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Questioning the Rise of Gelatinous Zooplankton in the World's Oceans

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During the past several decades, high numbers of gelatinous zooplankton species have been reported in many estuarine and coastal ecosystems. Coupled with media-driven public perception, a paradigm has evolved in which the global ocean ecosystems are thought to be heading toward being dominated by “nuisance” jellyfish. We question this current paradigm by presenting a broad overview of gelatinous zooplankton in a historical context to develop the hypothesis that population changes reflect the human-mediated alteration of global ocean ecosystems. To this end, we synthesize information related to the evolutionary context of contemporary gelatinous zooplankton blooms, the human frame of reference for changes in gelatinous zooplankton populations, and whether sufficient data are available to have established the paradigm. We conclude that the current paradigm in which it is believed that there has been a global increase in gelatinous zooplankton is unsubstantiated, and we develop a strategy for addressing the critical questions about long-term, human-related changes in the sea as they relate to gelatinous zooplankton blooms.

Keywords: bloom, media, jellyfish, salp, global synthesis

The enigmatic gelatinous zooplankton are widely heralded as key members of ocean ecosystems (Hamner et al. 1975, Mills 1995, Purcell et al. 2007), yet their ecological roles are often grossly oversimplified and misunderstood. Basic similarities among body designs—specifically, water contents of 95% or higher (compared with 60%–70% for the marine vertebrates and crustaceans) and a planktonic lifestyle—make it easy to lump the approximately 2000 species (Daly et al. 2007, Mills 2011) into a single, catch-all category: the *gelatinous zooplankton*, which includes groups such as the jellyfish (cnidarian medusae), ctenophores (comb jellies), and pelagic tunicates (the invertebrate chordates that include salps, doliolids, and pyrosomes; hereafter, we will focus on the salps). In fact, the distinct morphologies of the species categorized as gelatinous zooplankton can yield ecological outcomes as vastly different as, say, lumping lions and gazelles into a single ecological group called *mammals*. The apparent sudden appearance and disappearance of gelatinous zooplankton in population “blooms” (figure 1)—a distinct feature of this group—contributes to their negative reputation as sentinels of ecological disturbance.

To some marine ecologists (e.g., Jackson et al. 2001, Richardson et al. 2009; also see supplemental box S1 available online at <http://dx.doi.org/10.1525/bio.2012.62.2.9>), a paradigm seems to have developed in which ocean ecosystems are seen as heading toward being dominated largely

by “nuisance” jellyfish. We present a broad overview of gelatinous zooplankton in a historical context to reconsider how their population changes may reflect human-mediated alteration or perturbation of global ocean ecosystems. To this end, we consider information relating to the following questions: What is the evolutionary context of contemporary gelatinous zooplankton blooms? What is the human perception of changes in jellyfish, ctenophore, and salp populations? What do the data allow us to say—or not to say—to support the current paradigm (i.e., is there sufficient data available to have established the paradigm), and why should we care? In the conclusion, we develop a strategy for addressing the critical questions about long-term, human-related changes in the sea as they relate to gelatinous zooplankton blooms.

Gelatinous zooplankton blooms have ancient origins and are not a new phenomenon

Following a call for further studies of the role of fishes and jellyfishes and their possible role in maintaining the natural ecology of the sea (Parsons 1993), Mills (1995) suggested that the jellyfish, which are ubiquitous in nearly all marine ecosystems, may be positioned to increase in areas that have been subjected to overharvesting and environmental perturbations. At about the same time, Pauly and colleagues (1998) suggested that marine food webs were being restructured,

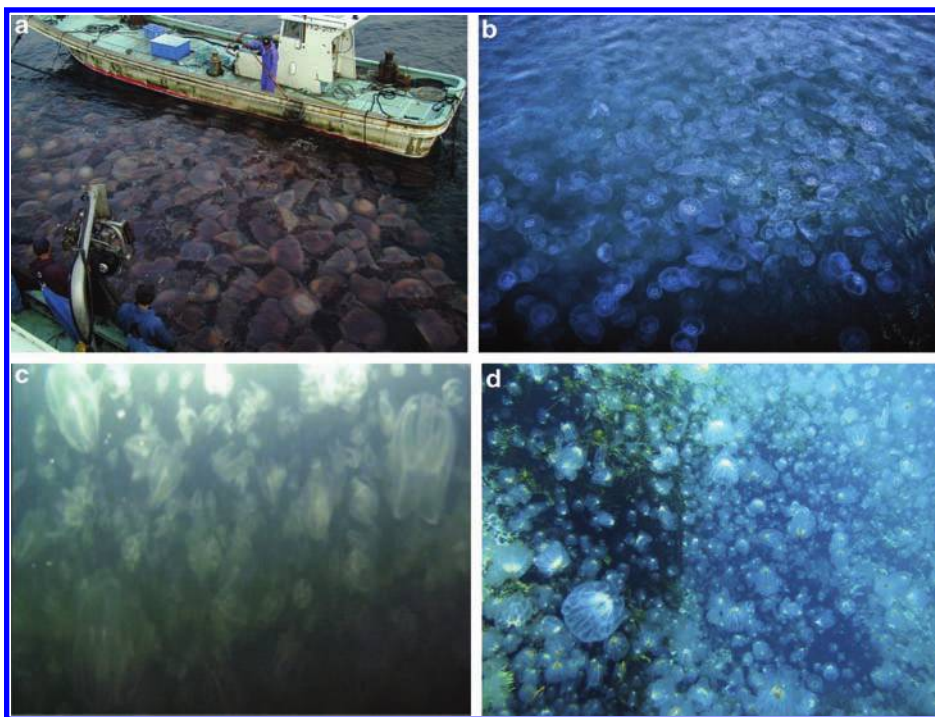


Figure 1. Examples of modern-day jellyfish that regularly form blooms. (a) *Nemopilema nomurai* medusae off the coast of Japan. (b) *Aurelia* sp. 1 medusae bloom off the coast of Japan. (c) *Mnemiopsis leidyi* ctenophores in the Baltic Sea. (d) *Cyclosalpa* sp. salps off the coast of New Zealand. Photographs: www.seacology.co.nz.

particularly at higher trophic levels, by fishing activities, and spectacular blooms of jellyfish were reported in the Black Sea (Vinogradov et al. 1989), in the eastern Mediterranean Sea (Lotan et al. 1994), in the Bering Sea (Brodeur et al. 1999), and off Japan (Uye and Ueta 2004), and increased densities of salps were reported in the Southern Ocean and northwest Atlantic Ocean (see figures 1 and 2; Atkinson et al. 2004, Madin et al. 2006). These reports partially led to the perception that modern gelatinous zooplankton blooms are increasing in number at a global scale. Note that we use the term *bloom* to mean both true and apparent blooms, defined as the “normal and/or abnormal seasonal abundance... directly attributable to population increase due to reproduction and growth” and “increase[d]... abundance... associated with temporary or transient physical or chemical phenomena,” respectively (Hamner and Dawson 2009 [p. 164], see also Graham et al. 2001).

The modern popular perception that gelatinous zooplankton are positioned—almost uniquely among metazoans—to take advantage of future global change (box S1; Mills 1995) raises the following question: In what circumstances is being gelatinous beneficial in the plankton? First, the evolution of a planktonic lifestyle and gelatinous body plan could be driven by ecological benefits derived from feeding, distribution, predator avoidance (e.g., being invisible), or breaking cycles of parasitism (Strathmann et al. 2002). From the paleontological perspective, the diversification of

phytoplanktonic food (energy) resources may have been a major selective pressure for the evolution of filter-feeding meso- and macrozooplankton (Butterfield 1997), and among the zooplankton, filter-feeding coupled with a gelatinous body plan (i.e., low organic content per individual) is arguably more energetically efficient than specialist raptorial predation, especially when low concentrations and a patchy distribution of food predominate, as in the past, present, and probably future open ocean (Acuña 2001, Ducklow et al. 2009) and in more turbid waters (Eiane et al. 1999). Planktonic gelatinous predators, in turn, would also benefit indirectly from any factors that benefit their filter-feeding prey.

Rapid numerical increase is another common character across gelatinous zooplankton groups that is also deeply rooted in evolutionary time. Asexual propagation occurs in various modes (strobilation and the production

of benthic buds and podocysts in Scyphozoa, coloniality and the budding of frustules and medusae in Hydrozoa, complex asexual budding in Chordata), and patches of animals may accumulate in the plankton if asexual propagation exceeds physical dilution. The distribution of sexually reproductive adults in the plankton, as opposed to the benthos, also meant that the vertical dimension in which sexual reproduction had to succeed had expanded. Although a planktonic sexual stage has increased potentials for dispersal and gene exchange between populations, it has the added costs of increased gamete dilution and new sources of predation. Behavioral and physical concentration are considered effective means of minimizing gamete dilution by free-spawning individuals otherwise incapable of copulation (Mills 1983). Interestingly, at least some hermaphroditic ctenophores have the ability to self-fertilize, which may facilitate rapid numerical expansion during favorable conditions (Costello et al. 2006, Condon and Steinberg 2008).

Origination and persistence are also important metrics of evolutionary success. The paleontological record for the soft-bodied and unlikely-to-fossilize gelatinous zooplankton is discontinuous and difficult to interpret, making it hard to affix a firm time frame to the group's origins. Nonetheless, fossils and evolutionary inference suggest that the Ctenophora originated during the Early Cambrian, about 540 million years ago (mya; Chen et al. 2007); medusae likely arose during the Middle- to Late-Cambrian period,

about 540–520 mya (e.g., Hagadorn et al. 2002); and pelagic tunicates appeared during the Neogene, 20–30 mya (Rigby and Milsom 2000). Therefore, being gelatinous evolved independently, multiple times, and in many disparate taxa (also in radiolarians, polychaetes, mollusks, chaetognaths, and holothurians), and this trait has been conserved for perhaps more than 500 million years in the case of jellyfish. This extremely long history suggests that the different gelatinous zooplankton groups are evolutionary success stories capable

of withstanding the global events that led to the disappearance of the trilobites, ammonites, and marine reptiles.

Apparent ancestral traits enabling rapid numerical expansion and exploitation of environments with pulsed food resources (Butterfield 1997) would suggest that mass occurrences of gelatinous zooplankton have an ancient origin. Indeed, fossilized mass strandings of scyphozoan jellyfishes show that dense accumulations of medusae occurred in shallow-water marine habitats at least as early as the Upper Cambrian (figure 2; Hagadorn et al. 2002). Phylogenetic reconstruction (Dawson and Hamner 2009) and—allowing for the vagaries of taphonomic processes—fossil specimens of cnidarian medusae both suggest that mass appearances of jellyfish occurred at least as early as the Middle Cambrian and were essentially concurrent with or quickly followed the evolution of medusae. It is reasonable to infer that mass appearances also characterized the early evolution of other gelatinous zooplankton that also occur en masse today and are not solely modern phenomena.

Gelatinous zooplankton blooms and the human frame of reference

Humans have a history of paradoxical fascination with jellyfish. Asian and Greek mythologies converge in depicting jellyfish as repulsive creatures, perhaps influenced by ancient human perceptions of jellyfish. Medusa, originally a beautiful maiden in Greek mythology, was transformed by an enraged Athena into an ugly creature with serpents as hair who would turn anyone who observed her to stone. Modern human narratives have perpetuated a negative perception of jellyfish, such as in the early 1900s, when politicians were negatively referred to as “jellyfish,” and this mindset is accentuated by negative reports about jellyfish in the global media (box S1).

Gelatinous zooplankton blooms appear to have occurred frequently over the past two centuries, with historical monographs

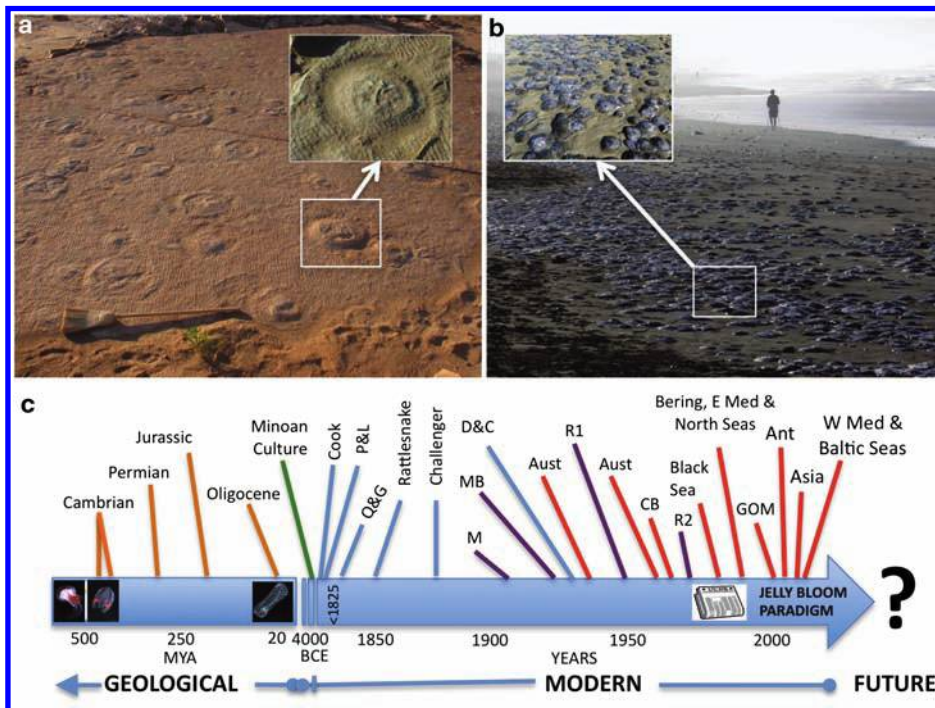


Figure 2. Historical versus modern perspective of gelatinous zooplankton blooms. (a) Fossil deposit of scyphozoan medusae. Photograph: J. W. Hagadorn, www3.amherst.edu/~jwhagadorn. (b) Photograph of a modern jellyfish (*Aurelia*) stranding on a San Francisco beach, November 2010. Photograph: Ocean Beach Bulletin, www.oceanbeachbulletin.com. (c) Time line showing records and evidence of jellyfish blooms over geological and modern time scales. The geological time period records—namely, those from the Cambrian, Permian, Jurassic, and Oligocene periods—refer to the age of fossilized medusae strandings (orange lines) from Stasinska (1960), Pickerill (1982), Nel et al. (1987), Gand et al. (1996), and Gaillard et al. (2006). The records from Minoan Culture are based on apparent depictions of medusae blooms on ancient pottery (green line). The records from historical expeditions and voyages (blue lines), historical monographs and media reports (purple lines), and scientific publications (red lines) reference current and historical jellyfish or salp blooms. The pictures on the time line refer to the first appearance of ctenophores (the ctenophore image), cnidarian medusae (the medusa), and pelagic tunicates (the salp) in the fossil record (see the text for references), and significant increases in global media reports (the newspaper) on jellyfish (see figure 3). Asia refers to Japan, China, and Korea; Ant, Antarctica; Aust, Sheard (1949) and Kott (1957); BCE, before current era; CB, Chesapeake Bay; Challenger, Herdman (1888); Cook, Beaglehole (1963); D&C, Dakin and Colefax (1933); E, eastern; GOM, Gulf of Mexico; M, Mayer (1910); Med, Mediterranean Sea; MYA, millions of years ago; P&L, Péron and Lesueur (1816); Q&G, Quoy and Gaimard (1824); R1, Russell (1953); R2, Russell (1970); Rattlesnake, Macgillivray et al. (1852); W, western.

using a variety of superlative epithets, including “extremely abundant” and “vast swarms” to describe occurrences of hydromedusae, scyphomedusae, and salps (see the time line in figure 2; Herdman 1888, Mayer 1910, Galigher 1925, Russell 1953, 1970). Although some recent reports of mass occurrences suggest a variety of human-related causes, such as eutrophication, climate change, overharvesting of fish, and translocations (e.g., Mills 2001, Pauly et al. 2003, Purcell et al. 2007, Richardson et al. 2009 and the references within it), others have found no evidence of unnatural blooms—for example, of *Crambionella orsini* (e.g., Daryanabard and Dawson 2008)—or have shown decreases in the numbers of jellyfish and salps (Mills 2001, Lavaniegos and Ohman 2003, Brodeur et al. 2008). It seems possible, therefore, that the perceived increase in the number of jellyfish blooms may be a case of shifting baselines (e.g., Jackson et al. 2001), such that the public perception is shaped in the absence of a historical baseline and through a lack of continuity in the collective memory.

Therefore, because the paleontological and historical records show mass occurrences of gelatinous zooplankton in the scientific literature, we sought to determine the origins of the modern public perception that the magnitude and frequency of gelatinous zooplankton have increased and to determine to what degree those perceptions are supported by the available data.

A paradigm based on perception?

A major impediment to detecting trends in jellyfish populations is the lack of a defined baseline, due to a scarcity of long-term data on gelatinous zooplankton blooms, resulting in a continuously sliding frame of reference, which refers only to the observer’s immediate past and ignores reports of recurrent blooms in the more-distant past. This perceptual bias is most clearly reflected in media reports that localized outbreaks of gelatinous zooplankton were unknown for decades, despite an apparent long history of reports from that region (e.g., recent fish kills in the British Isles by *Pelagia noctiluca* outbreaks). Examples of mass jellyfish strandings exist in the older scientific literature; for example, Galigher (1925) casually mentions the “hordes of jellyfish which appear annually” (p. 94) along the shores of Monterey Bay, California, as though it were common knowledge.

Gelatinous zooplankton blooms are episodic and seasonal and exhibit high interannual variability, and witnessing a bloom can be a chance event (see Mills 2001). Recently, however, observational efforts in marine ecosystems—formal scientific research, as well as casual public observation—are increasing exponentially, which provides increasing opportunities to observe and report gelatinous zooplankton blooms that might not have been noticed with fewer observers or lower levels of sampling effort. Online reports of jellyfish blooms, even from personal blogs with limited credibility, get an immediate global audience equivalent to that of a reputable news or science report (box S1). Moreover, as our knowledge of the diversity of gelatinous species

grows, and as we start to study species for the first time, the absence of prior data on the species may be misinterpreted as a complete absence of that species over time. For instance, claims of the occurrence of an invasive ctenophore, *Mnemiopsis leidyi*, in Baltic Sea waters were ultimately attributed to the misidentification of a native species and to a lack of prior observation (Gorokhova et al. 2009 and the references within it), whereas the same nonnative species of ctenophore was first misidentified as the related species *Bolinopsis infundibulum* in the Black Sea (see Vinogradov et al. 1989). The rare black jellyfish, *Chrysaora achlyos*, was also known for many years (Martin and Kuck 1991) before it was rediscovered and described (Martin et al. 1997).

There is an understandable bias of both popular and scientific literature toward reporting notable events (e.g., jellyfish blooms), whereas years with less-notable events (e.g., low-levels of gelatinous zooplankton) make for poor news and unremarkable science. This reporting bias contributes to a perception of increased frequency of jellyfish and salp blooms. The public and the media are alert to jellyfish and salp blooms because some gelatinous taxa are particularly conspicuous organisms. Some jellyfish species also painfully sting or, in rare cases, kill humans, which raises the general apprehension toward and awareness of these animals, and deaths resulting from one or a few jellyfish can give a false impression of the presence of a bloom event. The presence of dense gelatinous zooplankton aggregations, however, is not necessarily caused by an actual increase in numbers in a particular region, because many “nuisance” jellyfish behaviorally maintain aggregations, and these abundance spikes may be localized and not representative of the entire region in question (Graham et al. 2001, Dawson and Hamner 2009). Moreover, in some taxa, aggregations are also a natural outcome of the production of a cohort of young medusae or ctenophores, which are kept or brought together by wind-driven and hydrodynamic processes (Graham et al. 2001, Costello et al. 2006, Condon and Steinberg 2008). Therefore, although media and scientific reports of massive numbers of jellyfish may be newsworthy, they should not be misinterpreted as an indication that gelatinous zooplankton abundance has deviated from their typical ranges.

In a number of recent review articles, potential drivers have been discussed that might lead to increases of gelatinous zooplankton (e.g., Mills 2001, Purcell et al. 2007, Richardson et al. 2009). Richardson and colleagues (2009) concluded that the rise in the numbers of jellyfish and salps is both a symptom and a necessary and unavoidable outcome of the cumulative human impacts that have caused a deterioration of the ocean ecosystem. A closer examination of these articles, however, reveals that the data necessary to test such statements are unavailable, which is even acknowledged in the articles. Indeed, most statements about an increased number of jellyfish blooms are based on local and sometimes regional studies, which are often focused on only a few well-studied (e.g., *Aurelia* spp.), high-visibility (e.g., *Nemopilema nomurai*), or invasive (e.g., *M. leidyi*)

species, and a global analysis has not yet been attempted. Given the dearth of knowledge about gelatinous zooplankton in major ocean basins, do these studies truly represent the entire range of fluctuations exhibited globally by modern populations? Moreover, some of the regions that provide the strongest evidence that jellyfishes were rising in number (e.g., Bering Sea; Brodeur et al. 1999, 2008) exhibited subsequent declines, leading to the conclusion that the apparent increasing trends were probably part of low-frequency oscillations driven by natural climatic cycles that may cause large-scale regime shifts in the ocean (box S1, Purcell et al. 2007, Brodeur et al. 2008).

Although authors of correlation analyses are often careful to present their conclusions with suitable caveats, these become mere footnotes when the conclusions are translated into bold headlines by the media and by reviews in the scientific literature. Such reports have, in turn, generated a greater demand for scientific research on the subject, reflected in the recent growth of review articles in the field (figure 3, box S1). This increased interest allows the publication of these results in higher-profile journals, which, by their stature, propagate these statements and engage a wider community, whereas the empirical foundation on which the conclusions rest has eroded (see Brodeur et al. 1999, 2008). Rising awareness of changes in gelatinous zooplankton in the ocean eventually leads to an expansion of the research community conducting and publishing research on jellyfish and salp abundance. Beyond the small base of a few dozen scientists conducting traditional research in marine laboratories, research universities, and museums, gelatinous zooplankton now draws attention from a growing interdisciplinary community that addresses population increases and their causes and broader consequences for society (Purcell et al. 2007).

At the same time that scientists are grappling with questions about changes in gelatinous zooplankton population dynamics, media reports about the impacts of jellyfish on human activities are on the rise. To compare the relative scientific effort and public awareness, we performed a media search on the Web of Science, using the search terms *jellyfish*, *ctenophore*, and *salp*. Our search results showed that scientific publications about gelatinous zooplankton have approximately doubled each decade since 1941 (figure 3a). To estimate public perception, we used the same search terms in a search with Google News. The frequency of media reports on gelatinous zooplankton from coastal ecosystems is remarkably high, and there is a consistent message throughout many of the major international media outlets (box S1). News reports on gelatinous zooplankton have also increased in number dramatically—by over 500%—in the past two decades (figure 3b), and the headlines are often alarmist (box S1). In contrast, scientific publications on jellyfish outbreaks, although they increase in a manner proportional to that of media reports, are outnumbered by public media reports by a factor of ten. This could be because scientific reports lag behind media reports in general, yet the trend holds when the above numbers of jellyfish reports are

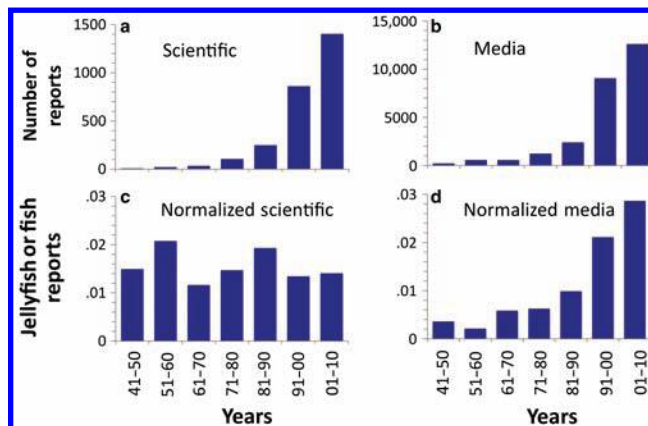


Figure 3. Scientific and media reports about gelatinous zooplankton from 1941 to 2010. (a) Scientific publications reported in the Web of Science. (b) Media reports from Google News. (c) Scientific publications on jellyfish and salps, normalized to the number of fish publications and are presented as a ratio. (d) Media reports on jellyfish and salps, normalized to the number of fish reports. The data were normalized by dividing the number of jellyfish reports by the number of fish reports for each decade. The searches were performed in May 2010; the search terms were jellyfish, ctenophore, salp, or fish.

standardized against a different topic, *fish*. Fish-related publications also grew over time, but the relevant growth rates of both scientific publications and media reports are comparable. This normalization shows that scientific publications about jellyfish and salps have not changed appreciably over time, whereas media reports have increased in number and are potentially driving public perception (figures 3c, 3d).

What do the data allow us to say about gelatinous zooplankton blooms?

Among the community of gelatinous zooplankton researchers, there is a lack of consensus on when, where, and whether the numbers of the gelatinous zooplankton have increased from their historical levels. This lack of consensus derives from the shortage of long-term data sets (defined as longer than 20 years) on jellyfish and salp abundance and biomass, and the fact that the available long-term data suggest a nuanced relationship between variability in gelatinous zooplankton and short-term changes in environmental parameters (e.g., seasonal hypoxia, interannual climate variability; Lavaniegos and Ohman 2003, Atkinson et al. 2004, Costello et al. 2006, Brodeur et al. 2008, Kogovšek et al. 2010). Long-term data do suggest that some gelatinous zooplankton oscillate around some ecosystem-specific baseline (Goy et al. 1989 for medusae; Lavaniegos and Ohman 2003, Atkinson et al. 2004 for salps), and that external factors such as climatic cycles (e.g., the North Atlantic Oscillation, El Niño; Purcell et al. 2007, Brodeur et al. 2008, Kogovšek et al. 2010) and the effects of overharvesting (Pauly et al. 2003, Lynam

et al. 2006) are likely to drive deviations from these natural cycles. Ecosystems can respond to external environmental parameters and stressors with baseline shifts (Jackson et al. 2001). There is also growing evidence to suggest that climate alters the phenology of jellyfish, causing temporal shifts in bloom formation and trophic mismatches in the food web (Edwards and Richardson 2004, Costello et al. 2006, Condon and Steinberg 2008). Therefore, without knowledge of historical ecosystem baselines, it is very difficult to determine whether the number of gelatinous zooplankton blooms have increased (e.g., in the northern Adriatic Sea; Kogovšek et al. 2010) or whether they are undergoing a longer-term (e.g., decadal) fluctuation driven by climate or other cycles (Purcell et al. 2007, Brodeur et al. 2008).

Another challenge is the difficulty in quantifying gelatinous zooplankton population biomass even on short time scales. Jellyfish and salp blooms are generally short lived and patchy. Furthermore, traditional net sampling is often ineffective for fragile taxa, especially ctenophores, because they can be damaged or destroyed unless special precautions are taken (Hamner et al. 1975). Alternative methods, including the use of towed optical instruments, remotely operated vehicles, acoustics, and blue-water diving have proven valuable for studying these fragile organisms and will continue to be critical in the characterization of the occurrence of gelatinous zooplankton in the future (see Hamner et al. 1975, Madin et al. 2006, Ducklow et al. 2009 and the references within it). But collectively, scientists not specialized in gelatinous species have not even attempted to quantify jellyfish or salp populations in most global waters, particularly the open-ocean gyres. Therefore, the fundamental aspects of the ecology and life cycle of most gelatinous species remain unstudied and unknown. The public perception that jellyfish and salp outbreaks are increasing in number and the deficiency in scientific understanding underscore the importance of synthesizing the existing data on gelatinous zooplankton populations. Rigorous analyses are required in order to establish causal relationships between true blooms and environmental variables. In particular, understanding climate and anthropogenic effects on gelatinous zooplankton abundance represents a significant challenge for future research.

Gelatinous zooplankton in the future sea: Why should we care?

Understanding how gelatinous zooplankton populations will behave (i.e., decrease, increase, or stay the same) or how they will be perceived in the future is imperative because many gelatinous species influence ecosystem processes, human activities, and economies. Although jellyfish blooms are often perceived as negative events (box S1), changes in jellyfish and salp abundance (both increases and decreases) can generate positive and negative outcomes, depending on the species. For example, increases in populations sizes of venomous species in tourist regions could be detrimental to tourism-dependent industries, yet prior to synthetic

production, harvesting of the hydromedusa (*Aequorea* spp.) for the biomedically important green fluorescent protein and photoproteins relied on abundant stocks of this species, which have decreased locally (see Mills 2001). Similarly, increased jellyfish biomass could be detrimental to some fish stocks but could benefit juvenile stages of some commercially important fish (e.g., Lynam and Brierley 2007), could sustain healthy sea turtle and other fish populations (e.g., pink salmon), and could also stimulate revenue for medusa-based fisheries as a replacement ecosystem service. Some medusa fisheries are now overharvested in spite of heavy regulation (Dong et al. 2010), or the medusa have been replaced by other jellyfish species, which also affects export and trade, and can strain international relationships (e.g., seasonal dispersal of the giant jellyfish [*N. nomurai*] from Chinese waters into Japanese fishing grounds; Uye 2008 and the references within it).

The effects of gelatinous zooplankton on ecosystems, biogeochemical cycles, and human activities occur over a wide range of disparate time scales. For example, coastal fisheries operating on monthly scales are driven by seasonal productivity and energy-transfer efficiency within the food web (Pauly et al. 1998); however, many of the potential alterations to food webs caused by gelatinous zooplankton occur over much shorter time scales (figure 4). These processes are equally important to understand, because in the short term, jellyfish and salps can shunt energy away from higher trophic levels, thereby limiting fisheries production (Condon et al. 2011). Furthermore, the mismatch in time scales can also influence socioeconomics, management, and policy development for the ecosystems affected by gelatinous zooplankton. Industrial and societal prioritization and decisionmaking typically occur over annual to decadal periods, yet many of the anthropogenic and problematic effects that drive these political (e.g., reduced tourism, loss of fisheries) and research (e.g., jelly-mediated carbon flux, food-web processes) priorities are not considered sufficiently important or are overlooked because they occur over much shorter time scales (days to weeks) than sampling efforts or public perception (figure 4).

Even if the magnitude of gelatinous zooplankton blooms does not change over time, their effects on the environment and society may still be felt. Many ecosystems are exhibiting phase shifts created by environmental, climate, and anthropogenic stressors (e.g., see Ducklow et al. 2009), and these shifts could result in gelatinous zooplanktivores' having relatively greater influence on ecosystem functioning as they exploit emerging resources in the food web. For example, in systems such as the oligotrophic Sargasso Sea, where the numbers of large autotrophs have declined but those of picoautotrophs have increased (see Condon et al. 2011), filter-feeding pelagic tunicates that specialize on small cells (Acuña 2001, Sutherland et al. 2010) may be able to filter and consume more primary producers without necessarily increasing in numbers. Without identifying all aspects of how gelatinous zooplankton blooms influence society, food

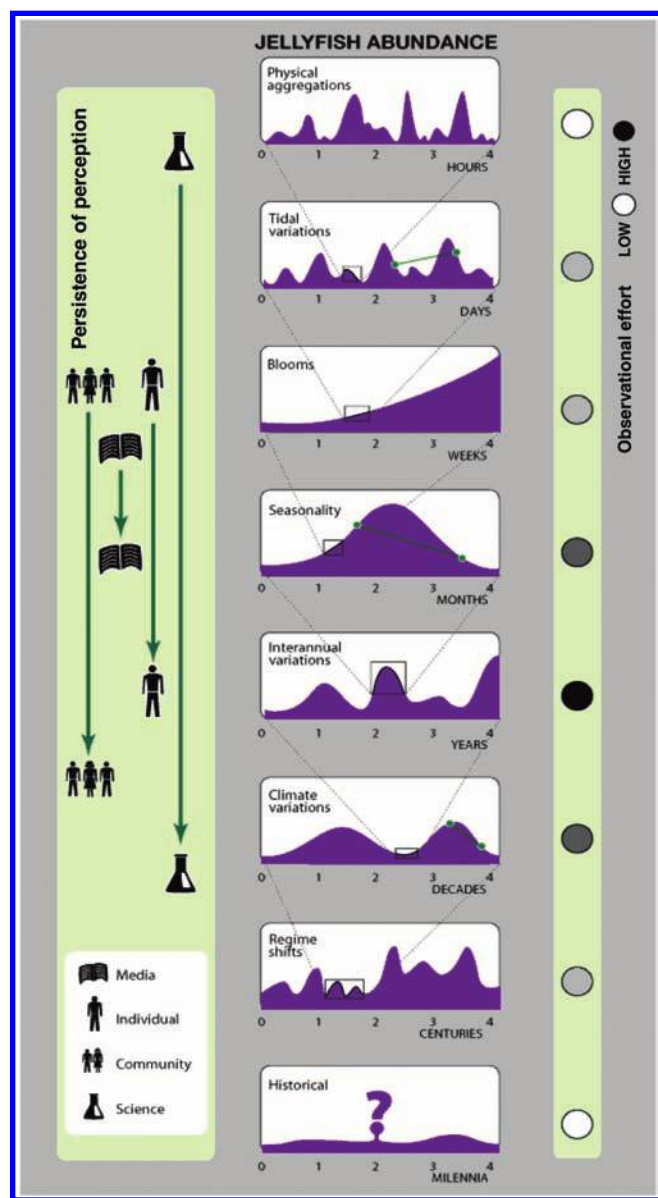


Figure 4. Heuristic illustration of the scales of variability in jellyfish abundance related to the scales of perception by humans. Gelatinous zooplankton populations exhibit large variations across all time scales from thousands of years to less than hours. How humans perceive the variations depends largely on their scale of interactions. Individuals largely perceive changes in jellyfish abundance over very short time scales, which is reflected mainly by media reports. Yet these scales of perception include only a portion of the variability that exists over much longer time scales, which leads to the potential for mismatches among public perception, scientific reporting, and fact.

webs, or biogeochemical cycles across all appropriate temporal scales, it is difficult to effectively manage ecosystems and fisheries and to apply necessary policy changes in regions affected by gelatinous zooplankton.

Finally, there are the many unknown factors or unexplored consequences concerning gelatinous zooplankton that have implications for human activities and marine systems. We know that jellyfishes are important keystone predators in some ecosystems (Condon and Steinberg 2008, Pauly et al. 2009), but we know little about their roles in pelagic and benthic food webs, the fate of gelatinous zooplankton biomass, and how these factors feed into large-scale biogeochemical processes, such as oceanic carbon sequestration and ocean acidification (Ducklow et al. 2009 and the references within it). Furthermore, it is likely that gelatinous zooplankton can increase biodiversity (e.g., the jelly-carbon shunt stimulates the increased diversity of microbial and planktonic communities; Condon et al. 2011) or cause localized near extinctions (e.g., high predation on copepods; Condon and Steinberg 2008), yet the underlying mechanisms are poorly understood. These combined factors could have important consequences for human activities and ecosystem functioning, depending on the timing, magnitude, and extent of gelatinous zooplankton.

A synthetic approach to redefining the paradigm

A clear need exists to assess historical, current, and future trends in medusa, ctenophore, and salp abundance across the world's oceans, as well as their roles in ecosystems, and the societal and ecosystemic consequences of their proliferation. Consequently, we are creating a global database of gelatinous zooplankton records (the Jellyfish Database Initiative [JEDI]), compiled from as many records as possible, contributed by ourselves; by researchers worldwide; and from online databases of zooplankton records such as the Ocean Biogeographic Information System (www.iobis.org; see Grassle 2000), scientific literature, and historical records (e.g., nineteenth- and early twentieth-century expedition reports). The relevant metadata vary widely in scope, extent, and type, ranging from a single specimen held in a museum collection to continuous, quantitative records of abundance from long-term studies from many regions around the world (figure 5). The database also reveals where records of jellyfish and salps are scarce or absent in terms of chronological and geographical coverage (figure 5).

In view of the inconsistent data, we must decide the best strategy for testing the paradigm that ocean ecosystems have changed or will change to be dominated by gelatinous zooplankton because of a variety of human perturbations to the sea. Our initial synthesis suggests that analyses can include data for over two-thirds of the world's ocean surface, with multiple regional examples of long-term, continuous records (figure 5). Although it is tempting to focus solely on those high-resolution data, we are using a strategy that maximizes the availability of all data, which would allow global trends in gelatinous zooplankton to be analyzed as robustly as possible. First, we are examining patterns in abundance in data sets for which continuous observations are available. In a few instances, these data have been collected for more than 50 years (figure 5), which allows testing of hypotheses

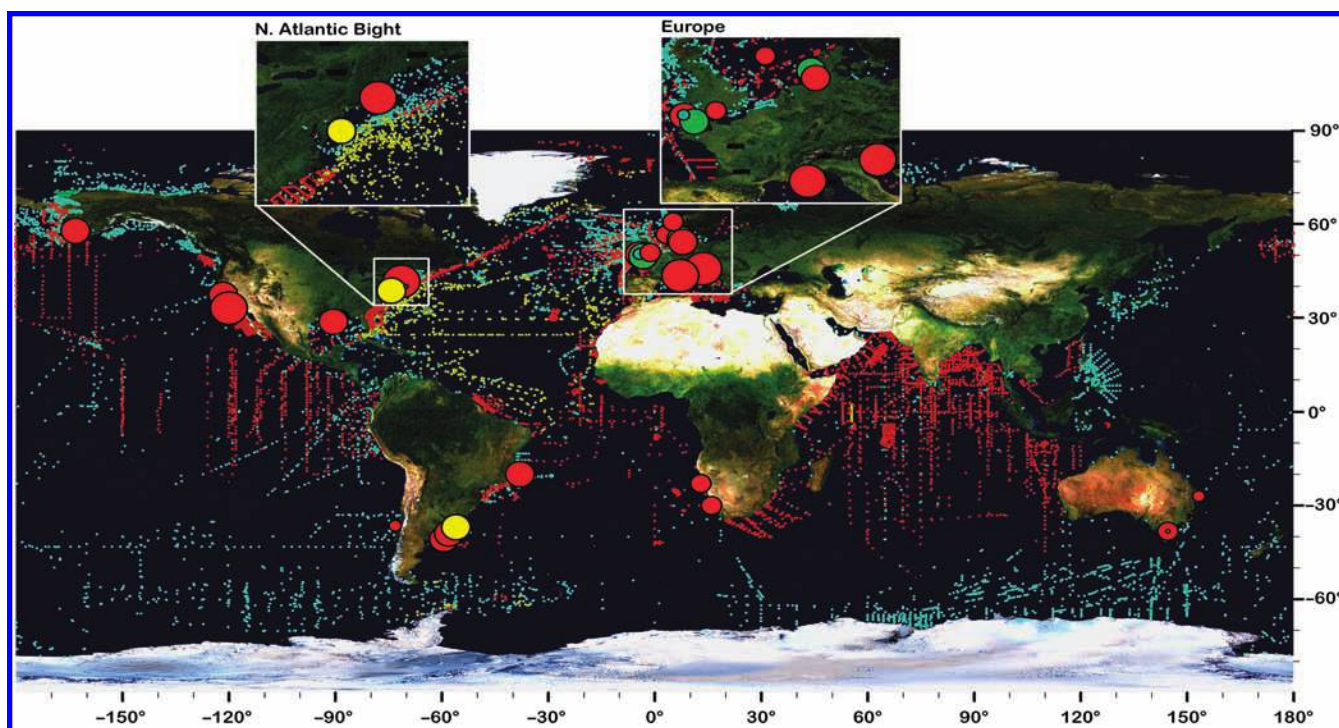


Figure 5. Distribution of the Jellyfish Database Initiative (JEDI) metadata sets. Gelatinous zooplankton groups to be represented in JEDI include cnidarian medusae, ctenophores, salps, doliolids, pyrosomes, and larvaceans, and the types of metadata represented include quantitative (green), categorical (yellow), presence–absence (red), and presence-only (light blue) data. Point size illustrates the relative duration of each data set or of the individual records, with longer time series represented by larger points: The time-series lengths range from 1 to 200 years. Contributors to JEDI are acknowledged under the umbrella of the JEDI Development Team. The current list of contributors may be viewed at www.jellywatch.org/blooms.

about forcing factors, such as climatic patterns and fishing intensity, operating over decadal time scales. Second, because many sets of high-resolution gelatinous zooplankton data correspond to areas that also contain categorical observations of (i.e., data organized into defined data ranges as defined by the specific study), the presence or absence of, or proxies for gelatinous zooplankton (e.g., salp fecal pellets in sediment traps indicate the presence of salps), we are assessing the congruence among sets of differing data types to determine whether it is appropriate to extrapolate trends identified in high-resolution data to the chronological and geographic range of all available data.

Clearly, this challenging task will require a concerted effort from the research community and collaboration among the scientific community, policymakers, economists, and the media. The JEDI, for instance, has been designated to provide baseline data and a data-set repository that will extend far into the future, such that scientists will be able to revisit questions about jellyfish and salp abundance, which will provide a platform to advance our understanding and that will allow us to develop paradigms about blooms of gelatinous zooplankton. Furthermore, this new data-rich source of information will facilitate the bridging of gaps between science and policy, which is both timely and highly desirable in our opinion. We hope that this effort will generate similar

enthusiasm for jellyfish research in the wider scientific community and in the public and will provide answers to the question, “Are the numbers of gelatinous zooplankton rising in the world’s oceans?”

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The authors are members of the Jellyfish Working Group (JWG), convened by the National Center for Ecological Analysis and Synthesis (NCEAS). Our common interest is to examine the supposition that the number of jellyfish blooms has increased globally. The JWG is an open program, allowing anyone wishing to participate the opportunity to do so (www.jellywatch.org/blooms). The JWG aims to serve the wider scientific community through producing the cooperative Jellyfish Database Initiative; establishing links; and mediating cooperation among science, outreach, and policy; providing training and infrastructure for present and future research endeavors; and making recommendations for future activities. We thank Lucas Brotz and three anonymous reviewers for their contributions to the manuscript. Funding for NCEAS and the JWG comes from National Science Foundation Grant no. DEB-94-21535, from the University of California at Santa Barbara, and from the State of California. MND was supported in part by National Science Foundation Grant no. DEB-07-17071.

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