unprecedented invasion of the siphonophore *Muggiaea atlantica* into the German

Table 2. Natural diets of some co-occurring hydromedusae in late spring 1987, Friday Harbor, Washington, USA, as determined from gut contents of field-collected animals. All species of medusae were collected from the same water masses. Since the same pool of potential prey was available to all species of hydromedusae, differences in diets reflect selectivity on the part of the medusae. Mechanisms for prey selection are discussed by Mills (1981b) and Purcell and Mills (1988). The number of medusae of each species examined is designated by "n". Prey consumed is presented as percentage of the total number of prey items in the guts. From unpublished data of the author.

Predator species	Prey consumed	
	%	Principal types
Aequorea victoria (n = 100)	90	Hydromedusae and ctenophores
Catablema nodulosa (n = 90)	78	Hydromedusae
	11	Invertebrate eggs
Mitrocomella polydiademata (n = 125)	45	Larvaceans and houses
	40	Invertebrate eggs
Phialidium gregarium (n = 125)	73	Invertebrate eggs
	11	Larvaceans and houses
Bougainvillia principis (n = 125)	85	Barnacle nauplii
Aglantha digitale (n = 36)	71	Copepods and copepod nauplii
	27	Invertebrate eggs, especially copepods

Bight in 1989. The population of this small, copepod-eating siphonophore reached 500 m^{-3} in summer 1989, temporarily reducing resident copepods to near zero. Although such a bloom has not yet been repeated, Greve warns of the potential for general disruption of this pelagic ecosystem if the normal dominant gelatinous predator *Pleurobrachia pileus* is replaced by *Muggiaea atlantica*, whose ecology is quite different, not being susceptible to the ctenophore-specific secondary carnivore *Beroe gracilis*.

Parsons (1979) questioned whether the removal of top predators by the world's fisheries might favour the establishment of increased numbers of jellyfish. *Nanomia* blooms in the Gulf of Maine might be an interesting example of such a phenomenon. In the Black Sea, predatory fishes were removed from the system, but the remaining small planktivorous fishes seem genuinely to have been outcompeted by newly arrived *Mnemiopsis* ctenophores. The result, however, in these two situations appears to be the same – domination of a previously highly productive ecosystem by jellyfishes following human-mediated events such as over-fishing, introductions of alien species to a new environment, and general

Table 3. Natural diets of some siphonophores as determined from gut contents of field-collected animals. The number of colonies of each species examined is designated by "n". Prey consumed is presented as percentage of the total number of prey items in the guts. Most siphonophores appear to be highly selective carnivores (discussed further by Purcell (1981a, 1984)).

Predator species	Location (season)	Prey consumed		Reference
		%	Principal types	
Nanomia bijuga (n = 53)	Gulf of California	25 20 16	Copepods Chaetognaths Shrimp	Purcell (1981a)
Nanomia bijuga (n = >100)	Central California	Mostly Euphausiids		B. H. Robison (pers. comm.)
Rosacea cymbiformis (n = 47)	Gulf of California	58 25	Copepods Crab zoea larvae	Purcell (1980, 1981c)
Rhizophysa eysenhardti (n = 646)	Gulf of California (summer)	100	Fish larvae	Purcell (1981b)
Bassia bassensis (n = 60)	Gulf of California	100	Copepods	Purcell (1981a)
Muggiaea atlantica (n = 117)	Washington State (Oct. 1980)	100	Copepods	Purcell (1982)

habitat degradation. Parsons (1993) pointed out that studying "the role of jellyfish, teleosts, and other predators in maintaining the natural ecology of the sea is practically a nonexistent research enterprise".

Jellyfishes in fjords

Medusae, siphonophores, and ctenophores form a major part of the macroplankton of temperate fjords, which are generally considered to be high productivity systems. Extensive year-round collections in the San Juan Archipelago, between British Columbia, Canada, and Washington State, USA, yielded nearly 65 different species of medusae, siphonophores, and ctenophores in the region (Mills, 1981a and unpublished). Mackie and Mills (1983) and Mackie (1985) reported an assemblage of about 6–8 hydromedusae, 3–5 siphonophores, and 4–5 ctenophores which were sufficiently abundant to be easily seen and counted from a manned submersible in fjords of British Columbia, Canada. Occurring in horizontal bands of varying thicknesses, some of these species reached localized densities of up to 10 animals m^{-3}. They clearly formed an important community of mesopelagic predators, about which little is known.

Norwegian fjords appear to have a very similar assemblage of gelatinous predators to those found in the fjords of British Columbia, but characterization of these jellyfishes is only now in progress (F. Pagès, pers. comm.). Fosså (1992) describes a Norwegian fjord whose ecology appears to have changed in response to

an unusual population increase of a normally resident jellyfish. While many Norwegian fjords are populated by the cosmopolitan and usually deep-water scyphomedusa *Periphylla periphylla*, only a small number of fjords contain large *P. periphylla* populations. This medusa has been present in Lurefjorden near Bergen since at least the 1940s, but in 1973 it suddenly experienced a population explosion, that, as measured by the nuisance factor in fishing nets, has continued to increase over the past 20 years. Presumably as a result of the increased numbers of medusae (which feed nearly exclusively on copepods (Table 4)), the pelagic fish community in Lurefjorden is now different from nearby fjords not dominated by jellyfish. The two species of mesopelagic fish, *Maurolicus muelleri* and *Benthosema glaciale*, known to be important copepod predators in nearby fjords, are not present in Lurefjorden, where the whiting, *Merlangius merlangus*, often reported to be associated with medusae, is the dominant larger fish. It seems quite likely that the increased presence of *P. periphylla* has driven these changes.

Feeding by medusae, siphonophores, and ctenophores

A limited number of field studies have reported the natural diets of one or more jellyfishes in a particular ecosystem. A representative selection of this information, chosen for large sample sizes, is given in Tables 2–5. Whereas scyphomedusae and ctenophores appear to be fairly generalist predators, eating a wide variety of

Table 4. Natural diets of some scyphomedusae as determined from gut contents of field-collected animals. The number of medusae of each species examined is designated by "n". Prey consumed is presented as percentage of the total number of prey items in the guts (except Brewer data, where % is number of medusae containing that type of prey). Although most scyphomedusae that have been studied feed to some extent on all available zooplankton, nearly all authors below saw evidence of varying degrees of selectivity in their studies on scyphomedusae.

Predator species	Location (season)	Prey consumed		Reference
		%	Principal types	
Aurelia aurita	Kiel Bight		All zooplankton esp. mollusc larvae and copepods	Schneider and Behrends (1994)
Chrysaora quinquecirrha (n = 390)	Chesapeake Bay, USA (summers 1987–1990)	55–71	Copepods (also sometimes numerous rotifers, cladocerans, ctenophores, polychaetes, and bay anchovy eggs)	Purcell (1992)
Cyanea capillata (n = hundreds)	Connecticut (springs 1980–1986)	80–85 15–30 2–12 10	Copepods Decapods and mysids Amphipods Fish	Brewer (1989)
Periphylla periphylla (n = 39)	Norway (March 1992)	97	Copepods	Fosså (1992)
Pseudorhiza haeckeli (n ≈ 35)	S. Australia (summers 1984–1986)	41 33	Fish eggs and larvae Copepods	Fancett (1988)
Stomolophus meleagris (n = 165)	Gulf of Mexico (summers 1986–1987)	63 16 9 8	Bivalve veligers Copepods and nauplii Tintinnids Gastropod veligers	Larson (1991)

available zooplankton, individual species of hydromedusae and siphonophores tend to have highly specialized diets, but these latter animals usually occur in multi-species assemblages that may together have a more general effect. A bias exists in many feeding studies, because the diet of the gelatinous predator was examined near some harvestable resource. Studied in a different location, a predator might show different dietary preferences. An example of this is the NE Pacific hydromedusa *Aequorea victoria*, shown by Purcell (1989) to consume herring larvae in bays where herring are known to spawn, but never found by the present author to consume any kind of larval fishes in a nearby habitat without spawning herring. We do not yet have sufficient knowledge to distinguish between the effects of excessive predation by a bloom of one or the other of these groups of jellyfishes, if such exists.

Conclusions

Medusae, siphonophores, and ctenophores are present in all of the world's oceans, often in great numbers. It appears that these resident jellyfishes are in a position to take advantage of changes in local ecology, and that newly introduced alien jellyfishes can also sometimes take great advantage of imbalances brought about by pollution, overfishing, or other major environmental change. Systems previously dominated by many species of fishes seem capable of switching over to domination by jellyfish with surprising ease and rapidity. We do not know whether these switches are reversible by human-mediated environmental change. Our knowledge of the specific biology and ecology of most medusae, siphonophores, and ctenophores can be described as non-existent to fragmentary, so that our understanding of how jellyfishes contribute to either healthy or radically altered ecosystems is still poor.

Acknowledgements

Table 5. Natural diets of some ctenophores as determined from gut contents of field-collected animals. The number of each species examined is designated by "n". Prey consumed is presented as percentage of the total number of prey items in the guts. With the exception of *Beroe*, ctenophores that have been studied tend to be generalists and their diets appear to reflect prey availability.

Predator species	Location (season)	Prey consumed		Reference
		%	Principal types	
Pleurobrachia bachei (n = >1000)	California (year round 1971)	79 12	Copepods Cladocera	Hirota (1974)
Pleurobrachia pileus (n = 1352)	Scotland (spring 1966)	56 25 7 6	Copepods Cladocera Barnacle larvae Invertebrate eggs	Fraser (1970)
Mnemiopsis leidyi (n = 3300)	Virginia USA (year round 1965–1967)	55 11 11 9 8	Copepods Barnacle nauplii Mysids Annelid larvae Bivalve larvae	Burrell and Van Engel (1976)
Mnemiopsis leidyi (n = 192)	Black Sea (May–June 1990)	46 37 12	Bivalve larvae Cladocera Copepods	Tiskhon-Lukanina, *et al.* (1992)
Beroe spp. (n = hundreds)	Worldwide (year round)	100	Ctenophores, salps	G. R. Harbison (pers. comm.)

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