Jellyfish blooms: are populations increasing globally in response to changing ocean conditions?

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Abstract

By the pulsed nature of their life cycles, gelatinous zooplankton come and go seasonally, giving rise in even the most undisturbed circumstances to summer blooms. Even holoplanktonic species like ctenophores increase in number in the spring or summer when planktonic food is available in greater abundance. Beyond that basic life cycle-driven seasonal change in numbers, several other kinds of events appear to be increasing the numbers of jellies present in some ecosystems. Over recent decades, man's expanding influence on the oceans has begun to cause real change and there is reason to think that in some regions, new blooms of jellyfish are occurring in response to some of the cumulative effects of these impacts. The issue is not simple and in most cases there are few data to support our perceptions. Some blooms appear to be long-term increases in native jellyfish populations. A different phenomenon is demonstrated by jellyfish whose populations regularly fluctuate, apparently with climate, causing periodic blooms. Perhaps the most damaging type of jellyfish increase in recent decades has been caused by populations of new, nonindigenous species gradually building-up to 'bloom' levels in some regions. Lest one conclude that the next millennium will feature only increases in jellyfish numbers worldwide, examples are also given in which populations are decreasing in heavily impacted coastal areas. Some jellyfish will undoubtedly fall subject to the ongoing species elimination processes that already portend a vast global loss of biodiversity. Knowledge about the ecology of both the medusa and the polyp phases of each life cycle is necessary if we are to understand the true causes of these increases and decreases, but in most cases where changes in medusa populations have been recognized, we know nothing about the field ecology of the polyps.

Introduction

For the purposes of this article, the term 'jellyfish' is used in reference to medusae of the phylum Cnidaria (hydromedusae, siphonophores and scyphomedusae) and to planktonic members of the phylum Ctenophora. Though not closely related, these organisms share many characteristics including their watery or 'gelatinous' nature, and a role as higher-order carnivores in plankton communities; I also cite one example of fragments of the benthic portion of a hydrozoan that occur in high numbers up in the water column, functioning more or less like small jellyfish in terms of their diet. I will not discuss the salps or other planktonic tunicates, which also have bloom characteristics in their appearances and disappearances in the water column, but which are herbivores feeding on very small particles, and have many other quite different aspects to their life cycles.

As parts of the oceans become increasingly disturbed and overfished, there is some evidence that energy that previously went into production of fishes may be switched over to the production of pelagic Cnidaria or Ctenophora (Mills, 1995). Commercial fishing efforts continue to remove top-predator fishes throughout the world oceans (Pauly et al., 1998), and it seems reasonable to watch concomitant trends in jellyfish populations, as jellyfish typically feed on the same kinds of prey as do many either adult or larval fishes.

Increases in jellyfish populations that will be detailed in this paper include some cases where native species have increased in local or regional ecosystems. Increases in jellyfish in some other cases have been the result of recent introductions followed by population explosions of nonindigenous species into coastal ecosystems. Decreases in jellyfish populations have also been documented in local or regional ecosystems in which the habitat has been degraded, typically by increased development, industrialization and pollution, but the proximate causes of these declines may not be evident. Although environmental degradation typically leads to species loss, eutrophication can apparently also sometimes lead to increases of jellyfish in local environments; such cases typically involve only single species and may sometimes in fact be nonnative species (see Arai, 2000). Decreasing levels of oxygen (hypoxia) in some bodies of water, often associated with eutrophication, may also favor increases in jellyfish populations (Purcell et al., 2001b.) Finally, there is a small amount of evidence suggesting that some jellyfish blooms may also turn out to be indicators of climate-induced regional regime shifts (Shimomura, 1959; Brodeur et al., 1999), rather than a response to anthropogenic change.

To some extent, what we interpret as a jellyfish bloom may reflect our expectations about an ecosystem. The life cycles of jellyfish lead to the transient appearance of 'blooms' in nearly all cases. Most medusae are budded from benthic polyps – that asexual reproduction process is usually seasonal, with the period of medusa budding varying from days to months long, but nearly always resulting in seasonal appearance and disappearance of medusa populations (with a few exceptions, most medusae appear to live less than one year). Even holoplanktonic species like ctenophores increase in number in the summer when planktonic food is available in greater abundance, giving rise to a form of jellyfish 'bloom'. While locally appearing and disappearing with great annual regularity, medusa and ctenophore populations also undergo interannual fluctuations, some years bringing much larger populations of each species than others. On top of the interannual population variation, there is now evidence for some species showing overall net gains or losses in numbers in certain locations over many-year periods. This last type of population trend is the one I am addressing in the present paper. Blooms resulting from aggregations enhanced by physical oceanographic processes will be reviewed elsewhere in this volume (Graham et al., 2001). Many of the species included have both planktonic (medusa or ctenophore) and benthic (polyp) phases of their life cycles and both parts must be considered in order to understand the changes taking place. Unfortunately, in most cases, we have information about only the planktonic phase of each life cycle.

There seems to be general agreement that man's activities are having measurable effects on the oceans in many places and certainly in most coastal habitats. Jellyfish populations (hydromedusae, scyphomedusae and ctenophores) respond to these changes, yet the general awareness of these phenomena is still embryonic and few data are available. Local increases in jellyfish abundance seem to be of two sorts. In some cases, species that have always been present suddenly experience severe increases or 'blooms', often with little evidence of what caused the population increase. In other cases, introductions of nonindigenous species to an ecosystem can lead to their unchecked population growth; several recent increases of medusa and ctenophore populations can be attributed to such circumstances. The following selected examples illustrate increases of native jellyfish species and nonindigenous species, as well as decreases in some other species.

Intrinsic increases in species native to an ecosysem

Chrysaora, Cyanea and Aequorea *populations in the Bering Sea*

Scientists working on Alaskan fisheries for the U.S. National Oceanic and Atmospheric Administration (NOAA) realized about 5 years ago that there is an unprecedented biomass of large jellyfish in the Bering Sea this decade. Biomass, especially of the scyphomedusae *Chrysaora melanaster* Brandt, 1835 [combined with less abundant *Cyanea capillata* (Linnaeus, 1758) and hydromedusae *Aequorea aequorea* (Forsskål, 1775)], has been estimated in NOAA's eastern shelf trawl samples from 1975 to 1999. After remaining more or less constant throughout the 1980s, the combined medusa biomass has increased more than 10-fold over the 1980s values during the 1990s (Brodeur et al., 1999). This increase has been confirmed by other researchers and fishermen who have worked for decades in the Bering Sea and report never having seen such high numbers as in recent years (R. D. Brodeur, pers. comm.). There is very little historic mention of *C. melanaster* in the Bering Sea

since its initial description from Avachinsky Bay on Kamtschatka (south of the Aleutians) more than 160 years ago, but at least in the 1990s, this has become the dominant jellyfish in the Bering Sea pelagic ecosystem.

The Bering Sea is a very productive region, accounting for up to 5% of the world's total fishery production and 56% of the U.S. fishery production of fish and shellfish (National Research Council, 1996). There is some public debate over whether or not the Bering Sea is being overfished, with no consensus in sight. Changes in numbers of pollock and other fishes are thought to be effecting an entire trophic cascade in the North Pacific, including the feeding of sea lions, and eventually seemingly causing some killer whales to shift diets to sea otters (Estes et al., 1998).

The dramatic increase in *C. melanaster* is very likely in exchange for some other member(s) of the ecosystem. It is not known at this time what process is facilitating the jellyfish increase, but data imply a correlation with a climate shift in the area that occurred about the same time (Brodeur et al., 1999). Nothing is known about the ecology of the polyp of *C. melanaster*, which is the only life cycle phase present during the colder months of the year, and which could be driving the change. Alternatively, medusae might be surviving better or growing faster, thus accounting for the huge increase in biomass.

Chrysaora *and* Aequorea *populations in the Benguela Current, Southern Africa and Namibia*

Similar increases in populations of *Chrysaora hysoscella* (Linnaeus, 1766) and *Aequorea aequorea* medusae are implied to have taken place in the Benguela Current off the west coast of Southern Africa during the 1970s (Fearon et al., 1992). The evidence in that case is circumstantial; in fact, the increase is hypothesized only in that these prominent members of the 1980s Benguela Current plankton did not even appear in comprehensive data records from the 1950s and 1960s, and thus their populations are assumed to have previously been very low or nonexistent. High numbers seen in the 1970s have persisted through the 1980s and into the late 1990s off Namibia where both species are still abundantly present, to the point of negatively impacting the fishing industry (Sparks et al., 2001; H. Mianzan, pers. comm.).

In general, there is a long history of removing and discarding jellyfish from net plankton samples because they encumber the smaller planktonic study-species. Additionally, a net full of large scyphomedusae may tear upon recovery and be very costly to repair or replace, so large jellyfish populations are usually systematically avoided by those who study the general plankton (or fish). Such traditions make the 20-year Bering Sea data set that much more remarkable, but also lend some uncertainty to the purported mid-century absence of jellyfish data in the Benguela Current.

Pelagia *in the Mediterranean*

Pelagia noctiluca (Forsskål, 1775) is a small scyphomedusa with fairly cosmopolitan distribution and is apparently endemic to the Mediterranean, as well as other locations (Kramp, 1961). *P. noctiluca* blooms in the Mediterranean have been especially noteworthy because the medusae sting and the summer blooms are considered highly offensive to summer bathers. A several-year bloom in the early 1980s stimulated two 'Jellyfish Blooms' meetings in Athens in 1983 and 1991 (Vućetić, 1983; Boero, 1991). The Mediterranean location of this bloom phenomenon provided an unusually complete simple binary (presence/absence) database covering more than two centuries from which the fluctuation pattern could be teased out (information came from research by European scientists and associated collection data at 4 nearby museums and field laboratories) (see Goy et al., 1989b).

This is perhaps the only species of jellyfish for which regular population fluctuations are known. In the western and central Mediterranean Sea, population peaks have occurred on average every 12 years between 1785 and 1985, with each peak enduring over several years (Goy et al., 1989b). The authors found eight population highs separated by seven low *P. noctiluca* periods and conclude that climatic factors between May and August including low rainfall, high temperature and high atmospheric pressure appear to correlate well with *P. noctiluca* blooms, these factors occurring during the reproductive period for this species and likely influencing it, at least indirectly. Years without large numbers of *P. noctiluca* off southern France seem to be typified by higher numbers of a variety of other species of medusae, siphonophores and ctenophores, but not apparently in such high numbers as might themselves be described as blooms (Morand & Dallot, 1985; Goy et al., 1989a; Buecher et al., 1997).

Pelagia noctiluca appears to have been historically much less common in the Adriatic portion of the Mediterranean, where substantial blooms have been noted only in 1910–1914 and 1976–1986 (Purcell et al., 1999b). *P. noctiluca* densities in the northern Adriatic in 1984–1985 reached typical offshore densities of about 20 per m^3, with probably wind-driven nearshore accumulations of up to 600 medusae per m^3 (Zavodnik, 1987).

Periodic fluctuations of *Pelagia noctiluca* have not been described from elsewhere in the world, although the species is common in warm waters world-wide. It is possible that fluctuating *P. noctiluca* populations also occur elsewhere, but have not been recorded yet.

Stomolophus nomurai *in the Sea of Japan*

Shimomura (1959) described a very large bloom of very large rhizostome medusae, *Stomolophus nomurai* (Kishinouye, 1922), in the Sea of Japan in 1958. This species seems to be tolerant of a wide temperature range, occurring that year in temperatures from 12–28 °C, and the bloom extended from the Sea of Japan even to waters off Hokkaido. The medusae occurred from the surface to 200 m, being deeper in the day and nearer the surface at night. The bloom, which was a serious fisheries nuisance, lasted well into the winter, ending in December in the Sea of Japan and in January on the Pacific side of Japan. Individual medusae were to 200 cm in diameter, weighed up to 40 kg, and were visible every few m of surface at peak abundance. Fishermen are reported to have caught 20 000–30 000 *S. nomurai* medusae per day during the yellow tail fishery in October and November 1958. While Shimomura reported that local occurrences of this species occur most years, he also cited a bloom of similar magnitude from 20 years earlier, when hindsight indicates that it signaled a regime shift and the end of a several-year sardine peak. Another very large and unpredicted bloom of *S. nomurai* occurred in the Sea of Japan in 1995, with small numbers seen also in 1972 and 1998 (M. Omori & Y. Hirano, pers. comm.). The biology of this very impressive species is so little-known that the whereabouts of the polyps and whether or not there is a small annual production of medusae *somewhere* is not known.

Siphonophores Muggiaea *in the German Bight and* Apolemia *off the coast of Norway*

Greve (1994) described a seemingly unprecedented invasion of the small calycophoran siphonophore, *Mug-*

giaea atlantica Cunningham, 1892, into the German Bight, North Sea, where it is typically absent or found only in very low numbers. *M. atlantica* is commonly collected in the adjoining western English Channel, but its sudden presence in numbers up to 500 per m^3 in waters west of Helgoland in July, 1989 seems unexplainable in terms of the understanding of local oceanographic processes. Although other populations of the pelagic ecosystem seemed unaffected by the unusual presence of all of these siphonophores, Greve (1994) pointed out that the usual dominant carnivore in the system is the ctenophore *Pleurobrachia pileus* (O. F. Müller, 1776), which is secondarily controlled by another ctenophore, the highly specific ctenophore-feeder *Beroe gracilis* Künne, 1939. If *M. atlantica* were to replace *P. pileus* as the dominant carnivore, its population would be unlikely to be preyed upon by *B. gracilis*, thus altering the balance in this pelagic ecosystem.

Similarly perhaps, Båmstedt et al. (1998) report an unusual mass occurrence of the virulant and very long siphonophore *Apolemia uvaria* (Lesueur, ?1811) along much of the Norwegian west coast beginning in November, 1997 and lasting at least into February, 1998. The primary effect reported of this invasion was killing of penned (farmed) salmon, although such high numbers of large siphonophores probably also preyed heavily on the coastal zooplankton community.

Although both the *Muggiaea atlantica* and *Apolemia uvaria* events in the North Atlantic were rare and peculiar, they very likely represent changes in local hydrography (Edwards et al., 1999), as does the nearly-annual stranding of the oceanic, neustonic, hydroid *Velella velella* (the by-the-wind-sailor), which is blown ashore in huge numbers by prevailing winds nearly every year in mid-to-late spring along most of the beaches of Washington, Oregon and California. Peculiar winds or ocean currents are certainly capable of causing the appearance of local jellyfish blooms by advecting unusual species into new areas. Whether such species remain in a system long enough to cause long-term changes in the plankton community determines to some extent our interest in the events and whether or not they are seen as 'blooms'.

Siphonophore Nanomia *in the Gulf of Maine*

Twice in the last two decades, unusually high numbers of the siphonophore *Nanomia cara* A. Agassiz, 1865 have been reported by observers in manned submersibles in the Gulf of Maine (Rogers et al., 1978;

Mills, 1995). The 1975 observations were corroborated by fishermen whose trawl nets were being clogged by the high numbers of siphonophores. The authors respectively reported maximum densities of 1–8 siphonophores per m^3 in 1975–1976 and up to 50–100 per m^3 (concentrated near the bottom) in 1992–1993. In both cases, access to submersibles for observations was limited and follow-up counts were not performed. It is not known if such high numbers of *N. cara* occur with some regularity or if some special ecological factors in the environment, for instance the poor fishing conditions of the early 1990s (resulting from decades of overfishing), might be related. Further study of *N. cara* in the Gulf of Maine is planned for the next few years (M. Youngbluth, pers. comm.).

Pelagic hydroid fragments in the Gulf of Maine

Beginning in 1994, immediately following observations of high numbers of *Nanomia cara* in Wilkinson Basin in the Gulf of Maine (Mills, 1995), another team of scientists found unusually high numbers of floating bits of hydroid colonies suspended in the water column about 150 km to the southeast, on Georges Bank (Madin et al., 1996), where floating hydroids do not typically form a noticeable element in the zooplankton. In fact, from May to June 1994 the net zooplankton in the region was dominated by fragments of hydroid colonies, primarily *Clytia gracilis* (M. Sars, 1850), but also including other *Clytia* and *Obelia* species. A shore-based observer reports large numbers of hydroid polyps washing ashore most autumns since 1990 on the south shore of Nantucket Island, in the same general oceanic system (J. T. Carlton, pers. comm.). Shipboard feeding experiments in 1994 indicated that the unexpected hydroids in the water column might be eating half of the daily production of copepod eggs and 1/4 of the production of copepod nauplii, potentially affecting recruitment of fishes whose larvae normally feed on these copepods (Madin et al., 1996). A careful search of the literature and unpublished data sets by L. P. Madin revealed that similar floating hydroids were reported in the same area by Bigelow in 1913, 1914, 1916, and also recorded in 1939–1940, in the 1980s, and every year since 1994 (L. P. Madin, pers. comm.). Nevertheless, the phenomenon is not well known, and not well understood. The intriguing question of whether these bits of usually-bottom-living animals have been broken up and become resident in the water column as a result of increased trawling activities on the bottom remains un-

answered (Mlot, 1997), but it seems that the numbers of 'jellies' may have increased in recent decades in these important, but now decimated, fishing grounds.

Scyphomedusae in the northern Gulf of Mexico

Graham (2001) found some evidence for recent increases in large scyphomedusan jellyfish near the coasts of Alabama, Mississippi, Louisiana and Texas in the Gulf of Mexico by examining bycatch data from routine government shrimp and groundfish surveys from 1985 to 1997. He presents data that suggests localized increases in both number and distribution (increasingly offshore) of *Chrysaora quinquecirrha* (Desor, 1848) medusae in high productivity waters near the Mississippi River delta during the summer months and more general numerical increases in *Aurelia aurita* (Linnaeus, 1758) over much of the study area in the autumn months of the study period. It will likely take at least another decade for these trends to sort out and to fully understand the importance of the apparent increases in medusae in the northern Gulf of Mexico. The additional arrival of a new large jellyfish, the Indo-Pacific rhizostome *Phyllorhiza punctata* von Lendenfeld, 1884, in large numbers from coastal Alabama to Louisiana throughout summer 2000 (W. M. Graham, pers. comm.) may further change the pelagic ecosystem dynamics in this economically important fishing area.

Pelagic Cnidaria and Ctenophora in the Southern Ocean

Pagès (1997) suggests in a review of gelatinous zooplankton in the pelagic system of the Southern Ocean that recent several-year periods in which the pelagic ecosystem seems to have been dominated by Cnidaria and Ctenophora may alternate regionally with periods dominated by krill and/or salps. For example, in the Antarctic Polar Frontal Zone in the South Georgia sector, in summer 1994, gelatinous carnivores, together with myctophid fish, were the most abundant nektonic organisms. At the Weddell Sea ice edge in autumn 1986, salps, medusae and ctenophores accounted for 3/4 of the wet weight and 1/3 of dry weight of the micronekton/macrozooplankton in the upper 200 m. Pagès (1997) notes that in spite of reports of such high densities, no comments on the apparent importance of these animals in the pelagic system have been put forth.

In the Antarctic pelagic ecosystem, the greatest scientific effort has been on the commercially valuable

krill, with some reluctant study of salps in years when krill were few and salps dominated (Loeb et al., 1997). In some years when salps were locally abundant (1991, 1993), medusae, siphonophores and/or ctenophores were also important players either in nearby regions or even different water layers than the salps. Pagès (1997) found it difficult to put together enough data to even document the apparent recent increase in carnivorous jellies and there is certainly too little data yet to understand the nature or regularity of these apparent fluctuations. Scientists who study carnivorous pelagic jellies are rarely included in studies of the Southern Ocean.

Mesopelagic and deep-sea jellyfish

If we can barely define the extent of blooms in the visible uppermost layers of the sea, what can be said about midwater jellies? Do they form periodic blooms? Are the huge numbers of *Periphylla* present since the 1970s in a Norwegian fjord reported by Fosså (1992) an invasion of a new habitat, or a bloom of a pre-existing population? Will the 'new' population maintain at its present level, or increase, or fall off?

Jarms et al. (1999) and Youngbluth & Båmstedt (2001) report population increases of the characteristically-midwater *P. periphylla* medusae in Lurefjorden during the 1990s (relative to the data of Fosså, 1992), indicating further changes in the jellyfish population in that fjord, growing in recent years through recruitment within the fjord. Other fjords in Norway also host small numbers of *P. periphylla* medusae, but for reasons that are not clear, have not suffered the explosion that has disrupted fisheries in Lurefjorden, and remain dominated by mesopelagic fishes. Whether Lurefjorden is a special case or represents one of several possible outcomes in such isolated waters is still unknown. Eiane & Bagøien (1999) compare the jellyfish-dominated Lurefjorden with a nearby fish-dominated fjord and note that light levels below 100 m in Lurefjorden are substantially lower and may, therefore, disadvantage visual predators such as fish, giving jellyfish an advantage in exploiting the food web in that particular situation.

In the open ocean, although total biomass drops off with depth (Angel & Baker, 1982), specific biomass and species diversity of medusae and siphonophores (and probably ctenophores) apparently increases with depth at least to several thousand m (Thurston, 1977; Angel & Baker, 1982). Our very rough knowledge of the midwater pelagic ecosystem typically includes only a sketchy understanding of changes over time. Raskoff (2001) has examined a unique decade-long record of the midwater gelatinous fauna in Monterey Bay, California, and found evidence for changes in the mesopelagic jellyfish populations during two El Niño events in the 1990s that might be interpreted as short-term blooms. It is not yet clear if the influence of man's activities extends in general to the deep water column, and how or when we will be able to read the signals if it is.

Burd & Thomson (2000) report increased abundance of medusae in the water column above hydrothemal vent fields compared to the same depths in surrounding waters. Such population differences most likely relate to increased nutrient availability above vent sites and may be better interpreted as site-specific patchiness rather than as blooms.

Increases in nonindigenous species that recently invaded an ecosystem

Rhopilema *and other scyphomedusae in the Mediterranean*

Rhopilema nomadica Galil, Spanier, & Ferguson, 1990 is a large (to 80 cm diameter) scyphomedusa that has become increasingly abundant in the eastern Mediterranean over the past two decades (see below) (Lotan et al., 1992). Like *Pelagia noctiluca*, another jellyfish resident in the Mediterranean (see above), *R. nomadica*'s presence creates an environmental hazard to fishermen and bathers alike, because it has an unpleasant sting and can be present in such large numbers as to clog fishing nets. First recorded in 1976 in the Mediterranean, the origin of this new hazardous jellyfish is surprisingly unclear. Although assumed to have arrived via the Suez Canal, *R. nomadica* is rare in the Red Sea and is not known from elsewhere [it was only recently described, after its arrival to the Mediterranean (Galil et al., 1990)]. Its reproductive potential in the eastern Mediterranean appears to be very high (Lotan et al., 1992) and it has been present in large numbers off the coast of Israel every summer since 1986 (Lotan et al., 1994).

The population has so far remained in the eastern Mediterranean, where it can now be found in coastal areas from Egypt to Turkey (Kideys & Gücü, 1995; M. Fine, pers. comm.). The jellyfish blooms in Mersin Bay, Turkey, of the mid-1980s, although not identified to species by Bingel et al. (1991) were attributed to a

new population of *R. nomadica* (Lotan et al., 1994). In contrast to the fluctuating population peaks demonstrated as typical of *Pelagia noctiluca*, there is no question that the 'bloom' of *Rhopilema nomadica* is simply a population explosion in a new habitat.

Two other species of scyphomedusae have recently become established in the Mediterranean Sea (and elsewhere) – these are *Phyllorhiza punctata* of the warm western Pacific and the epi-benthic, Indo-Pacific species *Cassiopea andromeda* (Forsskål, 1775) (M. Fine, pers. comm.). Little is yet known about the population dynamics of these newer populations.

Increasingly common new estuarine hydromedusae in San Francisco Bay and the Chesapeake Bay

Three species of hydromedusae, all apparently indigenous to the Black Sea, *Maeotias marginata (=inexspectata)* Ostroumoff, 1896, *Blackfordia virginica* Mayer, 1910, and *Moerisia* sp., have now become established in both San Francisco Bay and the Chesapeake Bay in North America (Calder & Burrell, 1967, 1969; Mills & Summer, 1995; Mills & Rees, 2000; Rees & Gershwin, 2000). All three species occur in very low salinity regions of these two large estuary systems. In San Francisco Bay, such regions were not previously inhabited by (native) jellyfish (Smith & Carlton, 1975), whereas in the Chesapeake Bay the nonindigenous species join native low-salinity jellyfish populations (Purcell et al., 1999c). The impacts of these new residents (known in the Chesapeake Bay since the 1960s–70s, but only discovered in San Francisco Bay in the 1990s) are largely still unknown, and their ubiquity in these ecosystems has only recently been recognized (Purcell et al., 1999a; Rees & Gershwin, 2000).

Originally located in one tributary to San Francisco Bay (Mills & Summer, 1995), *Maeotias marginata* is now known to be present in at least 4 equally-low salinity sloughs in the region (J. T. Rees, pers. comm.). *Moerisia lyonsi* Boulenger, 1908 has become so numerous in parts of the Chesapeake Bay that it has become an accidental nuisance in experimental mesocosms (Purcell et al., 1999a); a related (or possibly the same) species is still a rarity in San Francisco Bay (Rees & Gershwin, 2000). *B. virginica* is now known to be present in two tributaries to San Francisco Bay, as well as a variety of other harbors all over the world (Mills & Sommer, 1995), but little is known about its effect in these ecosystems.

Medusae and ctenophores in the Black Sea

Pollution, eutrophication and many anthropogenic alterations of the natural environment have vastly altered the Black Sea and its adjacent Sea of Azov in the past 50 years (Zaitsev & Mamaev, 1997). This system provides 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' – medusae and ctenophores. By the 1960s, largely due to the effects of pollution combined with over fishing, many of the native fishes in the Black Sea had become uncommon, including the jellyfish-eating mackerel *Scomber scombrus*. Perhaps directly related to the loss of this and other fishes, and to increasing eutrophication, the Black Sea has experienced severe outbreaks of three different species of 'jellyfish' in the past 3 decades (Zaitsev & Mamaev, 1997).

The first, little publicized, bloom was of the Mediterranean (and presumptively Black Sea native) scyphomedusa, *Rhizostoma pulmo* (Macri, 1778). In the late 1960s and early 1970s, this species (with bell diameters to 40 cm) reached abundances of 2–3 per m^3 in nearshore waters, later washing ashore and leaving 1–1.5 m high piles along beaches in late summer and early fall (Zaitsev & Mamaev, 1997).

For unexplained reasons, the *Rhizostoma pulmo* population dropped back to some lower 'non-bloom' level by the mid-1970s, but at the same time, the resident population of *Aurelia aurita* began to increase, perhaps in response to the generally increasing salinity, as large amounts of incoming fresh water were diverted for irrigation (Studenikina et al., 1991). Increasing numbers of commercial benthic and pelagic fish populations were also crashing during this period, leaving *A. aurita* as one of the top water-column predators. Its population peaked in the late 1980s, with a biomass estimated at 300–500 million tons, when it was estimated to be eating 62% of the annual production of the Black Sea zooplankton, most of which had previously been supporting fishes (Vinogradov et al., 1989; Zaitsev & Mamaev, 1997).

Perhaps because of a several year influx of additional fresh water in the 1980s, the *Aurelia aurita* population began to decline in the late 1980s when the salinity became unfavorably low (Studenikina et al., 1991), but at about the same time the Atlantic American (New England to Argentina) ctenophore, *Mnemiopsis leidyi* A. Agassiz, 1865, was accidentally introduced in the Black Sea, probably via ballast

water from a grain ship. This ctenophore is more eury-haline than *A. aurita* and was apparently not adversely affected by the lowering salinity. The nonindigenous *M. leidyi* population first peaked in the late 1980s to early 1990s with an estimated biomass of over a billion tons (300–500 animals per m^3 observed in some regions), while in the same period the *A. aurita* population dropped to less than 1/20 of its earlier peak value (Vinogradov et al., 1989; Zaitsev, 1992; Zaitsev & Mamaev, 1997). Nearly all of the zooplankton production in the Black Sea at that time had gone from feeding fishes to feeding ctenophores, and commercial fisheries in the Black Sea became nearly non-existent.

Economic turmoil in Russia during the 1990s has interrupted a regular sampling program in the northern Black Sea, so it is not entirely clear how jelly populations have fared this decade. Both Russian and Turkish scientists are now sampling regionally to follow events in the Black Sea. Kovalev & Piontkovski (1998), Mutlu et al. (1994) and Shiganova (1998) give data that indicate continuing very high numbers of jellies in the system, but with peaks alternating this decade from *Mnemiopsis leidyi* to *Aurelia aurita* and then back to *M. leidyi* by the mid-1990s. Kideys et al. (2000) review data from the past decade including new data from the southern portion of the Black Sea, where *M. leidyi* and *A. aurita* numbers have dropped in the late 1990s. Purcell et al. (2001a) review the history and biology of *M. leidyi* in the Black Sea basin and compare it with the same species in its native North American estuaries elsewhere in this volume.

The arrival of the ctenophore *Beroe ovata* Bruguière, 1789 in the Black Sea in 1997 (Finenko et al., 2001; Shiganova et al., 2001) promises to redirect the story there yet again. This species already appears to be having some local effect on *Mnemiopsis* populations. *B. ovata* is well known in the Mediterranean, but had not previously been recorded in the Black Sea; in some ways its extension into the Black Sea might be seen as yet another nonindigenous species there.

The gradual domination of the Black Sea and Sea of Azov pelagic systems by jellies is a story that combines outbreaks of both native and introduced medusae and ctenophores. There is little doubt that extensive anthropogenic alterations over time have led to severe disruptions in the functioning pelagic ecosytem, and the absence of jellyfish predators has undoubtedly fueled these imbalances. *Mnemiopsis leidyi* was newly observed in the Caspian Sea in 1999 (Volovik, 2000, T. A. Shiganova, pers. comm.), and it is predicted that again, a highly unique pelagic ecosystem with a large number of endemic species and important fisheries resources, may be massively disrupted by the arrival of this ctenophore.

Aurelia *blooms around the world*

In addition to the 1980s bloom in the Black Sea, *Aurelia 'aurita'* populations have recently swelled to huge numbers in many coastal areas worldwide, often causing significant economic damage. Although it is usually considered to be a cosmopolitan species, I currently favor a theory of 19th and 20th century introduction of *A. aurita* to harbors throughout the world via shipping, citing the fairly recent nuisance status of this species in many areas. 'Rediscovery' of *A. labiata* Chamisso and Eysendardt, 1821, another species that is apparently endemic to the Pacific Coast of North America (L. A. Gershwin, pers. comm.) adds weight to the idea of a more restricted original range of *A. aurita*, probably in the North Atlantic. Understanding the biogeography of all of the *Aurelia* species requires serious molecular genetic study. Several researchers are undertaking aspects of the problem at this time (see Dawson & Martin, 2001), and the situation may eventually be sorted out.

Aurelia sp. is known to have been present in Japan at least since 1891 (Kishinouye, 1891) and was first mentioned in Tokyo Bay in 1915 (Hirasaka, 1915). The species in Japan is generally thought to be *A. aurita* and is well-known by individuals in the American aquarium display business to culture differently than the west coast of North America species, *A. labiata* (Japanese material strobilates nearly all of the time in the laboratory, wheras *A. labiata* polyps from the west coast of North America strobilate only occasionally). Whether or not *A. aurita* is indigenous to Japan is not known, but summer blooms of this species in Japanese bays have caused increasing socio-economic problems since the 1950s. Shimomura (1959) documents disruptions of fisheries in the Sea of Japan by *A. aurita* blooms as early as 1950. Matsueda (1969) describes power plant restrictions and temporary shut-downs throughout Japan due to clogging of intake screens by *A. aurita* medusae beginning in the mid-1960s as increasing numbers of power plants used seawater cooling systems. This technology highlighted the already-occurring summer *A. aurita* blooms, whose origins in time are obscure. Problems in net fishing and power plant operations in Tokyo Bay from exceedingly high *A. aurita* numbers are described by Yasuda (1988). Omori et al. (1995) note that the importance of

A. aurita in the pelagic ecosystem in Tokyo Bay began in the 1960s when the dominant copepods switched from *Acartia omorii* Bradford and *Paracalanus* spp. to the smaller *Oithona davisae* Ferrari & Orsi. This switch had many food web ramifications which may have included an increasingly favorable situation for *A. aurita* in Tokyo Bay (although this is not proven). Feeding and digestion by *A. aurita* in Tokyo Bay has recently been studied by Ishii & Tanaka (2001). Similar general zooplankton changes may explain the increasing importance of *A. aurita* in bays throughout Japan in the latter half of this century, but the blooms may have already occurred in some places decades earlier (M. Toyokawa, pers. comm.).

Aurelia 'aurita' has caused upsets in power plants throughout the world. Besides Japan, shut-downs due to medusae clogging the seawater intake screens have been reported in the Baltic region, Korea, India, Saudi Arabia, Australia and more (Möller, 1984a; Rajagopal et al., 1989; Y. Fadlallah & S. Baker, pers. comm.). Half of the Philippines lost power on December 10, 1999 when large numbers of *Aurelia* sp. were sucked into the cooling system of a power station there (The Economist, Dec. 18, 1999, pp. 36–37). The 'bloom' nature of such events can be seen at many levels. *A. aurita*, like most jellyfish, has a more or less annual cycle, so the clogging problem peaks annually during the months that medusae are largest and also most abundant. There is also some variation between years, with clogging being much more problematic in some years than others. The final issue is whether or not the entire clogging phenomenon is becoming increasingly severe over a period of several to many years.

It appears that *Aurelia aurita* may become especially abundant in highly eutrophic areas, and if so, increasing eutrophication of some harbors may increase *A. aurita* globally in coming decades. Elefsis Bay in Greece supports a uniquely high *A. aurita* population in the Mediterranean, which is assumed to correlate to the high eutrophication there (Papathanassiou et al., 1987). Sewage effluent, in this case from Athens, provides both inorganic and organic nutrients that are available to medusae both directly and indirectly through the food web (Wilkerson & Dugdale, 1984).

Aurelia aurita has been extensively studied in a variety of locations in the North Sea and Baltic Sea (Hay & Hislop, 1980; Möller, 1980, 1984a,b; Gröndahl, 1988; Schneider & Behrends, 1994; reviewed by Lucas, 2001), where it is implied that it is a natural endemic species. Such *A. aurita* populations

fluctuate enormously throughout the year as annual medusa populations mature and die fairly synchronously, but the scientific literature contains no evidence or mention of long-term changes in these *A. aurita* populations in recent decades. Schneider & Behrends (1994) discuss large, interannual variations in the *A. aurita* medusa populations in Kiel Bight, but their data (1978–1993) and discussion gives no hint of gradual or abrupt increase in the Baltic Sea populations over time. Such lack of change in comparison with *A. aurita* populations in Japan is noteworthy and possibly indicative of longer residence time of *A. aurita* in northern Europe, or of different scenarios of anthropogenic disturbance and biological response in bays in Europe and Asia.

Recent decreases in jellyfish populations

Decreases in either jellyfish abundance or species richness or both have been reported in a variety of locations worldwide in the past decade. Examples enumerated below come from both the community/ecosystem level and from the level of a single taxon in a fairly restricted location.

Hydromedusae in the northern Adriatic Sea

Benović et al. (1987) report a decrease in hydromedusa abundance and species richness in the northern Adriatic, which they believe correlates with declining water quality resulting from increasingly eutrophic nearshore conditions. There is a long tradition of marine plankton work in the North Adriatic and the fauna is well-known. Since the 1960s, there has been a trend in those waters toward growing oxygen depletion in near-bottom water, while at the same time the near-surface water was becoming increasingly hypersaturated with oxygen. The authors report a substantial loss of metagenic anthomedusae (22 species) and leptomedusae (9 species), out of a total of 42 known regional species of hydromedusae, have disappeared from the northern Adriatic from 1910 to 1984. All of the affected species have benthic polyps that may have been eliminated by the low oxygen bottom water, while the holoplanktonic (without benthic hydroids) trachymedusae and narcomedusae were only slightly affected by changes in the water column. The effects on polyps are all inferred, with no actual polyp studies available. The continuation of this study for more than another decade, through 1997 (Benović et al.,

in press), shows that the biodiversity of hydromedusae in the northern Adriatic has remained low in spite of evidence for seasonal immigration by medusae of species previously established there. Low oxygen conditions on the bottom remain unfavorable to benthic polyps living in the northern Adriatic.

Medusa biodiversity in St. Helena Bay, west coast of South Africa

Buecher & Gibbons (2000) examined hydromedusa, scyphomedusa and ctenophore populations within this oceanically-influenced bay in a set of 264 samples taken from 1988 to 1997. The area is important as a major recruitment center for commercial pelagic fish in the southern Benguela ecosystem. The authors identified a total of 53 species of pelagic Cnidaria and Ctenophora from the Bay, but show a decided trend towards a loss of species richness of this gelatinous fauna during the 10-year study period, with 21–24 species present each of the first 5 years, declining to only 11 or 12 species present the last 2 years. No reason for this decrease in biodiversity over the 10-year study period was proposed, and although it is likely that a decrease in sample numbers may account for loss of numerous rare species in later years, it is also possible that an undefined change in the ecosystem is recorded in this loss of biodiversity.

Aequorea victoria *in Washington State and British Columbia*

Aequorea victoria (Murbach & Shearer, 1902) (sometimes locally reported as *A. aequorea* or *A. forskalea* in the literature) has been perhaps the most abundant medusa both numerically and in terms of biomass in parts of the Puget Sound/Strait of Georgia inland marine waters of Washington State, U.S.A., and British Columbia, Canada. Between the early 1960s and the mid-1990s, hundreds of thousands of these medusae were collected by various different laboratory groups in order to extract natural *aequorin* and green fluorescent protein (gfp), respectively luminescent and fluorescent proteins that have proved useful in biological and medical research. Annual collections varied enormously, but it is estimated that 25 000 to 150 000 *Aequorea* mature medusae were harvested nearly every summer during that period in and around Friday Harbor, Washington (J. F. Blinks & O. Shimomura, pers. comm.). Only the largest specimens were collected, not out of special concern for their ecology but because the protein yield per individual was more

favorable. Since the early 1990s, both the numbers and maximum sizes of *Aequorea* medusae in the Friday Harbor area have fallen off gradually, but continuously, so that in the late 1990s, there have not been enough animals for commercial collections (although the ability to manufacture *aequorin* and gfp has also now largely supplanted the need for collection). Finding even 1000 *Aequorea* medusae over several weeks would have been difficult during the summers of 1997, 1998, and 1999, and average size was much smaller than in earlier year (few were as large as the minimum size example painted onto remaining collecting screens from the 1970s); in summer 2000, numbers have been the lowest yet (C. E. Mills, pers. obs.).

In trying to assess this obvious population decrease in which little real population data is available, it should be noted that we also have no idea what might be the functional geographic limits of the *Aequorea victoria* population that is resident in and near Friday Harbor. We do not know if the decline is a slow response to nearly three decades of collections or (more likely) if it is the result of an unrelated environmental change. Furthermore, there is virtually no field data about the polyp phase of *A. victoria*, outside of a few isolated field collections over the decades. As in the cases of *Polyorchis penicillatus* (Eschscholtz, 1829), *Spirocodon saltatrix* (Tilesius, 1818) (below) and *Chrysaora melanaster* (see above), one cannot determine whether the change has been effected by the medusa or polypoid phase of the life cycle of this species. We have no sense of when, if ever, the *A. victoria* medusa population will rebound.

The family Polyorchidae in the North Pacific

The hydrozoan family Polyorchidae is comprised of five species of anthomedusae that have historically inhabited many of the protected bays and inlets between about 30° and 55° N Latitude on both sides of the north Pacific Ocean (Uchida, 1927; Kramp, 1961; Rees & Larson, 1980; Y. M. Hirano, pers. comm.; C. E. Mills, unpublished). On the Asian side of the Pacific, two species have non-overlapping distributions: the medusa *Spirocodon saltatrix* used to be commonly found from southern Kyushu to the top of Honshu (Japan), and *Polyorchis karafutoensis* Kishinouye, 1910 occurs from central Hokkaido to northern Sakhalin Island (Russia). On the west coast of North America, *Polyorchis penicillatus* has been collected from the northern Gulf of California and San Diego to the Aleutian Islands, and is joined by *Polyorchis haplus*

Skogsberg, 1948 and *Scrippsia pacifica* Torrey, 1909 in California.

All of these large, easily recognized, hydromedusae seem to assume the same ecological role, spending much of their time perched on their tentacles and feeding on the bottom, but also swimming and feeding in the water column some of the time. All of them presumably have a benthic polyp phase in their life cycle, but it is not known for any species, in spite of many attempts to raise the easily-obtained planula larvae in the laboratory from field-collected medusae. The polyp could be the most vulnerable part of the polyorchid life cycle, yet we know nothing about it.

Spirocodon saltatrix is now uncommon or rare throughout most of its range in Japan (Y. M. Hirano, pers. comm.) and *P. penicillatus* is much less abundant in some Washington and British Columbian bays and probably throughout California than it was only a couple of decades ago (a strong showing of *P. penicillatus* in some central California bays in the winter of 1999–2000 now clouds the picture slightly). There is too little information about the remaining 3 species to speculate on the robustness of their present populations.

The problem of marine habitat loss as a result of coastal development is sadly exemplified by this family of large, showy hydromedusae. Once well-known in shallow bays along more than 1500 linear miles of coastlines on both sides of the North Pacific Ocean, these medusae are now increasingly rare. The general urbanization of many bays, accompanied by dredging and filling, and construction of marinas and tourist facilities along most of this range has all contributed to a vast degradation of their habitat. Additionally, both *S. saltatrix* and *P. penicillatus* have been favorite research animals and heavily collected from many of their previous haunts; one cannot discount the possibility that over-collection by scientists has led to their demise in some bays. These large medusae are correspondingly highly fecund, producing around 10 000 eggs per day for much of their lives; it is possible that some aspect of their ecology requires this huge egg/embryo input in order to maintain stable local populations. One wonders how long into the next millennium this family of unusual semi-benthic medusae will manage to persist.

Conclusions

It has been said that many biologists who have observed marine communities over a period of time believe they have seen significant declines in populations of some species, but that they do not have the data to confirm or refute these impressions (Thorne-Miller & Catena, 1991). Even though relatively few scientists study pelagic medusae or ctenophores, many cases of upsets in medusa or ctenophore populations have been documented as man's influence on the oceans becomes increasingly apparent. The problem of ocean change is very real.

It is unfortunate that we have so little population and ecological data about medusae and ctenophores in the field that we usually cannot presently distinguish between natural fluctuations and long term, possibly irreversible, change. Even in the case of *Chrysaora melanaster* in the Bering Sea, with an unusual 25 year data set (1975–1999), it would require data from the preceding 20 years, when the international fin-fishing effort was considerably less, to understand if man's influence in the Bering Sea is driving the ecosystem toward a long-term increase in medusae. Seemingly enormous numbers of jellyfish are now being harvested in Southeast Asia for the global market (Omori & Nakano, 2001). We know nothing about the population biology of these species; in many cases, we do not even know the species names of the commodity-products coming to market, and certainly we do not know how these populations are responding either to to harvest pressure or to nearshore changes in recent decades. Uye & Kasuya (1999) suggest that numbers of indigenous ctenophores, especially *Bolinopsis mikado* (Moser, 1907), may be rising in some Japanese coastal waters; this situation bears following in coming years.

Although Cnidaria and Ctenophora are low on the phylogenetic tree, they generally feed high on marine food chains, directly competing in many cases with fishes for food. Massive removals of fishes from ecosystems might be expected to open up food resources for gelatinous predators, which seems in some cases to be what has happened. Further interactions between jellyfishes and fish are explored by Purcell & Arai (2001), elsewhere in this volume. Although some jellyfishes are preyed upon by fishes, others of the carnivorous jellies prey nearly exclusively other jellies, forming a somewhat independent food web named the 'jelly web' by B.H. Robison (Robison & Connor, 1999).

Largely through the aquarium industry's handsome efforts to display jellyfish, the general public is becoming much better acquainted with this group of animals at the same time that jellyfish seem to be increasing their presence on the world stage of ocean ecosystems. If I could offer one piece of advice to young scientists seeking a project on pelagic Cnidaria, it would be to study the population dynamics of some of the common and abundant species that occur in coastal regions throughout the world, whose populations must be substantially influenced by changes in their local ecosystems, and about which we know next to nothing beyond their names.

Acknowledgements

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