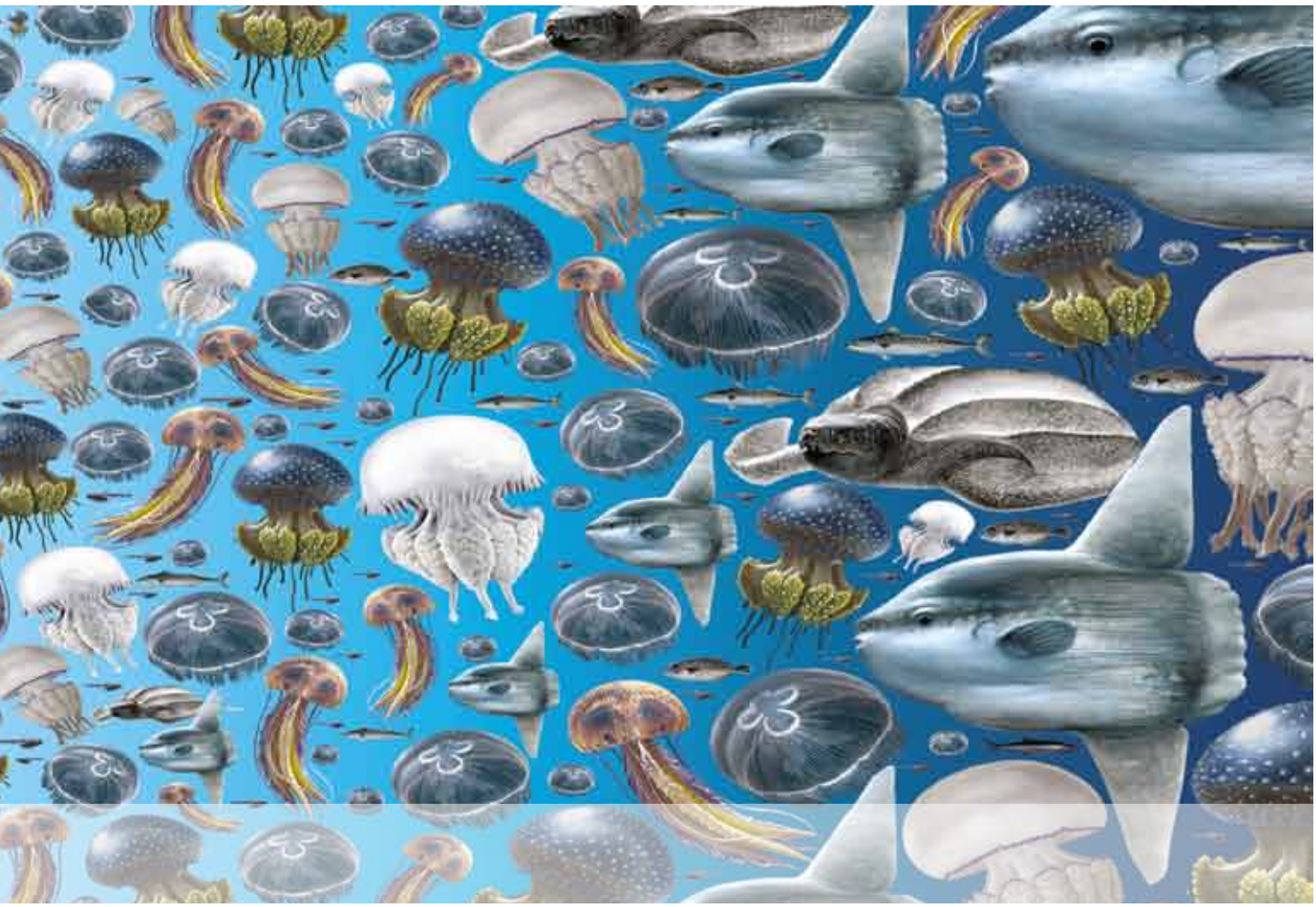
GENERAL FISHERIES COMMISSION FOR THE MEDITERRANEAN

ISSN 1020-9549

STUDIES AND REVIEWS

No. 92 2013



REVIEW OF JELLYFISH BLOOMS IN THE MEDITERRANEAN AND BLACK SEA

Cover photo and design
Cover picture: “Decrease of large fish releases jellyfish from competition with their larvae. Increased jellyfish availability favors medusivorous species, whose populations increase at the expenses of gelatinous plankton” art by A. Gennari, graphics by F. Tresca.
Cover design: A. Nastasi.

STUDIES AND REVIEWS **No. 92**

GENERAL FISHERIES COMMISSION FOR THE MEDITERRANEAN

REVIEW OF JELLYFISH BLOOMS IN THE MEDITERRANEAN AND BLACK SEA

by

Ferdinando Boero

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

Rome, 2013

ISBN 978-92-5-107457-2

PREPARATION OF THIS DOCUMENT

This document stems from the Workshop on Algal and Jellyfish Blooms in the Mediterranean and Black Sea, organized by the General Fisheries Commission for the Mediterranean (GFCM) in Istanbul (Turkey) 6-8 October 2010. The purpose of this document is to provide an updated overview of the jellyfish blooms phenomenon in the Mediterranean and Black Sea and to illustrate how the problem is affecting our societies. It is clear that a new type of human approach to marine ecosystems in general is needed to prevent and face a phenomenon such as the jellyfish blooms. Sources are referenced in the bibliography. Additional insight obtained through author's own experience, "jelly-news" reported by the mass media and the public opinion has also been used throughout the document.

ACKNOWLEDGEMENTS

The author truly thanks the GFCM Executive Secretary Abdellah Srour, the GFCM Secretariat for the support provided and all the participants who attended the GFCM Workshop on Algal and Jellyfish Blooms in the Mediterranean and Black Sea (6-8 October 2010, Istanbul, Turkey): Muharrem Aksoy, Yelda Aktan, Hamdi Arpa, Levent Artüz, Muharrem Balcı, Neslihan Balkıs, Zekiye Bırıncı Özdemır, Nihayet Bizsel, Silvia Casabianca, Kenan Cinar, Derya Denle, Nazli Demirel, Esra Fatma Denizci Toslak, Turgay Durmuş, Haydar Fersoy, Eyuphan Firat, Bella Galil, Emine Gülhan, İlknur Gültekı, Ali Guney, Asma Hamza, Sinem İnce, Melek Isinibilir, Alpaslan Kara, Belgin Karaşahın, Getin Keskın, Vahdettin Kürüm, Sami Lakkis, Victor T. Langenberg, Mustafa Mantikci, Ilker Marangoz, Volodymyr Myroshnychenko, Elif Murat Dalkara, Yıldız Özçalkap, Süleyman Özdemır, Duyşen Özel, Zeki Ozer, Ramazan Ozkaya, Antonella Penna, Stefano Piraino, Çolpan Polat Beken, Sevim Polat, Mehmet Sezer, Nüket Sıvrı, Basak Sözer, Hamid Taleb, Seyfettin Tas, Fatma Telli Karakoç, Benin Toklu Alıçlı, Bülent Topaloğlu, Cihan Toslak, Vildan Tüfekçı, Muhammet Türkoğlu, Jan Van Dalfsen, Banu Yalim, Bülent Yasar, Noyan Yilmaz, Ahsen Yuksek, Mustafa Zengın.

A special thank goes to Aurora Nastasi from the GFCM Secretariat who assisted me in writing and editing the Workshop report as well as this review.

The Commission for the Scientific Exploration of the Mediterranean Sea (CIESM) is acknowledged for sponsoring the pilot phase of the Jellywatch in Italian waters in the years 2009, 2010, and contributing financially to the early versions the poster on which the campaigns were based. Materials used to write this report stem also from the 7th Framework Programme EU projects Jason, Sesame, Vectors, Perseus and CoCoNet.

Boero F.
Review of jellyfish blooms in the Mediterranean and Black Sea.
Studies and Reviews. General Fisheries Commission for the Mediterranean. No. 92.
Rome, FAO 2013. 53 p.

ABSTRACT

Gelatinous plankton is formed by representatives of Cnidaria (true jellyfish), Ctenophora (comb jellies) and Tunicata (salps). The life cycles of gelatinous plankters are conducive to bloom events, with huge populations that are occasionally built up whenever conditions are favorable. Such events have been known since ancient times and are part of the normal functioning of the oceans. In the last decade, however, the media are reporting on an increasingly high number of gelatinous plankton blooms. The reasons for these reports is that thousands of tourists are stung, fisheries are harmed or even impaired by jellyfish that eat fish eggs and larvae, coastal plants are stopped by gelatinous masses. The scientific literature seldom reports on these events, so time is ripe to cope with this mismatch between what is happening and what is being studied. Fisheries scientists seldom considered gelatinous plankton both in their field-work and in their computer-generated models, aimed at managing fish populations. Jellyfish are an important cause of fish mortality since they are predators of fish eggs and larvae, furthermore they compete with fish larvae and juveniles by feeding on their crustacean food. The Black Sea case of the impact of the ctenophore *Mnemiopsis leydi* on the fish populations, and then on the fisheries, showed that gelatinous plankton is an important variable in fisheries science and that it cannot be overlooked. The aim of this report is to review current knowledge on gelatinous plankton in the Mediterranean and Black Sea, so as to provide a framework to include this important component of marine ecosystems in fisheries science and in the management of other human activities such as tourism and coastal development. Fact sheets on the most important gelatinous plankters of the Mediterranean and Black Seas are included as an appendix.

CONTENTS

1. INTRODUCTION 1
   1.1. Jellyfish 1
      1.1.1. Cnidaria 1
      1.1.2. Ctenophora 2
      1.1.3. Chordata 3
   1.2. The blooms 4
   1.3. Ecosystem “malfunctioning” 5
   1.4. The grand picture 7
   1.5. The impact of gelatinous plankton on fish populations 8
   1.6. Measures and estimates of predation impacts of gelatinous plankton on fish 8
   1.7. Jellyfish as keystone predators 12
   1.8. Gelatinous plankton as a source of food 12
2. JELLYFISH BLOOMS IN THE MEDITERRANEAN AND BLACK SEA 14
   2.1. The Black Sea and *Mnemiopsis*, a paradigmatic example 14
   2.2. Jellyfish bloom cases in the Mediterranean Sea 15
   2.3. Lessons from the history of the Adriatic Sea 16
3. CURRENT KNOWLEDGE AND RESEARCH NEEDS 19
   3.1. Analysis of the possible drivers of the phenomena 19
   3.2. Methods to monitor and forecast blooms 22
   3.3. Further studies on blooms 25
   3.4. Negative (and positive) impacts of jellyfish blooms on human activities 26
      3.4.1. Fisheries 26
      3.4.2. Public health 27
      3.4.3. Tourism 28
      3.4.4. Food market 28
      3.4.5. Cooling systems of factories 29
      3.4.6. Cage aquaculture 29
      3.4.7. Positive impact of gelatinous plankton 29
      3.4.8. The species 30
4. DEVELOPING A SCIENTIFIC FRAMEWORK IN SUPPORT OF MANAGEMENT INSTRUMENTS TOWARDS ELIMINATING OR MITIGATING THE EFFECT OF BLOOMS 31
   4.1. Human impacts and ecosystem functioning 31
   4.2. Multiple stressors 31
   4.3. The ecosystem approach 32
   4.4. Recommendations for management 32
   4.5. Conclusion 35
5. INVENTORY OF EXISTING BIBLIOGRAPHY ON THIS ISSUE AND LIST OF RELEVANT PUBLICATIONS ANNEXED TO THE REPORT 36
6. APPENDIX: THE MAIN GELATINOUS PLANKTERS OF THE MEDITERRANEAN AND THE BLACK SEA 44

FIGURES AND TABLES

Figure 1. Life cycle of a pelago-benthic jellyfish (after Boero *et al.*, 2008).....2

Figure 2. A ctenophore: *Leucothoea* (art by A. Gennari) 3

Figure 3. A pelagic tunicate: *Salpa* (art by A. Gennari) 3

Figure 4. The pathway *phytoplankton → herbivorous crustacean plankton → carnivorous zooplankton → fish* (art by A. Gennari, graphics by F. Tresca) 4

Figure 5. The pathway *phytoplankton → crustacean plankton → jellyfish* (art by A. Gennari, graphics by F. Tresca) 5

Figure 6. The pathway *phytoplankton → herbivorous gelatinous zooplankton* (art by A. Gennari, graphics by F. Tresca) 6

Figure 7. The three main pathways determining marine ecosystem functioning (art by A. Gennari, graphics by F. Tresca) 7

Figure 8. Fishing down marine food webs (after Pauly *et al.*, 1998) 12

Figure 9. Revised version of the scenario of fishing down marine food webs. Future ecosystems are predicted to be dominated by jellyfish (after Pauly *et al*., 2009).....12

Figure 10. The decrease of large fish releases jellyfish from competition with their larvae. Increased jellyfish availability favors medusivorous species, whose populations increase at the expenses of gelatinous plankton (art by A. Gennari, graphics by F. Tresca) 13

Figure 11. *Mnemiopsis leydi* (art by A. Gennari) 14

Figure 12. *Pelagia noctiluca* (art by A. Gennari) 15

Figure 13. Periodicity of *Pelagia noctiluca* blooms. Open circles: years without *Pelagia*. Closed circles: years with *Pelagia*. Solid line: probability of *Pelagia* blooms (after Goy *et al*., 1988) 15

Figure 14. Ecological history of the Adriatic Sea. Period 1: fish-dominated. Period 2: jellyfish-dominated. Period 3: dinoflagellate-dominated (red tides), with overfishing of benthic molluscs. Period 4: bacteria-dominated, with mucilages. Period 5 (erratic): thaliacean-dominated. Period 6 (present): lower production (art by A. Gennari, graphics by F. Tresca) 17

Figure 15. Bloom of *Rhopilema nomadica* in the Levant Sea, coasts of Israel (courtesy of Bella Galil) 19

Figure 16. Bloom of *Carybdea marsupialis* in correspondence of coastal defences along the Adriatic coast of Italy 20

Figure 17. *Phyllorhiza punctata*, recently recorded from the western Mediterranean (art by A. Gennari) 21

Figure 18. *Catostylus tagi* photographed at Pantelleria Island (picture by Maria Ghelia) 21

Figure 19. *Marivagia stellata* (after Galil *et al*., 2010) 22

Figure 20. The poster of the CIESM jellywatch (2009 version). (Concept by Ferdinando Boero, art by A. Gennari, graphics by F. Tresca) 24

Figure 21. Jellyfish in the Mediterranean hit the cover of Time magazine, on 4 November 2009.....25

Figure 22. Graphic representation of the presence of jellyfish along the Italian coast in the summer 2010. *Pelagia* dominates the western basin but it is absent from the Adriatic, where *Rhizostoma* and *Carybdea* are dominant (Boero, unpublished). 25

Figure 23. The nets of Japanese fishermen are often impaired by swarms of *Neopilema nomurai* 26

Figure 24. Press release on the sinking of a fishing vessel by giant jellyfish 27
Figure 25. Report on the first case of lethal sting by a gelatinous plankter in the Mediterranean Sea. It occurred in Sardinia at the end of August 2010. The probable responsible was *Physalia* .. 27
Figure 26. Jellyfish barrier to protect tourists from being stung 28
Figure 27. A jellyfish dish 28
Figure 28. Jellyfish clogging the cooling system of a power plant 29
Figure 29. The author playing with *Aurelia aurita* in the Varano Lake, S. Italy (picture by Roberto Rinaldi, taken from the TV broadcast Linea Blu) 30
Figure 30. The main species of gelatinous plankton in the Mediterranean and Black Seas, from the CIESM Jellywatch poster 30

Table I. Field predation rates of *Aurelia aurita* based on stomach contents and digestion rates (after Arai, 1997) 8
Table II. Stomach contents of field-caught *Aurelia aurita* of various sizes and at different sites, as percentage of prey numbers (after Arai, 1997) 9
Table III. Stomach contents of field-caught specimens of *Pelagia noctiluca* of various sizes and at different sites, as percentage of prey numbers (after Arai, 1997) 10
Table IV. Gut content of Narcomedusae collected in situ (after Larson *et al*., 1989) 10
Table V. Numbers of fish eggs and larvae eaten per day by single specimens of various gelatinous predators (after Arai and Purcell 2001) 11

1. INTRODUCTION

1.1. Jellyfish

The word "jellyfish" is a popular term defining what marine biologists call gelatinous macrozooplankton. The word "gelatinous" refers to the general consistency of these animals: their body is mostly made of extracellular matrix (often called mesoglea), i.e. the matrix that holds cells together and that is present in all animals, including us, but that, in these organisms, is the greatest portion of the whole body. Jelly refers just to gelatine. This body architecture is shared by animals that are very far from each other, in terms of evolutionary history. The fossil record tells us that true jellyfish are the oldest animals among those that are still living today, being represented in fossils that date back to the Pre-Cambrian. They are referred to the phylum Cnidaria (Cartwright *et al.*, 2007). Vertebrates, including us, are referred to the phylum Chordata, and some chordates, namely the Tunicata, are also members of gelatinous macrozooplankton, with the Thaliacea and the Appendicularia. Gelatinous macrozooplankton, furthermore, comprises also the Ctenophora, or comb jellyfish. The representatives of these three phyla are the bulk of gelatinous macrozooplankton and, together, make up what we call "jellyfish" (Boero *et al.*, 2008). The following paragraphs contain a textbook-knowledge account of the three phyla, summarizing the information that is relevant for the scopes of this report.

1.1.1. Cnidaria

The true jellyfish are the planktonic stages of three cnidarian classes: the Hydrozoa, the Scyphozoa, and the Cubozoa. Most Scyphozoa and all Cubozoa fall within the category of macro- and even megazooplankton, since they are large enough, as adults, to be perceived by the naked eye, ranging from 2 mm (e.g. some small medusae) to 2 m in bell diameter, and several metres of tentacle length, of the largest medusae. Some Hydrozoa are macroplankters too, but many species belong to the mesozooplankton, being smaller than 2 mm. Gelatinous mesozooplankton is usually not perceived by a casual observer, unless when its representatives reach high densities.

Jellyfish move by jet propulsion, contracting their bells, or umbrellas. The umbrella usually carries tentacles on its margin and has a manubrium hanging in its cavity. The mouth is at the end of the manubrium. The tentacles catch the prey and bring it to the manubrium.

Cnidarians do have stinging cells, i.e. cells armed with cnidocysts, little capsules containing an inverted filament that can be everted to inject a venom into their victims (either preys or predators or... us). With very few exceptions, cnidarian jellyfish are carnivores, and use their cnidocysts to kill their prey that, according to the species, can be either other jellyfish, or crustaceans, or fish eggs and larvae, or anything reaching a viable size for the predator. Some, however, are microphagous or even contain zooxanthellae. Cnidarian jellyfish, also called medusae, have complex life cycles that often involve a benthic stage: the polyp. Jellyfish life histories often involve larval amplification. The adult medusae reproduce sexually, and each fertilization leads to the formation of a planula larva (Fig. 1).

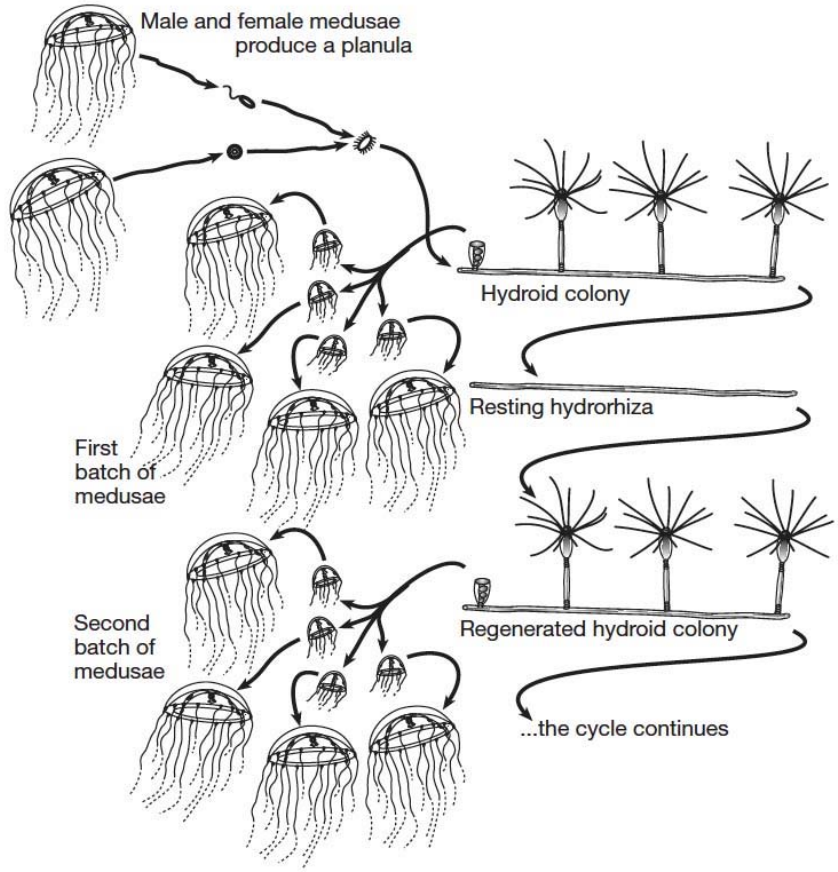


Figure 1. Life cycle of a pelago-benthic jellyfish (after Boero *et al.*, 2008).

The larva settles and leads to a colony that can become quite large, feeding on other animals. A single colony, through asexual reproduction, can produce thousands of small medusae that, then, will grow to maturity. "Amplification" means that each fertilization event does not lead to a single adult but, instead, to many adults, due to asexual reproduction in the polyp stage. The sexually competent medusa is the adult, whereas the polyp stage, where the amplification occurs, is a larva. Hence: larval amplification.

Many Hydrozoan species have suppressed the medusa stage and are sexually mature as polyps. Whereas some Hydrozoans and Scyphozoans do not have a polyp stage, and spend their whole life as medusae. The Hydrozoa produce medusae by lateral budding, the Scyphozoa by strobilation, and the Cubozoa by complete metamorphosis of a polyp into a medusa.

Besides medusae, the Cnidaria can contribute to gelatinous macrozooplankton as floating or swimming colonies, such as the hydroids *Velella* and *Porpita*, or siphonophores like *Physalia*.

1.1.2. Ctenophora

Gelatinous macrozooplankton is usually equated to stinging jellyfish, and its presence causes major concern about own safety in non-marine biologists, due to fear of potential stings. Many members of gelatinous zooplankton, however, are not Cnidaria, and do not sting. The Ctenophores (Fig. 2) do not have a bell and a manubrium, and do not move by pulsations, they just share a gelatinous appearance with the Cnidaria. Ctenophores move by ciliary propulsion, through what zoologists call "ctenes" or combs. Hence the popular name: comb jellies. They

can be a few centimetres, or even 50 or more centimetres, being globular, or similar to a dirigible, or ribbon like. Ribbon like ones, of the genus *Cestum*, can move also by snake like movements, but the other members of the group usually glide, appearing motionless and, in spite of that, moving. Their bodies are characterized by iridescent glows that are caused just by the flapping combs, the propulsors of the animal. Ctenophores have two tentacles armed with colloblasts, cell organelles that, instead of containing a venom, as the cnidocytes of Cnidaria, contain a glue that holds on their victims. Like cnidarian jellyfish, they also feed on other gelatinous plankters, on crustaceans, or on fish eggs and larvae, being comparable to true jellyfish in their feeding habits. Ctenophores have no impact on human health, and cannot cause any direct harm to us. Ctenophores are holoplanktonic (some are benthic, but will not be considered in the present account), there whole life cycle taking place in the water column.

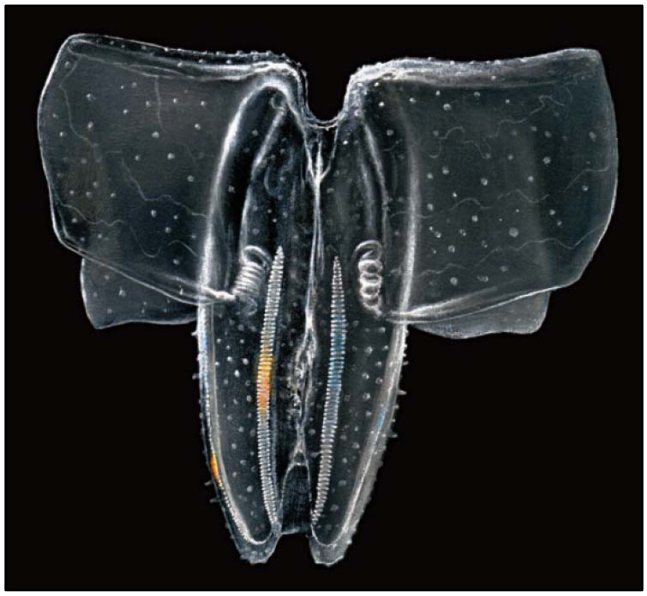


Figure 2. A ctenophore: *Leucothoea* (art by A. Gennari).

1.1.3. Chordata

Pelagic tunicates (Fig. 3) are members of the phylum Chordata; they comprise the Thaliacea and the Larvacea, or appendicularians. The Larvacea are of small size, but can be present in very high quantities. The Thaliacea, namely salps, doliolids and pyrosomes, are of much larger size, pyrosome colonies and salp chains reaching several metres in length. Pelagic tunicates are much different from both Cnidaria and Ctenophora in their feeding habits, they are filter feeders upon protists (usually phytoplankton), bacteria and even viruses. Their life cycles are holoplanktonic and involve both sexual and asexual reproduction, with the possibility of high biomass increases due to formation of large colonies. Apparently, just as for Ctenophora, the pelagic tunicates do not have benthic stages.

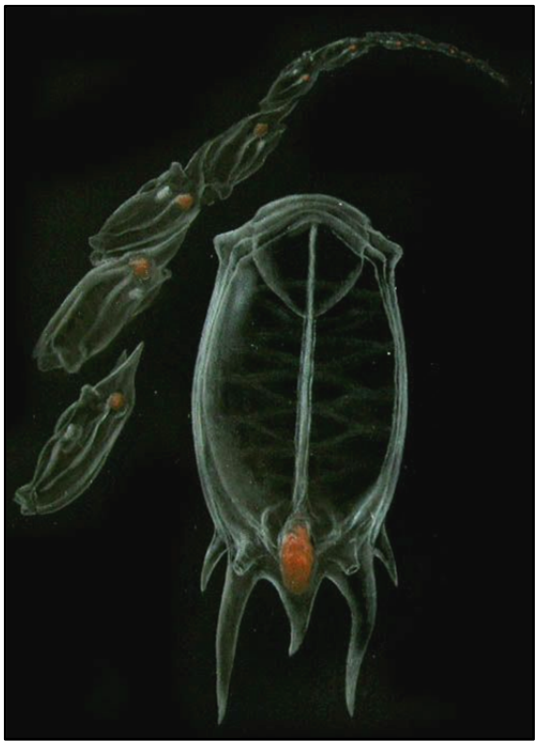


Figure 3. A pelagic tunicate: *Salpa* (art by A. Gennari).

1.2. The blooms

The whole functioning of marine ecosystems is based on blooms, i.e. on pulses of primary and secondary production due to the sudden increase in the population size of some key species. The spring bloom of phytoplankton, in temperate seas like the Mediterranean and the Black Seas, is determined by a peak of primary production of planktonic protists (the phytoplankton) that are usually diatoms or flagellates. The phytoplankton pulse is followed by a zooplankton pulse that takes advantage of the phytoplankton. Crustaceans, especially copepods, are the main representatives of herbivorous zooplankton. The zooplankton peak sustains the rest of the food web, being predated upon by carnivorous plankters. Among these, fish larvae and juveniles are prominent, eventually to become the well-known representatives of nekton: the fish. The pathway *phytoplankton → herbivorous crustacean zooplankton → carnivorous zooplankton → fish* (Fig. 4) is the backbone of marine production and sustains also our exploitation of marine resources, through fisheries. The species forming the nodes of this pathway are part of a system that functions due to production pulses (the blooms). If the pathway is sustained, the ecosystem produces fish that, in their turn, realize complex pathways within the fish universe. Small fish are fed upon by larger fish, and most of the nekton seems to be self-sufficient. But this is just an impression. Primary production must be at the base of food webs, and primary production is mainly the phytoplankton pulses. The impression of self-sufficiency of the fish domain reveals its weakness if we consider fish as life cycles, and not just as the adults we feed upon. Fish larvae and juveniles are often carnivorous, but they feed on preys that are herbivorous: the copepods and other crustaceans that rely on the phytoplankton pulses. An ecosystem cannot function with carnivores only!

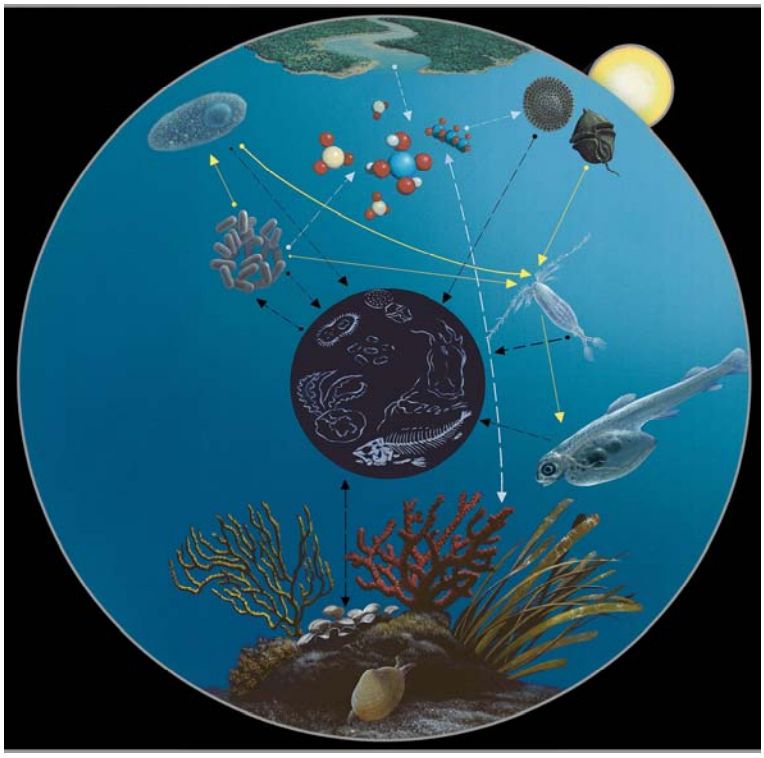


Figure 4. The pathway *phytoplankton → herbivorous crustacean plankton → carnivorouszooplankton → fish* (art by A. Gennari, graphics by F. Tresca).

1.3. Ecosystem "malfunctioning"

The term "malfunctioning" is obviously anthropocentric. All ecosystems do function, otherwise they would cease to exist. If they function so as to satisfy our expectations, they are considered as functioning well, whereas if they cease to do so, then they are labeled as functioning in a bad way (malfunction means just this: bad functioning).

Jellyfish are the oldest animals, among the ones that are currently present on the planet. They were present since the Pre-Cambrian and are not so different from their ancestors. Having passed through more than 500 millions of years of natural selection, with no big changes in their body organization, these animals are simply perfect! Simple and perfect. They also express their populations in pulses, like most of the representatives of marine systems. Jellyfish blooms, thus, are a quite normal phenomenon. The evolution of highly efficient animals, such as fish, however, probably posed a limit to their prevalence in the oceanic realm, with the triumph of the *phytoplankton → herbivorous crustacean zooplankton → fish* pathway that we like so much. A system based on pulses, however, is almost reset at each seasonal cycle. Such systems have been called "lottery systems" (see Boero, 1994; Fraschetti *et al.*, 2003 for reviews). There is a "prize", represented by the primary production pulse, and the winners are those who better utilize it, channeling its energy into their representatives, so as to build another pulse. For the fish to be the winners, their larvae and juveniles must tap from the secondary production of crustaceans. Jellyfish compete with the fish larvae and juveniles for the use of this resource. Furthermore, they can also feed on the eggs and larvae of the fish. We have seen that jellyfish have life cycles with larval amplification (Fig. 1). They can be produced in great quantities, so as to rapidly build huge populations. Hence: jellyfish blooms.

The lottery game in marine systems is based on the match or mismatch of the secondary or tertiary producers with the pulses that are at the base of marine ecosystems (Cushing, 1990). If the jellyfish produce a pulse with a good match with the pulse of crustaceans, and the fish do not, then the jellyfish can take over, and their bloom is reinforced. The bloom of jellyfish will compete with the fish larvae and juveniles and limit their growth, but it can also impact directly on the fish, since the blooming jellyfish will predate also on their eggs and larvae (Moller, 1984). When this happens, the *phytoplankton → herbivorous crustacean zooplankton → fish* pathway is disrupted, with the onset of the *phytoplankton → herbivorous crustacean zooplankton → jellyfish* pathway (Fig. 5).

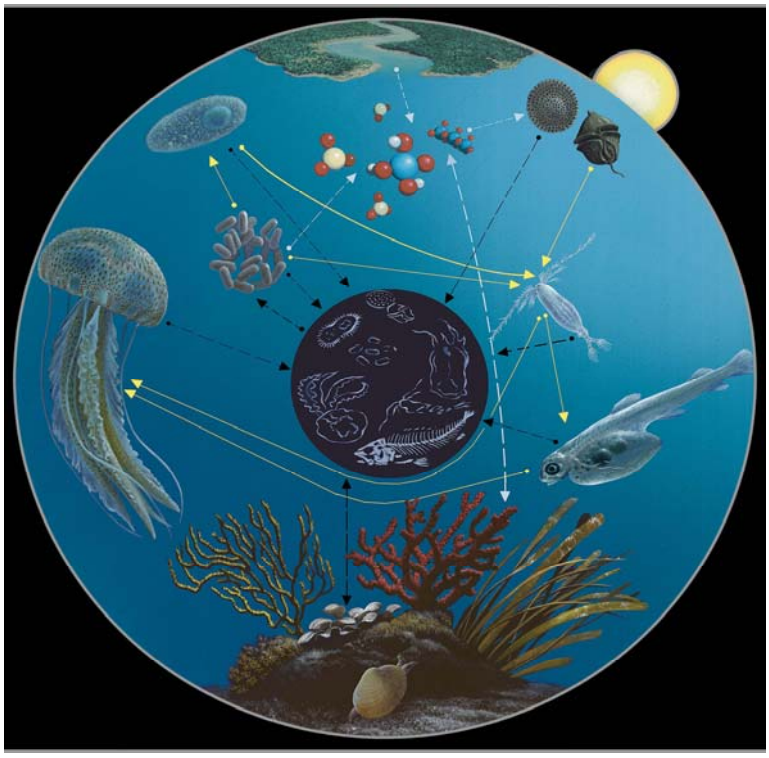


Figure 5. The pathway *phytoplankton → crustacean plankton → jellyfish* (art by A. Gennari, graphics by F. Tresca).

The fish, however, can rely on their "internal" pathways and most of them can stand the failure of one cohort, since they are long lived and can spawn for several years. The loss of one cohort can be buffered by the adult individuals that, usually, are invulnerable to jellyfish or that even feed upon them. Jellyfish, instead, are short lived and the individuals that make up a single pulse cannot persist and must reproduce successfully, starting from scratch, to produce another pulse in the subsequent favorable season. Fish, instead, can "hold their breath" and try again a year later.

When systems work in this way, jellyfish blooms are "accidents" that do not disrupt in a radical way the functioning of the *phytoplankton → herbivorous crustacean zooplankton → fish* pathway. Hence they can be disregarded, as they have been so far by fisheries biologists. They have an impact, of course, but of limited entity.

The "jellyfish" considered here are the carnivorous ones, namely Cnidaria and Ctenophora. The same pattern can be present also for herbivorous jellyfish, namely the Chordata. They feed directly on the phytoplankton and when they are particularly abundant they compete with the copepods, depleting the *phytoplankton → herbivorous crustacean zooplankton → fish* pathway, with the production of a short circuit in it: the *phytoplankton → herbivorous gelatinous zooplankton* pathway (Fig. 6).

At the end of their peak, pelagic tunicates usually contribute to what we call marine snow and fall to the benthos, almost skipping the pelagic trophic pathways (besides the bacteria that feed on them while they are falling towards the bottom).

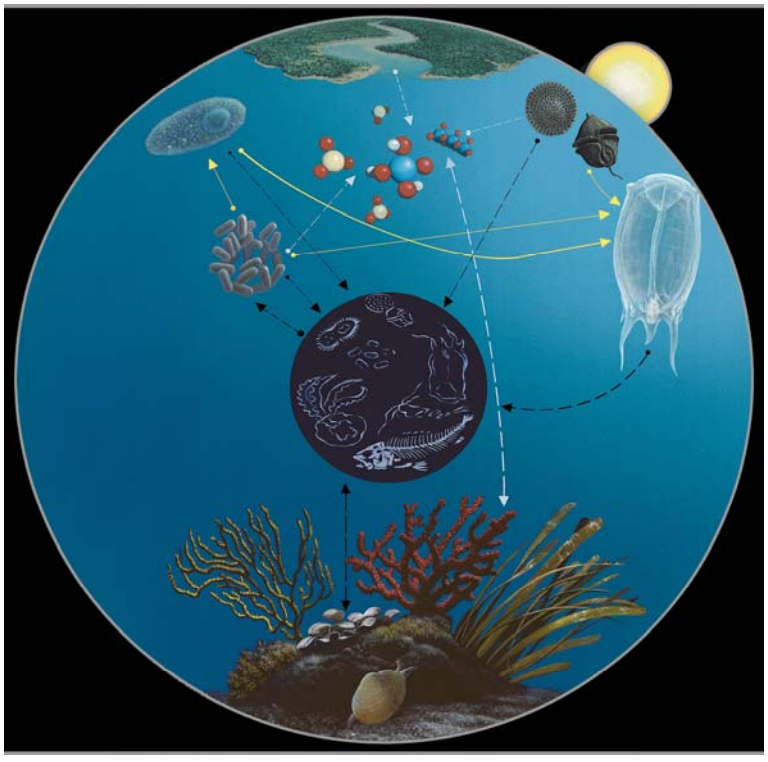


Figure 6. The pathway *phytoplankton → herbivorous gelatinous zooplankton* (art by A. Gennari, graphics by F. Tresca).

1.4. The grand picture

Marine ecosystems functioning, thus, takes place through three main pelagic pathways: the *phytoplankton → herbivorous crustacean zooplankton → carnivorous zooplankton → fish* pathway, the *phytoplankton → herbivorous crustacean zooplankton → carnivorous gelatinous zooplankton* pathway, and the *phytoplankton → herbivorous gelatinous zooplankton* pathway (Fig. 7). These pathways are not mutually exclusive, but one can prevail over the others. Usually, the first one (ending up with fish) prevails and determines what we consider as a "normal" situation (Fig. 4). The other two pathways, one ending up with carnivorous gelatinous zooplankton (Fig. 5) and the other with herbivorous gelatinous zooplankton (Fig. 6), from time to time can go through episodic success that, normally, cannot disrupt the prevailing pathway, ending up with fish. These blooms might even enhance the diversity in the nekton, as hypothesized above. The scientific literature is replenished of records of "anomalous" blooms of gelatinous plankton that, traditionally, have been considered as freaks in the functioning of marine systems. As a matter of fact, they are not freaks, they are part of the manifold possibilities in which marine ecosystems work. The evolutionary lineages interacting in these systems coexist since millions of years and can cope with each other.

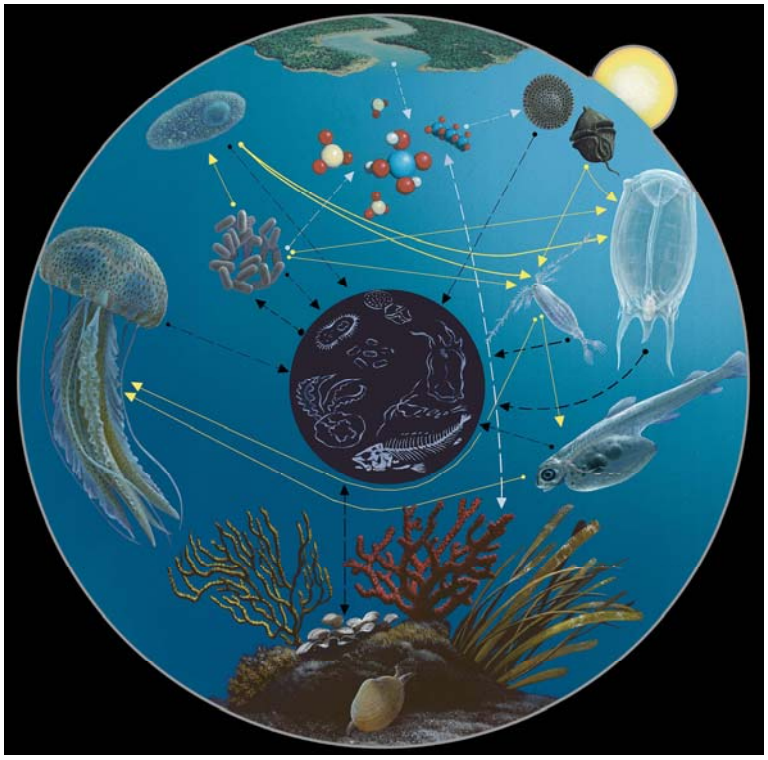


Figure 7. The three main pathways determining marine ecosystem functioning (art by A. Gennari, graphics by F. Tresca).

1.5. The impact of gelatinous plankton on fish populations

Summarizing, the impact of gelatinous zooplankton on fish populations can be: *i*) *positive*, due to a keystone effect that prevents the monopolization of overly successful fish species at the expenses of others, so maintaining fish biodiversity high. This effect occurs when fish and jellyfish coevolved in the same environmental context and if the jellyfish are abundant just for short periods; *ii) negative*, due to predation on and competition with fish larvae and juveniles (predation occurs also on fish eggs) if the jellyfish are not coevolved with the resident fish or if the fish populations are not "healthy", due to overfishing, and the jellyfish blooms are abnormally large and long-lasting. A different kind of competition might be exerted by thaliaceans, since they overexploit the phytoplankton and deplete resources for the crustacean grazers that are fed upon by fish larvae and juveniles.

1.6. Measures and estimates of predation impacts of gelatinous plankton on fish

The species of gelatinous plankton are in the thousands, and most of them are Hydromedusae (see Bouillon *et al.*, 2004; Bouillon *et al.*, 2006), followed by the Scypozoa and Cubozoa (see Arai, 1997), the Tunicata (see Bone, 1998), and the Ctenophora (see Harbison *et al.*, 1978). In comparison to the very high diversity of this compartment of plankton, the number of species whose biology and ecology have been investigated is exceedingly small. For most of them we barely know that they exist, and often even their life cycles are unknown.

These predators, furthermore, are very opportunistic since they are equipped with tentacles armed with cnidocysts or colloblasts that can catch almost anything, from unicellular organisms to much larger prey. Some are very specialized in their diets, but most of them feed on anything they can find.

The study of the trophic role of gelatinous plankton, and especially the carnivorous one, is made in two ways. The simplest one consists in collecting animals in the field and inspecting their gut, listing all the food items they contain. Feeding rates are measured in the laboratory, offering food to the animals and evaluating their clearing rates from a given volume of water and the time of digestion of the offered prey. These studies have been made on few species and at specific places (Tab I and II for *Aurelia aurita*). If a jellyfish species lives both in the North Sea and in the Mediterranean Sea, as is the case of *Pelagia noctiluca* (Tab. III), the study of its diet in the North Sea does not necessarily reflect its diet in the Mediterranean Sea, since the available food items might be very different. So, what has been found at one place cannot be automatically extended to all the places where a given species occurs.

Table I. Field predation rates of *Aurelia aurita* based on stomach contents and digestion rates (after Arai, 1997).

Size	Prey	Items/day
6-25 mm	fish larvae	1,6
16-40 mm	fish larvae	0,6
36-50 mm	fish larvae	15,9

Table II. Stomach contents of field-caught *Aurelia aurita* of various sizes and at different sites, as percentage of prey numbers (after Arai, 1997).

Specimens - size	Prey	%
40: 28-160 mm	copepods	45
	tintinnids	30
	veligers	11
	Oikopleura	5
	cladocera	3
	Noctiluca	3
	chetognats	3
961: 80-260 mm	copepods	56
	herring	30
	cladocera	13
	hydromedusae	1
1200: 36-50 mm	crustacea	63
	herring	34
20: large	copepods	77
	veligers	22
189: 10-150 mm	copepods	48
	hydromedusae	34
	eggs	12
	diatoms, ciliates	< 6
55: 28-34 mm	copepods	100
17: 2.5 mm	rotifers	93
	tintinnids	7

Table III. Stomach contents of field-caught specimens of *Pelagia noctiluca* of various sizes and at different sites, as percentage of prey numbers (after Arai, 1997).

Specimens - size	Prey	%
50: 10-40 mm	fish eggs	43
	copepods	29
	cumacea	14
	chatognats	14
51	copepods	67
	cladocera	11
	chaetognats	10
	gastropods	3
	euphausiids	2
	fish larvae	1
	mysids	1
38	copepods	44
	decapods	39
	cladocera	7
	fish eggs/larvae	3
	chaetognats	2
	amphipods	1

Some species, as the scyphozoan *Drymonema dalmatinum*, apparently feed only on other jellyfish, since Larson (1987) inspected 13 specimens and found only medusae in their guts. The same seems true also for Narcomedusae in general (Tab. IV).

Table IV. Gut content of Narcomedusae collected in situ (after Larson *et al.*, 1989).

Species	Prey	Place
Aegina citrea	salps	NW Atlantic
Aegina citrea	ctenophores	Arctic
Aegina citrea	hydromedusa	NE Pacific
Cunina duplicata	doliolids	NW Atlantic
Cunina proboscidea	salps, doliolids	NW Atlantic
Pegantha laevis	salps	NW Atlantic
Solmaris corona	doliolids	NW Atlantic
Solmissus albescens	pteropods	Mediterranean
Solmissus incisa	cteophore	Bahamas
Solmissus marshalli	hydromedusa	NE Pacific
Solmundella bitentaculata	pteropods	Antarctic

These gelatinous plankton eaters might be a natural mitigation of the impact of the predation pressures of their prey on crustacean and fish plankton, as largely demonstrated for the main predator of *Mnemiopsis leyidi* in the Black Sea: the ctenophore *Beroe ovata* (see, for instance, Shiganova *et al.*, 2004).

Purcell and Nemazie (1992) showed that the only prey of the hydromedusa *Nemopsis bachei* are copepodites of *Acartia clausi*, even though they stated that the observed predation could not affect significantly the population size of the copepods. Also *Pelagia noctiluca*, the main former of jellyfish blooms in the Mediterranean Sea, feeds mostly on copepods, even though Sabatés *et al.* (2010) report that 12 percent of its diet is made of fish larvae.

Arai and Purcell (2001) reviewed the available information on the impact of predation of gelatinous predators on fish (Tab. V).

Table V. Numbers of fish eggs and larvae eaten per day by single specimens of various gelatinous predators (after Arai and Purcell, 2001).

Species	Prey per day
Physalia physalis	120
Rhizophysa eysehardti	9
Aequorea victoria	91±147
Nemopsis bachei	4±3
Aurelia aurita	1,6
Chrysaora quinquecirrha	343±419
Mnemiopsis leidyi	42±33

Gelatinous herbivorous filter feeders (namely Thaliacea and Appendicularia) are extremely efficient in removing phytoplankton from the water column and, when present in huge swarms, they can impair the potential for feeding by crustaceans (see Bone, 1998 for a monograph). Harbison and McAlister (1979), with laboratory experiments, showed that Thaliaceans of various species do perform clearing rates of 100 percent.

1.7. Jellyfish as keystone predators

Bony fish do have very high fecundities. If a species "wins" the lottery and perfectly matches with the onset of energy availability during a seasonal cycle, its larvae and juveniles can monopolize the system. If the species is a large carnivore, it will deplete the lower levels of the food web. Either large or small as adults, all fish are small when they are eggs and larvae, and all are liable of jellyfish predation. Jellyfish presumably feed on the fish eggs and larvae that are most abundant during their peak, when jellyfish predation is maximal. In doing so, jellyfish reduce the size of the populations of the previous "winners" and release the rest of the nekton guild from their potential monopolization of nektonic biodiversity, as suggested by Piraino *et al.* (2002). If this were true, as suggested also by Purcell and Decker (2005), carnivorous gelatinous plankton might enhance the diversity of nekton, with a keystone role as a whole guild, and not as a single species.

1.8. Gelatinous plankton as a source of food

Growing evidence shows that also gelatinous plankton contributes to pelagic food webs as food for higher-level predators (Arai, 2005), but chances are good that their contribution to the sustaining of pelagic food webs is much lower than that of fish.

In the revised figure of Pauly *et al.* (2009) (Fig. 9), illustrating the process of fishing down marine food webs, jellyfish eating species, such as *Mola mola* and *Caretta caretta* are shown in the place of tuna, as in the classical version by Pauly *et al.* (1998) (Fig. 8).

It is not clear, though, if these species are really disappearing, as suggested by the figure, since *Mola mola* is not so present in fisheries catches, due to low market prices. If jellyfish are increasing, it might be expected that the species feeding on them, such as *Mola mola*, are liable to increase, due to higher food availability. Of course, the increase in jellyfish presences might be due to high pressures on their predators, as hinted by Pauly *et al.* (2009) picture, so that they are released from predation. But pressures are even higher on their competitors (commercial fish) that use their same food when they are larvae and juveniles.

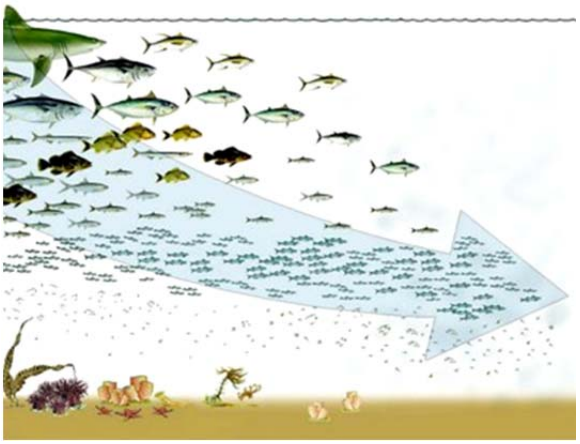


Figure 8. Fishing down marine food webs (after Pauly *et al.*, 1998).

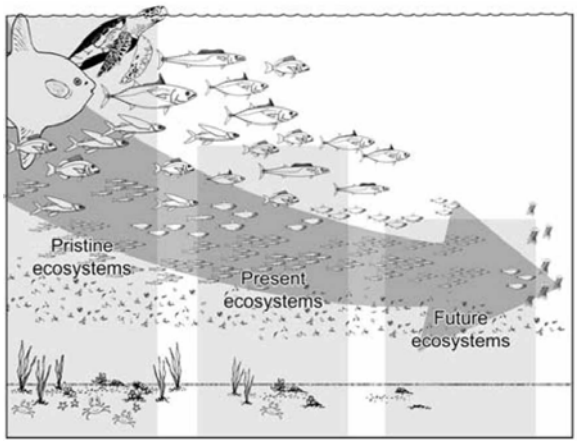


Figure 9. Revised version of the scenario of fishing down marine food webs. Future ecosystems are predicted to be dominated by jellyfish (after Pauly *et al.*, 2009).

Furthermore, Pope *et al.* (2010) suggested that shark overfishing releases sunfish from predation and increased jellyfish presences enhance their thriving possibilities. Unfortunately, estimates of sunfish populations are rather vague and their possible increase is highly hypothetical, just as their possible decrease!

Dulcic *et al.* (2007), however, reported an increase in recent years in the records of *Mola mola* in the Adriatic Sea. Garibaldi *et al.* (2010), and Orsi Relini (2010 a, b) recently reported an increase of medusivorous fishes in the Ligurian Sea. The leatherback turtle, *Demochelys coriacea*, is a specialized eater of gelatinous plankton and is apparently increasing in abundance due to higher food availability (Jones *et al.*, 2011). These increases in medusivorous species might be a response of marine communities to the current abundance of gelatinous plankton, with increases in the populations sizes of the species that take advantage from jellyfish as a source of food (Fig. 10) (for reviews see Arai, 2005; Ates, 1988). Some fish species that feed on jellyfish, such as *Mola mola*, are not of great commercial importance and, as reported by Orsi Relini *et al.* (2010a) they appear to be negatively affected by the habit of feeding on jellyfish, their perianal area becoming reddish due to the ingestion of great quantities of *Pelagia noctiluca*.

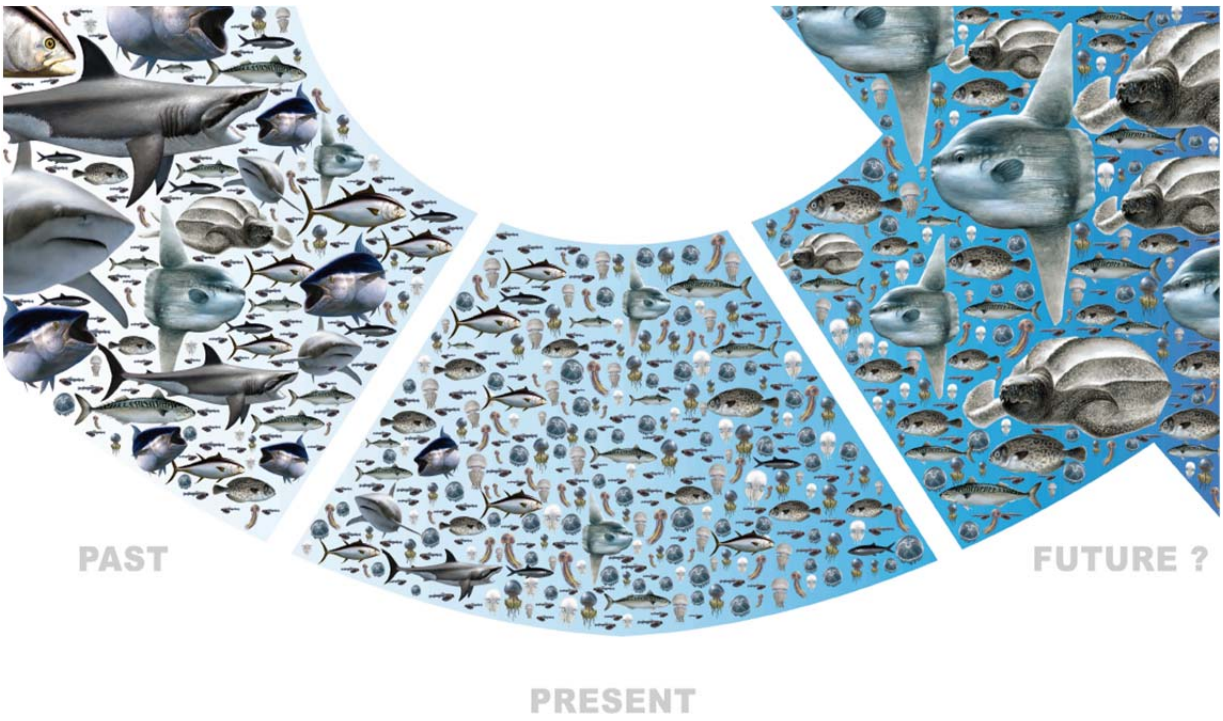


Figure 10. The decrease of large fish releases jellyfish from competition with their larvae. Increased jellyfish availability favors medusivorous species, whose populations increase at the expenses of gelatinous plankton (art by A. Gennari, graphics by F. Tresca).

In conclusion, the situation envisaged by Mills (2001) with the regime shift from a fish to a jellyfish ocean (and embraced also by Pauly *et al.*, 2009) seems to evolve towards the rise of medusivorous species, from gelatinous plankton eating other gelatinous plankton such as *Beroe ovata* feeding on *Mnemiopsis leidyi* (see below) to fish and reptiles with jellyfish-based diets.

2. JELLYFISH BLOOMS IN THE MEDITERRANEAN AND BLACK SEA

2.1. The Black Sea and *Mnemiopsis*, a paradigmatic example

The ctenophore *Mnemiopsis leidyi* (Fig. 11) was first detected in the Black Sea in 1982 (Peredalov, 1983). This species is typical of the Atlantic coast of the USA, and was probably brought to the Black Sea as a clandestine passenger in the ballast waters of US oil tankers. The Black Sea has several native gelatinous plankters but, evidently, they coevolved with their prey and predators and they never caused serious problems. *Mnemiopsis*, instead, built huge populations and put the Black Sea fisheries on their knees, depleting the nekton by feeding on fish eggs and larvae (direct predation) and on their crustacean prey (competition), as reported, for instance, by Kydeis (1994) and Shiganova (1997). For the first time, it was undeniable that fisheries can be severely affected by gelatinous plankton (besides the clogging of fishing nets during episodic blooms).

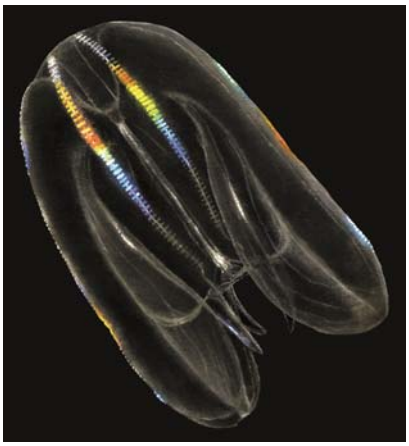


Figure 11. *Mnemiopsis leydi* (art by A. Gennari).

The problem was almost solved by another ctenophore invader, *Beroe ovata*, presumably coming from the same Atlantic ecosystem where *Mnemiopsis* thrives (Finenko *et al.*, 2000). *Beroe* feeds on *Mnemiopsis* and its arrival in the Black Sea mitigated the impact of the alien, just as it probably does in the original ecosystem of both species (Shiganova *et al.*, 2004). For the first time, with the case of *Mnemiopsis*, it became clear that the predation and competition of gelatinous zooplankton can have an overwhelming impact on fish populations and, hence, on fisheries.

Meanwhile, in other parts of the world, and especially along the USA coasts, plankton ecologists had been showing that gelatinous plankters do feed on fish eggs and larvae and proposed estimates for their impact on fish populations (e.g. Purcell, 1985). But these claims apparently passed unnoticed by fisheries ecologists, who continued to envisage man as the sole cause of decrease of fish populations.

Between the extreme of zero impact allotted to gelatinous plankton by traditional fisheries ecologists and the total impact allotted to *Mnemiopsis* there is probably some intermediate measure.

2.2. Jellyfish bloom cases in the Mediterranean Sea

The presence of jellyfish blooms in the Mediterranean is known since the beginning of the study of marine life. Goy *et al.* (1988) made an extensive bibliographic search, looking for accounts of blooms of the mauve stinger (*Pelagia noctiluca*) (Fig. 12) in the literature dealing with Mediterranean Sea biota.

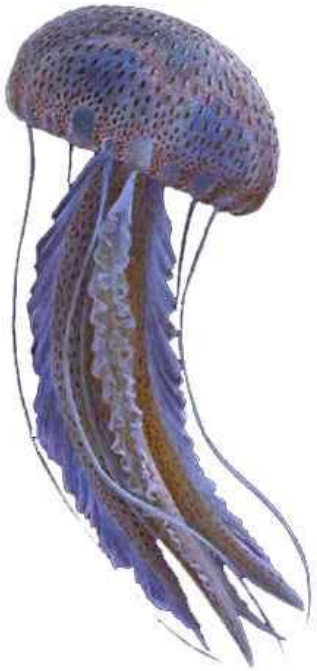


Figure 12. *Pelagia noctiluca* (art by A. Gennari).

The first account found by Goy *et al.* (1988) dates back to 1775 (Forskal, 1775) and in the same report the authors list 55 records of *Pelagia noctiluca* blooms in the period 1775–1987, identifying a possible periodicity of about 12 years in the occurrence of these episodes of apparently abnormal abundance of this species (Fig. 13).

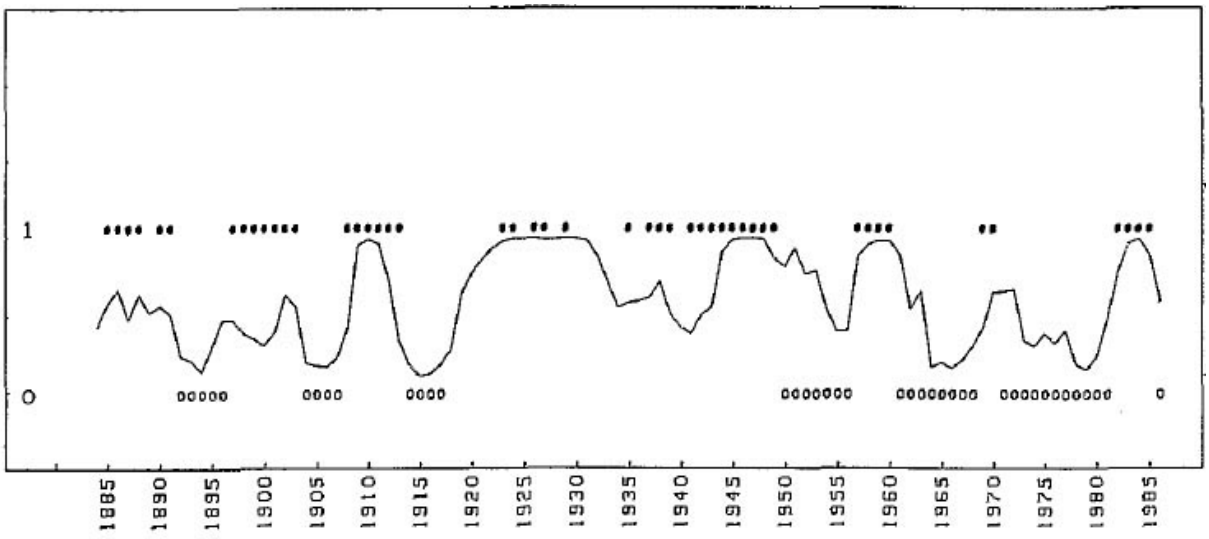


Figure 13. Periodicity of *Pelagia noctiluca* blooms. Open circles: years without *Pelagia*. Closed circles: years with *Pelagia*. Solid line: probability of *Pelagia* blooms (after Goy *et al.*, 1988).

This species is present in swarms also in other European waters. Russell (1970), for instance, reports an account by Cole (1952) who stated: "the sea looked as if converted into a solid mass of jellyfish".

In spite of the interest of some authors to report on these events, however, chances are good that most of these blooms simply passed unnoticed. The reasons for this are manifold:

- Blooms can occur in restricted areas where the jellyfish are concentrated in large quantities, but where no researchers are active at that time.
- Blooms are observed but no accounts are published, simply because the observation is not considered as having sufficient interest for a scientific publication.
- Blooms are reported in papers only with a few lines, being considered as simple anecdotes, their record being very difficult to trace.

Interest in these phenomena started in the early 1980s, when a basin-wide massive occurrence of *Pelagia noctiluca* affected almost the whole Mediterranean basin, including the Adriatic Sea, where the blooms of *Pelagia* had been noticed starting from 1977 (Malej and Malej, 2004). The United Nations Environmental Programme (UNEP), through the Mediterranean Action Plan (MAP) launched a project that made money available to study these phenomena. Research activities culminated into two Workshops that took place in 1983 (UNEP, 1984) and in 1987 (UNEP, 1991) respectively. In those workshops, and in several papers published in scientific journals by the participants to the project, all available information on *Pelagia noctiluca* blooms in the Mediterranean were assembled, culminating in the review by Goy *et al.* (1988) reporting about the periodic occurrence of *Pelagia* blooms.

The massive blooms of *Pelagia* of the early 1980s, however, soon reached an end, and the situation went back to "normal", or, better, went into other directions and jellyfish were soon forgotten. The people who studied these events changed their topics of research (due to lack of fund availability) even though jellyfish blooms appeared every once in a while, without sparking any interest from funding agencies.

In 2001, the Mediterranean Commission (CIESM) organized a workshop on Gelatinous plankton blooms (CIESM, 2001), linking the blooms of *Pelagia* of the early 1980s with the blooms of the alien ctenophore *Mnemiopsis leidyi* in the Black Sea that started in the same period and that continued in a massive way. The rationale of the CIESM workshop was to consider these blooms as part of a general trend, along with what had been already highlighted by Mills at a global level (1995; 2000).

2.3. Lessons from the history of the Adriatic Sea

During the *Pelagia* years, the Adriatic Sea was particularly struck by the blooms, with lots of studies by Italian, Slovenian and Croatian researchers (see CIESM, 2001 for references). As described by Boero (2001) and Boero and Bonsdorff (2007), *Pelagia* blooms eventually came to an end, to be replaced by a period of red tides, caused by dinoflagellate blooms, coupled with events of anoxic crises, followed then by a period of mucilages (Fig. 14).

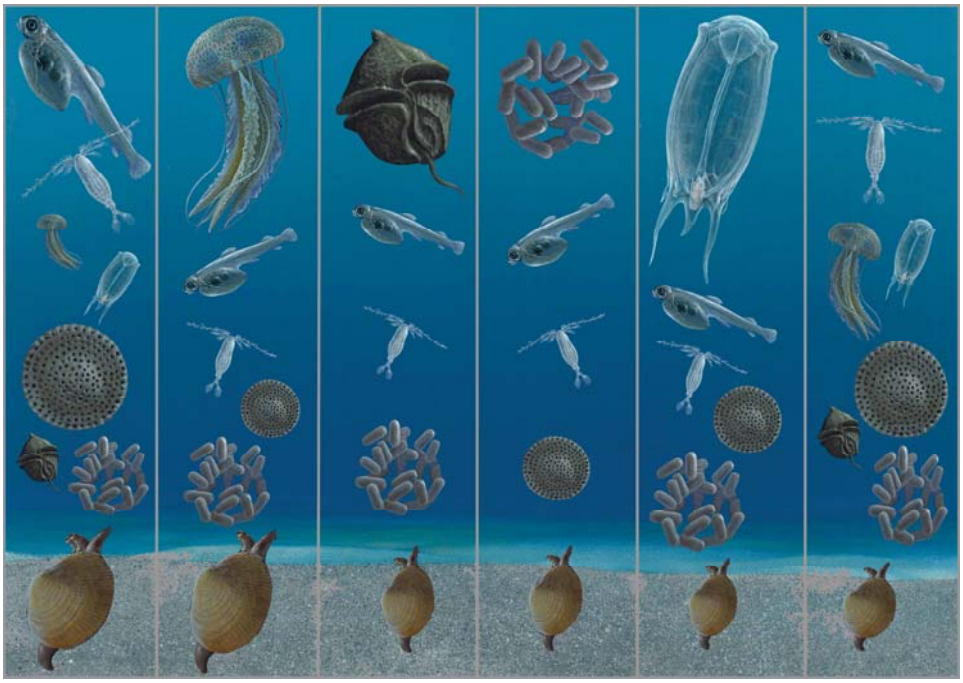


Figure 14. Ecological history of the Adriatic Sea. Period 1: fish-dominated. Period 2: jellyfish-dominated. Period 3: dinoflagellate-dominated (red tides), with overfishing of benthic molluscs. Period 4: bacteria-dominated, with mucilages. Period 5 (erratic): thaliacean-dominated. Period 6 (present): lower production (art by A. Gennari, graphics by F. Tresca).

The scenario hypothesized by Boero (2001) and Boero and Bonsdorff (2007) was that the persistence of *Pelagia* blooms in the first half of the 1980s had a similar effect to that of *Mnemiopsis* in the Black Sea, but that the real impact of the blooms was not properly evaluated. Fishermen lamented net clogging by jellyfish aggregates, so impairing their functioning. This interpretation of jellyfish impact on fisheries presumed that the fish were there, but that they were not caught because the jellyfish impaired fishing gears. In the Black Sea, instead, *Mnemiopsis* did not clog fishing nets, and it was immediately apparent that fish were not caught simply because there were no more fish! *Pelagia* is a very efficient predator of fish eggs and larvae, and of their crustacean food (see, for example Sabatés *et al.*, 2010) and it is highly probable that fish populations were depleted by *Pelagia* predation during the early 1980s blooms. Jellyfish replaced a very important sink of carbon fluxes (i.e. fish), as it happened many times in the past, at more or less regular intervals (Goy *et al.*, 1989). Past *Pelagia* blooms, however, were not so devastating as those of the 1980s and did not lead to the same series of phase shifts that affected the Adriatic Sea in the 1980s (Fig. 14). Fish, in fact, are longer lived than jellyfish and the nektonic food webs they form are very complex and partly self-sustained, since large fish feed on smaller fish, getting much farther from the base of trophic networks than jellyfish. During their blooms, jellyfish first draw most energy from the system and then go through massive mortalities, at the end of the favorable period. Large fish are almost immune to jellyfish predation and even if they skip one reproductive event, they still have time to engage successful reproduction when the jellyfish eventually disappear. The success of jellyfish, in this framework, is temporary, and the fish dominate the scene again as soon as jellyfish decrease. As remarked above, jellyfish blooms might even be beneficial to fish populations, playing a keystone role in avoiding the monopoly of few species ensuing from abnormal reproductive success. Fish, however, are subjected to another predatory pressure, at the other end of their life cycles. Humans catch adult fishes with increasingly efficient gear. This pressure on the adults might be compensated by the very high fecundity of teleosts, so that even a few remaining adults can repopulate the oceans with their astonishing production of eggs and larvae.

Fish, then, are well equipped to cope with gelatinous predators, escaping them with the larger size of their adults and with longer life spans than those of gelatinous plankton. Fish are also well equipped to cope with human predation, due to their small size at the beginning of their life cycle and to their very high fecundity rates. But if the attack to fish occurs at both sides of the spectrum, with gelatinous plankton decimating the eggs, larvae, and juveniles and predating on their crustacean food, and with fisheries decimating the reproductive adults, then the defeat of fish might be more serious than when "attacks" are isolated.

The reason for the defeat of fish in the Adriatic history of the 1980s and 1990s might be just due to gelatinous plankton blooms coupled with overfishing. A series of *Pelagia* blooms disrupted the recruits of Adriatic fish and overfishing reduced the reproductive adults to a threshold that made recovery of fish populations less effective than in the past. Of course, as already stressed, multiple causality is paramount in determining these events, and surely also pollution and eutrophication did play a relevant role in determining the state of the Adriatic Sea. The series of phase shifts in the Adriatic Sea history, with an amazing phylogenetic regression in the dominance of Adriatic biota (fish, jellyfish, dinoflagellates-red tides, bacteria-mucilages) might well be due to the disruption of the food web based on the microbial loop, continuing to crustaceans, and then ending up into fish larvae and juveniles, sustaining nektonic food webs and, hence, fisheries. In the past, the system could cope with episodes of jellyfish abundance, but in the case of the early 1980s blooms, the system went in another direction and is still not back to what was "normal" in pre-*Pelagia* years.

Another outstanding case of jellyfish outbreak in the Mediterranean is that of *Rhopilema nomadica* in the Levantine Basin (see below).

3. CURRENT KNOWLEDGE AND RESEARCH NEEDS

Mills (1995, 2001) was the first to highlight a global regime shift from a fish to a jellyfish ocean. Since then, scant investments have been made to support research on these events, besides noticeable exceptions, such as the Black Sea, due to the appalling case of *Mnemiopsis*.

3.1. Analysis of the possible drivers of the phenomena

The knowledge on gelatinous plankton blooms is very sparse in the Mediterranean and Black Sea regions, with the exception of special periods in which funds have been made available to study these phenomena, especially in the Black Sea, due to the invasion of *Mnemiopsis leidyi.* The opportunities provided by traditional plankton sampling campaigns are not completely appropriate because they are focused on mesozooplankton, privileging crustacean plankton and, eventually, small jellyfish. A bloom of large jellyfish of any kind might impair plankton nets in no time or, if the specimens are sparse, might not be evaluated in the right way. The knowledge of these phenomena, thus, seriously needs focused sampling techniques to improve our knowledge that, currently, is mostly linked to episodic observations that can be considered as anecdotal. The absence of focused projects on gelatinous plankton, and the inadequacy of the sampling gear to monitor plankton abundance and composition (focused on crustaceans), are conducive to a widespread lack of reliable information. Of course, when jellyfish blooms are recorded, the information is reliable, but the reverse is not true: the absence of records of jellyfish blooms is not a guarantee that these phenomena did not occur. Many researchers, for instance, if interviewed, do have memories of events of gelatinous plankton blooms, even though they never published accounts on them, since the projects they were working at did not consider gelatinous plankton and, also, because of low acceptance rates of articles reporting on such events, especially by highly ranked journals. The improvement of knowledge requires focused projects on these phenomena, by using the methods that will be described in the following section. As reported above, there is a global regime shift from a fish to a jellyfish ocean (Mills, 2001). The causes for this trend are not necessarily linked exclusively on global trends, but there are currently many phenomena that are occurring at a global scale and that might favor jellyfish blooms, namely:

Global warming, on the one hand, should enhance species that thrive at tropical latitudes but, on the other hand, species that are favored by cold waters should be in distress. If the species of warm water affinity are more and more abundant, and expand their natural ranges, such as *Rhopilema nomadica* (Fig. 15) in the Levantine Basin of the Mediterranean Sea, it is also true that species of temperate affinity, like *Mnemiopsis leyidi* are also increasing, even in the warmest portions of the Mediterranean Sea.

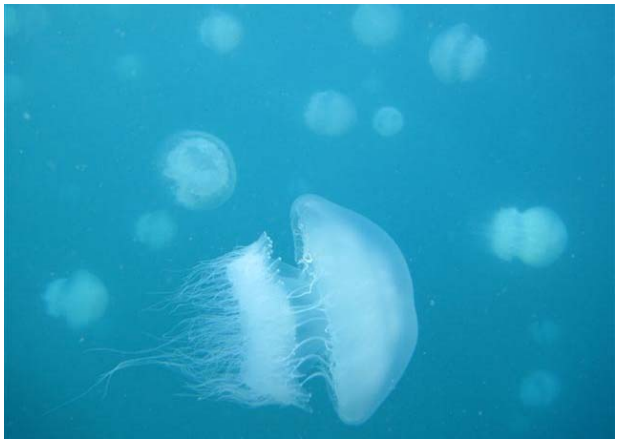


Figure 15. Bloom of *Rhopilema nomadica* in the Levant Sea, coasts of Israel (courtesy of Bella Galil).

So, global warming is conducive to increases in the abundances of some species but, apparently, it does not have a negative impact on species that are not of tropical affinity. The favor to species of warm water affinity resides primarily in the presence of newly available conditions that allow the establishment of species of tropical affinity that entered the basins recently. Furthermore, the favorable windows for sexual reproduction are becoming wider, allowing further population increases.

Global overfishing is removing top predators from the oceans (Fig. 10). Fish larvae compete with jellyfish in eating crustacean zooplankton and if the adult populations are large, the number of produced larvae and juveniles might overwhelm the gelatinous plankton, outcompeting it. A lower abundance of fish, however, might release jellyfish from their competition and, if the jellyfish populations increase, a vicious circle is started, since they predate on their competitors, further reducing the resilience of the fish populations already impacted by overfishing.

There are also other causes that have been called for the increase of gelatinous plankton, and they are mostly local, such as the following:

Eutrophication has been invoked as a cause for jellyfish abundance. In the Mediterranean, however, an increase in nutrients in the water is usually conducive to algal blooms, and the link with gelatinous plankton blooms can be just circumstantial. The red tides and the mucilage events that characterized the ecology of the Adriatic in the last 20 years have been ascribed just to eutrophication and they did not lead to jellyfish blooms but, instead, they followed the *Pelagia* years and occurred in the absence of gelatinous plankton or, eventually, favored salps and other microphagous gelatinous plankters that, however, remained mostly unstudied.

Increased space for polyps ensuing, for instance, from the widespread use of hard coastal defenses and from the increase in tourist harbors can enhance jellyfish production by the benthic stages, when present in the life cycle. Furthermore, this might allow the persistence of species in certain areas, year after year. The cubozoan *Carybdea marsupialis*, for instance, has been recorded only recently from the Adriatic Sea (Boero and Minelli, 1986) but, in the last few years it is very abundant in correspondence of the coastal defenses that were built to prevent coastal erosion (Fig. 16). It is highly probable that the coastal defenses are a proper settling place for the polyps, so enhancing the spread of this stinging species.

Figure 16. Bloom of *Carybdea marsupialis* in correspondence of coastal defenses along the Adriatic coast of Italy.

Transport of non-indigenous species (NIS) is a very particular case, and applies well to the Black Sea, that became severely affected by the introduction of the alien ctenophore *Mnemiopsis leyidi*, then mitigated by the arrival of another ctenophore NIS (*Beroe ovata*) that feeds on *Mnemiopsis*. These ctenophores are typical of the Atlantic coast of the American continent and reached the Black Sea due to direct human transport, presumably via the ballast waters of oil tankers. The widespread use of scenic jellyfish in public aquaria, such as *Phyllorhiza punctata* (Fig. 17), might lead to "escape" of polyps or even planulae, eventually leading to population outbreaks, but this possibility is purely hypothetical (Bolton and Graham, 2006).

Figure 17. *Phyllorhiza punctata*, recently recorded from the Western Mediterranean (art by A. Gennari).

Widening of the natural area of non-indigenous species is different from the previous case, since species can change their natural distribution while reaching areas where they had been previously unrecorded. The main recipient of non-indigenous species in the whole Mediterranean area is the eastern basin, now called Levantine basin in its extreme eastern portion. The opening of the Suez Canal, and the low diversity of that part of the Mediterranean basin, made so that the Red Sea species, expanding their natural range through the artificial waterway of the Suez Canal, thrived at the newly reached site, building up huge populations. This is the case of *Rhopilema nomadica*, a scyphozoan jellyfish (Fig. 15) that was described as new to science by Galil *et al.* (1990) from the Levantine basin but that was immediately considered as having entered the Mediterranean Sea through the Suez Canal, even if the species has never been found outside the Mediterranean area. Obviously, without human intervention (i.e. without the opening of the Suez Canal) no Indo-Pacific species would have widened its natural range so as to reach the Mediterranean Sea. In spite of this, these species cannot be considered as having been transported directly by humans, such as those introduced via aquaculture, aquarium trade, fouling, ballast waters, etc. Their reaching the Mediterranean might be considered as being human-mediated, via the construction of a connection between their natural area and another one, so allowing their expansion there, where the conditions are conducive to their thriving. Other species, such as the recently recorded scyphozoan jellyfish *Catostylus tagi* (Fig. 18), entered from the Gibraltar Strait (Boero, 2011) and so really widened their natural range with no mediation by human action.

Figure 18. *Catostylus tagi* photographed at Pantelleria Island (picture by Maria Ghelia).

Overall, overfishing and global warming are probably the most important drivers of increased jellyfish presence in the global ocean and, with due exceptions, also in the Mediterranean and the Black Sea. The various drivers do not act in isolation and they might reinforce with each other. The Levant basin, however, is a noticeable exception, since it hosts mostly species that entered from the Suez Canal, and new species are still being found, like *Marivagia stellata*, having the Mediterranean Sea as type locality, but having arrived there from other locations where they have been undetected by science (Galil *et al.*, 2010) (Fig. 19).

Figure 19. *Marivagia stellata* (after Galil *et al.*, 2010).

3.2. Methods to monitor and forecast blooms

Jellyfish blooms became a matter of concern in the early 1980s in the whole Mediterranean sea. On that occasion, UNEP launched a programme and considered them a sort of biological pollution, promoting jellyfish research within the framework of the MED POL initiative. The results of these researches were summarized in UNEP (1984; 1991). On that occasion, however, researchers were not much experienced on these topics, and the expertise was more or less improvised. The episodic occurrence of such phenomena, in fact, prevented the building of specific capacities on this topic, since they would have been underutilized for most of the time. Marine scientists focused more on events that were rather predictable, such as phytoplankton blooms or crustacean zooplankton blooms, not to speak about fisheries sciences. The researchers that had previous experience on gelatinous plankton, furthermore, usually dealt with small jellyfish (i.e. the Hydrozoa) that are more stable in presence, albeit they do not have the same impact of the large jellyfish, in case of blooms.

Long term samplings, however, are usually carried out at various parts of the world and the examination of the samples might give an indication of the taking over of gelatinous plankton on the rest of the trophic networks, as highlighted by Brodeur *et al.* (1999) for the Bering Sea and by Licandro *et al.* (2010) for the Northeast Atlantic and the Mediterranean Sea. It is often the case, however, that large gelatinous organisms are considered as a nuisance for plankton sampling, since they clog the nets and spoil the rest of the plankton. Thus, it can happen that sampling sessions are just interrupted, waiting for the bloom to disappear! In this way precious information is usually lost and, furthermore, such behavior by researchers suggests that the lack of records of blooms might not necessarily mean that the blooms did not occur but that they were simply not recorded, even deliberately.

The UNEP-MED POL project suddenly came to an end due to the end of the jellyfish outbreaks of the early 1980s, and no other project on gelatinous plankton has been launched

in the Mediterranean region so far. Only recently, due to the increase of gelatinous plankton outbreaks, activities did start again. The most noticeable one is the already mentioned Jellywatch, launched by CIESM in Italian waters, that was supported by the magazine Focus:
http://www.focus.it/meduse/
In Catalunya, the local government launched Projecte Medusa:
http://www.icm.csic.es/bio/medusa/index.html
At Malta the project is called Spot the Jellyfish:
http://193.188.45.233/jellyfish/index.html
In Ireland it is Ecojel:
http://www.jellyfish.ie/index.asp

The best structured one is the Calalan Projecte Medusa, with relatively high funding that led to the availability of well-equipped laboratories to rear jellyfish under controlled conditions, reconstruct their life cycles, and make experiments on their physiological requirements. In 2011, the European Union's Seventh Framework Programme financed the project "Vectors of change", and one task of the project regards just the investigation of gelatinous plankton blooms at European scale. Other EU projects, namely Perseus and CoCoNet, still within the Seventh Framework Programme, do have the study of gelatinous plankton among their scopes, supporting the concept that was initiated under the CIESM umbrella.

The study of gelatinous macrozooplankton requires completely different techniques from those employed for crustacean plankton (see Purcell, 2009 for a review). In general, the current ways that scientists employ to assess the presence and the abundance of gelatinous macrozooplankton are visual censuses from various means:

1. **Blue diving**: divers stay at a given depth, linked to a rope fixed to a buoy or a boat, and count jellyfish in a fixed period of time (Hamner, 1975). Samples are obtained by using plastic bags.
2. **From boats:** cruises with boats (from small vessels to ferries) follow predefined paths, and jellyfish are counted during these mini-cruises, by identifying them from the boat. Samples can be obtained from small vessels by using buckets or plastic bags.
3. **From airplanes:** jellyfish are visible from small airplanes flying at low heights and large areas can be inspected in a relatively short time (Houghton *et al.*, 2006).
4. **From beaches:** it is possible to see stranded jellyfish by walking along beaches, also near shore gelatinous plankton is visible from the coast.
5. **From submersibles:** this very expensive method is revealing an astonishing abundance and diversity of gelatinous plankters in deep waters. Photographic records and collections of specimens are possible and the chances to find new species are high (Larson e*t al.*, 1992).
6. **By videocameras:** this allows prolonged observation periods from a fixed station (Benfield *et al.*, 1996).

Echosound measures are also possible, even though it is not so easy to identify the species in question (e.g. Brieley *et al.*, 2005).

Radio tracking is being used to follow tagged individuals of large and sturdy species, leading to precious information on their movement patterns (e.g. Gordon and Seymour, 2009). This implies that some individuals are captured, tagged, and released.

Licandro *et al.* (2010) used data from the **Continuous Plankton Recorder** to reconstruct jellyfish abundances in the historical period sampled by the CPR. These automatic methods, however, might not account for blooms of large organisms that are distributed in the water column in a spaced manner, as it is often the case for gelatinous plankters.

Citizen science (Silvertown, 2009) is an alternative method to evaluate the presence and abundance of gelatinous macrozooplankton.

The advantages are:

- public involvement in science
- coverage of large areas almost indefinitely
- no costs
- large amount of data
- easy documentation through pictures
- if a species is recorded, it means that it occurs at a given place and at a given time
- if a species is not recorded when other species are recorded, chances are good that that species was really absent

The disadvantages are:

- great efforts in mass media involvement, requiring good communication skills
- not homogeneous data quality
- unknown research effort: if no species are recorded, it does not mean that they were absent (negative data can be due to absence of observers)
- mostly based on shore observations

The advantages of citizen science approaches are especially evident for gelatinous plankton since people are very easily aware of it, and the species in the Mediterranean Sea are mostly easy to identify with some reliability. Citizen science has been used to monitor jellyfish presence along the Italian coastline (8 500 km) during 2009–2011 and the results were impressive, with thousands of records of all the main species, the records of new species from the Mediterranean or for the Italian fauna. Citizen science is a very good tool to assess the presence of gelatinous plankton, especially along the coast. The CIESM Jellywatch, carried out by F. Boero for three years (2009–2011) was based on a poster (Fig. 20) distributed across Italy through an intense media campaign. The results of the Jellywatch (carried out especially in Italy and Israel) led to the records of new species from the Mediterranean or to a better evaluation of their distribution, with new records from the western basin, showing the expansion of tropical species that thrived already in the Levantine basin.

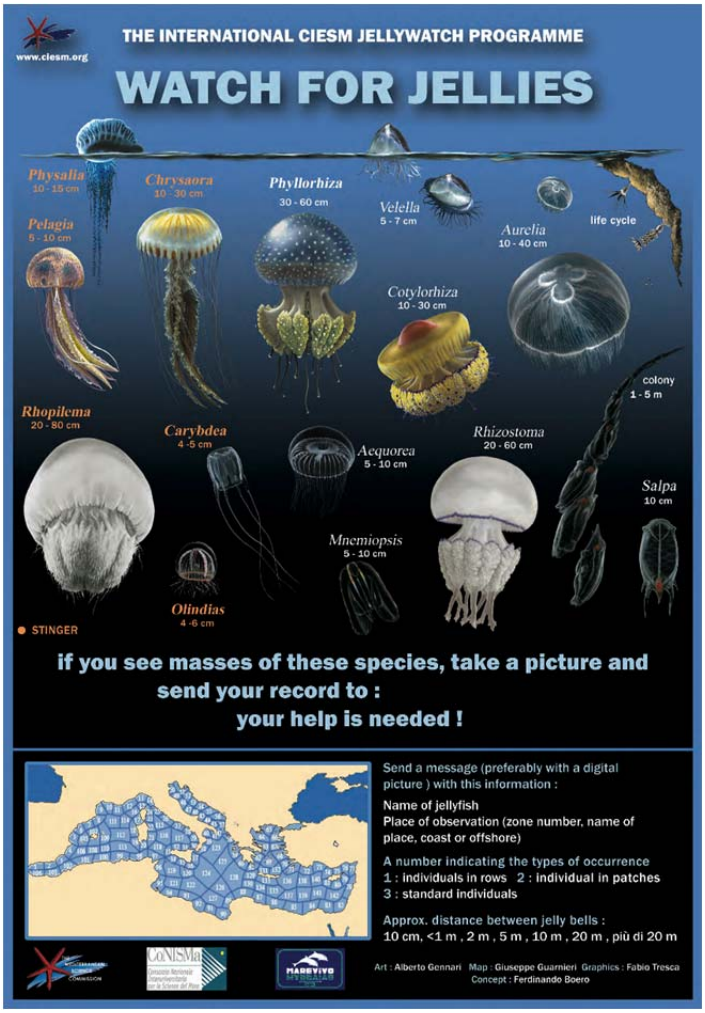


Figure 20. The poster of the CIESM jellywatch (2009 version). (Concept by Ferdinando Boero, art by A. Gennari, graphics by F. Tresca).

The discovery of abundant populations of *Mnemiopsis leydi* both in Israel (Galil *et al.*, 2009) and in Italy (Boero *et al.*, 2009) showed that the alien ctenophore successfully colonized the whole Mediterranean. The result was covered by the media of the whole world, reaching the cover of Time Magazine (Faris, 2009) (Fig. 21). The campaigns of 2010 and 2011 were even more successful due to the involvement of the popular science magazine Focus, that even opened a web page dedicated to the jellywatch, and published Meteomedusa, a weekly report on the presence of jellyfish along the Italian coast, ensuing from the records of the readers. In 2011, a smartphone app of meteomedusa was launched and it was downloaded 26 000 times.

Figure 21. Jellyfish in the Mediterranean hit the cover of Time magazine, on 4th November 2009.

3.3. Further studies on blooms

Citizen science is probably the best method to assess the presence of gelatinous blooms across large spaces, but further studies are of course needed to better understand the processes leading to these phenomena. Research projects on gelatinous plankton typically must involve the assessment of:

1. the genetic status of relevant species to evaluate genetic fluxes across different populations (e.g. Stopar *et al*., 2010) and to ascertain the mechanisms of colonization by NIS;
2. the position of the various species into food webs (what they eat, who eats them);
3. the physical conditions that are more conducive to proliferations;
4. the links between current regimes and jellyfish transport and accumulation;
5. the importance of benthic stages, when present;
6. the existence of natural products that might be used by humans (from food to drugs);
7. the impact on human health;
8. the impact on local economies (from fisheries to tourism).

Jellyfish outbreaks or even simple presences are almost impossible to forecast. During the *Pelagia* years, the abundance of this species gave the impression that it would have dominated the Mediterranean Sea for decades but, eventually, the blooms came to an end in a very abrupt way, being replaced by dinoflagellate blooms, at least in the Adriatic (Fig. 14).

Figure 22. Graphic representation of the presence of jellyfish along the Italian coast in the summer 2010. *Pelagia* dominates the western basin but it is absent from the Adriatic, where *Rhizostoma* and *Carybdea* are dominant (Boero, unpublished).

In the past, these outbreaks have been correlated to El Niño or to the North Atlantic oscillation, and, if this were the case also in this historical period, it might even be possible to attempt some prediction. The abundance of jellyfish in almost all the oceans of the world, and the persistence of the phenomenon, however, suggest that these correlations with periodic events are probably not so important, even if they have been so in the past.

The large scale citizen science study, covering the Adriatic, the Ionian, the Tyrrhenian and the Ligurian Seas, shows that species distribution can be very different in the various basins (Fig. 22), and such distributions are not consistent from year to year. If these events were driven by meteorological drivers (i.e. by the short-term expression of climatic conditions), it is clear that predictions are impossible, since we cannot predict the weather over the medium-long term. However, since the gelatinous plankters are transported by the currents, it might be possible to forecast that a bloom observed at a given part of the basin might be transported to another part of the basin by the prevailing currents.

During the citizen science study, the Meteomedusa web page showed the records of jellyfish along the Italian coast in almost real time. Those maps, of course, did not predict the future, but showed the present and gave an idea of jellyfish presence at a basin scale. The coupling of both current and wind regimes with the distribution of species at a given moment, might lead to give indications of possible future scenarios in the short term.

3.4. Negative (and positive) impacts of jellyfish blooms on human activities

The risks involved in the increase of gelatinous plankton blooms are manifold, since these events affect humans in several ways. In general, jellyfish blooms are perceived negatively, but in some cases they might have positive impacts on human activities. The interactions of gelatinous plankton blooms and human activities of any kind involve:

3.4.1. Fisheries

During blooms, the gelatinous masses are so thick that they can clog fishing nets in no time, impairing their functioning (Fig. 23). The masses can become so heavy to destroy the gear and, in one case, the press reported that, in Japan, a vessel sank due to the weight of the jellyfish present in the net that it was pulling up (Fig. 24).

Figure 23. The nets of Japanese fishermen are often impaired by swarms of *Neopilema nomurai*.

Purcell *et al.* (2007) provide a long list of documented events of jellyfish negative impact on various fishing gear such as beach seine, seine net, set net, trawl, gill and dip nets, prawn trawls. The effects are invariably clogging and or fouling of nets. Besides impairing the functioning of the nets, jellyfish require laborious operation for their removal from gear and subsequent disposal.

The Telegraph

HOME NEWS SPORT FINANCE COMMENT BLOGS CULTURE TRAVEL

Royal Wedding | UK | World | Politics | Obituaries | Earth | Science | Health Nev

Earth News | Environment | Climate Change | Wildlife | Outdoors | Picture Galler

Earth

Japanese fishing trawler sunk by giant jellyfish

A 10-ton fishing boat has been sunk by gigantic jellyfish off eastern Japan.

Nomura's jellyfish: The crew of the fishing boat was thrown into the sea when the vessel capsized, but the three men were rescued by another trawler

By Julian Ryall in Tokyo 7:00AM GMT 02 Nov 2009

Comments

The trawler, the Diasan Shinsho-maru, capsized off Chiba`as its three-man crew was trying to haul in a net containing dozens of huge Nomura's jellyfish.

Figure 24. Press release on the sinking of a fishing vessel by giant jellyfish.

Fisheries can be affected also by indirect damage by predation, since many Cnidaria and Ctenophora species are recorded as predators of fish eggs, larvae, and juveniles. Predation is particularly intense during gelatinous plankton blooms, and fish recruitment can be impaired almost completely, so affecting fisheries due to failure of reproductive processes. Fisheries also suffer from indirect damage due to competition, since the predation of jellyfish on crustacean plankton (the main food source for juvenile fish) reduces the success of recruitment of fish due to shortage of resources for the early stages of their life cycles. The same can be true for herbivorous gelatinous macrozooplankton (i.e. the Thaliacea) which, depleting phytoplankton populations, decreases the food availability for crustacean plankton, presumably reducing its abundance, so affecting the feeding opportunities of its predators, namely the larvae and juveniles of fish.

3.4.2. Public health

In 2010, the first casualty due to the sting of a gelatinous plankter (*Physalia physalis*) occurred in Sardinia (Fig. 25). Besides this extreme event, hundreds of thousands of tourists are stung more or less severely by jellyfish, mainly by *Pelagia noctiluca* and under a lesser extent by other species such as the already mentioned *Physalia physalis*, the cubozoan *Carybdea marsupialis* etc. De Donno *et al.* (2009) made a survey along the Salento Peninsula and estimated the impact of jelly stings by analyzing the statistics of first aid stations on the shore. Purcell *et al.* (2007) made a bibliographic survey on cases of stings at a world level. The figures are appalling, ranging from 15 000 cases in Japan in 1961, to 45 000 cases of treatment along the French riviera in the period 1984–1987, the peak of *Pelagia* years in the Mediterranean. More than 14 000 cases of treatment have been reported for the Mediterranean coast of Spain in August 2006. The reactions are of various kinds, depending on the species and on the sensitivity of the stung individual. The risk is not so high, in terms of extreme events, but it is anyway a nuisance and a sting can spoil a vacation.

Prima vittima di medusa nel Mediterraneo

Gli avvistamenti di Physalia physalis nell'estate 2010

Villaputzu (Cagliari). Una donna di 69 anni esce dall'acqua dopo essere stata punta da una medusa. Sente un grande bruciore, chiede aiuto, perde conoscenza e muore. È la prima vittima di medusa registrata nel Mediterraneo. Si deve parlare di allarme meduse? Secondo gli esperti no, ma occorre prestare attenzione e sapere cosa fare in caso di incontro con queste gelatinose creature. (Focus.it, 26 agosto 2010)

È forse il primo caso di "puntura" mortale di una medusa nel Mediterraneo quello occorso a una donna di 69 anni a Villaputzu, in provincia di Cagliari.

«La *Physalia Physalis*, questo il nome scientifico della medusa responsabile, c'è sempre stata ma ora è più presente» spiega Ferdinando Boero, il biologo marino dell'Università del Salento a capo del progetto di avvistamento "Occhio alla medusa". Ma non si tratta propriamente di una medusa killer, sebbene sia tra le più urticanti presenti nei nostri mari: chi viene colpito raramente vede l'animale, sente solo una fortissima scarica, causata dai filamenti lunghi anche 20 metri della medusa. E non si tratta nemmeno di una vera medusa: è infatti una colonia di forme polipoidi e medusoidi che convivono galleggiando sul pelo dell'acqua.

In alcuni casi però l'incontro con Physalia, detta anche caravella portoghese, può portare al ricovero in ospedale, ma finora nessuno era morto.

Gli avvistamenti di *Physalia Physalis* tratta dal meteo-meduse di Focus. È stata avvistata a Porto Ercole (metà luglio), al largo della Corsica (giugno e agosto), Torre dei corsari (Arbus, a maggio), Funtanamare (Gonnesa, in marzo), al largo dell'isola di San Pietro (marzo), Villaputzu (agosto), al largo di Palermo (luglio), nello stretto di Messina (marzo) e a Malta e Gozo (marzo e giugno rispettivemente)

Figure 25. Report on the first case of lethal sting by a gelatinous plankter in the Mediterranean Sea. It occurred in Sardinia at the end of August 2010. The probable responsible was *Physalia*.

3.4.3. Tourism

Sea-based tourism is one of the main sources of income in the whole Mediterranean Sea. If stinging jellyfish persist, stung tourists can cancel their reservations or reduce the length of their stay, with a reduction of revenues from tourism.

Along some coasts, e.g. France and Spain, anti-jellyfish barriers have been put in operation, so as to defend portions of space just in front of beaches (Fig. 26). The efficacy of these systems is debatable, since the jellyfish can be mashed against the barriers, and be dispersed as a soup of stinging material right into the "protected" area. For especially noxious species (especially *Physalia physalis*, that floats on the sea surface) direct removal has been experimented, both from the sea and from the beaches, where these siphonophores easily strand, while retaining their stinging capabilities. Damages to tourism are regularly reported by the press, but evaluations of the economic damage are apparently not available.

Figure 26. Jellyfish barrier to protect tourists from being stung.

3.4.4. Food market

The impairment of fish recruitment obviously impacts on the food market, due to low availability of fish. Furthermore, as remarked by Orsi Relini *et al.* (2010a), fish that eat medusae such as *Pelagia* are characterized by red perianal areas and nothing is known about the possible changes in their value as food. The negative issues, however, might be counterbalanced by positive ones, since jellyfish are an important fisheries yield in some parts of the world (Morikawa, 1984; Hsieh *et al.*, 2001), due to their high value as delicacy food in some markets (Fig. 27). Kingsford *et al.* (2000), however, lament high variability in catches. Dong *et al.* (2008), in fact, report about stock enhancement of edible fish populations in China. *Rhopilema esculentum* is a popular food in China and is the object of intensive aquaculture practices (You *et al.*, 2007).

Figure 27. A jellyfish dish.

3.4.5. Cooling systems of factories

Power plants and other industries are often placed on the shores of water bodies and the Mediterranean is not an exception. In this way, industries take advantage of marine waters to cool their engines. The intaking pipes convey water into the cooling systems that can be clogged by jellyfish, sucked by the powerful pumps that suck water into the systems (Fig. 28). The presence of jellyfish forces the plant to stop functioning for the time of the cleaning of the pipes. Purcell *et al.* (2007) review reports of power stations affected by jellyfish blooms in Japan, Philippines, China, India, Baltic Sea, Gulf of Oman, Qatar, Arabian Gulf, USA.

Figure 28. Jellyfish clogging the cooling system of a power plant.

3.4.6. Cage aquaculture

Adult fish are usually immune from gelatinous plankton impact, since they can swim faster than jellyfish and escape from them. If closed in a cage, however, fish cannot escape. It happened already, both in the North Sea and in the Mediterranean Sea, that swarms of *Pelagia noctiluca* have exterminated aquacultured specimens. The jellies are brought by the current towards the nets, and are then crushed through them, so that the water into the cages becomes a soup of stinging tentacles and manubria that enter the gills of the fish and eventually kill them. Baxter *et al.* (2011) studied the interaction of salmon with *Aurelia aurita* which, indeed, caused gill damage to the fish. Purcell *et al.* (2007) listed impacts on aquaculture, with cases of damage to bivalves, prawns, shrimp, salmons, trout, and fish in general.

3.4.7. Positive impact of gelatinous plankton

As already stressed, carnivorous gelatinous plankters presumably act as selective agents, removing weak individuals from the populations of the species they prey upon. Furthermore, since they prey on the most abundant food items, they reduce the numerousness of potential monopolizers, acting as keystone predators.

Some large jellyfish, such as *Rhizostoma pulmo* and *Cotylorhiza tuberculata* are often accompanied by juvenile fish of various species. This aspect is worth further investigation since these species might prove fish recruitment enhancers by providing benefits to fish juveniles in terms of protection and even of feeding opportunities.

Another positive impact of the presence of jellyfish might be linked to tourism (Dawson *et al.*, 2001). Jellyfish, furthermore, are the main attraction in most marine aquaria since their beauty and elegance fascinate many people. Many artifacts are now inspired by jellyfish and there is a tendency to recognize them as beautiful animals. This tendency is not to be under evaluated. In the nineteenth century, and in the first half of the last century, whales were seen as monsters, as testified by Melville's masterpiece "Moby Dick". Nowadays, those who kill whales are seen as criminals, and whale watching is increasingly widespread, being a source of income at places where whales are regularly present. Of course, it is not advisable to enter in the water if there is a bloom of *Pelagia* or even if there are just a few specimens of *Physalia*, but the other jellyfish of the Mediterranean and the Black Sea are less stinging than these two dangerous stingers. Jellyfish watching (Fig. 29) might become a tourist attraction, as it is at Palau (Dawson *et al*., 2001).

Figure 29. The author playing with *Aurelia aurita* in the Varano Lake, S. Italy (picture by Roberto Rinaldi, taken from the TV broadcast Linea Blu).

The information assembled and organized during the Jellywatch exercise of citizen science (see above) can be used also to make people aware of the properties of the various species, giving the opportunity to enjoy encounters with beautiful wild animals that are also among the very few ones that do not escape while we approach. Furthermore, cnidarians (especially sea anemones) also already used as food in some parts of the Mediterranean. Jellyfish are a delicacy in several oriental cuisines where they have a high commercial price. Jellyfish, furthermore, are the animals with the highest proportion of extracellular matrix in their bodies (the jelly) and the biotechnological opportunities that they offer are still largely unexplored. Piraino *et al.* (1996) carefully described the ontogeny reversal in the species *Turritopsis dohrni*, a rather exceptional phenomenon of cell transdifferentiation and redifferentiation leading to the metamorphosis of a jellyfish into a polyp (the preceding stage in the life cycle). Further research showed that this possibility is more widespread than previously thought (Piraino *et al.*, 2004), with promising perspectives in the fields of aging and even in oncological research.

3.4.8. The species

The main species of gelatinous plankters occurring in the Mediterranean and Black Seas are figured in the CIESM Jellywatch poster, whose concepts have been developed by Ferdinando Boero with the aid of the pictorial artist Alberto Gennari and the graphic artist Fabio Tresca (Fig. 30). In the Appendix to this report, the species of major concern are listed in alphabetical order, with information about their main features.

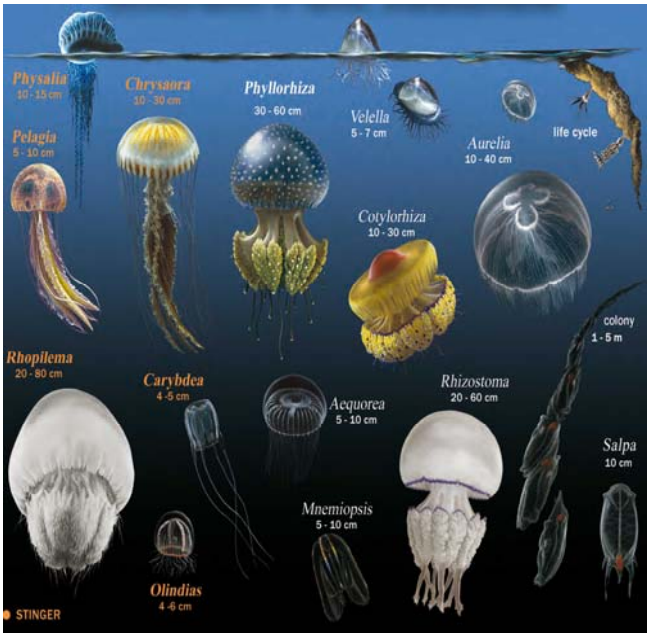


Figure 30. The main species of gelatinous plankton in the Mediterranean and Black Seas, from the CIESM Jellywatch poster.

4. DEVELOPING A SCIENTIFIC FRAMEWORK IN SUPPORT OF MANAGEMENT INSTRUMENTS TOWARDS ELIMINATING OR MITIGATING THE EFFECT OF BLOOMS

4.1. Human impacts and ecosystem functioning

Man removes the fish in an industrial way, with more and more sophisticated technologies. It is worthwhile considering that, in the ocean, we are still hunters and gatherers, and we draw resources from natural populations, as we did in pre-agriculture periods also in terrestrial systems. The natural populations of the species we hunted on, however, could not cope with our pressure when we became too efficient as hunters, and we had to shift to agriculture, due to depletion of natural resources ensuing overexploitation. Marine systems, due to their faster turnovers, can support a stronger pressure than terrestrial ones, but they too have their limits in supporting us. Overfishing means that we are fishing at a faster rate than the turnover rate of the populations we predate upon. We have seen that fish, if not stressed, can cope well with the competition of gelatinous macrozooplankton, being overwhelmed by it just episodically and being able to recover at a fast pace. But, in the last 50 years, we have overexploited most of the oceans (Jackson *et al.*, 2001). After having depleted the populations of large fish, we are now "fishing down marine food webs" as evocated by Pauly *et al.* (1998) (Fig. 8). This has released gelatinous zooplankton from fish competition, and the blooms of gelatinous plankton, once episodic, are becoming the rule (Mills, 1995; 2000). Besides removing the fish, so leaving space to the jellyfish, we are introducing species into ecosystems that did not coevolve with the resident species (see Purcell *et al*., 2007, for a list of introduced gelatinous predators). If these aliens are voracious carnivores, they might disrupt the "normal" functioning of ecosystems, channeling towards their own populations the resources that should go to the fish. If we introduce one of these species in a system that is already stressed by overfishing, the impact will be even greater.

4.2. Multiple stressors

In experimental ecology, impacts are usually evaluated in isolation. In the real life, however, several impacts (each having almost negligible effect) can sum to each other so as to impair the impacted system. If the impact of fisheries (on adult fish) is not associated to the impact of predation and competition on early stages in fish life cycles, it might happen that a fisheries impact that is predicted as bearable by the exploited populations can become unbearable when summed to the impact of gelatinous plankton predation and competition. Under these circumstances, gelatinous plankton impacts might be the proverbial straw that broke the camel's back. The logic of the ecosystem approach should be just this: it is not sufficient to analyze the impact of fisheries on single species, as if there were no other predators of those species out there. Humans surely are the most efficient predators of adult fish. So efficient that it is not necessary to evaluate the predation pressure of other predator species. But the case of *Mnemiopsis* shows that gelatinous predators of fish eggs and larvae can have a high impact on fish populations. So, the first step to apply the ecosystem approach to fisheries should be to consider fish as life cycles and evaluate potential impacts on the whole array of life stages that defines each species. If this is done, then the importance of gelatinous zooplankton becomes immediately apparent, both as a competitor and as a predator of fish.

4.3. The ecosystem approach

The highly advocated ecosystem approach requires that it is tenuous to focus on single ecosystem nodes, disregarding the rest. The appreciation of ecological links is crucial for the management of the resources. If something "goes wrong" and the resources we expect to extract from the ecosystems (e.g. the fish) are not produced anymore, we must single out the processes that led to a different functioning of the ecosystems. The reasons for such malfunction (from our point of view) are often ascribed to direct human pressure, and usually the blame falls on overfishing. But they might also be the result of different ways of ecosystem functioning that are less directly dependent on our pressures. Stability is nonsense: in nature nothing remains the same. Boero (1994) distinguished between normal fluctuations, such as the seasonal ones, leading to recurrent patterns of biodiversity expression, and variations, i.e. changes in biodiversity expression that might be labeled as regime shifts, deviations from the norm of fluctuations. Furthermore, Boero (1996) analyzed the importance of episodic events in determining the changes we observe when dealing with the history of a system. Jellyfish blooms have been "normal" episodes in the history of marine ecosystems, but now they seem to have become the rule (Mills, 2001). Boero *et al.* (2008) reached the conclusion that "irregularities rule the world, sometimes", since history is governed by contingencies. History, in fact, would not exist if natural systems were governed by rules that constrain them into a restricted range of possible developments. Contingencies (such as jellyfish blooms) lead to changes in the systems, and history is just this: deviation from the norms dictated by constraints (Boero *et al.*, 2004). As it often happens in complex systems (and ecosystems are the most complex systems of the planet) the causes for a pattern might be multiple, with a blend of different pressures. Most analyses are correlational, so we might find a correlation between one activity (e.g. fishing) and an ecosystem response (e.g. the decline of fish), but this correlation might not be the only cause of the observed pattern. Correlation does not imply causation, or might hide multiple causality. With the ecosystem approach we should disentangle the possible causes of the observed patterns, so as to enforce proper management, based on a good knowledge of the functioning of the ecosystems that we want to manage, of course considering the history of the system we want to manage. If fisheries science focuses just on fish, the results of management might not be as good as expected. The problems in resource extraction from natural fish populations might be due also to mismanagement due to lack of knowledge about the functioning of the system that sustains the resources that we are directly interested in. The ecosystem approach to fisheries, thus, must invoke the study of the whole ecosystem, because the fish are just an epiphenomenon that cannot persist in isolation from the rest of the ecosystem. Management, thus, cannot be divorced from understanding patterns and processes.

4.4. Recommendations for management

The management of natural events is based on several steps:

1. Identification of the phenomenon ensuing from perceived symptoms (in this case: jellyfish blooms are increasing).
2. Identification of the causes (in this case the causes are multiple and are not the same for all species, at all places).
3. Alleviation of the symptoms (but this does not solve the problem).
4. Removal of the causes.
5. If the causes are difficult to remove, adaptation to the new situation is the only solution.

The drivers of jellyfish blooms, as described in Section 3 of this report, are many and concur to determine a situation that, contrary to the past, seems persistent and of global scale. It is obvious that "local" management can only alleviate the symptoms but will not remove the causes.

In the past, jellyfish blooms have been studied episodically, since their occurrence was episodic, and most of the times the studies started after the onset of the blooms, and came to an end when the phenomena became less evident. Obviously, this research strategy is not conducive to a good understanding of these phenomena. So, the first strategy to manage jellyfish blooms is to incorporate jellyfish research into fisheries research, and treat the jellyfish just as the fish are treated, with monitoring of their diversity, life cycles, fluctuations etc. Early warning of the onset of blooms might lead to better understanding of the triggering conditions that, eventually, might be artificially modified, if possible, so as to impair the population boom.

Richardson *et al.* (2009) proposed a series of management measures to cope with jellyfish blooms. They listed in a table the management responses, the research needs, the benefits and the risks and issues. Their contributions are as follows:

- **Develop jellyfish products for food and medicine**

In other words: *If you cannot fight them... eat them*. Some jellyfish species are a food source in some countries (e.g. China) and the development of conservation and packaging practices to sell them where they are appreciated might be a wise strategy, adapting the fishing fleets and the commercial network behind them to take advantage of sudden abundances of this product-to-be. Jellyfish are widely diverse and some species might contain chemicals that are conducive to the development of new drugs and other biotechnological products based on active molecules. Jellyfish are the oldest among the living animals and contain the premises of the evolutionary "innovations" that characterize the whole metazoan evolution (Boero and Piraino, 2010), their basic features might hide important potentials, as suggested by the discovery of the so-called "immortal jellyfish" (Piraino *et al.*, 1996), a species with promising features in the field of aging prevention.

- **Use cutting nets to destroy the jellyfish**

This practice is used to physically destroy jellyfish that, transported by the currents, are pushed against these nets and are destroyed then. This might be a solution to defend power plants, since the fragments transported into the cooling systems might not clog them (but this is far from being certain). The pieces of jellyfish might lead to regeneration of new jellyfish through asexual reproduction (Boero *et al*., 2002). Furthermore, jellyfish fragments retain their stinging properties and can become even more lethal for, for instance, fish kept in aquaculture cages.

- **Destroy the polyps**

Many species do have polyp stages (Fig. 1) that are the real "seeds" where blooms come from. Also polyps, however, do have very high potentials for asexual reproduction from fragments, and attempts at destroying them might even exacerbate the phenomena. The use of chemicals and other practices can be problematic (Sandifer *et al.*, 1974) and, furthermore, antifouling paints contain chemicals that cause serious problems to biodiversity in general and cannot be used on a wide scale. The great abundance of the stinging cubozoan *Carybdea marsupialis* along the Adriatic coast of Italy (Boero, unpublished observation) is probably linked to the hundreds of kilometres of coastal defenses that have been established to prevent beach

erosion. The availability of hard bottom habitats in a region previously dominated by soft bottoms might have favored the establishment of the species that, in fact, was unknown from the Adriatic sea before 1986 (Boero and Minelli, 1986). To clean 500 km of coastal defenses is surely unfeasible. Di Camillo *et al.* (2010) however, reported that ship wrecks in the Adriatic are the ideal substrate for the polyps of *Aurelia aurita* and estimated that the extensive blooms of this species in their study area might well be sustained by just one wreck. They did not find the polyps growing on any other substrate. In this case, of course, the removal of the wreck(s) might remove the cause for the blooms of this species. The disappearance of species with polyps, however, might pave the way for species that do not have a polyp stage, such as the mauve stinger *Pelagia noctiluca*. The study of jellyfish presence in Italian waters in 2009-2011 (Boero, unpublished), for instance, showed that *Pelagia* was almost absent from the Adriatic Sea, whereas it was very abundant in the western coasts of the Italian peninsula. Instead of *Pelagia*, *Aurelia* was most abundant in the Adriatic, together with *Carybdea*. Both species are polyp formers, whereas *Pelagia* is not. Their presence might have outcompeted *Pelagia* which, when these species are absent or less abundant, might find less restrictions to the numerical increase of its populations.

- **Biocontrol agents**

The use of chemicals to kill jellyfish or polyps is not advisable, since active substances (which are anyway still not developed) will almost surely induce resistance in the target species, while impacting even more on their potential predators. The control of noxious species such as *Mnemiopsis leidyi* by focused predators such as the ctenophore *Beroe ovata* might lead to consider the introduction of predators into systems heavily invaded by some gelatinous plankter. These practices have been used on land, but with very debatable success. In several cases, in fact, the supposed controller became a pest itself once it destroyed the target species! It seems, as shown in a previous section of this document, that medusiphagous species (fishes and turtles) are increasing, due to greater food availability. The natural systems, thus, are answering to the fish-jellyfish regime shift and might provide a buffer to it without any need of intervention from our side. Of course, medusiphagous species should be somehow protected, so that they can continue to play their role. Many of them, however, are already protected (marine turtles) or do have little commercial value (the sun fish).

- **Prevent any activity that might promote the spread of gelatinous plankters**

Many species became a nuisance when they were introduced into basins with communities that had not coevolved with their ecological traits. The case of *Mnemiopsis* is the most famous one. CIESM (2002) reviewed the ways non-indigenous species can be spread by ships, both as fouling on their hulls, or as resting stages. Policies have been designed to prevent the spread of NIS through ships, and they must be extended also to leisure boats. Jellyfish can be transported as polyps growing on animals that are shipped around the world, such as oysters (Edwards, 1976), or they can be spread through aquarium trades (Bolton *et al*., 2006). Obviously these activities must be carefully controlled to prevent the spread of potentially noxious species.

Other ways to prevent jellyfish risks, especially for fisheries activities might be:

- **Design nets that are not clogged by gelatinous plankton**

The efficacy of such nets is probably very debatable, since it is very difficult to sort jellyfish from fish.

• **Employ selective fishing gear**
The use of hooks is probably the most effective way to avoid jellyfish interference with fisheries activities. If jellyfish are around, it is advisable to shift from nets to hooks.

• **Set early warning systems**
The identification of swarms, and the prediction of their movements based on knowledge of oceanographic patterns, can lead to adaptive measures to cope with the presence of gelatinous plankton. This is extremely important for cage aquaculture, with the employment of protective barriers against jellyfish. Also fisheries activities might be regulated when particularly intense events do occur.

The management measures described above are aimed at mitigating local effects of gelatinous plankton blooms, and might be useful to cope with them but, surely, not to avoid their occurrence, especially for indigenous species, whereas the control of artificial transport is itself a definitive measure. The prevention of these phenomena must act directly on their causes that, we have seen, are manifold. Richardson *et al.* (2009) suggest to reduce:

- **Eutrophication**
- **Overfishing**
- **Global warming**

These obvious measures would undoubtedly improve environmental quality at large and might, thus, also reduce the present prevalence of jellyfish. The mitigation of these impacts cannot be obtained by single-country initiatives and its enforcement is far from being universally agreed upon, as many world summits showed, since the Rio Convention in 1992. Aquaculture, furthermore, is widely proposed as a valid alternative to fisheries to satisfy the demand of fish by the food market. In fact, it is suggested that the development of aquaculture will release natural populations from the pressures of overfishing. As remarked by various authors (see Boero, 2009), however, aquaculture species are invariably carnivores (especially in the Mediterranean area) and they are fed with pellets that derive from smaller fish taken from natural populations. After having taken the larger fish, thus, we are fishing down marine food webs (Pauly *et al.*, 1998) to feed the fish that we rear. Cage aquaculture, furthermore, enhances eutrophication (Pusceddu *et al.*, 2007), so exacerbating both nutrient enrichment and overfishing.

4.5. Conclusion

The possibility of enjoying the goods and services offered by natural biodiversity depends on the rate we utilize them. The natural resources are renewable but the rate we consume them cannot be higher than the rate they renew themselves. One of the paradigms of current economy is growth. Production, income, and consumption must grow, in order to have a healthy economy. The expectation, thus, is infinite growth. Obviously this is not possible, since our planet is finite, and the biomass ecosystems can produce is limited. The growth of human populations is exerting an unbearable pressure on natural systems that, obviously, are on the edge of collapse. The scientific community is warning about this problem since the times of Malthus and Darwin, but it is apparently unheard by decision-makers, economists having much greater influence than ecologists. However, if the principles we invented to regulate our activities (economy, with its infinite growth) are in conflict with natural principles (ecology, with the finiteness of natural systems), we can only expect that we will be defeated.
Jellyfish are just a symptom of this situation, another warning that Nature is giving us!

5. INVENTORY OF EXISTING BIBLIOGRAPHY ON THIS ISSUE AND LIST OF RELEVANT PUBLICATIONS ANNEXED TO THE REPORT

Abed-Navandi D. & Kikinger R. 2007. *First record of the tropical* Scyphomedusa Phyllorhiza punctata *Lendenfeld, 1884 (Cnidaria: Rhizostomeae) in the Central Mediterranean Sea.* Aquatic Invasions, 2(4): 391–394

Arai M.N. 1997. *A Functional Biology of the Scyphozoa*. Chapman & Hall, London, 316 pp.

Arai M.N. 2005. Predation on pelagic coelenterates: a review. *Journal of the Marine Biological Association of the United Kingdom*, 85:5 23–536

Ates R.M.L. 1988. *Medusivorous fishes, a review*. Zoologisches Mededelingen, 62: 29–42

Banaszak A.T., Iglesias Prieto R. & Trench R.K. 1993. *Scrippsiella velellae*, new species (Peridiniales) and *Gloeodinium viscum*, new species (Phytodiniales) dinoflagellate symbionts of two hydrozoans (Cnidaria). J*ournal of Phycology,* 29(4): 517–528

Bat L., Satilmis H.H., Birinci-Ozdemir Z., Sahin F. & Ustun F. 2009. Distribution and population dynamics of *Aurelia aurita* (Cnidaria; Scyphozoa) in the southern Black Sea. *North-Western Journal of Zoology,* 5(2): 225–241

Baxter E.J., Sturt M.M., Ruane N.M., Doyle T.K., McAllen R., Harman L. & Rodger H.D. 2011. Gill damage to Atlantic salmon (*Salmon salar*) caused by the common jellyfish (*Aurelia aurita*) under experimental challenge. *PLoS ONE*, 6(4) e18529. doi:10.1371/journal.pone.0018529

Bayer F. 1963. Observations on pelagic molluscs associated with the siphonophores *Velella* and *Physalia*. *Bulletin of Marine Science*, 13(3): 454–466

Bayha K.M. & Graham W.M. 2009. A new Taqman PCR-based method for the detection and identification of scyphozoan jellyfish polyps. *Hydrobiologia*, 616: 217–228

Benfield M.C., Davis C.S., Wiebe P.H., Gallager S.M., Lough R.G. & Copley N.J. 1996. Video plankton recorder estimates of copepod, pteropod and larvacean distribution from a stratified region of Georges Bank with comparative measures from a MOCNESS sampler. *Deep-Sea Research II*, 43: 1925–1946

Boero F. 1994. Fluctuations and variations in coastal marine environments. *P.S.Z.N.I: Marine Ecology*, 15(1): 3–25

Boero F. 1996. Episodic events: their relevance in ecology and evolution. *P.S.Z.N.I: Marine Ecology*, 17: 237–250

Boero F. 2001. Adriatic ecological history: a link between jellyfish outbreaks, red tides, mass mortalities, overfishing, mucilages, and thaliacean plankton? In: *Gelatinous Zooplankton outbreaks: theory and practice*. CIESM Workshop Series, 14: 55–57

Boero F. 2009. Recent innovations in marine biology. *Marine Ecology - An evolutionary perspective,* 30 (suppl. 1): 1–12

Boero F. 2011. New species are welcome, but...what about the old ones? *Italian Journal of Zoology*, 78(1): 1–2

Boero F., Belmonte G., Fanelli G., Piraino S. & Rubino F. 1996. The continuity of living matter and the discontinuities of its constituents: do plankton and benthos really exist? *Trends in Ecology and Evolution*, 11(4): 177–180

Boero F., Belmonte G., Bussotti S., Fanelli G., Fraschetti S., Giangrande A., Gravili C., Guidetti P., Pati A., Piraino S., Rubino F., Saracino O., Schmich J., Terlizzi A. & Geraci S. 2004. From biodiversity and ecosystem functioning to the roots of ecological complexity. *Ecological Complexity*, 2: 101–109

Boero F. & Bonsdorff E. 2007. A conceptual framework for marine biodiversity and ecosystem functioning. *Marine Ecology - An evolutionary perspective*, 28 (Suppl. 1): 134–145

Boero F., Bouillon J., Gravili C., Miglietta M.P., Parsons T. & Piraino S. 2008. Gelatinous plankton: irregularities rule the world (sometimes). *Marine Ecology Progress Series*, 356: 299–310

Boero F., Bouillon J., Piraino S. & Schmid V. 2002. Asexual reproduction in the Hydrozoa (Cnidaria). In: Hughes R.N., ed. *Reproductive Biology of Invertebrates XI: Progress in Asexual Reproduction*, pp. 141-158, Oxford & IBH Publishing Co, New Delhi

Boero F. & Piraino S. 2010. From Cnidaria to "Higher Metazoa" in one step. In: De Salle R. & Schierwater B., eds. *Key Transitions in Animal Evolution,* pp. 162-174. CRC Press, Boca Raton

Boero F., Putti M., Trainito E., Prontera E. & Piraino S. 2009. First records of *Mnemiopsis leidyi* (Ctenophora) from the Ligurian, Thyrrhenian and Ionian Seas (western Mediterranean) and first record of *Phyllorhiza punctata* (Cnidaria) from the western Mediterranean. *Aquatic Invasions,* 4(4): 675–680

Boero F. & Minelli A. 1986. First record of *Carybdea marsupialis* (L., 1758) (Cnidaria, Cubozoa) from the Adriatic Sea. *Bollettino del Museo civico di Storia naturale di Venezia*, 35: 179–180

Bone Q. 1998. *The biology of pelagic tunicates*. Oxford University Press, Oxford.

Bouillon J., Medel M.D., Pagès F., Gili J.M., Boero F. & Gravili C. 2004. Fauna of the Mediterranean Hydrozoa. *Scientia Marina*, 68 Suppl. 2: 1–449

Bolton T.F. & Graham W.M. 2006. Jellyfish on the rocks: bioinvasion threat of the internationsl trade in aquarium live rock. *Bioinvasions*, 8(4): 651–653

Bouillon J., Gravili C., Pagés F., Gili J.M. & Boero F. 2006. An introduction to Hydrozoa. *Mémoires du Muséum national d'Histoire naturelle*, 194: 1–591

Brierley A.S., Boyer D.C., Axelsen B.E., Lynam C.P., Sparks C.A.J., Boyer H.J., Gibbons M.J. 2005. Towards the acoustic estimation of jellyfish abundance. *Marine Ecology Progress Series*, 295: 105–111

Brodeur R.D., Mills C.E., Overland J.E., Walters G.E. & Schumacher J.D. 1999. Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. *Fisheries oceanography*, 8(4): 296–306

Cartwright P., Halgedahl S.L., Hendricks J.R., Jarrard R.D., Marques A.C., Collins A.G. & Lieberman B. 2007. Exceptionally Preserved Jellyfishes from the Middle Cambrian. *PLoS ONE,* 2(10): e1121 doi:10.1371/journal.pone.0001121

CIESM. 2001. Gelatinous zooplankton outbreaks: theory and practice. *CIESM Workshop Series 14*, 112 pp., Monaco

CIESM. 2001. Alien marine organisms introduced by ships in the Mediterranean and Black Seas. *CIESM Workshop Series*, 20, 136 pp, Monaco

Cole G.J. 1952. *Pelagia* in Manx waters. *Nature*, 170: 587

Cushing D.H. 1990. Plankton production and year-class strength in fish populations - an update of the match mismatch hypothesis. *Advances in Marine Biology*, 26: 249–293

Daskalov G.M., Grishin A.N., Rodionov S. & Mihneva V. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences of the United States of America*, 104(25): 10518–10523.

Dawson M.N., Martin L.E. & Penland L.K. 2001. Jellyfish swarms, tourists, and the Christ-child. *Hydrobiologia*, 451: 131–144

Dawson M.N. & Jacobs D.K. 2001. Molecular evidence for cryptic species of *Aurelia aurita* (Cnidaria, Scyphozoa). *Biological Bulletin*, 200: 92–96

De Donno A., Idolo A., Bagordo F. 2009. Epidemiology of jellyfish stings reported to summer health centres in the Salento peninsula (Italy). *Contact Dermatitis,* 60: 330–335

Di Camillo C.G., Betti F., Bo M., Martinelli M., Puce S. & Bavestrello G. 2010. Contribution to the understanding of seasonal cycle of *Aurelia aurita* (Cnidaria: Scyphozoa) scyphopolyps in the northern Adriatic Sea. *Journal of the Marine Biological Association of the United Kingdom*, 90(6): 1105–1110

Dong J., Jiang L., Tan K., Liu H., Purcell J.E., Li P. & Ye C. 2009. Stock enhancement of the edible jellyfish (*Rhopilema esculentum* Kishinouye) in Liaodong Bay, China: a review. *Hydrobiologia*, 616: 113–118

Dulcic J., Beg Paklar G., Grbec B., Morovic M., Matic F. & Lipej L. 2007. On the occurrence of the ocean sunfish *Mola mola* and slender sunfish *Ranzania laevis* in the Adriatic Sea. *Journal of the Marine Biological Association of the United Kingdom*, 87: 789–796

Edwards C. 1976. A study in erratic distribution: the occurrence of the medusa *Gonionemus* in relation to the distribution of oysters. *Advances in Marine Biology*, 14: 251–284

Faris S. 2009. A gelatinous invasion. *Time*, November 2: 47–48

Finenko G.A., Romanova Z.A. & Abolmasova G.I. 2000. The ctenophore *Beroe ovata* is a new invader to the Black Sea (in Russian). *Ecol Morya*, 50: 19–22

Forsskal P. 1775. Medusae. In: *Descriptiones Animalium, avium, amphibiorum, piscium, insectorum, vermium. Postmortem auctoris edidit Carsten Niebuhr*. Hauniae, Vol. 1, pp. 106–111

Fraschetti S., Giangrande A., Terlizzi A. & Boero F. 2003. Pre- and post-settlement events in hard- and soft-bottom community dynamics. *Oceanologica Acta*, 25(6): 285–296

Fuentes V.L., Dror L.A., Bayha K.M., Atienza D., Edelist D., Bordehore C., Gili J.M. & Purcell J.E. 2010. Blooms of the invasive ctenophore, *Mnemiopsis leidyi*, span the Mediterranean Sea in 2009. *Hydrobiologia*, 645: 23–37

Galil B.S., Spanier E. & Ferguson W.W. 1990. The Scyphomedusae of the Mediterranean coast of Israel, including two Lessepsian migrants new to the Mediterranean. *Zoologisches Mededelingen*, 64(7): 95–105

Galil B., Gershwin L.A., Douek J. & Rinkevich B. 2010. *Marivagia stellata* gen. et sp. nov. (Scyphozoa: Rhizostomeae: Cepheidae), another alien jellyfish from the Mediterranean coast of Israel. *Aquatic Invasions*, 5(4): 331–340

Galil B., Kress N. & Shiganova T. 2009. First record of *Mnemiopsis leidyi* A. Agassiz, 1865 (Ctenophora; Lobata; Mnemiidae) off the Mediterranean coast of Israel. *Aquatic Invasions*, 4: 356–362

Garcia J.R. 1990. Population dynamics and production of *Phyllorhiza punctata* (Cnidaria: Scyphozoa) in Laguna Joyuda, Puerto Rico. *Marine Ecology Progress Series*, 64: 243–251

Garibaldi F., Orsi Relini L. & Relini G. 2010. Medusivorous fishes of the Ligurian Sea 2. The specialist, *Schedophilus medusophagus* Cocco, 1939. *Rapports CIESM*, 39:525

Gordon M.R. & Seymour J.E. 2009. Quantifying movement of the tropical Australian cubozoan *Chironex fleckeri* using acoustic telemetry. *Hydrobiologia*, 616: 87–97

Gould P., Ostrom P. & Walker W. 1997. Food of flesh footed shearwaters *Puffinus carnipes* associated with high-seas driftnets in the Central North Pacific Ocean. *Emu,* 97(2): 168–173

Goy J., Morand P. & Etienne M. 1989. Long-term fluctuations of *Pelagia noctiluca* (Cnidaria, Scyphomedusa) in the western Mediterranean Sea. Prediction by climatic variables. *Deep-Sea research*, 36(2): 269–279

Haddad M.A. & Nogueira M. 2006. Reappearance and seasonality of *Phyllorhiza punctata* von Lendenfeld (Cnidaria, Scyphozoa, Rhizostomeae) medusae in southern Brazil. *Revista Brasileira de Zoologia*, 23(3): 824–831

Hamner W.M. 1975. Underwater observations of blue-water plankton: logistics, techniques, and safety procedures for divers at sea. *Limnology and Oceanography*, 20(6): 1045–1051

Harbison G.R., Madin L.P. & Swanberg N.R. 1978. On the natural history and distribution of oceanic ctenophores. *Deep-Sea Research*, 25: 233–256

Harbison G.R. & McAlister V.L. 1979. The filter-feeding rates and particle retention efficiencies of three species of *Cyclosalpa* (Tunicata, Thaliacea). *Limonology and Oceanography*, 24(5): 875–892

Herut B., Galil B. 2000. The coast of Israel, southeast Mediterranean, in: Sheppard C.R.C., ed. *Seas at the Millennium: an environmental evaluation*. Volume 1. Regional chapters: Europe, The Americas and West Africa. pp. 253–265

Houghton J.D.R., Doyle T.K., Davenport J. & Hays G.C. 2006. Developing a simple, rapid method for identifying and monitoring jellyfish aggregations from the air. *Marine Ecology Progress Series*, 314: 159–170

Hsieh Y.-H.P., Leong F.-M. & Rudloe J. 2001. Jellyfish as food. *Hydrobiologia*, 451: 11–17

Jackson J.B.C., Kirby M.X., Berger W.H., Bjorndal K.A., Botsford L.W., Bourque B.J., Bradbury R., Cooke R., Erlandson J., Estes J.A., Hughes T.P., Kidwell S., Lange C.B., Lenihan H.S., Pandolfi J.M., Peterson C.H., Steneck R.S., Tegner M.J. & Warner. R. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293: 629–638

Jones T.T., Hastings M.D., Bostrom B.L., Pauly D. & Jones D.R. 2011. Growth of captive leatherback turtles, *Dermochelys coriacea*, with inferences on growth in the wild: implications for population decline and recovery. *Journal of Experimental Marine Biology and Ecology*, 399: 84–92

Kemp P.F. 1986. Deposition of organic matter on a high-energy sand beach by a mass stranding of the cnidarian *Velella velella* (L.). *Estuarine and Coastal Shelf Science*, 23(4): 575–579

Kideys A.E. 1994. Recent dramatic changes in the Black Sea ecosystem: The reason for the sharp decrease in Turkish anchovy fisheries. *Journal of Marine Systems*, 5:171–181

Kikinger R. 1992. *Cotylorhiza tuberculata* (Cnidaria: Scyphozoa) – Life history of a stationary population. *PSZN I: Marine Ecology*, 13: 333–362

Kingsford M.J., Pitt K.A. & Gillanders B.M. 2000. Management of jellyfish fisheries, with special reference to the order Rhizostomeae. *Oceanography and Marine Biology*, 38: 85–156

Kogovsek T., Bogunovic B. & Malej A. 2010. Recurrence of bloom-forming scyphomedusae: wavelet analysis of a 200-year time series. *Hydrobiologia*, 645: 81–96

Kokelj F. & Plozzer C. 2002. Irritant contact dermatitis from the jellyfish *Rhizostoma pulmo*. *Contact dermatitis*, 46: 179–180

Kremer P. 1977. Respiration and excretion by the ctenophore *Mnemiopsis leidyi*. *Marine Biology*, 44: 43–50

Kremer P. 1994. Patterns of abundance for *Mnemiopsis*. US coastal waters: a comparative overview. *ICES Journal of Marine Science*, 51: 347–354

Larson R.J. 1987. First report of the little-known scyphomedusa *Drymonema dalmatinum* in the Caribbean Sea, with notes on its biology. *Biological Oceanography*, 4: 447–454

Larson R.J. 1980. The medusa of *Velella velella* (Linnaeus, 1758) (Hydrozoa, Chondrophorae). *Journal of Plankton Research*, 2(3): 183–186

Larson R.J. 1988. Feeding and functional morphology of the lobate ctenophore *Mnemiopsis mccradyi*. *Estuarine Coastal and Shelf Science,* 27(5): 495–502

Larson R.J., Matsumoto G.I., Madin L.P. & Lewis L.M. 1992. Deep-sea benthic and benthopelagic medusae, recent observations from submersibles and a remotely operated vehicle. *Bulletin of Marine Science*, 51: 277–286

Larson R.J., Mills C.E. & Harbison G.R. 1989. In situ foraging and feeding behavior of Narcomedusae (Cnidaria: Hydrozoa). *Journal of the Marine Biological Association*, United Kingdom, 69(4): 785–794

Licandro P., Conway D.P.V., Daly Yahia M.N., Fernandez de Puelles M.L., Gasparini S., Hecqu J.H., Tranter P. & Kirby R.R. 2010. A blooming jellyfish in the northeast Atlantic and Mediterranean. *Biology Letters*, 6: 688–691

Lotan A., Ben-Hillel R. & Loya Y. 1992. Life cycle of *Rhopilema nomadica* a new immigrant scyphomedusan in the Mediterranean. *Marine Biology*, 112(2): 237–242

Lotan A., Fine M. & Ben-Hillel R. 1994. Synchronization of the life cycle and dispersal pattern of the tropical invader scyphomedusan *Rhopilema nomadica* is temperature dependent. *Marine Ecology Progress Series*, 109: 59–65

Lucas C.H. 2001. Reproduction and life history strategies of the common jellyfish *Aurelia aurita*, in relation to its ambient environment. *Hydrobiologia*, 451: 229–246

Lilley M.K.S., Houghton J.D.R. & Hays G.C. 2009. Distribution, extent of inter-annual variability and diet of the bloom-forming jellyfish *Rhizostoma* in European waters. *Journal of the Marine Biological Association*, United Kingdom, 89(1): 39–48

Malej A. 1989. Behaviour and trophic ecology of the jellyfish *Pelagia noctiluca* (Forsskal, 1775). *Journal of Experimental Marine Biology and Ecology,* 126: 259–270

Malej A. & Malej A. 2004. Invasion of the jellyfish *Pelagia noctiluca* in the northern Adriatic: a non-success story. Chapter 16. In: Dumont H.J., Shiganova T.A., Niermann U., eds. .*Aquatic invasions in the Black, Caspian and Mediterranean Seas*, Kluwer Academic Publications, Netherlands, pp. 273–285

Mariottini G.L. & Pane L. 2010. Mediterranean jellyfish venoms: a review on Scyphomedusae. *Marine Drugs*, 8: 1122–1152

Mills C.E. 1995. Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. *ICES Journal of Marine Science*, 52(3–4): 575–581

Mills C.E. 2001. Jellyfish blooms: Are populations increasing globally in response to changing ocean conditions? *Hydrobiologia*, 451: 55–68

Moller H. 1984. Reduction of larval herring population by jellyfish predator. *Science*, 224: 621–622

Morikawa T. 1984. Jellyfish. *FAO INFOFISH Marketing Digest*, 1: 37–39

Orsi Relini L., Garibaldi F., Lanteri L. & Relini M. 2010a. Medusivorous fishes of the Ligurian Sea 1. Chub mackerels and other pelagic fish species sometimes "have the medusa" *Pelagia noctiluca*. *Rapports CIESM*, 39: 612

Orsi Relini L, Palandri G & Relini M. 2010b. Medusivorous fishes of the Ligurian Sea 3. The young giant, *Mola mola* at the Camogli tuna trap. *Rapports CIESM*, 39: 613

Paspaleff B.W. 1938 Uber die Entwicklung von *Rhizostoma pulmo* Agassiz. *Trud chernomorsk biol Sta Varna*, 7: 1–25

Parker D.M., Cooke W.J. & Balazs G.H. 2005. Diet of oceanic loggerhead sea turtles (*Caretta caretta*) in the central North Pacific. *Fishery Bulletin*, 103(1): 142–142

Pauly D., Christensen V., Dalsgaard J., Froese R. & Torres F. 1998. Fishing down marine food webs. *Science*, 279 : 860–863

Pauly D., Graham W., Morissette L. & Palomares Deng M.L. 2009. Jellyfish in ecosystems, online databases, and ecosystem models. *Hydrobiologia*, 616(1): 67–85

Piraino S., Boero F., Aeschbach B. & Schmid V. 1996. Reversing the life cycle: medusae transforming into polyps and cell transdifferentiation in *Turritopsis nutricula* (Cnidaria, Hydrozoa). *Biological Bulletin*, 190 (3): 302–312

Piraino S., Fanelli G. & Boero F. 2002. Variability of species' roles in marine communities: Change of paradigms for conservation priorities. *Marine Biology*, 140: 1067–1074

Piraino S., De Vito D., Schmich J., Bouillon J. & Boero F. 2004. Reverse Development in Cnidaria. *Canadian Journal of Zoology*, 82(11): 1748–1754

Pope E.C., Hays G.C., Thys T.M., Doyle T.K., Sims D.W., Queiroz N., Hobson V.J., Kubicek L. & Houghton J.D.R. 2010. The biology and ecology of the ocean sunfish *Mola mola*: a review of current knowledge and future research perspectives. *Reviews in Fish Biology and Fisheries*, 20(4): 471–487

Purcell J.E. 1984. Predation on fish larvae by *Physalia physalis,* the Portuguese Man-of-War. *Marine Ecology Progress Series*, 19: 189–191

Purcell J.E. 1985. Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. *Bulletin of Marine Science*, 37(2): 739–755

Purcell J.E. 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. *Journal of the Marine Biological Association of the United Kindgom*, 85: 461–476

Purcell J.E. 2009. Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. *Hydrobiologia*, 616: 23–50

Purcell J.E. & Decker M.B. 2005. Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987–2000. *Limnology and oceanography*, 50: 376–387

Purcell J.E. & Arai M.N. 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia*, 451 (Dev. Hydrobiol., 155): 27–44

Purcell J.E., Shiganova T.A., Decker M.B. & Houde E.D., eds. 2001. The ctenophore *Mnemiopsis* in native and exotic habitats: US estuaries versus the Black Sea basin. Developments in Hydrobiology, *Hydrobiologia*, Vol 155, 451:145–176

Purcell J.E. & Nemazie D.A. 1992. Quantitative feeding ecology of the hydromedusan *Nemopsis bachei* in Chesapeake Bay. *Marine Biology*, 113(2): 305–311

Purcell J.E., Uye S. & Lo W.T. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series*, 350: 153–174

Pusceddu A., Fraschetti S., Mirto S., Holmer M. & Danovaro R. 2007. Effects of intensive mariculture on sediment biochemistry. *Ecological Applications*, 17(5): 1366–1378

Rapoza R., Novak D. & Costello J.H. 2005. Life-stage dependent, *in situ* dietary patterns of the lobate ctenophore *Mnemiopsis leidyi* Agassiz 1865. *Journal of Plankton Research*, 27(9): 951–956

Revelles M., Cardona L., Aguilar A. & Fernàndez G. 2007. The diet of pelagic loggerhead sea turtles (*Caretta caretta*) off the Balearic archipelago (western Mediterranean): relevance of ling-line baits. *Journal of the Marine Biological Association of the United Kindgom*, 87: 805–813

Richardson A.J., Bakun A., Hays G. & 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

Rippingale R.J. & Kelly S.J. 1995. Reproduction and survival of *Phyllorhiza punctata* (Cnidaria: Rhizostomeae) in a seasonally fluctuating salinity regime in western Australia. *Marine and Freshwater Research,* 46: 1145–1151

Roohi A., Kideys A., Sajjadi A., Hashemian A., Pourgholam R., Fazli H., Khanari A.G. & Eker-Develi E. 2010. Changes in biodiversity of phytoplankton, zooplankton, fishes and macrobenthos in the southern Caspian Sea after the invasion of the ctenophore *Mnemiopsis leidyi*. *Biological Invasions*, 12: 2343–2361

Rottini Sandrini L. & Stravisi F. 1981. *Preliminary report on the occurrence of* Pelagia noctiluca *(Semaeostomeae, Pelagiidae) in northern Adriatic.* Rapports et procès-verbaux des réunions. Commission internationale pour l'exploration scientifique de la mer Méditerranée, 27(7): 147–148

Russell F.S. 1970. *The medusae of the British Isles. Pelagic Scyphozoa with a supplement to the first volume on Hydromedusae.* Cambridge University Press, Cambridge, 1–284

Pérez-Ruzafa A., Gilabert J., Gutérrez J., Fernàndez A.J., Marcos C. & Sabah S. 2002. Evidence of a planktonic food web responses to changes in nutrient input dynamics in the Mar Menor coastal lagoon, Spain. *Hydrobiologia*, 475/476: 359–369

Sabatés A., Pagés F., Atienza D., Fuentes V., Purcell J.E. & Gili J.M. 2010. Planktonic cnidarian distribution and feeding of *Pelagia noctiluca* in the NW Mediterranean Sea. *Hydrobiologia*, 645(1): 153–165

Sandifer P.A., Smith T.I.J. & Calder D.R. 1974. Hydrozoans as pests in closed-system culture of larval decapod crustaceans. *Aquaculture*, 4(1): 55–59

Shiganova T.A. 1997. *Mnemiopsis leidyi* abundance in the Black Sea and its impact on the pelagic community. In: Ozsoy E. & Mikaelyan A., eds. *Sensitivity of the North Sea, Baltic Sea and Black Sea to anthropogenic and climatic changes*, pp. 117–130. Dordrecht/ Boston/ London: Kluwer Academic Publishers

Shiganova T.A., Dumont H.J.D., Mikaelyan A., Glazov D., Bulgakova M.Y.V., Musaeva E.I., Sorokin P.Y., Pautova L.A., Mirzoyan Z.A. & Studenikina E.I. 2004. Interaction between the invading ctenophores *Mnemiopsis leidyi* (A. Agassiz) and *Beroe ovata* Mayer 1912, and their influence on the pelagic ecosystem of the northeastern Black Sea. In Dumont H., Shiganova T. & Niermann U., eds. *The ctenophore* Mnemiopsis leidyi *in the Black, Caspian and Mediterranean Seas and other aquatic invasions*. NATO ASI Series, 2. Environment. Kluwer Academic Publishers: 33–70

Silvertown J. 2009. A new dawn for citizen science. *Trends in Ecology and Evolution*, 24 (9): 467–471

Siokou-Frangou I., Sarantakos K. & Christou E.D. 2006. First record of the syphomedusa *Rhopilema nomadica* Galil, 1990 (Cnidaria: Scyphozoa: Rhizostomeae) in Greece. *Aquatic Invasions*, 1(3): 194–195

Stein M.R., Marraccini J.V. & Rotschild N.E. 1989. Fatal Portuguese man-o'-war (*Physalia physalis*) envenomations. *Annals of Emergency Medicine*, 18: 312–315

Stopar K., Ramsak A., Trontelj P. & Malej A. 2010. Lack of genetic structure in the jellyfish *Pelagia noctiluca* (Cnidaria: Scyphozoa: Semaeostomeae) across European Seas. *Molecular Phylogenetics and Evolution*, 57: 417–428

Turk V., Lucic D., Flander-Putrle V. Malej A. 2008. Feeding of *Aurelia* sp. (Scyphozoa) and links to the microbial food web. *Marine Ecology*, 29: 495–505

UNEP. 1984. *Workshop on Jellyfish Blooms in the Mediterranean*. 31 October – 4 November 1983, Athens

UNEP. 1991. *Jellyfish blooms in the Mediterranean*. Proceedings of the II Workshop on Jellyfish in the Mediterranean Sea. MAP Technical Reports Series, No.47; UNEP, Athens

Woltereck R. 1904. Ueber die Entwiklung der *Velella* aus einer in der Tiefe vorkommenden Larve. *Zoologieches Jahrbucher Suppl.*, 7: 347–372

Wilson D.P. 1947. The Portuguese Man-of-War, *Physalia physalis* L., in British and adjacent seas. J*ournal of the Marine Biological Association of the United Kingdom* 27: 139–172

You K., Ma C.0, Gao H., Li F., Zhang M., Qui Y. & Wang B. 2007. Research on the jelly-fish (*Rhopilema esculentum* Kishinouye) and associated aquaculture techniques in Chi-na: current status. *Aquaculture International*, 15(6): 479–488

6. APPENDIX: THE MAIN GELATINOUS PLANKTERS OF THE MEDITERRANEAN AND THE BLACK SEA

For each species[1], the following information is given:

- **Geographic status** (in respect the Mediterranean and Black Sea region)**:** Indigenous, non-indigenous, cryptogenic.
- **Ways of introduction:** (If indigenous, not applicable).
- **Life cycle**
- **Presence patterns:** regular - occasional - seasonal.
- **Behaviour:** e.g. vertical migrations.
- **Ecophysiology**
- **Genetic characterization**
- **Association with other species**
- **Diet:** food, nutrients.
- **Predators**
- **Documented blooms (one, several, many)**
- **Geographic distribution in the Mediterranean and the Black Sea**
- **Documented impacts**
- **Possible impacts**
- **Gaps in knowledge**
- **Management measures**

[1] All pictures provided are by A. Gennari.

Aurelia aurita (Linnaeus, 1758)

Geographic status: indigenous.

Ways of introduction: not applicable.

Life cycle: typical scyphozoan life history, with benthic scyphopolyps that asexually strobilate ephyrae that grow into sexual medusae, the females of which brood larvae that settle into the shallow coastal benthos within a few days of being released (Dawson and Jacob, 2001). Large developmental plasticity (e.g. podocysts, pseudoplanulae, reverse development) (Piraino *et al.*, 2004).

Presence patterns: the main period of strobilation, resulting in release of ephyrae, starts in the late winter/early spring. The ephyrae released develop into medusae by early spring, which endure till summer or early autumn. Prolonged or even semi-continuous periods of strobilation have been reported in some areas, resulting in the presence of ephyrae in the water column for much of the year (Lucas, 2001). Occasional medusae in midwinter (Galil *et al.,* 1990).

Behaviour: very common in the mixed layer down to the subthermocline in the Black Sea. Small individuals are mostly found above the thermocline, while larger individuals (up to 40 cm umbrella diameter) below (Bat *et al.*, 2009). Exhibits a consistent pattern of diel vertical migration (Malej *et al.*, 2007).

Ecophysiology: poorly known.

Genetic characterization: molecular studies revealed cryptic species (Dawson and Jacob 2001).

Association with other species: unknown.

Diet: small copepods, copepodites, larvae of Gastropoda, Bivalvia, Cirripedia, nauplii, Appendicularia, fish eggs and larvae (Malej *et al.*, 2007).

Predators: probably fish, not well documented.

Documented blooms (one, several, many): many, both in the Mediterranean and the Black Sea.

Geographic distribution in the Mediterranean and Black Sea: common inhabitant of nearshore waters circumglobally between about 50 °N and 55 °S (Turk et al., 2008; Dawson and Jacob, 2001). Common in the Adriatic Sea, also in closed basins (Mliet Island, Lake of Varano). Occasionally abundant in the Black Sea and in the western and central Mediterranean.

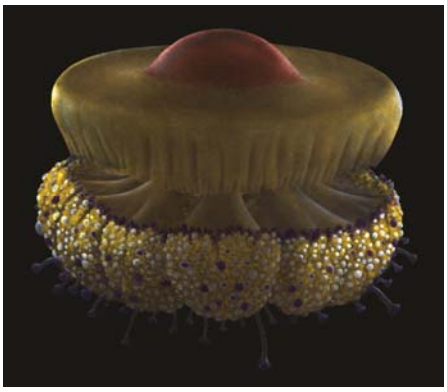
Documented impacts: Aggregations may clog cooling water intakes of coastal power plants and block fishing nets (Dong *et al.*, 2010).

Possible impacts: impoverishment of plankton communities.

Gaps in knowledge: distribution of polyps (Di Camillo *et al.*, 2010).

Management measures: reduce polyp growth.

Cotylorhiza tuberculata (Macri, 1778)



Geographic status: indigenous.

Ways of introduction: not applicable.

Life cycle: Occurrence, growth, maturation, and aging of medusae indicate an annual life cycle. Ephyrae are released during strobilation peaks in spring and summer; exceptionally high growth rates lead to medusa diameters of up to 40 cm after six months. Due to symbiotic zooxanthellae, the medusae are potentially autotrophic. The gonochoristic medusae mature during summer; a sexual dimorphism is evident by brood-carrying filaments in females. The life span of the medusae is about half a year, while scyphistomae are potentially perennial. The observed annual metagenetic cycle is a life history adaptation to a highly seasonal environment (Kikinger, 2008).

Presence patterns: June to September (Pérez-Ruzafa *et al.*, 2002), occasionally in winter (Galil *et al.*, 1990).

Behaviour: poorly known.

Ecophysiology: poorly known.

Genetic characterization: poorly known.

Association with other species: juvenile fish are often associated with it, and it might enhance recruitment success in some species.

Diet: microphagous and photosynthetic due to the presence of symbiotic microalgae.

Predators: *Caretta caretta* (Revelles *et al.*, 2007).

Documented blooms: formed blooms in the past, although they were not documented very frequently (Kogovsek et al., 2010).

Geographic distribution in the Mediterranean and Black Sea: throughout the Mediterranean Sea (Galil *et al.*, 1990).

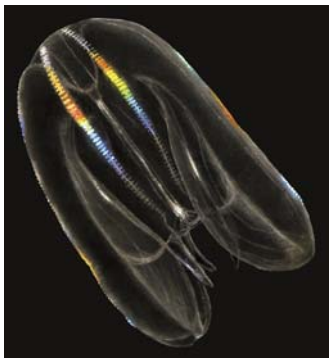
Documented impacts: none.

Possible impacts: it might have a positive effect on fish recruitment by providing shelter to juveniles.

Gaps in knowledge: impact on food chains.

Management measures: limit substrates conducive for polyp settlement, such as dead mollusc shells.

Mnemiopsis leidyi (Agassiz, 1865)



Geographic status: non indigenous; originating from the western Atlantic (Purcell *et al.*, 2001), in coastal waters over a wide latitudinal range (40°N–46°S), it invaded the Black Sea in the 1980s, followed by subsequent invasions of the other large water bodies in the Mediterranean basin (Shiganova *et al.*, 2001, Galil *et al.*, 2009).
Ways of introduction: ballast water (Shiganova, 1998).
Life cycle: size changes from 0.5 mm to more than 50 mm in length and development from the cydippid larval stage to adult lobate morphology (Rapoza *et al.*, 2005).
Presence patterns: population sizes in temperate locations small during cold winter temperatures, and increase with reproduction in the spring (Kremer, 1994).
Behaviour: usually at a depth shallower than 20 m during all months. The ctenophore was found in the deepest layer, at 50–100 m, only in summer months (Roohi *et al.*, 2010).
Ecophysiology: metabolism and growth of *M. leidyi* are clearly influenced by temperature (Kremer, 1977). *Mnemiopsis* is found in an extremely wide range of environmental conditions (winter low and summer high temperatures of 2°C and 32°C, respectively, and salinities of 2–38 per thousand) (Purcell *et al.*, 2001).
Genetic characterization: two of the sequenced ctenophores (SAL-1 and HAF-1) contained an ITS composite genotype that was previously found in invasive *M. leidyi* from the Black Sea (south western Black Sea and Gelendzhik Bay, Russia) and the Sea of Azov (various locations), as well as in native ctenophores from the United States, possibly indicating common recent ancestry (Fuentes *et al.*, 2009).
Association with other species: unknown.
Diet: feeds on a variety of prey (Larson, 1988); Cladocera, copepods, bivalve larvae, crab larvae, diatoms, dinoflagellates, fish eggs and fish larvae (Purcell *et al.*, 2001).
Predators: *Beroe ovata*, *Chrysaora quinquecirrha*, *Cyanea capillata*, *Peprilus alepidotus* and butterfish *Pronotus triacanthus* (Fuentes *et al.*, 2010).
Documented blooms: blooms of the invasive ctenophore, *Mnemiopsis leidyi*, occurred in 2009 along the Mediterranean Sea coasts of Spain and Israel (Galil *et al.*, 2009; Fuentes *et al.*, 2010). In the framework of the CIESM Jellywatch campaign in the summer of 2009, *M. leidyi* was recorded from the Ligurian, Tyrrhenian, and Ionian Seas, including swarming episodes that, together with those reported from Spain in the same period, suggest a great success of the species in the estern Mediterranean (Boero *et al.*, 2009).
Geographic distribution in the Mediterranean and Black Sea: present since more than two decades in the Black Sea, became abundant in the whole Mediterranean since 2009.
Documented impacts: invasion of regions outside its historical distributions have resulted in dramatic planktonic community alterations and destruction of fisheries in regions such as the Black Sea (Shiganova *et al.*, 2003). Interfered with operation of desalination plants in Israel (Galil *et al.*, 2009).
Possible impacts: unknown.
Gaps in knowledge: establish how many colonization events did occur, was there an adaptation to Mediterranean conditions?
Management measures: discharge ballast waters in the mid-Atlantic and fill ballast tanks in regions where putative aliens are less frequent.

.

Pelagia noctiluca (Forskål, 1775)

Geographic status: indigenous.

Ways of introduction: not applicable.

Life cycle: holoplanktonic.

Presence patterns: regular, mostly in summer, first sightings in February, present until October. Possibly, it spends the winter in deep water, or as resting stages. Occasionally winter swarms (Galil *et al.*, 1990).

Behaviour: forms enormous swarms, carried by currents, known to move vertically in the water column, especially in winter.

Ecophysiology: poorly known.

Genetic characterization: mixed populations throughout the Mediterranean (Stopar *et al.*, 2010).

Association with other species: unknown.

Diet: zooplankton, including ichtyoplankton.

Predators: several fish species (undocumented quantitatively).

Documented blooms: many.

Geographic distribution in the Mediterranean and Black Sea: abundant especially in the western Mediterranean, occasionally in the eastern basin.

Documented impacts: human health, tourism, fisheries, aquaculture, power plants.

Possible impacts: not applicable (all the negative impacts of jellyfish are directly applicable to this species, so no putative ones remain).

Gaps in knowledge: where are they when they are not present? Are there areas from where the blooms spread? Are there resting stages?

Management measures: reduce overfishing, especially of medusivorous species. Instruct first aid stations on beaches how to alleviate stings. Increase public awareness.

Phyllorhiza punctata (von Lendenfeld, 1884)

Geographic status: non indigenous.

Ways of introduction: unknown. The records from the Levantine Basin suggest entry from the Red Sea through the Suez Canal, whether by drift or transported by vessels (ephyrae with ballast water, scyphistomae attached to hulls) (Abed-Navandi and Kikinger, 2007; Galil *et al.*, 2009).

Life cycle: poorly known for the Mediterranean (see Garcia, 1990; Ripingale and Kelly, 1995).

Presence patterns: found off the Israeli coast in January, July and October (Galil *et al.*, 2009). In Brazil, the presence in late winter and spring of all size classes suggested a prior period of continuous ephyrae release synchronized to seasonal high water temperatures and extended photoperiod (Haddad and Nogueira, 2006).

Behaviour: unknown.

Ecophysiology: poorly known.

Genetic characterization: Bayha and Graham (2009) characterized the polyps.

Association with other species: algal endosymbionts (zooxanthellae) (Garcia, 1990; Galil *et al*., 2009) and thus autotrophy may be important for this species.

Diet: zooplankton.

Predators: unknown.

Documented blooms: several (e.g. Gulf of Mexico), but not in the Mediterranean Sea.

Geographic distribution in the Mediterranean and Black Sea: both in the eastern and the western basins, so far only occasional.

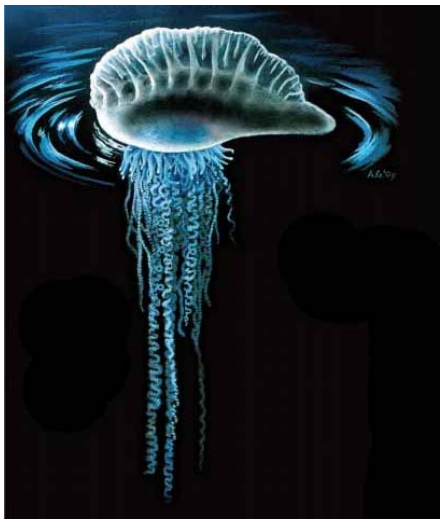
Documented impacts: none in the Mediterranean Sea. In the Gulf of Mexico it clogged fishing nets.

Possible impacts: may harm fisheries by predating on fish eggs and larvae and their prey, zooplankton (Boero *et al.*, 2009).

Gaps in knowledge: very little is known about this species in the Mediterranean Sea.

Management measures: common in marine aquaria displays. Control aquarium trade.

Physalia physalis (Linnaeus, 1758)



Geographic status: non indigenous, native of tropical and subtropical areas (Wilson, 1947).

Ways of introduction: enters the Mediterranean occasionally, through the Strait of Gibraltar (suggested by distribution patterns).

Life cycle: an "individual" is actually a colony of unisexual organisms. Every individual has specific gonozooids (sex organs or reproductive parts of the animals, either male or female). Each gonozooid is comprised of gonophores, which are little more than sacs containing either ovaries or testes. *Physalia* are dioecious. Their larvae probably develop very rapidly to small floating forms. Fertilization is assumed to occur in the open water, because gametes from the gonozooids are shed into the water. This may happen as gonozooids themselves are broken off and released from the colony. The release of gonozooids may be a chemical response occurring when groups of individuals are present in one locality. Critical density is probably required for successful fertilization. Fertilization may take place close to the surface. Most reproduction takes place in the fall, producing the great abundance of young seen during the winter and spring.

Presence patterns: occasional in the Mediterranean Sea, more abundant in recent years.

Behaviour: transported by wind, it floats on the surface.

Ecophysiology: powerful venom, occasionally lethal.

Genetic characterization: poorly known.

Association with other species: *Lepas fascicularis* and *L. pectinata*, *Caretta caretta*, *Nomeus gronovii* (Wilson, 1947).

Diet: larval fish comprised 70 to 90 percent of the prey types found in stomach contents of *Physalja physalis*. It feeds also on chaetognaths and small squids (Purcell, 1984).

Predators: *Glaucus atlanticus, Janthina janthina, Caretta caretta*.

Documented blooms: several, especially in the Atlantic, but also in the Mediterranean Sea.

Geographic distribution in the Mediterranean and Black Sea: mostly in the western basin, but may pass Sicily Channel and reach Malta.

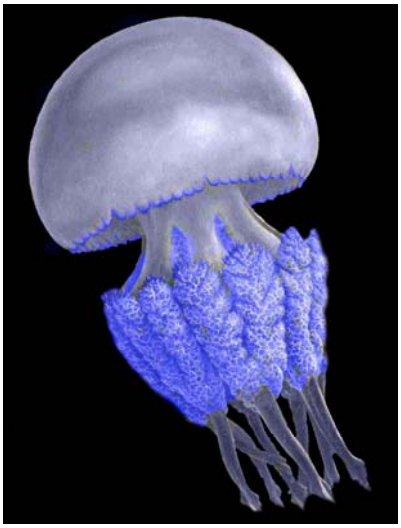
Documented impacts: lethal (Stein *et al.*, 1989), one case reported in the Mediterranean (Sardinia, summer 2010).

Possible impacts: potential impact on commercial fishing in the area. A popular food choice for the Man o' War is larval fish: if too many fish are consumed in their larval stage, there won't be many adult fish for humans to harvest.

Gaps in knowledge: dependence of Mediterranean populations on Atlantic propagules, impact on food chains.

Management measures: close bathing facilities when the species is present. Collection and disposal on land.

Rhizostoma pulmo (Macri, 1778)



Geographic status: indigenous.

Ways of introduction: not applicable.

Life cycle: Fertilization external, planulae appear after 2 days, settle polyps reproduced asexually mainly by podocysts. Strobilation is induced by temperature cue. During transformation from newly released ephyra to young medusa, velar lappets appear and increase in number (Paspaleff, 1938). Reverse transformation of ephyrae into scyphopolyps has been observed (Paspaleff, 1938).

Presence patterns: seasonal, occurring usually in late spring when the temperature increase to 25.5°C (Galil *et al.*, 1990; Mariottini and Pane, 2010).

Behaviour: poorly known.

Ecophysiology: swarms seemed to correlate with high temperature and nutritional factors connected to the abundance of zooplankton, which is the food for this microphagous jellyfish (Mariottini and Pane, 2010).

Genetic characterization: unknown.

Association with other species: the crab *Liocarcinus vernalis* is often transported by this jellyfish.

Diet: diatoms (Lilley *et al.*, 2009).

Predators: unknown, probably many fish species.

Documented blooms: annual blooms (Kogovsek *et al.*, 2010). During the years of the bloom in the Mediterranean Sea, *Rhizostoma pulmo* occurred in large numbers in the northern Adriatic Sea, in open sea and along the coastline, as well as in the southern Adriatic Sea and the northern Ionian Sea, mainly in winter. *Rhizostoma pulmo* was indicated to be the largest and most abundant jellyfish in Lebanese coastal waters, occurring usually in late spring when the temperature increase up to 25.5°C, staying in Lebanese waters up until mid-August and disappearing later on (Mariottini and Pane, 2010).

Geographic distribution in the Mediterranean and Black Sea: mainly Adriatic Sea, Ionian Sea, Ligurian Sea, eastern Mediterranean, Tunisian waters, western Mediterranean and Black Sea (Mariottini and Pane, 2010). During the last decade, in some eastern Mediterranean waters *Rhizostoma pulmo* has been replaced by *Rhopilema nomadica* (Herut and Galil, 2000).

Documented impacts: many economic problems and also health implications (Mariottini and Pane, 2010). After a contact cutaneous pain, erythematous with subsequent small vesicles (Kokelj and Plozzer, 2002). The stings are much milder than those of *Pelagia noctiluca*.

Possible impacts: unknown.

Gaps in knowledge: triggering of blooms.

Management measures: reduce eutrophication, utilization as a food.

Rhopilema nomadica (Galil, 1990)

Geographic status: East African species. It was first recorded along the coastlines of Israel in 1977 (Galil et al., 1990). At present is found along the Levantine Basin with a single record off the Peloponnesus, Greece (Galil *et al.*, 1990; Siokou-Frangou *et al.*, 2006).

Ways of introduction: invasion through the Suez Canal.

Life cycle: life cycle from planula to ephyra to young medusa described. Strobilation considered dependent on temperature, with rapid strobilation between 18–20°C and declining at 24–26°C. The rise of water temperature supports the strobilation in spring, while inhibited in winter and in summer (Lotan *et al.*, 1992).

Presence patterns: huge swarms are formed each summer since the mid-1980s along the SE Levantine coast (Galil *et al.*, 1990; 2010).

Behaviour: poorly known.

Ecophysiology: laboratory studies support the possibility that synchronization and annual occurrence are controlled by seasonal changes in water temperature regimes, leading to rapid strobilation and release of ephyrae during springtime. The sensitivity of the polyps to low temperatures might explain why its dispersal is limited to the eastern Mediterranean (Lotan *et al.*, 1994), but this sole reason is probably too simplistic.

Genetic characterization: unknown.

Association with other species: juveniles of *Alepes djedaba*, a carangid fish that entered through the Suez Canal, are commonly found in association with *R. nomadica*, taking shelter under its umbrella and among the filamentous mouth arms (Galil *et al.*, 1990).

Diet: unknown.

Predators: unknown.

Documented blooms: many, in the Levantine Basin.

Geographic distribution in the Mediterranean and Black Sea: south-eastern Mediterranean.

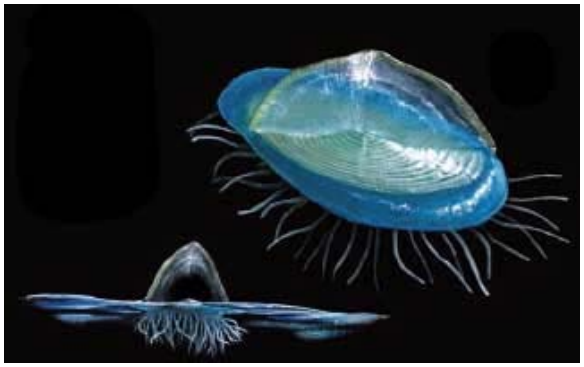
Documented impacts: the swarms adversely affect tourism, fisheries and coastal installations. The summer swarming results each year in envenomation victims suffering burning sensation, eurythema, papulovesicular and urticaria-like eruptions that may last weeks and even months after the event. Coastal trawling and purse-seine fishing are disrupted for the duration of the swarming due to net clogging and inability to sort yield. Jellyfish-blocked water intake pipes pose a threat to desalination plants, cooling systems of port-bound vessels and coastal power plants (Galil *et al.*, 1990; Galil, 2007; Mariottini and Pane, 2010).

Possible impacts: impoverishment of plankton communities.

Gaps in knowledge: distribution of polyps triggering of blooms, competing species and predators, etc.

Management measures: reduce suitable substrates for polyps, reduce overfishing.

Velella velella (Linnaeus, 1758)



Geographic status: indigenous, circumglobal in warm and temperate waters.

Ways of introduction: not applicable.

Life cycle: the floating stage is a polyp colony. It produces medusae that reproduce sexually (Larson, 1980), the larvae sink in deep water, and then migrate towards the surface while the colony is formed, going through several growth stages (Voltereck, 1904).

Presence patterns: present in spring, early summer.

Behaviour: wind-transported.

Ecophysiology: poorly known.

Genetic characterization: poorly known.

Association with other species: *Scrippsiella velellae* (Peridiniales) (Banaszak *et al.*, 2006).

Diet: iponeuston, including fish eggs and larvae.

Predators: *Caretta caretta* (Parker *et al.*, 2005); *Puffinus carneipes* (Gould *et al.*, 1997); *Ianthina janthina* (Bayer, 1963).

Documented blooms: many, also in the Mediterranean Sea.

Geographic distribution in the Mediterranean and Black Sea: eastern and western Mediterranean (Bouillon *et al.*, 2004).

Documented impacts: stranded swarms form masses of putrescent material.

Possible impacts: might impair the recruitment of some fish species, if the blooms match the period of presence of fish eggs and larvae.

Gaps in knowledge: the studies on the life cycle are very old. Little has been done in recent years.

Management measures: The stranded colonies enrich the sands of beaches (Kemp, 1986). This species is affected by oil pollution.

Gelatinous plankton is formed by representatives of Cnidaria (true jellyfish), Ctenophora (comb jellies) and Tunicata (salps). The life cycles of gelatinous plankters are conducive to bloom events, with huge populations that are occasionally built up whenever conditions are favorable. Such events have been known since ancient times and are part of the normal functioning of the oceans. In the last decade, however, the media are reporting on an increasingly high number of gelatinous plankton blooms. The reasons for these reports is that thousands of tourists are stung, fisheries are harmed or even impaired by jellyfish that eat fish eggs and larvae, coastal plants are stopped by gelatinous masses. The scientific literature seldom reports on these events, so time is ripe to cope with this mismatch between what is happening and what is being studied. Fisheries scientists seldom considered gelatinous plankton both in their field-work and in their computer-generated models, aimed at managing fish populations. Jellyfish are an important cause of fish mortality since they are predators of fish eggs and larvae, furthermore they compete with fish larvae and juveniles by feeding on their crustacean food. The Black Sea case of the impact of the ctenophore Mnemiopsis leydi on the fish populations, and then on the fisheries, showed that gelatinous plankton is an important variable in fisheries science and that it cannot be overlooked. The aim of this report is to review current knowledge on gelatinous plankton in the Mediterranean and Black Sea, so as to provide a framework to include this important component of marine ecosystems in fisheries science and in the management of other human activities such as tourism and coastal development. Fact sheets on the most important gelatinous plankters of the Mediterranean and Black Seas are included as an appendix.

ISBN 978-92-5-107457-2 ISSN 1020-9549

9 789251 074572

I3169E/1/01.13