Jellyfish and Ctenophore Blooms Coincide with Human Proliferations and Environmental Perturbations

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Abstract

Human populations have been concentrated along and exploiting the coastal zones for millennia. Of regions with the highest human impacts on the oceans (Halpern et al. 2008), 6 of the top 10 have recently experienced blooms or problems with jellies. I review the time lines of human population growth and their effects on the coastal environment. I explore evidence suggesting that human activities—specifically, seafood harvest, eutrophication, hard substrate additions, transport of nonindigenous species, aquaculture, and climate change—may benefit jelly populations. Direct evidence is lacking for most of these factors; however, numerous correlations show abundant jellies in areas with warm temperatures and low forage fish populations. Jelly populations fluctuate in ∼10- and ∼20-year cycles in concert with solar and climate cycles. Global warming will provide a rising baseline against which climate cycles will cause fluctuations in jelly populations. The probable acceleration of anthropogenic effects may lead to further problems with jellies.

INTRODUCTION

Jellyfish: swimming umbrella- or bell-shaped medusae that catch planktonic prey with stinging nematocysts; the sessile polyp stage asexually produces medusae and polyps

Jelly: used in this article to refer to all pelagic cnidarians and ctenophores

The evidence that humans have changed the Earth's terrestrial and aquatic biosphere is overwhelming. That humans also have changed the atmosphere and climate has been accepted among scientists for more than a decade (Stott et al. 2010). Obvious human modification of the Earth may have begun with extermination of megafauna (e.g., mammoths) early in the Holocene epoch ~10,000 years ago, which led to early agriculture, the establishment of settlements, and increasing deforestation in the late Holocene. The time frames of human environmental modifications differ greatly among the continents: human populations numbered in the tens of millions in East Asia, India, Europe, and Africa more than 2,000 years ago, whereas the population in North America did not reach 1 million until European settlement after 1500 (Durand 1977). Human effects accelerated with the Industrial Age after ~1750 (Kutzbach et al. 2010). Since ~1950 and especially after ~1970, increasing regions of the Earth's coastal waters have been progressively degraded by humans.

Humans began to notice jellyfish as potential problems only relatively recently during the post-1950 period. Jellyfish directly interfere with several human enterprises—specifically, tourism by stinging swimmers (Fenner et al. 2010), fishing by clogging nets (Nagata et al. 2009, Dong et al. 2010), aquaculture by killing fish in net pens (Doyle et al. 2008, Delannoy et al. 2011), and power production and desalination by clogging water-intake screens (Daryanabard & Dawson 2008). It seems clear that human problems with jellyfish have increased recently (Purcell et al. 2007) (**Figure 1**).

Whether jelly populations per se have increased is less clear. Jelly population sizes typically show dramatic interannual fluctuations; however, determination of true fluctuations or increases and the causes have been hampered by the short duration (<10 years) of most available data
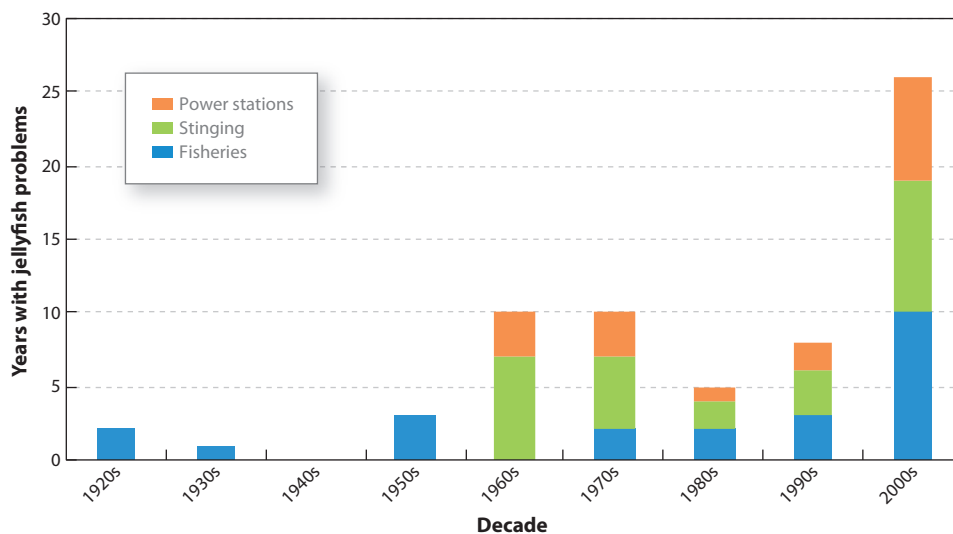

Figure 1

Number of years in each decade with published reports of human problems with jellyfish in Japan. Fisheries and aquaculture problems are combined. Problems can occur every year in three categories (power stations, stinging, and fisheries); therefore, the highest possible score is 30, except in the 2000s (27). Adapted from Purcell et al. (2007), updated to include 2000–2008.

sets. Henson et al. (2010) concluded that time series of ∼40 years are necessary to distinguish trends due to global warming from natural interannual and decadal variability. Therefore, few jelly data sets are sufficiently long to evaluate if a population has increased over time. A recent analysis indicated that jellyfish populations showed increasing trends after 1950 in >70% of the 45 large marine ecosystems (Brotz et al. 2012). The objective of the National Center for Ecological Analysis and Synthesis (NCEAS) Jellyfish Working Group is analysis of data from around the world to test whether jellyfish populations have increased globally (Condon et al. 2012).

Reviews have proliferated recently speculating that jellies have benefited from human-caused changes, including climate change, eutrophication, overfishing, coastal construction, and species introductions (Purcell et al. 1999, 2001, 2007; Arai 2001; Mills 2001; Pauly & Palomares 2001; Purcell 2005; Graham & Bayha 2007; Richardson et al. 2009; Dong et al. 2010; Uye 2010; C.M. Duarte, K.A. Pitt, C.H. Lucas, J.E. Purcell, S.-I. Uye, et al., manuscript submitted). Most of these factors are occurring simultaneously around the world. In addition to the paucity of long-term data on jelly abundances, the interactions of multiple concurrent factors confound determination of their relative importance to jellies. Because these factors were reviewed recently, I focus on research published after Purcell et al. (2007). In the present review, I explore recent evidence that regions recently experiencing jelly blooms are those that developed high human populations early and have the greatest environmental degradation.

BRIEF HISTORIES OF HUMAN AND JELLYFISH POPULATIONS

Human populations left relatively good records of their locations and abundance, first by bones, tools, and art, and later in writings. The estimated global human population numbered ∼256 million in 14 AD, with most in East Asia (China plus Japan, 75 million), India (70 million), Europe (37 million), Southwest Asia (34 million), and Africa (23 million) (Durand 1977). Although populations in those regions continued to grow, human populations in the Americas were low until European colonization. By 1500, only 1 million humans were estimated to live in North America; however, the other regions had grown substantially. By 1750, populations had increased greatly in East Asia (233 million), India (100 million), Europe (102 million), and Africa (100 million), but the North American population was only 2 million, with half in the northeastern United States (Durand 1977, Tanton 1994). After 1750, human populations increased rapidly in all regions (**Figure 2**). The most dramatic increase between 1750 and 2010 was in North America (176-fold), as compared with approximately 6- to 10-fold in the other regions. Populations have been concentrated near the coasts. Coastal areas have been densely populated for 2,000 years in East Asia, India, Europe, and parts of Africa. By contrast, a few parts of the Americas, such as the northeastern United States, have had high populations for only about 100 years.

Large strandings of jellyfish occurred in the Cambrian period at least 500 Mya (Young & Hagadorn 2010), before vertebrates evolved. Unfortunately, jellyfish fossils are too scarce to deduce their population sizes. Qualitative scientific records of their populations and proliferations date from ∼200 years ago in the Mediterranean Sea (Goy et al. 1989, Kogovšek et al. 2010), but such long records are extremely rare. Semiquantitative multiyear records began only recently (∼1960) and also are rare (Cargo & King 1990, Molinero et al. 2005, Brodeur et al. 2008a, Licandro et al. 2010). In the Mediterranean Sea, Chesapeake Bay, and Bering Sea, the long-term records show that jellyfish populations fluctuate in conjunction with climatic factors (Goy et al. 1989, Cargo & King 1990, Brodeur et al. 2008a).

Eutrophication: addition of surplus nutrients and organic matter that often increases phytoplankton biomass and decreases water transparency and DO concentrations

Bloom: an unusually high abundance compared with other years; also referred to as an outbreak
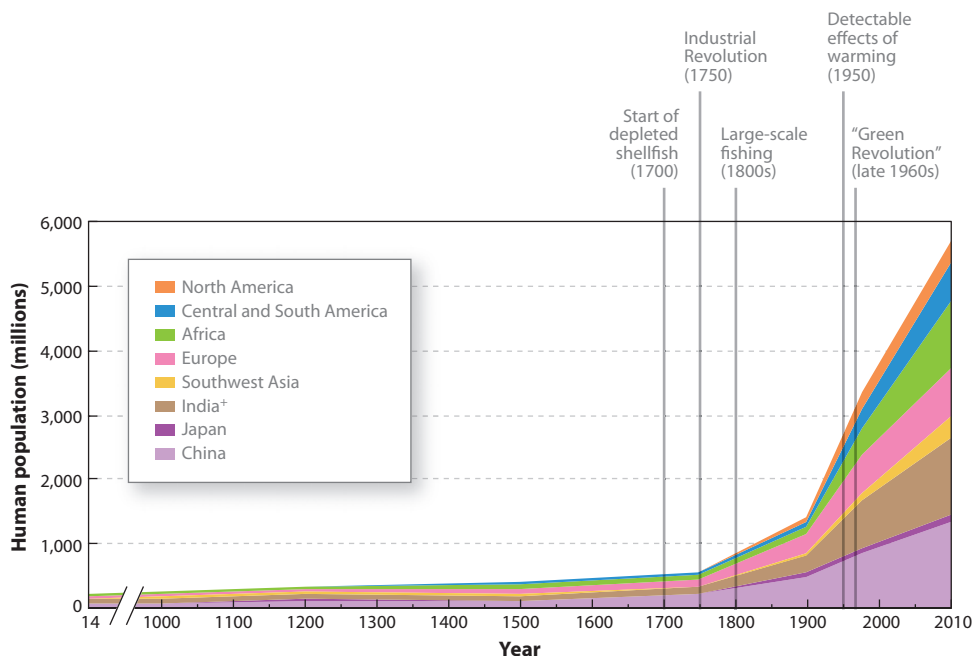
Figure 2

Human population growth from 14 AD. Although appreciable human degradation of the environment had already occurred by 1400 in heavily populated areas, damage accelerated with mechanical harvesting of shellfish and fish as well as the development of engines that burned coal and powered factories and ships, which led to global warming. Although organic fertilizers had been used in agriculture for millennia, the global availability of chemically synthesized inorganic fertilizers lead to the "Green Revolution" and coastal eutrophication. Data from Durand (1977) and the World Census in 2010 (**http://en.wikipedia.org/wiki/ World_population**).

HUMAN ACTIVITIES AND THEIR POTENTIAL EFFECTS ON JELLYFISH

Seafood Harvesting: Removal of Competitors and Predators

Reductions of shellfish and finfish populations over human history have altered coastal plankton food webs. Humans may have unintentionally benefited jelly populations by increasing the zoo-plankton foods available to them and by removing their predators. The greatest effects historically were where humans proliferated earliest. Harvesting accelerated after engines were developed and populations increased further.

Shellfish. Exploitation of aquatic organisms, including fish, shellfish, and algae, may be the earliest disturbance by human populations on costal ecosystems (Jackson et al. 2001). Mounds of bivalve shells (middens) found worldwide reveal prehistoric human utilization of marine resources at least 125,000 years ago (Erlandson & Fitzpatrick 2006). Resource use expanded and intensified after development of mechanical harvesting and boat transport. Oysters in Ireland were depleted by humans in Dublin by the early 1700s; by the early 1900s, few oysters remained around Ireland; and in the early 1920s, a disease mostly eliminated the remaining oysters (Went 1962). In Chesapeake Bay in the United States, oysters declined after peak harvests in 1800 owing to overharvest and

disease (Newell 1988). Ecosystem changes from such overharvest may be profound but generally unnoticed. Water-column filtration by oysters in Chesapeake Bay was 100 times greater in 1870 than in 1988 (Newell 1988). Oysters filter phytoplankton and sediments from the water and reduce regeneration of nutrients, thereby ameliorating the effects of eutrophication (Newell et al. 2005). Thus, extensive bivalve harvests may have amplified effects of concurrent eutrophication of coastal waters. Uneaten phytoplankton could then enhance zooplankton populations, which then could benefit predators of zooplankton, such as jellies.

Fish. Declining finfish fisheries have garnered more recent attention than have shellfish fisheries (Pauly & Palomares 2001), perhaps because many commercially viable shellfish fisheries were depleted earlier. Progression to offshore harvesting of fish required greater sophistication of early humans. Boats were used for long-distance transport at least 50,000 years ago (Erlandson & Fitzpatrick 2006). The range and intensity of harvest increased dramatically with technological advances, such as trawls and engine-powered ships in the eighteenth and nineteenth centuries, when severely depleted fish stocks were commonly reported (Jackson et al. 2001). Jackson et al. (2001) state, "Evidence from retrospective records strongly suggests that major structural and functional changes due to overfishing occurred worldwide in coastal marine ecosystems over many centuries." Historical records show that fishing pressure on ecosystems globally was fairly constant from 1950 to 1970, but increased markedly thereafter (Swartz et al. 2010) (**Figure 3**). In most ecosystems, the largest, predatory fish were depleted first, followed by the forage fish— a phenomenon called fishing down marine food webs (Pauly & Palomares 2001, Pauly et al. 2009). Fishing down is observed in the catches as different target species, decreased fish sizes, and decreased trophic levels.

Jellyfish and the overharvest of seafood. The potential link between fishing down and jelly increases is clear. Logically, reduction of piscivorous fish favors zooplanktivorous fish; however, these small forage fishes are heavily fished for human food and to produce oil and meal for aquaculture feeds (Metian & Tacon 2009). Catches of forage fish increased 8.8-fold between 1950 and 2006 (**http://www.seaaroundus.org**). Forage fish were key functional groups in the Northern Adriatic Sea food webs (Libralato et al. 2010), but they constitute the highest catches in the Mediterranean Sea (Palomera et al. 2007), which suggests serious ecosystem consequences for their overharvest. Similarly, Brodeur et al. (2011) examined interannual variability of energy transfer by jellyfish and forage fish in the Northern California Current. Jellyfish had a major impact on lower trophic levels but transferred relatively little production to higher trophic levels compared with forage fish. Thus, predominance of jellyfish would decrease production of vertebrates important to humans.

When the populations of forage fish are reduced by fishing, zooplanktivorous jellies have flourished, presumably owing to reduced competition for food, as for *Mnemiopsis leidyi* ctenophores in the Black Sea (Daskalov et al. 2007). This potential link was suggested many years ago (Möller 1980), but competition has been tested directly only once to my knowledge (i.e., for larval herring; Purcell & Grover 1990). The diets of jelly and forage fish species are similar, with overlaps ranging from 0.2% to 73.4% (Purcell & Sturdevant 2001, Brodeur et al. 2008b) and from 84% to 89% for *M. leidyi* and Caspian anchovy (Darvishi et al. 2004). Competition requires that resources are limiting, which is difficult to demonstrate. Competition for food often has been inferred from inverse relationships among zooplankton, fish, and jellies (e.g., Daskalov et al. 2007).

The inverse biomasses of *M. leidyi* and fishes are striking in the southern Black Sea, where anchovy (potential competitor) catches in 1989 were 20% of those in 1988 and mackerel (potential predator) catches in 1991 were 20% of those in 1990; meanwhile, the ctenophore live biomass surged in 1990 (Mutlu 2009). Daskalov et al. (2007) identified two top-down-triggered regime

Forage fish: small zooplanktivorous fish, such as herrings, anchovies, and menhaden

Ctenophores: gelatinous zooplanktivores that differ from jellyfish by lacking an attached stage, being hermaphroditic, and not stinging
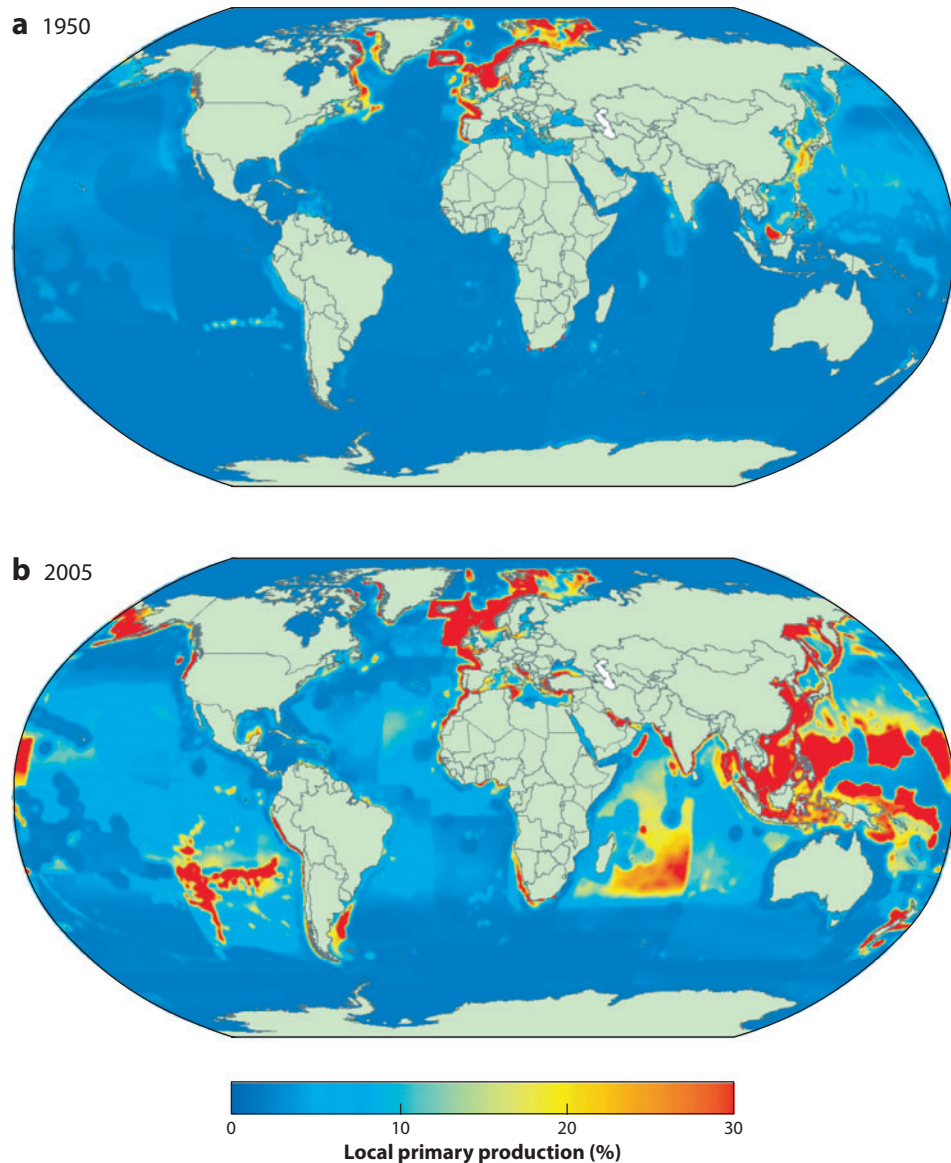
Figure 3

Primary production required to sustain global marine fisheries landings expressed as percentage of local primary production in (*a*) 1950 and (*b*) 2005. Adapted from Swartz et al. (2010).

shifts in the Black Sea between 1950 and 2000. The first, depletion of pelagic piscivorous fish in the early 1960s and 1970s, resulted in increasing zooplanktivorous fish in 1964–1977. Fishing effects were greatest in 1977–1988 and reduced the populations of the zooplanktivorous fish. After 1990, fishing efforts decreased owing to the shortage of fish, and these stocks started to recover. The authors conclude that observed increases in jellies—first of *Aurelia aurita* medusae in 1977–1980 and second of *M. leidyi* ctenophores in 1989–1994—were "triggered by intense fishing resulting in system-wide trophic cascades."

The fishing effort in the East China Sea increased in 1990–2002, causing a severe decline in the trophic level of fisheries from 3.5 in 1965 to 2.7 in 2000 (Jiang et al. 2008). Blooms of jellyfish increased over the past 10 years, and fisheries increasingly targeted fish in the family Stromateidae, which are well-known predators of jellies (Purcell & Arai 2001). An Ecopath model for 1997–2000 showed strong interactions between large jellyfish, stromateoids, and zooplanktivorous fish.

Removal of predators of jellyfish and ctenophores. In addition to competitors of jellies, their predators also have been depleted by fishing, either intentionally (as for mackerels) or accidentally (as for sea turtles that are caught in nets or on longlines). Leatherback sea turtles, which forage on jellies, have been severely reduced in the Pacific by many factors, including harvesting, fishing, and trash pollution (Spotila et al. 2000). Other predators of jellies include 124 species of fish, including commercial species, and 34 other animals (Purcell & Arai 2001, Arai 2005; see also Pauly et al. 2009).

Nutrient Additions

Humans have increased the nutrients in coastal waters by clearing forests, increasing the populations of large animals, fertilizing soil for agriculture, and changing the natural drainage. Humans have disposed of their wastes in waterways throughout history. Increased eutrophication has accompanied increases in human populations over time, with acceleration after the development of synthetic fertilizers.

Land clearing. The different timescales of human perturbations are evident in comparisons between regions developed in antiquity (the Northern Adriatic) and the first region in North America (the Chesapeake Bay; Stevenson et al. 1999). In the Northern Adriatic region, the primeval forest was cleared for grazing and agriculture approximately 3,000 years ago. Dams and water diversions led to a historical increase in sediment loading, which markedly increased with development of hydropower. The coastal areas were most intensively developed, and the percentage of the population near the coast increased from 60% in 1880–1931 to 80% in 1981 as the population doubled. The first permanent European settlement in North America was beside Chesapeake Bay (1608); however, large-scale land clearing occurred after the mid-1700s, leading to extensive sedimentation into the bay and its tributaries. Thus, extensive land clearing—which greatly increases erosion and reduces the soil's ability to hold nutrients—was ~1,800 years earlier in Europe than in northeast North America.

Eutrophication. Along with land clearing for agriculture came fertilization of the fields, which was with manure in the Northern Adriatic from Roman times until the importation of guano as fertilizer in 1840–1880 (Stevenson et al. 1999). In Chesapeake Bay, fertilizer use also increased in the 1800s. Agriculture progressed rapidly after the advent of tractors in the 1890s. Fertilizer use increased greatly following development of commercially produced synthetic fertilizer in the early 1900s. Since the Industrial Revolution, human activity has approximately doubled the amount of biologically available N globally (Howarth 2008) (**Figure 4**). There is great variation among regions, with increases up to 10- to 15-fold in some areas. Although agriculture is still the largest N source in many regions of the world, in the northeast United States, N inputs are ~20% atmospheric, 30% from nonpoint sources, 35% from wastewater, and 15% agricultural.

Although civilizations developed basic sewage treatment (settlement of solids) as early as 3500 BC, most people threw waste into the streets (Lofrano & Brown 2010). The sewer and wastewater systems of the Romans were abandoned after their empire fell in 476 AD. In Europe,
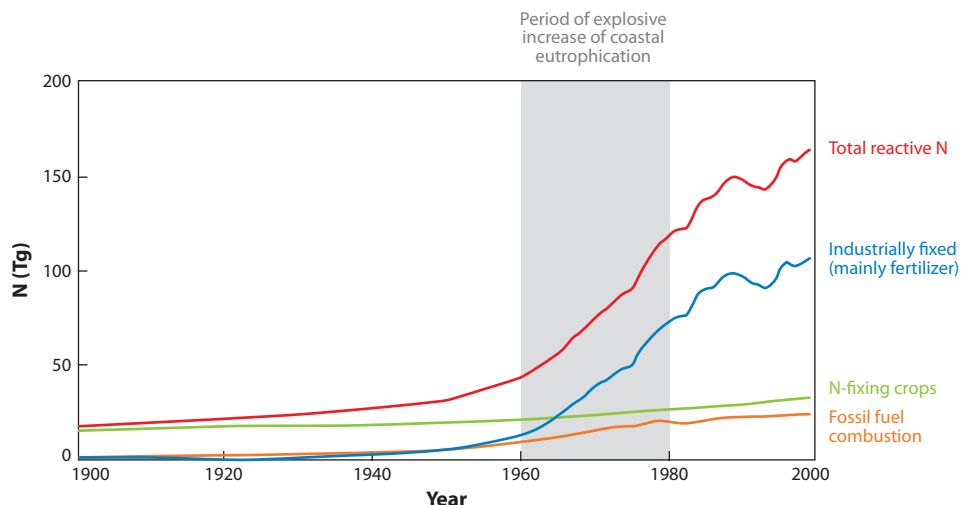
Figure 4

Global additions of anthropogenically fixed N and the period of explosive increase of coastal eutrophication. Adapted from Boesch (2002).

waste was emptied into the streets and wastewater was discharged without treatment for centuries; cesspits were in general use until 1880, and rivers were used as sewers. People in the early United States continued these European practices.

With larger populations came larger sanitation problems (Lofrano & Brown 2010). Most major cities in Europe had treatment facilities by World War I, but both world wars delayed progress and damaged existing systems. After the wars, wastewater treatment progressed in the United Kingdom, but not in the rest of Europe. In the United States, settlement of solids was the most common waste treatment until 1972, when secondary treatment was mandated. Most developed nations now have progressed to nutrient removal; however, some still lack good sanitation practices, such as Canada, where large cities dump some of their untreated sewage directly into the waterways (Halifax, St. John's, Saint John), only settle and skim off large debris (Montreal, Vancouver), or lack even primary sewage treatment (Victoria) (Sierra Leg. Def. Fund 2004).

In the twenty-first century, safe drinking water and sanitation are still unavailable to large populations in developing countries as well as to rural and poor populations in developed countries. Raw sewage disposal into estuaries in India has been the usual practice throughout history, and treatment of sewage from large cities before disposal is recent (Ramaiah et al. 2007). Most cities in developing countries like India have large numbers of channels that carry untreated wastewater from domestic, municipal, and industrial sources that is used by farmers for irrigation (Saha et al. 2010). Chen et al. (2002) summarized conditions of the Yangtze River Delta in China from ~1986 to 1997: "The appearance of black and odorous conditions in rivers in the urban areas has increased due to serious pollution by organic matter with consequent high oxygen demand."

Evidence of eutrophication. The Thames was polluted by the early 1300s, and the 1539 plagues in Europe were due to contaminated drinking water (Lofrano & Brown 2010). By 1550, the Venice Lagoon was heavily polluted and anoxic in summer. In Chesapeake Bay, increased nutrient concentrations were observed in sediment cores beginning in 1850–1900, and changes in the diatom communities were observed before 1900 (Stevenson et al. 1999). The exponential growth

of fertilizer use in 1960–1990 (**Figure 4**) caused the exponential increase in the incidence of coastal marine eutrophication globally (Vaquer-Sunyer & Duarte 2008). Eutrophication recently has been reduced in some regions, causing oligotrophication (Nixon 2009), but these systems have not returned to pre-eutrophication states (Duarte et al. 2009). Howarth (2008) concludes that excess fertilizer and manure application to agricultural soils is a main driver of coastal eutrophication.

Jellyfish and eutrophication. Eutrophication is one of the major global pollution problems (Howarth 2008). In addition to increased nutrients, eutrophication is associated with altered nutrient ratios and increased turbidity. Most simply, increased nutrients often lead to greater biomass at all trophic levels. More food for polyps and jellies increases growth, asexual reproduction, and sexual reproduction rates. Eutrophication also causes complex changes in the food web. Accumulating evidence suggests that high N:P ratios shift the phytoplankton community from a diatom- to a flagellate-based food web, which may favor jelly blooms (Purcell et al. 2007). Eutrophication is also connected with size reduction of the zooplankton community, which may be detrimental to fish (visual predators that prefer large zooplankton), thereby benefiting jellies (nonvisual predators that consume both small and large zooplankton). To my knowledge, only one study compares feeding by fish (jack mackerel) and jellyfish (*A. aurita*) in different levels of turbidity; feeding on anchovy larvae by the fish was significantly reduced in the most turbid water, whereas feeding by jellyfish was unaffected by turbidity (R. Ohata, R. Masuda & Y. Yamashita, manuscript submitted).

Decreased light penetration may alter the feeding environment to benefit nonvisual gelatinous predators over visually feeding fish. Light penetration in Norwegian fjords with extremely high abundances of the mesopelagic medusa *Periphylla periphylla* is lower than in fjords with two species of visual zooplanktivorous fish (Eiane et al. 1999, Sørnes et al. 2007, Asknes et al. 2009). The photosensitivity and behaviors of the jellyfish lead to their retention in the fjords (Sørnes et al. 2007). Norwegian coastal waters have darkened owing to freshening since 1935, especially where dissolved oxygen (DO) concentrations also declined (Asknes et al. 2009). The differences in darkening among fjords are due to their water sources. North Atlantic water with high transparency occurs in fjords with fish, but the Norwegian coastal water contains high concentrations of colored dissolved organic matter (DOM) that attenuates light and occurs in fjords with predominantly jellyfish. Eutrophication in the Baltic and North Seas may contribute to this problem because their waters join to form the Norwegian Coastal Current. Mass occurrences of *P. periphylla* developed in the 1970s, and the number of fjords with them appears to be increasing.

Jellies may contribute to eutrophication and be able to use it directly because they excrete and take up nutrients (ammonium and phosphate) and DOM (Pitt et al. 2009). Condon et al. (2010) concluded that excretion of nutrients by ctenophores and scyphomedusae combined supported <4% of daily primary production in Chesapeake Bay. Nutrient excretion by jellyfish with symbiotic dinoflagellates (zooxanthellae) is only approximately 7% that of azooxanthellate jellies because nutrient recycling occurs between the jellyfish and algae (Pitt et al. 2009). Few studies address excretion of DOM by jellies. In Chesapeake Bay, ctenophores excreted high percentages (25.2% and 18.3%) of their body C and N in mucus and contributed up to 18% and 28% per day to labile DOM in summer, but excretion of DOM by scyphomedusae was only 3% per day (Condon et al. 2010). Ctenophore and phytoplankton production of labile dissolved organic C (DOC) were comparable and could be utilized for bacterial production in this eutrophic estuary. Similarly, the epibenthic, zooxanthellate jellyfish, *Cassiopea*, released little DOC but large amounts of particulate organic C and particulate organic N in mucus that induced high bacterial growth (Wild et al. 2010).

The uptake of DOM by jellyfish or ctenophores seldom has been studied (Pitt et al. 2009). Labile DOM concentrations in marine environments are small, and probably are an insignificant source of C for azooxanthellate species. By contrast, zooxanthellae in medusae can assimilate dissolved

inorganic C (DIC) from the water column, and species like *Cassiopea* spp. can utilize nutrient pools that are unavailable to azooxanthellate species. *Cassiopea* sp. medusae actively extracted and took up inorganic nutrients from the sediment (Jantzen et al. 2010) and occurred in high abundances (31 medusae m^{-2}) in tropical habitats (Niggl & Wild 2010). In Bermuda, the sizes and densities of *Cassiopea* spp. medusae and the nutrient concentrations were greater where human densities were high than where they were low (Stoner et al. 2011). This study is, to my knowledge, the first direct test of eutrophication effects on jelly populations. These studies suggest that zooxanthellate medusae may flourish in habitats with high inputs of organic matter.

Jellyfish and hypoxia. Reduced DO in coastal environments is one serious consequence of eutrophication. The number of coastal sites reporting hypoxia globally increased dramatically beginning in the 1980s (Vaquer-Sunyer & Duarte 2008). Fish avoid or die in waters of ≤2–3 mg O$_2$ per liter, but many jellies are tolerant of ≤1 mg O$_2$ per liter (Purcell et al. 2007). Additional evidence confirms the tolerance of jellies to hypoxic conditions and defines limitations to their use of hypoxic habitats. The swimming bell contraction rate of *A. aurita* medusae was constant over the DO levels from 1.0 to 5.8 mg O$_2$ per liter; by contrast, gill ventilation rates and swimming speeds in Spanish mackerel decreased at ≤4 mg O$_2$ per liter, indicating stress (Shoji et al. 2005). Feeding rates on fish larvae increased at low DO for the medusae but decreased for the fish. In Hiroshima Bay, the greatest abundances of these medusae were where bottom-layer DO concentrations were the lowest (2–3 mg O$_2$ per liter), suggesting no adverse effects (Shoji et al. 2010). Settlement of *A. aurita* planulae was quickest and highest in the lowest DO concentration tested (0.2 mg O$_2$ per liter); however, the polyps survived <7 days. At 2 mg O$_2$ per liter, however, budding of new polyps was less than at 4.5 mg O$_2$ per liter, and no strobilation occurred (Ishii et al. 2008). In Tokyo Bay, one of the most eutrophic in Japan, most polyps were ≤2 m above the bottom where mussel biomass was lowest (Ishii & Katsukoshi 2010). This high tolerance of low DO concentrations allows recruitment in hypoxic bottom waters that cannot be tolerated by other species.

Large (but not small) *M. leidyi* ctenophores had lower growth and egg production in low DO concentrations (1.5 and 2.5 mg O$_2$ per liter) than in saturated DO, but *Chrysaora quinquecirrha* medusae growth was unaffected (Grove & Breitburg 2005). Clearance rates of *M. leidyi* on fish eggs and larvae were the same at low and high DO concentrations (1.5 and 7 mg O$_2$ per liter), and ctenophore densities were high in the bottom layer even in low DO (Kolesar et al. 2010).

Jellies may provide positive feedbacks to hypoxia. First, pelagic cnidarians and ctenophores feeding on zooplankton would reduce grazing on phytoplankton, which could increase the flux of ungrazed phytoplankton to the benthos, where it would decompose; anoxic sediments release phosphate and ammonium that fuel phytoplankton and further reinforce hypoxia. This was illustrated in a Danish fjord, where years with exceptionally severe hypoxia were those with blooms of *A. aurita* medusae (Møller & Riisgård 2007). The same scenario may occur in Chesapeake Bay, where predation was sufficient to reduce zooplankton in summers when ctenophores predominated, but not when medusae predominated (Purcell & Decker 2005).

A second positive feedback to hypoxia may be decomposition of gelatinous blooms, which has been investigated only recently. Decomposition of jelly blooms could cause large releases of inorganic and organic nutrients and lead to localized hypoxic or anoxic conditions (Pitt et al. 2009). DOC release rates by decaying medusae were >10 times those of living medusae. Decomposition of jellyfish stimulated bacterial and ammonium production in Northern Adriatic waters (Tinta et al. 2010). The effects of jelly decomposition on the benthos could be severe when large biomasses occur. Jelly-falls, masses of moribund gelatinous species, are reviewed by Lebrato et al.

DIC: dissolved inorganic C

Hypoxia: conditions of low DO concentrations (≤2 mg O$_2$ per liter) that are stressful to most marine life

Strobilation: asexual production of small medusae (ephyrae) from polyps

(2012). Because of their high biomass during blooms, decomposition of jellies may be important periodically to nutrient recycling.

Substrate Additions

From the time humans began using boats at least 50,000 years ago, they probably also built harbors. Harbors provide an ideal habitat for the sessile stages of scyphozoans (polyps) and hydromedusae (hydroids), which are found attached to hard surfaces in harbors today (C.M. Duarte, K.A. Pitt, C.H. Lucas, J.E. Purcell, S.-I. Uye, et al., manuscript submitted). In addition to surfaces for polyps, harbors and aquaculture lagoons provide calm, eutrophic water that retain jellies (Lo et al. 2008). Early and continuing human modification of shorelines also included structures to protect against erosion, retain sediments, and provide transportation (Bulleri & Chapman 2010) that also host these populations (Willcox et al. 2008). The extent of cnidarian use of these structures is unknown, because the small cryptic benthic stages may not be identified (Carlton 2009). Man-made structures are especially susceptible to nonindigenous species (NIS), perhaps because they are carried by boats to the structures (Bulleri & Chapman 2010).

Over time, humans have increased coastal hard substrates dramatically. Planulae of six scyphozoan species preferentially settled on artificial substrates (Holst & Jarms 2007, Hoover & Purcell 2009); *Cotylorhiza tuberculata* planulae did not demonstrate strong preference, but *Chrysaora quinquecirrha* planulae settled only on natural surfaces (Astorga et al. 2012; C.M. Duarte, K.A. Pitt, C.H. Lucas, J.E. Purcell, S.-I. Uye, et al., manuscript submitted). The numbers of artificial structures currently are growing at rates of 3.7%–28.3% per year. The energy industries also provide surfaces for colonization by cnidarians, including oil rigs and power-plant cooling-water intakes, and more recently offshore wind-, tidal-, and wave-power installations. Wind energy is experiencing especially rapid expansion (28.3% per year). Because of climate-change-induced sea level rise and more powerful storms, and the exponentially growing human population with its increasing energy demands, additions of substrates can be expected to increase in the future.

Transportation of Nonindigenous Species

Recognition of NIS did not begin until marine biologists appeared in the 1700s and 1800s, although considerable transport probably occurred earlier: "From the 1500s to the 1800s, ocean-going ships were floating zoos and botanical gardens" (Carlton 2009). Restriction of accidental NIS transport in ballast water was not implemented until 1973 and continues to be a leaky effort (David & Gollasch 2008). More stringent requirements were approved in 2004 but are not yet in force. As with all anthropogenic factors, shipping activities and the potential for transport greatly increased over time. A stochastic population model showed that approximately 300 ports could be invaded from a random port within 50 years of the initial invasion, illustrating the great potential for additional invasions (Kaluza et al. 2010).

The earliest reported jellyfish introduction was in 1838 (**Supplemental Table 1**; follow the Supplemental Material link from the Annual Reviews home page at **http://www.annualreviews.org**). The scyphozoan *Phyllorhiza punctata* is native to Southeast Asia and Australia but now is established in the central and eastern Pacific, Caribbean, U.S. Atlantic coast, and Mediterranean Sea (Verity et al. 2011). *Aurelia* spp. also were introduced multiple times, as clarified by molecular studies (Dawson 2003). Hydromedusan species may have been introduced extensively; however, the hydroids are cryptic and difficult to identify, and their small medusae also generally are unnoticed. The most damaging introduced jelly is the ctenophore *M. leidyi*. It appeared in the Black Sea in the early 1980s, but its range expanded to the Mediterranean Sea in the 1990s and to northern Europe from new introductions in the 2000s (Costello et al. 2012).

NIS: nonindigenous species (introduced species, aliens, and invaders)

Supplemental Material

Aquaculture

Aquaculture combines effects of fishing, eutrophication, substrate addition, and NIS transport. In addition to reduction of forage fish for feed, aquaculture is a source of nutrients and organic matter, which could increase zooplankton available to jellies. That fish farms can cause local eutrophication and that they can damage the benthos is clear (Buschmann et al. 2009), but effects on the plankton food web are not well known. Bivalve culture also has environmental costs (Dumbauld et al. 2009). Sheltered habitats, such as bays and fjords, are preferred locations for aquaculture; unfortunately, because of reduced water circulation, these semienclosed habitats can retain eutrophication and jellies. On the other hand, bivalve farming reduces nutrients and improves coastal water quality, as long as the sediments below the farm remain oxic with intact nitrification and denitrification processes (Lindahl & Kollberg 2009).

Aquaculture installations provide habitats for the attached polyp and hydroid stages, although little documentation exists. Three species of medusa-producing hydroids were quantified in aquaculture installations (Chaplygina 1993). A hydroid species that plagues salmon culture in the North Sea, *Ectopleura larynx*, liberates actinula larvae (not swimming medusae), and cleaning the net cages breaks up the hydroids into the water, both of which damage the fish's gills (Guenther et al. 2010).

Increasing aquaculture is a consequence of declining overexploited wild stocks and increasing human populations. The most intensive coastal aquaculture is in China (>500 kg km^{-1} of coastline produced annually), followed by Southeast Asia, Indonesia, the Philippines, Japan, and Egypt (25–500 kg km^{-1} per year) and Spain, France, Ireland, and Norway in Europe (25–50 kg km^{-1} per year) (Bostock et al. 2010). By contrast, aquaculture in the Americas is intensive only in Chile (50–100 kg km^{-1} per year). Because aquaculture is a rapidly expanding industry (**Figure 5**), all of its possible effects can be expected to increase in the future.
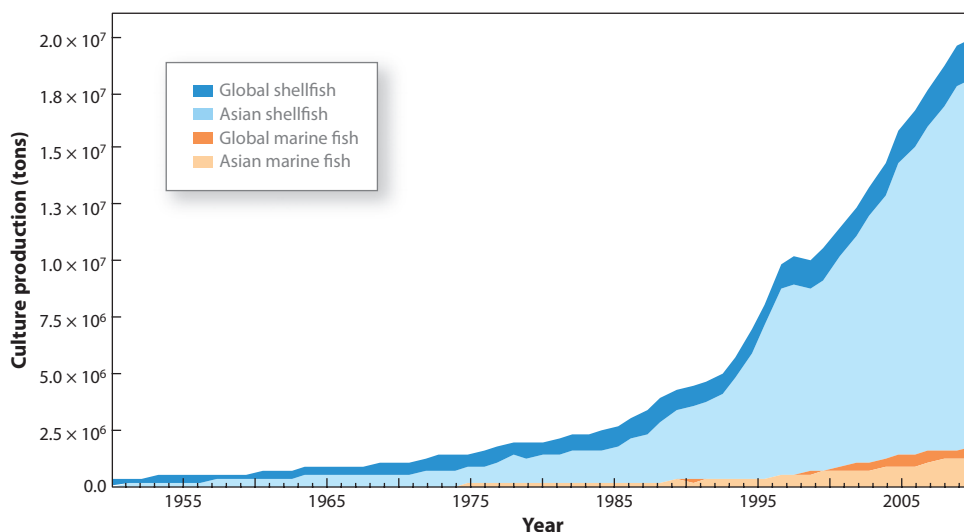

Figure 5

Global and Asian shellfish and marine fish aquaculture production from 1950 through 2008. Figure updated from Purcell et al. (2007); data taken from the Web site of the Food and Agriculture Organization of the United Nations, Fisheries and Agriculture Department (**http://www.fao.org**).

Climate Change

Humans first modified the atmospheric C budget centuries ago by deforestation for fuel, buildings, and agriculture. The net effect of land cover change (−0.15°C between 1850 and 2000) was much less important than other forcings, including anthropogenic (greenhouse gases +1.3°C and sulfate aerosols −0.5°C) and natural (volcanic aerosols −0.2°C and solar insolation +0.2°C) (Matthews et al. 2004). The 2000s have been the warmest decade in the instrumental record (Arndt et al. 2010). Climate models project that global warming due to human influences will be 0.1°C–0.2°C per decade and that sea surface temperatures (SSTs) will rise nearly everywhere (Intergov. Panel Clim. Change 2007). Among the various factors potentially affecting jelly populations, the most information is available on the effects of temperature because of its long history of routine use in the field and laboratory.

SST: sea surface temperature

CPR: Continuous Plankton Recorder

Climate and jellyfish populations in situ. Data exist for few of the ∼1,400 species of pelagic cnidarians and ctenophores; however, several studies add evidence of greater abundances of jellies in warm, high-salinity conditions (**Supplemental Table 2**). In agreement with previous studies, scyphomedusae that were more abundant included *C. quinquecirrha* in Chesapeake Bay (Decker et al. 2007) and *A. aurita* and *Cyanea* spp. in the North Sea west of Denmark (Lynam et al. 2010). *A. aurita* and *Cyanea* spp. also were more abundant during warm years in the southern part of the North Sea and in the Irish Sea (Lynam et al. 2010, 2011). High abundances of *Pelagia noctiluca*, *A. aurita*, and *Rhizostoma pulmo* in 2003 coincided with exceptionally warm temperatures and low river flow in the Northern Adriatic Sea (Kogovšek et al. 2010). Pacific black sea turtle landings were high during every El Niño and warm event between 1970 and 1988 when they foraged on *Chrysaora plocamia* medusae in southern Peru (Quiñones et al. 2010). Several holoplanktonic jelly species also have been most abundant in warm, high-salinity conditions in the Mediterranean Sea (Molinero et al. 2005, 2008). The 1980s had many outbreaks of jellies, with seasonal peaks three times larger than other years from 1966 to 1993. The fluctuations were attributed to temperature and stratification, and changes in the zooplankton were attributed to top-down effects (predation). Because García-Comas et al. (2011) found synchronous fluctuations in environmental parameters, copepods, jellyfish, siphonophores, chaetognaths, and decapod larvae from the same collection in 1974 to 2003 (30 years), they attributed the cause to climate-driven bottom-up effects (primary production).

Several recent studies have utilized Continuous Plankton Recorder (CPR) nematocyst counts in the long-term CPR database. Species can be identified when the samples are reanalyzed by microscopic or molecular techniques (Baxter et al. 2010, Licandro et al. 2010). In the studies testing multiple driving forces (below), SST was always significant, and was most important in the Irish Sea. Lynam et al. (2010) reported an increase in jellyfish and nematocysts since ∼1994 in the Irish Sea, which concurs with studies in the North and Mediterranean Seas that include recent years (Licandro et al. 2010, Kogovšek et al. 2010); however, Gibbons & Richardson (2009) attributed this recent increase to the ascending part of a 20-year cycle, which they observed from CPR samples (1946–2005) across the North Atlantic and North Sea. Thus, the recent jellyfish proliferations in the North Atlantic and Mediterranean Sea, which are linked climatically by the North Atlantic Oscillation, may decline when the climate regime shifts in the future. Solar and lunar activity occur in ∼10- and 20-year cycles that affect climate on the Earth (Yndestad 2009, El-Sayed Aly 2010), which could explain the ocean productivity and jelly cycles observed. Nevertheless, the large-scale cycles that control global climate now fluctuate against the background of ocean warming, which may raise the baseline populations of jelly species that favor warm conditions.

Supplemental Material

Not all jelly species in all locations are most abundant in warm years (**Supplemental Table 2**). Maximum abundances of *Chrysaora melanaster* medusae occurred at moderate SSTs in the eastern Bering Sea (Brodeur et al. 2008a). Other species show negative correlations with temperature. High abundances of two species occurred in the Northern California Current during cool years with strong upwelling and high productivity (Suchman et al. 2012). The greatest abundances of 22 taxa of meroplanktonic hydromedusae occurred during the upwelling period during one year in the Bay of Panama (Miglietta et al. 2008). In the North Sea, where the annual minimum and maximum SSTs were ∼1°C and 15°C, more *Pleurobrachia pileus* ctenophores were reported with warming, but in South Africa (SST range 11°C to 19°C), the highest densities occurred during the coldest year sampled. Regional differences in climate effects on abundances of *A. aurita* and *Cyanea lamarckii* medusae were due to incursions of cool oceanic water in the northern North Sea, versus association of those species with warm conditions in the southern part (Lynam et al. 2010). The ctenophore *Pleurobrachia rhodopis* was abundant at lower temperatures than favored by five hydrozoan species and *P. noctiluca* in the northwest Mediterranean (Molinero et al. 2008). Environmental modeling can be used to predict the distributions of jellies resulting from changing conditions and from introductions (Siapatis et al. 2008, Bentlage et al. 2009).

Climate effects on polyps. Experimental data show that, in most cases, increasing temperatures increase asexual production of jellyfish (Purcell et al. 2009, 2012). Since the earlier review (Purcell et al. 2007), new studies bring the total scyphozoan species tested to 13, with *Aurelia* spp. tested from diverse climates. Temperature significantly affected budding of new polyps. In some species tested (*A. aurita* from the Baltic Sea, *Cassiopea andromeda*), new bud production predominated in cool temperatures and was inversely related to temperature and strobilation, which increased as temperatures rose. In others, bud production increased with temperature when strobilation was absent or reduced in warm temperatures (*A. aurita* from the northwest Mediterranean and Japan, *C. tuberculata*). In other polyps, there appeared to be a negative effect of unusually high temperatures, with decreased production of both polyps and ephyrae.

Podocyst production is another asexual method of increasing polyp numbers, but little is known because of their tiny size (0.1–0.7 mm) and crypsis (Arai 2009). Podocyst production by *A. aurita* occurred only by unfed polyps and increased with temperature; salinity had no effect (Htun et al. 2012). They concluded that podocysts contributed little to population increase but enabled survival in stressful conditions.

Of the scyphozoan species tested, most polyps strobilated over broad temperature ranges (Holst 2012, Purcell et al. 2012). Polyps from habitats from cool climates—*Aurelia aurita*, *Aurelia labiata*, *Chrysaora quinquecirrha*, *Chrysaora hysoscella*, and *Cyanea* spp.—strobilated at temperatures ≤15°C, which correspond to late-winter to early-spring temperatures in their habitats. Unlike the other species, polyps of boreal *Cyanea capillata* did not strobilate at 15°C, and more polyps strobilated at colder temperatures. In these species, polyps produced more ephyrae at warmer temperatures. By contrast, polyps from tropical climates (*Mastigias* sp., *A. aurita* from Taiwan) had highest ephyra production at intermediate temperatures. Numbers of ephyrae produced per polyp differed substantially among species and habitats, ranging in *Aurelia* spp. from 18–35 ephyrae in cool climates to ∼3–7 ephyrae in a tropical climate. Warm temperatures also shorten the times until strobilation of the scyphozoan species tested, which would result in medusae appearing earlier seasonally.

Environmental effects on asexual reproduction rates have been studied for few hydromedusan species, which have diverse reproductive methods. Production of polyp and medusa buds increased and accelerated with temperature in estuarine *Moerisia lyonsi* (in Ma & Purcell 2005). By contrast, production of medusae from *Proboscidactyla ornata* medusae was greatest at intermediate temperature, consistent with the seasonal production pattern (Kawamura & Kubota 2008). In

summary, ocean warming may increase the populations of many jellies and change the timing and length of their seasons and distributions.

Consequences of global warming also include changed cloud cover and rainfall, melting of glaciers and pack ice, and earlier seasonal melting of snow pack that will alter the salinity and light regimes (Intergov. Panel Clim. Change 2007). Increased jellyfish populations have been attributed to salinity changes in semienclosed bodies of water owing to climate variations as well as human perturbations (Purcell et al. 2007). Many species above were most abundant in years with high salinity as well as warm temperatures. Production of medusae by polyps is affected by salinity (Purcell et al. 2007, 2009; Holst & Jarms 2010; Prieto et al. 2010). Light, which seldom has been considered to affect jellyfish population size, also accelerates strobilation (Purcell 2007, Liu et al. 2009).

Few field studies test environmental effects on polyps. *Aurelia* sp. polyps strobilated earlier in Tasmania when prestrobilation temperatures were warmer in 2004 than in 2003 (Willcox et al. 2008). Strobilation in situ occurred in 35% more *A. labiata* polyps and began ~23 days earlier in 2005 when temperature, salinity, light, and food were higher than in 2004 (Purcell et al. 2009), which far exceeded predictions from laboratory results (6% and 2 days; Purcell 2007). Thus, favorable conditions coincided in 2005 and increased and accelerated strobilation relative to other years. Strobilation in many species occurs as temperature, light, and plankton production increase.

Combined Effects

All of the above factors are occurring together in coastal regions globally. How they may interact and affect jelly population sizes is unknown, but they may act synergistically (Jackson et al. 2001, Kirby et al. 2009). Some recent studies examine effects of additional forcing factors in combination with climate on jelly population sizes (**Supplemental Table 2**). Analysis of CPR data on plankton and nematocysts plus temperature from 1949 to 2005 and cod spawning stock biomass in the North Sea showed that the decline of cod (presumably due at least in part to overfishing), which coincided with a temperature increase in the mid-1980s, caused a trophic cascade that led to "a proliferation of jellyfish" after the mid-1980s (Kirby et al. 2009). The cod spawning stock biomass, catch, and recruitment also declined in the 1980s in the Irish Sea, following the precipitous herring stock decline in the mid-1970s (Lynam et al. 2011). The highest nematocyst frequencies in CPR samples (1970–2007) occurred ~1982–1990 after the herring collapse. Recent jellyfish biomass (1994–2009) increased while zooplanktivorous fish stocks were low. Jellyfish abundance correlated positively with SST and copepod biomass and negatively with February–May precipitation. Thus, ecosystem changes from overfishing and warming correlated with high jellyfish abundance.

⊙ Supplemental Material

Jellyfish biomass in the eastern Bering Sea increased continuously during the 1990s but then declined precipitously in 2000; the onsets of the outburst and decline coincided with transitions between climatic regimes, with jellyfish flourishing in moderate conditions (Brodeur et al. 2008a). The jellyfish population size in the preceding year, SST, sea ice, current, wind mixing, and the abundances of zooplanktivorous juvenile walleye pollock and zooplankton all correlated with jellyfish population size. Warmer conditions prevailed in the 2000s, which had moderate jellyfish populations. Thus, fish abundances and climate influences correlated with jellyfish abundances in the eastern Bering Sea.

Oguz & Gilbert (2007) examined a suite of factors to determine causes of abrupt transitions in the Black Sea ecosystem from 1960 to 2000. Changes in the fish communities were caused by overfishing, first of piscivorous species before 1973 and then of zooplanktivorous species during the 1980s. Eutrophication began in the early 1970s, was intense during the 1980s, and decreased during the 1990s. A warm regime was replaced by a cold regime after 1980, and intense warming returned in 1995. The accidentally introduced the ctenophore *M. leidyi* was first discovered in the

early 1980s, but its population dramatically increased in 1989 at the time of the zooplanktivorous fish collapse and the climate shift. *M. leidyi* was the dominant zooplanktivore until ~1998, when reduced fishing enabled the zooplanktivorous fish to begin recovery and a predator of ctenophores, *Beroe ovata*, arrived and began to limit the *M. leidyi* population. Oguz et al. (2008) concluded that a combination of overfishing, nutrient enrichment, and climate shift to a warm regime was involved in the 1989–1990 anchovy collapse and outbreak of *M. leidyi*.

Japan's fisheries have suffered great losses during the 2000s because huge numbers of the giant jellyfish *Nemopilema nomurai* are carried into Japanese waters, possibly from the East China Sea (Uye 2010). In the East China Sea, the Korean fish catch in 2004 was less than half of that in the mid-1980s, SSTs increased 1.7°C between 1976 and 2000, and nutrient loading (dissolved inorganic N and P) has increased rapidly while silica decreased, with toxic dinoflagellate blooms increasing from <5 per year to 58 in 2003. Although no analyses were made, all of these factors may have contributed to the Asian jellyfish increases.

Present Conditions

The Earth's population today totals 7 billion humans, 27 times that in 14 AD when this story began. The highest populations throughout history have been in Asia, India, Europe, and Africa. Today, these regions contain ~70% of the world population. Thousands of years of human exploitation in these regions have had environmental costs, which now may be reflected in problems with jellies. Although changes associated with technological advances proceeded along similar time lines after the Industrial Revolution, the sizes of the populations contributing to the effects were dramatically greater in Europe and Asia than in North America. In 1750, ~102 million people lived in Europe and ~233 million lived in East Asia, but only 2 million lived in North America. Population growth since 1750 was more rapid in North America, which had 352 million people in 2010, but Europe (733 million) and Asia (1 billion) still have larger populations.

Halpern et al. (2008) recently combined anthropogenic effects to identify marine ecosystems with large effects and the major causes (**Figure 6**). The forcing factors included climate change (SST, UV, acidification), organic and inorganic pollution, several methods of fishing, benthic structures (oil rigs), commercial shipping, and species invasions. They concluded that the strongest forcing factors were climate change and overfishing. They did not include other factors relevant to this review, including hypoxic zones, coastal engineering (piers, walls), aquaculture, and sedimentation. Six of the top 10 rankings of total impact scores coincide with locations that have had jelly blooms (**Table 1**). Below those rankings are eight other locations (#18–96) with notable recent jelly blooms. Most of these locations have high human population densities, high N loading, out-of-balance fisheries, and hypoxia.

The eastern Bering Sea is ranked #2, where jellyfish increased throughout the 1990s but then abruptly declined after 2000 (Brodeur et al. 2008a). This region would be affected almost exclusively by fishing and climate change (**Figures 3** and **6**).

Ranks #3 and #6 are the East China and Yellow Seas, which have suffered from all of the anthropogenic drivers for centuries. Blooms of *N. nomurai*, which had previously occurred only in 1920, 1958, and 1995, have been nearly annual since 2000 and severely interfere with Chinese fisheries (Dong et al. 2010). They were abundant in 2003 with cool water of moderate salinity, but not in 2005 with warm water of low salinity. The medusae are carried northward into the Sea of Japan (#18) where they fill the nets of Japanese fisheries (Uye 2010). *Cyanea nozakii*, a warm-water, high-salinity species, also has increased since 2000 in the East China and Yellow Seas and now is widely distributed and interferes with fishing. A bloom of *C. nozakii* in 2004 was thought to be the main cause of an 80% decline in edible jellyfish (*Rhopilema esculentum*) with direct economic
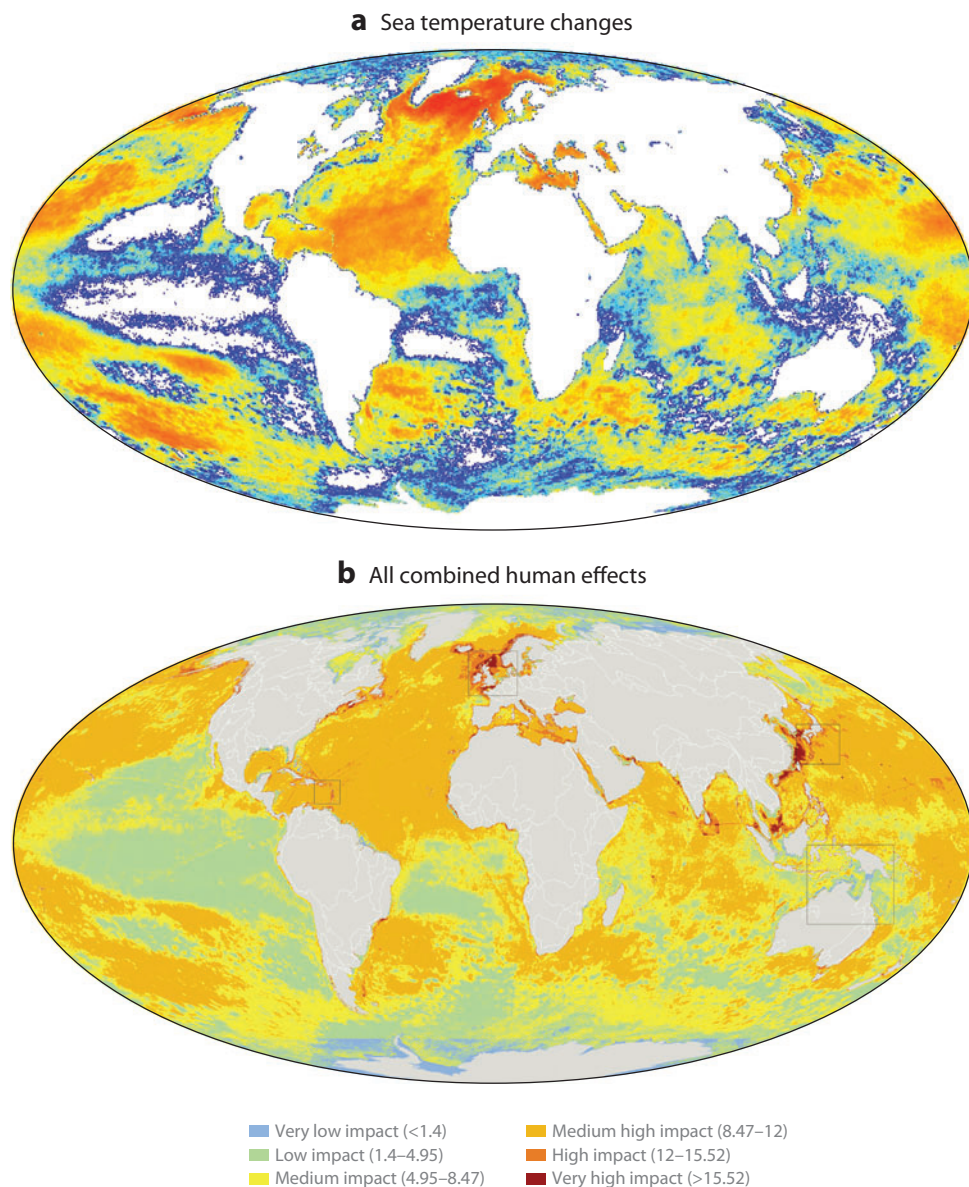
a Sea temperature changes

b All combined human effects

■ Very low impact (<1.4)	■ Medium high impact (8.47–12)
■ Low impact (1.4–4.95)	■ High impact (12–15.52)
■ Medium impact (4.95–8.47)	■ Very high impact (>15.52)

Figure 6

Global maps of (*a*) temperature changes and (*b*) cumulative human impacts. Red indicates very high impacts and blue indicates very low impacts. Adapted from Halpern et al. (2008).

losses of US$70 million. Blooms occurred of *A. aurita* in 2004–2009 and of *Cyanea* spp. in 1999, 2003, and 2004, when it constituted 98.4% of the fisheries catch in May. In the Seto Inland Sea of Japan, problem blooms of *A. aurita* have occurred since the 1950s, but increased noticeably in the 1980s (Mills 2001, Purcell et al. 2007, Uye 2010). The Seto Sea was not a location in Halpern et al. (2008), but it has high population density and nutrient loading (**Table 1**). Asian waters are affected by all of the environmental problems.

Table 1 Rankings of scores of human impacts, population densities, and environmental indicators where notable jellyfish blooms occur

Location	Region	Total score	Rank	Human density (people per km²)	FiB Index[h]	N load[i] (metric tons per year per km²)	Hypoxia[j]
Eastern Bering Sea	Arctic	9,073,790	2	0.1[a]	1.53	<0.1[e]	—
East China Sea	Asia	8,718,290	3	214[a]	1.67	3.0	S
North Sea	Northeast Atlantic	8,695,670	4	482[a]	−0.04	4.1	M
Celtic Seas	Northeast Atlantic	6,842,880	5	464[b]	1.8	3.2	M
Yellow Sea	Asia	4,624,850	6	156[a]	1.56	5.6	S
Baltic Sea	Northeast Atlantic	3,774,150	9	49[c]	0.24	6.2	WP
Sea of Japan	Asia	2,303,360	18	337[d]	0.38	<0.25[e]	S
Northern Gulf of Mexico	Gulf of Mexico	1,889,980	25	21[a]	0.32	15.5	WS
Western Mediterranean Sea	Western Mediterranean	1,649,190	34	102[a]	0.32	0.3	L
Black Sea	Black Sea	1,550,430	37	89[e]	0.14	6.2	WP
Adriatic Sea	Western Mediterranean	1,420,020	43	217[a]	−0.94	3.1	L
Levantine Sea	Eastern Mediterranean	724,402	76	44[f]	1.03	—	L
Namib	Temperate South Africa	643,684	84	12[f]	3.54	<0.1[e]	S
Gulf of Oman	Indo-Pacific	473,233	96	58[f]	7.42	—	S
Chesapeake Bay	Eastern United States	—	—	56[g]	—	14.5	WS
Seto Inland Sea of Japan	Asia	—	—	643[g]	—	10.0	S

Rankings of total scores from 180 locations (after Arctic and Southern Ocean locations were omitted), from Halpern et al. (2008).

[a]EarthTrends Environmental Information (**http://earthtrends.wri.org**).

[b]River Severn; estimated from population of watershed in Environ. Agency (2011) and area of watershed in Eur. Environ. Agency (2001).

[c]Sweitzer et al. (1966).

[d]Int. EMECS Cent. (1999).

[e]Eur. Neighb. Partn. Instrum. (2007).

[f]Estimated from area of watershed with country populations at **http://en.wikipedia.org/wiki/World_population**.

[g]Breitburg et al. (2009).

[h]Fishing in Balance (FiB) Index from the Sea Around Us Project (**http://www.seaaroundus.org**). Scores in 1950 are assumed to be zero. The FiB Index assesses whether catch rates are in balance with ecosystem production. FiB Index = 0 indicates higher production at lower trophic levels, so fishing is in balance. FiB Index > 0 indicates that the fishery has expanded or that bottom-up effects are occurring, so there is more catch than expected. FiB Index < 0 occurs when the fishing impact is so high that the ecosystem function is impaired.

[i]Calculated from Breitburg et al. (2009) with human populations.

[j]Breitburg et al. (2009). Abbreviations: M, minimal; L, localized; S, seasonal; P, persistent; W, widespread.

The North (#4), Celtic (#5), and Baltic (#9) Seas of northern Europe also have long histories of human exploitation of the environment and recent increases of jellies (Lilley et al. 2009; Lynam et al. 2010, 2011; Bastian et al. 2011). Abundances of *Rhizostoma octopus* in the Irish Sea were much higher in 2003, which was an exceptionally warm year, than in 2004 or 2005 (Lilley et al. 2009). In a 30-year record of ctenophores in the southern North Sea, the beginning of the blooms abruptly shifted in 1987–1988 up to eight weeks earlier when spring SSTs were 1°C–2°C warmer (Schlüter et al. 2010). Few studies address medusae in the Baltic Sea, perhaps because low salinities limit their populations (but see Barz & Hirche 2005, Holst & Jarms 2010); however, several address

jellyfish in fjords of Denmark (Möller & Riisgård 2007, Riisgård et al. 2011). *M. leidyi* ctenophores have been found since 2006 in southern North Sea and Baltic waters as a new introduction from North America (Costello et al. 2012). The northern European waters are affected by all of the environmental problems.

Human civilizations have used the Mediterranean Sea for 4,000 years. The western Mediterranean (#34) and Adriatic (#43) Seas have climatic connections with northern Europe and similar patterns of jellyfish increases. Most species documented show high abundances in warm, high-salinity conditions. Currently, the Mediterranean has high abundances of at least five scyphozoan species (Kogovšek et al. 2010, Fuentes et al. 2011) and a cubozoan species (Bordehore et al. 2011). *M. leidyi* ctenophores bloomed from Spain to Israel in 2009 (Fuentes et al. 2010). The Levantine Sea (#76) has experienced many NIS invasions through the Suez Canal from the Red Sea (Graham & Bayha 2007, Galil et al. 2010). *Rhopilema nomadica* first appeared in the 1990s and now forms annual problem blooms. In the Benguela Current off Namibia (#84), jellyfish may have replaced heavily fished forage fish (Lynam et al. 2006). In 2002, *Crambionella orsini* medusae bloomed throughout the Gulf of Oman (#96) and the Persian Gulf and caused problems in fisheries, desalination plants, and coastal power plants (Daryanabard & Dawson 2008). Little information exists for jelly populations in many highly ranked locations [Sunda Shelf (#1), India, South America] so it was not possible to evaluate effects of environmental degradation over most of the globe.

The combined effects of climate, nutrient inputs, and fishing will determine the amounts of food available to jellies and their population sizes in the future. Climate changes, mainly warming SSTs and shoaling mixed layer depths, have reduced phytoplankton in most of the oceans over the last century and especially since 1950 (Boyce et al. 2010). These effects may be less pronounced in coastal areas, where increased melting, precipitation, and human populations will deliver additional nutrients, and shallow depths allow nutrient replenishment from the seafloor. Thus, reduced primary production may limit fish and jelly production over parts of the oceans in the future, but perhaps not in coastal regions where the species discussed in this review live.

SUMMARY POINTS

1. High human populations in Asia, India, Europe, and Africa have exploited coastal waters for at least 3,000 years. Combined, these regions now contain ∼70% of the world population. Populations reached high densities in parts of the American continents only during the last century. The Industrial Revolution accelerated population growth and environmental impacts globally after 1750. Human effects on the marine environment (fishing, eutrophication, construction, shipping, aquaculture, climate change) intensified after 1950.

2. Problems with jellyfish were reported in the 1950s in Japan and have increased in the 1980s and 2000s, especially in Japan, China, and Europe.

3. Anthropogenic effects are interrelated and occur simultaneously in most coastal waters. Direct evidence linking jelly blooms to possible human causes is lacking in most cases; however, correlative evidence suggests connections.

4. Overfishing is a key environmental driver that could positively affect jellies. Several correlations show inverse biomasses of jelly and forage fish, probably because of reduced competition for zooplankton when forage fish are depleted.

5. Eutrophication is a pervasive global problem with many possible benefits for jellies. Correlative evidence suggests increased jellies where transparency is reduced, nutrients are high, and DO concentrations are low.

6. Temperature is an important driver. High populations of many jelly species and high asexual production of medusae by polyps occur in warm conditions. Jellyfish and ctenophore populations fluctuate with climate cycles, which will now occur on a rising baseline of ocean warming. Warming may increase the population sizes of many species and change the timing and length of their seasons as well as their distributions.

7. Several locations ranked as the most impacted by humans have had notable jelly blooms. Few jellyfish population data are available for much of the globe.

8. The amount of food available determines the abundances of jellies and fish. Although warming SSTs and shoaling mixed layer depths may continue to reduce ocean production, nutrient delivery in coastal areas may counteract this effect.

FUTURE ISSUES

1. Human population and demands from coastal areas will continue to increase. In the conflict of interests between human economics and preservation of the environment, economics usually prevails. Therefore, all of the anthropogenic forcing factors discussed here probably will escalate. Despite efforts to restore the environment, earlier conditions have not returned. We need to understand how present ecosystems, including jellyfish, will change under continued anthropogenic forcing.

2. Locations with severe environmental degradation also have had jelly blooms; therefore, it is likely that problems with jellies will continue. Data on jelly populations are unavailable for most of the oceans. Because of their importance in ecosystems and negative interactions with human interests, it is important to increase efforts on their study.

3. Anthropogenic climate warming will continue. Solar and lunar cycles now are at lows. When the cycles ascend in the coming decade, ocean temperatures will reach new highs. Because many temperate jelly populations respond positively to warming, and temperature has the strongest effect in most studies, it is important to better understand the effects of warming.

4. With high populations of jellyfish, interest in new commercial products will increase. Additional species suitable for human food (Kitamura & Omori 2010) and animal feeds, as well as for new uses in medicine and biotechnology, could be utilized.

DISCLOSURE STATEMENT

ACKNOWLEDGMENTS

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RELATED RESOURCES

DockWatch (Dauphin Isl. Sea Lab): **http://dockwatch.disl.org**

Forecasting Sea Nettles (Natl. Ocean. Atmos. Inst.): **http://chesapeakebay.noaa.gov/forecasting-sea-nettles**

Hydrozoa Directory (P. Schuchert): **http://www.ville-ge.ch/mhng/hydrozoa**

JelliesZone (D. Wrobel): **http://www.jellieszone.com/index.htm**

JellyWatch (CIESM): **http://www.ciesm.org/marine/programs/jellywatch.htm**

JellyWatch (Monterey Bay Aquar. Res. Inst.): **http://www.jellywatch.org**

Medusozoa (L. Gershwin): **http://www.medusozoa.com**

Scyphozoan Wiki (M. Dawson): **http://scyphozoan.ucmercedlibrary.info**

Siphonophores (C. Dunn): **http://www.siphonophores.org**

STOPJELLY (Popul. Outbreak Mar. Life): **http://tnfri.fra.affrc.go.jp/kaiyo/POMALweb/e-stopjelly.html**

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Errata

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