

GENERAL FISHERIES COMMISSION FOR THE MEDITERRANEAN



COMMISSION GÉNÉRALE DES PÊCHES POUR LA MÉDITERRANÉE

GENERAL FISHERIES COMMISSION FOR THE MEDITERRANEAN

Thirty-fifth Session

Rome, Italy 9-14 May 2011

REVIEW OF JELLYFISH BLOOMS
IN THE MEDITERRANEAN AND BLACK SEAS*
(GFCM Studies and Reviews No. 92)

(Draft)

*Available in English only

Compiled by FERDINANDO BOERO

INDEX:

I. INTRODUCTION	
1. Jellyfish	4
i. Cnidaria	. 4
ii. Ctenophora	5
iii. Chordata	5
2. The blooms	
3. Ecosystem "malfunctioning"	
4. The grand picture	
5. The impact of gelatinous plankton on fish populations	8
6. Estimates of predation of gelatinous plankton on fish	. 8
7. Jellyfish as keystone predators	10
8. Gelatinous plankton as a source of food	
II. JELLYFISH BLOOMS IN THE MEDITERRANEAN AND BLAC	K
SEAS	
1. The Black Sea and <i>Mnemiopsis</i> , a paradigmatic example	
2. Jellyfish bloom cases in the Mediterranean Sea	
3. Lessons from the history of the Adriatic Sea	
III. CURRENT KNOWLEDGE AND RESEARCH NEEDS	
1. Possible drivers of the phenomena	
i. Global warming	
ii. Global overfishing	
iii. Eutrophication	
iv. Increased space for polyps	
v. Transport of Non Indigenous Species	16
vi. Widening of the natural area of Non Indigenous Species	
2. Monitoring and forecasting methods	
1. Blue diving	
2. From boats	
3. From airplanes	
4. From beaches	
5. From submersibles	
6. By videocameras	
ii. Echosound measures	
iii. Citizen science	
3. Further studies on blooms	
4. Negative (and positive) impacts of jellyfish blooms on human activities	
i. Fisheries	
ii. Public health	
iii. Tourism	
iv. Food market	
v. Cooling systems of factories	
vi. Cage aquaculture	
vii. Positive impact of gelatinous plankton	
5. THE SPECIES	. 24
IV. SCIENTIFIC SUPPORT TO MANAGEMENT	. 25
1. Human impacts and ecosystem functioning	
2. Multiple stressors	
3. The ecosystem approach	
4. Recommendations for management	. 26
i. Develop jellyfish products for food and medicine	26
ii. Use cutting nets to destroy the jellyfish	27

iii. Destroy the polyps	27
iv. Biocontrol agents	27
v. Prevent activities promoting the spread of gelatinous plankters	27
vi. Design nets that are not clogged by gelatinous plankton	
vii. Employ selective fishing gear	
viii. Set early warning systems	
ix. Reduce Eutrophication	
x. Reduce Overfishing	
xi. Reduce Global warming	
5. Conclusion	28
V. BIBLIOGRAPHIC INVENTORY: LIST OF RELEVANT PUBI	LICA
TIONS	29
VI. APPENDIX: THE MAIN GELATINOUS PLANKTERS OF	
MEDITERRANEAN AND THE BLACK SEAS	35
Aurelia aurita (Linnaeus, 1758)	36
Cotylorhiza tuberculata (Macri, 1778)	
Mnemiopsis leidyi (Agassiz, 1865)	
Pelagia noctiluca (Forskål, 1775)	39
Phyllorhiza punctata (von Lendenfeld, 1884)	40
Physalia physalis (Linnaeus, 1758)	41
Rhizostoma pulmo (Macri, 1778)	42
Rhopilema nomadica Galil, 1990	43
Velella velella (Linnaeus, 1758)	44
VII ACKNOWI FDGFMENTS	

I. INTRODUCTION

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.

i. 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 the 2 m in bell diameter, and several m 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).

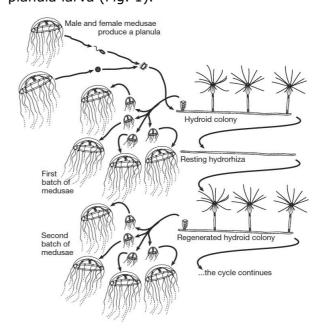


Fig. 1. Life cycle of a pelago-benthic jellyfish. See text for explanation. After Boero et al. (2008)

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 the siphonophores.

ii. Ctenophora

Gelatinous macrozooplankton is usually equated to stinging jellyfish, and its presence causes major concern about own safety in non-marine biologists, due to the fear the potential stings generate in us. 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.



Fig. 2. A ctenophore: Leucothoea. Art by Alberto Gennari

Ctenophores move by ciliary propulsion, through what zoologists call "ctenes" or combs. Hence the popular name: comb jellies. They can be a few cm, or even 50 or more cm, 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.

iii. Chordata

Pelagic tunicates (Fig. 3) are members of the phylum Chordata, they comprise the Thaliacea and the Larvacea, or appendicularians.



Fig. 3. A pelagic tunicate: *Salpa*. Art by Alberto Gennari

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 meters 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.

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 bloom 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 \rightarrow 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 prey that are herbivorous: the copepods and other crustaceans that rely on the phytoplankton pulses. An ecosystem

cannot function with carnivores only!

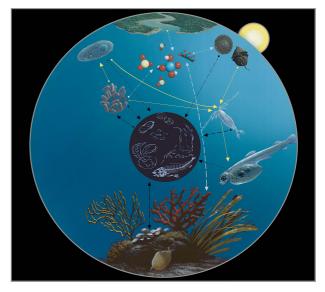


Fig. 4. The pathway phytoplankton - herbivorous crustacean plankton - fish. Art by Alberto Gennari, graphics by Fabio Tresca

3. Ecosystem "malfunctioning"

The term "malfunctioning" is obviously anthropocentric. All ecosystems do function, othewise 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 labelled 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 guite 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 \rightarrow 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 win-

ners 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* \rightarrow *herbivorous crustacean zooplankton* \rightarrow *fish* pathway is disrupted, with the onset of the *phytoplankton* \rightarrow *herbivorous crustacean zooplankton* \rightarrow *jellyfish* pathway (Fig. 5).

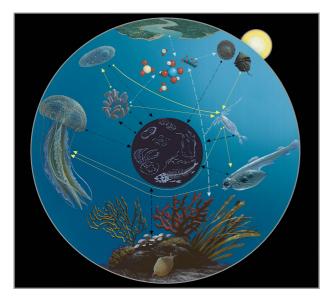


Fig. 5. The pathway phytoplankton - crustacean plankton - jellyfish. Art by Alberto Gennari, graphics by Fabio Tresca

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 favourable 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 *phyto-plankton* \rightarrow *herbivorous crustacean zoo-plankton* \rightarrow *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 $phytoplankton \rightarrow herbivorous\ crustacean\ zo-oplankton \rightarrow fish\ pathway, with the production of a short circuit in it: the <math>phytoplankton \rightarrow herbivorous\ gelatinous\ zooplankton\ pathway\ (Fig. 6).$



Fig. 6. The pathway phytoplankton - herbivorous gelatinous zooplankton. Art by Alberto Gennari, graphics by Fabio Tresca

At the end of their peak, pelagic tunicates usually contribute to what we call marine snow and fall to the benthos, almost jumping the pelagic trophic pathways (besides the

bacteria that feed on them while they are falling towards the bottom).

4. The grand picture

Marine ecosystems functioning, thus, takes place through three main pelagic pathways: the *phytoplankton* \rightarrow *herbivorous crustacean zooplankton* \rightarrow *fish* pathway, the *phytoplankton* \rightarrow *carnivorous crustacean zooplankton* \rightarrow *carnivorous gelatinous* zooplankton pathway, and the *phytoplankton* \rightarrow *herbivorous gelatinous zooplankton* pathway (Fig. 7).

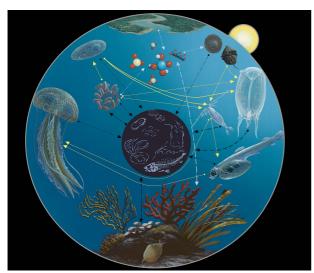


Fig. 7. The three main pathways determining marine ecosystem functioning. Art by Alberto Gennari, graphics by Fabio Tresca.

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 which, 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.

5. The impact of gelatinous plankton on

fish populations

Summarizing, the impact of gelatinous zooplankton on fish populations can be:

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. 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.

6. Estimates of predation 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, 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 in specific

places (Tab I and II for Aurelia aurita). If a

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

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.

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

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

Some species, as the scyphozoan *Drymone-ma dalmatinum*, apparently feed only on other jellyfish, since Larson (1987) inspected GFCM

13 specimens and found only medusae in

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

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)

their guts. The same seems true also for Narcomedusae in general (Tab. IV).

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	Medit.
Solmissus incisa	cteophore	Bahamas
Solmissus marshalli	hydromedusa	NE Pacific
Solmundella bitenta- culata	pteropods	Antarctic

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

These gelatinous plankton eaters might be a natural mitigation of the impact of the predation pressures of their prey on crustacean

JELLYFISH BLOOMS

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 clausa*, 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% of its diet is made of fish larvae.

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

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

Arai and Purcell (2001) reviewed the available information on the impact of predation of gelatinous predators on fish (Tab. V). Gelatinous herbivorous filter feeders (namely Thaliacea and Appendicularia) are extremely effient 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%.

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.

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.

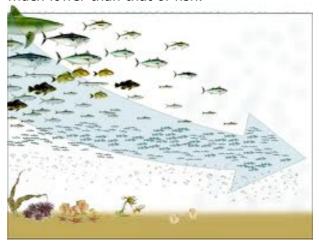


Fig. 8. Fishing down marine food webs. After Pauly et al. (1998)

In the revised figure of Pauly et al (2009) (Fig. 8), illustrating the process of fishing down marine food webs, jellyfish eating species, such as *Mola mola* and *Caretta caretta* (Fig. 9) are shown in the place of tuna, as in the classical version by Pauly et al. (1998). 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 (Fig. 9). But pressures are even higher on their competitors (commercial fish), that use their same food when they are larvae and juveniles.

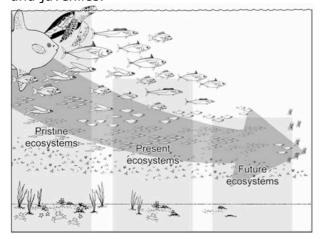


Fig. 9. Revised version of the scenario of fishing down marine food webs. Future ecosystems are predicted to be dominated by jellyfish. After Pauly et al. (2009)

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 (for reviews see Arai 2005; Ates 1988) (fig. 10).

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



Fig. 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 Alberto Gennari, graphics by Fabio Tresca

the ingestion of great quantities of *Pelagia* noctiluca.

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 medusiphagous 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.

II. JELLYFISH BLOOMS IN THE MEDITERRANEAN AND BLACK SEAS

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).



Fig. 11. Mnemiopsis leydi. Art by Alberto Gennari

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).

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 envisaged 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. 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.

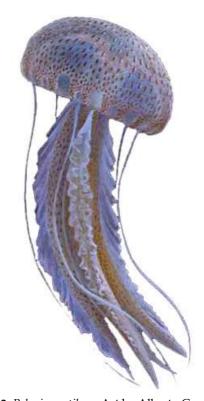


Fig. 12. Pelagia noctiluca. Art by Alberto Gennari

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).

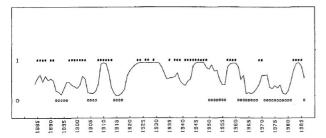


Fig. 13. Periodicity of *Pelagia noctiluca* blooms. Open circles: years without *Pelagia*. Closed circles: years with *Pelagia*. Solid line: probability of *Pelagia* blooms. After Goy et al. 1988.

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 Eighties, 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 Eighties, 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 availablity) 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 Eighties 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).

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).

The scenario hypothesized by Boero (2001) and Boero and Bonsdorff (2007) was that the persistence of *Pelagia* blooms in the first half of the Eighties 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

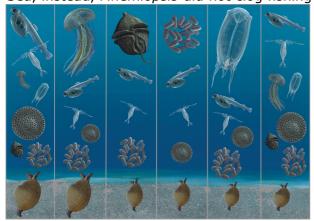


Fig. 14. Ecological history of the Adriatic Sea. Period 1: fish-dominated. Period 2: jellyfish-dominated. Period 3: dinoflagellate-dominated (red tides), with overfishing of benthic molluscs. Period 4: bacteria-dominated, with mucilages. Period 5 (erratic) thaliacean-dominated. Period 6 (present) lower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

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 Eighties blooms. A very important sink of carbon fluxes (i.e. fish) was replaced by jellyfish, 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 Eighties and did not lead to the same series of phase shifts that affected the Adriatic Sea in the Eighties (Fig. 12). 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 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 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 Eighties and Nineties 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, bacteria) migh 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 Eighties blooms, the system went in another direction and is still not back to what was "normal" in pre-Pelagia years.

III. CURRENT KNOWLEDGE AND RESEARCH NEEDS

Mills (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*.

1. 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 which, currently, is mostly linked to episodical observations that can be considered as anedoctal. 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:

i. Global warming

Global warming, on the one hand, should enhance species that thrive at tropical latitudes but, on the other hand, species that are favoured 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



Fig. 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 favourable windows for sexual reproduction are becoming wider, allowing further populations increases.

ii. Global overfishing

Overfishing is removing top predators from the oceans (Fig. 8). 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:

iii. Eutrophication

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, favoured salps and other microphagous gelatinous plankters that, however, remained mostly unstudied.



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

iv. Increased space for polyps

The widespread use of hard coastal defences and the increase in tourist harbors can enhance jellyfish production from 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 cor-

respondence of the coastal defences that were built to prevent coastal erosion (Fig. 16). It is highly probable that the coastal defences are a proper settling place for the polyps, so enhancing the spread of this stinging species.

v. Transport of Non Indigenous Species

A very particular case, that 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).



Fig. 17. *Phyllorhiza punctata,* recently recorded from the Western Mediterranean. Art by Alberto Gennari.

vi. Widening of the natural area of Non Indigenous Species

This is different from the preceeding case, since species can change their natural distri-

bution 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 estreme 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.



Fig. 18. *Catostylus tagi* photographed at Pantelleria Island. Picture by Maria Ghelia.

In spite of this, these species cannot be considered as having been transported directly by humans, such as those introduced via acquaculture, 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.

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).



Fig. 19. Marivagia stellata. After Galil et al. (2010)

2. Monitoring and forecasting methods

Jellyfish blooms became a matter of concern in the early Eigthies 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 under utilized 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 highighted by Brodeur et al. (1999) for the Bering Sea and by Licandro et al. (2010) for the Noertheast 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.

After the UNEP-MEDPOL project, that suddenly came to an end due to the end of the jellyfish outbreaks of the early Eighties, no other project on gelatinous plankton has been launched in the Mediterranean region. 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.ht ml

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 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 the year 2011, the European Union financed the project Vectors of change, and one task of the project regards just the investigation of gelatinous plankton blooms.

The study of gelatinous macrozooplankton requires completely different techniques from those employed for crustacean plankton (see Purcell 2009 for a review).

i Visual censuses

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 nearshore 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 et al 1992).
- **6. By videocameras**. This allows prolonged observation periods from a fixed station (Benfield et al 1996).

ii. Echosound measures

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

Radiotracking 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 authomatic 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.

iii. Citizen science

Citizen science (Silvertown 2009) is an alternative method to evaluate the presence and

abundance of gelatinous macrozooplankton. The adantages 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:

- need for great efforts in mass media involvement
- · 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



Fig. 20. The poster of the CIESM jellywatch (2009 version). Concept by Ferdinando Boero, Art by Alberto Gennari, Graphics by Fabio Tresca.

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 and 2010 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 during two years (2009-2010) 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. The discovery of abundant populations of Mnemiopsis leydi both in Israel (Galil et al 2009) and in Italy (Boero et a. 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 campaign of 2010 was 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



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

3. Further studies on blooms

the records of the readers.

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 poplations (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. 12).

In the past, these outbreaks have been correlated to El Nino 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 Thyrrenian and the Ligurian Seas, showed that species distribution was very different in the various basins (Fig. 22), and such distributions were not even 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 driven by the currents, it might be possible to forecast that a bloom observed in a given part of the basin might be transported to another part of the basin by the prevailing currents.



Fig. 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).

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 the situation 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.

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:

i. 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



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

weight of the jellyfish present in the net that it was pulling up (fig. 24).

The Telegraph



Japanese fishing trawler sunk by giant jellyfish

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



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 iellyfish.

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

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.

Fisheries can be affected also by indirect damageby 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.

ii. Public health

In 2010 the first casualty due to the sting of a gelatinous plankter (*Physalia physalis*) occurred in Sardinia (Fig. 25).



Fig. 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*.

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 extenct 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.

iii. Tourism

Sea-based tourism is one of the main souces 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.



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

Along some coasts, e.g. France and Spain, anti-jellyfish barriers have been put in operation, so 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 specially 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.

iv. 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).



Fig. 27. A jellyfish dish.

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).

v. 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, Quatar, Arabian Gulf, USA.



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

vi. Cage aquaculture

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 acquacultured 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.

vii. 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 numerosity of potential monopolizers, acting as keystone predators.

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 and

people are greatly attracted by their beauty and elegance. Many artifacts are now inspired by jellyfish and there is a tendency to recognize them as beautiful animals. This tendency is not to be underevaluated. In the XIX 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 trourist attraction, as it is a Palau (Dawson et al 2001).



Fig. 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, and do have a high commercial price. In China they are even farmed.

Jellyfish, furthermore, are the animals with the higherst proportion of extracelluar 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.

5. 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).



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

In the Appendix to this report, the species of major concern are listed in alphabetical order, with information about their principal features.

IV. SCIENTIFIC SUPPORT TO MANAGEMENT

1. Human impacts and ecosystem functioning

Man removes the fish in an industrial way, with more and more sophisticated technologies. It is worth while 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. 9). This has released gelatinous zooplankton from fish competition, and the blooms of gelatinous plankton, once episodical, 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 over-fishing, the impact will be even greater.

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 unbeareable 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 stages. 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.

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 malfunctionings (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 labelled 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 fuctioning 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. 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)
- 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 episodical, 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:

i. 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 nework behind them to take advantage of sudden abundances of this product-to-be. Jellyfish do have a wide species diversity and some species might contain chemicals that might become conducive to the development of new drugs and other biotechnological pro-

ducts 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.

ii. 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 them. 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.

iii. Destroy the polyps

Many species do have polyp stages (Fig. 1) that are the real "seeds" from where blooms come. 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 km of coastal defences that have been established to prevent beach erosion. The availability of hard bottom habitats in a region previously dominated by soft bottoms might have favoured 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 defences is surely unfeasible. Di Camillo et al (2010) however, reported that ship wreks 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 and 2010 (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.

iv. 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 showed in a previous section of this document, that medusiphagous species (fishes and turtles) are increasing, due to greater food availablity. 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).

v. Prevent activities promoting 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:

vi. 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.

vii. 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.

viii. Set early warning systems

The individuation 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 which, we have seen, are manifold. Richardson et al (2009) suggest to:

ix. Reduce Eutrophication x. Reduce Overfishing xi. Reduce 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 im-

pacts 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.

It is common perception, furthermore, that aquaculture is 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, aquacultured species are invariably carnivores (especially in the Mediterranean area) and they are fed by 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.

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 exherting an unbearable pressure on natural systems that, ovbiously, 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!

V. BIBLIOGRAPHIC INVEN-TORY

- 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 MN 1997. A Functional Biology of the Scyphozoa. Chapman & Hall, London, 316 pp.
- Arai MN 2005. Predation on pelagic coelenterates: a review. Journal of the Marine Biological Association of the United kingdom 85: 523-536
- Ates RML 1988. Medusivorous fishes, a review. Zoologisches Mededelingen, 62: 29-42
- Banaszak AT, Iglesias Prieto R, Trench RK 1993. *Scrippsiella velellae*, new species (Peridiniales) and *Gloeodinium viscum*, new species (Phytodiniales) dinoflagellate symbionts of two hydrozoans (Cnidaria). Journal of Phycology 29 4: 517-528
- Bat L, Satilmis HH, 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 EJ, MM Sturt, NM Ruane, TK Doyle, R McAllen, L Harman, HD Rodger 2011. Gill damage to Atlantic salmon (Salmon salar) caused by the common jellyfish (Aurelia aurita) under experimental challenge. Plos O n e 6 (4) e 18529. 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 KM, Graham WM 2009. A new Taqman PCR-based method for the detection and identification of scyphozoan jellyfish polyps. Hydrobiologia 616: 217-228
- Benfield MC, Davis CS, Wiebe PH, Gallager SM, Lough RG, Copley NJ 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, S. 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 MP, 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: RN Hughes (ed.), Reproductive Biology of Invertebrates XI: Progress in Asexual Reproduction, Oxford & IBH Publishing Co. New Delhi: 141-158.
- Boero F, Piraino S 2010. From Cnidaria to "Higher Metazoa" in one step. in: DeSalle R, Schierwater B (eds) Key Transitions in Animal Evolution. CRC Press, Boca Raton, pp 162-174.
- 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 MD, Pagès F, Gili J-M, Boero F, Gravili C 2004. Fauna of the Mediterranean Hydrozoa. Scientia Marina 68 Suppl. 2: 1-449.
- Bolton TF, Graham WM 2006. Jellyfish on the rocks: bioinvasion threat of the international 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 AS, Boyer DC, Axelsen BE, Lynam CP, Sparks CAJ, Boyer HJ, Gibbons MJ, 2005. Towards the acoustic estimation of jellyfish abundance. Marine Ecology Progress Sereries 295: 105-111.
- Brodeur RD, Mills CE, Overland JE, Walters GE, Schumacher JD 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 SL, Hendricks JR, Jarrard RD, Marques AC, Collins AG, Lieberman B 2007. Exceptionally Preserved Jellyfishes from the Middle Cambrian. PLoS ONE 2(10): e1121 doi:10.1371/journal.pone.0001121
- CIES, 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 GJ 1952. *Pelagia* in Manx waters. Nature 170: 587.
- Cushing DH 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 GM, Grishin AN, 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 MN, Martin LE, Penland LK 2001. Jellyfish swarms, tourists, and the Christ-

- child. Hydrobiologia 451: 131-144
- Dawson MN, Jacobs DK 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 CG, 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 JE, 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 occurence 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 GA, Romanova ZA, Abolmasova GI 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 VL, Dror LA, Bayha KM, Atienza D, Edelist D, Bordehore C, Gili JM, Purcell JE 2010. Blooms of the invasive ctenophore, *Mnemiopsis leidyi*, span the Mediterranean Sea in 2009. Hydrobiologia 645: 23-37
- Galil BS, Spanier E, Ferguson WW 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 LA, 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 JR 1990. Population dynamics and production of *Phyllorhiza punctata* (Cnidaria: Scyphozoa) in Laguna Joyuda, Puerto Rico. MarinEcology Progress Series64: 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 MR, Seymour JE 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.
- HaddadMA, 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 WM 1975. Underwater observations of blue-water plankton: logistics, techniques, and safety procedures for divers at sea. Limnology and Oceanography 20 6: 1045-1051
- Harbison GR, Madin LP, Swanberg NR 1978. On the natural history and distribution of oceanic ctenophores. Deep-Sea Research 25: 233-256.
- Harbison GR, McAlister VL 1979. The filterfeeding 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: 1. Regional chapters: Europe, The Americas and West Africa. pp. 253-265
- Houghton JDR, Doyle TK, Davenport J, Hays GC 2006. Developing a simple, rapid method for identifying and monitoring jellyfish aggregations from the air. Marine Ecology Progress Series 314: 159-170
- Hsieh Y-HP, Leong F-M, Rudloe J 2001. Jellyfish as food. Hydrobiologia 451: 11-17.
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629–638.
- Jones TT, Hastings MD, Bostrom BL, Pauly D, Jones DR 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 PF 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 AE 1994. Recent dramatic changes in the Black Sea ecosystem: The reason for the sharp decrease in Turkish anchovy fisheries. J Mar Syst 5:171–181
- Kikinger R 1992. *Cotylorhiza tuberculata* (Cnidaria: Scyphozoa) Life history of a stationary population. PSZN I: Marine Ecology 13: 333-362
- Kingsford MJ, Pitt KA, Gillanders BM 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 RJ 1987. First report of the little-

- known scyphomedusa *Drymonema dal-matinum* in the Caribbean Sea, with notes on its biology. Biological Oceanography 4: 447-454
- Larson RJ 1980. The medusa of *Velella velella* (Linnaeus, 1758) (Hydrozoa, Chondrophorae). Journal of Plankton Research 2 3: 183-186
- Larson RJ 1988. Feeding and functional morphology of the lobate ctenophore *Mnemiopsis mccradyi*. Estuarine Coastal and Shelf Science 27 5: 495-502
- Larson RJ, Matsumoto GI, Madin LP, Lewis LM, 1992. Deep-sea benthic and benthopelagic medusae, recent observations from submersibles and a remotely operated vehicle. Bulletin of Marine Science 51: 277-286
- Larson RJ, Mills CE, Harbison GR 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 DPV, Daly Yahia MN, Fernandez de Puelles ML, Gasparini S, Hecqu JH, Tranter P, Kirby RR 2010. A blooming jellyfish in the neotheast 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 CH 2001. Reproduction and life history strategies of the common jellyfish *Aurelia aurita*, in relation to its ambient environment. Hydrobiologia 451: 229-246
- Lilley MKS, Houghton JDR, Hays GC 2009. Distribution, extent of inter-annual variability and diet of the bloom-forming jellyfish *Rhizostoma* in European waters. Journal of the Marine Biological Association of the 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: Aquatic invasions in the Black, Caspian and Mediterranean Seas (H. Dumont et al. eds.), Kluwer Academic Publ.

- Netherlands, 273-285
- Mariottini GL, Pane L 2010. Mediterranean jellyfish venoms: a review on Scyphomedusae. Marine Drugs 8: 1122-1152
- Mills CE 1995. Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. ICES J. mar. Sci. 52 3-4: 575-581.
- Mills CE 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 BW 1938 Uber die Entwicklung von Rhizostoma pulmo Agassiz. Trud chernomorsk biol Sta Varna 7: 1–25
- Parker DM, Cooke WJ, Balazs GH 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 ML 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 EC, Hays GC, Thys TM, Doyle TK, Sims DW, Queiroz N, Hobson VJ, Kubicek L, Houghton JDR 2010. The biology and eco-

- logy 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 JE 1984. Predation on fish larvae by *Physalia physalis*, the Portuguese man of war. Marine Ecology Progress Series 19: 189-191
- Purcell JE 1985. Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. Bulletin of Marine Science 37 (2): 739-755
- Purcell JE 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 JE 2009. Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. Hydrobiologia 616: 23-50
- Purcell JE, Decker MB 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 JE, Arai MN 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia, 451 (Dev. Hydrobiol., 155), 27–44
- Purcell JE, Shiganova TA, Decker MB, Houde ED (eds) 2001 The ctenophore *Mnemiopsis* in native and exotic habitats: US estuaries versus the Black Sea basin. Developments in Hydrobiology, Vol 155. Hydrobiologia 451:145–176
- Purcell JE, Nemazie DA 1992. Quantitative feeding ecology of the hydromedusan Nemopsis bachei in Chesapeake Bay. Marine Biology 113, 2: 305-311
- Purcell JE, Uye S, Lo WT 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 JH 2005. Lifestage 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 AJ, Bakun A, Hays G, Gibbons MJ 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends in Ecology & Evolution 24 6: 312-322
- Rippingale RJ, Kelly SJ 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 AG, 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, F. Stravisi. 1981. Preliminary report on the occurrence of Pelagia noctiluca (Semaeostomeae, Pelagiidae) in northern Adriatic. Rapports et Proces-Verbaux des Reunions Commission Internationale pour l'Exploration Scientifique de la Mer Mediterranee. 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 AJ, 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., F. Pagés, D. Atienza, V. Fuentes, JE Purcell, JM Gili 2010. Planktonic cnidarian distribution and feeding of *Pelagia noctiluca* in the NW Mediterranean Sea. Hydrobiologia 645 (1): 153-165
- Sandifer PA, Smith TIJ, Calder DR 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 Sensitivity of the North Sea, Baltic Sea and Black Sea to anthropogenic and climatic changes. (ed. E. Ozsoy and A. Mikaelyan), pp. 117–130. Dordrecht /Boston/ London: Kluwer Academic Publishers
- Shiganova TA, Dumont HJD, Mikaelyan A,

- Glazov D, Bulgakova MYV , Musaeva EI, Sorokin PY , Pautova LA, Mirzoyan ZA and Studenikina EI (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 Eds. Dumont H, Shiganova T and Niermann U: 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 ED 2006. First record of the syphomedusa *Rhopilema nomadica* Galil, 1990 (Cnidaria: Scyphozoa: Rhizostomeae) in Greece. Aquatic Invasions 1 3: 194-195
- Stein MR, Marraccini JV, Rotschild NE 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; Athens. 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 vorkomenden Larve. Zoologieches Jahrbucher Suppl. 7: 347-372.
- Wilson DP 1947. The Portuguese Man-of-War, Physalia physalis L., in British and adjacent seas. Journal of the Marine Biological Association of the United Kingdom 27: 139-172
- You K, Ma C, Gao H, Li F, Zhang M, Qui Y, Wang B 2007. Research on the jellyfish (*Rhopilema esculentum* Kishinouye) and associated aquaculture techniques in China: current status. Aquaculture International 15 (6): 479-488

VI. APPENDIX: THE MAIN GE-LATINOUS PLANKTERS OF THE MEDITERRANEAN AND THE BLACK SEAS

For each species, the following information is given:

- •Geographic status in respect the the Mediterranean and Black Seas region: Indigenous, non indigenous, cryptogenic.
- •If non indigenous: way of introduction
- •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
- •Geographic distribution in the Mediterranean and the Black Sea
- Documented impacts
- Putative impacts
- •Gaps in knowledge
- Putative impacts

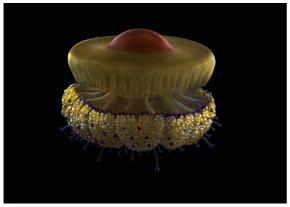
Aurelia aurita (Linnaeus, 1758)



- 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 enduretill 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 (food nutrients): 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).
- *Putative 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 (food nutrients): microphagous and photosynthetic due to the presence of symbiotic microalgae.
- Predators: Caretta caretta (Revelles et al., 2007).
- Documented blooms (one, several, many): 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.

- Putative 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)

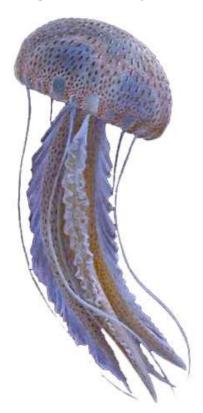


- Geographic status: non indigenous; originating from the Western Atlantic (Purcell et al. 2001), in coastal waters over a wide latitudinal range (40°N–46°S), it invaded the Black Sea in the 1980s, followed by subsequent invasions of the other large water bodies in the Mediterranean basin (Shiganova 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 cyclippid 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‰) (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 (food nutrients): 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 (one, several, many): 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 Western 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).
- Putative 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. Ocassionally 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 (food nutrients)*: zooplankton, including ichtyoplankton.
- *Predators*: several fish species (undocumented quantitatively).
- Documented blooms (one, several, many): 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.
- Putative impacts: not applicable (all the negative impacts of jellyfish are directly ap-

plicable 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.

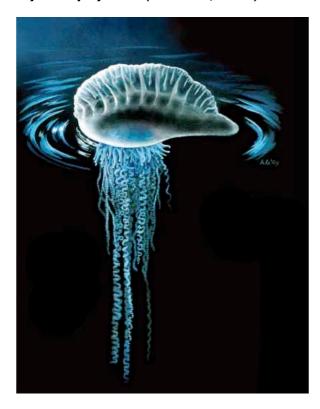
Phyllorhiza punctata (von Lendenfeld, 1884)



- 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 Noqueira, 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 (food nutrients): zooplankton.
- Predators: unknown.
- Documented blooms (one, several, many): 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.
- *Putative 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.

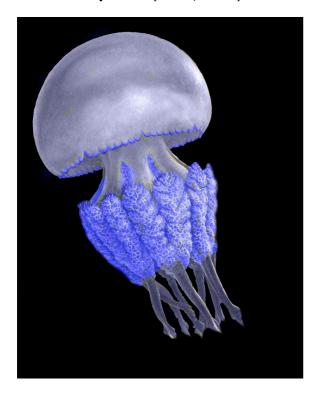
Physalia physalis (Linnaeus, 1758)



- 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 (food nutrients): larval fish comprised 70 to 90% 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 (one, several, many): 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).
- Putative 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: dependance 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 (food nutrients): diatoms (Lilley et al., 2009).
- *Predators*: unknown, probably many fish species.

- Documented blooms (one, several, many): 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 & 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.
- Putative impacts: unknown.
- Gaps in knowledge: triggering of blooms.
- Management measures: reduce eutrophication, utilization as a food.

Rhopilema nomadica Galil, 1990



- Indigenous or non indigenous or cryptogenic: 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 (food nutrients): unknown

- Predators: unknown.
- Documented blooms (one, several, many): many, in the Levant 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).
- *Putative 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*: prsent 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 (food nutrients)*: 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 (one, several, many): 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.
- Putative 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.

VII. ACKNOWLEDGEMENTS

This report stems from the Workshop on Algal and Jellyfish Blooms in the Mediterranean and the Black Sea, organized by GFCM at Itanbul, Turkey, on 6-8 October 2010.

Stefano Piraino provided precious advice. Giacomo Milisenda helped in the compilation of the Appendix.

The Commission for the Scientific Exploration of the Mediterranean Sea (CIESM) sponsored the pilot phase of the Jellywatch in Italian waters in the years 2009, 2010, contributing financially to the making of the poster on which the campaigns were based. Materials used to write this report stem also from the EU projects Jason, Sesame, Vectors; and on a PRIN project of MIUR.