The Jelly Ocean

Predicting the future roles of gelatinous plankton in ocean food webs

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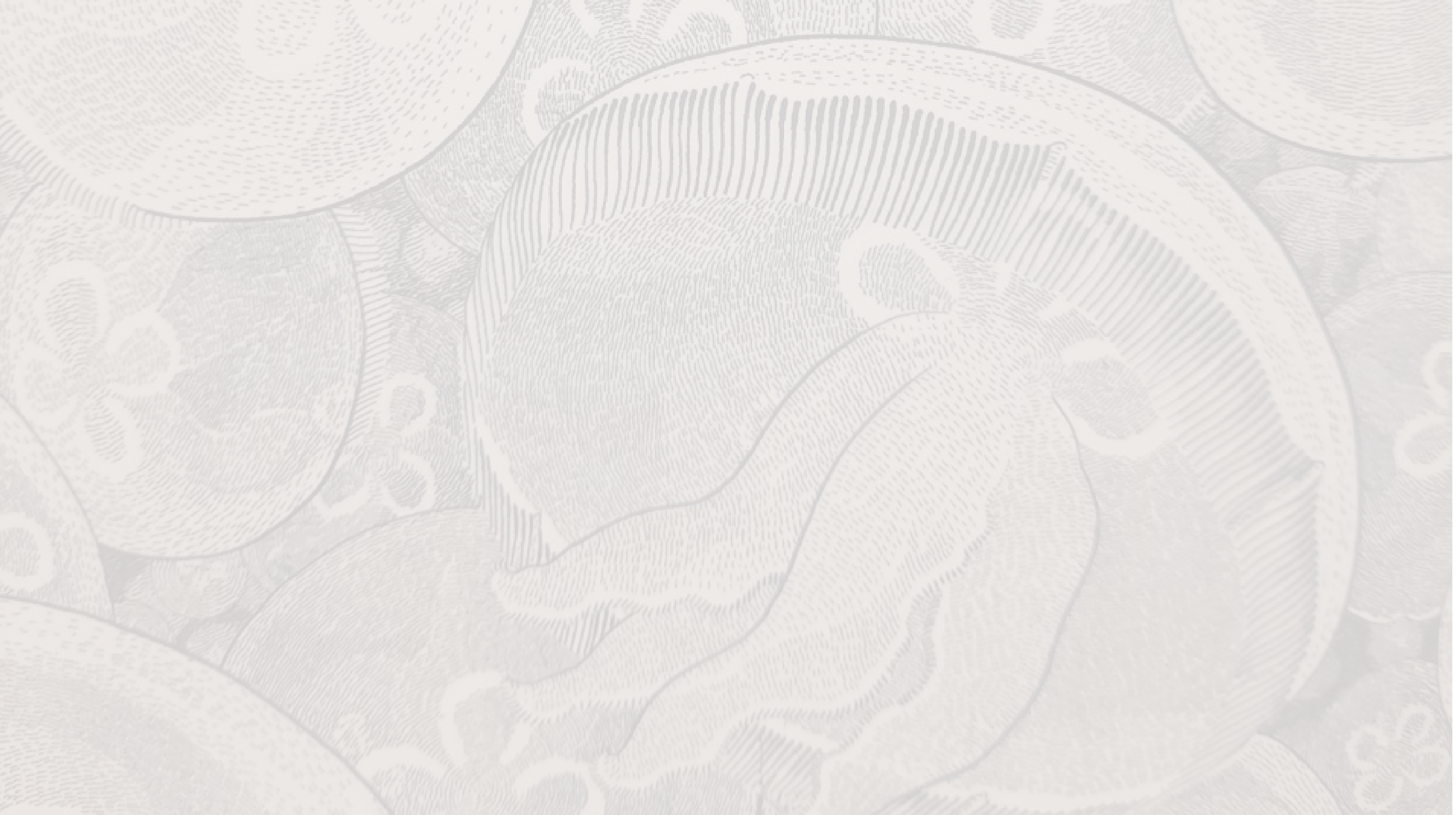

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Abstract

Jellyfish (gelatinous zooplankton encompassing species from various taxa) have historically been viewed as a trophic dead-end. However, a recent apparent increase in jellyfish bloom size and frequency has sparked interest in the way jellyfish interact with other species in the ocean food web. By summarizing the current knowledge on these interactions it is clear that jellyfish are not a trophic dead-end, but an important linkage in food webs as prey, predator, competition and part of the carbon pump. A change in jellyfish abundance is therefore likely to greatly impact various ecosystems and species. This calls for the implementation of jellyfish in ecosystem-based management and predictive models. To fill in knowledge gaps standing in the way of such implementation further regional, species specific monitoring of jellyfish is required.

Introduction

Understanding the role of all links in marine food webs is essential in future efforts in regulating ocean ecosystems. However, there are still plenty of species of which their roles and relations to other species are relatively unknown (Link, 2007 and references within). Scientific interest is often primarily aimed at species with a high economic value (either for consumption or as a tourist attraction), who are considered a key-stone species, or who show a strong decline in abundance. But overlooking species is something to watch out for, as there have been plenty of instances where previously considered unimportant species turned out to have major effects on their surroundings (Link, 2007; Nunoo et al, 2009). One of the groups that has been historically overlooked are a group of gelatinous zooplankton, commonly known as jellyfish. The definition of jellyfish is still quite broad, but Gibbons & Richardson, 2013 proposed only using this definition for members of the Medusozoa and Ctenophora taxa who inhabit the pelagic zone (Table 1). In these taxa there are species of which the life history and ecology is fairly well researched (Lucas, 2001; Hubbot et al, 2017; Schnedler-Meyer et al, 2018; Goldstein & Steiner, 2019), but they are not routinely monitored as other marine species are.

Table 1 : the terms *Jellyfish* and gelatinous zooplankton are not synonymous to each other. Ctenophora, Medusozoa and Thaliacea are all gelatinous zooplankton with a high water content. But, since they differ in various, fundamental ways as this table describes (including physiology, habitat, biology and ecology, and possible interaction with and effect on humans and their affairs such as fisheries) they cannot all be grouped together as *jellyfish*. Based on this information Gibbons & Richardson proposed using the term *jellyfish* exclusively for pelagic Ctenophora and Medusozoa as they are most comparable in their digestive and nervous systems, occupy a similar habitat (shelf and coast), their impact on humans resembles each other and are expected to have convergent responses to anthropogenic drivers.[a]Excluding Platyctenida. [b]Most Scyphozoa and Cubozoa, some Hydrozoa; ?, unknown.

	Taxon		
	Medusozoa	**Ctenophora**[a]	**Thaliacea**
	e.g. *Pelagia, Nemopilema, Chironex, Aequorea*	**e.g. *Mnemiopsis***	**e.g. *Salpa, Pyrosoma***
Environment	Meroplanktic[b]	Holoplanktic	Holoplanktic
Habitat where they form blooms	Coastal and shelf	Coastal and shelf	Shelf and oceanic

Reproduction	Benthic polyp, asexual; pelagic medusa sexual	Sexual; hermaphroditic	Alternating sexual and asexual zooids
Nervous system	Simple	Simple	Complex
Closed digestive system	No	No	Simple
Diet	Protists—vertebrates	Protists—vertebrates	Bacteria—protists
Impacts			
Coastal plant	Yes	Yes	No
Vessels at sea	Yes	?	Yes
Fishing operations	Yes	?	No
Fish populations	Yes: directly and indirectly	Yes: directly and indirectly	?: indirectly
Fish kills	Yes	No	No
Tourism	Yes	?	No
Health	Yes	No	No
Anthropogenic drivers			
Sprawl	Yes: polyps	No	No
Invasives	Yes: e.g. *Phyllorhiza punctata*	Yes: e.g. *Mnemiopsis leidyi*	No
Fishing	Yes: reduction in predation and competition release niche space	Yes: reduction in predation and competition release niche space	Unknown but unlikely: reduction in predation; not known competitors with fish
Eutrophication	Yes: change in size structure of food web, increase in prey base; increase in turbidity	Yes: change in size structure of food web, increase in prey base; increase in turbidity	No: increased prey base irreversibly clogs gills, leading to "starvation"
Ocean warming	Yes: stratification reduces size structure of food base; warming encourages polyp proliferation and faster medusa growth rates	Yes: stratification reduces size structure of food base; warming leads to faster individual, and likely population, growth rates	Yes: stratification reduces size structure of food base; warming leads to faster individual and population growth rates
Hypoxia	Yes: polyps and medusae tolerant to some hypoxia; polyps can encyst	Yes: ctenophores tolerate, and continue to feed; but growth rates reduced	Unlikely: high oxygen demand as zooids move and feed near constantly

note. From: "Beyond the jellyfish joyride and global oscillations: advancing jellyfish research" by Mark J. Gibbons, Anthony J. Richardson in *Journal of Plankton Research*, Volume 35, Issue 5, September/October 2013, Pages 929–938, https://doi.org/10.1093/plankt/fbt063

This might have to do with jellyfish having been historically seen as a “trophic dead-end”: it was assumed that, due to the low energy density of jellyfish, predators would prefer to eat other prey (Verity & Smetacek, 1996). However, they are recently gaining interest due to jellyfish blooms that seem to be higher in frequency and in number. Which becomes very apparent when looking at the the abundance of jellyfish showing up in fish landings. (Brotz et al. 2012; Condon et al. 2013) (Figure 1). Population fluctuations are not uncommon in a lot of jellyfish species, but the recent blooms have resulted in negative interactions with society by stinging swimmers, clogging aquaculture installations and blocking aquatic infrastructure such as cooling pipes (Purcell, 2012).

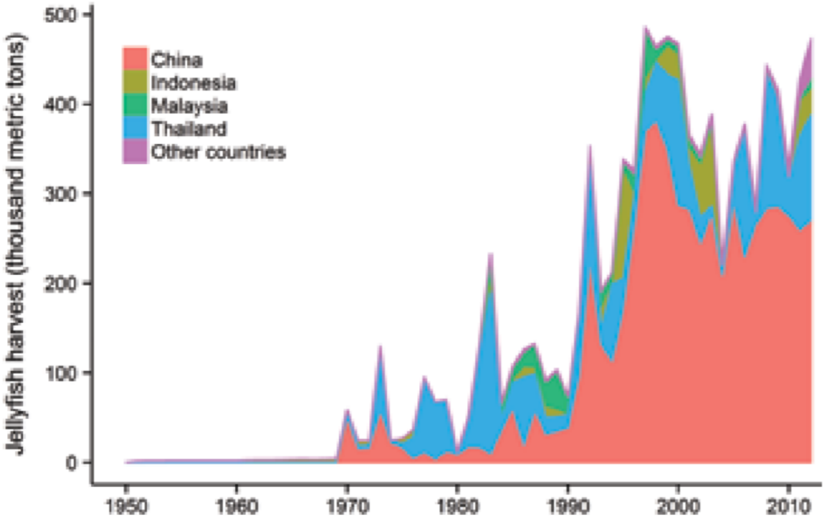


Figure 1 Landings of jellyfish from 1950 to 2012 by country (adapted from the Food and Agriculture Organization of the United Nations; www.fao.org/fishery/statistics/software/fishstatj/ en).

Aside from these direct interactions with humans there also seems to be a connection between increased jellyfish abundance and drops in commercial fish stocks (Cowan & Haude, 1993; Purcell and Arai, 2001; Angel et al, 2016). The blooms have even significantly impacted marine ecosystems through this alteration of community structure and thus disrupting the normal path with which energy flows through the system (Richardson et al. 2009; Utne-Palm et al. 2010).

The health and stability of marine ecosystems is a necessity for food security, economic development and species conservation. In order to preserve this the monitoring of just the economically interesting species is not sufficient and food web linkages (including jellyfish) ought to be included in research and predictive models (Pitcher et al., 2009; Chiaverano 2016; Lamb et al., 2019).

This essay is therefore aimed to present the current knowledge on the role of jellyfish in the marine food web and to predict the way trophic pathways might be altered by increasing jellyfish blooms. Aside from that the final section will be dedicated to current knowledge gaps that require further research in order to make models used for ecosystem-based management more precise.

Background on jellyfish, their life history and recent changes in abundance

Gelatinous plankton, more commonly known as jellyfish, is a term encompassing many species. Jellyfish are widespread and each species has a unique ecology and relation to other species and its environment. Not all species are as well researched as others, mainly species that have many interactions with humans or with other species of interest are studied. To gain the correct knowledge on the role of jellyfish in each environment research would have to be done on separate species, but as this knowledge is currently lacking, this essay will focus on the global trends and phenomena observed in jellyfish. This is in an attempt to summarize evidence of jellyfish affecting ecosystems and food webs in general, providing an incentive to look closer at the roles of separate species.

Firstly it is important to look at the life history of jellyfish as they inhabit different environments during their life, thus also playing different roles in the food web. Although species have their differences, the majority follows a similar, but complex, life cycle. In an extremely simplified scenario the medusa phase (the adult jellyfish) mainly reproduces sexually by releasing eggs and sperm in the water, with fertilized eggs then starting the planula larval stage. Planula larvae turn into polyps that are primarily sessile, but can float freely in some species. The polyp stage can last years depending on environmental conditions. When conditions are favourable the polyp can reproduce asexually, forming many buds each having the potential to become an ephyra larvae by separating itself from the polyp. The ephyra larvae live free floating and can then develop into the adult medusa stage once more. The transitions to different stages are triggered by a variety of environmental (light, nutrients) and hormonal factors. (Strauss, 2020)

The complexity of this life cycle causes the jellyfish to interact in a variety of ways with different species in each of the life cycle stages. It also means that increases in number can be caused by higher reproduction rates in the polyp phase and the medusa stage, and/or by higher survival rates in the planula and ephyra larval stages. A big issue in monitoring the role of the jellyfish, is that they are often unnoticed until they are in the medusae stage.

As mentioned previously a higher frequency of jellyfish outbreaks have been observed worldwide (Graham, 2001; Mills, 2001; Link & Ford 2006; Lynam et al., 2006), with increases in blooms mainly appearing in the coastal waters of the Far East (Kang & Park, 2003; Uye & Shimauchi, 2005; Xian et al., 2005). Brotz et al., 2012 compiled data from fishery landings using Large Marine Ecosystem (LME) creating a map displaying where on the globe jellyfish populations seem to increase (Figure 3)

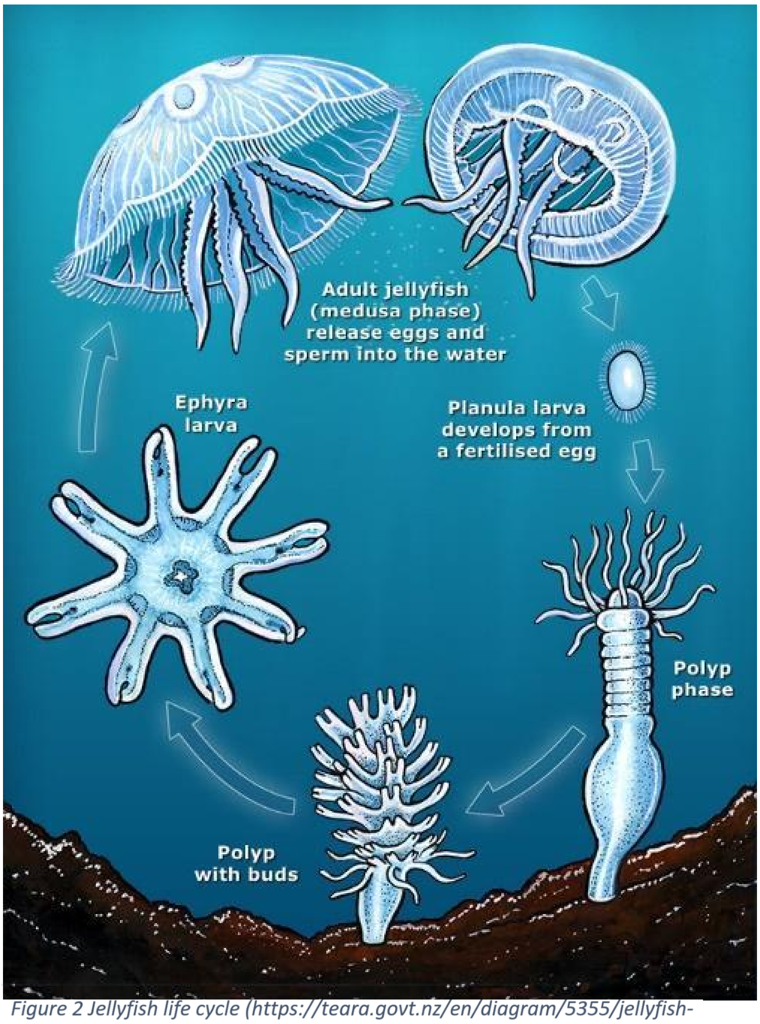


Figure 2 Jellyfish life cycle (https://teara.govt.nz/en/diagram/5355/jellyfish-life-cycle

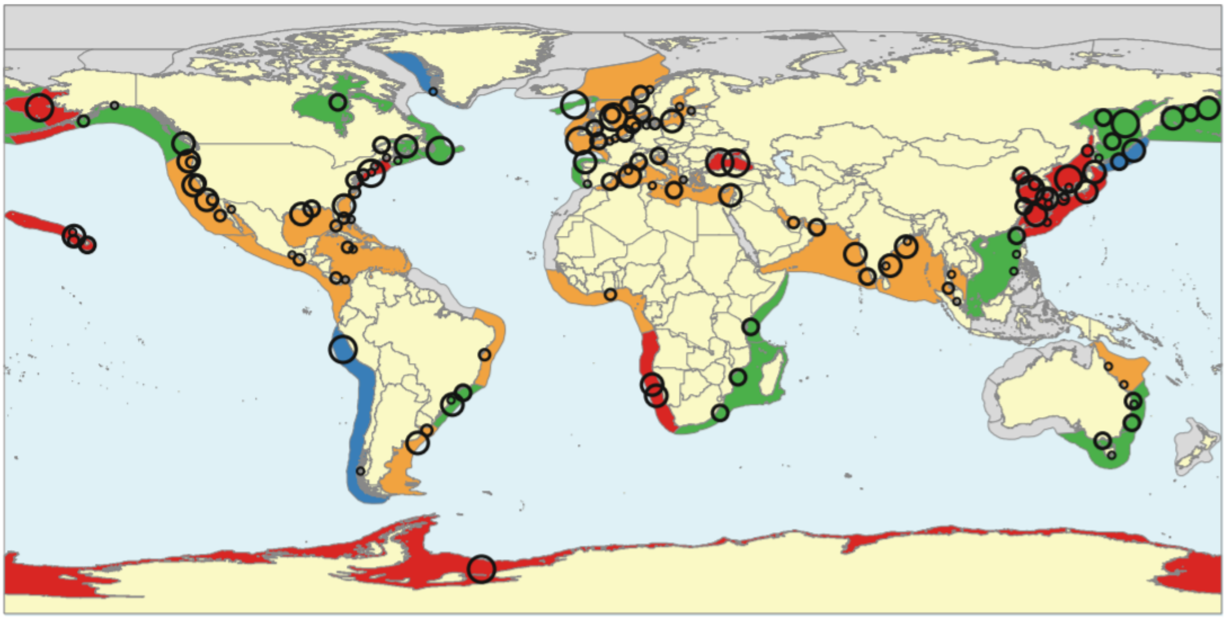


Figure 3 Brotz et al., 2012 Created a map of population trends of native and invasive species of jellyfish by LME. Red increase (high certainty), orange increase (low certainty), green stable/variable, blue decrease, grey no data. Circles represent discrete chronicles with relative sizes reflecting the Confidence Index. Circle locations are approximate, as some were shifted to avoid overlap; the circle for the Antarctic LME summarizes circumpolar observations

There are a variety of phenomena considered to be responsible for this observed increase of jellyfish. Some of them directly related to the food web, others not so much. All potential causes are summarised in figure 4 and explained in short here

1. Overfishing : Not only do jellyfish and regular fish compete for zooplankton, fish are also known to predate on polyps, ephyrae and even smaller individuals of jellyfish (Pucell & Arai 2001). By removing competition and predators the jellyfishes' survival increases. The interaction between jellyfish and foraging fish and predators and effects of overfishing will be further examined later on.
2. Translocations : exchanges of ballast water (which contains organisms) can cause certain organisms to be introduced to new habitats (Graham & Bayka, 2007). In systems where planktivorous fish were overexploited, the introduction of jellyfish by means of ballast water has led to strong increases of jellyfish abundance (Daskalov et al., 2007). Most notoriously was the introduction of the spotted jellyfish (*Phyllorhiza punctata*) from the Pacific Ocean into the Gulf of Mexico through translocation (Graham & Bayka, 2007) Through aerial surveys in 2000 from May to September a total of 5 million jellyfish spread over 150 km2 were estimated. This equates to 40000 tonnes in wet weight. The blooms were so massive that they would clog shrimp nets, resulting in millions of dollars in economic losses.
3. Eutrophication : Eutrophication in coastal zones enables phytoplankton blooms, which can lead to jellyfish blooms (Purcell et al. 2001). In some ecosystems an environment with low silicate concentration and increased nitrogen and phosphorus concentrations seems to favour non-siliceous phytoplankton (primarily flagellates) over diatoms (Harashima et al. 2006). This shift in species of primary production also alters the species in secondary production (Cushing, 1989), altering the food web in a way that seems to benefit jellyfish as they are better at predating these species than other fish are (Parsons &Lalli, 2002; Sullivan & Gifford,

2004; Colin et al., 2005; Malej et al., 2007). The blooms caused by eutrophication also have an effect on the oxygen availability of the environment; blooms can sink to the seafloor, where the degradation by bacteria results in local benthic hypoxia (Dias & Rosenburg, 2008). Jellyfish and their polyps tolerate hypoxia (Purcell et al., 2001) and some species benefit from enhanced feeding rates (Decker et al., 2004). Enhanced feeding success in low-oxygen environments because its less-tolerant prey (copepods) are more vulnerable to predation [Decker et al. 2004]. With the number of dead zones worldwide having doubled each decade since the 1960s, primarily owing to eutrophication (In 2008 there was 245,000 square kilometres of deadzone) (Dias & Rosenburg, 2008), there is an increasing number of habitats available that are more suitable for jellyfish than for fish.

4. Climate change : Global warming results in more environments with strong water column stratification. This divide in a warmer, low-nutrient top layer and a colder, nutrient-rich lower layer could create an environment that once again benefits flagellates as they can move vertically whereas diatoms cannot (Cushing, 1989). As mentioned already in the section on eutrophication, a flagellate based food web tends to favour jellyfish further down the web (Parsons & Lalli, 2002). Apart from the effects of global warming on the food web, ephyarae production and medusa growth seem to be accelerated by warmer temperatures (Purcell et al., 2007). A review by Purcell et al. 2007 looked at 15 species of temperate jellyfish and found that 11 of those species were higher in abundance during periods of warmer water.
5. Habitat modification : The polyps of jellyfish require a hard substrate, meaning that an increase in such habitats could increase polyp proliferation. Direct evidence for this process is still limited, but it has been demonstrated in the coastal zones of Taiwan (Lo et al., 2008). Furthermore, petroleum platforms seem to be an excellent place for polyps to adhere to, as they can attach themselves to the depth most suitable to them (Graham, 2001). With ever increasing numbers of coastal projects, the number of habitats attractive to polyps could also increase.

The dangerous side of these processes is that they could create a feedback loop resulting in an alternative stable state, shifted to a more gelatinous ocean. This loop is further explained later on.

With these processes in mind, each potential relation of jellyfish in a food web will be discussed and predictions on future shifts in these food webs will be made. This includes competition with foraging fish, predation on jellyfish and bloom-waste sinking to the ocean floor. Different linkages will first be discussed separately to keep things simple. But the entire web will be put together in a later paragraph to provide a more in depth understanding of the importance of jellyfish.

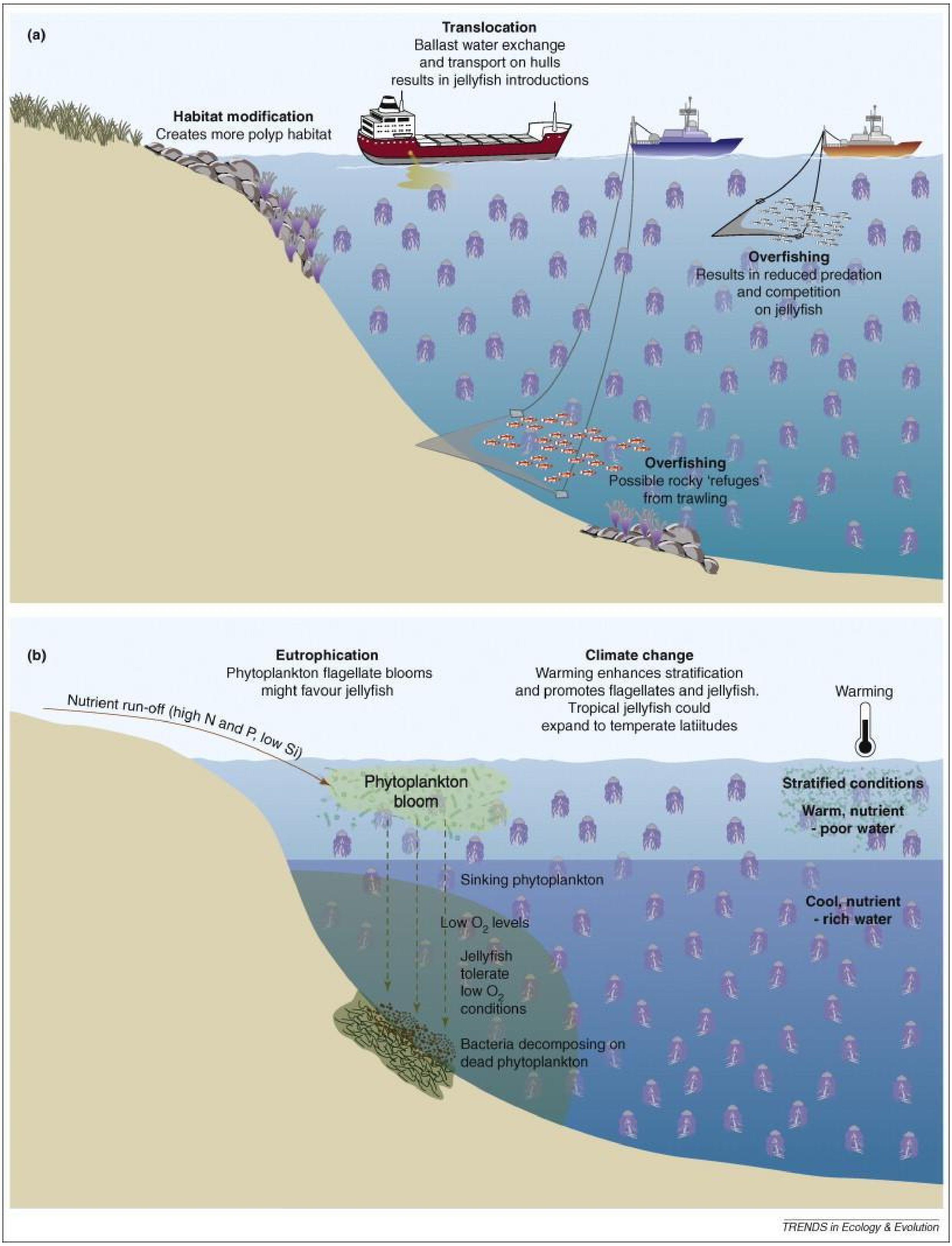


Figure 4 Probable mechanisms promoting jellyfish outbreaks. (a) Summary of the impacts of habitat modification, translocations and overfishing on jellyfish outbreaks; (b) Summary of the impacts of eutrophication and climate change on jellyfish outbreaks. Jellyfish symbols represent jellyfish blooms. From Richards et al. 2009

Jellyfish and competing fishes

The first interaction to be described is the competition between jellyfish and foraging fish. This interaction potentially could have major impacts on entire oceanic food webs and cause a shift towards a gelatinous zooplankton dominated system in the future. A shift that will then affect all other relations between jellyfish and other species.

There seemed to have been an equilibrium between small filter-feeding pelagic fish and jellyfish that is upheld by them competing for food and both feeding on the others eggs and larvae. Jellyfish being capable of consuming >30% of fish egg or larvae during periods of jellyfish bloom (Purcell and Arai, 2001). Modelling studies imply that significant quantities of biomass and energy can flow through jellyfish, a trophic pathway which does not involve commercially important fish (Ruzicka et al. 2012; Robinson et al. 2014, 2015). This means that in the absence of such fish, jellyfish could take over the system. And historically, they have: The first case was reported in the early 90’s in Japanese waters. The collapse of a previously massive sardine population was immediately followed up with the infestation by Nomura jellyfish (Kawasaki, 1993). Then, in the northern Benguela upwelling system, intense fishing severely decreased sardine stocks and jellyfish now dominate this system (Lynam et al, 2006). The collapse of anchovy stocks in the Black Sea and the Caspian sea were both followed by an explosion of ctenophores (Shiganova, 1998; Daskalov et al., 2007). A similar pattern leads to an ever increasing abundance number of jellyfish in the Bering Sea (Brodeur et al., 2008) while the local herring stock decreases (Donelly et al., 2003). And these are just a few documented instances. From these patterns it would not be farfetched to suggest that the jellyfish populations are limited (or held in check) via the competition for food and (very likely) the predation on polyps, ephyrae and small medusa by these filter-feeding fish. This would then imply that the effects of heavy fishing on such fish species in combination with the other processes causing jellyfish increase could amplify the shift in equilibrium until a ‘tipping point’ (Hughes, T.P. et al., 2005; Bakun et al., 2006, Bakun, 2006). After this point the jellyfish start to overwhelm the previous system as their more vulnerable life-stages are significantly less predated on and they themselves are predating far more on fish larvae and eggs (Arai, 1997). This lack of regulation and ever increasing numbers would open the door to new waters (or seafloor habitat in sessile species) to infest. After establishing, this infestation by jellyfish might prevent the presence of competitive or predatory fish (Bakun, 2006), resulting in diverse fish communities being replaced by a relative monoculture of jellyfish. Once again gaining the upper hand in the system, multiplying rapidly and infesting new waters, creating a seemingly endless expanding process.

This creates a feedback mechanism specific to marine environments, where the prey becomes the predator, explained by Bakun and Weeks (Bakun et al., 2006): ‘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.’

If such a switch were to occur the ocean ecosystems would revert back to a state very similar to the ecosystems of the Cambrian, with some authors being convinces that this will be the eventual outcome of the effects of anthropogenic stressors to the marine environment (Figure 5) (Parsons et al., 2002;)

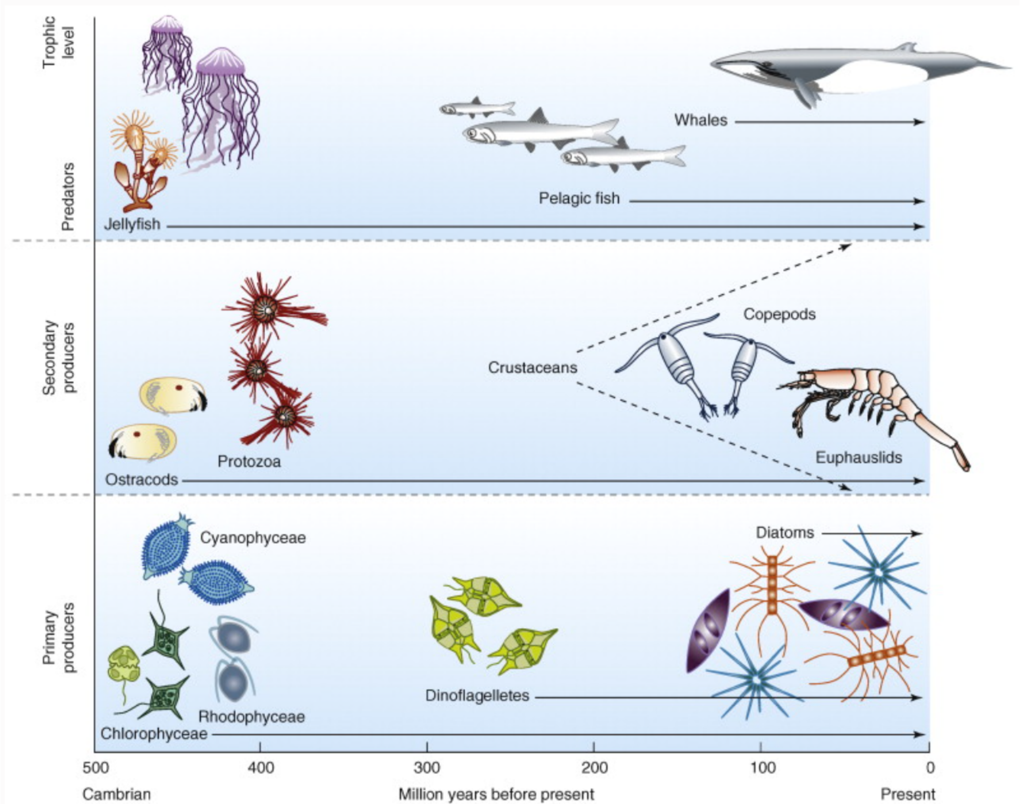


Figure 5 The evolution of pelagic food chains from the Cambrian (simple food chains, with jellyfish as the top predators) to the present (more-complex food chains, with fish and higher animals as top predators). (Richardson et al., 2009)

A recent modelling study aimed at understanding and predicting such a shift implied that in systems with low primary production the system would be fish-dominated and during periods of high primary production, fishing and turbidity the system would be jellyfish-dominated (Schnedler-Meyer et al., 2016). This model compares well with observed trends and predicted a global susceptibility index for the likelihood systems could get overrun with jellyfish.

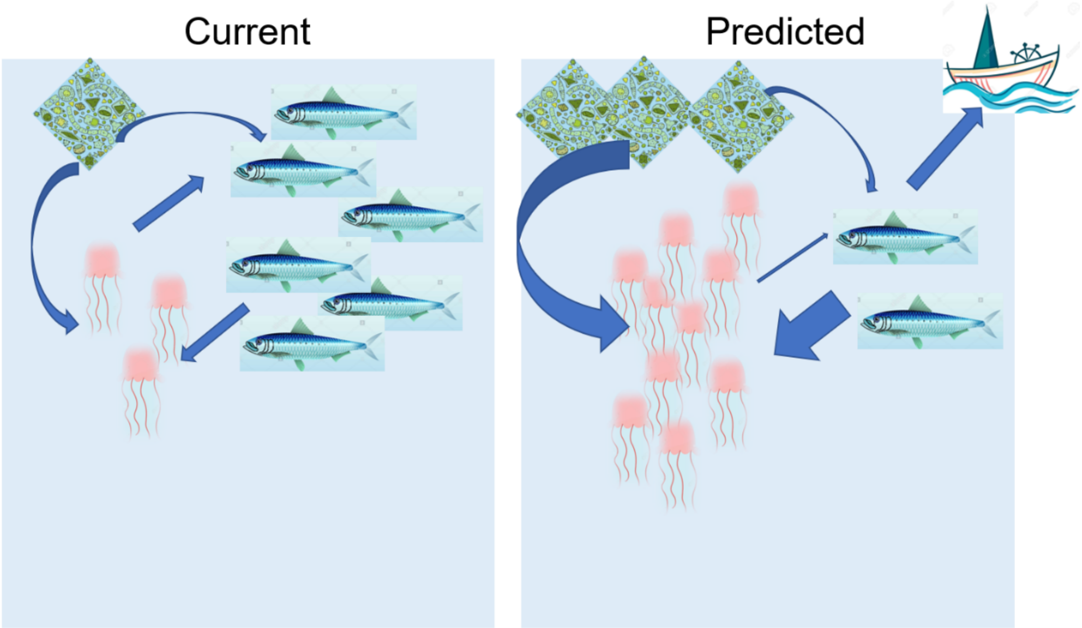


Figure 6 Foodweb comparing the current situation and predicted situation. Thickness of arrows indicate the amount of consumption

Jellyfish and predators

For the predation section the focus will be on predation on adults as this essay primarily looks at the effects of an increase in bloom frequency and size on the food web and as information on predation on polyps is limited (this is a knowledge-gap that will be discussed later).

Jellyfish have historically been classified more so as consumers in the food web and not so much as possible food source for other species, they were seen as a trophic dead-end (Verity & Smetacek, 1996). This argument was based on the overall low nutritional value of jellyfish, especially the gelatinous 'bell' of the animals. Meaning that predators would need to consume very large volumes to reach their metabolic demands. To give an example on this; when comparing the energy densities between scyphozoan jellyfish and various fish species, jellyfish energy densities average 0.10–0.18 kJ per g wet mass^{-1} whereas various fish average 2.4–5.8 kJ per g wet mass^{-1} (Doyle et al., 2007). In simple terms: if a predator wants to ingest the same energy content it would ingest when eating fish, it would have to eat 25-30 times as much volume in gelatinous tissue. The sheer volume necessary to digest when having a diet primarily consistent of jellyfish would mean that a predator would need to have a large 'belly full of jelly'. This would result in reduced streamlining and lower manoeuvrability, leaving the jellyfish-predator at higher susceptibility of becoming prey itself (Verity & Smetacek, 1996). The animals most known for consuming jellyfish, the leatherback turtle (*Dermochelys coricae)* and the ocean sunfish (*Mola mola*) are both massive, weighing a few hundred kilograms. This size could help defending them against predators, even if they are slowed down after a feeding session (Verity & Smetacek, 1996). This could count as evidence that only those species that are big enough could feed on a primarily jellyfish-based diet.

However, there seem to be a few benefits of feeding on jellyfish that would make them a prey option to species other than leatherback turtles or ocean sunfishes. An experiment performed over 20 years ago showed evidence that jellyfish are very easy to digest, possibly up to 20 times as fast as shrimp (Arai et al., 2003)(figure 7). In other words: the low-energy density in jellyfish might be compensated for by the speed at which they are digested. This could result in predators reaching comparable rates of energy acquisition when feeding on jellyfish instead of crustaceans or fish. But this rapid digestion is not the only reason an opportunistic predator could switch to jellyfish from a crustacean/fish-based diet. Jellyfish are i) extremely abundant during a bloom, ii) very slow-moving compared to most other food-sources, iii) fast-growing, with many taxa taking very little time to grow full size. These three qualities make the energy expended for catching a sufficient amount of jellyfish much lower than the energy expended when catching fish or other prey items. Thus feeding on jellyfish (mainly under bloom-circumstances) could be strategically more beneficial.

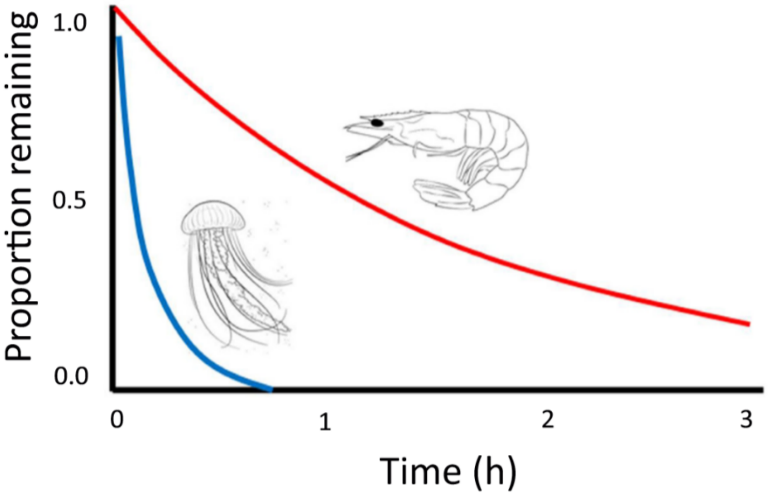


Figure 7:The digestion time of jellyfish in comparison to shrimp

So then who feeds on jellyfish, how much of their diet is gelatinous, and, if the oceans do shift to a more gelatinous state, who can cope?

The first part of this question is fairly simply in theory: who eats who? But in practice it can be a bit more difficult to determine whether an animal eats jellyfish. The most direct evidence for a species predating jellyfish is through observations; you spy a turtle feasting on a jellyfish bloom and its confirmed. But most activity in the ocean goes unnoticed by human eyes, so food webs need to be pieced together from data retrieved through different paths. Current methodologies used to increase our understanding of the role of jellyfish in food webs are:

Animal borne cameras (Thiebot el al., 2016; Thiebot et al., 2017): Over the past two decades cameras have gotten significantly smaller (some only weighing 15 grams), making it possible to track feeding behaviours of a large variety of species. This method gives insights on individual prey capture and thus capture rate, energy expenses per capture and ingestion rates. In addition it also shows if predators are feeding selectively on parts of prey or if they are consumed as a whole. The limitations that come with this technique are the lengths of camera footage (not showing all the individual eats) and the fact that devices need to be recovered, which could be difficult.

Stable isotope analysis (SIA) of predator tissue (Cardona et al., 2012; González et al., 2014): this method has been used for decades to assess diets (Philips et al., 2014; McInnes et al., 2016), but has only recently gained traction for understanding the dietary importance of jellyfish due to recent improvements in analysis(Parnell et al., 2010). In short SIA is based on the way the isotopic composition of the tissue of the predator is influenced by the isotopic composition of the prey. In food web analysis stable isotopes of carbon and nitrogen are used most commonly (Chiaradia et al., 2016; Nielsen et al., 2018). This technique can give information on the feeding history of a predator over weeks or even months. But when only using two isotopes the isotopic signatures of different prey can come out ambiguous, leading to a distorted view of the predators' diet (Pitt et al., 2009)

Molecular analysis of fecal samples and stomach content (Jarman et al., 2013; Sato et al., 2015; McInnes et al., 2016;Lamb et al., 2017): In order to examine the dietary behaviour of both terrestrial and aquatic systems, DNA metabarcoding is widely used (Dahl et al., 2015; Kartzinel et al; 2015; Schneider et al., 2017). With the rapid digestion jellyfish undergo they are not likely to be recognizable as part of a predators diet by simple microscopic gut inspections, but there will still be DNA left that can be traced using this method. Specific parts of the genome can be used as 'barcodes'; target regions with enough variability to distinguish taxonomic groups, DNA residue from stomach or fecal samples can then be identified through next-generation DNA sequencing (Thomas et al., 2016). This method does require a wide 'library' of species barcodes, so that all ingested species can be identified. An additional benefit from this method is that the abundance of each species found in the samples can also be determined. A limitation is the availability of samples from oceanic creatures as fecal samples are just washed away.

Remotely operated vehicles (ROV's)(Smolowitz et al., 2015; Hoving & Haddock, 2017): ROV's are deployed to obtain data from the ocean floor. Especially camera footage from these vehicles has been useful in identifying predator-prey relations in usually unobservable territories (Smolowitz et al., 2015; Smith et al., 2016)

With the use of these methods, the consumption of various types of jellyfish all throughout the world's oceans has been observed in a high number of studies (Figure 8).

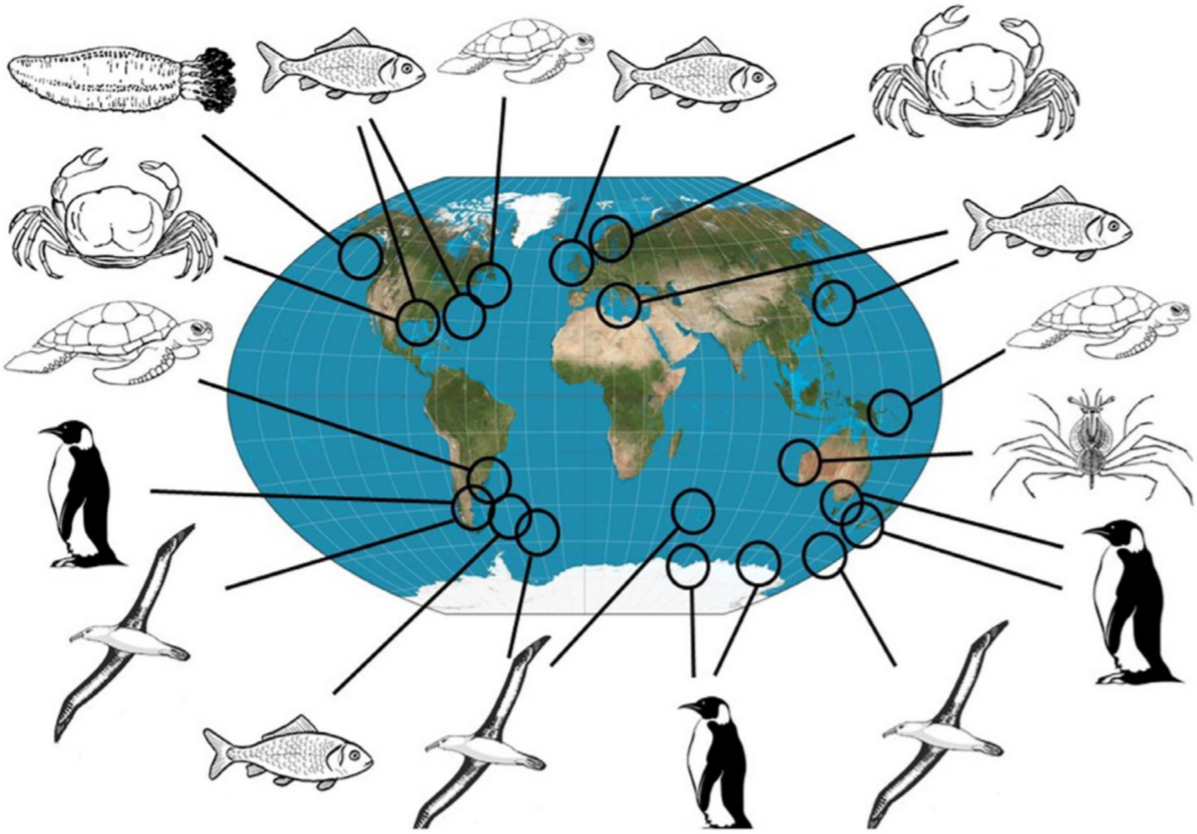


Figure 8: From Hays et al 2018: Illustrative examples of recent work using modern techniques (such as stable isotope analysis of predator tissue, remotely operated vehicles, animal-borne cameras and molecular analysis of stomach content and fecal matter) showing the general location of some of these studies and taxa that have been found to consume jellyfish. Illustrated schematically are flying sea birds [McInnes et al., 2017], penguins [Jarman et al., 2013;McInnes et al., 2016;Thiebot et al., 2016; Thiebot et al., 2017], fish including fish larvae [Arkhipkin, 2013González et al.,2014;Milisenda et al., 2014;D'Ambra et al., 2015;Lamb et al., 2017;Ayala et al., 2018], turtlesFosette et al., 2012;Haeslip et al., 2012;Gonzalez et al., 2014],crab[Sweetman et al., 2014;Archer et al., 2018],rocklobsterlarvae[O'Rorke et al., 2012],andseacucumber[Smith et al., 2014].

These observed predators can mainly be grouped in the following: i) those who feed primarily on jellyfish ii) those who will opportunistically feed on jellyfish iii) those who do not feed on jellyfish. Below each group their characteristics will be described, as well as the effects of a more gelatinous future on said group.

1) Predators with a jellyfish-based diet

As previously mentioned these are animals on which there is evidence they primarily feed on jellyfish. The leatherback turtle and ocean sunfish are the most known of this group. Species who predate on jellyfish as their main food source need to be large enough to have a digestive system capable of handling the quantity of tissue that needs to be digested to reach their daily energy requirements. Since jellyfish appear in blooms and vary heavily in abundance through time and space, these predators need to be adapted to periods of relative fasting. The importance of size on surviving a jellyfish-based diet is further proven by new research methodologies; in recent DNA metabarcoding and SIA studies, the diet of the ocean sunfish (previously thought an obligate jelly-feeder) seemed more variable (Syväranta et al., 2011; Harrod et al., 2013;Sousa et al., 2016), but shifted towards a more gelatinous diet as individuals grew larger (Nakamura & Sato, 2014). DNA barcoding showed that gelatinous zooplankton made up 76% of the DNA found in the guts of the leptocephali larvae (the larvae of the European eel *Anguilla Anguilla,* an endangered species) living in the Sargasso Sea (Ayala, 2018). Showing they have an important role for this species' survival.

In the scenario of a more gelatinous future, this group of predators will likely benefit. Not just by blooms becoming larger, thus having higher quantities of food, but also through the increasing frequency of blooms making periods of fasting shorter, having an overall lower energy expense.

2) Opportunistic predators

The newer methodologies have unveiled a wide variety of species predating jellyfish of which this was previously unknown. Animal borne camera's showed footage of four species of penguin consuming salps, ctenophores and scyphozoan jellyfish, with some species having jellyfish represent 42.4% of their prey capture events (Thiebot et al. 2017). These kinds of empirical foraging data (including prey encounter rate, handling time, consumption and selection) can be incentive to more field-based studies on the optimal foraging equilibrium (Dick et al., 2013). Take for example a recent study on two albatross species which found that jellyfish made up roughly 20% of the diet of these birds during breeding season (McInnes et al., 2017). SIA studies show jellyfish being a possibly important component of more popular fish species such as the Atlantic bumper (*Chloroscombrus chrysurus*), bluefin tuna (*Thunnus thynnus*), swordfish (*Xiphias gladius*) and the little tunny (*Euthynnus alletteratus*) (Cardona et al., 2012).

A recent, but old school analysis of 69 000 stomachs of 107 species of fish showed that 39 of them consumed jellyfish regularly, of which 23 species had not been documented as doing so before (Diaz-Briz et al., 2017). Indicating that the importance of jellyfish in diets is still underestimated.

For some predators it is uncertain whether jellyfish were consumed on purpose or merely 'by-catch' when hunting for crustaceans or small larvae which tend to live in and around the bodies of jellyfish (Sato et al., 2015) But on the other hand the concentration of small preys attracted and caught by the jellyfish might increase their energetic value to predators.

The effects of a more gelatinous ocean on these species is hard to predict. What we have seen in the past few decades looks like an increasing importance of jellyfish in diets of species that previously consumed them less often. Gut content analyses done on several Pacific fish species during a 15-year period showed higher consumption rates of jellyfish during years with warmer temperatures, concluding that these predators might be able to switch to a more jellyfish-rich diet when other food sources are lacking (Brodeur et al., 2018). The same trend can be seen in the diet of the Atlantic cod (*Gadus morhua*), in which the consumption of ctenophores steadily increases over the past 30 years (Eriksen et al., 2017).

The long term effects are mainly based on how well each species can make the switch. This is something that would have to be studied for each individual species as some might be able to fully compensate their diet with jellyfish whereas some might be able to partially compensate during a short time, but will eventually lack nutrition.

3) Predators who do not feed on jellyfish

As mentioned above, gut analysis studies have found some species not consuming any jellyfish: the other 68 species out of the 107 fish species studied (Diaz-Briz et al., 2017). There are many more species that cannot or will not consume jellyfish. This might be a problem if jellyfish do indeed take over large parts of the overall second production. These species could very well be at danger of deceasing in numbers as they are out competed by species who can add jellyfish to their menu.

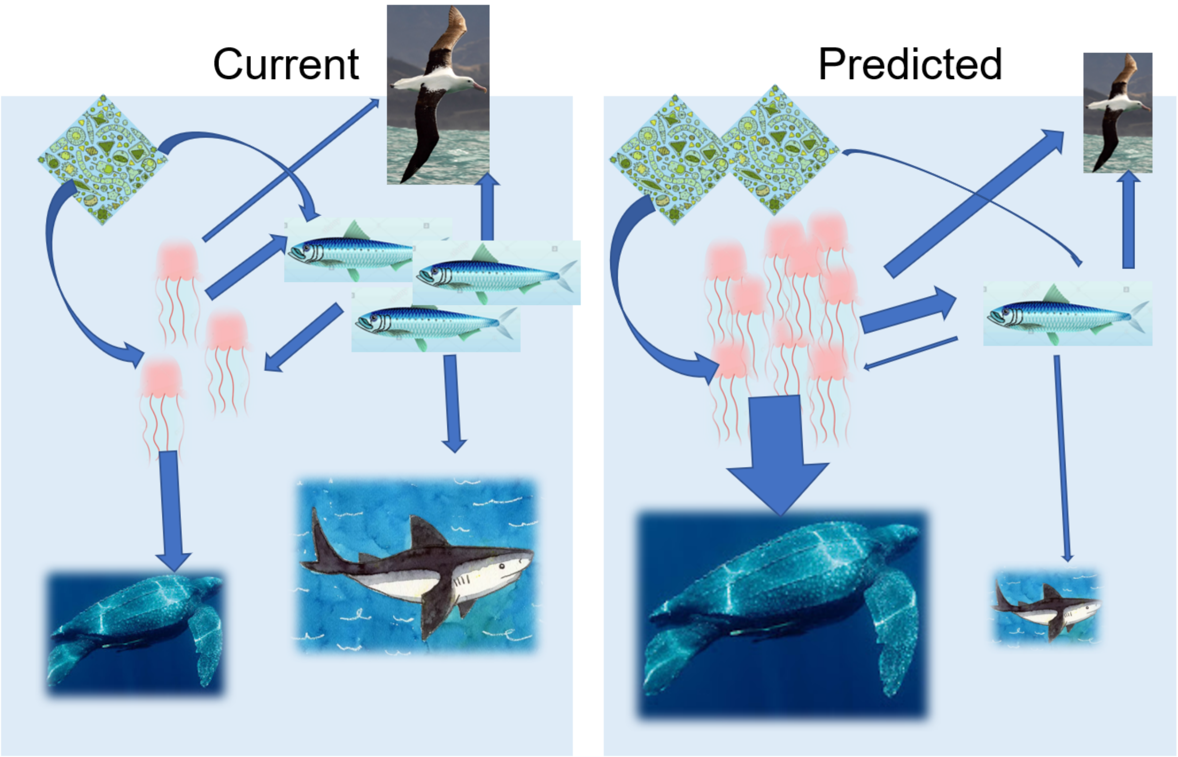


Figure 9 Foodwebs for the current situation and predicted situation. Thickness of arrows indicate size of consumption. The size of the animals indicate the abundance. The Leatherback Seaturtle represents predators who prefer jellyfish. The Albatross represents opportunistic predators. The shark represents predators who cannot live of jellyfish

Jellyfish and the benthic "waste-disposal" community

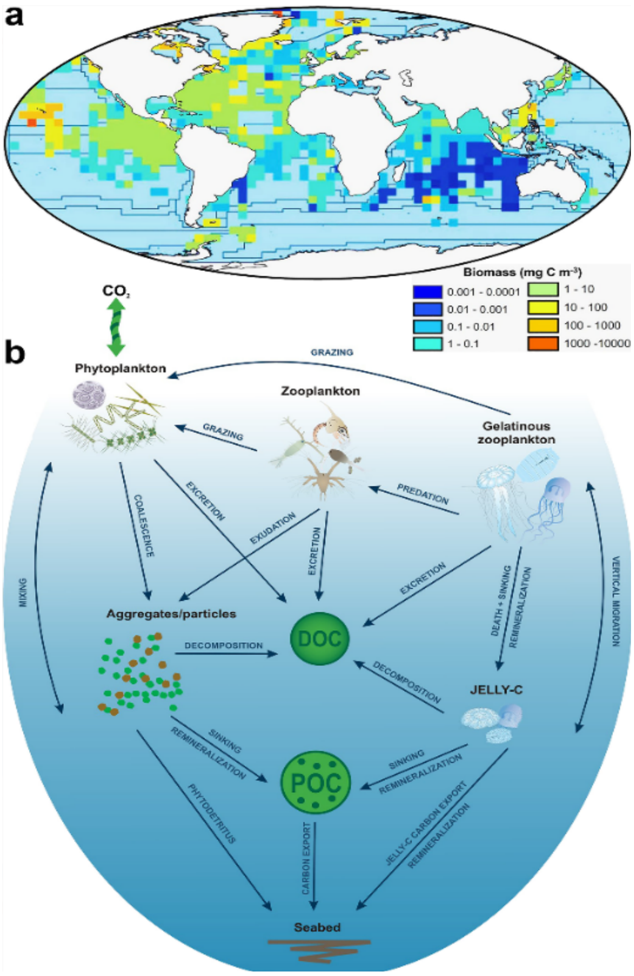
Jellyfish blooms can be massive, depending on the species, with cnidarian medusae blooms reaching biomass densities of 50 kg wet weight per 100 m^3 (*Lilley et al., 2001*). With the entire bloom reaching a biomass of several million tonnes (*Lynam et al., 2006*). Whereas many species whose carcasses end up on the seafloor live and die at different times, a bloom of jellyfish is usually followed by a mass death, causing a massive flux of organic material to the seafloor. Such a bloom collapsing and decomposing at the same time would have to influence the benthic community and chemical environment. Jellyfish were first believed to sink to the bottom fairly slow, but it turns out they sink 500 to 1600 meters a day depending on the species (Helmholtz Centre for Ocean Research Kiel (GEOMAR) 2013)

A recent study by Lebrato et al. from 2019 compiled jellyfish biomass data collected from studies from 1934 to 2011 (over 90,000 data points) to model the nutrient influx caused by the collapse of jellyfish blooms. A summary of the biomass data and the way nutrients from jellyfish (named Jelly-C) fit into the ocean food web can be found in figure 10. Through their review they concluded that the permanent and fast transfer of carbon by jellyfish is a significant part of the global biological soft-tissue pump, and needs to be included in biochemical ocean models.

In general these collapsed blooms seem to be a big part of the diet of a variety of species. Through camera footage the rapid consumption of jellyfish carcasses by benthic creatures including, crabs, fish, shrimps, worms and amphipods was observed (*Sweetman et al., 2014*). Dead jellyfish seem to be a significant component of the diet of the lobster *Nephrops norvegicus*, a species that is commercially exploited in the Norwegian fjords (*Dunlop et al., 2017*). And even several benthic fish in the Northwest Atlantic consume dead jellyfish (*Smith et al., 2016*).

As much as some species benefit from this nutrient transport, the sudden big change in environmental conditions caused by the downfall of a bloom is not in everyone's favour. An experimental study by Chelsea et al. from 2016 measured the presence of three different species in places with and without jellyfish carcasses. In figure 11 the abundance of said species under different conditions is visualized and shows clear difference between how attracted these species are to the jellyfish carcasses.

Especially with very large surges of carcasses the regular benthic community seems to be overwhelmed, causing a shift in community structure. Several studies saw a decrease in macrofauna and a severe increase in bacteria (*Blanchet et al., 2014; Sweetman et al., 2016; Wenjin et al., 2018*). So can we expect to see more and more of this change in community caused by jellyfish in a changing ocean? Winder et al. performed a study in 2017 to estimate the effects of temperature increase and ocean acidification and found that these processes would increase the amount of gelatinous zooplankton followed by a change in the rest of the carbon flux. The effects they visualized in figure 12 (where jellyfish are referred to as appendiculars) are very much what could be predicted for the future.



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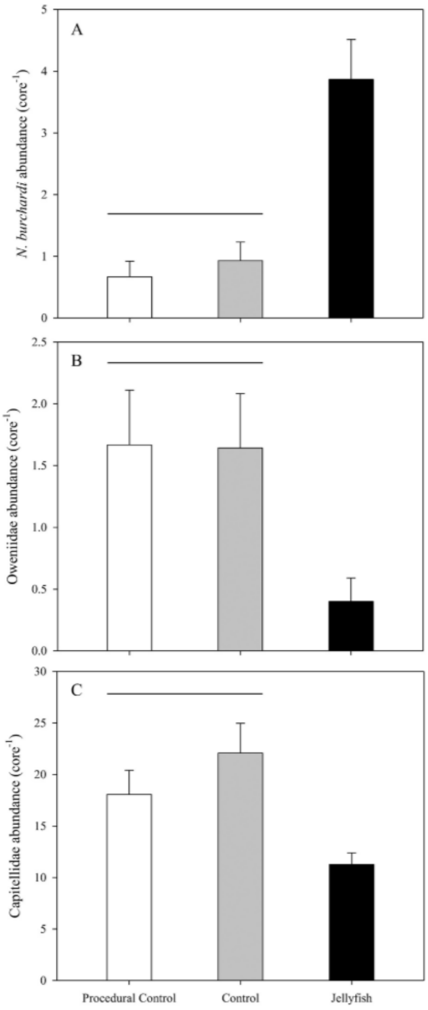

Figure 10: Global summary of gelatinous biomass and how jelly-C fits in the biological pump. (a) Upper ocean (200 m) depth-integrated global gelatinous zooplankton biomass on 5° grid cells displayed over the Longhurst Provinces modeled (light-blue/empty means no data available). Data are replotted as per Lucas et al. ("https://agupubs-onlinelibrary-wiley-com.proxy-ub.rug.nl/doi/full/10.1029/2019GB006265?sid=worldcat.org" \l "gbc20938-bib-0056" 2014) to model jelly-C export per Longhurst Province under John Wiley and Sons License Number 4575870755047. (b) A schematic representation of the biological pump and the biogeochemical processes that remove elements from the surface ocean by sinking biogenic particles including jelly-C. The diagram is adapted from a JGOFS U.S. cartoon to accommodate and describe jelly-C sinking and export. Symbols are courtesy of the Integration and Application Network ("http://ian.umces.edu/symbols/" http://ian.umces.edu/symbols/).

Figure 11 Mean abundance over three days of three species. In the jellyfish (black), control (grey), and procedural control (white plots).

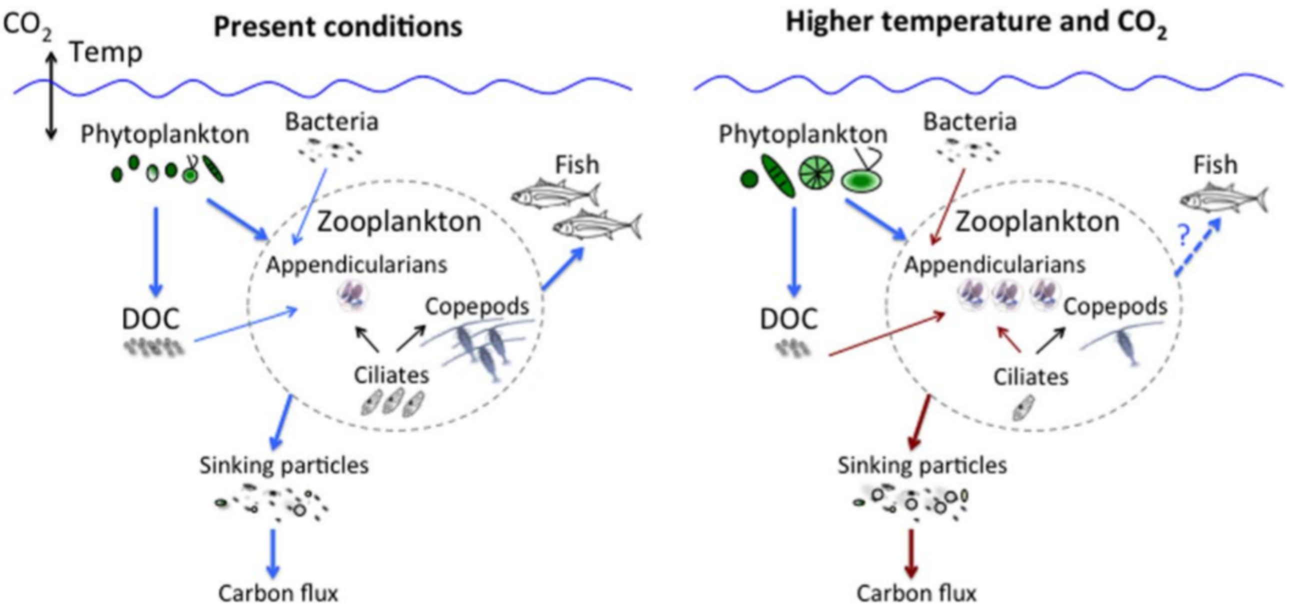

Figure 12: Foodweb describing current situation and future predictions. Appendiculars means jellyfish. The red arrows indicate a change in the foodweb.

Summary of all food webs and future predictions

Figure 13 describes current relations and possible changes after an increase in jellyfish abundance. This is an overly simplified visualisation of reality as many of the groups linked to jellyfish are also linked to each other (e.g. species predating on jellyfish also predate on fish that are competing with jellyfish). Meaning that a change jellyfish abundance could have an even larger effect than already predicted.

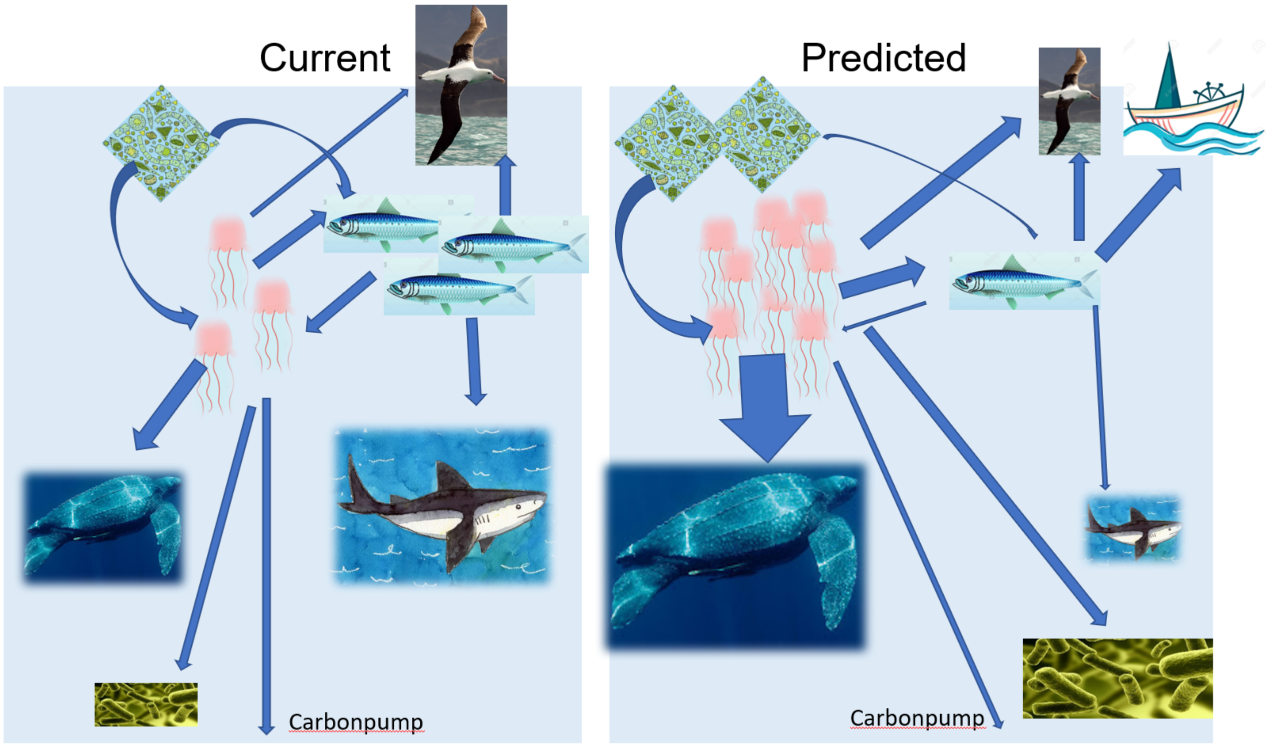

Figure 13 Final foodwebs with all previously discussed factors implemented. Sizes of arrows represent size of consumption.

How to implement jellyfish in ecosystem-based management

Taking into consideration the current role of jellyfish in food webs and the predicted changes to said food web by the likely future increase of jellyfish blooms, the inclusion of jellyfish in ecosystem-based management seems to be a necessity. Ideally jellyfish would be implemented in predictive models, which is something that is still often forgotten. A review from Lamb et al. 2019 looked at how often jellyfish were included in models (in particular Ecopath models) and although they saw an increase in models implementing jellyfish (either as part of a plankton group or separately)(figure 14), their role was often underestimated. Something that would have to change as jellyfish seem to impact ecosystems far more than was believed. Including jellyfish in models would, for example, give more accurate predictions on fish stock.

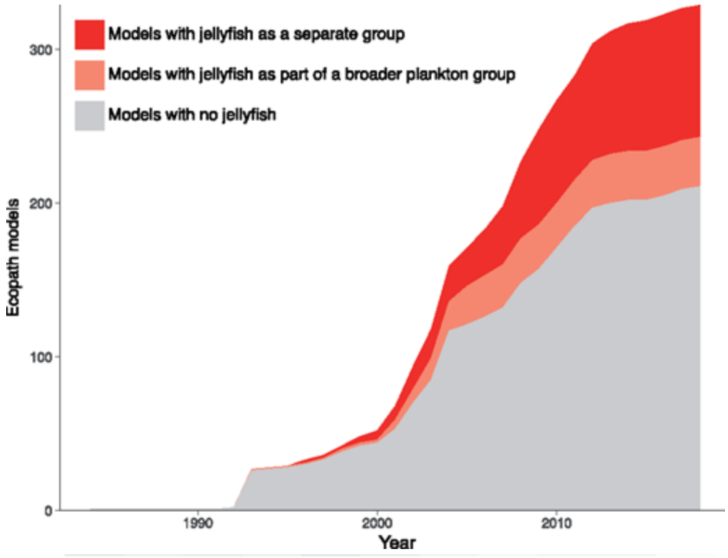

Figure 14: Number of models that implemented jellyfish over time

Unfortunately there are still a vast number of knowledge gaps regarding the exact roles of jellyfish in the food web, which would be very interesting for future research. Firstly, the overall monitoring of jellyfish is very species selective and limited to areas where there are fisheries (coastal). As mentioned before, abundance is usually only measured in species that are of economic interest, are causing issues for humans, or have a clear interaction with other species humans find interesting. Considering the countless numbers of species that fall under the jellyfish umbrella this would most certainly result in a skewed image of the global effects of increasing jellyfish blooms. To prevent this monitoring would have to be done regionally.

Then, there are the effects of a more gelatinous ocean on opportunistic jellyfish-predators. There is very limited knowledge on how these species are affected by a change in diet and which species would be able to cope with a long term change in diet and which species would not. The methods described earlier could help to fill these gaps, but especially long term monitoring would be essential to predict the fate of each predatorial species.

The final problem lays in the complexity of the jellyfish life-cycle. Most data on jellyfish food web roles and abundance is based on adults. However, the polyp stadia also affects the size of blooms. On top of that, they are also feeding and being eaten.

In conclusion the roles of jellyfish are still underestimated and ought to be taken more seriously, especially considering the apparent shift towards a more gelatinous ocean. To solve this, species-specific, regional research is required that would garner information to be implemented into models necessary for ecosystem-based management.

The main issue currently standing in the way of advancements is the loose language used in all of the papers I have read. They all talk of “some species are somewhat increasing in some areas” or “some species are increasing globally”. But these are all vague answers to the vague question “are jellyfish increasing in abundance?”. The debate would strongly benefit from tightening language and drawing clear lines.

Acknowledgements

I would first like to thank my supervisor Karin de Boer for her endless patience and pep talks, especially during the current pandemic. I would further like to give credit to a few of my friends; Hedwig, Ilse and Manon, who bullied me into a better work ethic. And last but not least, a very special thank you to the Gorillaz, who made the song Superfast Jellyfish on the album The Plastic Beach. A song that resulted in an obsession for jellyfish that kept me motivated during the writing process.

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