Review

The jellyfish joyride: causes, consequences and management responses to a more gelatinous future

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Human-induced stresses of overfishing, eutrophication, climate change, translocation and habitat modification appear to be promoting jellyfish (pelagic cnidarian and ctenophore) blooms to the detriment of other marine organisms. Mounting evidence suggests that the structure of pelagic ecosystems can change rapidly from one that is dominated by fish (that keep jellyfish in check through competition or predation) to a less desirable gelatinous state, with lasting ecological, economic and social consequences. Management actions needed to stop such changes require tactical coping strategies and longer-term preventative responses based on fundamental and targeted research on this understudied group.

Blooming jellyfish

Jellyfish are important and often conspicuous components of ecosystems. Although they have historically been viewed as trophic dead ends, some 124 fish species and 34 species of other animals are reported to feed either occasionally or predominately on jellyfish [1]. Of these, 11 fish species are jellyfish specialists, and some critically endangered animals, such as the leatherback turtle *Dermochelys coriacea*, target jellyfish blooms [2]. Juveniles of some fish species find safe refuge from predation by living on or nearby jellyfish (Figure 1a). These interlopers feed on the prey and parasites of jellyfish, potentially enhancing fisheries recruitment in some situations, with jellyfish acting as multiple ‘fish-attracting’ devices [3]. Jellyfish have been eaten by humans since 300 AD in China, and ~425 000 tonnes y^{-1} are harvested globally (1996–2005) for human consumption in Southeast Asia [4]. Jellyfish fisheries exist in 15 countries, including China, India, Indonesia, Japan, Malaysia and the Philippines, with export industries in Australia and the USA.

Although dense jellyfish aggregations are a natural feature of healthy pelagic ecosystems [5], a picture is now emerging of more severe and frequent outbreaks in many areas. Unfortunately, jellyfish are fragile and difficult to sample, hampering the collection of time series [6], although available information suggesting that aggregations are on the increase is persuasive. More frequent jellyfish outbreaks have been reported worldwide [7–11], particularly in coastal waters of the Far East [12–15].

Jellyfish outbreaks can have many deleterious consequences, including losses in tourist revenue through beach closures and even the death of bathers [16]; power outages following the blockage of cooling intakes at coastal power plants [16]; blocking of alluvial sediment suction in diamond mining operations [11]; burst fishing nets and contaminated catches [11]; interference with acoustic fish assessments [17]; killing of farmed fish [8]; reduction in commercial fish abundance through competition and predation [11]; and as probable intermediate vectors of various fish parasites [6]. Most dramatic are recent outbreaks

Glossary

Cnidaria: invertebrate phylum that contains animals such as anemones and corals but also a range of jellyfish, including large scyphozoan jellyfish (up to 2 m in diameter) and smaller hydromedusae (only a few mm in diameter). Generally have alternating polyp and medusa life stages. Stinging cells or cnidoblasts (nematocysts) concentrated in the tentacles and mouth appendages are used to poison or stun prey.
Ctenophora: invertebrate phylum, sometimes called comb jellies or sea gooseberries, that propel themselves through the sequential beating of their rows of cilia (comb rows). Have colloblasts, cells which discharge a glue to ensnare prey. Ctenophores are holoplanktonic, remaining in the plankton their entire life.
Ephyrae: the initial larval free-swimming stage of a medusa produced asexually from the benthic polyp.
Eutrophic: waters that have high nutrient levels, often leading to increased primary production and algal biomass, and a reduction in water transparency and concentration of dissolved oxygen.
Filter feeding: ingestion of small particles, usually plankton, often by small pelagic fish.
Flagellate: single-celled organisms that use whip-like flagella for propulsion. Most contain chlorophyll and are photosynthetic, whereas some feed partially or even wholly on organic material.
Jellyfish: free-swimming gelatinous animals belonging to the phyla Cnidaria and Ctenophora.
Medusa: the mobile, bell-shaped stage of cnidarians that actively swim through muscular contraction of their bells.
Pelagic: living in the water column, as opposed to near or on the seafloor.
Polyp: the benthic stage of cnidarians with a general body plan of a cylindrical body and a ring of tentacles surrounding an oral opening.
Statoliths: calcium carbonate structures in the margin of the swimming bell of medusa used to sense gravity and so help in maintaining orientation.

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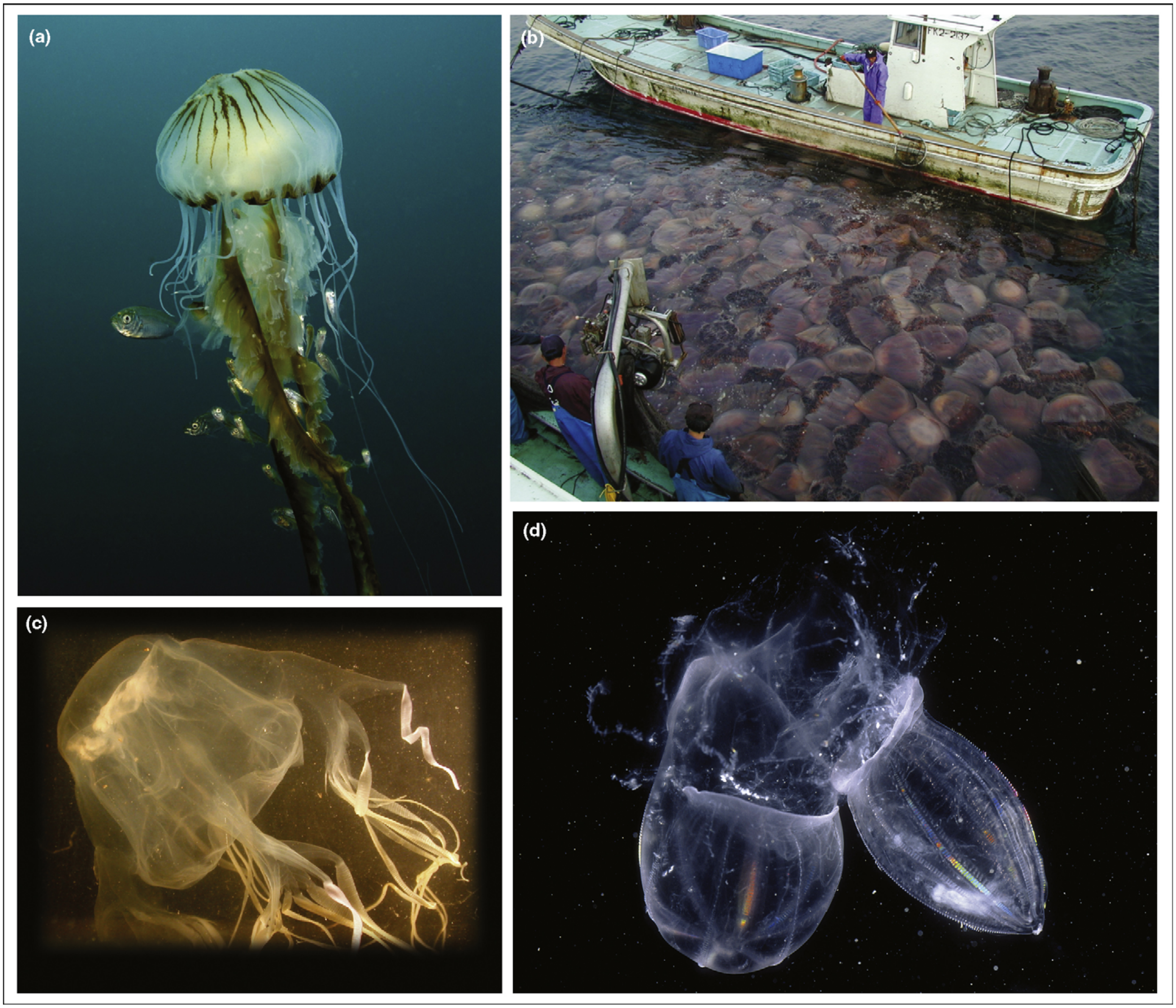

Figure 1. Examples of common jellyfish, their ecosystem roles and impacts on humans. **(a)** *Chrysaora* spp. acting as a fish-aggregating device for juvenile horse mackerel *Trachurus trachurus* (Carangidae). **(b)** Nomura *Nemopilema nomurai* clogging fishing nets in Niu, Fukui Prefecture (Japan), October 2003. **(c)** The box jellyfish *Chironex* spp., which can kill bathers and results in beach closures in North Queensland (Australia) during the summer. **(d)** Two individuals of the predatory comb jelly *Beroe* (bottom and right) feeding on another comb jelly *Mnemiopsis* (centre). Reproduced, with permission, from J. Collins [76] (a); Y. Taniguchi (b); Lisa Gershwin (c); and Peter Parks/ imagequestmarine.com (d).

in the Sea of Japan of the giant Nomura jellyfish *Nemopilema nomurai* (up to 2 m in diameter and weighing 200 kg), which are clogging and bursting fishing nets (Figure 1b).

Here we discuss the current evidence for anthropogenic stresses leading to more frequent and severe jellyfish blooms. Circumstantial support coupled with direct observations suggests that overfishing, eutrophication, climate change, translocations and habitat modification are causing jellyfish outbreaks. We detail a possible mechanism whereby jellyfish can form an alternative stable state in marine ecosystems through a self-enhancing feedback loop, replacing the more common and productive food webs dominated by higher trophic-level organisms such as fish. Finally, we describe the research required to investigate ways of first controlling, and then preventing jellyfish blooms to avoid large-scale disruptions to pelagic ecosystems. We use a broad definition of jellyfish that includes cnidarians and ctenophores (Box 1).

Are humans responsible for jellyfish increases?

Available evidence suggests a suite of human activities might act separately and potentially synergistically to result in outbreaks of some jellyfish species (Figure 2). Of these human activities, there is convincing evidence for the role of species translocations, overfishing and eutrophication in increasing jellyfish blooms, particularly in coastal areas. More speculative is evidence for the roles of climate change and habitat modification in promoting outbreaks.

Overfishing

The annual removal globally of between 100 and 120 million tonnes of marine life (fish, invertebrates, discarded

Box 1. Jellyfish taxonomy, ecology and life cycles

The term 'jellyfish' refers to free-floating gelatinous animals belonging to the phyla Cnidaria and Ctenophora (comb jellies). Although many Cnidaria actively swim through muscular contraction of their bells and Ctenophora propel themselves through the sequential beating of cilia, neither can progress against currents and are, thus, defined as zooplankton. Jellyfish range in size from a few mm (*Aglaura* and *Obelia* spp.) to 2 m (*Nemopilema nomurai*; Figure 1a, main text) in diameter. Ctenophores are armed with colloblasts, which discharge a glue to ensnare prey, whereas cnidarians have stinging cells (nematocysts) concentrated in their tentacles that are used to poison or stun prey. Because of these stinging cells, cnidarians pose more threats to people than do ctenophores.

Jellyfish have complex life cycles, which vary with taxonomy [63]. Ctenophores are generally holoplanktonic, remaining in the plankton their entire life. They can be abundant in shelf waters, although some are restricted to the deep sea. Ctenophores are fragile and are thus poorly known, with ~150 species currently described. Although some cnidarians are also holoplanktonic, most are meroplanktonic, spending only a portion of their life cycle in the water column. Their archetypal life cycle is an alternation of life-history stages between a small, cryptic, benthic polyp and a conspicuous, free-swimming, open-water medusa. The polyp produces medusae by asexual budding, whereas the medusa reproduces sexually. This alternation of stages means jellyfish can be present even when they are not obvious to the casual observer.

The Cnidaria comprise three main groups of jellyfish, all of which can pose problems to human health. Most species of the Class Scyphozoa, which includes the large, bell-shaped jellyfish commonly washed up on beaches, have a polyp stage that buds off small medusae. They are found in all pelagic environments, but attain greatest abundances near the coast. Approximately 200 species have been described. Jellyfish of the Class Cubozoa are cuboidal and most are fist size or smaller, although a few are much larger, such as the deadly Australian sea wasp *Chironex*, which has a polyp stage in its life cycle; however, unlike other cnidarians, the polyp develops into a single medusa without budding. There are ~20 species, restricted to temperate and tropical shelf waters. Super-Class Hydrozoa is a diverse group that includes colonial siphonophores, such as the Portuguese-man-of-war *Physalia*. Most are thumbnail size and display both life-cycle stages, but in others the medusa or polyp is lost. Hydrozoa are found in all oceans and have 3700 described species.

bycatch and illegal and unreported species) over the past two decades [18] could be encouraging jellyfish outbreaks. Enduring fishery-related stock collapses appear to be occurring with increasing frequency worldwide [19]. Many fish compete for the same zooplankton prey as jellyfish [20], and fish are also predators of jellyfish, with benthic and reef fish species ingesting polyps, and pelagic fish species eating ephyrae and small individuals [20]. However, the removal of such fish opens up ecological space for jellyfish. For example, in the productive northern Benguela upwelling system off the coast of Namibia, intense fishing has decimated sardine stocks, and this once-productive fisheries system is now dominated by jellyfish such as *Chrysaora* [11]. It is likely that the collapse of the sardine stocks lowered the predation pressure on jellyfish and increased their available food resources [21,22].

Intensive trawling of the seafloor might further contribute to jellyfish blooms, as large numbers of potential competitors and predators of jellyfish are removed from heavily trawled soft-bottom habitats, while any nearby hard substrate (e.g. rocky outcrops), which is difficult to trawl, could possibly afford jellyfish polyps 'refuges' from fishing. However, further research is needed to determine whether this is the case. In Box 2, we discuss generalisations from pertinent case studies to explain why some prominent fisheries collapses lead to jellyfish outbreaks and others do not, and find that the trigger is often overexploitation of a dominant small zooplanktivorous fish in a situation where a similar small filter-feeding fish replacement is not available.

Eutrophication

Coastal eutrophication encourages phytoplankton blooms that can ultimately lead to jellyfish outbreaks [23]. The addition of excessive nutrients from fertiliser runoff and sewage into coastal waters can alter pelagic communities. Nutrients added to the coastal zone are rich in nitrogen and phosphorus but poor in silica. Under such conditions, the silica deficiency hypothesis suggests that non-siliceous phytoplankton, such as flagellates (cells with one or two flagella that include harmful red-tide species), proliferate and replace diatoms [24], resulting in a reduction in the size of primary and secondary producers [25]. It has been hypothesised that such a food web supports fewer fish, marine mammals, turtles and seabirds because of the smaller average food size and longer food chain [25], and is more favourable for jellyfish than for fish [26]. Jellyfish can survive in such environments for many reasons (Table 1), including their ability to feed on a range of prey, including protists [27] such as flagellates [28,29], and will thrive given the high total amount of food available.

Large phytoplankton blooms resulting from nutrient enrichment can sometimes sink to the seafloor, where their bacterial degradation can cause localised hypoxia [30]. The greater tolerance of polyps and medusae than of fish to low-oxygen conditions ensures that jellyfish survive and even reproduce during hypoxic events, which fish are unable to do (Table 1). The ctenophore *Mnemiopsis leidyi* can even benefit from enhanced feeding success in low-oxygen environments because its less-tolerant prey (copepods) are more vulnerable to predation [31]. During the summer of 2007 in the Gulf of Mexico, nutrient-rich outflows from the Mississippi River resulted in large phytoplankton blooms and 25 000 km^2 of oxygen-depleted waters [32]. Such 'dead zones' are thought to favour jellyfish [9] because of their lower oxygen and food demands compared with those of commercially valuable fish and shellfish. With the number of dead zones worldwide having doubled each decade since the 1960s, primarily owing to eutrophication [30], there is an increasing number of habitats available that are more suitable for jellyfish than for fish.

Climate change

Global warming might also favour some jellyfish species. Warming of the sea surface can enhance water column stratification, leading to nutrient-poor surface waters where flagellates, because of their ability to migrate vertically into nutrient-rich deeper waters, can outcompete diatoms [25]. Such flagellate-dominated food webs might be more favourable for jellyfish than for fish [26]. Warmer temperatures also accelerate medusae growth and ephyrae production [16]. Purcell *et al.* [16] found that the abundance of 11 out of the 15 temperate jellyfish species that

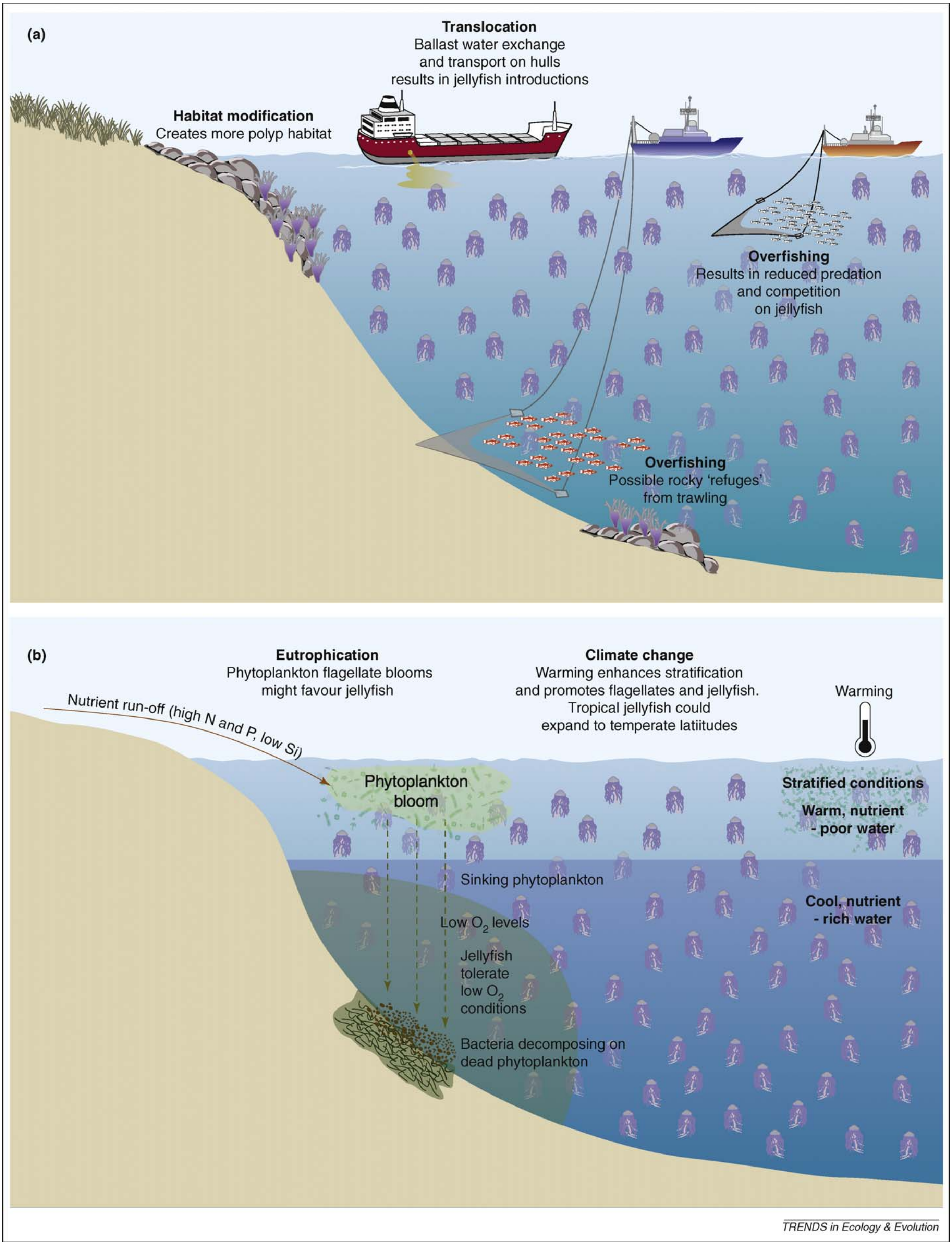

Figure 2. Probable mechanisms promoting jellyfish outbreaks. **(a)** Summary of the impacts of habitat modification [49], translocations [42] and overfishing [22] on jellyfish outbreaks; **(b)** Summary of the impacts of eutrophication [16] and climate change [16] on jellyfish outbreaks. Jellyfish symbols represent jellyfish blooms.

Box 2. Why does the collapse of some fisheries cause jellyfish outbreaks and others not?

Major jellyfish outbreaks have followed overexploitation and collapse of a locally dominant, small filter-feeding fish stock (e.g. anchovy, sardine or herring) in situations where another rapidly responding, similar fish species is not available as an adequate replacement. For example, in the northern Benguela upwelling system, where intense fishing decimated sardine stocks and jellyfish now dominate [11], maximum anchovy abundance has historically been limited to ~10% of maximum sardine biomass [64] (possibly because the weakly swimming anchovy might be incapable of coping as well as the larger sardine in this highly energetic upwelling system [21]). There is thus no obvious filter-feeding replacement for sardine in this ecosystem. This pattern was replicated in the energetic ocean context off Japan, where anchovies have not historically built populations comparable to those of sardines [64], and where the infestation of giant Nomura jellyfish has occurred following the collapse of what was an enormous Japanese sardine population [65]. When translocated ctenophores exploded in abundance following the anchovy collapse in the Black Sea [10], there was no obvious replacement. A similar episode of anchovy collapse and ctenophore explosion occurred in the Caspian Sea [43] and, following a similar general pattern, there was a decade-long increase in jellyfish abundance in the Bering Sea [55] following a lasting decline in herring abundance [66].

Equally informative are fishery collapses that have not led to jellyfish outbreaks. With the collapse of the largest fish stock in the world, the Peruvian anchoveta (*Engraulis ringens*) during the 1970s [64], there was no switch to increased jellyfish outbreaks. One possible explanation is that there were healthy stocks of an alternate rapidly responding filter-feeding species (i.e. highly migratory sardines) that quickly built up a large biomass and spread throughout the system to replace the collapsed anchoveta [64].

Finally, many of the instances in which fisheries collapses have not led to jellyfish outbreaks involve predatory rather than planktivorous fish [19]. Many fisheries collapses in the North Atlantic shelf and peripheral seas have been of bottom-dwelling predators such as cod and haddock. In these cases, the filter-feeding small pelagic prey of the collapsed species have increased rapidly (e.g. herring off New England [22] and sprat in the Baltic Sea [51]). Lower predatory fish biomass can release predation pressure on planktivorous fish, enabling their biomass to increase (top-down control) and, thus, lead to increased predation on, and competition with, jellyfish. Thus, many well-known collapses of piscivorous fish should have favoured increased planktivorous fish abundance and could have suppressed rather than encouraged jellyfish outbreaks.

they reviewed increased as waters warmed. Gibbons and Richardson [33] showed that variations in jellyfish abundance over 50 years in the oceanic North Atlantic are temperature dependent, with more jellyfish occurring in warmer years.

Warming could also expand the distribution of many of the most venomous tropical jellyfish species toward subtropical and temperate latitudes. For example, the northeast Australian coast is home to two types of box jellyfish: the sea wasp *Chironex* (Figure 1c) and the species complex known as irukandji; stings from both can be fatal and can force beach closures. The general global warming trend here has been exacerbated by the strengthening of the warm southward-flowing East Australia Current over the past 60 years [34], a situation that appears to be caused by altered circulation patterns in response to climate change [35]. There is growing concern that box jellyfish might expand southward toward more populated areas, with severe repercussions for the tourist industry [36].

Another aspect of climate change that could influence jellyfish is ocean acidification, a result of increased atmospheric CO_2 concentrations dissolving into the oceans and altering its carbonate balance. A recent study in the central North Sea suggested that jellyfish increase in abundance as pH declines; this was interpreted as the negative impact of more acidic conditions on calcifying plankton opening up ecological space for jellyfish [37]. However, a more comprehensive analysis over a larger area showed no significant relationship between jellyfish abundance and acidity [38]. More acidic conditions could potentially negatively affect jellyfish, given that most scyphozoan and some hydrozoan medusae use calcium carbonate statoliths for orientation. Whether statoliths are negatively affected by reduced pH, as is likely for other calcium carbonate structures of marine plankton (e.g. pteropod shells), or whether they are sufficiently protected within the jellyfish, is currently unknown.

Climate change will also influence climate variability, which, in turn, will affect jellyfish populations. Jellyfish appear to be sensitive to climate variability, with their abundance being related to large-scale climate indices such as the North Atlantic Oscillation (NAO) [39], El Niño Southern Oscillation [40] and the Pacific Decadal Oscillation [41]. Attrill *et al.* [37] found that jellyfish in the North Sea were positively related to the NAO phase, and predicted that, because some climate models project an increased frequency of positive NAO conditions, jellyfish might also increase.

Translocations

The human-assisted movement of species to new marine areas is most commonly caused by the exchange of ballast water (containing organisms) between regions and the transport of fouling biota (e.g. polyps) on ship hulls [42]. Some jellyfish, especially ctenophores, are robust to ballast water exchange, and have often increased in abundance once translocated to new areas where the dominant planktivorous fish in the system has been removed [43]. For example, following the anchovy stock collapse in the Black Sea, apparently due to overfishing, the abundance of the ctenophore *Mnemiopsis*, which had been introduced some years earlier, abruptly exploded to dominate the pelagic ecosystem [44]. Currently, the same invasive jellyfish has made its way to the Caspian Sea, where it is has been a factor in the commercial extinction of the beluga caviar industry [45] and in the reduction in the sturgeon and anchovy kilka [46]; it has now invaded both the Baltic and North Seas [47,48]. Elsewhere, scyphozoan jellyfish blooms have begun appearing in areas previously free of invading jellyfish species. For example, the spotted jellyfish *Phyllorhiza punctata* from the Pacific Ocean has become a nuisance following its translocation into the Gulf of Mexico [42]. Aerial surveys of the gulf in May–September 2000 estimated a total of 5 000 000 jellyfish over 150 km^2, equivalent to 40 000 tonnes wet weight. The greatest economic impact was clogging of shrimp nets, which contributed to millions of dollars of economic losses.

Habitat modification

Because cnidarian polyps require a hard substrate for attachment, an increase in the amount of suitable benthic habitat could theoretically lead to polyp proliferation.

Table 1. Attributes of jellyfish that enable them to survive and thrive in harsh environments

Processes	Attributes	Ecosystem implications
Feeding	Jellyfish as a group have broad diets, from protists [27–29] to fish eggs and larvae [52]	Dietary versatility enables jellyfish to survive in patchy food environments and on prey (e.g. flagellates) better than many fish; might encourage red-tide blooms, such as *Noctiluca*, by grazing their mesozooplankton competitors [77]
	Jellyfish consume prey that are stung (cnidarians) or stuck (ctenophores) that cannot escape	Even prey that escape ingestion might subsequently die because of toxins or be incapacitated and subsequently eaten
	Most large medusae cannot retract their tentacles (but ctenophores can)	Prey might continue to be killed on passive contact even when a jellyfish is not feeding
	Unlike most predators, jellyfish do not exhibit feeding satiation at natural prey densities [52]	Potential to kill large number of fish eggs and larvae
	Jellyfish can feed in turbid water	Enables jellyfish to outcompete some fish in murky coastal water [78]
	Large jellyfish have few obligate predators (e.g. sunfish, some turtles)	Limited top-down control of jellyfish, with little energy transfer from large jellyfish to higher trophic levels
Growth	Jellyfish grow faster than most other metazoans [26], equal to or faster than small fishes [79]	Respond quickly to favourable environmental conditions
	Medusae shrink when starved [52] and resume normal growth and reproduction within days of feeding [80]	Jellyfish survive starvation well, responding rapidly once favourable food conditions return, whereas fish quickly lose condition and are susceptible to predation when starved
Reproduction	Fragmented polyps regenerate [52]	Possible rapid increase in numbers when broken (e.g. following trawling disturbance)
	Ctenophores are hermaphroditic and reproduce at a young age	Populations grow exponentially under favourable conditions
Survival	Jellyfish and their polyps tolerate hypoxia [23] and some species benefit from enhanced feeding rates [31]	Continue to grow in hypoxic environments [81], such as anoxic dead zones, where few jellyfish predators survive
	Some hydrozoan polyps can 'shut down' and encyst for up to 40 years [82] under adverse conditions [52,60]	Jellyfish can persist in a system unseen, surviving adverse conditions and germinating when good conditions return [60]

Although direct evidence to support this is scant, it has been demonstrated off the coast of Taiwan [49] in association with mariculture operations. Further, Graham [9] asserts that the petroleum platforms in the Gulf of Mexico, which extend from the seafloor to the surface, provide polyps with the opportunity to attach at a depth where physical conditions are ideal for growth. Coastal development is expanding and the additional defences needed to combat future sea-level rises could result in a further increase in suitable polyp habitat.

Self-enhancing feedback: the never-ending jellyfish joyride

Jellyfish have a suite of successful attributes that enable them to survive in disturbed marine ecosystems and to rebound rapidly as conditions improve (Table 1). These attributes include a broad diet, fast growth rates, the ability to shrink when starved, the capacity to fragment and regenerate, and the ability to tolerate hypoxia. These are characteristic of opportunistic 'weed species' and would appear to give jellyfish an edge over fish in environments stressed by climate change, eutrophication and overfishing [22]. Based on many of these attributes, a mechanism can now be hypothesised to describe how local jellyfish outbreaks might spread, displace fish and thus form an alternate ecosystem state.

The most prominent regional jellyfish outbreaks of recent decades have followed collapses of formerly dominant local stocks of small filter-feeding pelagic fishes (Box 2). Thus, it is not unreasonable to suggest that jellyfish proliferations are held in check via a combination of competition for planktonic food and (perhaps) predation on ephyrae, small medusae or polyps by filter-feeding fishes. If this is the case, heavy fishing and other aspects of global change that appear to favour jellyfish could act to increase the abundance of jellyfish relative to that of filter-feeding fish until a crucial 'tipping point' [22,50,51] is reached. Here, jellyfish begin to overwhelm any significant control of their vulnerable life-cycle stages by fish predators, while progressively eliminating that control via their predation on fish eggs and larvae [52]. Moreover, as jellyfish abundance increases, successful sexual combination of planktonic reproductive products becomes more efficient. For jellyfish with entirely pelagic life cycles, this might involve infesting recirculating ocean currents, permanent eddy structures and other retention zones. For those species with obligate sessile stages, it might entail sequential colonisation of new seafloor habitat. A rapidly self-enhancing feedback loop could then ensue in which the jellyfish infestation spreads by sequentially invading habitats where fish might have formerly controlled jellyfish numbers.

Once established, a jellyfish infestation might quickly exclude competitive or predatory fish stocks, resulting in a durable regime shift in ecosystem structure and operation [51], with diverse fish communities replaced by a relative monoculture of jellyfish. As uncontrolled growth continues, local overproduction is available for export to new areas, where the jellyfish could again overwhelm resident predators and precipitate local outbreaks.

This type of feedback mechanism, where the hunted becomes the hunter, is specific to marine environments, as illustrated by Bakun and Weeks [22]: 'Imagine trying to maintain stability in an African veldt ecosystem if antelopes and zebras were to voraciously hunt and consume the young of the adult lions and cheetahs that prey on them.' The potentially durable switch to a jellyfish-dominated system is reminiscent of the ancient, rudimentary ecosystems of the Cambrian, and has convinced some authors [26,53] that human stressors are propelling marine ecosystems 'way back to the future' (Box 3).

Box 3. The jellyfish joyride: way back to the future?

Parsons and Lalli [26], building on arguments first proposed elsewhere [53,67], have speculated that anthropogenic stressors threaten to push modern marine ecosystems back to those of the Cambrian. They have suggested that climate change, eutrophication and overfishing are acting synergistically to create an environment that is reminiscent of that presumed to have existed >550 million years ago (MYA). The recently oxygenated oceans [68] of the Cambrian were warmer and more eutrophic [69] than they are today, and phytoplankton production was dominated by cyanobacteria and flagellates [70]. Fish were absent, as were most of the modern zooplankton orders [71], which only began to appear during the Mesozoic Era, and radiated during the Cenozoic at a time when diatoms and large phytoplankton cells began to dominate primary production [26]. Clupeomorph fishes, such as anchovy, herring and sardine, which currently dominate the filter-feeding fisheries globally, only appeared during the Cretaceous ~100 MYA [72].

We can trace the evolution of jellyfish back to between 540 and 500 MYA from fossil evidence [73], and possibly to the pre-Ediacaran period of >1000 MYA [74]; molecular evidence suggests that ctenophores might be at the base of all metazoan life [75]. At the time of the Cambrian, jellyfish were likely to have been among the top predators of marine systems, and although this might not have been the case since modern finfishes evolved, they have persisted, possibly as a result of a suite of attributes that makes them efficient competitors in harsh environments (Table 1, main text).

If Parsons and Lalli [26] are right, then human activities are shifting the balance from highly evolved ecosystems dominated by diatoms and fish to the more ancient, rudimentary flagellate and jellyfish-dominated systems reminiscent of the Paleozoic (Figure I). It is ironic that the same activities that are driving rapid industrialisation and technological achievements are threatening to push marine ecosystems way back to the future.

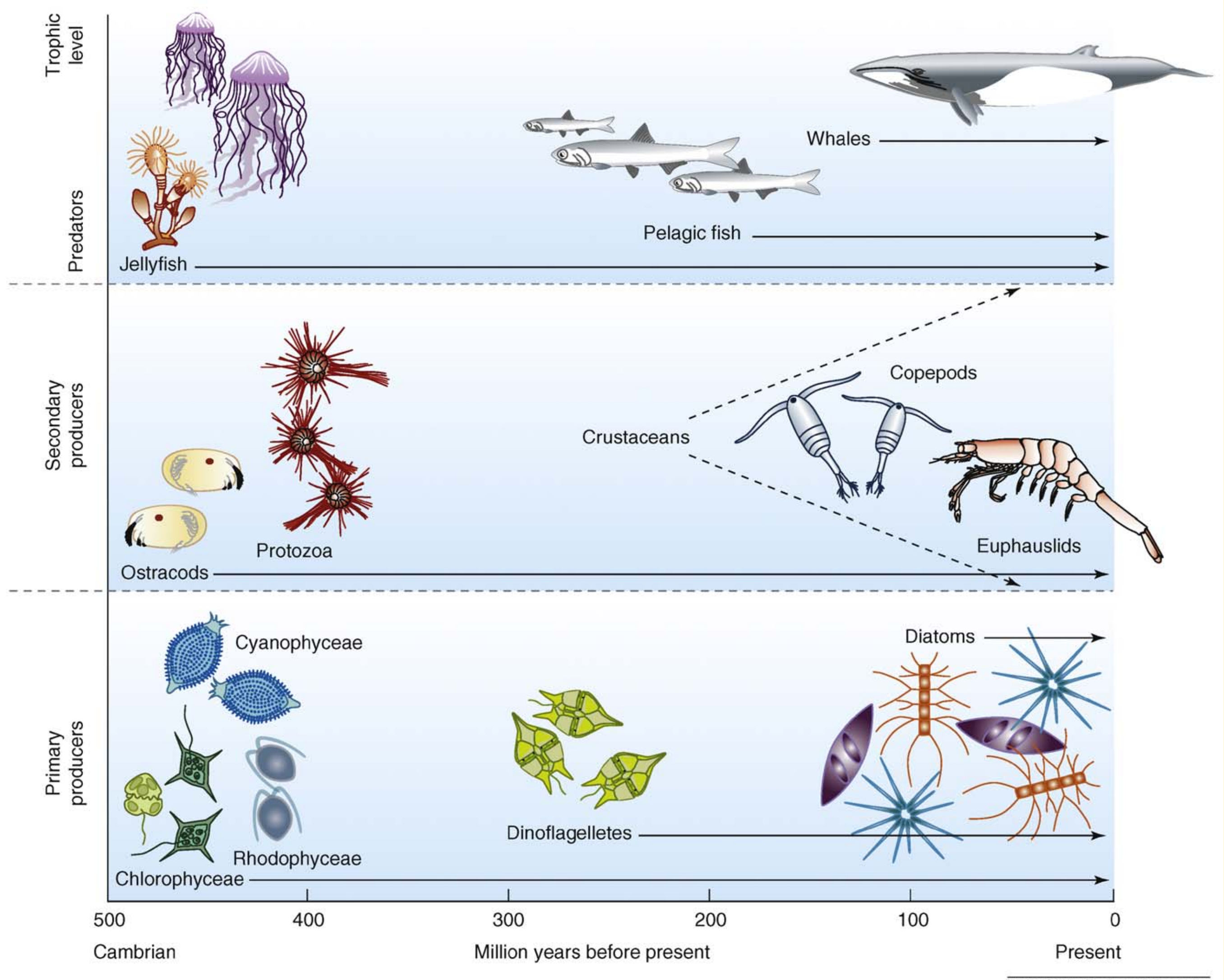

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Figure I. The evolution of pelagic food chains from the Cambrian (simple food chains, with jellyfish as the top predators) to the present (more-complex food chains, with fish and higher animals as top predators). Redrawn, with permission, from Ref. [26].

Applying the brakes: potential management responses

The synergistic impact of multiple human activities causing more-frequent jellyfish blooms is likely to require a multifaceted integrated response beyond our current traditional management of single environmental issues and of single-species fisheries [43,54]. Although high jellyfish abundances caused by cyclical climate patterns are likely to return to more normal conditions [55], ecosystems that have rapidly switched to being dominated by jellyfish because of anthropogenic stressors might not return to a pre-jellyfish state without significant intervention.

One potentially appealing response is to harvest more jellyfish for human consumption. Jellyfish are important culturally as a gourmet food in Chinese banquets, and are the ultimate modern diet food [56]. Several species of scyphozoan jellyfish with mild stings are edible, but many other species could be utilised by improving processing techniques. Unfortunately, jellyfish harvesting in isolation is unlikely to return systems to their previous state if stresses that caused the ecosystem shift remain.

Rare insight into the potential holistic management response required to reverse a jellyfish stable state is provided by the massive outbreak of the introduced ctenophore *Mnemiopsis leidyi* in the Black Sea. It was first recorded in the Black Sea in 1982, and was probably introduced via ballast discharge by ships from the east coast of the USA [10]. The historically dominant zooplanktivore in the Black Sea is the European anchovy *Engraulis encrasicolus*. During the late 1980s, annual anchovy landings in the Black Sea increased to nearly 900 000 tonnes and represented >60% of the total fishery catch of the region in 1988. In 1989, apparently as a result of this heavy exploitation, the anchovy spawning biomass declined by >85%, followed by a marked increase in zooplankton biomass in 1990, in apparent response to the reduction in grazing pressure [10]. This enhanced food source for *Mnemiopsis* would have increased its production rate, and the collapse of the

Table 2. Potential management responses and directed research required to prevent ecosystems from abruptly switching to being dominated by jellyfish, and to return those ecosystems already dominated by jellyfish to pre-jellyfish states

Management responses	Research needs	Benefits	Risks and issues
Short-term tactical time frame			
Develop jellyfish products for food and medicine	Increased research into processing and marketing of inedible species and into medicinal efficacy	New industries and improved local economies; limit impact on fish recruitment and reduce biomass of spawning jellyfish	Does not address underlying problem; depends on international markets; might increase fishing pressure on non-problem species in healthy ecosystems
Use cutting nets to destroy jellyfish in the water column	Technology is in its infancy, but research needed on possibility of regeneration, impacts of resulting organic enrichment and bycatch	Destroy jellyfish, reducing spawning biomass	Does not address underlying problem; might not switch system from one dominated by jellyfish; possibility of regeneration; might impact non-problem jellyfish species
Destructively clean artificial hard structures and prevent settlement	Accelerate development of environmentally benign chemicals for anti-fouling; identify 'polyp' beds for problem jellyfish species	Destroy benthic polyps and prevent settlement, thereby reducing jellyfish numbers	Most polyp beds yet to be found so large-scale benthic surveys needed; not practical on a large scale; threat of toxic bioaccumulation
Use of biocontrol agents	Identify potential biocontrol agents for benthic polyps. Most biocontrol research is in terrestrial systems: what theory and lessons are transferable to marine ecosystems and what needs to be developed?	Selectively control jellyfish numbers and reduce spawning biomass	Most jellyfish nonselective predators, so risk of control agent outbreaks and impact on non-problem jellyfish species
Stop jellyfish reseeding programs[a]	Assess whether jellyfish reseeding programs cause problem jellyfish blooms, especially for countries downstream	Reduce likelihood of pushing systems (including those downstream) over tipping point to one dominated by jellyfish	Economic benefits for those countries currently reseeding must be balanced against potential risks
Enforce hull-cleaning measures and ballast water protocols[b]	Develop methods to treat ballast water to kill potential invasive species and improve protocols	Minimise accidental introductions of jellyfish and polyps	Impacts on oceanic ecosystems unknown
Stop or restrict trans-regional aquarium trade in live jellyfish	Identification of jellyfish species that pose little translocation risk	Reduce likelihood of accidental introductions	Jellyfish are major attractions, but perhaps only local species should be used
Long-term strategic time frame			
Reduce eutrophication	Research into jellyfish feeding ecology, and into how ecosystem resilience is enhanced by reducing multiple stressors on marine systems	Reduce algal blooms, increase O_2 in bottom waters and favour competitors and predators of polyps such as fish	Relatively easily managed in a region (cf. climate change)
Reduce overfishing	Ongoing development of an ecosystem approach to fisheries management; research into conservation of obligate jellyfish predators, such as some turtles and sunfish	Increase competitors and predators of benthic polyps and pelagic medusae; lessen polyp fragmentation	Difficult to control, especially in the open oceans
Minimise global warming	Ongoing research supporting energy efficiency and move toward energy sources with lower greenhouse gas emissions	Favour food webs dominated by diatoms and fish rather than by flagellates and jellyfish	Requires government responses globally; already committed to substantial warming because of the amount of CO_2 already emitted

[a] For example, 414 million juvenile jellyfish were released in Liaodong Bay (China) alone in 2005 and 2006 to promote jellyfish fisheries [83].

[b] A worldwide convention adopted in 2004 now requires ships to exchange ballast water in the open ocean before entering coastal areas.

zooplanktivorous anchovy might also have lessened predation pressure on susceptible *Mnemiopsis* life stages. It was at this point that the *Mnemiopsis* population exploded. This situation was exacerbated by extensive agricultural runoff in the Black Sea that led to anoxic bottom waters [30] that were likely to have favoured jellyfish. As *Mnemiopsis* feeds on fish eggs and larvae [57], its explosive outbreak contributed to the rapid collapse of Black Sea fisheries [43].

Two fortuitous changes in human impacts have enabled the Black Sea to at least partially recover from jellyfish infestation. First, another alien ctenophore (*Beroe*) was accidentally introduced and began feeding on *Mnemiopsis* (Figure 1d), reducing the overall jellyfish biomass [16]. This suggests that directed jellyfish removal (through biocontrol, massive harvesting, jellyfish destruction or restocking of predators such as fish) is beneficial (for holoplanktonic forms at least). The second fortuitous event was the economic upheaval following the fall of communism, which curtailed fertiliser application during the 1990s, reducing nutrient runoff and enhancing oxygen concentrations [30]. In combination with continued low anchovy harvest, these events have led to reduced jellyfish biomass, fewer hypoxia events and a partial return to an ecosystem state that is more similar to that found in the Black Sea before *Mnemiopsis* was introduced [30].

This example suggests that any single management intervention is unlikely to be effective. What is needed is a combination of coping strategies and longer-term preventative responses. We outline such a multitiered approach in Table 2, including the various management responses, their benefits and risks, and the research required to underpin them.

Future research

These management levers and the targeted research outlined in Table 2 need to be supported by innovative basic research in five key areas. First, much of the evidence for jellyfish outbreaks remains anecdotal [16]. There is an urgent need to establish long-term observation programs for jellyfish, similar to the monitoring for crustacean zooplankton [58]. Enhanced jellyfish observations are now possible through recent advances in acoustic, aerial, automated underwater, diving, molecular and video methods [59]. Such data provide indicators of jellyfish outbreaks and should be included in programs monitoring ecosystem health [6]. Proxy time series of jellyfish abundance might be possible from statoliths deposited in sediments, and could be efficiently located and counted using molecular markers.

Second, there needs to be more fundamental research on jellyfish ecology, their complex life cycles and ecosystem roles. We know neither the appearance nor location of the polyp stage for most species. A key question is whether the proliferation of hard structures around our coastlines is leading to more jellyfish outbreaks and, if so, for which species. Our knowledge of jellyfish diet is limited to a relatively small number of species, and it is essential to expand these temporally, spatially and across jellyfish taxa to model their dynamics and ecosystem linkages. Information on jellyfish predators is improving with new online databases [1], and this information might prove crucial for understanding processes controlling jellyfish numbers. It seems reasonable to presume that jellyfish are usually held in check by fish predation, but are they? Gathering knowledge on basic jellyfish ecology is hampered by the scarcity of scientists with an active research interest [6], a direct consequence of meagre funding in this area.

Third, expanded experimental work on jellyfish is needed to determine basic rate processes and effects of climate change. Despite the challenges of rearing jellyfish in the laboratory [6], knowledge of the impact of different temperatures on physiological processes of medusae and polyps is crucial. There is a need for laboratory experiments focussing on the sensitivity to pH of jellyfish statoliths and more directed work on polyp regeneration and encystment. There is even a shortage of basic information such as the growth efficiencies of jellyfish.

Fourth, few marine ecosystem models currently include jellyfish [1], and those that do rarely capture their complex life history and ecology [60] that is needed to simulate possible alternate fish–jellyfish stable states. Models focussed on jellyfish will help answer questions concerning the relative importance of fish and invertebrate predation and competition in holding jellyfish populations in check. Models must also be developed to include system stressors (e.g. fishing, eutrophication and global warming), so that virtual experiments can be conducted to assess the relative importance of these stressors, explore ecosystem resilience and evaluate different management strategies.

Last, a research area that has the potential for considerable human benefit and would help support basic jellyfish research is investigation of the efficacy of many traditional medicinal uses of jellyfish [56]. Jellyfish have been used to alleviate, cure or improve an array of ailments, including arthritis, bronchitis, burns, fatigue, gout, hypertension, menstruation pain and ulcers. Recent studies have confirmed that jellyfish collagen suppresses arthritis in laboratory rats [56] and stimulates autoimmune and inflammatory responses in humans [61], but most traditional medicinal uses remain untested.

Conclusion

Once on the ‘jellyfish joyride’, management actions appear to be difficult and uncertain, so the precautionary approach suggests that emphasis needs to be placed on prevention rather than cure. Directed and concerted early action could be crucial to avert large-scale alteration of pelagic ecosystems. The potential replacement of fisheries resources by jellyfish in many regions is concerning in a world with an expanding population in developing countries dependent upon protein from the sea. A sobering quote from Daniel Pauly, possibly the most widely cited fisheries biologist, portends the future if we do not act proactively and in an integrated fashion to apply the brakes on the jellyfish joyride: ‘My kids will tell their children: eat your jellyfish!’ [62].

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References

1 Pauly, D. *et al.* (2009) Jellyfish in ecosystems, online databases and ecosystem models. *Hydrobiologia* 616, 67–85
2 Houghton, J.D.R. *et al.* (2006) Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. *Ecology* 87, 1967–1972
3 Lynam, C.P. and Brierley, A.S. (2007) Enhanced survival of 0-group gadoid fish under jellyfish umbrellas. *Mar. Biol. (Berl.)* 150, 1397–1401
4 Fisheries, Aquaculture Information, Statistics Service (1999) *FishStatPlus.* FAO
5 Graham, W.M. *et al.* (2001) A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia* 451, 199–212
6 Hay, S. (2006) Marine ecology: gelatinous bells may ring change in marine ecosystems. *Curr. Biol.* 16, R679–R682
7 Link, J.S. and Ford, M.D. (2006) Widespread and persistent increase of Ctenophora in the continental shelf ecosystem off NE USA. *Mar. Ecol. Prog. Ser.* 320, 153–159
8 Mills, C.E. (2001) Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* 451, 55–68
9 Graham, W.M. (2001) Numerical increases and distributional shifts of *Chrysaora quinquecirrha* (Desor) and *Aurelia aurita* (Linne) (Cnidaria: Scyphozoa) in the northern Gulf of Mexico. *Hydrobiologia* 451, 97–111
10 Shiganova, T.A. (1998) Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. *Fish. Oceanogr.* 7, 305–310
11 Lynam, C.P. *et al.* (2006) Jellyfish overtake fish in a heavily fished ecosystem. *Curr. Biol.* 16, R492–R493
12 Ishii, H. and Tanaka, F. (2001) Food and feeding of *Aurelia aurita* in Tokyo Bay with an analysis of stomach contents and a measurement of digestion times. *Hydrobiologia* 451, 311–320
13 Uye, S. and Shimauchi, H. (2005) Population biomass, feeding, respiration and growth rates, and carbon budget of the scyphomedusa *Aurelia aurita* in the Inland Sea of Japan. *J. Plankton Res.* 27, 237–248
14 Kang, Y.S. and Park, M.S. (2003) Occurrence and food ingestion of the moon jellyfish (Scyphomoa: Ulmariidae: *Aurelia aurita*) in the southern coast of Korea in summer. *J. Korean Soc. Oceanogr.* 8, 199–202
15 Xian, W. *et al.* (2005) Jellyfish blooms in the Yangtze Estuary. *Science* 307, 41
16 Purcell, J.E. *et al.* (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Mar. Ecol. Prog. Ser.* 350, 153–174
17 Brierley, A.S. *et al.* (2001) Acoustic observations of jellyfish in the Namibian Benguela. *Mar. Ecol. Prog. Ser.* 210, 55–66
18 Pauly, D. and Watson, R. (2003) Counting the last fish. *Sci. Am.* 289, 42–47
19 Mullon, C. *et al.* (2005) The dynamics of collapses in world fisheries. *Fish Fish.* 6, 111–120
20 Purcell, J.E. and Arai, M.N. (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia* 451, 27–44
21 Bakun, A. and Weeks, S.J. (2004) Greenhouse gas buildup, sardines, submarine eruptions and the possibility of abrupt degradation of intense marine upwelling ecosystems. *Ecol. Lett.* 7, 1015–1023
22 Bakun, A. and Weeks, S.J. (2006) Adverse feedback sequences in exploited marine systems: are deliberate interruptive actions warranted? *Fish Fish.* 7, 316–333
23 Purcell, J.E. *et al.* (2001) Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a review. In *Coastal Hypoxia: Consequences for Living Resources and Ecosystems* (Rabalais, N.N. and Turner, R.E., eds), pp. 77–100, American Geophysical Union
24 Harashima, A. *et al.* (2006) Verification of the silica deficiency hypothesis based on biogeochemical trends in the aquatic continuum of Lake Biwa - Yodo River - Seto Inland Sea, Japan. *Ambio* 35, 36–42
25 Cushing, D.H. (1989) A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. *J. Plankton Res.* 11, 1–13
26 Parsons, T.R. and Lalli, C.M. (2002) Jellyfish population explosions: revisiting a hypothesis of possible causes. *Mer. (Paris)* 40, 111–121
27 Malej, A. *et al.* (2007) Direct and indirect trophic interactions of *Aurelia* sp (Scyphozoa) in a stratified marine environment (Mljet Lakes, Adriatic Sea). *Mar. Biol. (Berl.)* 151, 827–841
28 Colin, S.P. *et al.* (2005) Omnivory by the small cosmopolitan hydromedusa *Aglaura hemistoma*. *Limnol. Oceanogr.* 50, 1264–1268
29 Sullivan, L.J. and Gifford, D.J. (2004) Diet of the larval ctenophore *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). *J. Plankton Res.* 26, 417–431
30 Diaz, R.J. and Rosenburg, R. (2008) Spreading dead zones and consequences for marine ecosystems. *Science* 321, 926–929
31 Decker, M.B. *et al.* (2004) Effects of low dissolved oxygen on zooplankton predation by the ctenophore *Mnemiopsis leidyi*. *Mar. Ecol. Prog. Ser.* 280, 163–172
32 Rabalais, N.N. *et al.* (2002) Beyond science into policy: Gulf of Mexico hypoxia and the Mississippi River. *Bioscience* 52, 129–142
33 Gibbons, M.J. and Richardson, A.J. (2008) Patterns of pelagic cnidarian abundance in the North Atlantic. *Hydrobiologia* 616, 51–65
34 Ridgway, K.R. (2007) Long-term trend and decadal variability of the southward penetration of the East Australian Current. *Geophys. Res. Lett.* 34, 1–5
35 Cai, W. *et al.* (2005) The response of the Southern Annular Mode, the East Australian Current, and the southern mid-latitude ocean circulation to global warming. *Geophys. Res. Lett.* 32, L23706
36 Poloczanska, E.S. *et al.* (2007) Climate change and Australian marine life. *Oceanogr. Mar. Biol. Annu. Rev.* 45, 407–478
37 Attrill, M.J. *et al.* (2007) Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. *Limnol. Oceanogr.* 52, 480–485
38 Richardson, A.J. and Gibbons, M.J. (2008) Are jellyfish increasing in response to ocean acidification? *Limnol. Oceanogr.* 53, 2040–2045
39 Lynam, C.P. *et al.* (2004) Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. *Limnol. Oceanogr.* 49, 637–643
40 Raskoff, K.A. (2001) The impact of El Niño events on populations of mesopelagic hydromedusae. *Hydrobiologia* 451, 121–129
41 Anderson, P.J. and Piatt, J.F. (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar. Ecol. Prog. Ser.* 189, 117–123
42 Graham, W.M. and Bayha, K.M. (2007) Biological invasions by marine jellyfish. In *Biological Invasions (Ecological Studies)* (Vol. 193) (Nentwig, W., ed.), In pp. 239–256, Springer-Verlag
43 Daskalov, G.M. *et al.* (2007) Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proc. Natl. Acad. Sci. U. S. A.* 104, 10518–10523
44 Zaitsev, Y.P. (1992) Recent changes in the trophic structure of the Black Sea. *Fish. Oceanogr.* 1, 180–189
45 Stone, R. (2005) Science in Iran—attack of the killer jellies. *Science* 309, 1805–1806
46 Daskalov, G.M. and Mamedov, E.V. (2007) Integrated fisheries assessment and possible causes for the collapse of anchovy kilka in the Caspian Sea. *ICES J. Mar. Sci.* 64, 503–511
47 Boersma, M. *et al.* (2007) The first occurrence of the ctenophore *Mnemiopsis leidyi* in the North Sea. *Helgol. Mar. Res.* 61, 153–155
48 Haslob, H. *et al.* (2007) Invading *Mnemiopsis leidyi* as a potential threat to Baltic fish. *Mar. Ecol. Prog. Ser.* 349, 303–306
49 Lo, W.T. *et al.* (2008) Enhancement of jellyfish (*Aurelia aurita*) populations by extensive aquaculture rafts in a coastal lagoon in Taiwan. *ICES J. Mar. Sci.* 65, 453–461
50 Hughes, T.P. *et al.* (2005) New paradigms for supporting the resilience of marine ecosystems. *Trends Ecol. Evol.* 20, 380–386
51 Bakun, A. (2006) Wasp-waist populations and marine ecosystem dynamics: navigating the "predator pit" topographies. *Prog. Oceanogr.* 68, 271–288
52 Arai, M.N. (1997) *A Functional Biology of Scyphozoa.* Chapman & Hall
53 Parsons, T.R. (1979) Some ecological, experimental and evolutionary aspects of the upwelling system. *S. Afr. J. Sci.* 75, 536–540
54 Jackson, J.B.C. *et al.* (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–638
55 Brodeur, R.D. *et al.* (2008) Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. *Prog. Oceanogr.* 77, 103–111
56 Hsieh, Y.H.P. *et al.* (2001) Jellyfish as food. *Hydrobiologia* 451, 11–17

57 Rapoza, R. *et al.* (2005) Life-stage dependent, in situ dietary patterns of the lobate ctenophore Mnemiopsis leidyi Agassiz 1865. *J. Plankton Res.* 27, 951–956
58 Hays, G.C. *et al.* (2005) Climate change and marine plankton. *Trends Ecol. Evol.* 20, 337–344
59 Purcell, J.E. (2009) Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. *Hydrobiologia* 616, 23–50
60 Boero, F. *et al.* (2008) Gelatinous plankton: irregularities rule the world (sometimes). *Mar. Ecol. Prog. Ser.* 356, 299–310
61 Sugahara, T. *et al.* (2006) Immunostimulation effect of jellyfish collagen. *Biosci. Biotechnol. Biochem.* 70, 2131–2137
62 Weiss, K.R. (2006) A primeval tide of toxins. *LA Times*, 30 July
63 Day, M. *et al.* (2007) The phylum Cnidaria: a review of phylogenetic patterns and diversity 300 years after Linnaeus. *Zootaxa* 1668, 127–182
64 Schwartzlose, R.A. *et al.* (1999) Worldwide large-scale fluctuations of sardine and anchovy populations. *S. Afr. J. Mar. Sci.* 21, 289–347
65 Kawasaki, T. (1993) Recovery and collapse of the Far Eastern sardine. *Fish. Oceanogr.* 2, 244–253
66 Donnelly, C.P. *et al.* (2003) Possible effects of pollock and herring on the growth and reproductive success of Steller sea lions (*Eumetopias jubatus*): insights from feeding experiments using an alternative animal model, *Rattus norvegicus*. *Br. J. Nutr.* 89, 71–82
67 Greve, W. and Parsons, T.R. (1979) Photosynthesis and fish production: hypothetical effects of climatic change and pollution. *Helgol. Wiss. Meeresunters.* 30, 666–672
68 Fike, D.A. *et al.* (2006) Oxidation of the Ediacaran Ocean. *Nature* 444, 744–747
69 Brasier, M.D. (1992) Nutrient-enriched waters and the early skeletal fossil record. *J. Geol. Soc. London* 149, 621–629
70 Butterfield, N.J. (1997) Plankton ecology and the Proterozoic-Phanerozoic transition. *Paleobiology* 23, 247–262
71 Rigby, S. and Milsom, C.V. (2000) Origins, evolution, and diversification of zooplankton. *Annu. Rev. Ecol. Syst.* 31, 293–313
72 Maisey, J.G. (1991) *Santana Fossils: An Illustrated Atlas.* TFH Publications
73 Cartwright, P. *et al.* (2007) Exceptionally preserved jellyfishes from the Middle Cambrian. *PLoS ONE* 2, 1121–1127
74 Shukla, M. *et al.* (1991) Pre-Ediacaran fossil assemblages from India and their evolutionary significance. *Geol. Soc. India Mem.* 20, 169–179
75 Dunn, C.W. *et al.* (2008) Broad phylogenomic sampling improves resolution of the animal tree of life. *Nature* 452, 745–749
76 Collins, J. (2006) *Cool Waters, Emerald Seas.* Atrium
77 Pitt, K.A. *et al.* (2007) Jellyfish modify the response of planktonic assemblages to nutrient pulses. *Mar. Ecol. Prog. Ser.* 351, 1–13
78 Eiane, K. *et al.* (1999) Fish or jellies—a question of visibility? *Limnol. Oceanogr.* 44, 1352–1357
79 Palomares, M.L.D. and Pauly, D. (2009) The growth of jellyfishes. *Hydrobiologia* 616, 11–21
80 Hamner, W.M. and Jenssen, R.M. (1974) Growth, degrowth, and irreversible cell-differentiation in *Aurelia aurita*. *Am. Zool.* 14, 833–849
81 Grove, M. and Breitburg, D.L. (2005) Growth and reproduction of gelatinous zooplankton exposed to low dissolved oxygen. *Mar. Ecol. Prog. Ser.* 301, 185–198
82 Bouillon, J. *et al.* (2004) Fauna of the Mediterranean Hydrozoa. *Sci. Mar.* 68, 5–449
83 Dong, J. *et al.* (2008) Stock enhancement of the edible jellyfish (*Rhopilema esculentum* Kishinouye) in Liaodong Bay, China: a review. *Hydrobiologia* 616, 113–118

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