

CHAPTER 17

MACROJELLYFISH (SCYPHOZOA AND CTENOPHORA) IN TWO ENCLOSED MARINE SYSTEMS (THE SEA OF MARMARA AND ADRIATIC SEA): A REVIEW

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Abstract

Although geographically well apart, there are interesting similarities between the ecosystems of the Sea of Marmara and the Adriatic Sea. In this study, following an evaluation of the ecological problems as well as oceanography, productivity, plankton biomass of these seas, macro-jellyfish ecology of the two ecosystems were discussed comparatively. The Sea of Marmara and the Adriatic Sea are among the areas where increases in jellyfish and mucilage events have been observed in recent decades. Environmental problems such as global warming, oxygen depletion, eutrophication, overfishing, intense maritime traffic, and habitat destruction are causing opportunistic and alien species to increase in both abundance and number of species. As biodiversity declines due to habitat destruction, so does the ecosystem's means and ability to combat the invasion of alien species in both ecosystems. Accordingly, disruption of lower food chains can put pressure on the entire ecosystem and affect socio-ecological prospects. The

number of species of Scyphozoa and Ctenophora was found to be higher in the Adriatic Sea compared to the Sea of Marmara. Mass occurrences with a clear seasonal pattern and related to the geographical location were observed for *Aurelia aurita*, *Rhizostoma pulmo*, *Chrysaora hysoscella* and non-native *Mnemiopsis leidyi* in the Marmara Sea. However, although *A. aurita* and *R. pulmo* show widespread blooms according to the seasons and regions in the Adriatic Sea, *C. hysoscella* and *M. leidyi* produced blooms limited to a few areas. Negative and positive interactions of macrojellyfishes with human were also considered. Semi-enclosed seas such as the Sea of Marmara and the Adriatic Sea are representative of many temperate coastal waters where climate change and anthropogenic stressors are increasing, and the ecosystem has changed from a fish-dominated to a jellyfish-dominated ecosystem.

Keywords: Jellyfish, eutrophication, diversity, introduce, fisheries

1. Introduction

The Sea of Marmara and the Adriatic Sea are semi-enclosed marine systems located on the northern and northeastern edges of the Mediterranean Sea. While the Adriatic Sea cuts deeply into the European continent to the north, the Sea of Marmara is connected to another marginal basin, the Black Sea, to the east. Because of their geographic location, the influence of the surrounding land and limited exchange with the Mediterranean Sea, the Sea of Marmara and the Adriatic Sea have special characteristics that are important for biotic communities to settle and thrive.

Scyphozoa and Ctenophora are important members of marine ecosystems and have ecological and economic significance. In this chapter, we present an analysis of Scyphozoa and Ctenophora populations in the Adriatic Sea and the Sea of Marmara. We reviewed the available literature and compiled data on jellyfish species composition, temporal and spatial distribution, and mass occurrence of individual species in both sea basins. The Mediterranean Sea is known for its rich Scyphozoa and Ctenophora fauna (Galil et al., 1990; Daly Yahia et al., 2003; Boero, 2013; Gueroun et al., 2022), while in the marginal seas (Marmara and Adriatic) the number of species seems to be lower (Isinibilir and Yılmaz, 2017; Pestorić et al., 2021). In contrast to the lower species diversity, the Adriatic Sea and the Sea of Marmara are two regions where jellyfish blooms are quite common and sometimes have significant socioeconomic impacts.

We have organized this chapter as follows: First, we briefly describe the main features the Sea of Marmara and Adriatic Sea to characterize the biophysical environment for the observed jellyfish species, and then provide an overview of the Scyphozoa and Ctenophora species, which includes information on the species found in the Mediterranean and Black Seas. The spatial and temporal distribution in each of the two systems is then presented in more detail. Finally, data on the occurrence of blooms and the impact of human activities are described.

1.1. Oceanography, Productivity, and Plankton Biomass of the Sea of Marmara

The Sea of Marmara is a Turkish inland sea, with its connection to global waters provided by the Çanakkale Strait in its southwest, and to the Black Sea via the Istanbul Strait in the north. The Sea of Marmara has a width of 70 km, a length of 250 km, a surface area of 11,500 km², and a volume of 3,378 km³. It has an average depth of 400 m, with the deepest point reaching 1,390 m. The seabed topography of the Marmara Sea includes a broad continental shelf with a depth of 100 m along the southern coast, as well as three deep basins located in the north (from west to east: 1,100 m, 1,390 m, and 1,240 m).

The Marmara Sea contains two water masses separated by a density (salinity) interface called a halocline, which is located at approximately 25 m depth. Whilst the surface waters having about 22 psu salinity are under the strong influence of inflow from the Black Sea (Figure 1), lower water mass (at about 38 psu salinity) originates from the Mediterranean Sea (Beşiktepe et al., 1994). In the halocline, there is a sharp density stratification that prevents oxygen from reaching the lower layers from the surface. Except in the two shallow straits, where mixing occurs (Jarosz et al., 2013), the layers in the Sea of Marmara generally do not mix, as in the case in the Black Sea. However, there is a balance between the oxygen consumption caused by the settling of biogenic particulate matter from the surface to the lower layers and the oxygen-rich Mediterranean waters entering through the Çanakkale Strait. Despite the oxygen-deficient (suboxic) conditions in the Marmara halocline subsurface waters, which are continuously replenished by water inflows from the Çanakkale Strait (with an average renewal time of 6-7 years), permanent anoxic conditions similar to those in the Black Sea have not yet developed (Özsoy et al., 1988). However, in the past eutrophication and consequent hypoxia events were reported in some limited coastal and bay areas with limited interaction with the open sea (Baştürk et al., 1990). Such events have been more frequently observed in recent years (Balkıs et al., 2012; Turkoglu, 2013; Ediger et al., 2016).

The distribution of plankton fauna in the Sea of Marmara is influenced by the currents and water layers: The lower current brings species typical of the Mediterranean, while the upper current introduces species from the Black Sea.

The Sea of Marmara is renowned for its high fertility and productivity, making it one of the most productive seas in the Mediterranean basin. It exhibits chl-a values reaching as high as 20.0 $\mu\text{g L}^{-1}$ (Yalçın et al., 2017) and production values of 100 $\text{gC/m}^2/\text{y}$ (Ergin et al., 1993).

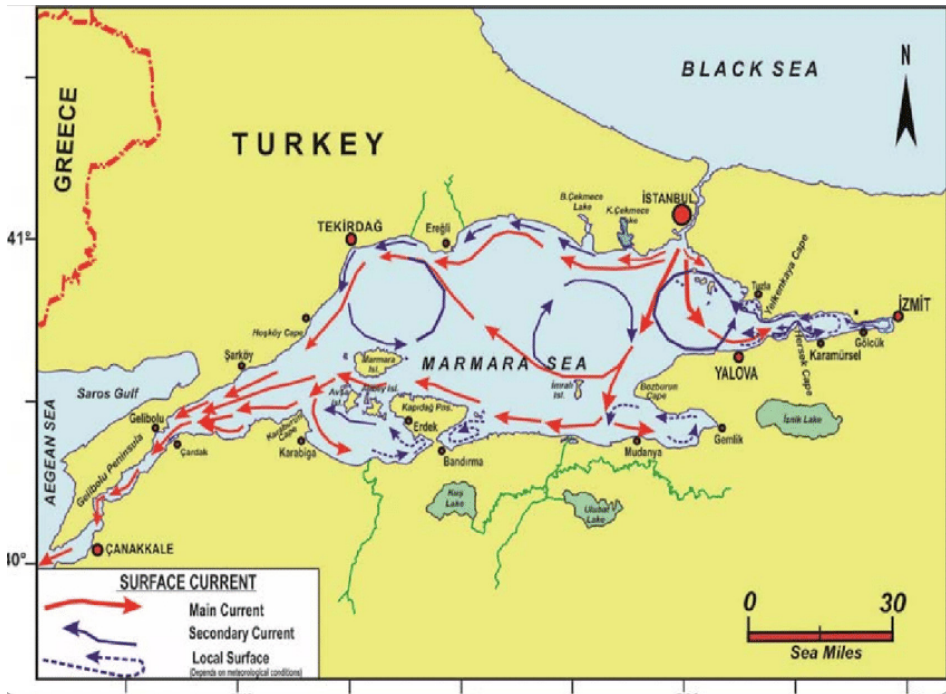


Figure 1. Surface currents of the Sea of Marmara (Meriç et al., 2018).

According to the results of research conducted to date, 273 phytoplankton species have been identified in the Sea of Marmara (Balkis and Tas, 2016). Although there are some seasonal differences according to the research findings in the Marmara Sea, the two main groups, diatoms, and dinoflagellates, have a contribution of more than 90% in the community (Tüfekçi et al., 2010). These two groups are also the phytoplankton groups that contribute the most to mucilage formation. In the Sea of Marmara, dinoflagellates are more abundant in summer and diatoms in winter; in the spring and autumn seasons, there may be increases in the species belonging to both groups depending on the environmental conditions (Tüfekçi et al., 2010; Balkis and Taş, 2016). During the mucilage event seen in 2007 and 2020/2021, the haptophyte *Phaeocystis pouchetii*, diatoms *Skeletonema costatum*, *Cylindrotheca closterium*, *Thalassiosira rotula*, *Proboscia alata*, *Rhizosolenia* sp., *Pseudosolenia calcar-avis*, *Ditylum brightwellii*, *Coscinodiscus* spp., *Leptocylindrus minimus*, *Chaetoceros* spp., *Cerataulina pelagica*, *Pseudo-nitzschia* cf. *seriata*, and the dinoflagellates *Gonyaulax hyalina* or *G. fragilis* (dinoflagellate) have been suggested as the potential species responsible for the mucilage production in the Sea of Marmara (Aktan et al., 2008; Tüfekçi et al., 2010; Balkis-Özdelice et al., 2021). Recently, Eker-Develi et al. (2023) identified mass occurrence of a

coccolithophorid species *Ochrosphaera neapolitana* during the intense bloom period in the Sea of Marmara and simultaneously showed its mucus production in the laboratory.

1.2. Oceanography, Productivity, and Plankton Biomass of the Adriatic Sea

The Adriatic Sea is the northernmost arm of the Mediterranean and is about 800 km long and 200 wide. It is connected to the Ionian Sea by the Strait of Otranto, which is 70 km wide and 789 m deep. The eastern coast of the Adriatic Sea is high and rocky, and because of the numerous islands, the coastline is very long. About 5,780 km of the Croatian part of the coast are divided into numerous bays and over 1,100 islands and rocks. Depending on the bathymetry and different oceanographic features, three basins of the Adriatic Sea are distinguished: the northern, the central and the southern (Figure 2). The biological characteristics of these basins are determined by the different morphology of the seabed, the meteorological characteristics, the hydrodynamics, and the influence of the mainland. Most of the Adriatic Sea (almost 3/4) is shallower than 200 m. The greatest depth of 1228 m was measured in the South Adriatic Pit. The basin has distinct morphological features both longitudinally and transversely. The Jabuka Pit, with a maximum depth of about 270 m, forms the boundary between the northern and middle Adriatic sub-basins. The southern sub-basin extends from the Palagruža sill to the Otranto sill. The western and eastern coasts each have a narrow continental shelf (width 20-30 km to the transition at 200 m depth) and a steep continental slope that reaches the mentioned maximum depth in the south. The southwestern Adriatic margin is characterized by a rugged morphology, topographic elevations, and numerous incisions (Trincardi et al., 2014) and sedimentary bedforms (Foglini et al., 2016), of which the Bari Canyon is the most developed.

The complexity of the oceanographic conditions of the Adriatic Sea derives from its geographical position, being deeply embedded in the European continent and consequently considered as a transition zone between the influences of the European continent and the oceanic effects of the Mediterranean Sea. Thermohaline circulation throughout the Adriatic Sea depends on large-scale atmospheric oscillations (Russo and Artegiani, 1996).

The southern Adriatic Sea is characterized by a quasi-permanent cyclonic circulation (Figure 2), the South Adriatic Gyre (Gačić et al., 1997). In winter, dense water (Adriatic Dense Water, AdDW) forms as a mixture of fresher Adriatic and saltier Ionian water due to convection processes. The deepest part of the southern Adriatic is not ventilated by winter convection, but mainly by the subsidence of the North Adriatic Dense Water (NadDW) through the Bari Canyon and other bathymetric features (Turchetto et al., 2012). The formation of the

AdDW and its discharge through the Strait of Otranto varies on an interannual time scale depending on winter air-sea heat fluxes (Manca et al., 2002).

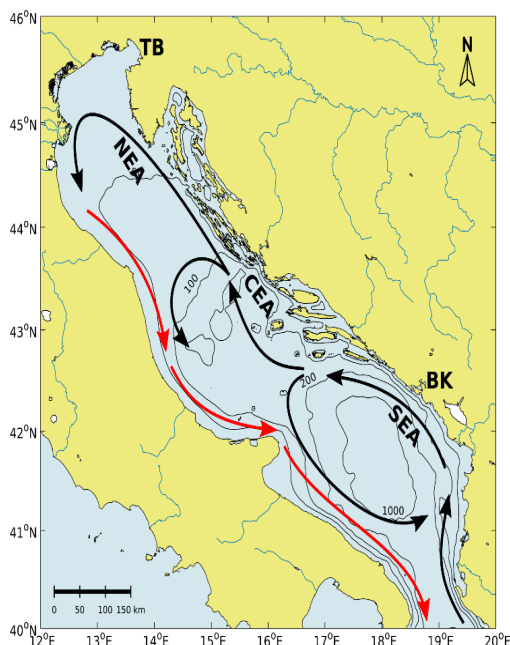


Figure 2. Surface currents (adapted from Civitarese et al., 2023) and bathymetry of the Adriatic Sea. The black arrows show the Eastern Adriatic Current and gyres, and the red arrows show the Western Adriatic Current. Isobaths are plotted at 50 m, 100 m, 200 m and 1000 m depth. Five research areas: TB - Gulf of Trieste, NEA - Northeastern Adriatic, CEA - Central Eastern Adriatic, SEA - Southeastern Adriatic, BK - Boka Kotorska Bay.

Depending on the circulation in the Ionian Sea, either water of high salinity of Levantine origin or water of lower salinity from the Atlantic Ocean is transported to the interior of the Adriatic Sea (Civitarese et al., 2010). The interaction between the Adriatic and the Mediterranean Sea resembles the bimodal oscillating system (BiOS), which is related to changes in the circulation of the North Ionian Gyre from cyclonic to anticyclonic mode and vice versa. This interaction has a great influence on the physical properties of the southern Adriatic Sea (Gačić et al., 2002). Due to the BiOS mechanism, thermohaline, and nutrient properties in the southern Adriatic Sea exhibit quasi-periodic variability (Civitarese et al., 2023). Levantine water entering the Adriatic Sea during the cyclonic phase of the North Ionian Gyre circulation is characterized by salinity above 38.75 psu, temperatures above 14 °C, and low nutrient content (Vilibić and Orlić, 2002; Civitarese et al., 2010). In contrast, the water of Atlantic origin associated with the anticyclonic phase is characterized by lower salinity.

The amount of nutrients entering the Adriatic depends on the circulation regime, with more nutrients entering during the anticyclonic phase and less during the cyclonic phase (Civitarese et al., 2023). Thus, the bimodal fluctuation system, winter convection, and the intrusion of either Levantine or Atlantic waters into the Adriatic regulate changes in the structure and activity of the plankton community of the southern Adriatic.

The southern Adriatic is an oligotrophic basin characterized by significant seasonal changes and fluctuations in phytoplankton abundance and biomass, reaching a maximum in spring (Antoine et al., 1995). A picophytoplankton community dominates, while microphytoplankton pulses are restricted to low salinity surface layers, deep chlorophyll maximum depths, and winter convection (Cerino et al., 2012; Jasprica et al., 2022). During a winter convection event, the area with the highest phytoplankton abundance appeared below the euphotic zone (Batistić et al., 2012), as did the abundance of microzooplankton (Lučić et al., 2017). The intensity of winter convection and spring bloom influences the downward fluxes of particles to the deepest part of the basin (Turchetto et al., 2012). The higher chlorophyll-a content, ranging from 0.3 mg m^{-3} to 0.7 mg m^{-3} and limited to the period from February to April, is short-lived and vertically restricted (Gačić et al., 2002). The mean annual chlorophyll content is in the range of $0.087 \pm 0.07 \text{ mg m}^{-3}$ (Viličić, 1989; Batistić et al., 2007).

According to climatological and circulatory characteristics (Artegiani et al., 1997), the central Adriatic is a transition basin between north and south. The coastal area is highly indented with many islands and bays, quite steep, so that the channel areas are relatively deep ($\sim 50 \text{ m}$) and characterized by relatively rapid aeration, including the penetration of open water masses. The oligotrophic character of the open waters of the central Adriatic is reflected in the composition of the phytoplankton communities, where the nanophytoplankton fraction dominates, while productivity in the channel areas is higher than in the open sea (Totti et al., 2000). The concentration of chlorophyll-a varies between 0.01 and 1.02 mg m^{-3} (Ninčević et al., 2002). On the other hand, nutrient enrichment in karst estuaries or in areas with strong anthropogenic pressure near large settlements and industrial areas leads to an increase in abundance and biomass of all components of the pelagic food web (Šolić et al., 2010; Vidjak et al., 2012). In the neritic region of the central Adriatic, chlorophyll-a concentrations in the surface layer ranged from 0.01 to 7.80 mg m^{-3} , with the highest values measured on the west coast (Pestorić et al., 2021). The composition and distribution of zooplankton in the central and southern Adriatic differ from that in the northern Adriatic and west coast. The basic characteristics are greater diversity, constancy of species, and low abundance with small annual fluctuations.

The northern Adriatic is the shallowest and most productive part of the Adriatic Sea. Nutrients, productivity, and plankton biomass in the northern Adriatic show strong gradients with distance from the major freshwater inflows discharging from the northwestern coasts. Primary production varies from about 100 to slightly less than 280 g C m⁻² year⁻¹ in the northwestern part and below 110 g C m⁻² yr⁻¹ in the central and eastern areas. Seasonal peaks are associated with peak river discharge, with average chlorophyll-a biomass peaking at about 2 µg L⁻¹ in spring and autumn (Brush et al., 2021a). Copepods are the most species-rich and abundant mesozooplankton group overall, while cladocerans predominate in summer and larvae of various benthic organisms (mollusks, Crustacea) are common in spring and autumn (Pierson et al., 2021).

2.1. Major Ecological Problems in the Sea of Marmara

Over the past few decades, the ecosystem of the Sea of Marmara has faced several anthropogenic challenges, including land-based pollution, eutrophication, overfishing, habitat loss, the introduction of invasive species and climate change. One of the most recent events that gained widespread attention from scientists, the media, and the public was the occurrence of large-scale mucilage events that persisted for several months in 2021 (Eker-Develi et al., 2023; Isinibilir-Okyar, 2023). The combination of strong stratification and pollution in the Sea of Marmara led to a critical drop in oxygen levels in the deeper waters, severely impacting metazoan life.

The cities that serve as the locomotives of Türkiye's industry and commerce, as well as the cities with significant agricultural activities, are mainly located around the Sea of Marmara. The population of the Marmara Region accounts for more than 30% of Türkiye's population, and the population growth rate is rather high in the cities surrounding the Sea of Marmara. The Marmara Region is the most industrialized region in Türkiye and is home to densely populated cities such as Istanbul, İzmit, Yalova, Gemlik, Mudanya, Bandırma, Erdek, Karabiga, Lapseki, Tekirdağ, and Silivri. In addition to the heavy urban activities, agricultural, commercial, and industrial activities also exert pollution pressure on the Sea of Marmara. Along with effluents from wastewater treatment facilities, rivers are among the most important particulate/dissolved pollution sources for this inland sea.

Habitat loss is one of the most significant threats to the Marmara Sea ecosystem. Both extensive land reclamation and coastal structures significantly altering the coastline, as well as illegal fishing activities, lead to the destruction of natural habitats on the seafloor. This situation causes significant damage to the underwater ecosystem by destroying their fishing

grounds and makes it impossible for small-scale fishermen operating in the region to sustain their fishing activities (Gül et al., 2019).

Rapid urbanization and coastal development worldwide have led to the degradation of natural coastal habitats, transforming them into anthropogenically altered habitats (Airoldi et al., 2009; Jordan et al., 2009). Coastal area reclamation and changes in coastal geomorphology not only result in alterations in sedimentation patterns but also significantly modify the biological and physical structure of nearshore habitats (Ten Brinke et al., 2004; Turner, 2006). Artificial habitats differ greatly from natural habitats in terms of their surface characteristics and structural complexity (Wen et al., 2010). Many anthropogenically modified coastal habitats are composed of concrete structures with much smoother surfaces compared to natural rocky reef substrates. This reduction in the presence of shelters, which are crucial for the aggregation and colonization of small fish and microhabitats, can lead to a decrease in biological diversity and an increase in opportunistic species (Bulleri, 2005; Wen et al., 2010).

The Turkish Straits System, consisting of the Istanbul and Çanakkale Straits and the Marmara Sea, is of strategic importance as the only waterway connecting the Black Sea to the Mediterranean Sea, and it is one of the most critical points for transfer of petroleum products worldwide. Approximately 3% of global oil trade is conducted through the Turkish Straits: each year, around 40,000 ships pass through the Çanakkale and Istanbul Straits. Petrochemical wastes such as bilge, slop, sludge, ballast waters, and domestic wastewater illegally discharged from ships pose a significant threat to the Marmara Sea, which has become highly sensitive to pollution load (Ünlü, 2016). In particular, the İzmit Bay hosts intense port activities and is home to approximately 36 ports and piers, making it the area with the highest ship traffic in the country (Ergüven et al., 2023). The Sea of Marmara is not only a region with intense local pressures (Ediger et al., 2016) but has also experienced an increase in seawater temperature in recent years (Altıok and Kayışoğlu, 2015; Altıok et al., 2021). As a result, the Marmara Sea has undergone changes in species diversity and is facing the pressure of invasive and opportunistic species (Balkıs-Özdelice et al., 2021; Dogan and Isinibilir, 2016; Isinibilir et al., 2010, 2015, 2021a, b, 2022), particularly impacting pelagic organisms and fishing activities (Altuğ et al., 2011; Çınar et al., 2011; Isinibilir, 2012; Isinibilir and Yılmaz, 2017).

2.2. Major Ecological Problems in the Adriatic Sea

The northern Adriatic is characterised by alluvial plains to the north and west and rugged mountains to the east. It has an extensive watershed (> 110,000 km²), is densely populated (> 25 million people), and is intensively used by industry, agriculture, and livestock in the west.

A high freshwater input brings sediments and dissolved inorganic and organic nutrients to this shallowest part of the Adriatic Sea. Annual river cycles are bimodal with peak discharge in spring (April - June) and autumn (October - December) (Zhang et al., 2021). This river-dominated sub-basin of the Adriatic Sea is subject to several anthropogenic pressures. These include nutrient enrichment with a long history of cultural eutrophication, which accelerated in the second half of the 20th century and has improved in recent decades (Mozetič et al., 2010; Viaroli et al., 2018). Analysis of oxygen depletion episodes showed that the frequency of hypoxia/anoxia events peaked in 1988-1991 and was prevalent in the western NA (Djakovac et al., 2015). In contrast to the Sea of Marmara, where large-scale mucilage events have occurred recently (Aktan et al., 2008; Eker-Develi et al., 2023), the accumulation of floating slime masses in the northern Adriatic has been documented since the first decades of the 18th century (Degobbis et al., 1995). More recently, the phenomenon reached its greatest spatial and temporal intensity in 1988-1992 but was less intense in subsequent years (Brush et al., 2021b). Significant threats to the ecosystem also include overfishing (Kennedy et al., 2021), coastal development associated with habitat degradation (Palinkas et al., 2021), increases in jellyfish blooms, and invasive species (Pearson et al., 2021).

The degree of pollution of the bays on the eastern coast of the Adriatic depends mainly on the depth of the water and the connection to the open sea (Kušpilić, 2005). Political and economic changes in southeastern Europe led to the cessation of the operation of large industrial facilities on the coast at the end of the last century. Today, the sources of pollution are mainly the rivers of the Adriatic basin and the sewage of the larger cities. The concentrations of organic pollutants and heavy metals in the rivers are much lower than in the rest of the Mediterranean (Kušpilić, 2005). Increasing eutrophication with degenerative consequences for benthic flora and fauna has been observed in cage fish farms (Matijević et al., 2006).

As a result of global changes, the Adriatic Sea is increasingly facing problems due to the introduction of new species, including alien species (through aquaculture and shipping) and species from other Mediterranean subregions that are expanding their geographical distribution (Pečarević et al., 2013; Vidjak et al., 2018; Palinkas et al., 2021).

Furlan et al. (2019) proposed the new Cumulative Impacts Index (CII), which combines the impacts of anthropogenic pressures and natural drivers on marine ecosystems. Anthropogenic pressures affecting ecosystems include smothering, sealing, abrasion and extraction of the seabed, underwater noise, introduction of non-native species, nutrient inputs, and introduction of hazardous substances. Impacts were categorized as physical, biological, chemical, and climatic. The multi-hazard assessment, which applied the CII to the Adriatic Sea, provided a

comprehensive assessment of marine areas and found that the most severe impacts were in the northern Adriatic Sea and on the western continental shelf (Furlan et al., 2019).

3. Jellyfish Diversity in the Marmara, Adriatic and Mediterranean Seas

The information on jellyfish in this chapter includes published records of jellyfish occurrences reported by scientists on research trips, as well as Citizen Science-based observations by divers, fishermen, locals, and students with the following semi-quantitative assignments: 0 no sightings, 1 sporadic occurrence of single organisms, 2 frequent sightings of single jellyfish and/or small aggregations, and 3 frequent sightings of large aggregations.

A total of 9 species of Scyphozoa (Discomedusae) were found in the Sea of Marmara, compared to 3 in the Black Sea, 14 in the Adriatic Sea and 24 in the Mediterranean Sea. Of these, eight species (*Aurelia aurita*, *Chrysaora hysoscella*, *Cotylorhiza tuberculata*, *Discomedusa lobata*, *Drymonema dalmatinum*, *Mawia benovici*, *Pelagia noctiluca*, *Rhizostoma pulmo*) were observed in both the Marmara Sea and the Adriatic Sea, several of which form large blooms (Table 1, Figure 3).

Table 1. Scyphozoa (Discomedusae) in the Mediterranean, Adriatic, Marmara, and Black seas: *Species forming bloom. + = Native, I = Introduced, ND = Newly Described				
Species	Mediterranean Sea	Adriatic Sea	Sea of Marmara	Black Sea
<i>Aurelia aurita</i> *	? (see text)	? (see text)	+	+
<i>Aurelia coerulea</i> *		I		
<i>Aurelia pseudosolida</i>		ND		
<i>Aurelia relicta</i> *		ND		
<i>Aurelia solida</i> *	I	I		
<i>Cassiopea andromeda</i>	I			
<i>Cassiopea polypoides</i>	I			
<i>Catostylus tagi</i>	I			
<i>Chrysaora hysoscella</i> *	+	+	I	I
<i>Chrysaora cf. achylos</i>	I			
<i>Chrysaora presudoocelata</i>	ND			
<i>Cotylorhiza erythraea</i>	I			
<i>Cotylorhiza tuberculata</i> *	+	+	I	
<i>Discomedusa lobata</i> *	+	+	I	
<i>Drymonema dalmatinum</i>	+	+	I	
<i>Marivagia stellata</i>	ND			
<i>Mawia benovici</i>		ND/I	ND/I	

<i>Pelagia noctiluca</i> *	+	+	I	
<i>Phacellophora camtschatica</i>	I			
<i>Phyllorhiza punctata</i>	I			
<i>Rhizostoma pulmo</i> *	+	+	+	+
<i>Rhizostoma luteum</i>	I			
<i>Rhopilema nomadica</i> *	I			
<i>Stomolophus meleagris</i>	I			

The species diversity of Ctenophora is also much greater in the Mediterranean and Adriatic Seas than in the Sea of Marmara and the Black Sea. So far, 16 species have been reported in the Adriatic Sea and 35 species in the Mediterranean Sea, compared to only four species in the Sea of Marmara (Table 2).

Table 2. Species list of Ctenophora in the Mediterranean, Adriatic, Marmara and Black seas.
*Species forming bloom + = Native, I = Introduced

Species	Mediterranean Sea	Adriatic Sea	Sea of Marmara	Black Sea
<i>Bathocyroe fosteri</i>	+			
<i>Beroe cucumis</i>	+			
<i>Beroe forskali</i>	+	+		
<i>Beroe mitrata</i>	+			
<i>Beroe ovata</i>	+	+		
<i>Beroe ovata</i> sensu Mayer	I	I	I	I
<i>Bolinopsis infundibulum</i>	+			
<i>Bolinopsis vitrea</i> *	+	+		I
<i>Callianira bialata</i>	+	+		
<i>Callianira ficalbi</i>	+	+		
<i>Ceroctena bicornis</i>	+			
<i>Cestum veneris</i> *	+	+		
<i>Cydippe ovata</i>	+			
<i>Charistephane fugiens</i>	+			
<i>Ctenella aurantia</i>	+			
<i>Deiopea kaloktenota</i>	+	+		
<i>Eschscholtzia pectinata</i>	+			
<i>Euplokamis stationis</i>	+			
<i>Eurhamphaea vexilligera</i>	+			
<i>Haeckelia bimaculata</i>	+			
<i>Haeckelia filigera</i>	+			

<i>Haeckelia rubra</i>	+	+		
<i>Hormiphora plumosa</i>	+	+		
<i>Lampaea pancerina</i>	+	+		
<i>Lesueuria vitrea</i>	+			
<i>Leucothea multicornis*</i>	+	+		
<i>Minictena luteola</i>	+			
<i>Mnemiopsis leidyi*</i>	I	I	I	I
<i>Ocyropsis maculate imaculata</i>	+			
<i>Pleurobrachia pileus</i>	+	+	+	+
<i>Pleurobrachia rhododactyla</i>	+	+		
<i>Pleurobrachia rhodopis</i>	+	+	+	
<i>Thalassocalyce inconstans</i>	+			
<i>Thoe paradoxa</i>	+			
<i>Velamen parallelum</i>	+			

Several Discomedusae and Ctenophora species form blooms in both the Sea of Marmara and the Adriatic Sea. The most common and with the greatest spatial and temporal extent are blooms of *Aurelia* and *Rhizostoma* (Figure 3) and the introduced Ctenophora *Mnemiopsis leidyi*.



Figure 3. Examples of jellyfish bloom in Istanbul strait in the Marmara (left: underwater photo of *Aurelia aurita* bloom by Hakan Kabasakal) and the Adriatic Sea (right: photo of *Rhizostoma pulmo* bloom taken by drone).

3.1. State of Jellyfish Species in the Sea of Marmara

The coastal areas of the Sea of Marmara exhibit a variety of jellyfish species, encompassing medusae from Scyphozoa and Ctenophora classes (see Tables 1 and 2). It is important to note that our research primarily focused on the coastal zones, and as a result, we did not

observe species belonging to the Coronatae group, which are typically found in deeper waters. However, in 2008, we detected the presence of the Coronatae species *Paraphyllina ransoni* in Izmit Bay (Isinibilir et al., 2010). Furthermore, our study unveiled the occurrence of *P. noctiluca*, a Scyphozoa species that is reported for the first time in the Sea of Marmara. The complete list of species, based on published data and our own observations, is given in Tables 1 and 2.

Scyphozoa (Discomedusae)

Aurelia aurita

The first record of *A. aurita* in the Sea of Marmara was reported from the Bosphorus in 1952 (Demir, 1954). *A. aurita* is a frequently occurring species (Figure 4) with high abundance in the upper layer of the Sea of Marmara, particularly in coastal areas and bays. It has been observed to reach very high biomass values along the Bosphorus, especially in coastal areas (Figure 3), such as 5111 g.m⁻² in April 2015 at the Strait of Istanbul (Isinibilir and Yılmaz, 2017). In June 1999, it reached a maximum biomass of 7000 g.m⁻² in the Bosphorus (Tarkan et al., 2000). In Izmit Bay, which experiences pressure from industry and maritime traffic, the maximum biomass recorded during 2001 and 2002 was 160.5 g.m⁻³ in the autumn 2002 (Isinibilir, 2012). In the southern part of the Sea of Marmara, the maximum abundance of *Aurelia* was found to be 11.0 ind.m⁻³ in June 2007 in Erdek Bay, a popular destination for holidaymakers in the region (Isinibilir, 2011). During the mucilage aggregation period in 2008, *Aurelia* was observed in very low numbers (0.4 ind.m⁻³) throughout the year (Isinibilir-Okyar et al., 2015).

When examining the distribution of planula and ephyra found in long-term zooplankton samples in the Marmara Sea between 2004 and 2022, significant differences were observed in abundance values. Planula larvae were detected between October and November, while ephyra larvae were found between February and May. The maximum abundance of planula (45 planula m⁻³) was recorded in October 2014, while the maximum abundance of ephyra (65 ephyra m⁻³) was observed in February 2015 (Isinibilir, unpublished data). These results suggest that the planula stage attaches itself to the substrate during the autumn and early winter, while the ephyra is released from the polyps during the late winter and spring months.

During our observations in 2006-2022, the jellyfish species *A. aurita*, was also found to be widespread in the Sea of Marmara (the northeast Marmara - NEM and İzmit Bay -IB), except for the easternmost areas as depicted in Figure 4. While they were observed throughout the year in NEM and IB, it was determined that their blooms occurred from January to July.

The period of lowest abundance and shortest bloom formation varied across regions, with the lowest recorded in 2006-2007 (Figure 4). Among all Scyphomedusae, *A. aurita* exhibited the most frequent bloom occurrences in the Marmara Sea (Figure 3). In IB and NEM, mass occurrences were primarily observed during winter and spring, lasting for up to four consecutive months in some years. In the southern Marmara (SM), *A. aurita* blooms occurred in June and July, particularly around Erdek Bay. Notably, extreme increases in *A. aurita* abundance were observed in January and February of 2019 and 2020. In the Southwestern Marmara (SWM), *A. aurita* was rarely found between February and July, with episodic mass events also recorded in January 2014 and October 2020 (Figure 4).

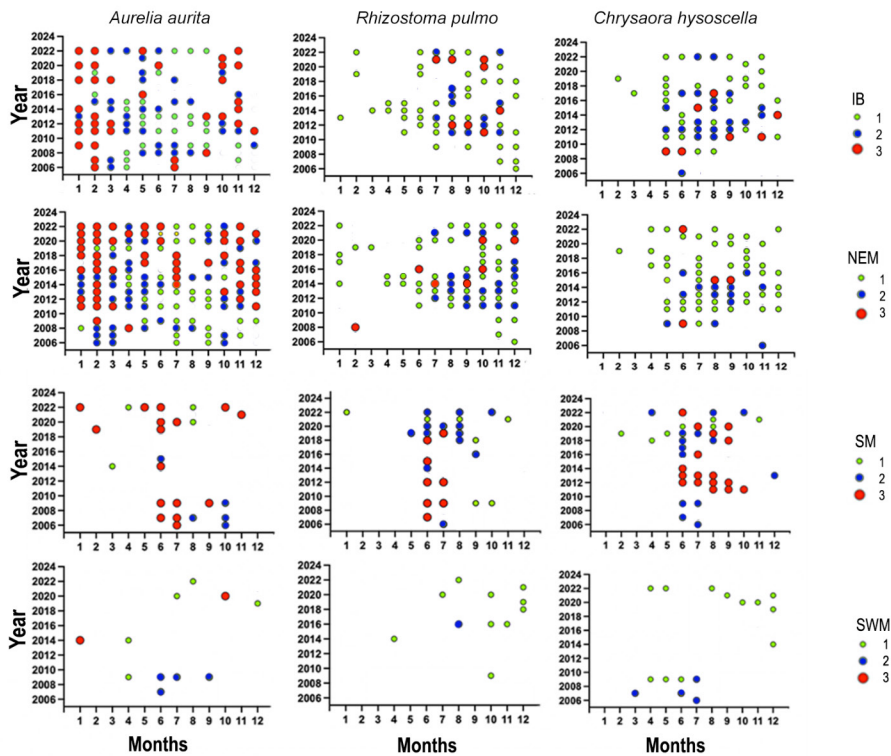


Figure 4. Monthly and annual variability (month/year) in relative abundance of three dominant Scyphozoa taxa in four investigated Marmara areas. (The data collection process involved research cruises as well as citizen science, which relied on observations from divers, fishermen, locals, and students: 0 no sightings, 1 sporadic occurrences of individual organisms, 2 frequent sightings of individual jellyfish specimens and/or small aggregations, and 3 frequent sightings of large aggregations).

Rhizostoma pulmo

R. pulmo is predominantly observed in high abundances in the Marmara Sea from July to December, particularly in the IB and NEM regions. However, it is rarely seen during the winter and spring months (Figure 4). In the SM region, *R. pulmo* is primarily observed during the warm seasons. Since 2015, episodic sightings of *R. pulmo* have been recorded in SWM (Figure 4).

Early reports by Isinibilir (2004, 2011) and Mavili (2008) indicated that *R. pulmo* is a common species in IB, NEM, and SM. In IB, small individuals of *R. pulmo* start to appear in surface waters towards the end of July and August when the seawater becomes warmer. They disappear in early January, and the bell diameter of specimens reaches its maximum in November and December (Isinibilir, 2004). Outbursts of *R. pulmo* were observed in the Erdek Bay in both July 2006 and June 2007 (Isinibilir, 2011).

An unusual mass mortality event of *R. pulmo* occurred on the coast of Istanbul in the Sea of Marmara in the first week of December 2020. The density of dead *R. pulmo* individuals was recorded as 45 ind.m⁻² in the area, with a mean diameter of 24.3 cm (Öztürk and Sümen, 2020).

Chrysaora hysoscella

The first observation of *C. hysoscella* in the southwest Sea of Marmara dates to 2000 (İnanmaz et al., 2002). Its abundance notably increased in the southwestern part of the Marmara Sea in 2007 and subsequently spread throughout the entire sea in 2009 (Isinibilir, 2015). The population of this species reached its peak in 2009, with over 1800 individuals per square kilometer recorded around the Strait of Istanbul in June 2009 (Isinibilir and Yılmaz, 2017).

C. hysoscella exhibits high population densities in IB, NEM, and SM (the southern Marmara) from May to December (Figure 4). Particularly in SM, large blooms of this species were observed from June to October during the period of 2011-2014. In the southwestern Marmara (SWM), *C. hysoscella* was frequently observed but did not form large aggregations. During dive surveys conducted around the Strait of Istanbul and Prince's Islands in July 2015, numerous young medusae of *C. hysoscella* were detected (Isinibilir and Yılmaz, 2017). After the mucilage event observed in the Sea of Marmara in 2007-2008 and 2021, an increase in the population and distribution of *C. hysocella* was observed in the following years.

Cotylorhiza tuberculata

Although an endemic species of the Mediterranean Sea, *C. tuberculata* is a relatively new and rare species in the Sea of Marmara. It was documented for the first time in the Marmara

Sea in September 2020 near Büyükkada, located in the northeastern part of the Marmara Sea (Isinibilir et al., 2021). Subsequently, on September 29, 2020, it was observed in the eastern basin of the Izmit Bay, specifically on the shores of Değirmendere (personal communication, İlker Acar, scuba-diver). In October 2021, two individuals of *C. tuberculata*, measuring 25 cm and 38 cm in diameter, were observed in Erdek Bay (Kale and Acarlı, 2022).

Drymonema dalmatinum

D. dalmatinum, a large-sized semaeostome jellyfish, has recently been observed in various regions of the Mediterranean, particularly in the Adriatic Sea. The earliest known records of *D. dalmatinum*, the only *Drymonema* sp. in the Mediterranean, date back to 1892 in the Gulf of Izmir (Antipa, 1892). In the Sea of Marmara, the genus *Drymonema* was initially recorded without species identification as *Drymonema* sp. in 2020 (Öztürk, 2020). One year later, on January 18, 2021, the presence of *D. dalmatinum* was reported based on fishermen's observations along the Maltepe coast in the northeastern part of the Sea of Marmara (Isinibilir et al., 2022).

Mawia benovici

M. benovici, formerly known as *Pelagia benovici*, has been documented in the Mediterranean region exclusively in the Adriatic Sea and the Ionian Seas (Avian et al., 2016; Chartosia et al., 2018; Piraino et al., 2014). In the Sea of Marmara, it was first observed in November 2019 at the entrance of the Çanakkale Bosphorus and Gemlik Bay (Isinibilir et al., 2022). This species is believed to be non-native to the Mediterranean and has also been reported off the coast of Senegal (Bayha et al., 2017). It is speculated that the species found in the Mediterranean may have originated from the west coast of Africa through commercial shipping or fishing activities (Bayha et al., 2017). According to Piraino et al. (2014), it is likely that *M. benovici* entered the Sea of Marmara through ship translocation via ballast waters.

Pelagia noctiluca

P. noctiluca was initially documented in the northeastern part of Gökçeada, North Aegean Sea in August 2008 and August 2009 (Öztürk and Topaloğlu, 2011). Subsequently, this species was observed in the Marmara Sea for the first time in November 2021 on the Hereke shores of Izmit Bay, at a depth of about 1-2 meters and a temperature of 15°C (personal communication, Tahsin Ceylan) and then near Paşalimanı Island, in the southern Marmara on 12th December 2021 (Bilecenoglu and Çınar, 2022). The introduction of *P. noctiluca* to this region may be attributed to the transportation of organisms via ballast waters, which is facilitated by the significant maritime traffic in Izmit Bay, hosting numerous commercial and military ports.

Discomedusa lobata

D. lobata was initially collected from the lower layer (25-90m) of the Gulf of Izmit in March 2011 (Isinibilir et al., 2015). Two years later, it exhibited high abundances, reaching approximately 1-2 ind. m⁻³ in the Sea of Marmara (Isinibilir et al., 2015). In November 2020, this species was once again observed on the shores of Değirmendere in the Gulf of Izmit (personal interview, İlker Acar). Furthermore, sporadic occurrences of individual organisms of *D. lobata* were reported around the Prince Islands in May 2020 (personal communication, N. Eda Topçu).

Ctenophora

Mnemiopsis leidyi

The earliest record of *M. leidyi* in the Sea of Marmara dates back to October 1992, with a biomass of 4.3 kg.m⁻² near the Dardanelles and more than twice that amount (9.7 kg.m⁻²) near the Strait of Istanbul (Shiganova et al., 1995). *M. leidyi* was reported from all 8 stations sampled from the entire Sea of Marmara in 1993 summer (Kideys and Niemann, 1994). In 2001-2002, the highest biomass in Izmit Bay was reported as 34.8 g.m⁻³ (Isinibilir, 2012).

In 2006, the average abundance of *M. leidyi* in Erdek Bay was 1.3 ind.m⁻³ (Isinibilir, 2011). The maximum abundance (58 ind.m⁻³) and biomass (353 g.m⁻³) of *M. leidyi* were recorded in the Izmit Bay in August 2008, just before the occurrence of the mucilage event in the Marmara Sea (Isinibilir, 2014).

In later years, it was reported to occur in all regions of the Sea of Marmara, except for the easternmost areas IB (Izmit Bay) and SEM (southeastern Sea of Marmara) (Figure 5). In 2008 and 2009, the bloom was observed during the summer, while in 2020 and 2021, it was seen only in June. In SEM, although the species is sparsely distributed, small aggregates are observed from May to September, with blooms occurring at different time intervals. In southern Marmara, the distribution of *M. leidyi* is restricted to the period from June to October. In SWM (southwestern Marmara), *M. leidyi* is found sporadically from June to October, but with a low number of individuals (Figure 5).

Beroe ovata

Beroe ovata is primarily observed from late summer to autumn, particularly in the IB and NEM (northeastern Marmara) regions of the Sea of Marmara. In the southern Marmara, its distribution is limited to the period between June and October (Figure 5). During the years 2006-2009, significant blooms of *B. ovata* were observed during the summer months. In southwestern Marmara, *B. ovata* was observed infrequently.

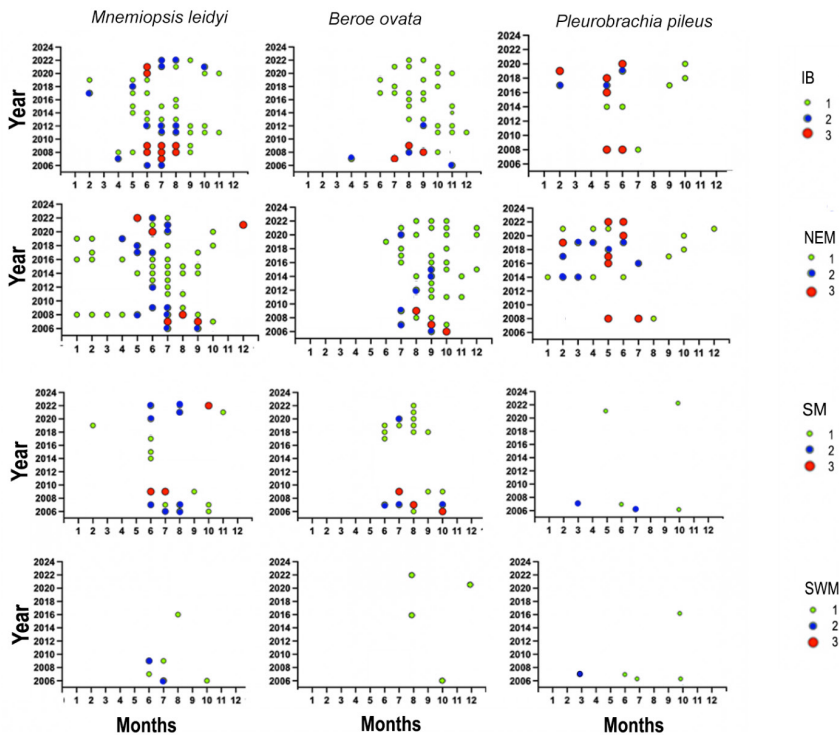


Figure 5. Monthly and annual variability (month/year) in relative abundance of three dominant ctenophore species in four investigated Marmara areas. (The data collection process involved research cruises as well as citizen science, which relied on observations from divers, fishermen, locals, and students: 0 no sightings, 1 sporadic occurrences of individual organisms, 2 frequent sightings of individual jellyfish specimens and/or small aggregations, and 3 frequent sightings of large aggregations).

The first recorded occurrence of *B. ovata* in the Marmara Sea was in October 1992, with maximum biomass of 60.5 g.m^{-2} (Shiganova et al., 1995). In the eutrophic Izmit Bay, the average biomass of *B. ovata* was reported as 15.5 g.m^{-3} with an average abundance of 44.5 ind.m^{-3} in 2001 (Isinibilir, 2012). In the southern part of the Sea of Marmara, its abundance was recorded as 1.03 ind.m^{-3} during the years 2006-2007 (Isinibilir, 2011).

Pleurobrachia pileus

Pleurobrachia pileus is primarily observed from late winter to early summer, particularly in the IB and NEM regions of the Sea of Marmara (Figure 5). Its presence is rarely observed in the SM and SWM regions. The first recorded occurrence of *P. pileus* was around the Strait of Istanbul and Prince Islands by Demir in 1952.

In Izmit Bay, the maximum mean abundance of *P. pileus* was recorded as 5.6 ind.m⁻³ in the autumn of 2002 (Isinibilir, 2012). The southern Sea of Marmara had its highest abundance of *P. pileus* in June 2007, reaching 9.5 ind.m⁻³ (Isinibilir, 2011). The most recent recorded maximum abundance of *P. pileus* in the Sea of Marmara was in the Izmit Bay in February 2019, with 38 ind.m⁻³. Additionally, the highest recorded biomass of *P. pileus* was around the Prince Islands in May 2017, reaching 511 g.m⁻³ (Isinibilir, unpublished data).

3.2. State of Jellyfish Species in the Adriatic Sea

Similar to the Marmara Sea, most data on jellyfishes in the Adriatic Sea come from the coastal sea (Pestorić et al., 2021). Among the species living in deeper open waters, the coronate species *Paraphylla intermedia*, *Periphylla periphylla* and *Nausithoe punctata* were recorded. Compared to the Scyphozoa and Ctenophora fauna in the Sea of Marmara, the number of species found in the Adriatic Sea is larger (Tables 1 and 2) and includes three newly described species, *Aurelia relictata*, *A. pseudosolida* and *M. benovici*, the latter of which was also recently recorded in the Sea of Marmara (Isinibilir et al., 2022). The status of the genus *Aurelia* in the Adriatic Sea has not yet been definitively clarified. Historical authors report the occurrence of the species *A. aurita* since the second half of the 19th century (Avian and Rottini Sandrini, 1994). However, recent analyses indicate that there are instead two introduced species (*A. coerulea*, *A. solida*) and two newly described species (*A. pseudosolida* and *A. relictata*) in the Adriatic (Scorrano et al., 2017; Garić and Batistić, 2022). Therefore, we use the designation *Aurelia* spp. in this chapter. Furthermore, there are few accurate data on the abundance or biomass of jellyfish in the Adriatic Sea. Therefore, we base our review on the description of the semi-quantitative analysis of abundance presented in Figures 4, 5, and 6. Data collection included both research cruises and Citizen Science based on observations by divers, fishermen, locals, and students: 0 no sightings, 1 sporadic occurrence of single organisms, 2 frequent sightings of single jellyfish and/or small aggregations, and 3 frequent sightings of large aggregations.

In the Adriatic, the most common Scyphozoa species are meroplanktonic *Aurelia* spp., *R. pulmo*, *C. hysocella*, *C. tuberculata*, and holoplanktonic *P. noctiluca*, and the ctenophores *Leucothea multicornis* and the introduced *M. leidyi* all form blooms frequently (Pestorić et al., 2021). With rare exceptions such as scyphomedusa *P. noctiluca* and the ctenophores *Cestum veneris* and *Bolinopsis vitrea* (Vioić et al., 2022), macrojellyfish are more common and numerous in the northern Adriatic (Figure 6). The complete list of species, based on published data and our own observations, is given in Tables 1 and 2.

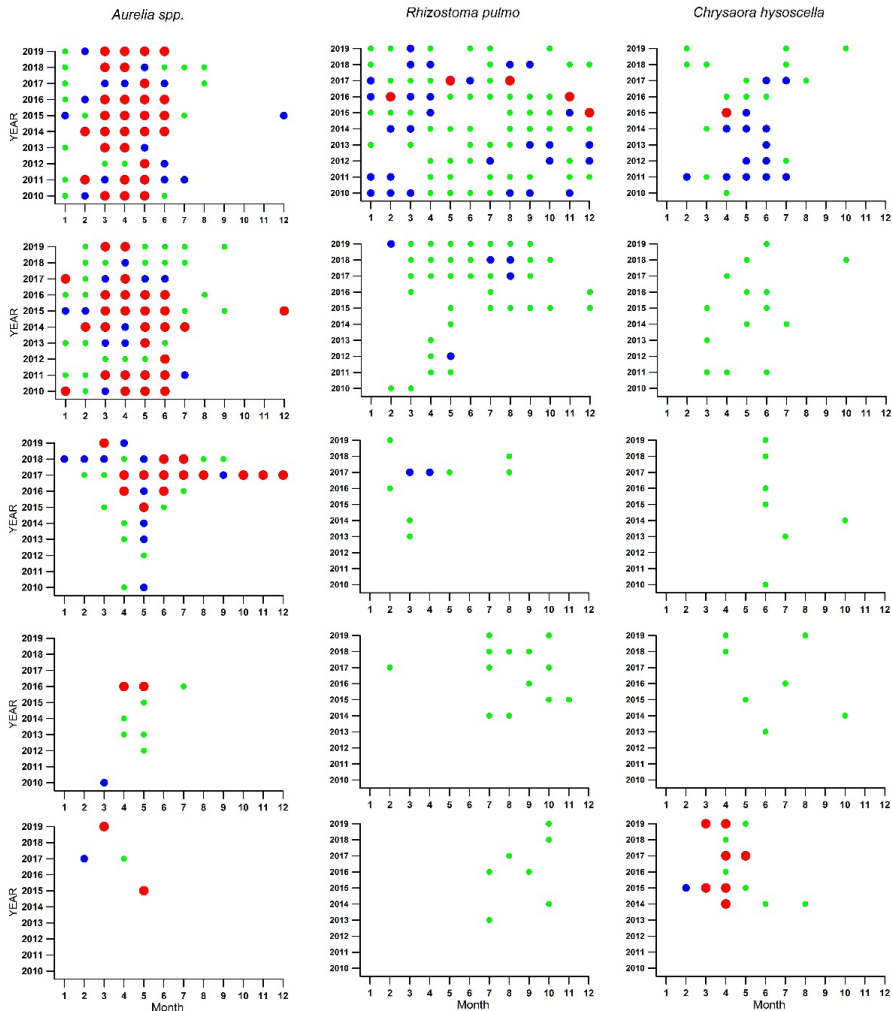


Figure 6. Monthly and annual variability (month/year) in relative abundance of three dominant Scyphozoa taxa in five investigated Adriatic areas. (The data collection process involved research cruises as well as citizen science, which relied on observations from divers, fishermen, locals, and students: 0 no sightings, 1 sporadic occurrences of individual organisms, 2 frequent sightings of individual jellyfish specimens and/or small aggregations, and 3 frequent sightings of large aggregations. (The abbreviations for the areas described in Fig 2.).

Scyphozoa (Discomedusae)

Aurelia spp.

As mentioned above, in contrast to the historical data for the Adriatic Sea, when only one species *A. aurita* was reported, publications today list four species, namely the introduced *A. coerulea* and *A. solida*, and two newly described species, *A. relicta* and *A. pseudosolida*.

One species, *A. relict*a, is endemic and its range is restricted to the sea lake of the southern Adriatic Island of Mljet. While the distribution of the introduced *A. coerulea* is restricted to coastal lagoons, marinas, and harbours, *A. solida* is typically distributed in more open waters (Scorrano et al., 2016). Extensive genetic and morphological data enabled the description of a new *A. pseudosolida* species from the northern Adriatic Sea (Garić and Batistić, 2022).

The observations presented in Figure 6 do not refer to specific environments such as Mljet Lake and lagoons and do not distinguish between species. *Aurelia* spp. is widespread in most of the Adriatic Sea, except the southernmost part, and shows a typical seasonal distribution with frequent blooms in winter and spring. A three-year study of the population dynamics of polyps *in situ* in the northern Adriatic Sea (Hočevár et al., 2018) showed production of buds and stolons in the warm part of the year, while strobilation was restricted to the colder months, with the highest production of ephyrae between November and January. This reproductive dynamic of polyps is consistent with the observed abundance of medusae in winter and spring.

Rhizostoma pulmo

This species is also widespread throughout the Adriatic but is much more common in the northern Adriatic (Figure 6). Unlike *Aurelia* spp. it is present throughout the year. It can form blooms in all times of the year, but they reach larger proportions during the cold season. Size measurements and finds of ephyrae in spring and autumn indicate several cohorts per year, and the largest specimens often overwinter. Similar to *Aurelia*, *Rhizostoma* blooms were also common in the past from the second half of the 19th century. The analysis of long-term time series showed that blooms in the northern Adriatic recurred in a period of about 8 to 12 years (Kogovšek et al., 2010), but that this period has recently shortened and we observe blooms annually in the last decade.

Chrysaora hysoscella

Unlike other meroplanktonic species, *C. hysoscella* seems to proliferate better in the southern Bay of Kotor (Figure 6), where it forms blooms more frequently than in the rest of the Adriatic Sea. It is most abundant in early spring and was rarely observed in autumn-winter period (Volić et al., 2019).

Cotylorhiza tuberculata

C. tuberculata, on the other hand, is a typical warm-water species, more common in the northern part of the Adriatic Sea and often blooming from July to September. Under laboratory conditions, temperature has been shown to have a crucial effect on polyp survival and asexual reproduction. An increase in temperature led to higher strobilation rates (Prieto

et al., 2010) and thus to the production of ephyrae. Therefore, we can expect this species to become even more successful as our oceans warm.

Drymonema dalmatinum

This species is rather rare in the northern Adriatic and is more frequently observed towards the south. It was observed from April to August and only occasionally in autumn (Malej et al., 2014). Interestingly, *Drymonema* is a voracious predator of other Scyphomedusae such as *Aurelia* (Larson, 1987) and *Rhizostoma* (Ciriaco et al., 2021), so the more frequent observations in the Adriatic may be related to the increase in jellyfish blooms in recent decades.

Mawia benovici

The new species found in the Adriatic Sea was originally described as *P. benovici* (Piraino et al., 2014), but it was later shown to be more closely related to g. *Sanderia*. Based on integrative taxonomy, Avian et al. (2016) placed this medusa in the new genus *Mawia*. *M. benovici*, rarely observed outside the Adriatic, was sighted mainly in the northern Adriatic during the colder season, but appeared in the Ionian Sea in June (Chartosia et al., 2018). As previously described, it is believed to have been introduced from the west coast of Africa (Bayha et al., 2017), probably as polyps on ship hulls (Tirelli et al., 2021).

Pelagia noctiluca

This holoplanktonic species is one of the most common Mediterranean scyphozoan species, typically more numerous and frequent in the western Mediterranean (Bergamasco et al., 2022). In the northern Adriatic, it is present with a small number of individuals and not every year. *P. noctiluca* is frequently observed in the southern Adriatic, where numerous ephyrae are also found in the surface layers of open waters (Garić, pers. comm.).

Discomedusa lobata

This species is most observed in the southern Adriatic Bay of Kotor, where it regularly forms blooms in winter and spring (Violić et al., 2019). In the colder part of the year, it is sporadically observed also in the northern Adriatic (Avian, 1992).

Ctenophora

Mnemiopsis leidyi

The first sighting of the invasive alien species *M. leidyi* in the Adriatic Sea was reported in October 2005 (Shiganova and Malej, 2009) in the Gulf of Trieste. Thereafter, this species was not found until 2016. Since then, it has formed extensive blooms in the northern Adriatic Sea every

year from July to November, often at densities of $> 20 \text{ ind.m}^{-3}$ (Malej et al., 2017; Shiganova et al., 2019; Budiša et al., 2021; Pierson et al., 2021). During the bloom period, carbon biomass can reach over 130 mg.C/ m^3 , exceeding that of mesozooplankton (Kogovšek et al., 2014). In the other parts of the Adriatic, except in the lagoons, *M. leidy* was observed less frequently.

***Pleurobrachia* spp.**

Three species of the genus *Pleurobrachia* (*P. pileus*, *P. rhodopsis* and *P. rhododactyla*) were observed in the Adriatic Sea, mainly in the northern Adriatic, although none of them is common (Shiganova and Malej, 2009). They were noted mainly in spring and autumn.

Bolinopsis vitrea

This species is not uncommon in the Bay of Boka Kotorska and in the northern Adriatic and is observed mainly in spring and autumn. *B. vitrea* formed blooms in Boka Kotorska in 2014 and 2020 (Lučić et al., 2012; Pestorić et al., 2021), while it is less abundant in the rest of the Adriatic.

Leucothea multicornis

Leucothea multicornis is abundant and often forms autumn and winter blooms in the Gulf of Trieste. It is quite common in the northern Adriatic, less so in the central and southern Adriatic.

Cestum veneris

Unlike most other Ctenophora species, which are more numerous in the northern Adriatic, *C. veneris* is more common in the central and southern Adriatic and occasionally forms blooms in the open waters of the southern Adriatic (Violčić et al., 2022). It has been rarely observed in the northern Adriatic (Rogelja et al., 2022).

***Beroe* spp.**

The taxonomy and distribution of the different species of g. *Beroe* in southern European seas has recently been studied in detail (Shiganova and Abyzova, 2021), but remains somewhat controversial. While *B. forskalii* is most abundant in the Adriatic Sea and appears to be native there, the occurrence of other species of *Beroe*, including the introduced species *B. ovata* sensu Mayer (Shiganova and Malej, 2009), is less clear.

Other Ctenophora species such as *Callianira bialata*, *Callianira ficalbi*, *Deiopea kaloktenota*, *Haeckelia rubra*, *Hormiphora plumosa*, *Lampaea pancerina* have been rarely mentioned recently, probably because there are no specialists for this group in the Adriatic countries.

4. Relations with Humans - Negative and Positive

The people who lived on the coasts of the Mediterranean knew jellyfish in ancient times and usually considered them harmful, as evidenced by the well-known ancient myth of Medusa. The reputation of jellyfish as ‘pests’ persists to this day, although recent research shows that they can have both positive and negative effects (Graham et al., 2014). Until recent decades, their important ecological impacts, such as providing shelter or substrate and other symbiotic associations, have been overlooked (Doyle et al., 2014). Similarly, recent research has shown that jellyfish can also be an important food source for various marine organisms (Arai, 2005; Lamb et al., 2017; D’Ambra and Merquiol, 2022), such as turtles, some fish, and even penguins, in addition to being a remarkable substrate for various microbes (Tinta et al., 2021). Recently, there has also been a growing number of publications on jellyfish as a food source for humans (Omori and Nakano, 2001; Brotz, 2011) and as a source of various active compounds (Leone et al., 2013; 2015; De Domenico et al., 2023). Jellyfish are also becoming increasingly popular in aquaristics and attract many tourists.

Interest in jellyfish in aquarium exhibits is quite high in Türkiye and has continued to grow after the establishment of the first jellyfish aquarium in Istanbul in 2009. In recent years, jellyfish have been collected from the sea and exhibited in aquariums (Şener Yavaş, personal communication). In this regard, they represent an important economic contribution and profit. Unfortunately, in the aquariums in Istanbul (except Sea Life Aquarium and EMAAR Aquarium), Antalya and Izmir, the jellyfish departments have been closed due to the difficulty of keeping jellyfish alive and economic difficulties (Ayhan Şentürk personal communication).

It is worth mentioning that the Sea of Marmara is not only an important fishing area but also a major recreational area for the coastal population, and the unsightly occurrence of jellyfish and mucilage accumulation on the shores has attracted great public attention and concern. An increase in jellyfish could affect tourist experience and destination choice, potentially leading to a significant decrease in tourism in an area frequently affected by jellyfish outbreaks. The frequent occurrence of jellyfish species, particularly *Rhizostoma pulmo* and *Chrysaora hysoscella*, has had a noticeable impact on tourism. As a result, some beach operators and local governments have been forced to install jellyfish nets, especially targeting *C. hysoscella*, as a precautionary measure (Isinibilir and Yılmaz, 2017) (Figure 7, top). In the Adriatic Sea, the most frequent stings are caused by *Pelagia noctiluca* (Figure 7, bottom).



Figure 7. *Chrysaora hysoscella*, holidaymakers and protective nets (top photos by Gökhan Karakaş and <https://www.yenicaggazetesi.com.tr/pusula-denizanasina-karsi-agli-koruma-19235h.htm>), and *Pelagia noctiluca* bloom (bottom left – video T. Makovec) and *Pelagia* sting (right – photo V. Malačič) from the Adriatic Sea.

The various negative effects of jellyfish blooms on fisheries are well known. In the northern Gulf of Mexico, the excessive proliferation of the invasive species *Phyllorhiza punctata* had a negative impact on the commercial shrimp industry during a two-month period in 2000, resulting in an estimated loss of \$10 million (Graham et al., 2003). In the summers of 2008 and 2009, the over abundance of *Chrysaora plocamia* jellyfish and their invasion of gillnets off the southern coast of Peru caused an economic loss of \$200,000 during a 35-day anchovy fishing period (Quiñones et al., 2013). In Japan, economic losses caused by *Nemopilema nomurai*, including reduced fish catches and damage to fishing nets, were estimated at approximately \$20 million in a single region (Kawahara et al., 2006).

A study conducted on the northern California coast found that 67% of fishermen reported a decrease in seasonal income due to jellyfish, and trawl fishermen fishing for salmon and shrimp in Oregon suffered economic losses of more than \$650,000 during the peak jellyfish season from June to September 2012 (Conley and Sutherland, 2015). Another study on

Morocco's Mediterranean coast found that 86% of fishermen were affected by jellyfish, resulting in additional time spent repairing damaged nets, seasonal loss of income, and an estimated annual direct loss of \$3.26 million to the fishing fleet in the port of M'diq (Mghili et al., 2022a).

The decrease in fish catches due to the invasive ctenophore *M. leidyi* was striking for the Black Sea and Caspian Sea (Kideys, 1994; Kideys et al., 2005). Assuming a cost of approximately 1 USD per kilogram of fish, the minimum economic loss for Türkiye alone would exceed 1 billion USD during the period from 1989 to 1993 in the Black Sea (Kideys et al. 2005). Similarly, due to the invasion from the same species, more than 70 percent decrease in the kilka catches of Iranian fishermen occurred during 1998 till 2001, with a minimum of 125 million USD in economic losses in the Caspian Sea.

A review article by Bosch-Belmar et al. (2020) lists 14 scyphozoan, 10 hydrozoan, one cubozoan, and one ctenophore species that affect fisheries and aquaculture. Major adverse impacts include interference with fishing gear, direct impacts on fishing operations, impacts on the health of farmed fish, and on aquaculture facilities. Based on available information, the Mediterranean Sea is the second most affected area after the North Pacific Ocean (Bosch-Belmar et al., 2020).

Other known negative impacts on human welfare include the problem of jellyfish intrusion blocking seawater-cooled condensers in coastal desalination plants, nuclear power plants, and coal-fired power plants (Graham et al., 2014). Some species pose a health risk to humans, and there are also negative impacts on coastal tourism. For example, lost revenue in north Queensland was estimated at \$49 million in 2002 (Gershwin et al., 2010).

4.1. Impact of Jellyfish on Fish Catches in the Sea of Marmara

The Sea of Marmara is of great value as Türkiye 's second most important fishing area, but the fishing industry has faced significant challenges in recent decades due to the proliferation of jellyfish. Apart from the well-documented effects of *Mnemiopsis leidyi* on small pelagic fish populations through bottom-up and top-down effects (Isinibilir et al., 2004; Kideys, 1994; Mutlu, 2009), the decomposition of a large *M. leidyi* biomass in the early 1990s may have contributed to the depletion of oxygen in the already oxygen-poor lower layers of the Sea of Marmara, negatively affecting demersal fisheries. In addition, the invasion of *Liriope tetraphylla* and subsequent shifts in the food web following the 2006-2007 bloom triggered a widespread mucilage phenomenon (Yilmaz, 2015) that resulted in significant losses to the fishing industry. The prevalence of mucilage caused by these events led to a disruption of the

small pelagic fishery in the Sea of Marmara, as purse seine nets became less efficient and, in some cases, even unusable due to the excessive weight of accumulated slime. As a result, fish landings halved in 2007-2008 compared to levels observed in the early 2000s (Figure 8).

While the amount of fish caught in the Sea of Marmara showed an increasing trend between 1980 and 2000, there has been a continuous decline since the 2000s. The highest catches were recorded at 83,293 tons in 1999, 72,947 tons in 2001, and 71,512 tons in 2002 (Figure 8). Increasing fishing pressure, illegal fishing, marine pollution, climate change, and invasive species have contributed to a significant decline in catches. In 2021, the total amount of fish caught in the Sea of Marmara was 14,400 tons. The most caught species are pelagic migratory fish, including anchovy (*Engraulis encrasicolus*) with 6,189 tons, horse mackerel (*Trachurus trachurus* and *T. mediterraneus*) with 2,011 tons, sardine (*Sardina pilchardus*) with 1.290 tons, bluefish (*Pomatomus saltatrix*) with 838 tons, Atlantic bonito (*Sarda sarda*) with 107 tons, Atlantic mackerel (*Scomber colias*) with 106.5 tons, and mullet (*Mugilidae*) with 41 tons. Most of these species are caught with gillnets and purse seines.

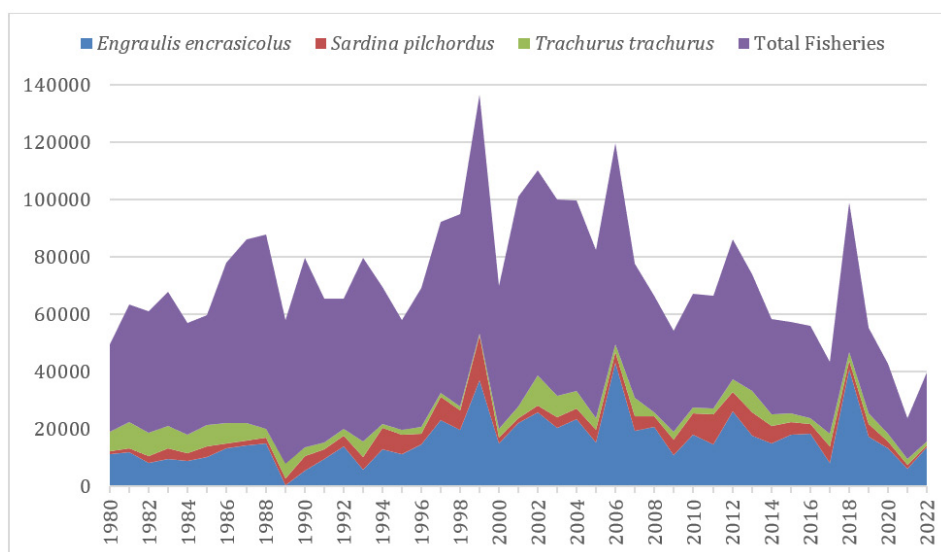


Figure 8. Annual small pelagic fish landing data (in tonnes) of the Sea of Marmara (1980-2020).
(Data from State Statistics Institute; www.tuik.gov.tr).

A total of 2676 fishing boats are registered in the Sea of Marmara. Of these boats, 86.70% (2320 boats) are small-scale fishing boats, 8.37% are trawlers (224 boats), 4.26% are gillnetters (114 boats), and 0.67% are carrier vessels (18 boats) (data from Turkish Statistical Institute 2023; www.tuik.gov.tr). Trawling has been prohibited in the Marmara Sea since 1971

by Fisheries Law No. 1380. However, trawlers registered in the Marmara region fish in the North Aegean or the western Black Sea, depending on the fishing season. Nevertheless, the use of trawl nets for shrimp fishing is allowed. Transport vessels have no right to fish, but they assist gillnet fishermen in their activities.

The proliferation of jellyfish in the Sea of Marmara has a negative impact on commercial fisheries. The most affected fishermen are those who engage in pelagic fishing with gillnets, purse seines and fyke nets. Although jellyfish can enter shrimp fishing gear when the shrimp trap is lifted, the impact is less severe compared to other fishing groups. Common problems faced by fishermen include clogged nets, torn nets, increased labor, reduced catches, difficulty retrieving nets from the sea, and removal of jellyfish mixed with the target catch. To address this problem, gillnet fishermen use a second net to remove jellyfish. These nets have a full mesh size of 72-80 mm, a thickness of 210d/72 and a length of 30x30 m and are equipped with clips at the end of the gillnet. After the operation, the jellyfish are removed from the second net and released back into the sea with a mushroom collar (Doğu, 2019; Kasapoğlu et al., 2020). Slipping is a well-known and practiced method worldwide in which unwanted species, unsuitable catches (undersized or of poor quality), or excess catches are released by sliding them over the floating net line after the net has been partially hauled in or “dried out” while still in the water (Lockwood et al., 1983; Stratoudakis and Marçalo, 2002). Although this method is not common in Turkish fisheries, it has been used since 2016 by all gillnet fishermen targeting anchovy and horse mackerel in the Sea of Marmara to remove jellyfish (*A. aurita*) between September and November (Sait Kanburoğlu, personal communication). In a study conducted by Kasapoğlu et al. (2020), the average amount of jellyfish hatched from the nets during each gillnet deployment was calculated to be 3,812.5 kg ($\pm 2,404.4$ kg) (minimum 500 kg/maximum 7,500 kg) (Figure 9).

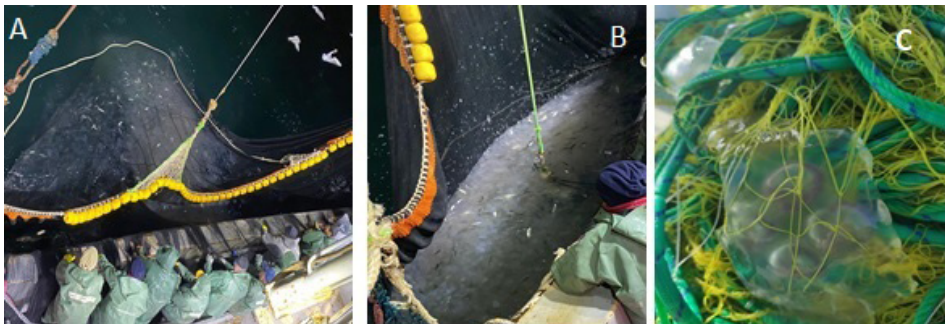


Figure 9. A, B. Jellyfish caught in purse seine nets during anchovy fishing in the Sea of Marmara (Photo: Sadettin Doğu), C: Jellyfish entering the gillnets of small-scale fishermen (Photo: Barış Köksalan).

Another fishing group that interacts with jellyfish is the small-scale fishermen who use alamana/voli nets. Unfortunately, this fishing group is not as favoured as the gillnet fishermen. Due to inadequate boat equipment, they struggle with jellyfish (*A. aurita* and *R. pulmo*). At times when jellyfish are proliferating, the nets used for voli fishing become clogged with jellyfish, making them heavier. As a result, these nets sink to the bottom instead of floating in the water column, making fishing impossible. In addition, the impact of the jellyfish makes it difficult to recover the nets from the sea. This situation leads to longer deployment times, higher fuel consumption, and net damage. In particular, if *A. aurita* gets into the gillnets, fishermen must remove it from the nets by hand. Otherwise, it is not possible to pull the nets filled with jellyfish through the net drum (Barış Köksalan, personal communication). While it normally takes 20 minutes to bring the nets on board, this process takes 2.5 hours due to the dense mass of jellyfish. As a result, fishermen haul is less during the day and fishing efficiency decreases. In addition, it has been reported that working conditions on small fishing boats pose a safety risk and that incidents have occurred under these conditions where the boat has been in danger of sinking (Erdoğan Kartal, personal communication).

The traditional fish traps (dalyan) used in the Strait of Istanbul between March and July are also infested with jellyfish. Especially in April and May, jellyfish enter the fish traps in large numbers, loosening the stakes that secure the traps and posing the risk of the traps collapsing (Mustafa Kılınç, personal communication). During times when jellyfish proliferate, fishermen must remove jellyfish from the traps every hour and throw them back into the sea. This situation causes fishermen to spend more time at sea (increased labour) (Figure 10).

Due to the sensitivity to jellyfish in the Sea of Marmara, trawling is prohibited. However, jellyfish have been observed in bottom trawls during research trawl surveys in the Sea of Marmara (Figure 11). In a fisheries survey conducted in the eastern Sea of Marmara between 2014 and 2022, jellyfish were found in a total of 194 trawl deployments at 139 stations. The most abundant jellyfish species was *A. aurita* with a frequency of 71.65%. The biomass of this species calculated for each station ranges from 0.24 to 11,975.04 kg.km⁻², and the abundance ranges from 39 to 132,009 ind.km⁻².



Figure 10. Jellyfish entering Beykoz Dalyan in the Bosphorus (Photo: Mustafa Kılınc).



Figure 11. Jellyfish entering the bottom trawl net in fisheries research (Photo: Saadet Karakulak).

Jellyfish proliferation in the Sea of Marmara has a direct impact on commercial fisheries and is estimated to cause significant economic losses. However, there is currently no scientific study that specifically addresses these economic losses. Extensive research is needed to assess fishermen's income losses and to understand their attitudes and behaviors regarding the hazards posed by jellyfish. In addition, jellyfish have also been reported to pose a threat to tourism and human health in certain areas (Mghili et al., 2022b). It is critical to conduct comprehensive studies on these issues.

Previous studies have reported interactions between jellyfish and various fishing gears, including longlines, trawls, gillnets, and purse seines (Purcell et al., 2007; Nagata et al., 2009; Conley and Sutherland, 2015). In this study, the interactions between jellyfish and fishing gears in the Sea of Marmara were found to be gillnets, voli nets, dalyans (traditional fish traps), and algarnas (a type of fishing net). Although trawling is prohibited in the Sea of Marmara, jellyfish have been observed in bottom trawl nets during fisheries research. Our results are the first evidence of jellyfish interactions with dalyans in the Sea of Marmara.

4.2. Impact of Jellyfish on Fish Catches in the Adriatic Sea

Several small pelagic fish are caught in the Adriatic (sardines, anchovies, sprats, and mackerel); among demersal fish, two species (hake and mullet) dominate, while catches of elasmobranchs, shad, and eels have recently declined. The catch in the Adriatic Sea fluctuated around 140,000 tonnes/year between 1992 and 2002 but increased to about 185,000 tonnes/year in 2016 (Kennedy et al., 2021).

There is limited information on the impact of jellyfish on fisheries in the Adriatic Sea. Palmieri et al. (2014) conducted a survey among fishermen in Chioggia, the main fishing port in northern Italy. The survey confirmed the negative impact of jellyfish blooms on fisheries and estimated economic losses from reduced fish catches at 8.2 million euros per year for the northern Adriatic trawl fleet. Other costs include additional fuel costs due to the shift in fishing activity (460,000 euros per year) and time lost repairing damaged equipment (89,000 man-hours per year). Nastav et al. (2013) took a different approach to jellyfish impacts and ran an input-output model to assess the impact of jellyfish blooms on the economy. Due to the small contribution of the fisheries sector to Slovenian GDP, the overall impact on the economy was not significant, although they found negative impacts on fisheries and lower value added in 2004, when a large bloom of *R.pulmo* lasted several months (Figure 12).



Figure 12. Catch by Slovenian fishermen in February 2004 (Photo: S. Radolovič).

Gill disorders in gilthead sea bream *Sparus aurata* studied with in vivo laboratory tests (Bosch-Belmar et al., 2016) suggest potential negative effects on this fish, which is commonly farmed in the Adriatic Sea. Jellyfish blooms can affect recreational activities and lead to economic losses (Palmieri et al., 2015), but no such studies have been conducted in Adriatic countries. In contrast, jellyfish are a popular attraction in Adriatic aquariums, as in many other countries around the world.

Since the first observation of *M. leidyi* in 2005 in the northern Adriatic Sea and its permanent establishment about 10 years later (Malej et al., 2017), several studies have been conducted on one of the worst and most widespread marine invasive species (Shiganova et al., 2019) in the Adriatic Sea. Due to their massive blooms, their ecological role is significant, including impacts on fish species. A study addressing potential impacts on zooplankton and anchovy in the northern Adriatic (Budiša et al., 2021) concluded that swarms of *M. leidyi* were associated with declines in anchovy populations, mainly due to competition for zooplankton food. In addition, *Mnemiopsis* blooms have been shown to have strong effects on increases in dissolved organic matter (Ciglenečki et al., 2021) and abundance of microbial plankton (Pagliaga et al., 2021).

5. Jellyfish Fishery

Jellyfish fisheries for human consumption are conducted in at least 21 countries worldwide. According to FAO data for 2018, the global jellyfish catch was 293,000 metric tons. The average annual catch between 2004 and 2013 was 318,000 metric tons (FAO, 2020). China is responsible for more than half of the global catch and plays a dominant role in the jellyfish market. It is followed by Thailand, India, Vietnam and Indonesia. These five countries account for more than 90% of the global jellyfish catch (Brotz, 2016). According to FAO statistics from 2007, 6617 tons of jellyfish in fresh, chilled, frozen, dried, and salted form were exported

around the world, with a value of over \$15 million (<ftp://ftp.fao.org>). The acceptance of jellyfish as a novel and sustainable food is also growing among non-Asian consumers (Torri et al., 2020). In recent decades, jellyfish have become an alternative source of income alongside fish worldwide. Rhizostomes are generally best suited for food, as the quality of mezoglea is considered high due to the intense composition of the tissue. It is estimated that about 80 species of rhizostomes offer commercially available products (Cheng, 1991).

The Sea of Marmara is home to two species of rhizostomes, namely *C. tuberculata* and *R. pulmo*. Of these two species, *R. pulmo* is widely recognized as a suitable and popular food source, enjoyed by people around the world.

The jellyfish fishery in Türkiye began in 1984 and lasted until 2006 (Kingsford et al., 2000; Figure 13). The annual catch averaged 1338 tons. In 2006, most jellyfish were caught in the Black Sea (51.13%), followed by the Sea of Marmara (43.26%), the Aegean Sea (4.92%), and the Mediterranean Sea (0.69%) (Turkish Statistical Institute data 2023; www.tuik.gov.tr). Fishing in the Sea of Marmara began in 1986 with an average annual catch of 517 tons. The fishery was conducted with scoop nets targeting a single species (*R. pulmo*). The fishing season began in July and lasted until early December. As the weather gets colder, the jellyfish migrate to deeper waters, limiting fishing activity. Each fishing boat caught about 7,000 specimens of *R. pulmo* per day. The jellyfish were processed in two processing plants in Türkiye (Karabiga/Çanakkale and Erdek/Bandırma) and exported to countries in the Far East (Japan, China, Korea) (Arpat Önsel, personal communication), which attracted much media attention during this period (Figure 14).

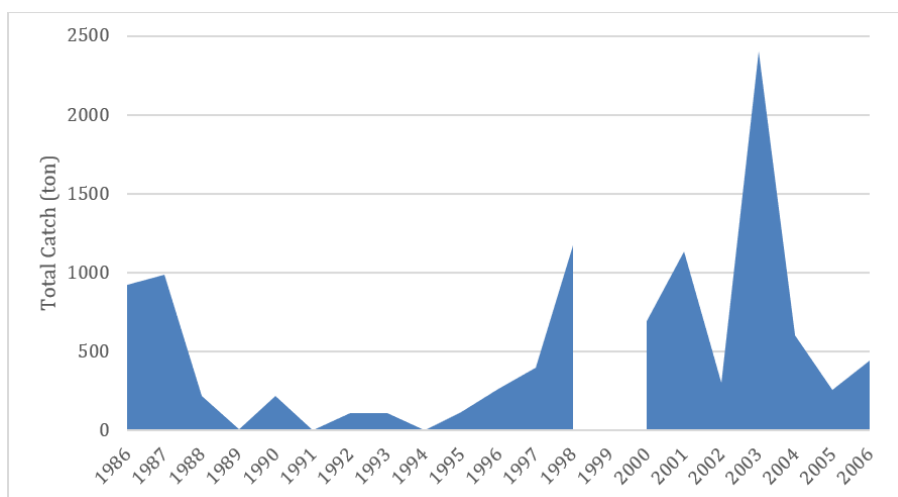


Figure 13. The amount of jellyfish caught in the Sea of Marmara.



Figure 14. Some news about jellyfish farming in Türkiye.

While jellyfish fishing has greatly increased worldwide, it is no longer practiced in Türkiye. However, given the growing jellyfish populations, promoting jellyfish fishing would be beneficial to both the ecosystem and the fishermen affected by jellyfish problems.

No data are available on jellyfish fisheries in the Adriatic (Brotz and Pauly, 2017), although it is inhabited by rhizostomid species such as *C. tuberculata* and *R. pulmo*, which are also caught elsewhere. Since these two species are particularly abundant in the northern Adriatic, their exploitation would probably be profitable.

6. Role of Artificial Marine Constructions and the Need for Long-Term Monitoring of Jellyfish

The increasing prevalence of hard substrate habitats near shore and in open waters created by humans could benefit jellyfish populations (Duarte et al., 2013). For example, newly created habitats resulting from coastal construction, roads and harbors, and other human activities can potentially provide substrate for benthic polyps. Because jellyfish polyps require a hard substrate for attachment, an increase in suitable benthic habitats could lead to an increase in polyps and thus jellyfish, as polyps are a critical stage in controlling jellyfish population dynamics. Especially in areas with soft (mud) or mobile (sandy-gravelly) substrate, it is important to avoid coastal fillings and similar shoreline construction activities. Such structures, including shipwrecks, may harbor polyp colonies that can cause localized problems (Isinibilir-Okyar, 2022).

In addition, offshore oil platforms, wind turbines, and other energy-related structures in open waters can facilitate the spread of some jellyfish species by providing stepping stones

for polyps in otherwise inaccessible environments (Dawson et al., 2005; Vodopivec et al., 2017). Solid waste materials such as plastic and metal, which have a long degradation period in nature, also serve as habitat for polyps (Shibata et al., 2015). Therefore, it is important to take measures to prevent solid waste from entering the marine environment.

Aubert et al. (2018) suggest including gelatinous zooplankton in monitoring programs, particularly in trawl-based fisheries research, to address knowledge gaps and biases in ecosystem assessments, especially given the adoption of an ecosystem approach to marine management under the Marine Strategy Framework Directive (MSFD) in European countries (MSFD EU Directive 2018). In accordance with EU Framework Directives, monitoring studies are being conducted in Türkiye and the Adriatic Sea. Gelatinous zooplankton can be included in trawl surveys, especially in the Sea of Marmara and Adriatic Sea where jellyfish blooms are more widespread and numerous. More knowledge of jellyfish population dynamics and distribution would allow prediction of jellyfish blooms and thus prevent greater damage in affected areas.

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