

## Jellyfish Population Explosions : Revisiting a Hypothesis of Possible Causes

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**Abstract :** A hypothesis is discussed that relates the production of large blooms of jellyfish (medusae and/or ctenophores) to specific food chains in the sea that are based on the production of nanophytoplankton. Evidence is given from the fossil record and from the contemporary ocean to show how this type of low-energy food chain contrasts with a high-energy food chain, which is based on diatom ecology and supports the large raptorial feeders, fish and whales. Recent anthropogenic effects on the ocean, including pollution and overfishing, are discussed in terms of the proposed hypothesis. Natural events that can lead to an abundance of jellyfish are also considered.

**Key words :** *jellyfish blooms, food chain energetics, eutrophication, overfishing, pollution, climate change, evolution of marine ecosystems*

### 1. Introduction

In recent years, there has been a spate of publications noting unprecedented population explosions of “jellyfish” (medusae and/or ctenophores) which have been increasing in frequency and expanding in geographic coverage (e.g. PURCELL *et al.*, 2001a). These high densities result from increases in numbers through reproduction, and are not aggregations caused by physical advection or behavioural activities as described by GRAHAM *et al.* (2001). Table 1 gives some examples of such blooms, but the subject has recently been reviewed in more detail by MILLS (2001). Some of these blooms have occurred in endemic species, others result after invasions by species brought into new areas in ballast water. A number of causes have been advanced, including eutrophication, overfishing, pollution, global warming, and increases in artificial substrates which expand the potential attachment sites for polyp stages in the life cycles of some species. We believe that a commonality underlying these enhancements of jellyfish populations may be indica-

tive of major fundamental changes in marine ecosystems that are pushing the world's oceans into a less desirable state with respect to marine resources.

We recognize that the many species of jellyfish have different diets and feeding methods, and that populations of those larger species that feed on large-sized food (macrozooplankton) in the sea can be enhanced simply by the removal of top-level fish that are direct competitors for food. However, many ctenophores (e.g. GREVE, 1970; HARBISON *et al.*, 1978) and medusae including the young of large species (e.g. FRASER, 1969; MILLS, 1995; PURCELL and ARAI, 2001; PURCELL and STURDEVANT, 2001) are known to feed on smaller-sized particles (mesozooplankton) such as small copepods and other small crustaceans, meroplanktonic larvae, fish eggs and fish larvae and even microzooplankton such as ciliates (STOECKER *et al.*, 1987), and their numbers are not directly controlled by fish removal except perhaps by removal of fish such as anchovies that are also low in food chains. Although turtles and some fish may eat jellyfish (e.g. PURCELL and ARAI, 2001), top-down control of population numbers does not seem to be prevalent for most species except for those that are eaten by other jellies

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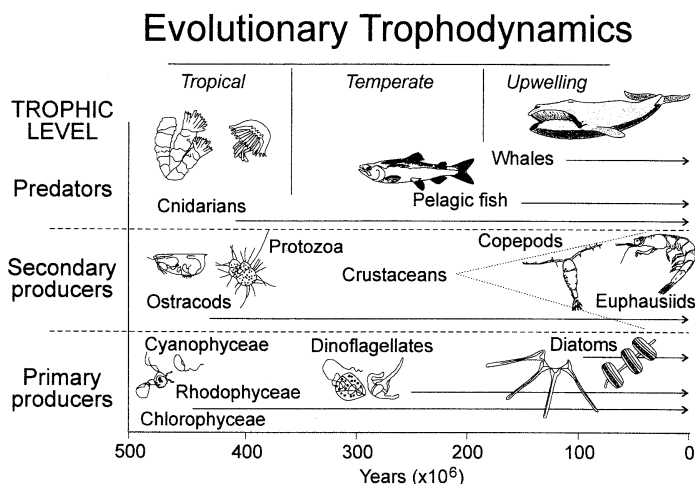


Fig. 1. The evolution of pelagic food chains in the ocean from the Cambrian to the present based on the fossil record and showing the approximate relationship in time between the evolution of low energy cnidarians (corals and "jellies") and higher energy requiring organisms (i.e. fish X 7, whales X 200) in association with the evolution of organisms at lower trophic levels from small to large primary producers. (Reprinted from PARSONS, 1979)

(PURCELL, 1991), as for example control of *Mnemiopsis* by *Beroe* (PURCELL *et al.*, 2001b; SHIGANOVA *et al.*, 2001; VINOGRADOV *et al.*, 2001). In order to find a general principle governing the outbreaks of jellyfish in different areas and at different times, we have re-examined the hypothesis put forward in 1977 by GREVE and PARSONS. These authors suggested that there are two basic food chains in the sea depending on the dominant type of primary producers. These are :

- (1) small flagellates\* → small zooplankton → jellyfish\*
- (2) large diatoms → large zooplankton → fish

These food chains represent pathways of energy flow in the pelagic ecosystem in the same sense as their use by others (e.g. RYTHER, 1969;

\* "Flagellates" include autotrophic flagellates as well as heterotrophic zooflagellates produced in the microbial loop through the consumption of picoplankton; all of these are  $<10 \mu\text{m}$  (i.e. nanoplankton). "Jellyfish" or "jellies" are not taxonomic categories, but are defined here and throughout this paper in an ecological sense to include all pelagic cnidarians and ctenophores.

SHELDON *et al.*, 1977) ; they are not a representation of a food web. One type of food chain in which flagellates are the dominant primary producers leads to production of jellies; we refer to this as a "low-energy" system. The other food chain, in which large phytoplankton prevail, leads to fish production and is a "high-energy" food chain. The concept of low- and high-energy food chains as described here (e.g. Fig. 1) does not depend on food chain length, but on the conditions for primary production and on the energy requirements of the terminal producer (s). RYTHER (1969) initially proposed that longer food chains (or increased number of trophic levels) were an impediment to the transfer of organic matter and resulted in lower terminal production. This is still a valid concept for very long food chains which involve active hunting and capture of prey at higher trophic levels. However, at the lowest trophic levels, as we have discussed in an earlier paper (PARSONS and LALLI, 1988), much higher ecological efficiencies between small-sized particles can result in almost equal energy flows in short and long food chains. As HEINBOKEL and BEERS (1979) have said, "relatively little of the energy and material fixed by

the nanoplankton may be lost to the larger consumers by the insertion of a ciliate extra link into the food chain". In our terminology, "high-energy" food chain refers to the terminal producers (i.e. fish or whales) as being high energy consuming organisms that must be supplied with an abundance of relatively large particles in order to meet their energy needs. Conversely, a "low-energy" food chain refers to terminal producers (e.g. jellies) that can feed efficiently off small particles in order to meet their lower metabolic demands. Hence the presence or absence of an additional link (e.g. picoplankton, including bacteria, being fed upon by zooflagellates) in the latter type of food chain is not nearly as important as the ecological conditions which favour the kind of primary producer. Thus the food chains depicted in Fig. 1 can be of equal length.

GREVE & PARSONS (1977) did not claim that these two different food chains were mutually exclusive, but suggested that one or the other could dominate at different times and/or in different ocean areas depending on environmental conditions. Environmental change causing shifts in dominance could either be induced by climate or pollution. Climate was cited in three references as causing at least two different conditions favoring flagellate production. The establishment of very stable, nutrient-poor water masses favors flagellate dominance, as these phytoplankton grow well under conditions of nutrient limitation. Flagellates also dominate in situations of light limitation, such as result from deep mixing of the water column. Diatom growth is at a disadvantage under both of these conditions, as physiological data have shown that high light intensity and abundant nutrients are necessary for diatoms to grow faster than flagellates. GREVE and PARSONS (1977) also cited literature references on grazing to further support their hypothesis that a flagellate-based, energy-poor food chain favors populations of jellyfish, and that an energy-rich food chain dominated by diatoms leads to fish production.

At the time of proposing this hypothesis, there was little evidence that large jellyfish population explosions were occurring in the sea, or that there were linkages with flagellate-

based food chains. However, GREVE and PARSONS gave some evidence concerning the preferential feeding of ctenophores on small prey items in the North Sea. They also pointed out that, on a seasonal scale in temperate waters, fish feeding and production maximize in early spring in association with diatom blooms, whereas jellyfish generally occur in large numbers later in the summer, when flagellates dominate in the nutrient-impoverished water column. This seasonal shift in the two different types of food chains has been noted in numerous publications (e.g., PARSONS *et al.*, 1970).

PARSONS later (1979, 1996) presented further evidence for the possible importance of these two food chains in pelagic marine ecology. These references drew attention to the size differential between small flagellates and large diatoms, which spans over six orders of magnitude in volumetric size. The first of these papers pointed out, that in evolutionary terms, the ancient ocean ( $500 \times 10^6$  ybp) was dominated by small phytoplankton (cyanobacteria, flagellates), small zooplankton and cnidarian ecology, including both coral reefs and pelagic jellyfish. It was argued that the later evolution of teleost fish (which appeared ca.  $300 \times 10^6$  ybp) and whales (ca.  $100 \times 10^6$  ybp) would have required a richer food chain in order to support the energy requirements of these animals (fish requiring approximately seven times and whales 200 times more energy than jellyfish on a weight specific basis according to FENCHEL, 1974). PARSONS (1979) suggested that this enrichment of the food chain of the pelagic environment came about from the evolution of larger phytoplanktonic forms, with diatoms appearing about 190 mya and becoming abundant by the time of the appearance of marine mammals (Fig. 1).

In contemporary terms, high and low energy food chains can be found in the present oceans. The greatest production of fish and whales in the world occurs in upwelling areas (e.g., the Peru Current or Benguela Current) on the western seabords of continents, whereas cnidarian ecology in terms of coral production is characteristic of convergent water masses on eastern seabords (e.g., the Caribbean and the Great Barrier Reef). These two different types

of ecologies are dominated by diatom and flagellate production, respectively. PARSONS (1996) further suggested that the fish/diatom food chain could be destabilized by overfishing. Two examples were given (AVIAN and SANDRIN, 1988; ZAITZEV, 1992) where jellyfish explosions had occurred in the ocean, although in neither case was it clear whether these may have been caused by overfishing, or by pollution to which diatoms are generally more susceptible than flagellates (e.g. THOMAS and SEIBERT, 1977).

Criticisms of GREVE and PARSONS' hypothesis on different ocean ecologies based on phytoplankton type have come mainly from two sources (LONGHURST, 1985; MILLS, 1995). Although LONGHURST (1985) agreed that different food chains developed seasonally in temperate waters, he did not believe there was definitive support for the existence of "two specific and separable pelagic food chains" elsewhere in the oceans. This may be partly a misinterpretation as GREVE and PARSONS did not claim that these food chains existed independently of each other, only that one or the other could dominate under different environmental conditions. LONGHURST also argued that he did not find a relationship between jellyfish and small zooplankton, and suggested that, on the contrary, jellies tend to eat larger organisms. More recent work has shown that there is considerable diversity in the diets of carnivorous cnidaria and ctenophores, and that many do indeed take small forms of zooplankton, predominantly small-sized copepods (e.g. GREVE, 1970; STOECKER *et al.*, 1987; MILLS, 1995; PURCELL and ARAI, 2001; PURCELL and STURDEVANT, 2001). The hypothesis being considered here was not intended to be mutually exclusive of jellyfish predation on larger zooplankton. It was intended to show that, in general, cnidarian ecology consumes small prey items compared with raptorial feeders, but there are certainly some biological exceptions.

In the second criticism, MILLS (1995) claimed that jellyfish are often abundant in upwelling (high-energy) environments. However, PAGÈS and GILI (1991) observed that the concentration of jellyfish in upwelled waters is the result of advection, not of increased reproduction. To quote these authors, "...a strong intrusion of

Angolan waters into the northern part of the Benguela system coincided with the abatement in the upwelling activity that characterizes the region. This important advective process facilitated penetration by large number of species and individuals of the gelatinous zooplankton...". MILLS (1995) also presented data indicating that the number of species of "jellies" found in high and low productive waters is about the same as observed from a submersible. However, the studies of the "high" productivity environment were in the N.W. Atlantic in July and August, when seasonal nutrient limitation would cause low productivity. In any event, the hypothesis being advanced here does not depend on the number of species but on the biomass of "jellies", which the author does not record. A further objection by this author is that "jellies" (quote) "... form a major part of the macroplankton of temperate fjords, which are generally considered to be high productivity systems." We agree that large concentrations of jellyfish are found at the head of many fjords but, as has been observed by a number of authors (e.g. PARSONS *et al.*, 1983; Hobson and MCQUOID, 2001), these areas generally have a low productivity, dominated by flagellate ecology. Where the impression of "high" productivity is gained, is from the frontal zone that sometimes occurs at the mouth of fjords. These areas are dominated by diatom ecology and by schools of fish, such as herring. Further, GRAHAM *et al.* (2001) have noted that aggregations of large medusae at fronts or other physical discontinuities must result from physical accumulation, because population increases of these animals is almost always decoupled from water column processes. MILLS (1995) also concluded that "jellies" are so ubiquitous that they are opportunistically positioned to utilize secondary production in the absence of fish. This may be correct, certainly in respect to their high reproductive rate. However, in coastal areas, changes caused by eutrophication, as discussed below, appear to enhance jellyfish production and not fish production. This indicates that a food chain favouring "jellies" occurs in these areas, rather than there simply being a vacancy for an opportunistic feeder at a higher trophic level.

**Table 1.** Some examples of jellyfish population explosions

Location	Date	Species	Suggested Causes	Reference
Bering Sea (eastern shelf)	1989 onward	Combined species, <i>Chrysaora melanaster</i> dominant	Climate change; overfishing	BRODEUR <i>et al.</i> , 1999
Black Sea	1970s- 1980s	<i>Rhizostoma pulmo</i> <i>Aurelia aurita</i>	Overfishing; eutrophication	KOVALEV & PIONTKOVSKI, 1998; SHIGANOVA, 1998; DASKALOV, 2002
	1982-	<i>Mnemiopsis leidyi</i>	Invasion & proliferation; overfishing	SHIGANOVA, 1998; DASKALOV, 2002
	1997-	<i>Beroe ovata</i>	Invasion & proliferation due to superabundant <i>Mnemiopsis</i> prey	SHIGANOVA <i>et al.</i> , 2001; VINOGRADOV <i>et al.</i> , 2001
Gulf of Mexico	1980s- 2000	<i>Chrysaora</i> <i>quinquecirrha</i> <i>Aurelia aurita</i>	Eutrophication; overfishing	GRAHAM, 2001 and pers. commun.
Mediterranean (western)	Periodic	<i>Pelagia noctiluca</i>	Climate change	GOY <i>et al.</i> , 1989
Tokyo Bay	1960s Onward	<i>Aurelia aurita</i>	Eutrophication	ISHII and TANAKA, 2001

## 2. Several Explanations for Population Explosions of Jellyfish based on the Energy Flow Hypothesis

Various causes of jellyfish population explosions have been advanced (see Table 1), but it is our contention that there is a general framework on which all of these events can be brought together, as outlined in the following sections.

### Pollution and Eutrophication Effects

There are two aspects to consider in respect to increases in jellyfish populations in coastal areas. Firstly, heavy metals and petroleum hydrocarbons are highest in coastal areas associated with urban runoff; secondly, agricultural and sewage eutrophication are also highest in coastal zones.

GREVE and PARSONS (1977) drew attention to Controlled Ecosystem Pollution Experiments (CEPEX) which showed that hydrocarbons tended to enhance flagellate production, and pointed out that this effect was also observed after some oil spills. However, concentrations of jellyfish in oil-polluted waters have not been recorded following these events. CEPEX experiments with heavy metal additions also decreased diatom populations, while flagellates

survived and accounted for most of the primary production. In addition, heterotrophic zooflagellates may also be produced under conditions of high organic pollution and a large bacterial biomass (FENCHEL, 1982). This microbial loop (AZAM *et al.*, 1983) may become especially dominant in some forms of coastal eutrophication. Organic enrichment leading to enhanced bacterial production was studied during the CEPEX experiments (PARSONS *et al.*, 1981). The addition of small amounts (1 to 5 ppm) of glucose caused a depression in photosynthesis, increased bacterial production, and a bloom of larvaceans, copepods and meroplanktonic larvae, followed by a large bloom of jellies (mostly *Pleurobrachia* and *Aequorea aequorea*). Thus, under experimental conditions, it may be concluded that the heterotrophic cycle is another possible contribution to jelly production.

Eutrophication of coastal waters now appears to be the most severe form of coastal pollution and could be a cause of enhanced jellyfish production. The subject was reviewed by PURCELL *et al.* (1999), and later by ARAI (2001) who concluded that cnidarian populations appear to increase in eutrophied areas, but such increases can not be unequivocally attributed

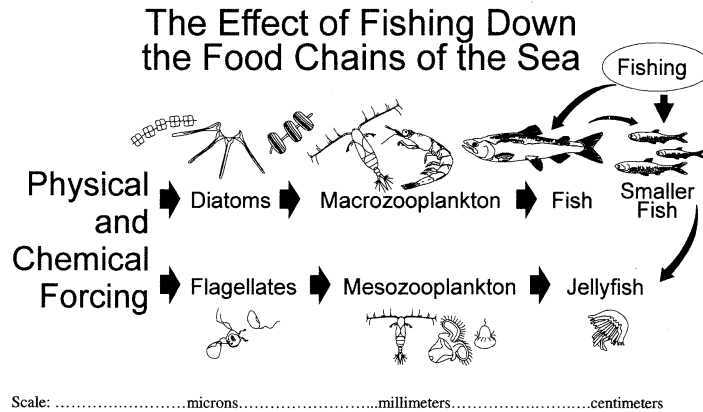


Fig. 2. The effect of overfishing on the high and low energy food chains of the sea. The elimination of large quantities of fish would initially cause an increase in the macroplankton and later a decrease in the diatom population through grazing. More nutrients then flow into the flagellate food chain resulting in an increased jellyfish population.

to nutrient enrichment since there are usually other coastal influences such as higher levels of heavy metals and hydrocarbons. In coastal eutrophication, the author correctly identifies the lack of silicate as the cause of flagellate blooms as diatoms require this nutrient for growth. Over the past four decades in eutrophied Tokyo Bay, a food chain based on microflagellates has developed which supports mainly small-sized copepods and jellyfish (*Aurelia aurita*), with very little fish production (NOMURA and MURANO, 1992; UYE, 1994; ISHII and TANAKA, 2001). This long-term change is what one would predict when eutrophication or pollution favors flagellate ecology and a low-energy food chain.

There are now a number of reports on the massive increases in jellyfish populations in the Black Sea (e.g. ZAITZEV, 1992; KOVALEV and PIONTKOVSKI, 1998; SHIGANOVA, 1998; SHIGANOVA *et al.*, 2001; VINOGRADOV *et al.*, 2001). In a modeling analysis of various causes for this effect, DASKALOV (2002) concluded that the two most probable causes were eutrophication and overfishing, with the latter being the stronger causative agent.

### Effects of Overfishing

The effects of overfishing on the high-energy food chain are shown in Fig. 2. The initial effect of overfishing in reducing fish size, either

within the fished population or by supplanting it with another smaller species in the fish catch, has been known for some time (e.g. HEMPEL, 1978; SHERMAN *et al.*, 1981). It is also common knowledge that the effects of overfishing may result in a variety of ecological changes, such as increased penguin populations in the Antarctic or decreased bird populations off Peru (for summary, see PARSONS, 1992). In Fig. 2, however, the specific case of what could happen to the diatom/fish food chain is illustrated. In the absence of fish to graze the large-sized zooplankters, the numbers of these animals would increase and exert pressure on the diatom population. Diatoms in turn would diminish, leaving more of the available nutrients to flow into the flagellate/jellyfish part of the food chain - a result that would increase the jellyfish population. This kind of oscillation between phytoplankton and zooplankton has been observed experimentally on lakes (e.g. MCQUEEN *et al.*, 1989) and has been the subject of computer simulations (e.g. HASTINGS and POWELL, 1991). Is there any evidence that this has happened in the natural marine environment?

BRODEUR *et al.* (1999) described a large increase in the population of jellyfish in the Bering Sea where there has been a substantial pollock fishery in recent years (SPRINGER, 1992). To account for this increase in jellyfish

numbers, BRODEUR *et al.* favor an explanation based on climate change. Certainly this is possible and is allowed for in Fig. 2, if the physical /chemical environment changes in such a way as to preferentially favor one or the other of the food chains. However, the alternative explanation that the increase in jellyfish has been the result of overfishing can not be dismissed. There are several pieces of circumstantial evidence which favor the latter explanation.

Firstly, SPRINGER (1992) noted that whereas fishing may have reduced the numbers of fish-eating birds and mammals in the area due to a lack of prey, plankton-eating auklets actually increased in abundance, which might indicate that the macroplankton community had increased as a result of the decreased predation by fish. Another unusual occurrence in the Bering Sea was the development of a massive bloom of coccolithophorid flagellates that was accompanied by a large increase in small crustaceans (e.g. STOCKWELL *et al.*, 2001). An explanation for this phenomenon does not necessarily require changes in the growth conditions for phytoplankton; it could also be generated by a lack of predator (i.e. fish) control of the food chain, which would force more nutrients into flagellate production if large crustaceans were to control diatom production (Fig. 2 and HASTINGS and POWELL, 1991). Once a food chain has been destabilized in such a manner, the role of climate as an additional influence in these effects can not be ruled out. However, the role of pollutants or eutrophication, such as may have caused changes in the Black Sea and in coastal waters, is probably not significant in the Bering Sea.

DASKALOV'S (2002) conclusion that overfishing was the primary cause of the increase in "jellies" in the Black Sea is important to the concept of food chains as originally suggested by GREVE and PARSONS (1977). DASKALOV concluded that size-selective effects were crucial to biomass dynamics. Large zooplankton consumed by fish had a pronounced effect on size structure of the food chain. He found that total zooplankton and phytoplankton biomass were determined mainly by the dynamics of the large size fractions at each trophic level, and that it was these that were most sensitive to

top-down control by fish. However, these conclusions were based on a mathematical model and one result of this model, the dominance of large phytoplankton cells in the presence of jellyfish, is not consistent with direct observations of others (e.g. ISHII and TANAKA, 2001). Other possible effects of overfishing are discussed by PURCELL and ARAI (2001); they reviewed the disappearance of mackerel in the Black Sea due to overfishing and the subsequent abundance of "jellies" on which the mackerel preyed. This type of direct predator /prey interaction with jellyfish does not appear to be common in the sea, but where it occurs, it must be included as a possible cause of jellyfish population explosions.

### Effects of Climate Change

Climate changes, whether induced by global warming or not, can have profound effects on marine ecosystems. BRODEUR *et al.* (1999) consider that the production of jellyfish in the Bering Sea, which started in about 1990 and has continued strongly ever since, was due to a regime shift brought about by a change in climate. They pointed out that the extent of ice cover in the Bering Sea is highly variable but, if the survival of early life stages of jellyfish depended on ice-associated phytoplankton blooms and attendant secondary production, then in terms of both its persistence and spatial extent, more favorable conditions existed after 1990, which was when the jellyfish population started to increase. If these events were associated with the physical/chemical regime in Fig. 2, then ensuing flagellate production could come about through quite different mechanisms, either by development of a very stable, nutrient-poor water column, or by formation of an unstable deeply-mixed water column (see PARSONS and TAKAHASHI, 1973 for discussion). Either condition favors flagellate growth over diatom production.

Jellyfish abundance in the Mediterranean Sea has been directly linked to climate by GOY *et al.* (1989), although an earlier report (AVIAN and SANDRIN, 1988) attributed an increase in jellyfish in the Adriatic Sea to overfishing. GOY *et al.* analysed long-term data sets and concluded that warmer waters gave

rise to more jellyfish, and suggested that this may have been due to increased production of microzooplankton.

### 3. Conclusions

It has not been our purpose to give specific reasons for any particular jellyfish population explosion listed in Table 1, but rather to establish a framework that could be used to explain any one of the observations. This framework is based on two very different pelagic food chains, which we believe evolved over time and which coexist in the contemporary ocean. These food chains are based on the amount of energy supplied by the different types of primary producers. The low-energy food chain is based on very small phytoplankton, generally referred to as flagellates (also as nanoplankton). These cells are at least six orders of magnitude smaller than the large phytoplankton, which are most often represented by the diatoms (or microplankton). Food chains based on very small phytoplankton support micro- and mesozooplankton that are mostly too little for large raptorial fish, because it is energetically too costly to feed on such small prey. Instead, these small zooplankton are easily fed on by the "jellies" of the sea. The conditions under which one or the other of these two food chains can dominate are determined by at least three events, including natural changes in the physical-chemical environment, various forms of pollution including eutrophication, and overfishing. Increased populations of medusae and/or ctenophores may develop wherever, or whenever, a flagellate-based food chain is favored. The effects of climate, pollution, and overfishing may, at times, act synergistically.

It is clear that several anthropogenic influences are having profound effects on our marine ecosystems. Industrial fisheries have removed, and continue to remove, vast numbers of the top-level predators of the sea; for the most part, these (teleost fish and whales) are the most recently evolved marine animals. These animals are also the most susceptible to pollution effects through bioaccumulation. By removal or debilitation of these top trophic levels, we not only provide more food to lower trophic levels, but we may also be changing the

species compositions of ecosystems. In the examples given here, medusae and/or ctenophores are becoming predominant in ecosystems formerly dominated by fish. It is well to remember, as PURCELL *et al.* (1999) have pointed out, that jellyfish may be superior competitors to fish in many respects as they feed continuously, do not satiate at natural food concentrations, usually have broad diets, often eat fish eggs and larvae, and shrink rather than die when food is limiting. Most are passive feeders that do not expend large amounts of energy in hunting and capturing food. Further, many medusae have both asexual and sexual reproduction, and all jellies have short generation times compared with fish. It is beginning to look as though the balance is being shifted from a highly evolved ecosystem in which fish or marine mammals occupy top trophic levels to an ecosystem in which environmental conditions and lessened competition favor the more ancient species like cnidarians and ctenophores.

One consequence of the establishment of the flagellate-jellyfish food chain is that the much lower energy demands of jellies compared with raptorial feeders (fish and whales), and their more rapid life cycles, can result in a rapid production of gelatinous biomass, much exceeding the total biomass of fish and whales. This is because jellies have a much lower metabolism, and consequently their total biomass can greatly exceed that of more metabolically expensive animals. It is important to remember that jellies have relatively few natural predators, and only a few species are commercially fished for human consumption. Control of jellyfish (or ctenophore) population size is primarily bottom-up control via the physical-chemical nature of the environment (temperature, salinity etc.), food availability and, for those species with a benthic stage in their life cycle, availability of suitable hard substrates. The development of huge jellyfish populations on a global scale is not a desirable result in a world where an expanding human population is demanding more and more protein from marine resources.

The hypothesis of GREVE and PARSONS that links jellyfish production to flagellate-based



food chains remains speculative, although we believe that additional evidence given in the present paper strengthens its validity. At present our knowledge of both natural and perturbed marine ecosystems remains underdeveloped to prove or disprove this hypothesis. However, certain observations and/or experiments could be undertaken to examine more closely the types of food chains discussed here. For example, it is essential that phytoplankton species composition be determined in areas undergoing anthropogenic change, as total primary productivity may not reveal differences leading to low- or high-energy food chains. Further, it is unlikely that the hypothesis holds for all species of jellies, especially not for those that are large-particle feeders and direct competitors with large raptorial fish. In this regard, it would be extremely useful to have more detailed information on diets of specific medusae and ctenophores in different types of ecosystems; such studies are presently being undertaken by Graham and Costello (in prep.). Until these types of information are available, the Greve and Parsons hypothesis remains unresolved.

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### References

- ARAI, N. M. (2001) : Pelagic coelenterates and eutrophication : a review. *Hydrobiologia*, **451**, 69–87.
- AVIAN, M. and L. R. SANDRIN (1988) : Fishery and swarmings of *Pelagia noctiluca* in the central and northern Adriatic Sea : Middle term analysis. *Rapports et Process-verbaux des Reunions. Commission internationale pour L'Exploration scientifique de la Mer Mediterranea*, **31**, 230–231.
- AZAM, F., T. FENCHEL, J.G. FIELD, J.S. GRAY, L. A. MEYER-REIL and L. A. THINGSTAD. (1983) : The ecological role of water column-microbes in the sea. *Mar. Ecol. Prog. Ser.*, **10**, 257–263.
- BRODEUR, R. D., C. E. MILLS, J.E. OVERLAND, G. E. WALTERS and J.D. SCHUMACHER (1999) : Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. *Fish.Oceanogr.*, **8**, 296–306.
- DASKALOV, G. M. (2002) : Overfishing drives a trophic cascade in the Black Sea. *Mar. Ecol. Prog. Ser.*, **225**, 53–63.
- FENCHEL, T. (1974) : Intrinsic rate of natural increase: the relationship with body size. *Oecologia*, **14**, 317–326.
- FENCHEL, T. (1982) : Ecology of heterotrophic microflagellates. II. Bioenergetics and growth. *Mar. Ecol. Prog. Ser.*, **9**, 35–42.
- FRASER, J. H. (1969) : Experimental feeding of some medusae and Chaetognatha. *J. Fish. Res. Bd Canada*, **26**, 1743–1762.
- GOY, J., P. MORAND and M. ETIENNE (1989) : Long-term fluctuations of *Pelagia noctiluca* (Cnidaria, Scyphomedusa) in the western Mediterranean Sea. Prediction by climatic variables. *Deep-Sea Res.*, **36**, 269–279.
- GRAHAM, W. M. (2001) : Numerical increases and distributional shifts of *Chrysaora quinquecirrha* (Desor) and *Aurelia aurita* (Linne) (Cnidaria : Scyphozoa) in the northern Gulf of Mexico. *Hydrobiologia*, **451**, 97–111.
- GRAHAM, W. M. and J. H. COSTELLO (In prep.) : A biogeographic synthesis of prey capture strategies among rhizostome and semeanostome scyphomedusae.
- GRAHAM, W. M., F. PAGÈS and W. M. HAMNER (2001) : A physical context for gelatinous zooplankton aggregations : a review. *Hydrobiologia*, **451**, 199–212.
- GREVE, W. (1970) : Cultivation experiments on North Sea ctenophores. *Helg. wiss. Meeresunter.*, **20**, 304–317.
- GREVE, W. and T.R. PARSONS (1977) : Photosynthesis and fish production : hypothetical effects of climatic change and pollution. *Helg. wiss. Meeresunter.*, **30**, 666–672.
- HARBISON, G.R., L.P. MADIN and N.R. SWANBERG (1978) : On the natural history and distribution of oceanic ctenophores. *Deep-Sea Res.*, **25**, 233–256.
- HASTINGS, A. and T. POWELL (1991) : Chaos in a three-species food chain. *Ecology*, **2**, 896–903.
- HEINBOKEL, J.F. and J.R. BEERS (1979) : Studies on the functional role of tintinnids in the Southern California Bight. III. Grazing impact on natural assemblages. *Mar. Biol.*, **52**, 23–32.
- HEMPEL, G. (1978) : North Sea fisheries and fish

- stocks—a review of recent changes. *Rapports et Process-verbaux des Reunions. Conseil international pour l'Exploration de la Mer*, **173**, 145–167.
- HOBSON, L.A. and M.R. McQUOID (2001) : Pelagic diatom assemblages are good indicators of mixed water intrusions into Saanich Inlet, a stratified fjord in Vancouver Island. *Mar. Geol.*, **174**, 125–138.
- ISHII, H. and F. TANAKA (2001) : Food and feeding of *Aurelia aurita* in Tokyo Bay with an analysis of stomach contents and a measurement of digestion times. *Hydrobiologia*, **451**, 311–320.
- KOVALEV, A.V. and S.A. PIONTKOVSKI (1998) : Interannual changes in the biomass of Black Sea gelatinous zooplankton. *J. Plankton Res.*, **20**, 1377–1385.
- LONGHURST, A.R. (1985) : The structure and evolution of plankton communities. *Prog.Oceanogr.*, **15**, 1–35.
- MCQUEEN, J.D., M.R.S. JOHANNES, J.R. POST, T.J. STEWARD and D.R.S. LEAN (1989) : Bottom-up and top-down impacts of freshwater pelagic community structure. *Ecol. Monogr.*, **59**, 289–309.
- MILLS, C.E. (1995) : Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. *ICES J. Mar. Sci.*, **52**, 575–581.
- MILLS, C.E. (2001) : Jellyfish blooms : Are populations increasing globally in response to changing ocean conditions? *Hydrobiologia*, **451**, 55–68.
- NOMURA, H. and M. MURANO (1992) : Seasonal variation of meso- and macroplankton in Tokyo Bay, central Japan. *La mer*, **30**, 49–56.
- PAGÈS, F. and J.M. GILI (1991) : Effects of large-scale advective processes on gelatinous zooplankton populations in the northern Benguela ecosystem. *Mar. Ecol. Prog. Ser.*, **75**, 205–215.
- PARSONS, T.R. (1979) : Some ecological, experimental and evolutionary aspects of the upwelling ecosystem. *South African J. Sci.*, **75**, 536–540.
- PARSONS, T.R. (1992) : The removal of marine predators by fisheries and the impact on trophic structure. *Mar. Poll. Bull.*, **26**, 51–53.
- PARSONS, T.R. (1996) : The impact of industrial fisheries on the trophic structure of marine ecosystems. *In* *Food Webs – Integration of Patterns and Dynamics*, Polis, G.A. and K.O. Winemiller (eds.), Chapman Hall, N.Y., pp. 352–357.
- PARSONS, T.R., L.J. ALBRIGHT, F. WHITNEY, P.J. LeB WILLIAMS and C.S. WANG (1981) : The effect of glucose on the productivity of seawater : An experimental approach using controlled aquatic ecosystems. *Mar. Environ. Res.*, **4**, 229–242.
- PARSONS, T.R. and C.M. LALLI (1988) : Comparative oceanic ecology of the plankton communities of the subarctic Atlantic and Pacific Oceans. *Oceanogr. Mar. Biol. Annu. Rev.*, **26**, 317–359.
- PARSONS, T.R., R.J. LeBRASSEUR and W.E. BARRACLOUGH (1970) : Levels of production in the pelagic environment of the Strait of Georgia, British Columbia : A review. *J. Fish. Res. Bd Canada*, **27**, 1251–1264.
- PARSONS T.R., R.I. PERRY, E.D. NUTBROWN, W. HSIEH and C.M. LALLI (1983) : Frontal zone analysis at the mouth of Saanich Inlet, British Columbia, Canada. *Mar. Biol.*, **73**, 1–5.
- PARSONS, T.R. and M. TAKAHASHI (1973) : Environmental control of phytoplankton cell size. *Limnol.Oceanogr.*, **18**, 511–515.
- PURCELL, J.E. (1991) : A review of cnidarians and ctenophores feeding on competitors in the plankton. *Hydrobiologia*, **216/217**, 335–341.
- PURCELL, J.E. and M.N. ARAI (2001) : Interactions of pelagic cnidarians and ctenophores with fish : a review. *Hydrobiologia* **451**, 27–44.
- PURCELL, J.E., W.M. GRAHAM and H.J. Dumont (eds.) (2001a) : *Jellyfish Blooms : Ecological and Societal Importance*. Reprinted from *Hydrobiologia*, **451** : 333 pp. Dordrecht : Kluwer Academic Publ.
- PURCELL, J.E., A. MAJEJ and A. BENOVIĆ (1999) : Potential links of jellyfish to eutrophication and fisheries. *Coastal Estuar. Stud.*, **55**, 241–263.
- PURCELL, J.E., T.A. SHIGANOVA, M.B. DECKER and E.D. HOUDE (2001b) : The ctenophore *Mnemiopsis* in native and exotic habitats : U.S. estuaries versus the Black Sea basin. *Hydrobiologia*, **451**, 145–176.
- PURCELL, J.E. and M.V. STURDEVANT (2001) : Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. *Mar. Ecol. Prog. Ser.*, **210**, 67–83.
- RYTHER, J.H. (1969) : Photosynthesis and fish production in the sea. The production of organic matter and its conversion to higher forms of life vary throughout the world oceans. *Science*, **166**, 72–76.
- SHELDON, R.W., W.H. SUTCLIFFE and M.A. PARANJAPÉ (1977) : Structure of pelagic food chains and relationship between plankton and fish production. *Fish. Res. Bd. Canada*, **4**, 2344–2353.

- SHERMAN, K., C. JONES, L. SULLIVAN, W. SMITH, P. BERRIEN and L. EJSYMONT (1981) : Congruent shifts in sand eel abundance in western and eastern North Atlantic ecosystems. *Nature*, **291**, 486-489.
- SHIGANOVA, T.A. (1998) : Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. *Fish. Oceanogr.*, **7**, 305-310.
- SHIGANOVA, T.A., Y.V. BULGAKOVA, S.P. VOLOVIK, Z.A. MIRZOYAN and S.I. DUDKIN (2001) : The new invader *Beroe ovata* Mayer 1912 and its effect on the ecosystem in the northeastern Black Sea. *Hydrobiologia*, **451**, 187-197.
- SPRINGER, A.M. (1992) : A review : Walleye pollock in the North Pacific - how much difference do they really make? *Fish. Oceanogr.*, **1**, 80-96.
- STOCKWELL, D.A., T.E. WHITLEGE, S.I. ZEEMAN, K.O. COYLE, J.M. NAPP, R.D. BRODEUR, A.I. PINCHUK and G.L. HUNT, Jr. (2001) : Anomalous conditions in the south - eastern Bering Sea, nutrients, phytoplankton and zooplankton. *Fish. Oceanogr.*, **10**, 99-116.
- STOECKER, D.K., P.G. VERITY, A.E. MICHAELS and L.H. DAVIS (1987) : Feeding by larval and post-larval ctenophores on microzooplankton. *J. Plank. Res.*, **9**, 667-683.
- THOMAS, W.H. and D.L.R. SEIBERT (1977) : Effects of copper on the dominance and the diversity of algae : Controlled ecosystem pollution experiment. *Bull. Mar. Sci.*, **27**, 23-33.
- UYE, S.-I. (1994) : Replacement of large copepods by small ones with eutrophication of embayments : cause and consequence. *Hydrobiologia*, **292/293**, 513-519.
- VINOGRADOV, M.E., E.A. SHUSHKINA and S.V. VOSTOKOV (2001) : Gelatinous macroplankton (jellyfish *Aurelia aurita*, ctenophores *Mnemiopsis leidyi* and *Beroe ovata*) in the Black Sea ecosystem. (Important aspects for the Caspian Sea modern ecology). 1st International Meeting of the Caspian Environment Programme. Baku, Azerbaijan, 24-26 April 2001. 5 pp.
- ZAITZEV, Yu. P. (1992) : Recent changes in the trophic structure of the Black Sea. *Fish. Oceanogr.*, **1**, 180-189.

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