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Comparative analysis of the ecosystems in the northern Adriatic Sea and the Inland Sea of Japan: Can anthropogenic pressures disclose jellyfish outbreaks?

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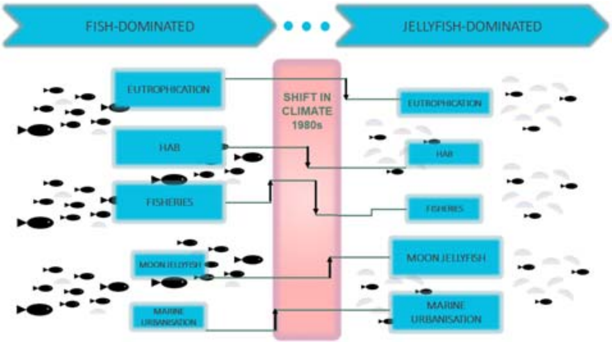
HIGHLIGHTS

- We reviewed environmental and ecosystem changes in two LTER sites in the N hemisphere.
- We examined the effects of anthropogenic pressures on moon jellyfish populations.
- A synchronous shift in climate was detected in the 1980s in both systems.
- Providing additional space for polyps, marine urbanisation-enhanced jellyfish population.
- Fish-dominated ecosystem switched to "jellyfish-permeated" environment.

GRAPHICAL ABSTRACT



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ABSTRACT

A prominent increase in the moon jellyfish (genus *Aurelia*) populations has been observed since 1980 in two semi-enclosed temperate seas: the northern Adriatic Sea and the Inland Sea of Japan. Therefore, we reviewed long-term environmental and biotic data from the two Long-Term Ecological Research (LTER) sites, along with the increase in the moon jellyfish occurrence to elucidate how these coastal seas shifted to the jellyfish-dominated ecosystems. The principal component analysis of atmospheric data revealed a simultaneous occurrence of similar climatic changes in the early 1980s; thereafter, air temperature increased steadily and precipitation decreased but became more extreme. Accordingly, the average seawater temperature from March to October, a period of polyps' asexual reproduction i.e. budding, increased, potentially leading to an increase in the reproductive rates of local polyp populations. Conspicuous eutrophication occurred due to the rise of anthropogenic activities in both areas from the 1960s onwards. This coincided with an increase of the stock size of forage fishes, such as anchovy and sardine, but not the population size of the jellyfish. However, by the end of the 1980s, when the eutrophication lessened due to the regulations of nutrients loads from the land, the productive fishing grounds of both systems turned into a state that may be described as 'jellyfish-permeated,' as manifested by a drastic decrease in fish landings and a prominent increase in the intensity and frequency of medusa blooms. A steady increase in artificial marine structures that provide substrate for newly settled polyps might further contribute to the enhancement of jellyfish population size. Elevated fishing pressure and/or predation by jellyfish on ichthyoplankton and zooplankton might jeopardize the recruitment of anchovy, so that the anchovy catch has

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never recovered fully. These semi-enclosed seas may represent many temperate coastal waters with increased anthropogenic stressors, which have degraded the ecosystem from fish-dominated to jellyfish-dominated.

1. Introduction

Human impacts on marine ecosystems have accelerated dramatically in recent decades. These anthropogenic impacts, such as eutrophication, pollution, overfishing, land use change, and habitat loss, act additively and synergistically with climate change and severely impact the structure and dynamic of ecosystems worldwide (Halpern et al., 2015; Halpern et al., 2008). Recent climate studies have shown patterns of the world's oceans warming over the past 100 years (Burrows et al., 2011; Levitus et al., 2009; Parmesan and Yohe, 2003) and an increased variance of precipitation (Dore, 2005), that, more and more over the last 3–4 decades, have been affecting the physiology and phenology of organisms, species-specific spatio-temporal distributions, community taxonomic compositions, and food web dynamics (Parmesan and Yohe, 2003; Poloczanska et al., 2013; Jourdan et al., 2018). The removal of large apex consumers by fisheries has, in many marine ecosystems, caused trophic downgrading and a reduction of the food chain length (Estes et al., 2011), or led to regime shifts or alternative states of the ecosystem (Estes et al., 2011; Travis et al., 2014) where energy-poor species may dominate (Lynam et al., 2006). In addition, excessive coastline modification has led to habitat loss affecting species richness and abundances (Airoldi et al., 2008), while the proliferation of the artificial underwater structures may offer opportunities for some opportunistic species (Duarte et al., 2013).

The depletion of fish stocks, the modification of the natural coastline, eutrophication, and warming temperatures (Richardson et al., 2009) have created opportunities for the expansion of jellyfish populations worldwide (Brotz et al., 2012; Kawahara et al., 2006; Kogovšek et al., 2010; Purcell, 2012; Uye and Ueta, 2004). Several attributes of jellyfish biology, such as the short life-span of medusae, sexual and asexual reproduction, broad diets, passive feeding, and low metabolic requirements (Arai, 1997), enable them to not only reproduce rapidly when conditions are favourable, but also to tolerate some environmental stressors better than other organisms – one example being fish (Shoji et al., 2005). In such perturbed ecosystems, the role of jellyfish becomes more important, shifting energy from energy-rich fish to energy-poor jellyfish (Uye, 2011). Increased jellyfish populations may compete with fish for food (Purcell and Arai, 2001; Shoji et al., 2009) and prey on fish eggs (Gordoa et al., 2013; Zenitani et al., 2013) and fish larvae (Milisenda et al., 2014; Purcell et al., 2014; Sabatés et al., 2010). In addition, by clogging nets and stinging (De Donno et al., 2014; Nastav et al., 2013; Uye, 2008; Uye and Ueta, 2004), they severely affect fisheries (Conley and Sutherland, 2015; Palmieri et al., 2014) and the tourist industry (Ghermandi et al., 2015).

The cosmopolitan moon jellyfish of the genus *Aurelia* has been noted as conspicuous scyphozoan forming notorious blooms in a variety of coastal environments between 70°N and 40°S (Kramp, 1965; Russell, 1970). As the majority of the scyphozoan species, the moon jellyfish has a bipartite life cycle, alternating between the benthic polyp stage and the free-swimming medusa stage. Tiny polyps reproduce asexually to form clones and increase their numbers, while through strobilation, a single polyp produces and releases multiple planktonic ephyrae which grow into medusae. Adult medusae reproduce sexually to form planulae that attach onto hard substrates and develop into polyps. Each life stage can thrive in a wide environmental window of temperature, salinity, and/or food availability, yet, there are specific key environmental factors that determine the ontogenetic processes (Arai, 1997; Lucas et al., 2012). Experimental studies show that warmer temperatures favour budding (Han and Uye, 2010; Hubot et al., 2017; Malej et al., 2012), while a decrease in temperature leads to a specific threshold that triggers strobilation of moon jellyfish polyps originating from temperate zones (Han and Uye, 2010; Lucas et al., 2012; Purcell et al., 2012). Moreover, an abundant food supply stimulates polyp reproduction (Han and Uye, 2010; Hubot et al., 2017) and ephyrae production (Ishii et al., 2004). Such physio-ecological properties facilitate the proliferation of polyps that consequently leads to massive medusae outbreaks.

A recent study that analysed long-term changes in jellyfish abundance (Condon et al., 2013) failed to demonstrate robust evidence for recent jellyfish increase on a global scale and suggested that jellyfish populations oscillated with about a 20-year periodicity. However, there are many regional cases to demonstrate the increase in jellyfish populations (Boero, 2013; Brotz et al., 2012; Kogovšek et al., 2010). Among areas that experienced increased incidence of jellyfish blooms were the northern Adriatic Sea (NAD) and the Inland Sea of Japan (ISJ). Intensive jellyfish blooms were attributed to the medusae of the genus *Aurelia*, specifically to *Aurelia* sp. 8 in the NAD and *Aurelia* sp. 1 in the ISJ (Dawson, 2003), that were recently designated as *A. solida* and *A. coerula*, respectively (Scorrano et al., 2017). Despite the apparently different species, the main period of strobilation in both areas overlaps: it starts in late autumn, concomitant with seawater temperature decrease to or below 15 °C. In situ observations revealed, that in the NAD strobilation occurs between November and March (Malej et al., 2012), while in the ISJ the strobilation starts in December and lasts until April with ephyrae still persisting in net samples in May (Makabe et al., 2014). Medusae are generally present from February until June in the NAD with very rare observations in January and July (Malej et al., 2012). In contrast, longer seasonal occurrence of medusa from February until November characterises the coastal waters of the ISJ (Uye and Shimauchi, 2005).

Both systems are important fishing grounds and recent jellyfish outbreaks had significant impact on local fisheries by clogging fishing nets, reducing the quality of the fish catch, and increasing the cost of fishing operations due to their displacement and reparation of fishing nets (Nastav et al., 2013; Palmieri et al., 2014; Uye and Ueta, 2004). We therefore, exploited a long-term time series of environmental and biotic parameters from the two LTER (Long-Term Ecological Research) sites to detect and evaluate the environmental changes that promoted massive moon jellyfish outbreaks in the recent decades. It is believed, that two mechanisms are controlling how large-scale drivers affect the plankton community, and may result in favouring jellyfish: 1) increased nutrient loads and changes in nutrient ratios (i.e. eutrophication) often lead to an increase in biomasses at different trophic levels, shift the phytoplankton community from a diatom-dominated system to a flagellate-based food web (Mozetič et al., 2012), and result in the dominance of small-sized zooplankters (Conversi et al., 2009; Kamburska and Fonda-Umani, 2009), which all may benefit jellyfish blooms (Purcell, 2012) (i.e. bottom-up control); and 2) overharvesting of forage fish relinquishes the competition for food between forage fish and jellyfish, leading to environmental conditions in which jellyfish flourish (Purcell, 2012) (i.e. top-down control). To investigate that, long-term changes in climate, nutrient loadings, and total fish catch were analysed. Finally, we hypothesised that the increasing seawater temperature together with marine urbanisation stimulated polyps' population in the way that resulted in an increase in frequency and intensity of medusae blooms.