THE CONTROVERSIES ARISEN FROM MISNOMER OF GELATINOUS ZOOPLANKTON IMPACTED BY CLIMATE CHANGE

Natascha Borgstein

18 January, 2021

Estuarine & Delta Systems (Royal NIOZ)

Dr. Lodewijk van Walraven (Royal NIOZ) & Dr. Karin de Boer (RUG)

ABSTRACT

Despite having been around for hundreds of millions of years, jellyfish appear to be simple organisms without much purpose. Nevertheless, recent evidence suggests that these organisms show incredible resilience to the effects of climate change, so much so that their numbers are now flourishing. In the recent years, more and more reports of jellyfish blooms and outbreaks are flooding the media despite rising sea temperatures, increased ocean acidity, pollution, and even overfishing. However, "jellyfish" is a much broader term than often realized, and therefore biases are easily formed around these apparent trends being reported. To encompass a wider array of organism, the term "gelatinous zooplankton" has become more commonly used by researchers. Even so, the extreme diversity and unique lifestyles of these species, that fall under the jelly-like description, sometimes makes assessing these trends rather challenging. In this review article I explore why there are conflicts regarding defining global gelatinous zooplankton abundances and the recent opportunities that could have allowed some groups to thrive more than others in this changing environment. I also offer more specific predictions for future trends based on published research and provide suggestions to mitigate further controversies in order to obtain more accurate and reliable future trend reports.

TABLE OF CONTENTS

Abstract	2
Introduction	4
General advantages of being gelatinous in the ocean (and major disadvantage)	5
Too diverse for single association	6
Recent trends in abundance	7
Flourishing in a changing climate	8
Opportunities from human interference1	10
Predictions and suggestions for the future1	1
Conclusions 1	13
Bibliography 1	14

INTRODUCTION

Reported to be generally unchanged for hundreds of millions of years (Gibbons et al., 2016), jellyfish seem to be masters of survival. Especially now, despite the plethora of damages the ocean is facing brought on by human interference and climate change (increasing temperatures, decreasing pH, increasing severity of weather events, eutrophication, hypoxia, overfishing) (Boero et al., 2016; Duarte et al., 2013; Richardson et al., 2009), jellyfish around the world are appearing more frequently in large numbers (Link & Ford, 2006; Mills, 2001; Richardson et al., 2009). However, many controversies are contained within these statements. I hope to illuminate the misleading controversies in this review in order to diminish inaccurate assumptions and offer suggestions for minimizing the underrepresentation of certain groups necessary to confidently define it as a global trend.

First and foremost, labeling an organism a "jellyfish" is not as simple as it seems. The common misconception is merely referring to organisms from the phylum Cnidaria (which include scyphozoansthe typical jellyfish, cubozoans- box jellyfish, and hydrozoans- hydroids) and Ctenophora (combjellies) as "jellyfish" (Condon et al., 2012b; Gibbons & Richardson, 2013). In reality there are many other phyla that fall under the "jellyfish" definition. Jelly-like and transparent appearance is a result of

convergent evolution, meaning that it is a trait which evolved independently and multiple times across various taxonomic groups (Condon et al., 2012b; Moroz, 2015). Nowadays, the term "gelatinous zooplankton" is more often used to generalize and include more of these groups. Although the definition of the two terms are the same, "gelatinous zooplankton" encompasses the broader taxonomic varieties containing these traits. In fact, at least eight marine phyla report to have gelatinous, jellylike individuals (Haddock, 2004) (see Figure. 1). The gelatinous trait of the Cnidarian phylum is estimated to have been conserved for more than 500 million years (Condon et al., 2012b). In the phylum Chordata, for example, certain species of Salps and Pyrosomes are gelatinous. Haddock (2004) also referred to individuals from the phyla Mollusca, Chaetognatha, Radiolaria, and Annelida, that have gelatinous



Figure 1. Representative members of gelatinous zooplankton. Organisms from at least eight phyla are included among the gelata. (a) Nemertean. (b) Phaeodarian radiolarian. (c) Salp with parasitic copepod. (d) Lobate ctenophore. (e). Narcomedusan hydrozoan. (f) Nudibranch mollusc. (g). Chaetognath. (h) Physonect siphonophore. (i) Coronate scyphozoan. (j) Polychaete [from Haddok, 2004].

characteristics in addition to the two typical gelatinous phyla of Cnidaria and Ctenophora as "gelatinous zooplankton". Sajikumar et al. (2016) also described a rare glass octopus (*Vitreledonella richardi*) in the phylum Mollusca, with having a transparent and gelatinous body. Verdes and Gruber (2017) likewise reported on two families of marine worms in the phylum Annelida: Acrocirridae and Flabelligeridae who have gelatinous, transparent bodies. With so many examples of distinctive and ancient organisms evolving with the gelatinous trait, it is evident that being gelatinous must be advantageous for phyla thriving in the ocean. I will discuss these benefits as well as elaborate on the fascinating diversity of organisms that fall under the term "jellyfish" or "gelatinous zooplankton" before addressing the purpose for my review, i.e. to explore why there are controversies around defining gelatinous zooplankton abundance trends and the opportunities that could have allowed some groups to thrive more than others.

GENERAL ADVANTAGES OF BEING GELATINOUS IN THE OCEAN (AND MAJOR DISADVANTAGE)

Arguably one of the greatest ecological advantages to having a gelatinous body in the pelagic ocean is for predator avoidance (Condon et al., 2012b). While living out in the open ocean, being transparent is an ideal camouflage when there is no place to hide from visual predators. Gelatinous zooplankton have a lot of visual predators, which include over 124 species of fish as well as 34 other types of marine animals such as sea turtles (Pauly et al., 2008; Purcell, 2012; Purcell & Arai, 2001). Concurrently, blending in with the surroundings is also advantageous for sneaking up on prey, as gelatinous zooplankton can be voracious predators targeting a large array of food (Purcell & Arai, 2001). The expense of having a gelatinous, clear body sacrifices the need for complex features. However, a lack of intricate structures also allows these organisms to be highly adaptable and regenerative (Sinigaglia et al., 2020). In terms of cnidarians and ctenophores, Pitt et al. (2013) explain that due to the fact that these organisms are mostly consistent of water, they do not have to wait for the construction of tissues in order to grow in size, unlike more complex organisms. Therefore cnidarians and ctenophores are able to grow much faster when compared to more complex organisms. On the other hand, this lack of complexity could also be viewed as a major disadvantage. For example, the low body carbon and muscle mass limits the propulsive capabilities for cnidarian species, especially in larger individuals (Costello et al., 2008; Gemmell et al., 2013). In other words, their overall swimming speed is restricted. It is particularly important to be transparent if not very mobile, as this camouflage can greatly enhance prey capture and predator avoidance. Nevertheless, a low body carbon accounting for less than 1% muscle mass in cnidarians (compared to most fish having over 50% muscle mass) does mean that gelatinous zooplankton are highly efficient swimmers that do not need to utilize much energy in order to generate a propulsive thrust (Gemmell et al., 2013). Thus, more energy can be spent on growth and reproduction rather than propulsion. These advantages could offer suggestions as to why high abundances of gelatinous zooplankton seem to be reported in the recent years despite the additional anthropogenic and climate challenges. Increased reports of gelatinous zooplankton outbreaks could furthermore be from the fact that there is more focus on these organisms after learning of the potential advantages they bring. However, because gelatinous zooplankton incorporate so many different species, as previously discussed, it is not recommended to make broad assumptions but rather look at a more specified level.

TOO DIVERSE FOR SINGLE ASSOCIATION

The term "jellyfish" or "gelatinous zooplankton" is used across the literature for simplicity, but often does not contain all of the gelatinous groups that were listed previously. Usually only one or more groups of interest are focused on during research, however still using "jellyfish" or "gelatinous zooplankton" when describing them. For example, Lilley et al. (2011) targeted scyphomedusae (cnidarians), ctenophores, hydromedusae, and tunicates, as their gelatinous zooplankton, whereas Condon et al. (2012b) concentrated mainly on salps from the phylum Chordata. A majority of literature, however, focuses solely on the two most-studied and readily available gelatinous phyla: Ctenophora and Cnidaria (for example: Duarte et al., 2013; Gibbons et al., 2016; Miller & Graham, 2012; Pauly et al., 2008; Pitt et al., 2013; Richardson et al., 2009).

As Richardson et al. (2009) emphasized, despite all being categorized as "jellyfish", the lifecycles vary drastically between the phyla or species depending on the specific taxonomy. For instance, cnidaria are mostly meroplanktonic, with all cubozoans and a majority of hydrozoans and scyphozoans consisting of a benthic polyp stage and a planktonic medusa stage (Miller & Graham, 2012; Richardson et al., 2009). On the other hand, a majority of ctenophores are holoplanktonic, i.e. they remain as free-swimming plankton for their entire life cycle. Siphonophores (another class of cnidarians) and salps, for example, also lack a sessile polyp phase (see Brotz et al., 2012). The bipartite life style in the majority of cnidarians also allows for an alteration of generations, described as metagenesis, whereby the sessile polyp reproduces asexually through budding whereas the free-swimming medusae reproduces sexually (Duarte et al., 2013; Miller & Graham, 2012; Richardson et al., 2009).

Even within the same phylum species are known to behave in different ways. For example, ctenophore *Mnemiopsis leidyi* is considered a cruising predator that feeds on slow moving or stationary prey, whereas ctenophore *Pleurobranchia bachei* is known as an ambush predator that deliberately pursues highly mobile prey (Purcell & Arai, 2001). Additionally, in the Cnidaria phylum, the varying number of stinging cells (called nematocysts) determines the type of prey captured. Purcell and Arai (2001) explained that certain siphonophores with only a few identical nematocysts targets soft-bodied

prey, whereas other siphonophores and hydromedusae each with more numerous, varied types of nematocysts go after hard-bodied prey.

The ranges in size of gelatinous zooplankton are just as drastic as their life histories. A glass octopus may reach a relatively large size of 45cm in length (Sajikumar et al., 2016), but a particular type of cnidaria known as a chain jelly (*Apolemia uvaria*) can grow up to 30 meters in total length (see Båmstedt et al., 1998)! Different species can vary in weight from no more than a few grams up to tens of kilograms (Lilley et al., 2011), which is impressive considering their bodies are made up of 95% or more of water (Condon et al., 2012b). Due to this high percentage of water and gelatinous body, these organisms are also osmoconformers, i.e. they maintain an internal environment that is equivocal to their surrounding environment (Graham et al., 2001), which is important to note for the later discussion.

RECENT TRENDS IN ABUNDANCE

Despite the fact that the common trend about gelatinous zooplankton abundances is that they are increasing globally, Condon et al. (2012a) explained that these "global" trends are actually inferred from trend reports in just a few diverse regions of the world such as the Bering Sea, North Sea, Black Sea of Japan, Sea, and Mediterranean. Therefore, in order to confidently state that gelatinous zooplankton are



Figure 2. Map of population frends of native and invasive species of jellyfish by Large Marine Ecosystem (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 [from Brotz et al., 2012].

increasing in numbers globally, further analyses should be performed in many more regions of the world, as I will discuss in a later section. Nevertheless, there does seem to be trends to more specified abundances of zooplankton blooms along shorelines, coastal margins, and in enclosed or semi-enclosed bodies of water (Graham et al., 2001; Gershwin, 2013). There are two types of these so-called blooms: a true bloom is when a rapid increase in gelatinous zooplankton abundance results from an extreme population burst. An apparent bloom is when the rapid abundance is a result of a re-distribution or re-dispersion of an otherwise stable population (Graham et al., 2001). The increase in instances of blooms along shorelines or other bordering areas are generally considered apparent blooms, as strong winds and surface currents compress the masses of organisms along the coasts, which may even result in mass

strandings along beaches (Graham et al., 2001). The water-filled bodies of gelatinous zooplankton remain in ionic balance with their surrounding seawater. This fine balance can be disrupted when temperature, salinity, or pressure gradients vary too frequently in enclosed or semi-enclosed bodies of water such as fjords, bays, harbors, and estuaries. Therefore, these are popular areas to observe apparent blooms since these organisms become stagnant (Graham et al., 2001; Gershwin, 2013). Not all gelatinous zooplankton are configuring in higher numbers, however. Brotz et al. (2012) compiled sources of data to create an analytical framework necessary to assess comprehensive trends observed since the 1950s of combined cnidaria, ctenophore, and salp abundances around global coastlines. Although 62% of their regions depicted an increase, still 7% showed clear decreasing trends (represented by the blue sections in Figure 2). Other reports, such as the one by Chiaverano et al. (2013) done at a beach in Hawaii, show oscillating bloom periods, with a significant increase in box jellyfish (Alatina moseri) aggregations from 1998 to 2001, yet a significant decrease from 2001 to 2006. No significant net increase or decrease could be determined from their 14-year study period. With continuing changes in climate and human interference, the ocean temperature, pressure, and salinity becomes even more dramatically off balance and pushed to extremes. Furthermore, overfishing also allows for gelatinous zooplankton to thrive and multiply with minimal impact for natural predators, and therefore contributes to true blooms (Lynam et al., 2006).

FLOURISHING IN A CHANGING CLIMATE

The numerous consequences resulting from climate change that were stated earlier appear to affect most ecosystems and organisms, including humans, in such negative ways (Galloway et al., 2004), so why is it that ctenophore and cnidarian populations, at least, seem to flourish so abundantly? The overarching reason is because as other ocean inhabitants (who compete with and feed on gelatinous zooplankton) are being effected, the previously occupied habitats of those suffering organisms are opened up to the hardy and resilient gelatinous zooplankton. To give a future perspective on the abundances of gelatinous zooplankton, I will expand specifically on how certain groups are so resilient towards to climate change.

One of the major consequences of climate change is ocean warming, driven by anthropogenic causes such as the extreme rates of deforestation and the burning of fossil fuels releasing excessive carbon dioxide and pollutants into the atmosphere (Galloway et al., 2004; Le Quéré et al., 2009). It is well known that tropical and shallow-water reef building corals are threatened by ocean warming due to their narrow range of temperature tolerance, and higher temperatures have been shown to slow their growth rate (Cantin et al., 2010). Boero et al. (2016), on the other hand, note a far broader temperature tolerance for many tropical gelatinous zooplankton species. Rather than be threatened by increasing temperatures, the metabolism of ctenophores and cnidarians increases, allowing them to reach the

medusa stage faster. In fact, each stage of the life cycle may be positively influenced by rising temperatures; *Aurelia labiata*, a type of moon jelly and widely studied cnidarian, not only show an increase in reproduction through asexual polyp budding and strobilation, but also an increase in the



number of strobilation cycles and larval production per individual polyp (Purcell, 2007). Experimental data also support the increase in asexual production of many cnidarians and ctenophores alongside the rise in temperatures (Purcell, 2012). With temperature induced increased reproduction rates and volumes, it is no wonder that over the past 50 years more cnidarians and ctenophores are abundant during the warmer years (Gibbons & Richardson, 2009) (see Figure 3). Furthermore, gelatinous tunicates, such as salps, have also shown higher abundances with ocean warming (Boero et al., 2016). These trends seem to hold true for varying temperature regions around the globe, including in the North Atlantic (Richardson et al., 2009), Irish Sea (Lynam et al., 2011), North Sea (Attrill et al., 2007), and Mediterranean (Licandro et al., 2010).

Alongside ocean warming is ocean acidification, where the increase of carbon dioxide in the atmosphere creates a decline in the pH of the ocean, making it more acidic (Euzen et al., 2017; Rockström et al., 2009). The lower pH significantly affects calcifying organisms such as snails and corals, as it lowers the amount of carbon ions available in the water that they require to build their shells and skeletons (Euzen et al., 2017; Langdon & Atkinson, 2005; Rockström et al., 2009). Cnidarians and ctenophores, however, do not possess

any calcified body parts and are therefore generally unaffected by the declining ocean pH, allowing them to flourish in those areas initially occupied predominantly by calcifying organisms (Attrill et al., 2007; Boero et al., 2016). Sure enough, Attrill et al. (2007) found a negative relationship between gelatinous zooplankton abundances and annual pH levels in the North Sea, meaning the number of individuals increased in those years and habitats where the pH had decreased (became more acidic). Although it is the surrounding climate that is having direct impact on the ocean environment, it is the unsympathetic actions of humans such as the excessive burning of fossil fuels and deforestation as previously mentioned, that have contributed significantly to increased rates of these changes. These same actions (and others) have also had indirect impact on the ocean's food webs.

OPPORTUNITIES FROM HUMAN INTERFERENCE

The generally careless nature of humans on land has literally spilled over into the oceans as runoff of the use of excessive amounts of rich nutrients are causing what is known as eutrophication (Rabalais et al., 2014). Population expansion and high demands for coastal development over the last years have been a big culprit of this runoff, resulting in a decreased amounts of dissolved oxygen concentration in those coastal areas (Rabalais & Turner, 2001). This state of hypoxia (oxygen depletion developing from eutrophication) poses a major threat to most fish species, but once again the resilience of cnidarians and ctenophores have allowed certain species to tolerate much lower oxygen concentrations (Condon et al., 2001; Grove & Breitburg, 2005). Fish and benthic invertebrates are two major predators of gelatinous zooplankton, as well as being competitors for settlement. However, since the predators are both sensitive to hypoxia, cnidarians and ctenophores have the advantage in lowered oxygen situations, and are therefore able to dominate the space in these stressful environments (Miller & Graham, 2012; Pauly et al., 2008). Similarly, the medusa stages of these gelatinous zooplankton benefit and an increase in abundance has been observed along the Norwegian coasts (Purcell, 2012). The prey capture rates of medusae are however unaffected as a result of hypoxia because although zooplankton sizes decrease, they are nonvisual predators that are not picky with what they eat (Daskalov et al., 2007; Miller & Graham, 2012). Large marine life such as fish, marine mammals, turtles, and seabirds are in fact visual predators who prefer larger zooplankton and are therefore negatively impacted by zooplankton size reductions (Purcell, 2012; Richardson et al., 2009). Even despite the decrease in dissolved oxygen, the coastal eutrophication stimulates an influx of phytoplankton blooms, that Richardson et al. (2009) mentioned can further boost gelatinous zooplankton outbreaks.

Overfishing is another example of how humans are providing an increase in opportunities for gelatinous zooplankton to flourish. Through over-harvesting of marine fish stocks humans are directly removing the gelatinous zooplankton's natural predators and competitors, consequently allowing more space for the zooplankton to prosper (Lilley et al., 2011; Purcell, 2012). For example, off the coast of Namibia, in West Africa, as a direct consequence of the once-productive sardine fisheries the coastlines have now become dominated by *Chrysaora hysoscella*, or sea nettles, due to the overharvesting and collapse of the sardine stocks that have lowered the predation pressure on these cnidarians (Lynam et al., 2006). One major destructive fishing practice known as bottom trawling destroys biogenic structures such as reefs, which are replaced over time with small benthic organisms. This process is once again advantageous for benthic polyp stages of cnidarians and ctenophores (Pauly et al., 2008). Despite scraping away bottom dwellings and thus taking away other potential hard areas which gelatinous

zooplankton prefer for settlement, the contemporary development of artificial structures adds additional available substrates.

Artificial structures like harbors, piers, floating docks, bridges, buoys, artificial reefs, and aquaculture installations all provide increased hard surfaces in otherwise soft-substrate dominated areas. Along with the appearance of more hard structures, there are more areas for larval stages of cnidarians and ctenophores to settle, and polyps or medusa stages to shelter (Duarte et al., 2013; Purcell, 2012). Studies by Holst and Jarms (2007) and Hoover and Purcell (2009) revealed that six cnidarian species even preferred to settle on artificial substrates rather than natural ones. Another advantage of artificial structures is the fact that they can reduce the distance between suitable larval settlement sites. The structures act as stepping stones among the long distances that these larval gelatinous zooplankton travel. As a result, the range of the spread of blooms can also be increased (Duarte et al., 2013). Over time, the exponentially increasing human population results in rapid more coastal development. Paired with the continuing rise in global sea levels, it is evident that the development of coastal defenses will also increase, thus resulting in even more suitable habitats for these organisms in the future (Richardson et al., 2009).

Expansive ocean travel by boats likewise aids in the spread of gelatinous zooplankton around the globe. More easily than perhaps realized, shipping across the oceans contributes to the spread of invasive species, which then cause serious damages to native ecosystem community structures. Gelatinous zooplankton (being generally small and lightweight) are easily picked up in the ballast water of ship hulls, translocated across the oceans, and dumped hundreds of miles away (Richardson et al., 2009). Without natural predators in these new habitats, these transported species are then able to thrive and take over native resources. Consequently, these intruders are labeled as invasive species (Daskalov et al., 2007). Examples of commonly invasive gelatinous zooplankton include *Phyllohiza punctata*, a cnidarian, in the Gulf of Mexico, and *Mnemiopsis leidyi*, a ctenophore invading the Black Sea (Daskalov et al., 2007; Lilley et al., 2011), each contributing to local tropic cascades. It is evident from all these diverse examples described previously that human actions must be modified in order to mitigate the potential overflow of gelatinous zooplankton in the oceans.

PREDICTIONS AND SUGGESTIONS FOR THE FUTURE

As referenced earlier, gelatinous zooplankton have a strong effect on other species around them. As gelatinous zooplankton are known to feed on the larvae and eggs of fish, Pauly et al. (2008) warned that the cnidarian and ctenophore outbreaks could over time diminish the availability of commercial fish. Evidence from (Brodeur et al., 2010) suggests that gelatinous zooplankton heavily influence the lower trophic levels (producers/ small consumers). However, due to their predominately (95%) water-filled bodies, gelatinous zooplankton contribute comparatively little to the higher trophic levels

(predators/large consumers), and their domination would decrease the abundance of marine vertebrates that are important to human consumption. Gelatinous zooplankton blooms are probable indicators of a degrading ecosystem, and so as the larger predators in the ocean are depleted and taken over, a type of chain reaction would occur in which the ocean would lose biodiversity (Gershwin, 2013). But is there enough evidence to speculate that this affect could happen globally? Although Condon et al. (2012a) concluded that a significant increase in gelatinous zooplankton was observed since the 1970s, the increase seen over the last decade is in line with the normal oscillating patterns gelatinous zooplankton populations tracked over the last century. According to Attrill et al. (2007), the frequency in occurrence of gelatinous zooplankton blooms is presumed to increase over the coming century in the North Sea as a result of the stronger influence of the North Atlantic Oscillations from warming oceans. However, Loveridge et al. (2020) offered a contradictory argument, using their experimental data, that cnidarian populations (specifically Aurelia aurita from around the United Kingdom) may actually decrease with increasing temperatures. Therefore, scattered local recognition of gelatinous zooplankton blooms (or lack thereof) could often be misinterpreted as representing a global trend when in fact it is simply the redistribution of a single population (Graham et al., 2001). Even the anthropogenic impacts discussed previously such as overfishing, coastal development, or translocations, show inconsistencies due to the lack of global knowledge of gelatinous zooplankton biomasses (Lilley et al., 2011).

There is simply a lack of a baseline, and this scarcity in long-term gelatinous zooplankton abundance data results in a perceptional bias from constantly shifting reference points over time (Condon et al., 2012a). Moreover, public observation is exponentially increasing with our expanding population, so logically there would be more recordings of blooms around the world compared to previous decades and centuries. Future research needs to be conducted in order to eliminate this perceptional bias by expanding the research to include the lesser-known species and underrepresented regions. For most of our vast ocean gelatinous zooplankton populations data are simply unavailable (Purcell, 2012). Especially regions in the Southern Hemisphere and open ocean gyres need to be further analyzed (Condon et al., 2012a). The general public is also naturally more attentive towards and interested in the highly-visible, invasive, and dangerous species because it impacts and threatens human lives directly (Condon et al., 2012b). Therefore, the rarer and unseen species may be highly underreported (Lilley et al., 2011). Problems with collecting this type of data include the fact that current collecting methods break up the fragile species and let the smaller species simply slip through. Only the larger species can be properly collected and separated from the enormous variety of plankton (Condon et al., 2012b; Gibbons & Richardson, 2013). More efficient collection methods are therefore needed in order to fill these knowledge gaps.

Whether or not the global trend of gelatinous zooplankton is increasing, better preparedness could moderate potentially hazardous outbreaks while, at the same time, provide ecological benefits. The extraordinary regenerative abilities and reproductive capabilities of gelatinous zooplankton

(especially cnidarians) could allow them to become sources of medicinal benefits in pharmaceutical, biotechnological, cosmetics, food, and feed industries (Leone et al., 2015; Purcell, 2012). Leone et al. (2015) hoped that by identifying these additional uses they would help resolve the negativity revolving around bloom-forming gelatinous zooplankton and paint the organisms in a more positive way. As an example, when chickens and pigs were given a diet including cnidarian feed compounds, there was an increase in muscle to bone ratio as well as increase in overall body tissue without any harmful side effects (Hsieh & Rudloe, 1994). Cnidarians also contain relatively large amounts of collagen, which may have beneficial effects on, for example, arthritis, hypertension, bone pain, ulcers, aging skin, and digestion (Gibbons et al., 2016; Leone et al., 2015). Additionally, the collagen in gelatinous zooplankton a purpose for direct human use hopefully inspires more people to learn about these diverse yet overlooked organisms and reinforce how they can be an incredibly versatile, sustainable, and feasible resource around the globe.

CONCLUSIONS

In the recent years people are beginning to understand the importance of studying global gelatinous zooplankton abundances, but there is much more research needed to fully understand their trends and ultimately their impacts. I have explored the biases that have been published thus far involving gelatinous zooplankton and described why some groups thrive despite the damaging effects of climate change. Overall, the most important adjustment that should be made moving forward is being more consistent with the labelling of "jellyfish" or "gelatinous zooplankton". These all-inclusive terms showcase a broad array of phyla that contain organisms with drastically different life cycles and behaviors. Most studies choose to focus only on cnidarians and ctenophores, but others such as Brodeur et al. (2010) do not even specify which gelatinous zooplankton or jellyfish they refer to. It is challenging, for example, to compare two different research papers in which both refer to "jellyfish" yet analyze two very different species since these comparisons can be misleading and the collective data may be too generalized or inaccurate. Nevertheless, it is reasonable to assume that as the excessive harvesting of marine fish continues there will be more food available and less predators present for the lower trophic levels (which include gelatinous zooplankton). Trends of species specifically in the Cnidaria and Ctenophora phyla show that it is logical to then assume that abundances could naturally increase over time simply because there is more space and resources with fewer competition to share it with (Pauly et al., 2008). More analysis is required to assess if these future predictions could also hold true for the other gelatinous zooplankton groups. Either way, the overwhelmingly negative repeated portrayals of these organisms in scientific literature (Doyle et al., 2014) have led to a lack of understanding regarding the benefits that certain gelatinous zooplankton can provide to ecosystems.

The incredible diversity of gelatinous zooplankton is overlooked when categorized into a general group based off of the findings from a few easy-to-study species. It is the duty of future researchers to gain a better, more detailed, and unbiased understanding of these organisms that we share this world with, in order to better understand, confront, and hopefully reverse the detrimental impact climate change is having on the environment.

BIBLIOGRAPHY

- Attrill, M. J., Wright, J., & Edwards, M. (2007). Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. *Limnology and Oceanography*, 52(1), 480–485. https://doi.org/10.4319/lo.2007.52.1.0480
- Båmstedt, U., Fosså, J. H., Martinussen, M. B., & Fosshagen, A. (1998). Mass occurrence of the physonect siphonophore *Apolemia uvaria* (Lesueur) in Norwegian waters. *Sarsia*, 83(1), 79–85. https://doi.org/10.1080/00364827.1998.10413673
- Boero, F., Brotz, L., Gibbons, M. J., Piraino, S., & Zampardi, S. (2016). 3.10 Impacts and effects of ocean warming on jellyfish. 25.
- Brodeur, R. D., Ruzicka, J. J., & Steele, J. H. (2010). Investigating Alternate Trophic Pathways through Gelatinous Zooplankton and Planktivorous Fishes in an Upwelling Ecosystem Using End-to-End Models. 7.
- Brotz, L., Cheung, W. W. L., Kleisner, K., Pakhomov, E., & Pauly, D. (2012). Increasing jellyfish populations: Trends in Large Marine Ecosystems. *Hydrobiologia*, 690(1), 3–20. https://doi.org/10.1007/s10750-012-1039-7
- Cantin, N. E., Cohen, A. L., Karnauskas, K. B., Tarrant, A. M., & McCorkle, D. C. (2010). Ocean Warming Slows Coral Growth in the Central Red Sea. *Science*, 329(5989), 322–325. https://doi.org/10.1126/science.1190182
- Chiaverano, L. M., Holland, B. S., Crow, G. L., Blair, L., & Yanagihara, A. A. (2013). Long-Term Fluctuations in Circalunar Beach Aggregations of the Box Jellyfish Alatina moseri in Hawaii, with Links to Environmental Variability. *PLoS ONE*, 8(10), e77039. https://doi.org/10.1371/journal.pone.0077039
- Condon, R. H., Decker, M. B., & Purcell, J. E. (2001). *Effects of low dissolved oxygen on survival and asexual reproduction of scyphozoan polyps (Chrysaora quinquecirrha).* 8.
- Condon, R. H., Duarte, C. M., Pitt, K. A., Robinson, K. L., Lucas, C. H., Sutherland, K. R., Mianzan, H. W., Bogeberg, M., Purcell, J. E., Decker, M. B., Uye, S., Madin, L. P., Brodeur, R. D., Haddock, S. H. D., Malej, A., Parry, G. D., Eriksen, E., Quiñones, J., Acha, M., ... Graham, W. M. (2012). Recurrent jellyfish blooms are a consequence of global oscillations. 9.
- Condon, R. H., Graham, W. M., Duarte, C. M., Pitt, K. A., Lucas, C. H., Haddock, S. H. D., Sutherland, K. R., Robinson, K. L., Dawson, M. N., Decker, M. B., Mills, C. E., Purcell, J. E., Malej, A., Mianzan, H., Uye, S., Gelcich, S., & Madin, L. P. (2012). Questioning the Rise of Gelatinous Zooplankton in the World's Oceans. *BioScience*, 62(2), 160–169. https://doi.org/10.1525/bio.2012.62.2.9

- Costello, J. H., Colin, S. P., & Dabiri, J. O. (2008). Medusan morphospace: Phylogenetic constraints, biomechanical solutions, and ecological consequences. *Invertebrate Biology*, 127(3), 265–290. https://doi.org/10.1111/j.1744-7410.2008.00126.x
- Daskalov, G. M., Grishin, A. N., Rodionov, S., & Mihneva, V. (2007). *Trophic cascades triggered by overfishing* reveal possible mechanisms of ecosystem regime shifts. 7.
- Doyle, T. K., Hays, G. C., Harrod, C., & Houghton, J. D. R. (2014). Ecological and Societal Benefits of Jellyfish. In K. A. Pitt & C. H. Lucas (Eds.), *Jellyfish Blooms* (pp. 105–127). Springer Netherlands. https://doi.org/10.1007/978-94-007-7015-7_5
- Duarte, C. M., Pitt, K. A., Lucas, C. H., Purcell, J. E., Uye, S., Robinson, K., Brotz, L., Decker, M. B., Sutherland, K. R., Malej, A., Madin, L., Mianzan, H., Gili, J.-M., Fuentes, V., Atienza, D., Pagés, F., Breitburg, D., Malek, J., Graham, W. M., & Condon, R. H. (2013). Is global ocean sprawl a cause of jellyfish blooms? *Frontiers in Ecology and the Environment*, *11*(2), 91–97.
- Euzen, A., Gaill, F., Lacroix, D., & Cury, P. (2017). The Ocean Revealed.
- Galloway, J. N., Dentener, F. J., Capone, D. G., Boyer, E. W., Howarth, R. W., Seitzinger, S. P., Asner, G. P., Cleveland, C. C., Green, P. A., Holland, E. A., Karl, D. M., Michaels, A. F., Porter, J. H., Townsend, A. R., & Voosmarty, C. J. (2004). Nitrogen Cycles: Past, Present, and Future. *Biogeochemistry*, 70(2), 153–226. https://doi.org/10.1007/s10533-004-0370-0
- Gemmell, B. J., Costello, J. H., Colin, S. P., Stewart, C. J., Dabiri, J. O., Tafti, D., & Priya, S. (2013). Passive energy recapture in jellyfish contributes to propulsive advantage over other metazoans. *Proceedings of the National Academy of Sciences*, 110(44), 17904–17909. https://doi.org/10.1073/pnas.1306983110
- Gibbons, M. J., Boero, F., & Brotz, L. (2016). We should not assume that fishing jellyfish will solve our jellyfish problem. *ICES Journal of Marine Science*, 73(4), 1012–1018. https://doi.org/10.1093/icesjms/fsv255
- Gibbons, Mark J, & Richardson, A. J. (2009). Patterns of jellyfish abundance in the North Atlantic. 15.
- Gibbons, Mark J., & Richardson, A. J. (2013). Beyond the jellyfish joyride and global oscillations: Advancing jellyfish research. *Journal of Plankton Research*, *35*(5), 929–938. https://doi.org/10.1093/plankt/fbt063
- Graham, W. M., Pagès, F., & Hamner, W. M. (2001). A physical context for gelatinous zooplankton aggregations: A review. In J. E. Purcell, W. M. Graham, & H. J. Dumont (Eds.), *Jellyfish Blooms: Ecological and Societal Importance* (pp. 199–212). Springer Netherlands. https://doi.org/10.1007/978-94-010-0722-1_16
- Grove, M., & Breitburg, D. (2005). Marine Ecology Progress Series 301:185. Mar Ecol Prog Ser, 301, 185-198.
- Haddock, S. H. D. (2004). A golden age of gelata: Past and future research on planktonic ctenophores and cnidarians. *Hydrobiologia*, 530–531(1–3), 549–556. https://doi.org/10.1007/s10750-004-2653-9
- Holst, S., & Jarms, G. (2007). Substrate choice and settlement preferences of planula larvae of Wve Scyphozoa (Cnidaria) from German Bight, North Sea. *Mar Biol*, 9.
- Hoover, R. A., & Purcell, J. E. (2009). Substrate preferences of scyphozoan Aurelia labiata polyps among common dock-building materials. *Hydrobiologia*, 616(1), 259–267. https://doi.org/10.1007/s10750-008-9595-6
- Hsieh, Y.-H. P., & Rudloe, J. (1994). Potential of utilizing jellyfish as food in Western countries. *Trends in Food Science & Technology*, 5(7), 225–229. https://doi.org/10.1016/0924-2244(94)90253-4

- Langdon, C., & Atkinson, M. J. (2005). *Effect of elevated pCO2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment.* 16.
- Le Quéré, C., Raupach, M. R., Canadell, J. G., Marland, G., Bopp, L., Ciais, P., Conway, T. J., Doney, S. C., Feely, R. A., Foster, P., Friedlingstein, P., Gurney, K., Houghton, R. A., House, J. I., Huntingford, C., Levy, P. E., Lomas, M. R., Majkut, J., Metzl, N., ... Woodward, F. I. (2009). Trends in the sources and sinks of carbon dioxide. *Nature Geoscience*, 2(12), 831–836. https://doi.org/10.1038/ngeo689
- Leone, A., Lecci, R., Durante, M., Meli, F., & Piraino, S. (2015). The Bright Side of Gelatinous Blooms: Nutraceutical Value and Antioxidant Properties of Three Mediterranean Jellyfish (Scyphozoa). *Marine Drugs*, 13(8), 4654–4681. https://doi.org/10.3390/md13084654
- Licandro, P., Conway, D. V. P., Daly Yahia, M. N., Fernandez de Puelles, M. L., Gasparini, S., Hecq, J. H., Tranter, P., & Kirby, R. R. (2010). A blooming jellyfish in the northeast Atlantic and Mediterranean. *Biology Letters*, 6(5), 688–691. https://doi.org/10.1098/rsbl.2010.0150
- Lilley, M. K. S., Beggs, S. E., Doyle, T. K., Hobson, V. J., Stromberg, K. H. P., & Hays, G. C. (2011). Global patterns of epipelagic gelatinous zooplankton biomass. *Marine Biology*, 158(11), 2429–2436. https://doi.org/10.1007/s00227-011-1744-1
- Link, J., & Ford, M. (2006). Marine Ecology Progress Series 320:153. Mar Ecol Prog Ser, 7.
- Loveridge, A., Lucas, C. H., & Pitt, K. A. (2020). Shorter, warmer winters may inhibit production of ephyrae in a population of the moon jellyfish Aurelia aurita. *Hydrobiologia*. https://doi.org/10.1007/s10750-020-04483-9
- Lynam, C. P., Lilley, M. K. S., Bastian, T., Doyle, T. K., Beggs, S. E., & Hays, G. C. (2011). Have jellyfish in the Irish Sea benefited from climate change and overfishing? *Global Change Biology*, 17(2), 767–782. https://doi.org/10.1111/j.1365-2486.2010.02352.x
- Lynam, Christopher P, Gibbons, J., Axelsen, B. E., Sparks, C. A. J., Heywood, B. G., & Brierley, A. S. (2006). Jellyfish overtake fish in a heavily fished ecosystem. 2.
- Miller, M.-E. C., & Graham, W. M. (2012). Environmental evidence that seasonal hypoxia enhances survival and success of jellyfish polyps in the northern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology*, 432–433, 113–120. https://doi.org/10.1016/j.jembe.2012.07.015
- Mills, C. E. (2001). Jellyfish blooms: Are populations increasing globally in response to changing ocean conditions? In J. E. Purcell, W. M. Graham, & H. J. Dumont (Eds.), *Jellyfish Blooms: Ecological and Societal Importance* (pp. 55–68). Springer Netherlands. https://doi.org/10.1007/978-94-010-0722-1_6
- Moroz, L. L. (2015). Convergent evolution of neural systems in ctenophores. *Journal of Experimental Biology*, 218(4), 598–611. https://doi.org/10.1242/jeb.110692
- Pauly, D., Graham, W., Libralato, S., Morissette, L., & Palomares, M. L. D. (2008). Jellyfish Blooms: Causes, Consequences, and Recent Advances. Springer Netherlands. https://doi.org/10.1007/978-1-4020-9749-2
- Pitt, K. A., Duarte, C. M., Lucas, C. H., Sutherland, K. R., Condon, R. H., Mianzan, H., Purcell, J. E., Robinson, K. L., & Uye, S.-I. (2013). Jellyfish Body Plans Provide Allometric Advantages beyond Low Carbon Content. *PLoS ONE*, 8(8). https://doi.org/10.1371/journal.pone.0072683
- Purcell, J. (2007). Environmental effects on asexual reproduction rates of the scyphozoan Aurelia labiata. Marine Ecology Progress Series, 348, 183–196. https://doi.org/10.3354/meps07056

- Purcell, Jennifer E. (2012). Jellyfish and Ctenophore Blooms Coincide with Human Proliferations and Environmental Perturbations. Annual Review of Marine Science, 4(1), 209–235. https://doi.org/10.1146/annurev-marine-120709-142751
- Purcell, Jennifer E., & Arai, M. N. (2001). Interactions of pelagic cnidarians and ctenophores with fish: A review. In J. E. Purcell, W. M. Graham, & H. J. Dumont (Eds.), *Jellyfish Blooms: Ecological and Societal Importance* (pp. 27–44). Springer Netherlands. https://doi.org/10.1007/978-94-010-0722-1_4
- Rabalais, N., Cai, W.-J., Carstensen, J., Conley, D., Fry, B., Hu, X., Quiñones-Rivera, Z., Rosenberg, R., Slomp, C., Turner, E., Voss, M., Wissel, B., & Zhang, J. (2014). Eutrophication-Driven Deoxygenation in the Coastal Ocean. *Oceanography*, 27(1), 172–183. https://doi.org/10.5670/oceanog.2014.21
- Rabalais, N. N., & Turner, R. E. (2001). Hypoxia in the northern Gulf of Mexico: Description, causes and change. In N. N. Rabalais & R. E. Turner (Eds.), *Coastal and Estuarine Studies* (Vol. 58, pp. 1–36). American Geophysical Union. https://doi.org/10.1029/CE058p0001
- Richardson, A. J., Bakun, A., Hays, G. C., & Gibbons, M. J. (2009). The jellyfish joyride: Causes, consequences and management responses to a more gelatinous future. *Trends in Ecology & Evolution*, 24(6), 312–322. https://doi.org/10.1016/j.tree.2009.01.010
- Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F. S. I., Lambin, E., Lenton, T. M., Scheffer, M., Folke, C., Schellnhuber, H. J., Nykvist, B., de Wit, C. A., Hughes, T., van der Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P. K., Costanza, R., Svedin, U., ... Foley, J. (2009). Planetary Boundaries: Exploring the Safe Operating Space for Humanity. *Ecology and Society*, *14*(2), art32. https://doi.org/10.5751/ES-03180-140232
- Sajikumar, K. K., Venkatesan, V., Jeyabaskaran, R., Muhammed, A., & Mohamed, K. S. (2016). First record of the glass octopus Vitreledonella richardi (Cephalopoda: Vitreledonellidae) from the Arabian Sea. *Marine Biodiversity Records*, 9(1), 53. https://doi.org/10.1186/s41200-016-0041-6
- Sinigaglia, C., Peron, S., Eichelbrenner, J., Chevalier, S., Steger, J., Barreau, C., Houliston, E., & Leclère, L. (2020). Pattern regulation in a regenerating jellyfish. *ELife*, 9, e54868. https://doi.org/10.7554/eLife.54868
- Verdes, A., & Gruber, D. F. (2017). Glowing Worms: Biological, Chemical, and Functional Diversity of Bioluminescent Annelids. *Integrative and Comparative Biology*, 57(1), 18–32. https://doi.org/10.1093/icb/icx017