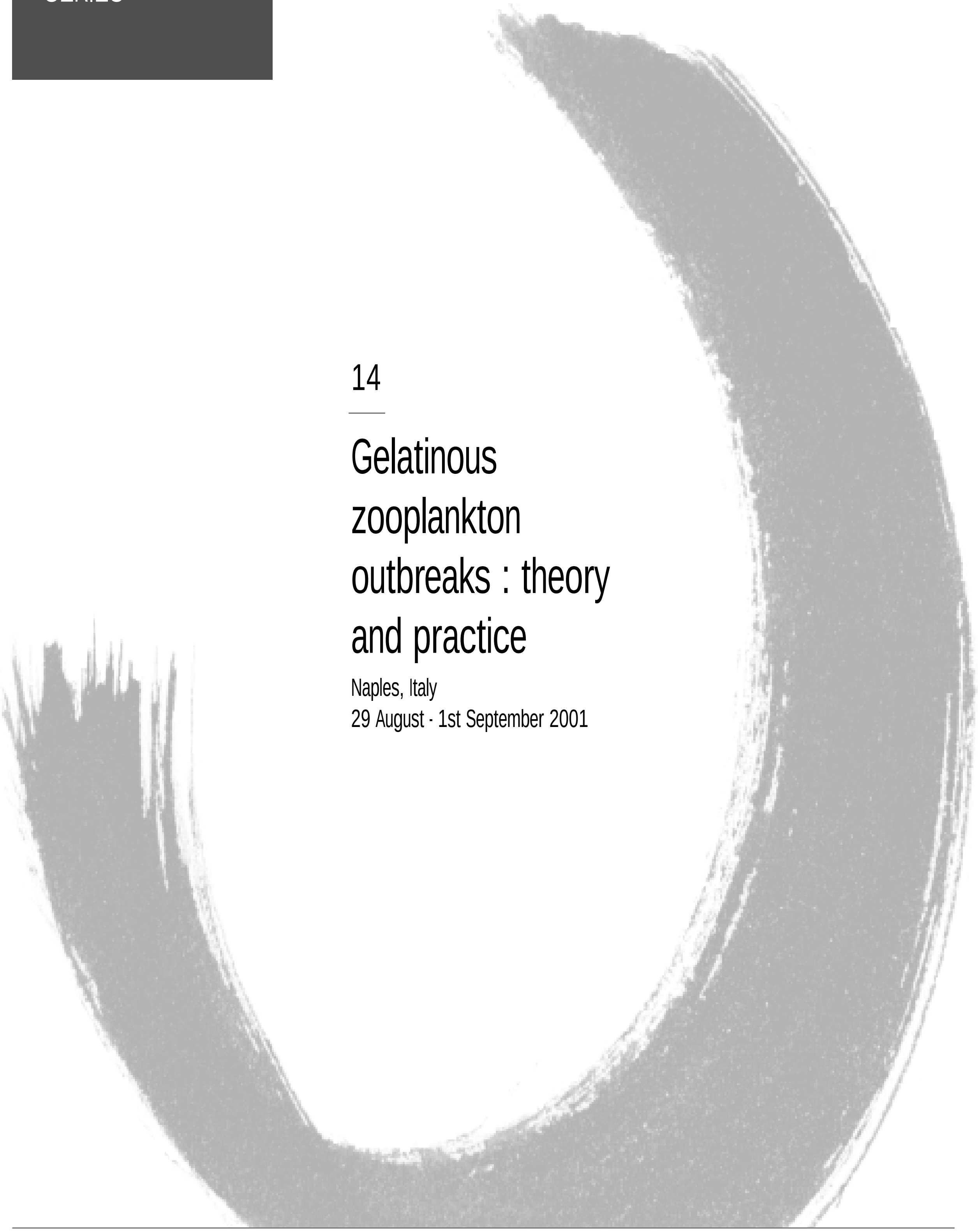
ISSN 1563-2727

CIESM
WORKSHOP
SERIES



14

Gelatinous zooplankton outbreaks : theory and practice

Naples, Italy
29 August - 1st September 2001

Commission Internationale pour l'Exploration Scientifique de la mer Méditerranée

CIESM Workshop Series

Gelatinous zooplankton outbreaks: theory and practice

Naples (Italy), 29 August - 1st September 2001

This is volume n°14 in the CIESM Workshop Series.

The collection offers a broad range of titles in the marine sciences, with a particular focus on emerging issues. The reports do not aim to present state-of-the-art reviews; they reflect the latest thinking of researchers gathered during four days at CIESM invitation to assess existing knowledge, confront their hypotheses and perspectives, and to identify the most interesting paths for future action.

To be cited as: CIESM, 2001. Gelatinous zooplankton outbreaks: theory and practice. CIESM Workshop Series, n°14, 112 pages, Monaco. <www.ciesm.org/publications/Naples01.pdf>

A collection edited by Frédéric Briand.

Publisher: CIESM, 16 boulevard de Suisse, MC-98000, Monaco.

CONTENTS

I - EXECUTIVE SUMMARY

II - WORKSHOP COMMUNICATIONS

1 - Dynamics of outbreaks : topological, spatial and physical constraints

2 - Tunicate outbreaks

3 - Jellyfish outbreaks

4 - Black Sea : *Mnemiopsis et al.* ...

I - EXECUTIVE SUMMARY

1. INTRODUCTION

The workshop was held in Naples from 29 August to 1st September 2001 in the magnificent “Sala degli Affreschi” of the Anton Dohrn Zoological Station. Nineteen scientists originating from twelve countries participated in the meeting at the invitation of CIESM.

In his opening presentation, the Director General of CIESM, Prof. Frédéric Briand, warmly thanked the President of the Zoological Station, Prof. Giorgio Bernardi, for his welcoming remarks and for the cordial hospitality extended to the participants. On their behalf he expressed his gratitude, and also great pleasure, for the opportunity to meet in one of the birthplaces of experimental marine science. It was particularly fitting that this seminar, which marked the first attempt of the new CIESM Workshop Series to address central plankton issues, would unfold here, a place so clearly associated with the historical development of plankton ecology. Ample thanks were expressed as well to Prof. Ferdinando Boero, Chair of CIESM Committee C6 on Littoral Environment and Workshop coordinator, for initially conceiving the theme of the meeting and providing, as usual, enthusiastic support towards its realization.

Aims and objectives

F. Briand went on to stress the prospective nature of this workshop. Rather than presenting a series of monologues on their research findings or “definitive” reviews, participants were encouraged to openly confront hypotheses, taking advantage of their different domains of expertise or geographic experiences, to enrich and enhance the originality of the discussions. From his own perspective, he was particularly looking for insights on some of the following issues:

- the extent to which gelatinous outbreaks are favoured by environmental disturbance, disequilibrium conditions, physical forcing, abundant food supply, or absence of top-down trophic control linked to overfishing;
- the time/space scale of such episodes;
- the identification of common evolutionary traits within the causative species;
- the resilience of pelagic communities to such events;
- the distribution of body mass and abundance at various trophic levels before, during and after outbreaks;
- the adequacy of available data sets and of current monitoring protocols.

F. Boero followed. He reminded everyone that the approach of the workshop was deliberately multidisciplinary. The aim was to integrate the views of plankton biologists, physiologists, system ecologists, and of physical oceanographers as well since the relation between gelatinous outbreaks and hydrodynamic forcing was of particular interest. In his overview of gelatinous plankton he emphasized many unresolved challenges, ranging from the major taxonomic difficulty of tracking the complex life stages of these organisms, identifying their function in benthic-planktonic coupling, to assessing their proper role and importance in current tropho-dynamic models.

These various questions run as an undercurrent through the following executive summary, which was drafted by Ferdinando Boero and Frédéric Briand, with sections contributed, where indicated, by Quentin Bone, Gabriel Gorsky and Tim Wyatt. Helpful editing comments were received as well from José Acuña, Emmanuelle Buecher, Patricia Kremer and Paul Nival; they are gratefully acknowledged.

2. BACKGROUND

2.1. Definitions (Quentin Bone)

Populations of gelatinous zooplankton, such as medusae, ctenophores, siphonophores, salps and appendicularians, vary much in abundance over an annual cycle in a more or less predictable manner, and tend to peak following the regular sequence of the phytoplankton spring pulse. In some years the expected plankton peak vastly exceeds the usual level and such unusual occasions are known as blooms. The term is also applied to sudden outbreaks of a particular species which comes to dominate the plankton for a period, and then resumes its normal seasonal abundance.

To recognise such events as “unusual occasions” requires knowledge of the “normal” baseline numbers. A further difficulty lies in the distinction between these two types of unusual events. Another resides in the botanical connotation of the term “bloom”. This led to some workshop members likening the concept of a bloom to that of a species, accepting the analogy with Tate Regan’s famous (1926) definition of a species as that which a good taxonomist says is a species. After much discussion it seemed sensible to retain the term plankton *blooms* only in relation to exceptional abundances of phytoplankton. The term *outbreaks* was deemed more appropriate to describe exceptional abundances (usually sudden and monospecific) of zooplankton, which can be seasonal or non-seasonal. This practice will be followed here, although this view was not shared by certain participants, especially F. Boero who argued that the term “jellyfish blooms” was perfectly acceptable as it remained embedded in the scientific literature, and that the distinction between blooms (multispecific, regular events) and outbreaks (monospecific, irregular events) should reflect extent of resource monopolization rather than systematics. Finally the term *accumulation* is applied to a mass of plankton organisms locally gathered by winds and currents.

2.2 A limited understanding (Quentin Bone)

Observations of vast concentrations of gelatinous organisms are not new: both Darwin and Huxley, on their respective voyages on the *Beagle* and *Rattlesnake*, sailed through areas of sea covered with salps, jellyfish, or siphonophores (Huxley, 1859). Yet it is only within the past few decades that the importance of the role of gelatinous organisms in marine food webs has become widely recognised, and attention directed to the causes and effects of their episodic pulses. Growing acceptance of the key role of gelatinous organisms has largely been due to innovations in observational techniques and to growing interest in trophic interactions.

More remains to be done. First, most gelatinous organisms, in particular ctenophores, are still sampled only in a fragmentary way by the usual standard nets, even with short hauls. Second, baselines from regular long-term biological and physical sampling, which are fundamental to understanding blooms and outbreaks, remain too few. In the Mediterranean, regrettably, long-term zooplankton time series (accompanied by physical observations) are only available from Villefranche-sur-mer (30 yrs for the “Filet Juday-Bogorov”; 23 yrs for the “Filet Régent”), Trieste (25 years), Naples (15 yrs) and from Chiavari (Genova) (13 years). The long term Plymouth series in the western Channel approaches since the beginning of the 20th century was only interrupted twice, first by the Kaiser and then by Hitler. The monthly samples continued until the Natural Environment Research Council (NERC) astonishingly ceased its funding in 1988.

Mainly from the study of exceptional outbreaks at only a few sites, some limited progress has been made in inferring the triggers and conditions for the formation of such events. A greater understanding of outbreaks will require improved observational and collecting techniques, plus long-term monitoring of the organisms and of relevant physical parameters such as mesoscale circulation, wind-stress and temperature. To avoid confusing causal relations with mere correlations, such studies should preferably be synoptic over a large scale.

Although outbreaks of gelatinous plankton organisms have often been seen in the Mediterranean there is still almost no information about their effective causes, or of correlations which would enable prediction of their occurrence (see Goy *et al*., 1989). Nor is there any detailed post-bloom study of the biological effects upon other surrounding planktonic organisms or of their effects on the benthos below. Quantitative data of the downward translocation of material from such occurrences through the water column are lacking.

2.3. Public and scientific perceptions

In general, phytoplankton blooms and pulses of copepods will pass unnoticed to the general public and, often, even to fishermen. Plankton accumulations will be noticed locally but have no great impact on human activities as they last only a short time. Gelatinous outbreaks, for their part, are immediately perceived as something unusual, falling outside the normal trends of species abundance in coastal waters. While thaliaceans usually thrive offshore and are seldom brought near the coastline, jellyfish are frequent along the coast and hence perceived more readily.

In the Mediterranean the importance of gelatinous zooplankton became evident in the early 1980's, the so-called "*Pelagia* years" (UNEP, 1984, 1991). Funds to investigate jellyfish outbreaks became suddenly available, due to widespread concern about the damage caused by the stinger *Pelagia noctiluca* to both tourists and fishermen. When the abundance of *Pelagia* went back to normality, funds were cut off .

Pelagia did not disappear completely, it simply became less evident, and scientists took note of episodic outbreaks in the hope of reviving the interest of funding agencies. Yet, despite record abundances of the scyphozoans *Aurelia, Chrysaora, Cotylorhiza, Pelagia, Rhizostoma*, the cubozoan *Carybdea*, the ctenophores *Cestus* and *Bolinopsis*, the pteropod *Creseis* and the urochordate *Thalia* (plus scattered records of siphonophores), they did not succeed: other planktonic massive events in the Adriatic sea – red tides and mucilages – had captured most of the attention.

The best, irrefutable, proof of the importance of gelatinous outbreaks came, in the form of a ctenophore, a decade later. *Mnemiopsis leidy*i appeared suddenly in the Black Sea and developed enormous populations that fed on both crustaceans (the food of many fish larvae and planktivorous fish) and fish eggs and larvae, impairing fish recruitment and largely contributing to the collapse of local fisheries. At about the same time, planktonic hydroids became abundant at George's Bank, and it was soon apparent that they did feed on cod eggs and larvae, adding to the concerns of a troubled fishery industry (Avent *et al*., 2001).

There lies a main problem in investigating the impact of gelatinous zooplankton on the dynamics of marine food webs: the long delayed reaction and the multiple paths between cause and effects (see fig. 1). It is not just public perception (tourists or fishermen), but also scientific perception which is to blame. Fisheries theory recognizes that egg and larval mortality rates may be the most important determinants of subsequent recruitment success, and that starvation of larvae may lead to increased vulnerability to predators; but the causes of starvation and sources of predation are poorly characterized. All nations, even the poorest ones, support research on fisheries, so as to understand the functioning of the systems impacted by this human activity and thus better manage coastal biological resources. Yet, very little, if any, of these funds is being spent to study the impact of gelatinous predators (see Purcell *et al*., 2001, for an overview).

Considering the large echo of the *Mnemiopsis* story, will this remain the case much longer? Published work on the impact of medusae and ctenophores on fish populations does exist, but not in the Mediterranean area. This may soon change as the Black Sea catastrophe provides an outstanding demonstration of the importance of gelatinous animals ... perhaps the only positive outcome of the "*Mnemiopsis* affair".

3. DYNAMICS OF OUTBREAKS

3.1 General considerations (Tim Wyatt)

Over the last thirty years, international scientific interest in outbreaks of planktonic organisms has been fostered by the growing realization that as our exploitation of the marine environment intensifies, some species can assume the roles of weeds or pests. This new perspective was first apparent with respect to microalgae, and there is a growing catalogue of phytoplankton species which

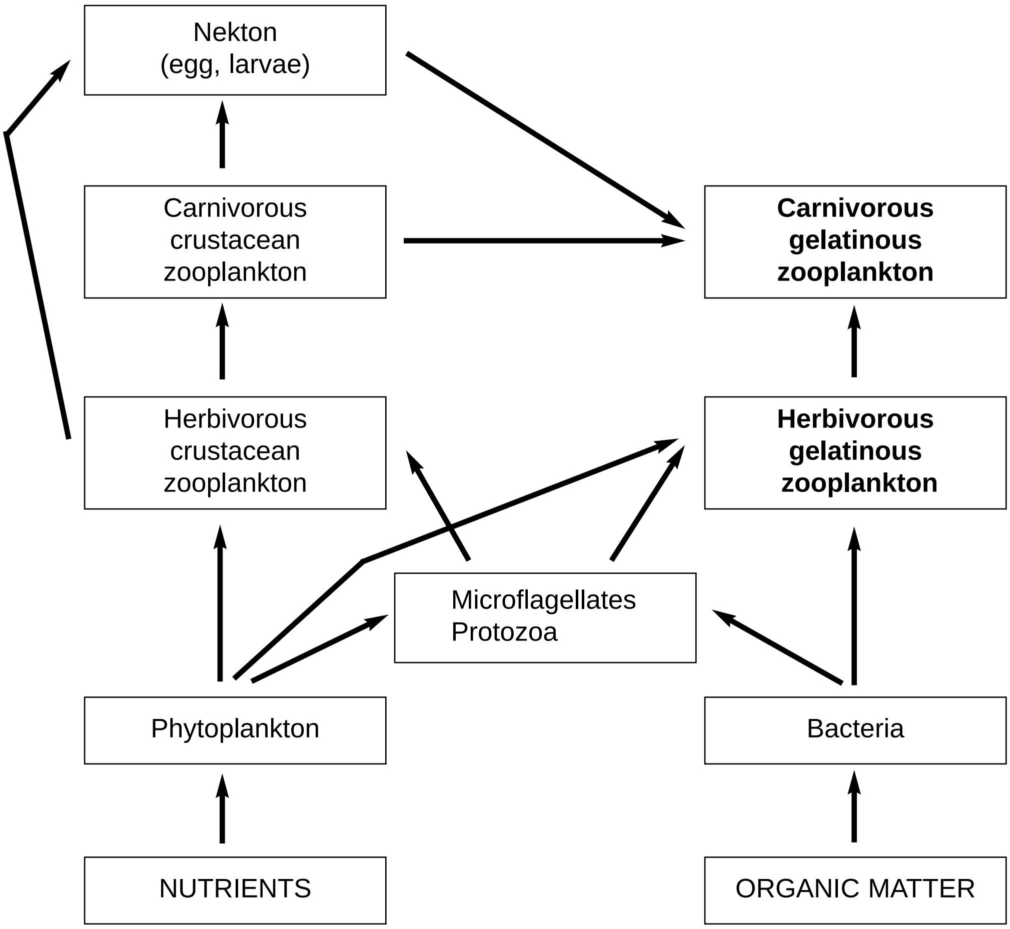


Figure 1. Simplified food web forming the basis of the pelagic food chain. Gelatinous animals are indicated in bold. By feeding on different compartments of the pelagic food web and acting as “sinks”, they are able to generate strong perturbations on the transfer of matter in the pelagic ecosystem.

affect human health, usually through consumption of fish and shellfish (and sometimes directly in the form of contaminated drinking water), and which have negative impacts on both the harvesting of wild marine resources and aquaculture. There are also microalgal phenomena such as *mare sporco* and toxic aerosols which affect the tourist industry. Certain species of the taxonomically diverse group of zooplankton colloquially known as “jellies” are now added to this catalogue of pests following premonitory warnings such as massive outbreaks of *Aurelia aurita* between 1977 and 1983, of *Pelagia noctiluca*, in the 1980s, in the Mediterranean and of *Mnemiopsis leidyi* (most likely an introduced species) in the Black Sea beginning in 1987.

Such outbreaks are often sporadic and of short duration, so that they tend to catch the scientific community off guard and discourage systematic long term studies (see section 2 above). There are thus few accounts of the environmental conditions which precede them, and empirically based answers to questions about how such events are triggered are frequently unsatisfactory. Theoretical studies too have been slow in coming to grips with these problems. An earlier generation, provoked by Hutchinson’s (1961) “paradox of the plankton” and the principle of competitive exclusion, was less interested in monospecific events than in the coexistence of many species. It was not outbreaks or blooms as such which required explanation but their absence (Slobodkin, 1989). This is no longer true, but many current studies of plankton population dynamics limit themselves to a phase of rapid growth driven by external forcing, and cannot therefore illuminate the effects of intrinsic regulatory mechanisms and life history strategies on these dynamics.

Further progress in understanding the population dynamics of jellies at the single species level should result from considering entire life cycles rather than only those stages which cause outbreaks. For example, in a simple life cycle where benthic and pelagic stages alternate, the former may make a significant or even essential contribution to the population in the water column (see Boero *et al.*, 1996). Then the success rate with which the water column is inoculated and the timing of this process become essential ingredients of the dynamics of the pelagic phase. The dynamics of the benthic phase are similarly determined by the pelagic phase, and its success in producing the appropriate stage for settlement. If sexual phases intervene, and if there are threshold densities necessary before life stage transitions can be accomplished, these processes and constraints too need to be taken into account. Acquisition of the quantitative data needed to make progress in understanding the population dynamics of jellies presents many challenging technical problems for field workers.

At the system level, changes in the composition and productivity of planktonic communities have been linked to such trends as climatic fluctuations, eutrophication, maritime traffic (through the associated transport of invasive species in ballast water) and trade in shellfish and other livestock, and aquaculture. There is also the strong probability that fishing pressure has now reached levels sufficiently intense to cause radical changes in the structure of marine food webs (Pauly *et al.*, 1998; CIESM, 2000); this trend is likely to favour jellies by releasing food resources that formerly supported fish stocks and their recruitment. If the details of such switches can be described, elucidation of the mechanisms involved could make a major contribution to fisheries science. New sampling procedures are revealing that jellies are much more abundant than conventional nets and other samplers indicated in the past, and that some of them have remarkably high growth rates. These findings are transforming our views of marine ecosystems, and providing an additional tool for exploring issues such as climate change and the impacts of human exploitation of the sea.

3.2. Life cycle "strategies"

Gelatinous plankton are characteristically sharply seasonal, with massive presences in a given period and almost no individuals during the rest of the year. Where are these animals when they are not there ? In other words, how can these organisms "escape into rarity" for a long time, then become extremely abundant during usually brief periods ? F. Boero argued that the answers are essentially two :

- Life history adjustment : to become rare when conditions are unfavourable and become abundant when conditions are favourable.
- Life cycle adjustment : to become dormant when conditions are unfavourable and become active (and abundant) when conditions are favourable. In this case, the total population size is more or less constant, the disappearance of active stages being compensated by the presence of resting stages.

Life history adjustment passes through sharp population bottlenecks, and is probably a risky way to face unfavourable conditions, whereas life cycle adjustment involves a period of rest or, at least, of permanence in another domain than plankton. This second strategy is very well known in most jellyfish, with life cycles passing through benthic polyps that represent a way to escape from plankton. Polyp stages, furthermore, are colonial and allow the sudden release of great numbers of medusae in short periods, leading to population pulses that can sometimes transform into outbreaks. The sudden release of many medusae is an optimal strategy to take advantage of favourable conditions that take place in a short period and disappear.

Despite the apparent advantages of life cycle adjustment, several holoplanktonic forms of gelatinous zooplankton seem to be able to survive at low population densities when conditions are unfavourable, then grow and reproduce rapidly when conditions are favourable.

- Hydrozoans and Scyphozoans, with few exceptions, exhibit life cycle adjustment, with a sharp tendency towards modularity in polypoid benthic stages. Notable exceptions to this rule are the holoplanktonic Trachymedusae and some Scyphozoa that do not have a polyp, like *Pelagia noctiluca*.
- Ctenophores do not have benthic resting stages and, as self-fertilizing hermaphrodites, are perfect candidates for life history adjustment.
- Salps, Doliolids, and Pyrosomes are holoplanktonic, alternating sexual and asexual repro-

duction, and so can increase population size very rapidly. In one doliolid species, life history adjustment to a special short cycle is known.

- Appendicularians are an exception to this, displaying life history adjustment, with sharp population reductions during unfavourable periods.

J. L. Acuña (this volume) explored this latter aspect in depth, presenting a theoretical model to explain appendicularian population dynamics through sequences of flushes and crashes. G. Gorsky (this volume) went further, focusing on behavioural traits as causal mechanisms of appendicularian outbreaks, calling attention to the problem of finding partners for fertilisation. Subtle behavioural interactions, linked also to the release of sperm attractants, are at the base of the event.

One would expect species with modular growth to be more prone to outbreaks than species without modularity. The sudden, massive appearance of ctenophores in the Black Sea shows the obvious limits of this prediction... while buttressing the view that “young” systems with species-poor fauna are particularly vulnerable to species introductions (the San Francisco Bay ecosystem provides another example of vulnerability to invasions).

3.3. The puzzling problem of seed populations

If we revisit the question “where are these species when they are rare ?”, presumably, there are seed populations, somewhere, constituting a pool of individuals that will trigger population increases. For some species with benthic stages, the answer is obvious: they are in the benthos, either in an active form or as resting stages. Most jellyfish, for instance, have polyp stages that can be active, so feeding and reproducing asexually, or can also undergo dormancy under negative conditions. For many species and higher groups, however, there are no known benthic stages, or resting stages in general, so that one has to expect that some individuals spend adverse conditions at particular places, when these species are generally absent or very rare. These “seed specimens” should remain more or less together, in order to be able to find each other and reproduce at the onset of the favourable season.

To complicate matters, species can have different life cycle patterns during and between outbreak periods. Bouillon *et al*. (1991), for instance, described an alternative life cycle pattern for the jellyfish *Laodicea indica* : during an outbreak, the planulae settled and gave origin to gonothecae that immediately budded new medusae, to fuel the population explosion, whereas, at the end of the outbreak, the planulae settled and metamorphosed into long-lived hydroid colonies. This suggests that what we see as a life cycle pattern during an outbreak is not necessarily the only pattern, and that species might behave in a different way in the aftermath. It would not be surprising, then, if resting stages were discovered as well in presumed holoplanktonic species, such as *Pelagia noctiluca* or thaliaceans and ctenophores.

Migration in space or time is not a requisite to maintain seed populations, which can also be based on widely spread, highly diluted numbers of individuals. Negative population growth rates of these seed populations during unfavourable periods can be compensated by explosive opportunistic growth during favourable periods or at favourable places (see Acuña, this volume). Survival of these populations will depend on fine evolutionary tuning between life cycle traits and the spatial-temporal structure of the habitat template.

4. TRIGGERING MECHANISMS OF OUTBREAKS

Knowledge is still fragmentary, seriously limiting our predictive capacity, but it is at least clear from experience that, for an outbreak to unfold, a certain number of favourable conditions must be met :

Climatic. The relative stability of the water column, which is largely conditioned by climatic factors, is a requirement for the development of a gelatinous zooplankton outbreak. First with respect to food supply, as net primary production is enhanced when the depth of the mixed layer is reduced; this largely accounts, through the distribution of temperature and rainfall, for the noted seasonality of phytoplankton peaks (Sverdrup, 1953). Next, to allow the survival and reproduction (see below) of these fragile animals. Due to limited data sets, there is unfortunately little statistical evidence firmly linking gelatinous massive events with climatic fluctuations (see Goy *et al*, 1989 for *Pelagia noctiluca* outbreaks in the Mediterranean). It will be most interesting to monitor the sensitivity of gelatinous outbreaks to global climatic change in years to come; such massive events may reveal pluri-annual trends in the state of the global environment.

Physical forcing. Hydrodynamics, winds, turbulence, advection, currents will all affect the availability of food resources, the rate of encounters of sexually reproducing individuals and the spatial scale of the outbreak extension. As indicated by P. Nival, the turbulence rate is particularly critical: it must not be too high, so as to favour gamete interactions and sexual reproductions, and yet high enough to scatter the eggs and expand the outbreak. In her presentation, based on long-time series in the bay of Villefranche, P. Licandro emphasized the importance of atmospheric forcing (wind, and pressure) in the occurrence of salp outbreaks. Further, when convergences bring together a sufficiently large number of individuals, these may well become the founders of an outbreak (or be taken for one!).

The potential contribution of physical models to understanding and even predicting gelatinous outbreaks was a subject of debate, intentionally stimulated by the participation of physical oceanographers. As A. Lascaratos remarked, marine biological phenomena are driven, to a large extent, by physical processes taking place in the vertical and horizontal dimensions. While it would be simplistic to suggest that plankton is “at the mercy” of physics, some recent hydrodynamic-biological models are able to generate quite realistic quantitative predictions of plankton dynamics (see G. Lacroix, this volume). To generate accurate qualitative predictions, however, it is clear that a detailed knowledge of the species biology and natural history is required. This was evidenced by F. Pagés (this volume) in presenting the case for the dominance of the jellyfish *Cotylorhiza tuberculata* in Mar Menor. In this lagoon, eutrophication cause recurrent outbreaks of the scyphomedusa – instead of the “expected” phytoplankton blooms – for two reasons: (a) its polyps find a proper substrate in the millions of empty oyster shells now paving the basin; and (b) its endosymbiotic zooxanthellae (captive phytoplankters) outcompete free phytoplankters in the uptake and assimilation of high-level nutrients.

Biological. Once the physical conditions are favourable, an opportunistic species must take advantage of a situation that, invariably, will not last very long. As outlined in section 3 (above), this is where adaptive reproductive strategies come into play. Asexual reproduction or self fertilization are surely the easiest way to produce in a short time the huge number of individuals recorded in an outbreak, even starting with a very low population density. For species that do not reproduce asexually, intense sexual reproduction will be needed to quickly produce the huge numbers observed. For many species with circannual internal rhythms of activity, the tuning of such rhythms with the onset of favourable conditions will be important in triggering an outbreak.

Ecological. A population explosion reflects the ability of a species to monopolize resources (i.e. capture them at a faster rate than competitors) while escaping predation. Clearly gelatinous species are quite adept at that. This led workshop participants to speculate on the relative merits of hypotheses based on body size, “hit and run” strategies, or peculiar density-dependent feeding behavior, without however reaching a clear consensus. Another possibility, raised in section 3.1, is that gelatinous outbreaks may become more frequent due to a combination of foodweb dynamics and overfishing. Although the passage from a “fish period” to a “jellyfish period” is not yet supported by solid evidence, it seems reasonable to speculate that jellyfish are indeed taking advantage of newly created spaces in marine foodwebs (see Mills, 1995). Indeed, E. Mutlu argues in this volume that the outburst of *Mnemiopsis* in the Black Sea was rather the outcome of overfishing on coastal over-wintering anchovies by Turkish purse seiners, than the cause of the collapse of the anchovy fisheries.

Predicting the occurrence of phytoplankton blooms is not an impossible challenge [spring plankton blooms are indeed quite predictable at temperate latitudes]. The really difficult task is to predict which particular species will proliferate in an environment which somewhat resembles a “lottery” (see Chesson and Warner, 1981). Do we have a situation where the winners are chosen randomly, or where some participants (in this case the species that were abundant in the previous favourable season) can buy many more tickets and thus have more chances to win ? In the latter case, we would predict that a set of dominant species will be recurrent for some time, at least until some drastic change occurs.

In the case of outbreaks, the lottery has only one winner. In some instances, the winner is an alien species originating from distant shores, as demonstrated by the successful invasion of the Red Sea jellyfish *Rhopilema nomadica* (Galil *et al.*, 1990) in the Levantine Basin or the dramatic, accidental introduction of the ctenophore *Mnemiopsis leidyi* in the Black Sea (G. Harbison, this volume). In the latter case, it appears that ballast waters brought another ctenophore to the Black Sea, *Beroe*, first recorded there in 1992 and now, it would seem, a rather efficient controlling agent of *Mnemiopsis* (see T. Shiganova, this volume). Both morphological and genetic comparisons concur in ascribing the species of the Black Sea to the *Beroe ovata* reported by Mayer from the United States, that is, a different animal from the nominal species with the same name reported by Chun from the Mediterranean. Apparently, there is a ctenophore highway linking the East coast of the American continent with the Black Sea !

More often, outbreaks are due to indigenous species: for example, two gelatinous species, *Pelagia noctiluca* and *Velella velella*, known for centuries in the Mediterranean, have caused massive outbreaks there in the past few years. Unfortunately, for most taxa we still ignore what constitute favourable conditions or, inversely, the causes of poor population growth (P. Kremer, this volume). This obviously calls for systematic eco-physiological research, to be carried both *in vitro* and *in situ*.

5. IMPACT OF GELATINOUS MASSIVE EVENTS

5.1. Main impact on human activities

While not the focus of the workshop, this aspect was touched upon by many discussions and presentations, which highlighted the usually devastating impact of enormous medusan numbers on human activities. Here follows a brief, synthetic listing.

5.1.1. Impact on fisheries via :

- net clogging. This is a highly visible impact: fishermen may collect enormous quantities of gelatinous organisms in a short time and their equipment will be often significantly damaged, as was demonstrated by astonishing photographs presented by E. Buecher from the northern Benguela current. In addition, usual fishing grounds will become unsuitable for exploitation until the outbreak is over. The economic damage is easily quantifiable in terms of lost days of activity, damaged gear and reduction of the catches.
- predation on fish food. The vast numbers of gelatinous grazers and predators will draw much energy from food webs, impairing the flux of matter and energy from either phytoplankton or crustacean grazers to the higher levels of the food web (see Fig. 1). In doing so, they will reduce the availability of food for exploited species. The economic damage due to this impact is not easily quantified.
- predation on fish eggs and larvae. This direct impact on fish populations has been demonstrated in several cases and may well be the main impact of gelatinous massive events. Mortality of larvae and juveniles is tractable (with adequate sampling) but hard to attribute to specific causes. As fishery recruitment models suggest, the failure of a year class might easily be due to something that happened somewhere else, some months or years before. Understanding these events requires models integrating proper knowledge of natural history. The outbreak of *Velella velella* that coloured in blue the beaches of the Western Mediterranean in the spring of 2000 likely had a large, but yet unnoticed, impact on the recruitment of many fish species with hyponeustonic eggs and larvae. The economic damage of such impacts is easily quantified when the effects are catastrophic —as was the case of *Mnemiopsis*— but is less tractable in other cases or when mixed causes of larval mortality come into play.

5.1.2. Impact on tourism

There is at least one known instance of a jellyfish outbreak generating tourism income – the “Aurelia lake” at Palau – but it was exceptional and of short duration. More generally, tourism and jellyfish do not mix well, and outbreaks have caused massive losses in tourism revenues, from the Levantine waters to the Mar Menor of southern Spain.

Jellyfish outbreaks are obvious and their effect on human perception is immediate, due to the painful stings they may inflict to swimmers. Much tourism in the Mediterranean Basin is linked to coastal visits and more or less prolonged sea bathing. When swimming is perceived as a "dangerous" activity, tourists simply go away and potential visitors will not come. The economic harm is evident and can be serious when tourism is the main revenue, as is the case of many coastal economies.

5.1.3. Impact on human health.

Certain Mediterranean jellyfish, like the hydrozoan *Olindias* spp., the scyphozoan *Pelagia noctiluca*, and the cubozoan *Carybdea marsupialis*, will inflict painful stings, resulting in direct harm to human health. Not only swimmers, but also fishermen handling gelatinous matter trapped in their nets, can suffer those stings. Fortunately, deadly jellyfish, like the cubozoan *Chironex*, are not present in the Mediterranean.

5.1.4. Impact on industrial activities.

Outbreaks of gelatinous animals can clog the suction pipes used by coastal industries and power plants to pump marine water in their cooling systems, thus impairing production.

5.2. Impact on the ecosystem

The impact of gelatinous zooplankton outbreaks on the functioning of the sea, and in particular on marine tropho-dynamics, are still largely a matter of speculation. It is reasonable, at least, to expect them to play a marked role on benthic-pelagic coupling (Marcus and Boero, 1998), and to seriously disrupt the "regular" transfer of matter and energy by acting as "sinks" in the pelagic food web (see Fig. 1).

5.2.1. Herbivore outbreaks

Except for appendicularians, gelatinous zooplankton grazers are not a constant in plankton samples. Thus their massive presence will be often considered as an outbreak even if it is a "normal" pulse accompanying a phytoplankton bloom. As the body of these animals is largely made of watery extracellular matrix, potential predators may have to ingest great quantities of material to have a low energetic return. Whether these gelatinous herbivores fuel the detrital or the microbial pathways, or whether they constitute an appreciable food source to marine turtles and certain fish, is unclear. Rapid progress is expected on this front as soon as quantitative population studies of their potential consumers become more systematic.

5.2.2. Carnivore outbreaks

Cnidarians and ctenophores are the main representatives of the gelatinous zooplankton carnivores. They channel secondary and tertiary production, competing for food with other zooplankers and with planktivorous fish, and they act as predators on many fish species, by feeding on their eggs and larvae. The outbreak of a jellyfish or ctenophore species will usually fill the water column with enormous numbers of voracious organisms that will feed on almost everything, exerting a major disruption on the whole foodweb (see hypothesis developed for the Adriatic by F. Boero, this volume).

6. URGENT PRACTICAL NEEDS

6.1. Upgraded sampling and monitoring

If gelatinous plankton constitutes an old, largely unresolved "black box" for planktonologists, it is largely due to dismal sampling yields. Traditional plankton nets are impaired within a few minutes when operating in a gelatinous outbreak and the collected samples will fast become an unrecognisable blob of little use to plankton studies. Sampling periodicity, furthermore, is often inadequate to intercept events that last a short time, as many gelatinous outbreaks do. Traditional sampling is crustacean-biased, in part due to a regrettable, but common lack of interaction betweeen scientists working on crustacean and gelatinous plankton.

Awareness of gelatinous plankton as something more relevant than a collection of weird transparent organisms came with the advent of blue diving and with the use of submersibles for underwater exploration (see Boero and Mills, 1997). The gelatinous organisms that were seen occasionally

Box 1. GELATINOUS ZOOPLANKTON - SAMPLING AND OBSERVATIONAL TECHNIQUES

by Gabriel Gorsky

I. Net sampling

a) standard WPII nets with mesh size larger than 200 µm are used for meso-zooplankton sampling (for details see SCOR-UNESCO Monographs on Oceanographic Methodology : Zooplankton Sampling 1968, UNESCO Press). Net sampling often proves destructive for fragile gelatinous structures but the damage will be reduced by using adapted cod ends.

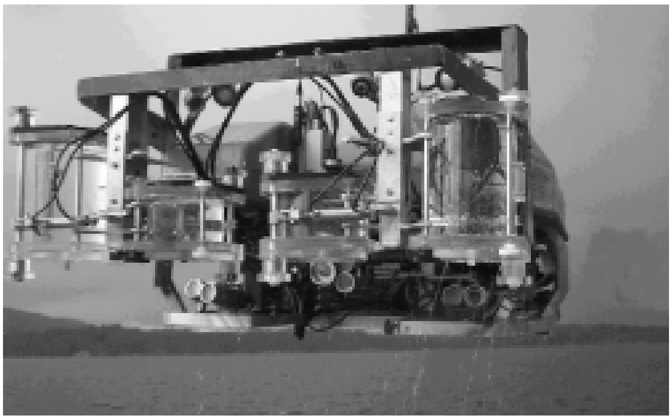
b) large collector nets (20-60 l) are used for sampling large gelatinous organisms. Their use is limited due to handling difficulties. When encountering dense populations of medusae, trawl nets are more appropriate.

c) multiple nets (MOCNESS BIONESS Hydrobios) are poorly adapted for sampling gelatinous plankton, especially for taxonomic purposes, due to their destructive nature.

II. Optical methods

a) Video profiling: this method is promised to an intense development in the future. Actually only a few towed systems are in use. One is the Video Plankton Recorder built at the Woods Hole Oceanographic Institution (Benfield *et al.*, 1996; Davis *et al*., 1996), which visualizes and quantifies small-size zooplankton. The Underwater Video Profiler constructed by the Laboratoire d'Océanographie in Villefranche sur mer (France), is another, allowing the visualization of the macrozooplankton from the surface to a depth of 1000 m (http://oceane.obs-vlfr.fr/~pvm). With the rapid progress of imaging technologies, the quality of the data collected by both instruments is constantly improving. However, although the quantitative data are of good quality, the images are not satisfactory yet for the taxonomists. They may be used for a rapid determination of dominant populations, but not for the identification of rare or new species.

b) Submersibles: manned submersibles are well suited for the qualitative *in situ* study of large gelatinous organisms. They allow good quality imaging and sampling of the animals. ROVs may also fulfill this task, but less easily due to the narrow field of vision, slow reaction, and laborious manipulation, among others.



*The Norway Aglantha ROV during medusa collections (*Periphylla periphylla*) in Norwegian fjords. The collecting devices are the hydraulic opening closing "Detritus samplers" from the HBOI (http://www.hboi.edu)*

c) Bioluminescence: the pattern of bioluminescent organelles may be used as a taxonomic descriptor and optical methods are in development for the acquisition and treatment of this signal. It has been successfully used on manned submersibles (Mixed Light Imaging System-MLIS, Widder 1992; see also: http://www.hboi.edu/marinesci/biolum.html).

d) AUV's: Autonomous vehicles are considered as the technology of the future in oceanography. Currently the degree of autonomy and the scientific instruments' load are the limiting factors. In the future, these vehicles will be able to detect patches of organisms and to use imaging techniques for taxonomic identification.

e) Aircraft observations: large superficial outbreaks of gelatinous organisms such as medusae or salps can be observed from aircrafts, allowing their extent and evolution in space and time to be measured.

III.Acoustics

Acoustics is not well adapted to the study of gelatinous organisms. Most of them are permeable to sound and do not produce a well-defined backscatter. Some gelatinous zooplankton such as the physonect siphonophores have a gas inclusion (pneumatophore), which can be detected acoustically. In fact, they are viewed as potentially significant sources of scattering in the ocean. Some pattern of the echo amplitudes may be specific to a faunistical group but the variability is still high.

from shipboards, or were occasionally collected in huge quantities with traditional samplings, proved to be more common than previously thought. The best way to observe gelatinous plankton is to look for them and this can be done in several ways : looking from shipboards, diving in blue water, observing from submersibles, using underwater automatic and video cameras.

The problem of obtaining intact samples remains acute for such fragile species. G. Gorsky provides here (see box 1) a brief but up-to-date review of sampling and observational techniques now available to the researcher... beyond the reliable, but quite limited, old-fashioned hand collecting.

Another crucial issue is the geographic coverage. In the future, it should be possible to determine the scale of outbreaks not only by satellite observations (unfortunately sensors specifically aimed at gelatinous plankton organisms have yet to be devised) but also by simultaneous observations at linked stations. In the Mediterranean, the development of an “early warning system” for the detection, monitoring and scientific investigation of gelatinous plankton outbreaks appears as a realistic goal, using the strength of the CIESM network and the synergy of its associated coastal research institutes on both north and south shores.

6.2. Experimental investigations of selected target species

This issue was addressed by a sub-group coordinated by P. Kremer. Part of our lack of understanding of gelatinous outbreaks is due to a lack of knowledge of the basic physiology, biology and ecology of the species concerned. Gelatinous zooplankton that are capable of producing outbreaks have a variety of life cycle and/or life history adaptations. Although we already have some understanding of these as well as trophic relationships, modes of reproduction, ecological energetics, and behavior, we still have only a rudimentary understanding of how they combine to control population dynamics.

A focused, extensive, investigation of a few selected species, mixing complementary *in situ* and *in vitro* studies, should prove highly beneficial. This would involve experiments that investigate not only how the animals respond when conditions are favourable, but also survival strategies when conditions are poor. Such target species should be cosmopolitan, easy to catch, easy to handle in the laboratory and possess a relatively short, tractable life cycle. Both carnivorous and herbivorous species, displaying either asexual or sexual reproduction modes, should be represented. *Thalia, Pleurobrachia, Clytia, Muggiaea, Oikopleura* and *Aurelia* would be good examples.

6.3. Expert training

The diversity of gelatinous plankton, if we exclude the highly diverse, small neritic hydromedusae, is in fact, rather low, likely underestimated due to the shortcoming in sampling and collection methods noted earlier. The known representatives of the phylum Ctenophora count only a few dozens; very few also are the oceanic hydromedusae (Narco- and Trachymedusae), the Scyphozoa, the Cubozoa, the Siphonophora and the Thaliacea in general. If their taxonomy is not fully settled, many species are cosmopolitan and most are well described in the scientific literature. Yet only very few people are able to properly identify gelatinous zooplankton species. This is quite paradoxical, when one considers the importance of this category on marine ecosystems, and their impact on human activities at large.

Specialists are not only few, most are far ahead in their career, and there are no new recruits in this scant research community. An international program to support the formation and training of marine zoologists in this area appears much needed (see Boero, 2001). There is a vast number of exciting questions on the gelatinous world that remain unanswered, which guarantees that investments in this direction will be fruitful. This field is very far from having been overexploited by the scientific community. For most species, for instance, the life cycle is unknown and current taxonomy covers just the pelagic stage. The problems of seeding populations, of the triggering mechanisms, are still wide-open. These issues will require new people and new ideas.

II - WORKSHOP COMMUNICATIONS

II - 1. Dynamics of outbreaks : topological, spatial and physical constraints

Conditions for blooming of pelagic species

Paul Nival and Gabriel Gorsky

Laboratoire d'Océanographie de Villefranche, Station Zoologique, Observatoire
océanographique de Villefranche/mer, France. Email: nival@obs-vlfr.fr

The occurrence of blooms of zooplankton species is most of the time impressive. However, their duration is usually short and the reasons for the anomalous development of species are still not clearly identified. In addition, these events are not tractable by the present planning of oceanographic research.

BLOOM

How to define a bloom? Spring bloom of phytoplankton means the increase (population growth) of different species which benefits from the increase in light, the decrease in vertical turbulence and the absence of grazers. These three conditions are certainly important for the development of a particular species which leads to its dominance in the community. Bloom of a zooplankton species corresponds to its ability to out-compete other species using the available food resources, avoiding predation and reproducing intensely.

Smayda (1997) suggested a definition for harmful phytoplankton blooms. Some remarks are valid for zooplankton species. A species is considered as a blooming species when it becomes conspicuous in the sea and when its is harmful to humans. However this condition depends on the size of the sample and on the sampling method used. During a bloom other species are more or less eliminated. However it might be a bias due to sampling problems like clogging of plankton nets by mucus.

There are large differences in the abundance of living quanta to qualify as a bloom (phytoplankton : $n > 5.10^8$ cells/m^3; doliolids : $n > 10^3/m^3$; salps : $n > 10^2/m^{3;}$ medusa : $n > 10/m^3$).

ASSEMBLAGE OF SPECIES

Different methods have been suggested to estimate the deviation of the species community from equilibrium: diversity index, rank-frequency graphs (Frontier et Pichot-Viale, 1991). However this picture of a climax as an attractor comes from the transposition of terrestrial observations and especially from plant ecology. The major differences between terrestrial communities and planktonic ones are:

- sensitivity to perturbations: the effect of wind that might have a strong influence on marine species (vertical transport in strong gradient of physical conditions) and negligible on terrestrial ones (consequence of roots and stem for plants, refuges in bottom substrate for animals);
- generation time: short for planktonic species. Thus, short term perturbations have a greater effect on these species than on long lived terrestrial species.

The rank-frequency curves show some regularities which are the combination of dynamics of the food web and biological properties of each species. How can one species depart from the whole community picture and dominate? One hypothesis is that the species assemblage is far from an equilibrium state and that there is some ecological space to be used either by one of the species of this community or by an introduced species.

FOOD WEB

The species assemblage depends on the available energy in the ecosystem and on the energy input. The community depends more or less on the primary producers, depending themselves on the regeneration of nutrients or on the physical forcing which produces the nutrient input. Physical forcing is necessary to keep the pelagic system running. As a consequence there is no steady state visible, even though it exists as an attractor of the species assemblage, and there is a permanent opportunity for a species to rush into a free ecological space.

The amount of matter in a body of water, and especially the intensity of the nutrient input, sets the maximum number of living quanta of a defined size. Beside the rank-frequency curve, the particle size frequency distribution in the sea gives another reference property to the species assemblage. There are more individuals per unit volume in small species than in large ones. The abundance decreases exponentially with size. Sheldon *et al.* (1972) have shown that biomass of individuals in a unit of logarithm of size is the same all over the size range of particles. Each species depends on the overall size spectrum of species and also on the energy flux produced by primary production.

It is classical to draw food webs to show how much matter is distributed among the species, to detect the major food chain which convey the major part of energy entering the food web. Most of these schemes, if not all, do not consider the different species, but guilds of species assumed to have the same role on matter transfer, or taxonomic groups provided that one species is common and dominate the quantitative role of the group. However, the biocenose is the result of an equilibrium between species interaction or competition. The strength of these interactions should be evaluated because a small amount of energy (auxiliary energy of Margalef, 1974) might push the species competition in different directions.

SPECIES INTERACTION - POPULATION DYNAMICS

One species can out-compete others through three processes:

- reproduction: a high spawning rate will give a burst in the population dynamics of the species;
- feeding: in order to maintain the high spawning rate and rapid growth of individuals, the food resource should be high. The blooming species should have a better access to food that the other species (feeding competition);
- mortality: mechanisms to reduce predation will allow each generation to produce a high proportion of reproducing adults.

A successful blooming species should be able to capture efficiently the matter distributed in a given size range. That is to capture the food of other species, and eventually of early life stages of its predators, to shed a large number of eggs or propagules, to escape predator at each life stage, to grow rapidly.

Feeding characteristics are important. A blooming species should catch food of any size. It should not be a specialist. One characteristics of the simple organisms as medusa or ctenophores is that they are not satiated. Ingestion rate is linearly related to concentration of prey available. There is no saturation threshold for these gelatinous organisms as in other species or it appears at very high concentrations of preys (Matsakis et Nival, 1989; Frid *et al.*, 1994). Purcell (1997) suggested that medusa feed on a large variety of prey types.

Wyatt and Jenkinson (1993) emphasise the life cycle which is neglected in most studies in marine productivity. The ability to bloom for a species might be related to special properties of its life stages. The picture of the coupled life cycle of ctenophores and copepods shows two opposite situations in these competing species. The game is played by the larvae and adults of each species. Depending on the number of adult individuals and the adjustment of the life cycle one or the other will win.

Not all species can bloom. Gelatinous plankton seem to have two important properties (figs. 1, 2). They are usually large so they are not subjected to predation by small species (except for the early life stages). They are able to feed on a large range of particle including the small particles (fig. 3). They usually have a high fecundity.

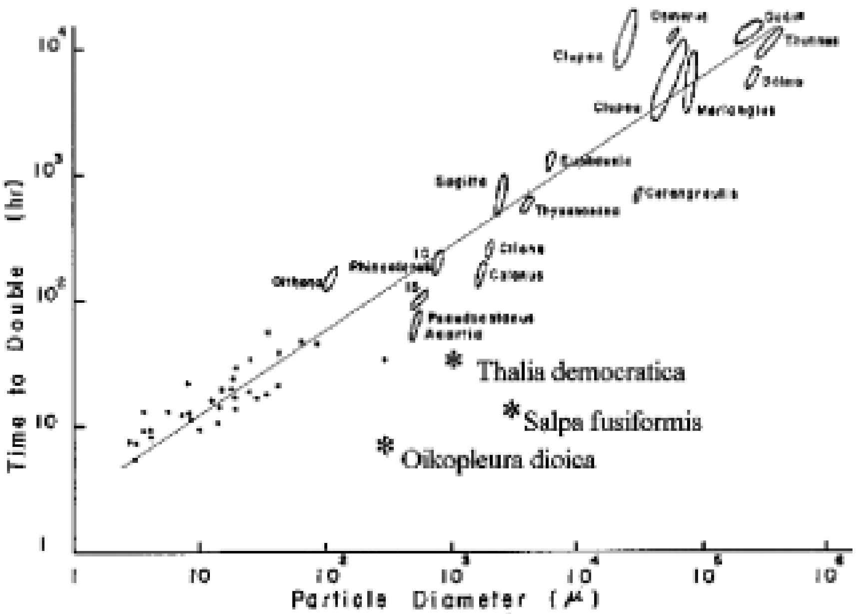


Fig. 1. Doubling time of some blooming species: The growth rate of the salps *Thalia democratica* and *Salpa fusiformis* (Braconnot *et al.*, 1988), and of the appendicularian *Oikopleura dioica* (Hopcroft and Roff, 1998) have been evaluated. Their doubling time is smaller than species of the same size and in the range of phytopankton species (stars on Sheldon *et al.* (1972) diagram).

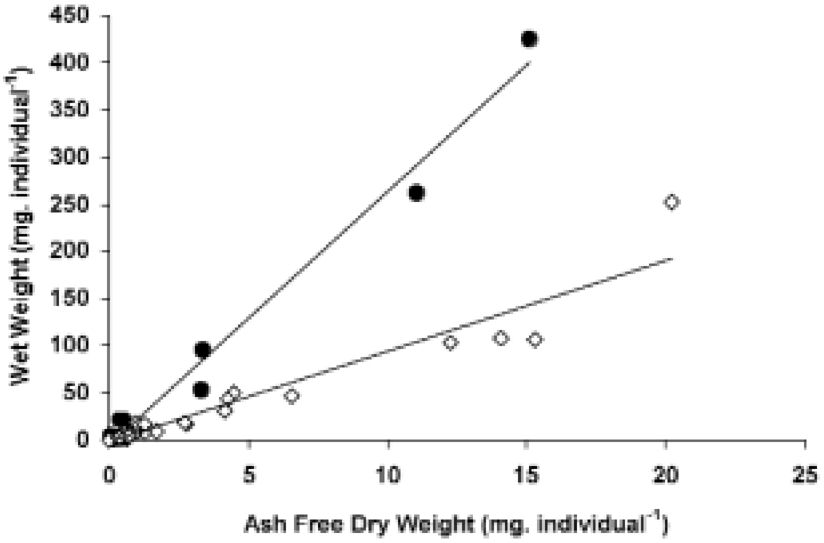


Fig. 2. Ash-free dry weight is a measure of the average metabolic rate of a species. Wet weight is more or less related to the size of the species. This graph based on data from Ikeda (1970) shows that gelatinous species appears larger in size than the other species of the same metabolic requirement. **Empty diamonds** correspond to crustacean and pteropods species, **dots** correspond to ctenophores, medusa, chaetognaths. We can assume that gelatinous species which appear large are facing less predators than expected.

ECOSYSTEM PERTURBATIONS - TRANSIENT SITUATION

To allow some free area in the ecological space, perturbations are necessary. If the strength of a perturbation in the community environment (wind, rain), or its frequency, is too high, the species assemblage will be faced with a new set of conditions, with a change in the proportions

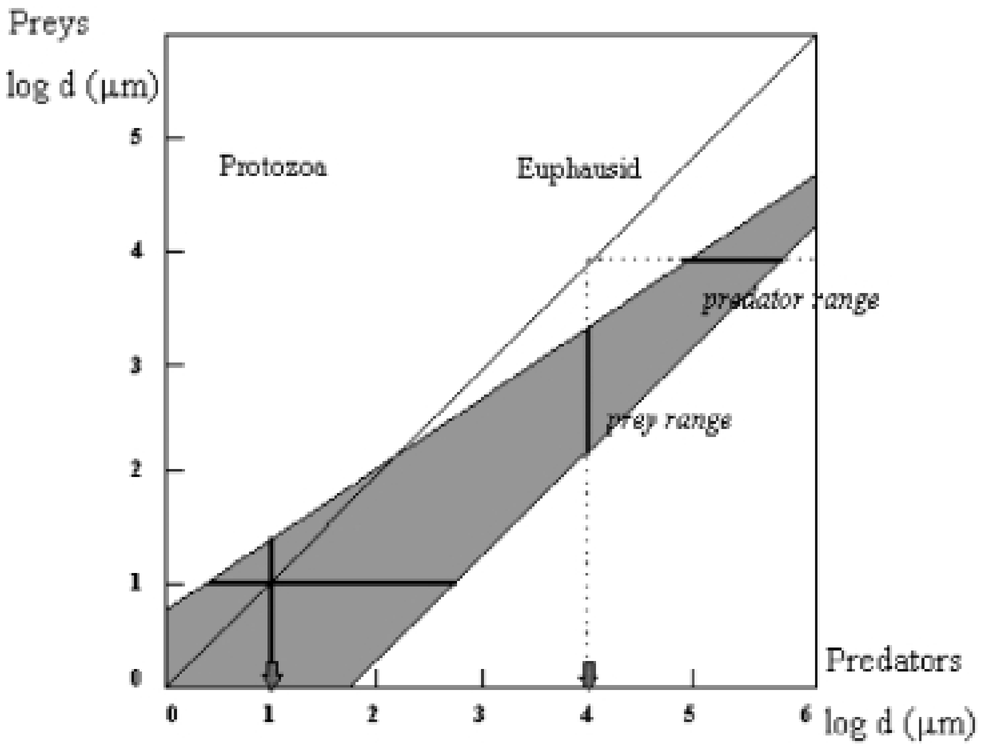


Fig. 3. This prey-size predator-size graph is based on the assumption that the logarithm of the range of preys of a species decreases with size. It is assumed that abundance of specie declines exponentially with size and that biomass of preys available for predators in an interval of log-size is constant. The **grey area** is assumed to take into account (1) that size of preys is more or less one order of magnitude less than the size of predator; (2) that unicellular animals are able to catch preys larger that their size. The range of preys for an Euphausid of size 104 mm is shown as a **black segment** on the vertical (preys) and horizontal (predators). We assume for instance that this crustacean cannot catch small organisms. The range of protozoan preys is larger, but so is the range of predators. The graph suggests that a gelatinous species of 104 mm in size, but having food requirements of a 102 mm species and the ability to prey in the small range of size, has a large food resource to invest in reproduction and a small predation risk.

of preys and predators, of resource and competitors. The sequence of hydrodynamic events set the transient characteristics of the species assemblage. Each hydrodynamic event shuffles the ecosystem and gives opportunity for a blooming species to develop.

An optimum turbulence rate will provide nutrients to the base of food web, without inducing high dispersion rate precluding bloom formation. For zooplankton species with sexual reproduction, mesoscale-turbulence favour the contacts between individuals, might scatter the eggs and increase the size of space invaded by the blooming species. However high rate of turbulence can inhibit gametes interaction and reproduction (decrease in the fertilisation success).

TIME SPACE CHARACTERISTICS

It is necessary to investigate the spatial extension of a bloom. Some species bloom every year (salps) for a relatively long period of time (month), others are producing short-lived blooms. However, the period of observation of the bloom from a fixed position gives a biased estimate of spatial extension and duration, depending on the current pattern. Zooplankton blooms might be viewed as patches of specific size which are embedded in the general water circulation. They should appear in a favourable spot and for some time circulate in the sea and develop. The life cycle characteristics are important elements (fig. 4). When they become obvious they might be in the declining phase of their dynamics and far from the source area. The distance covered, or the spatial extension, might be large.

The study of time-space scale characteristics of a bloom requires scientific cooperation, specific alert systems and permanent observation systems. It is compulsory to study the starting period of a bloom and not only its decline.

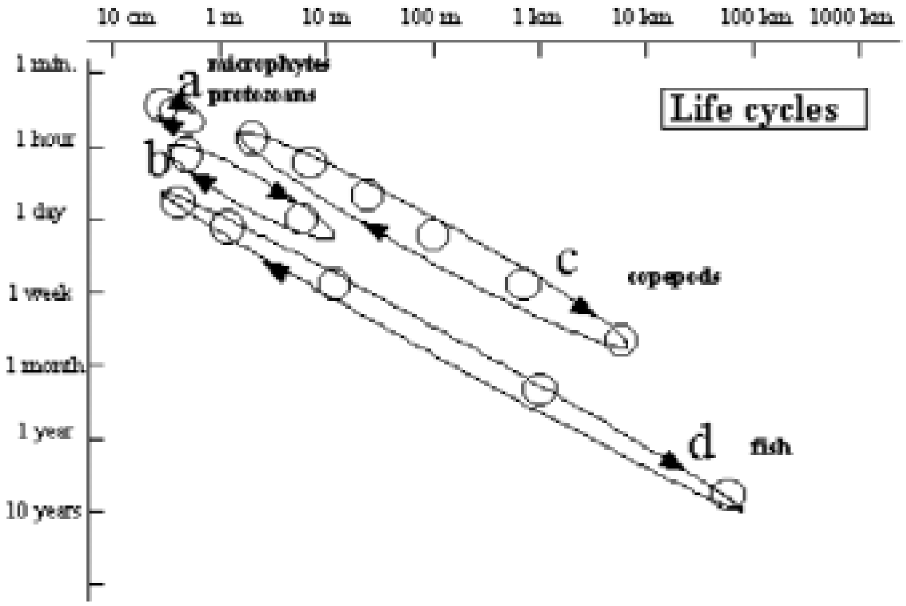


Fig. 4. The space and time scales of a species development depends on its size and doubling time. It interacts with physical processes of the same scale. However each individual develops from egg to reproductive adult through different stages which are affected by different processes such as spatial characteristics of their food, turbulence and transport and changes during the life cycle of the species. We can assume that the triggering mechanism of a bloom can be found at any time and space scale relevant to the life cycle of the species and be dependent on a large range of physical processes. **a, b, c, d** are species with different life cycles going through one (unicellular organisms) to several life stages of different duration (copepods, fish).

CONCLUSION

The following hypotheses deserve investigation:

- as a consequence of hydrodynamic perturbations, the ecosystem is most of the time in a transitory state therefore, there is a free space for blooming species;
- blooming zooplankton species have several specific properties (large food spectrum, high ingestion rate, high population growth rate, life stages able to compete with those of other species);
- the size of patches of blooming species depends on the physical properties and biological characteristics of the species (generation time and availability of food).

Topology and dynamics of plankton networks: are pelagic ecosystems robust?

Timothy Wyatt[1], Maurizio Ribera d'Alcala[2], Ferenc Jordán [3]

[1] *Instituto de Investigaciones Marinas, Vigo, Spain. Email: twyatt@iim.csic.es*
[2] *Stazione Zoologica "A. Dohrn", Napoli, Italy*
[3] *Collegium Budapest, Institute for Advance Studies, Budapest, Hungary*

Deep beneath the surface in the Stygian darkness of cold midwinter boreal and polar oceans, nothing much seems to be going on. The seed banks which will give rise to next spring's phytoplankton populations are dormant in the mud, and the mud eaters which might disturb them are in a state of torpor. Hundreds of meters below the surface, swarms of *Calanus* hang motionless in diapause, and the baby cod which will one day learn to eat their progeny have not yet been born. Thus the players in the classical food chain game are asleep and their roles are in abeyance. But time and space have been mapped. Biological clocks tick away and the celestial sphere turns. The winter solstice passes, days lengthen, winds abate. Prompted either by the wake-up signals of their clocks or by environmental cues, seeds start to hatch and diatoms inoculate the nutrient rich upper layers of the water, *Calanus* breaks its diapause and swims upwards in search of food, hormones regulate the final stages of gonad maturation in the cod, which have been navigating to their traditional spawning sites from overwintering grounds as far as 1000 km away. Everything is ready to build a food chain, but the links between its different components are yet to be made.

The diatom inoculum arrives in the upper lit layers and grow exponentially at the expense of the nutrients. But soon their growth is regulated as Calanus arrive and start to graze the diatoms down and reproduce. The cod spawn, their eggs hatch, and the larvae are soon feeding on the copepod nauplii. Thus links are reestablished one by one, and an ecosystem moves to another state. Some time later, the links start to disappear again as life cycle programmes run. The diatoms form spores which sink to the bottom, the fish larvae grow and move to other pastures, the copepods remain but must find other sources of food. All this of course is a gross oversimplification; all models are. In temperate and tropical waters, plankton webs are rarely set to "zero" as in our introductory scenario and the macroscopic appearance of the ecosystem remains a steady state. Nevertheless, thinking along these lines allows us to sketch a path from the population dynamics of single species to the complex behaviour of planktonic food webs and, ultimately, to the ecosystem structure. Luh and Pimm (1993) provide an approach to these processes of community assembly, where the sequence of states depends on "invasibility" and the parameters for each species are those of the Lotka-Volterra model, intrinsic growth rates, predation rates, competition).

It is customary to assume that the present state of an ecosystem is the result of a response to environmental forcing on different time scales. The environment is the context and the ecosystem is an adaptation to that context. The two together comprise an ensemble. Thus the environment defines a problem, and the state of the ecosystem represents a solution to that problem. As Alexander (1967) stressed in a different context, "*no one division of the ensemble into form and context is unique*", we can easily be led astray when we make such divisions, and our perception of the fit of solution to context may sometimes be strongly biassed by such arbitrary divisions. Traditionally, ensembles have been divided pragmatically. For example, in exponential single species models, the system is the species and the context consists of the everything else; in logistic models and in Lotka-Volterra predator-prey systems, the system comprises two nodes ("carrying capacity", species; prey, predator) and the link between them, and so on.

Most ecologists are familiar with networks in which the nodes are species or groups of species and other integrated components such as nutrient pools or detritus, and the links are flows of material or energy between them. Other network approaches deal with size classes or trophic levels. A convenient way to summarize the nodes and links of such a representation of a food web is to construct a matrix known as a cascade model. If we prepare such a matrix for a typical model planktonic web (table I), we note that the matrix is very sparse. In this case, the number of links is only $2*N$ out of a possible maximum of $N*N$.

Table I. Matrix showing material flow (links indicated by +) between nodes in a food web.
N = nutrient, DOM = dissolved organic matter, POM = particulate organic matter, B = bacteria, P = phytoplankton, Z = zooplankton (micro- or macro-), and HTL = higher trophic levels.

from/to	N	DOM	POM	B	P	Z(micr)	Z(macr)	HTL
N					+			
DOM				+				
POM								
B	+	+				+		
P		+				+	+	
Z(micr)	+	+	+				+	
Z(macr)	+		+					+
HTL	+							

It is common to assume that food webs are hardwired, and that the links represent material flows. But ecological links are not all simple flows of material or energy, and in addition many of them are time dependent as already indicated (Jordán, 2001). Non-material flows include information, signs which can lead to say predator avoidance or signals which might promote social cohesion or alarm. If we ignore information flow, which would taken us to a different kind of network (with multiple links among the same nodes) the ecological links can be classified into several categories according to the sign of the impact the processes have on the two nodes which are joined. Table II shows the main ones.

Table II. Classification of ecological links, and sign of feedback.

Nature of link	Sign of feedback
neutralism	0 0
commensalism	0 +, + 0
mutualism	+ +
competition	- -
amensalism	0 -, - 0
predation, parasitism	+ -, - +

The time dependence of the links is due to a number of causes, to disturbances which temporarily decouple some of the links (*e.g.*, upwelling, turbulent events, the onset of stratification,…), and to both strategic and tactical decisions by the living components of the ensemble, their inherited responses to predictable and unpredictable events. The creation and elimination of links and nodes results from life history strategies (hatching of spores, encystment, migration). Examples of the latter are the switching of grazers or predators from one resource to another as their relative abundance changes, the passing of thresholds which allow epidemic infection rates to occur, the formation of ecdysal cysts by dinoflagellates. Such events partly control succession and invasibility They also put severe constraints on the realizable states ecosystems can assume.

Given models of planktonic ecosystems which incorporate the features alluded to, the concept of robustness and stability need to be reconsidered. Stability usually refers to both *resistance*, the magnitude of a response to a perturbation, and to *resilience*, the rate at which the system returns to its original state (McArthur, 1955; Watt, 1964; Pimm, 1991). Both aspects are partly based on the idea of a climax community to which succession trends. But there are further limitations. In conventional models, trophic species do not admit life cycles, and trophic cycles themselves are forbidden (leading to Lindeman’s paradox, which stems from the neglect of feedbacks through detritivore and decomposer compartments, see Burns, 1989).

The effects of physics on the distribution of plankton at various scales

A. Lascaratos [1], G. Petihakis [2], G. Triantafyllou [1] and G. Korres [2]

1 Dept. of Applied Physics, Physical Oceanography Group, University of Athens, Greece
Email: alasc@oc.phys.uoa.gr
2 Institute of Marine Biology, Iraklio, Crete, Greece

It is believed that primary productivity is mostly a vertical process in the ocean. Indeed most of the processes involved (light transmission, photosynthesis, mineralization, water column-seabed interaction) have an important vertical component. This fact is also reflected in 3-D biological and ecological models which are in reality mainly 1-D models with the simple inclusion of advection terms (Lacroix and Nival, 1998). What then about the two horizontal dimensions? How important or critical are they in the distribution of biological parameters in the sea? The more data we have the more it becomes clear that the horizontal ocean flow field plays a very important role to what we would term as spatial (and temporal) distribution of phytoplankton, primary production, etc. (Krom *et al.*, 1992). The patchiness of such distributions which is related to dynamical flows of the sea is clearly a strong evidence that we cannot understand and interpret, in most cases, the biology if we do not understand the physics before. The concentration of phytoplankton for example in the center of cyclonic gyres is such an example. Would one go so far as to say that the distribution of biological parameters depends more on physics than on biology ? In other words, would one go to the (provocative) extreme of saying that the biology is in a “slave” mode to physics ? This is of course an open question which deserves careful attention. We have evidence of strong relation of fish catches to interannual variability of atmospheric and oceanic conditions. And there are very strong, actually dramatic, changes observed in the benthic populations in the Cretan Sea, themselves related to the Eastern Mediterranean transient that occurred at the end of 80’s-beginning of 90’s ? Obviously, physical forcing would be more valid even for phytoplankton and zooplankton “drifters” than for fishes which are less confined by the movements of the water.

This presentation has no clear answers to the above questions. It is rather intended to stimulate a discussion on those issues and address the right questions as a first and very important step towards possible resolution.

In this context we present here some preliminary results from a complex three–dimensional ecosystem model of the oligotrophic Eastern Mediterranean Sea, developed jointly by the Institute of Marine Biology of Crete and the University of Athens. We believe that these results might contribute to the discussion on the relation between the occurrence of blooms (their timing and their location) and the flow field. The simulation system comprises two on-line coupled sub-models: the three-dimensional Aegean Levantine Eddy Resolving MOdel, ALERMO, (based on POM) (Blumberg and Mellor, 1987) and the ecosystem model developed for the Cretan Sea (based on ERSEM) (Allen *et al.*, 2001). The computational domain covers the Eastern Mediterranean Sea between 22.5-27.7E and 34.8-41.0N, with 105 x 125 grid points, and constant grid spacing in latitude and longitude of 1/10 x 1/10 degrees. The vertical structure is resolved by 30 sigma levels with logarithmic distribution near the surface to correctly simulate the dynamics of the surface mixed layer.

For the initialisation, forcing, and boundary conditions, all available MODB and ECMWF data were objectively analysed to filter out spatial noise and interpolated to grid-points where data were missing. The initial conditions for the biogeochemical parameters are taken from the ecosystem model for the Cretan Sea while a uniform field of all state variables is applied to the model domain.

The biochemical model uses a "functional" group approach to describe the ecosystem where the biota is grouped together according to trophic level (subdivided according to size classes or feeding methods). A number of eighty (80) state variables have been chosen in order to keep the model relatively simple without omitting any component that may exert a significant influence upon the energy balance of the system. The ecosystem is considered to be a series of interacting complex physical, chemical and biological processes, which together exhibit coherent system behaviour. Biological functional growth dynamics are described by both physiological (ingestion, respiration, excretion, egestion, etc.) and population processes (growth, migration and mortality). The biological variables in the model are: phytoplankton, functional groups related to the microbial loop and zooplankton. Biologically driven carbon dynamics are coupled to the chemical dynamics of nitrogen, phosphate, silicate and oxygen. The phytoplankton pool is described by four functional groups based on size and ecological properties. These are diatoms (silicate consumers, size: 20-200µ), nanophytoplankton (2-20µ), picophytoplankton (<2µ) and dinoflagellates (>20µ). All phytoplankton groups contain internal nutrient pools and have dynamically varying C:N:P ratios. The nutrient uptake is controlled by the difference between the internal nutrient pool and external nutrient concentration. The microbial loop contains bacteria, heterotrophic flagellates and microzooplankton, each with dynamically varying C:N:P ratios. Bacteria decompose detritus and can compete for nutrients with phytoplankton. Heterotrophic flagellates feed on bacteria and picophytoplankton, and are grazed by microzooplankton. Microzooplankton also consume diatoms and nanophytoplankton and are grazed by mesozooplankton.

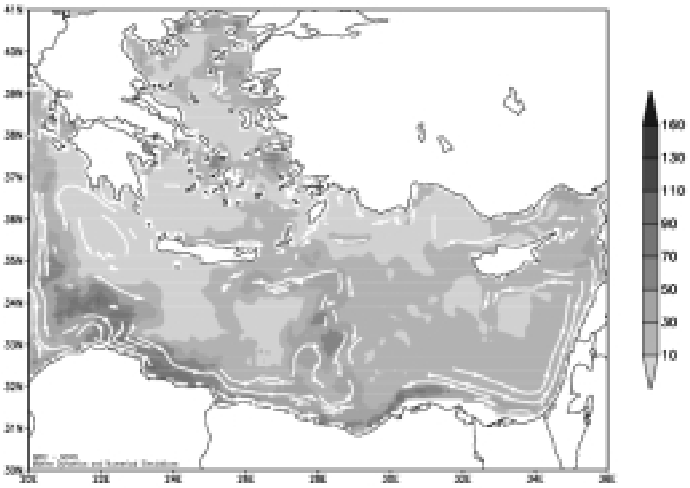


Fig. 1 : 4-13 February integrated Chlorophyll from 0-150m.

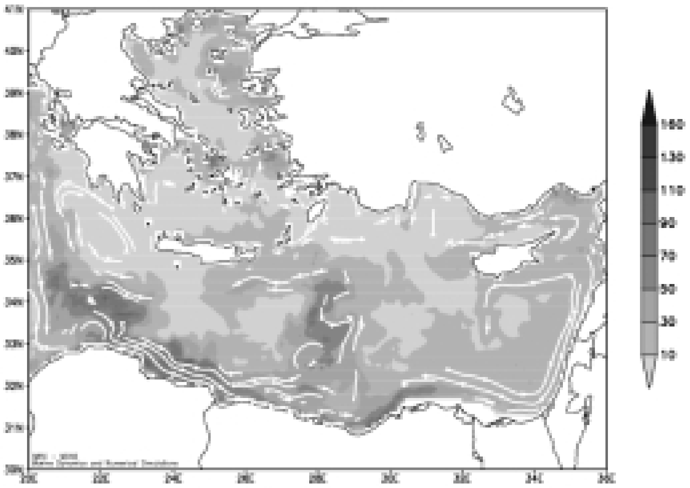


Fig. 2 : 14-23 February integrated Chlorophyll from 0-150m.

Results concerning the evolution of the integrated chlorophyll-a for the 0-150m layer from the beginning of February to the end of March at ten-day interval composites together with the flow field can be seen in figures 1 to 5. These results are in general agreement with previous studies concerning the circulation patterns and the productivity levels in the area (Becacos-Kontons, 1997; Psarra *et al.*, 2000;

Theocharis *et al.*, 1993). At the beginning of February (Fig. 1) high chlorophyll-a concentrations are mainly seen along the African coast off Libya and Egypt in a more or less patchy structure. At the same time a bifurcation of the circulation first to the north (at longitude 28 E) and then to the west can be observed. Progressively higher concentrations of chlorophyll-a (Figs. 2,3,4) can be seen along the path of this bifurcation.

The early bloom along the coasts of Africa might be related to higher temperatures and higher nutrient concentrations of Modified Atlantic Waters moving along the African coasts. The bloom observed in the open sea area between the African coasts and Crete seems to be either advected there by the currents or produced locally following the arrival of warm and nutrient-rich water masses. In both cases the role of the currents is very clear.

In the fourth image (6-15 March, Fig. 4) we observe some signs of weakening of the north African bloom while at the same time locally produced blooms develop along the southern coasts of Turkey. In the next and last picture (Fig. 5) local biological activity is very evident along the southern coasts of Turkey as well as at specific points in Crete. It seems, therefore, that we can differentiate “advected blooms” from “locally produced blooms”. We believe that our results, although preliminary, show that the flow field plays an important role on the time and place of occurrence of blooms.

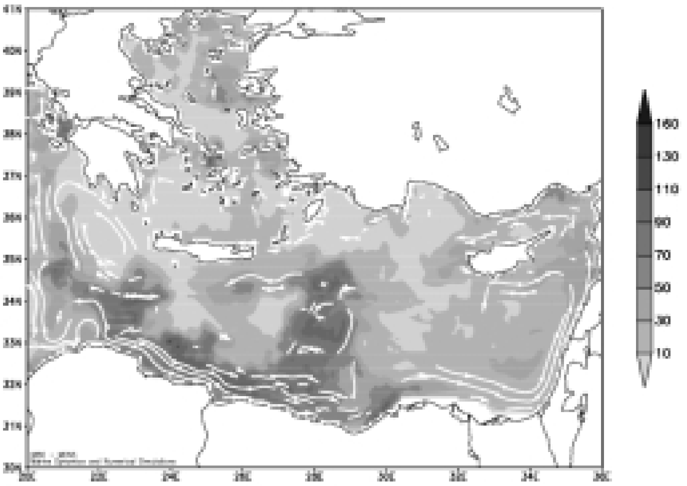


Fig. 3 : 24 February-5 March integrated Chlorophyll from 0-150m.

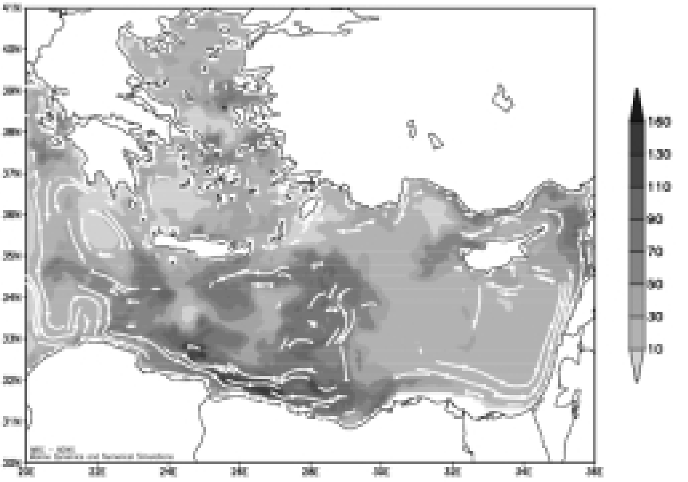


Fig. 4 : 6-15 March integrated Chlorophyll from 0-150m

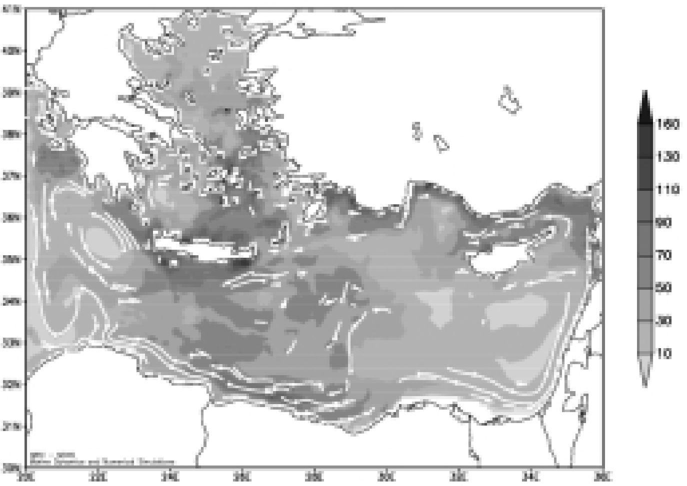


Fig. 5 : 16-25 March integrated Chlorophyll from 0-150m

Physico-biological coupling and plankton blooms : a modelling approach

Geneviève Lacroix[1], **Paul Nival**[2]

[1] *GHER, University of Liège, Belgium. Email: G.Lacroix@ulg.ac.be*
[2]*LOV, University of Paris VI, Villefranche-sur-mer, France*

INTRODUCTION

As is well known, the physical environment acts as a strongly constraining factor on ecosystem dynamics. The physico-biological interactions are numerous in the oceans and cover wide space and time scales (*e.g.* Mann and Lazier, 1991). Physical processes such as turbulence, vertical structure, freshwater run-off, upwellings, fronts, gyres, internal waves, residual circulation, … are as many mechanisms that force the ecosystems and, in particular, the dynamics of plankton blooms. Amongst such processes, turbulence can play a role at different levels, for instance on the vertical repartition of nutrients, nutrient uptake, grazing, formation of aggregates, … (*e.g.* Kiorboe, 1993). So it seems obvious to consider the physical environment when studying ecosystem dynamics and, in particular, the massive developments of gelatinous zooplankton.

The observations realized *in situ*, the experiences in laboratories and the satellites images, although indispensable to the understanding of the processes that govern plankton outbreaks, are not sufficient because limited in time and space. The use of modelling is a good way to complete the existing information and increase the comprehension of such events. One advantage of the models is that they “run” faster than the real marine environment does. Then, they can be used to study the planktonic response to some anthropic and/or environmental changes such as: an increase of the nutrients concentration, a change of the water temperature or the introduction of a foreign species (*e.g.* Oguz *et al.*, 2001). They allow also to test certain hypotheses and to study the relative importance of the processes considered. Depending on the objectives and the processes studied, they can cover the three spatial dimensions or not and their extension can be wide or, on the contrary, regional.

THE EXAMPLE OF A PLANKTON BLOOM IN THE LIGURIAN SEA

The biological production heterogeneity of the Ligurian Sea (Mediterranean Sea) is closely associated with local and regional hydrodynamical factors, especially those responsible for a high variability of the mixed layer depth in such a strongly stratified environment. Moreover, the overall system is dominated by a marked seasonal cycle as a result of the meteorological signal. The intensity and timing of winter-spring phytoplankton bloom, as well as the maximum biomass and the vertical repartition of others biological components – such as salps for instance –, perform a significant interannual variability. In order to study this variability associated with meteorological conditions, a modelling approach has been chosen. A coupled physico-biological model is applied to the Ligurian Sea and two simulations corresponding to different meteorological forcings (from October 1985 to September 1986 and from October 1986 to September 1987) have been performed in order to show how important can be the effect of interannual meteorological variability on the ecosystem dynamics.

MODEL

The coupled hydrodynamic-biological model — MODECOGeL —, implemented and validated for the northern Ligurian Sea using long term (1984-1988) experimental data from the French Frontal program surveys, is thoroughly presented in Lacroix (2001). The hydrodynamic model is a 1D version of the multi-levels, turbulent closure, G.H.E.R. (GeoHydrodynamics and Environment Research) model. Considering that the establishment and decay of the thermocline are strongly dependent on the atmospheric conditions, the model is forced by surface wind stress and heat fluxes computed from real meteorological conditions, a high rate sampling meteorological data allowing simulations that give confidence in the mixed layer dynamics (Lacroix and Nival, 1998). The ecosystem model is based on the L.O.V. (Laboratoire d'Océanographie de Villefranche) works. It takes into account 13 state variables based on size-classes (NO_3, NH_4, pico-, nano-, and microphytoplankton, nano-, micro-, and mesozooplankton, salps, heterotrophic bacteria, two classes of particulate organic matter and disolved organic matter). In order to see the effect of meteorological variability only, the initial conditions in both simulations are the same and come from data measured during Frontal.

RESULTS AND DISCUSSION

Among the results of the model, we will focus on distributions of turbulent kinetic energy (Figures 1a and 1b) and temperature (Figures 1c and 1d) for both simulations. The observation of the turbulent kinetic energy (tke) indicates that mixing was clearly more intense in winter and in the beginning of spring. An intense mixing (tke > 10^{-5} m^2/s^2) takes place as soon as the end of January. At this moment, the mixed layer depth reached more than 400 meters in 1986 and only 200 meters in 1987. In 1987, it was necessary to wait for the beginning of March to see the mixed layer depth reaching 400 meters. The middle of March 1986 and the beginning of May 1987 were marked by a strong wind event followed by a drop of the mixed layer depth respectively as deep as 400 and 150 meters. The beginning of the stratified period started earlier in 1986-1987 (April) than in 1985-1986 (May). The seasonal warming reached deeper layers in 1987 than in 1986, the later one being marked by a sharp thermocline.

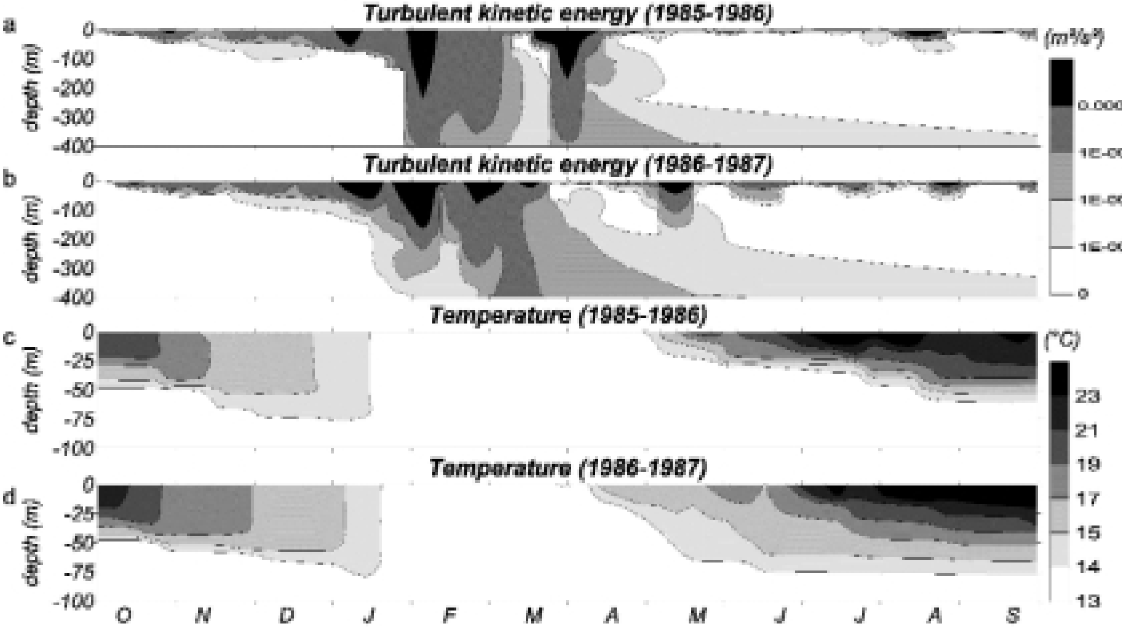

Turbulent kinetic energy (1985-1986)
Turbulent kinetic energy (1986-1987)
Temperature (1985-1986)
Temperature (1986-1987)

Figure 1. Time-depth evolution of the physical variables computed by the model. Turbulent kinetic energy (m^2/s^2) with meteorological conditions of 1985-1986 **(a)** and 1986-1987 **(b)**; temperature (°C) with meteorological conditions of 1985-1986 **(c)** and 1986-1987 **(d).**

Figure 2 shows the time-depth distribution of nitrate (Figures 2a and 2b), phytoplankton – expressed in chlorophyll with the use of a C:Chl ratio = 50 mgC $mgChl^{-1}$ – (Figures 2c and 2d) and salps (Figures 2e and 2f). The winter 1985-1986 was windier than in 1986-1987 and the mixing was so intense until February that it kept the phytoplanktonic production off. Nitrate came from deep layers as soon as the end of January in 1986 and only in March 1987. In 1986-1987, there is phytoplankton during all winter. As soon as the mixing decreases, the phytoplankton bloom can occur. The increase of phytoplanktonic biomass was faster in 1986 than in 1987 and the maximum appeared respectively in the middle of March 1986 and in the end of March 1987. The first year presented a second bloom in the middle of April just after the intense wind event. The same thing iwas observed in the middle of May 1987 but with a lower intensity. The observation of Figures 2e and 2f shows a high interannual variability in the salps biomass as well as in their vertical distribution.

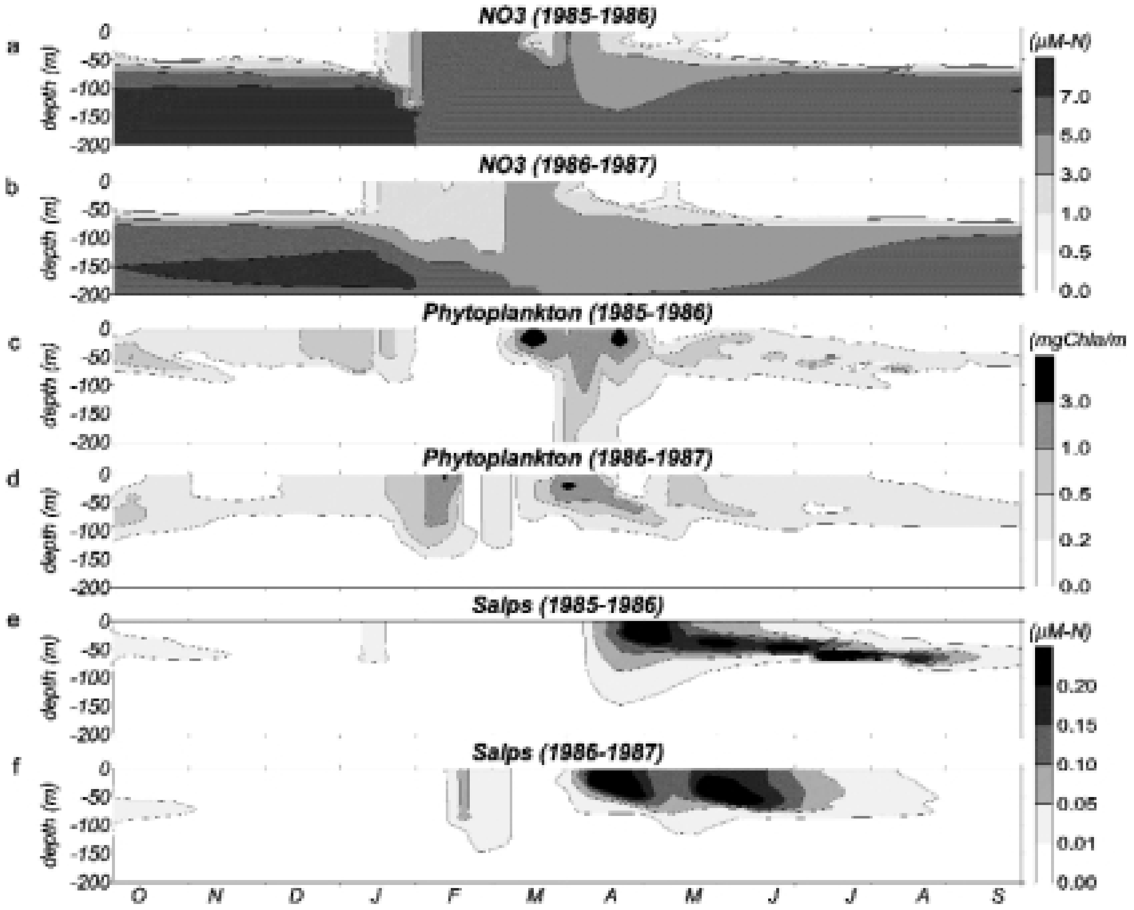


Figure 2. Time-depth evolution of the biological variables computed by the model. Nitrate concentration (µM-N) with meteorological conditions of 1985-1986 **(a)** and 1986-1987 **(b)**; phytoplankton biomass ($mgChl/m^3$) with meteorological conditions of 1985-1986 **(c)** and 1986-1987 **(d)**; salps biomass (µM-N) with meteorological conditions of 1985-1986 **(e)** and 1986-1987 **(f)**.

Since we took the same initial conditions for both simulations, we saw here the important role played by the meteorological conditions on the ecosystem dynamics and, in particular, on the timing of planktonic blooms and the vertical distribution of the plankton.

A better knowledge of the planktonic behavior should lead to a robust calibration of the biological model in the aim to improve it and then use it as a tool to study the response of the whole ecosystem dynamics to some environmental changes (increase of nutrients concentration, perturbation in the community structure, augmentation of water temperature, …).

II - 2. Tunicate outbreaks

Appendicularian outbreaks : accidents or rule ?

José Luis Acuña

Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo, Spain
Email: acuna@correo.uniovi.es

It has been more than a decade since the microbial loop-classical food chain dichotomy emerged as a clearly defined statement on the structure of marine pelagic ecosystems. Appendicularians were exceptional mesozooplankton within this conceptual scheme because of their capacity to capture very small particles. This has led many researchers to interpret that appendicularians are typical filter feeders associated with microbial-based pelagic systems. This interpretation is further reinforced by recent theoretical developments suggesting the ability of gelatinous bodies to endure the extreme food dilution characteristic of open-ocean, microbial based pelagic systems. However, this nearly consolidated perception of appendicularians as microbial-loop consumers does not live up to much evidence coming from other sources. On one side, the appendicularian functional response is similar to that of other zooplankton typical of rich, eutrophic habitats. In addition, extremely high densities of appendicularians are usually associated with blooms of phytoplankton (*e.g.* Seki, 1973; Nakamura, 1998; Dagg *et al.*, 1996), which suggests that there is an intricate relationship spanning the range from strict, microbial loop to classical food chain situations. What is the nature of this relationship ?

Perhaps our dichotomic division between microbial loop-classical food chains is hampering to some extent our attempts to understand appendicularian biology, blooms included. It is possible that appendicularians in particular, and many other gelatinous forms in general, are sublimate examples of “fugitive” species (*sensu* Hutchinson, 1951) that is, opportunistic forms able to survive situations of scarcity in time and space as resistance-dispersive stages, and to rapidly expand their populations during short, ephemeral and unpredictable benign periods associated with the initial stages of ecological successions (in this context, phytoplankton blooms; see Fig. 1). This is consistent with both gelatinous bodies being an adaptation to food scarcity (Acuña, 2001) and semelparity being a clear colonizing trait (Heron, 1972).

Appendicularians eat small particles that experience density increases during blooms of large phytoplankton, thus it is not surprising that the highest appendicularian densities are usually associated with blooms of large phytoplankton. Therefore, understanding appendicularian blooms requires a profound knowledge of the dynamics and successional properties of phytoplankton blooms. The disturbance regime in particular could prove of critical importance in triggering the development of appendicularian blooms. For certain disturbance frequencies, both phytoplankton and appendicularian populations could enter in a resonance mode leading to explosive population growth. There are examples of phytoplankton blooms that are not singular events, but sequences of stabilization-destabilization processes leading to a rather abrupt end. In his seminal 1953 paper, Sverdrup shows that the spring bloom occurs as a series of ephemeral pulses whose

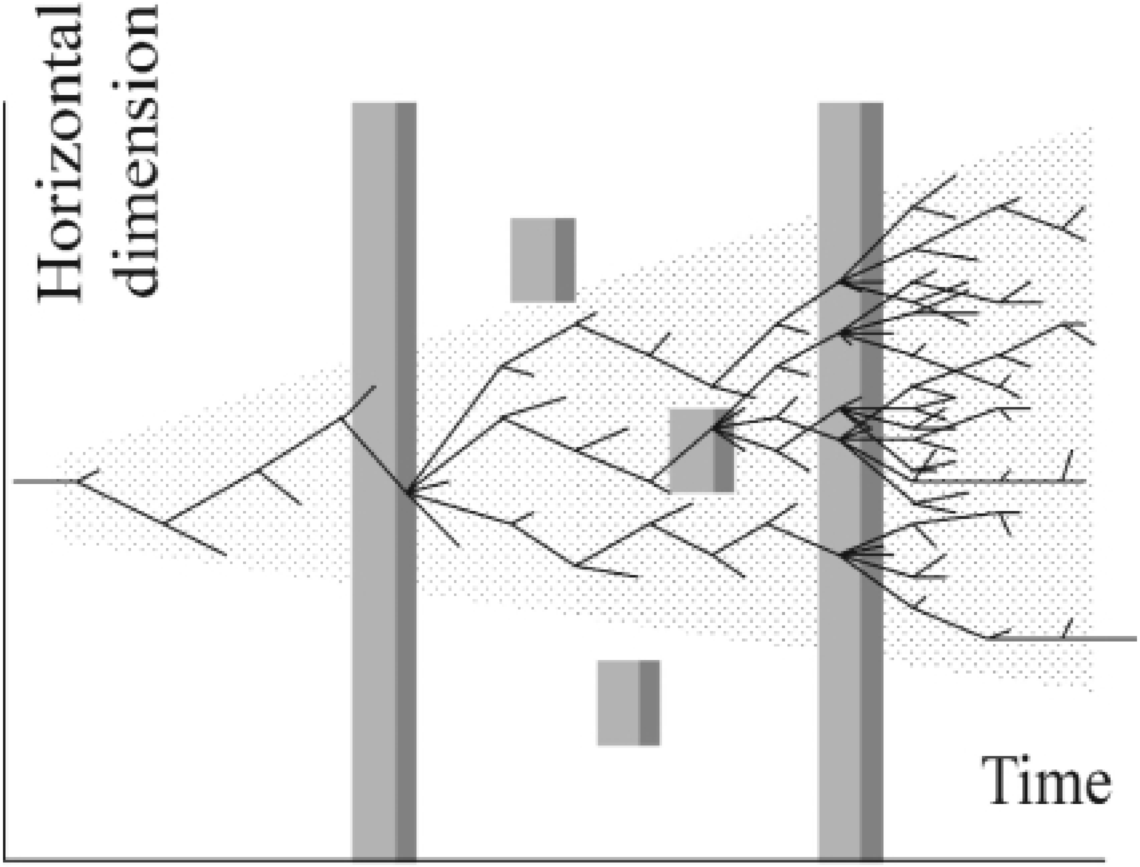


Figure 1. Hypothetical representation of the appendicularian fugitive strategy to monitor phytoplankton blooms in large portions of the spatio-temporal habitat template. Features in the figure (generation lengths, number of offspring, ...) are not real. The shaded rectangles represent phytoplankton blooms. There are two major bloom events which are ephemeral in time but continuous in space, the Spring and Autumn blooms, and several events which are ephemeral both in space and time during the summer stratification phase, corresponding to localized destratification processes. The lines represent single individuals. Each line branches into two other lines or descendants during periods of food scarcity, winter and summer stratification, although one of these individuals dies and does not reproduce. The remaining individual makes a living at very low food concentrations by means of its gelatinous strategy. However, if one animal happens to spend a significant portion of its life during a phytoplankton bloom, it generates five descendants, two of which die. The end result, and the basis of the strategy, is that a great portion of the spatio-temporal habitat template is monitored for blooms (dotted polygon) starting from a reduced, initial seed population, and ending in a limited number of survivors. Selection for opportunistic traits (i.e. short generation times) must be strong under these circumstances.

timing is determined by the vagaries of weather. Time lapses between the five destabilization events found by Sverdrup average 5±4 days (mean±SD, n=4), very similar to the appendicularian generation time (ca. 6 days at 15ºC, Paffenhöfer, 1975). Thus, the elements for an eventual build-up of dense appendicularian populations are altogether present during the spring bloom, and natural selection could in principle tune generation times to the average time interval between consecutive phytoplankton blooms. Addressing these types of problems requires a shift from the ecosystem to the population biology and evolutionary approaches, with the aid of knowledge gained from ecological analogues in terrestrial and freshwater systems. Characterization of seed populations and habitat templates in time and space may help to resolve some key aspects regarding the survival of the gelatinous inhabitants of the ocean, and their tendency to develop dense outbursts.

Changes in pelagic tunicate abundance and the possible ecological consequences

Quentin Bone

Plymouth Marine Laboratory, Plymouth, England. Email: qb@mba.ac.uk

Plankton workers have been long aware of irregular blooms or outbreaks of certain plankton species, which suddenly appear in enormous numbers. Seasonal blooms, though more or less regular, may vary enormously from year to year.

The pelagic tunicates have the most spectacular blooms in numbers of individuals. All share astonishing reproductive capacity to take advantage of favourable conditions, either with short generation times, or by alternating sexual and asexual stages or both. Or even, in the case of *Doliolum nationalis*, a special short cycle allowing very rapid invasion of the surroundings.

The effects of these tunicate blooms are twofold. First, the fine mesh of their feeding filters enables them to collect phytoplankton very efficiently. In slope and oceanic waters, phytoplankton biomass may be almost completely removed from the euphotic zone, whilst in coastal waters salp grazing deepens phytoplankton distribution and only reduces phytoplankton biomass, rather than removing it completely (Zeldis *et al.*, 1995). Haskell and his colleagues (1999) modelled the situation off the southeastern US continental shelf, concluding that doliolids reduced copepod populations both by eating their eggs and by out-reproducing them in cold conditions of upwelling.

Secondly, the relatively dense compacted faecal pellets (Yoon *et al.*, 1996) and discarded appendicularian houses transfer nutrient material in significant amounts to lower layers and the benthos. Calculated values for downward carbon transfer under salp blooms range up to 100-200mg/m^2/day. A significant N- spike seems to occur in the benthos after a salp bloom (Fernex *et al.*, 1996), but no quantitative studies exist on the effects on the benthos.

Successful studies on seasonal blooms, like those for salps and doliolids by the plankton analysts at Villefranche (*e.g.* Ménard *et al.*, 1994, 1997) require not only the plankton samples, but also sea and air data as well. Nor is it enough to have two or three years regular sampling data of different kinds, what is needed is as long a time series as possible (23 years in the case of the data analysed at Villefranche), and if possible, similar observations at different sites. Naturally these will involve intercalibration of what are often different sampling methods. Purely local events may result from very local conditions, whereas similar events over a large area strongly suggest physical forcing, such as temperature changes. Salp and doliolid blooms have been correlated with, and linked to, physical changes such as wind stress or temperature. Although it is evident that correlations cannot reasonably be regarded as causal without long-term data, even over periods of many years, cautious inferences of causality may be drawn. There are excellent historical data sets for the N. Sea and channel approaches (some for over 300 yrs).

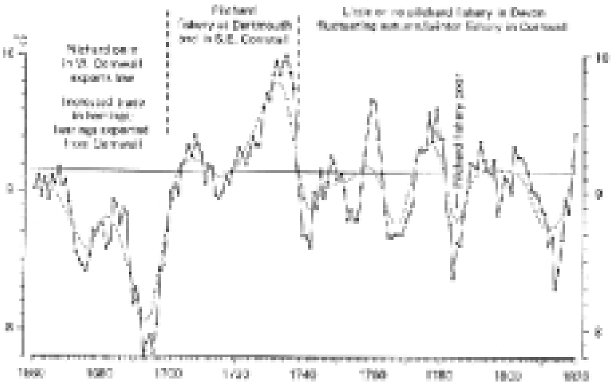


Figure 1. Fishery data for 1650-1820 compared with mean air temperatures for central England (From Southward *et al.*, 1988).

Using plankton and young fish data, (mainly from the 70 yr sample series at station E1 off Plymouth), Southward *et al.* (1995) present a very strong case for the efficient cause of the changes in the W. English channel plankton being gradual changes in sea temperature. Most recently, “global warming” since 1981 has been manifested by an annual mean temperature rise of 0.5°C. Interestingly, changes in the plankton from cold to warmer water species were mirrored by shorter term observations from rocky shore species such as barnacles and limpets.

Long-term time series for the Mediterranean plankton are few. A 17 year series continues for the Bay of Naples near the Stazione Zoologica, whilst in the Bay of Villefranche there is a continuing series from 1974 onwards (with a few interruptions).

This short presentation is really a plea for setting up and continuing plankton surveys in the Mediterraean. The continuous plankton recorder (CPR) route (MY/MZ) using a car transporter between Gibraltar and Genoa, was set up for one year by Paul Nival then funding ran out. The Plymouth Sir Alister Hardy Foundation (SAHFOS) was only able to support a further 5 months on the route, which then was abandoned.

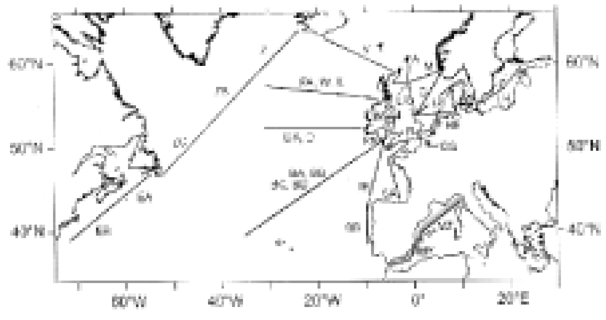


Figure 2. Continuous plankton recorder routes in 1998. Note a single route only in Mediterranean, (no longer running).

CPR surveys are not only important as a means of establishing “ground truth” for other monitoring methods such as satellite observations or small plane photography, but offer a synoptic view over the route followed. This is of especial importance when the spatial extent of blooms and their possible physical forcing are considered. Furthermore, compared with using research ships, CPR data are cheap. Monthly samples over a 450 mile route presently cost around £25,000 and this includes analysis of the records! At present no CPR routes in the Meditrerranean are contemplated so far as I am aware. The value of CPR data from the routes in the N. Sea to monitor an unusual doliolid bloom was well shown by Edwards *et al.* (1999).

In the late 1920’s and early 30’s striking changes took place in the plankton, in sea temperature and in phosphate levels off Plymouth. In the 1960’s the trend of rising temperature reversed, as did phosphate levels, the dominant chaetognath prior to the 1920’s returned, as did previously rare fish, such as cod. This Russell cycle was at first attributed to varying degrees of incursion of western water into the channel, but now seems very clearly basically related to climate change (Southward *et al.*, 1995). The point to be emphasised is that it is long term sampling, both biological and physical, that has led to a good understanding of the basis of the Russell cycle.

Without baselines, especially long term baselines, it is impossible to make sensible analyses of any changes, let alone venture any predictions.

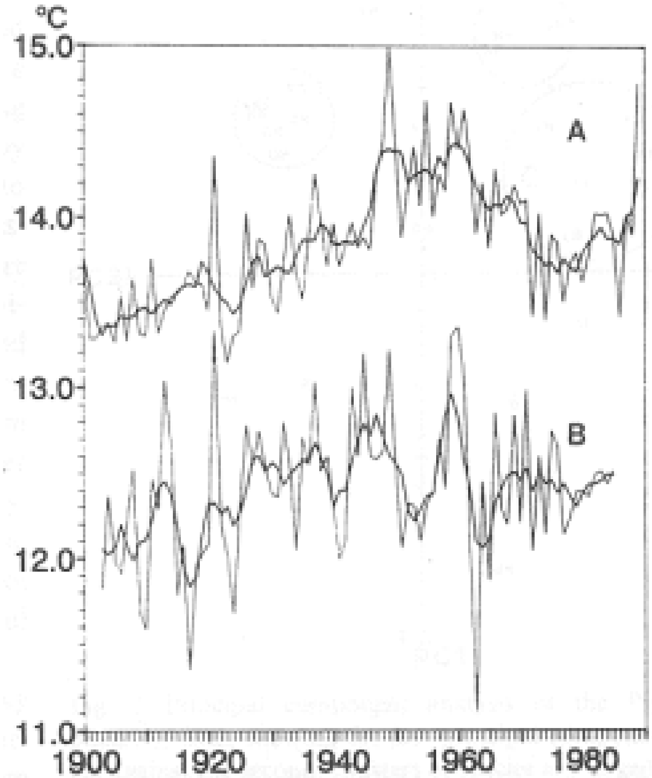


Figure 3. Trends in sea temperature since 1900. **Thin line**: annual means; **thicker line**: smoothed 5 year means. **A**: Bay of Biscay; **B**: Station E1 off Plymouth. Note that the E1 data cease in 1988 when the Natural Environment Research Council (NERC) inexplicably failed to fund this valuable long term data set, and also abandoned the CPR survey (From Southward *et al.*, 1995).

These long term observations enabled Southward and his colleagues (Southward *et al.*, 1995) over a period of some years to deepen our understanding of what had become known as the Russell cycle, in which the chaetognath indicator species *Sagitta elegans* and *S. setosa* monitored the relative abundance of cold and warm water in the channel. That is, it was supposed that their relative abundance and/or occurrence was related solely and directly to influx of water from the channel mouth into the coastal station of E1. More recent work by Southward and his group has shown that overall climate change was involved. Very fortunately, the surveys continued over a period of change, temperature rising to 1960 and then cooling to 1981 when temperatures rose again. Approximate annual mean change was +/-0.5°C. Alas, funding ceased in 1988 both for CPR surveys and fish surveys, as it did in many European countries. Other correlations with plankton or pelagic fish changes have been difficult to support. Solar forcing is acknowledged, but long data series do not support sun spot cycles, simply changes in annual mean temperatures, (Southward *et al.*, 1988).

A last example of value of long term surveys provided by CPR survey in the N. Sea, where a sudden appeaarance of doliolids signalled what seem to be changes in temperature of the water entering the N. Sea.

Aggregations and outbreaks of appendicularians

Gabriel Gorsky[1], Richard L. Miller[2] and Paul Nival[1]

1 LOV, CNRS/UPCM, Observatoire Océanologique, Villefranche sur mer, France
Email: gorsky@obs-vlfr.fr
2 Temple University, Dept. of Biology, Philadelphia, USA

Appendicularia and Thaliacea are holoplanktonic tunicates. Both groups are passive filter feeders. They feed indifferently on living and non-living particles of a given size range. In the case of the appendicularians (synonym - larvaceans), the retention efficiency is high even in the submicronic fraction of the size spectrum. The food particles are collected using an external system of nets continuously secreted by specialised epithelial cells of the animal's trunk. It is called the house and its structure optimises the water circulation, collection of food items and their transfer to the digestive system. The food collecting filter acts as a tangential flow filter and can concentrate ambient food particles up to 1000-fold. Appendicularians inhabiting superficial oceanic layers exhibit high metabolic activity and short life span. They are among the fastest growing metazoans on the planet. Hoptcroft and Roff (1995) estimated that the species *Oikopleura dioica* increases in average its biomass 10.7-fold in 24 h, and that its generation time at 29°C approaches one day. Appendicularians are shedding their gametes directly into the sea where fertilisation occurs. Population growth depends therefore directly on the fertilisation success. According to Omori and Hamner (1982), aggregation of drifting marine zooplankton may result from responses to temperature and salinity gradients and discontinuities, water mass motions, light intensity, predators, food distribution or social behaviour.

Appendicularians do not store energy in form of lipid deposits and they rely on constant food supply. In favourable feeding conditions and because of their short generation time they can rapidly form feeding aggregations. Platt *et al.* (1970) observed a considerable spatial heterogeneity in the chlorophyll distribution and showed a presence of plankton patches 0.5-1.5 miles in diameter. Wind-induced small eddies containing higher fluorescence values and high appendicularian concentrations were observed also near Villefranche/mer (NW Mediterranean). Thus, it is possible that wind or current induce accumulation of food allowing the evolution of an initial appendicularian concentration into aggregations that may initiate blooms.

According to our observations, atmospheric conditions play an essential role in the set up of a bloom. In order to evolve from an aggregation to a bloom, two conditions should be fulfilled:

1- food availability : food concentration (dependent on the light and nutrient availability) should support the feeding requirement of the growing population,

2- low turbulence conditions : persistent turbulence (wind forcing) during the starting phase of a bloom may prevent its development.

The impact of the climate and the turbulence on superficial populations may be illustrated by the effect on appendicularian mating aggregations. In laboratory as well as in the field more or less synchronous spawning behaviour was observed. Appendicularians autolyse their secretory cells, abandon their houses and aggregate in dense breeding patches. Alldredge observed more than 3000 ripe individuals l^{-1} in the windrows near California. Capitanio *et al.* (1997) found thousands of appendicularians in the stomach of large anchovies. Strong turbulence may disperse these dense patches and strongly decrease the fertilisation success. Our laboratory results show that approx. 1.10^5 sperms ml^{-1} are needed for a 50% fertilisation success. If the mean sperm concentration of *O. dioica* is about 2.10^6 sperms individual^{-1}, thus one male will fertilise 50% eggs in about 20 ml of water. About 50 males will be able to fertilise 50% eggs in 1 litre of water. 600 individuals/m^3 are considered as high larvacean concentration in Villefranche sur mer. In order to fertilise 50% of eggs, and in the case of homogenous distribution, all organisms from a spherical radius of 34 cm will have to concentrate in a spherical space of 12.4 cm in diameter (1 litre). If the natural concentration is of 10 individuals m^{-3}, all appendicularians in a spherical radius of 134 cm will have to concentrate in 1 litre. The lower the larvacean concentration, the longer the distance to join the mating aggregation. Strong turbulence and the consequent dispersion will result in low fertilisation rate and may slow down the population growth even if the nutritional conditions remain favourable. Thus, calm climatic conditions during the “key” periods may support appendicularian population growth, while inversely, turbulent conditions may prevent bloom formation. Uye and Ichino (1995) observed more than 50 000 *O. dioica* m^{-3} in the Inland Sea of Japan. At this concentration, according to our laboratory data, no swarming is necessary to achieve 50% fertilisation rate. Only the available food supply, predation or export may limit the population growth. Similar densities were observed in other coastal zones. Highly concentrated larvacean aggregations were also observed in the open ocean and at mesopelagic depths (personal observations). The short life span inducing the rapid population growth is also responsible for its rapid decline. However, because of the efficient retention of the small particulate organic matter and the important packaging activity (houses, faeces) when numerous, appendicularians play an important role in the transport of organic matter to the benthic ecosystem.

Clearly, additional research programs aimed at the data collection on diversity, distribution and abundance of marine organisms (i.e. Census of Marine Life program) are needed to improve our knowledge on the processes of animal aggregation in the oceans.

Interannual variations of some species of gelatinous zooplankton (Siphonophora and Thaliacea) in a coastal long-term series in the North-Western Mediterranean

P. Licandro[1,2], J.C. Braconnot[1], C. Carré[1], S. Dallot[1], M. Etienne[1], F. Ibanez[1], M. Moitié[1]

1 Lab. d'océanographie de Villefranche (LOV), Station Zoologique, Villefranche/mer, France
2 Stazione Zoologica A. Dohrn, Napoli, Italy. Email: licandro@alpha.szn.it

Fluctuations of gelatinous zooplankton can greatly affect the functioning of the planktonic system. Salps, which sometimes have blooms lasting days to months (Fraser, 1962; Berner, 1967; Madhupratap *et al.*, 1980; Heron and Benham 1984; Braconnot *et al.*, 1990; Menard *et al.*, 1994), can rapidly deplete large quantitites of phytoplankton standing stock and thus play an important role in biogeochemical cycles (Fernex *et al.*, 1996). Calycophoran siphonophores, one of the major carnivorous groups of plankton, can reach very high concentrations after a lag of several weeks from the peak in primary production (Sreekumaran-Nair *et al.*, 1992; Silguero and Robinson, 2000). There is limited information about the siphonophores because they can be easily destroyed by traditional sampling methods.

The analysis of historical data sets is fundamental in order to study occasional events like blooms of gelatinous organisms and their doubtless relationship with hydroclimatic factors. Long-term monitoring allows to quantify the extent of such events and to exactly identify when they occur.

For this reason from the longest planktonic data set in the Mediterranean, long term fluctuations of salps and siphonophores were studied in a coastal station (Point B) in the Ligurian Sea (Villefranche-sur-mer, North Western Mediterranean). Sampling was done from 1974 to 1999 (with an interruption between 1978 and 1983) at a maximum frequency of twice a day by vertically towing a Regent net (690 mm mesh size), from 75m depth to the surface. The major physical parameters (temperature and salinity at different depths) and meteorological variables (atmospheric pressure, air temperature, wind, rain and daily light intensity) were recorded in the same period.

Blooms of both salps (*Thalia democratica* and *Salpa fusiformis*) and siphonophores (*Muggiaea atlantica* and *Muggiaea kochi*) were observed in some periods during the 20 years studied.

Two great blooms of *Thalia democratica* were detected in 1990 (23313.3 ind. 100 m^{-3}) and in 1994 (23277.5 ind. 100 m^{-3}), while the major bloom of *Salpa fusiformis* (1858.7 ind. 100 m^{-3}) in 1999 was much lower and coincided with the annual peak of *T. democratica* (3657.3 ind. 100 m^{-3}).

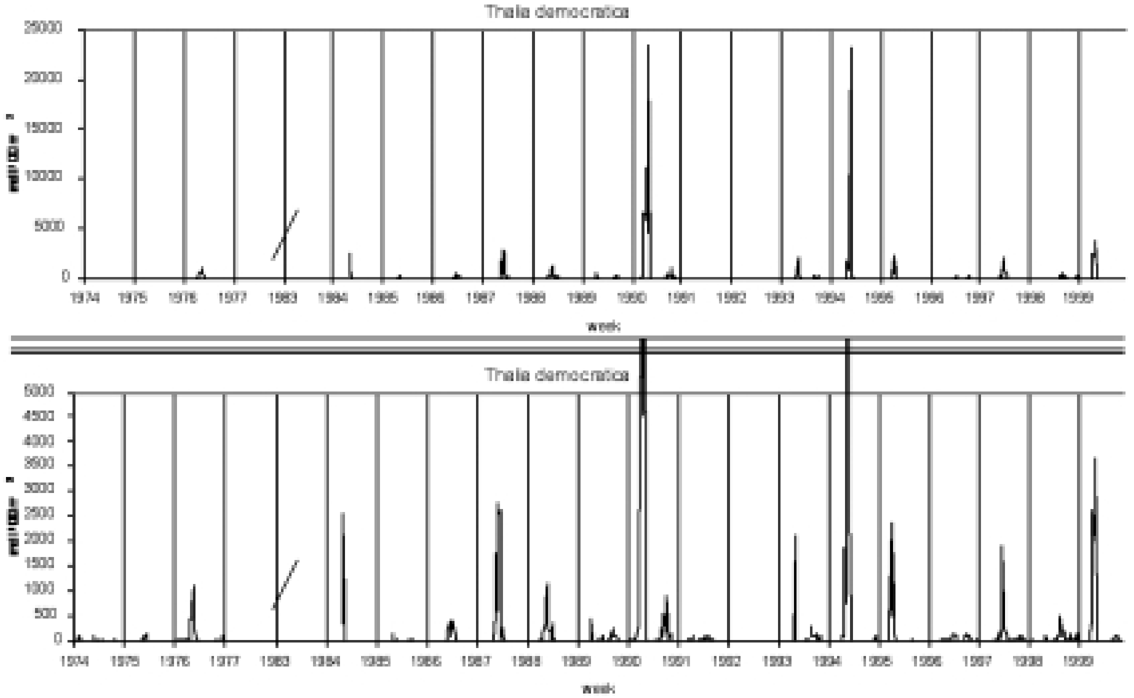


Fig. 1. Villefranche-sur-mer (Point B). Abundance (ind. 100 m^{-3}) of most important species of gelatinous zooplankton from 1974 to 1999 (interrupted from 1978 to 1983). Note the different scale for *Thalia democratica.*

M. atlantica, which predominated over *M. kochi* since 1987 (Carré and Carré, 1991), showed major interannual peaks in 1984 (4080.0 ind. 100 m^{-3}) and in 1990 (3276.7 ind. 100 m^{-3}), two weeks before the great bloom of *T. democratica.*

The impact of *T. democratica* bloom on the copepod community was studied during the spring 1990. A one order of magnitude decrease of copepods was observed during the salp bloom, as well as a diminution of the diversity of copepod community due to the rapid increase of the genus Sapphirina, which is parasitoid of salps.

The relationship between meteorology and fluctuations of salps was already pointed out in the Bay of Villefranche by Ménard *et al.* (1994) in the years 1967-1990, showing that winds, affecting the stratification of the water column, contributed to the unusual occurrence of massive abundance of salps. In that study a different type of net was used (Juday-Bogorov net, 330 mm mesh size). The actual analysis of the “Regent-net series”, which continued up to 1999, confirms the effect of wind and meteorological conditions on long-term fluctuations of salps (this time sampled by a net with an higher filtration rate). Most of their greatest interannual maxima can be related to unusual events of low atmospheric pressure and strong wind.

Furthermore, the preliminary analysis of long-term fluctuation of temperature, which decreased from the end of the 1970’s until 1990, may explain the increasing predominance of the siphonophore *M. atlantica*, which prefers relative cold waters (Purcell, 1982) and lower temperatures, over the congeneric species *M. kochi*.

II - 3. Jellyfish outbreaks

Adriatic ecological history: a link between jellyfish outbreaks, red tides, mass mortalities, overfishing, mucilages, and thaliacean plankton ?

Ferdinando Boero

Dipartimento di Biologia, Università di Lecce, Italia. Email: boero@unile.it

INTRODUCTION

The Adriatic Sea, in the last twenty years, went through a series of massive disruptions that greatly impaired local economies and ecosystem functions. The main cause of all this originates in eutrophication, caused by agricultural, industrial and urbanactivities leading to enormous nutrient overloads, mainly discharged by the Po River (Vollenweider *et al.*,1992). The years were characterised by jellyfish outbreaks, red tides, bottom anoxias leading to benthic mass mortalities and mucilages. The hypothesis developed hereafter sees Adriatic ecological history as a cascade of interconnected events.

THE SCENARIO

A more or less closed system that receives an overload of nutrients will invariably respond with a production increase. This quantitative prediction is of little value if not accompanied by a qualitative estimate. The Adriatic, before the1980's, was the most productive sea of the Mediterranean basin; this was due to high nutrient availability sustaining a high production consisting, for a long period, in fish and bivalves. Starting in the early 1980's, the Adriatic ecosystem dynamics displayed unusual properties.

The chain of "abnormal" events (Fig. 1)

The Pelagia years

During the early1980's, the massive presence of the scyphozoan *Pelagia noctiluca* affected the whole Mediterranean (see Goy, 1984a). This jellyfish outbreak had a great impact on Adriatic ecology. The effects on fisheries were enormous, since huge quantities of jellyfish clogged all nets in almost no time. Since *Pelagia* is a top predator, feeding on almost all plankton, including eggs and larvae of nekton and benthos (Larson, 1987), the impact on fish and also mollusc populations was presumably very large and resulted in lower production. Such an impact, however, was never estimated. The burst of studies on *Pelagia* lasted a few years to terminate abruptly, once the jellyfish population went back to normallevel.

Red tides

If three years of top predator outbreaks affected prey populations, then it is probable that, in the following years, the nutrients issued by the source (the river Po) were not all utilized by the usual components of the sink (fish and bivalves). Some opportunistic members of Adriatic communities took advantage of this increased nutrient load. This might explain the blooms of toxic dinoflagellates that impacted the northern Adriatic for many years (Marchetti, 1990), with catastrophic consequences on both fisheries and tourism. Harmful algal blooms resulted in both pelagic and benthic mass mortalities due to anoxic crises.

Mass mortalities

The mass mortalities in the water column led to accumulation of decaying organic matter on the bottom, leading, in turn, to mass mortalities of benthic organisms. Notably, powerful benthic filter feeders such as sponges and ascidians disappeared almost overnight (Stachowich, 1984), and it is probable that the same happened for bivalve populations (Ott and Herndl, 1995).

Bivalve overfishing

Faced with a decrease in bivalve yields, fishermen started to use very efficient tools to collect them, replacing traditional gear with powerful hydraulic dredges that collect specimens deeply buried in the sediment. The already depleted stock of benthic filter feeders became further impacted by overfishing. The absence of indigenous competitors might also explain the success of the imported bivalve *Tapes philippinarum*, a substitute of the local *Tapes decussatus*.

Mucilages

After a series of red tide years, it became easy to predict, after a particularly rainy spring and a consequent increase of terrestrial run offs, when a red tide would eventually occur. This prediction (made by the author during a workshop on red tides) failed in the year 1991 (?), when mucilages unexpectedly appeared.

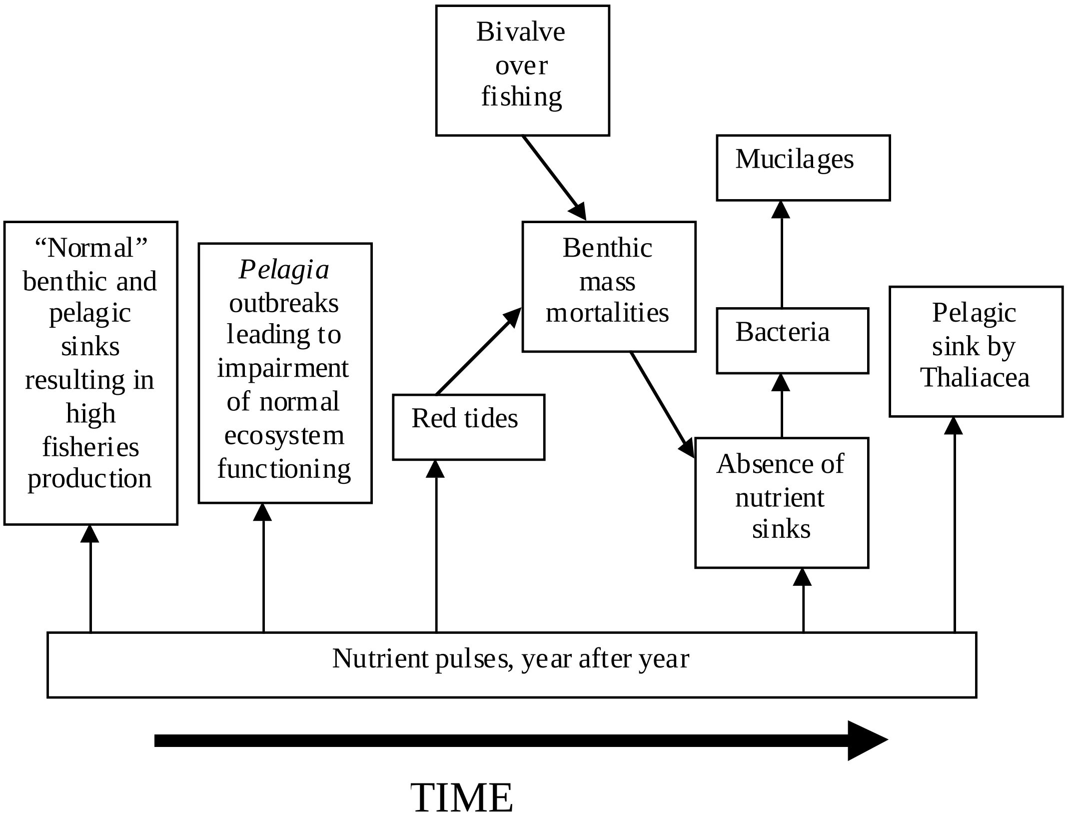


Fig. 1. The "history" of Adriatic abnormal events.

The cause of mucilages has been much investigated, particularly in the last ten years. Diatoms were the first obvious suspects, since diatoms cells were found trapped into the mucus. Another explanation is that mucilages are produced by bacterial activities (Herndl *et al.*, 1992), impaired by an overload of carbon in the water column. In both cases, anyway, the overload of nutrients is the trigger for the phenomenon.

In such a scenario, we might expect that mucilages should be present every year, at the end of the rainy season, fueled by the peak of nutrients brought at sea by terrestrial run-offs.

Sometimes this prediction works; sometimes it does not. Where do nutrients go when bacteria do not process them? An answer is “possibly into filter feeders”, this time not benthic but planktonic ones.

Thaliacean blooms

In the spring of 1998 a bloom of pelagic tunicates took place throughout the Adriatic, from Greece to the gulf of Trieste. The bloom occurred at some distance from the coast and passed almost unnoticed, so that there are no published records of it. the authror observed it while crossing the Adriatic from Dubrovnik to Bari and received accounts on its occurrence by Greek and Northern-Adriatic colleagues.

Thaliacea are very efficient filter feeders and can remove very small particles from the water column, including bacteria and particulate organic matter (Bone, 1998). In that year mucilages did not occur.

CONCLUSION

This historical reconstruction cannot be tested by proper experiments, but it possesses heuristic value It signals that it is wrong to treat each of the above-mentioned events as an isolated phenomenon, as if past history had no influence on future events. It also calls for the return to long-term series, so as to keep track of ecosystem history and thus detect patterns that might explain apparently unexpected (inexplicable !), phenomena : experimental ecology can identify the proximate causes of ecological events, but we need historical ecology to uncover their ultimate causes (Boero, 1994, 1996). The two approaches are not mutually exclusive and should be preferably conducted in parallel, fertilising each other.

The present reconstruction may also provide management recommendations for the recovery of the presently impaired Adriatic situation : since the reconstitution of an efficient sink of benthic filter feeders appears asa precondition for a return to normality, the management of their populations should aim at substantial biomass increases before a return to substantial fishing efforts.

Jellyfish outbreaks : natural cycle or stress response effect ?

Adam Benovic and Davor Lucic

Institute for Oceanography and Fisheries, Laboratories Dubrovnik, Croatia
Email: benovic@labdu.izor.hr

INTRODUCTION

The overall characteristic of the marine environment is its dynamic component of seasonality and consequent fluctuations in the abundance of plankton organisms. Under regular conditions it might be considered as successions of particular populations in phytoplankton and zooplankton communities in temperate seas. Generally, such temporal change is known as an annual ecological cycle. Appearance/disappearance of plankton populations do not correspond only to annual periods but also to longer time scales. When medium or long term cycles of populations, in any time scales, appear in a known average abundance, we consider it as regular conditions. At higher densities we consider such appearance as a bloom. A plankton bloom could be defined as: "*a dense concentration of plankton individuals which occurs in response to optimum growth conditions*" (Sumich, 1988). An open question is: "what is a dense concentration?" Whatever concentration we would take as "average", additional number of plankton individuals would probably be considered as "abnormal", "irregular", "unexpected" or "exceptional". These events could strongly bias the functionality of marine ecosystems and therefore attract wide public curiosity, but the causes of blooms and mechanisms involved are still a subject of debate among specialists.

CYCLE

Marine invertebrate swarms are world-wide phenomena (Steuer, 1910; Russel, 1970; Yasuda, 1970; Attrill and Thomas, 1996). Among many gelatinous plankton species observed regularly by fishermen and sea researchers, only those accounted as noxious are better researched and reported (Boero, 1991). "Normal" (annual?) blooms as well as absence of noxious species from ecosystems regularly do not draw special attention, neither in public nor in marine research. But the sudden appearance of a new species or massive reappearance of a known species would be immediately noticed, at least in local newspapers. Such events were noted recently in the Adriatic Sea, the most peculiar being the invasion of large numbers of *Muggiaea atlantica* in 1997 (Krsinic and Njire, in press). Although all appearance/disappearance of plankton species could not be quoted as a cycle, hypothetically we may consider it so. Comprehensive data on the problem of massive appearance of a jellyfish, *Pelagia noctiluca* in the Mediterranean (1976-1986) gave us a basis to point out the time scale as a reference (UNEP, MED-POL II, 1984) of gelatinous plankton cycles. We believe that occurrences that were documented by Goy (1984b) and Goy *et al.* (1991) showing cycling of *Pelagia noctiluca* from 1876 to 1986 in the western Mediterranean hypothetically could correspond to other gelatinous plankton cycles.

STRESS

Sélie (1950) used the term "stress" to describe "*the non-specific response of the body to any demand made upon it*". Although the word "stress" has became widely used and its meaning seems very obvious, it is not always clear whether it is seen as a cause or an effect (Stebbing, 1981, 1982). In any of the possible definitions, we would consider stress as a force that causes strong reactions of individual/populations/communities. The minimum extent of a force, or combination of a few forces, that trigger strong reactions could be related to "hormesis". Hormesis, known from the 19th century but without a generally accepted hypothesis, is "*the stimulation of growth processes by low concentrations of toxic agents*" of various kinds, from "very toxic" as Cu to "normal" like salinity (Stebbing, 1991), or "*increase in reproduction to escape the effect of sublethal agents*", whatever they are (Boero, 1991). In addition, at the level of chemical class, hormesis could be defined as "*low-dose stimulation followed by higher-dose inhibition*" (Calabrese and Baldwin, 1998).

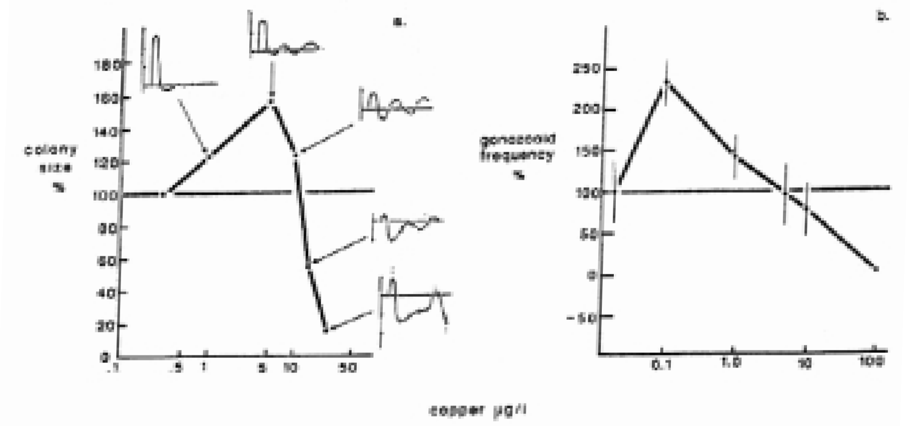


Fig.1. Examples of stimulation of **(a)** asexual reproduction and **(b)** sexual reproduction in *Laomedea flexuosa* in response to low levels of copper (from Stebbing, 1991).

EVIDENCE

In the Adriatic Sea swarms of large numbers of gelatinous plankton were noticed in the past (Steuer, 1910) but also in recent years (Benovic *et al.*, 2000a; Krsinic and Njire, in press). Table 1 lists some evidence reported by fishermen and other marine professionals.

Table 1. Some evidence of larger numbers of gelatinous plankton

Date	Observed species	Comment
21.09.95	*Cotylorhiza tuberculata*	In harbour of Dubrovnik; after strong south winds
10.10.96	*Pelagia noctiluca*	Near island of Lokrum; strong incoming current from Otranto; swarm of ca. 4 ind./m^3
15.05.97	*Pelagia noctiluca*	Near island of Kolocep; after strong south winds
18.05.97	*Pelagia noctiluca*	Near island of Korcula; large swarms; calm weather
12-16.05.97	Unknown species (probably *Aurelia aurita*)	At many localities in the north Adriatic (Porec, Rovinj, Pula); large swarms
26.08– 02.09.98	*Cotylorhiza tuberculata*	Along the coast in south Adriatic; massive event; specimens suspended in incoming current
26.03.99	*Cestus veneris*	Near island of Korcula; massive stranding on beaches after strong south wind
14.10.99.	*Cestus veneris*	Swarms near beaches in Dubrovnik; calm weather; strong currents
27.10.00.	*Rhizostoma pulmo*	In harbour of Dubrovnik; calm weather
15– 25.05.01.	*Aurelia aurita* and *Thalia democratica*	In the Bay of Ston; massive events near shellfish farms
05– 12.09.01	*Craspedacusta sowerbyi*	In the small freshwater lake Kuti in the River Mouth of Neretva; massive event

DISCUSSION AND HYPOTHESIS

Examples from Table 1 can be related to the Adriatic main sea current bringing water masses northward from the Otranto strait along the Croatian coast and transfering gelatinous plankton near shores. This is probably true when we consider *Pelagia noctiluca, Cotylorhiza tuberculata* and *Thalia democratica* that in the southern Adriatic Sea regularly appear in a few year cycles. It is more difficult to account for *Aurelia aurita*, and specially *Cestos veneris*; these events were not noticed in the last 30 years. In addition, higher salinity and warmer winter surface temperatures were recently noted in the Adriatic Sea (Gacic *et al.*, 1996). Do we have here examples of short-term and long-term cycles, or might we consider hormesis? In the north Adriatic, disappearance of many hydromedusae (Benovic *et al.*, 1987) and disruption of the ecosystem have been documented (Degobbis *et al.*, 1995). Expected repopulation of missing species has not revived previous hydromedusan fauna (Benovic *et al.*, 2000b). This is probably because of too strong and frequent stress effects that could destroy populations (Stebbing, 1982), and that could correspond to the “higher-dose inhibition” of chemical hormesis effect. Although North Adriatic anoxia has caused mass mortalities in benthic fauna (Travizi, 1998), some echinoderms continuously produce large numbers of pluteus larvae in the autumn (Lucic, pers.comm.), and masses of *Aurelia aurita* in the spring (Malej, pers.comm.). In land-locked sea-water lakes on the Island of Mljet (Benovic *et al.*, 2000a) the most common (until 1991) neritic copepod *Pseudocalanus elongatus* is now completely missing from the ecosystem (Lucic, pers. comm.). At the same time, *Aurelia* sp. became a major plankton organism reproducing throughout the year in population numbers and individual sizes nowhere previously recorded (Benovic *et al.*, 2000a). What mechanisms triggered this occurrence? We offer the hypothesis that, among other causes noticed in the Adriatic Sea (Benovic *et al.*, 1987), salinity change (Fig. 2) has triggered the hormesis effect in Mljet lakes.

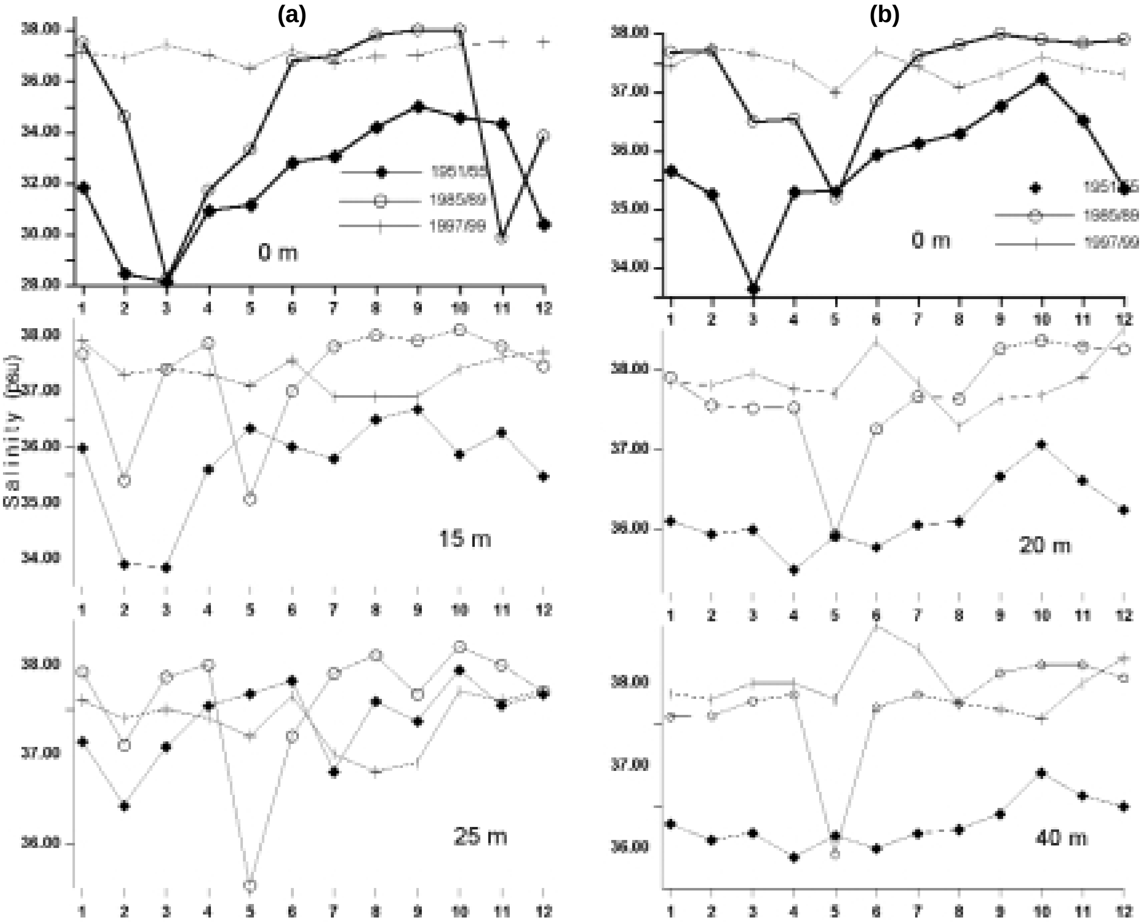


Fig. 2. Salinity changes in sea water lakes Malo jezero **(a)** and Veliko jezero **(b)** on the Island of Mljet (South Adriatic Sea). For geographical map and sampling sites, see Benovic *et al.* (2000 a).

Vucetic (1983) and Stebbing (1991) proposed hormesis as a possible cause of *Pelagia* blooms, but Boero (1991) challenged this by stating: "*Hormesis can be effective only if the source of disturbance is restricted in space*". Since we do not know the initial place of the larval production (of primordial swarm) for *Pelagia noctiluca* and *Cestus veneris*, we cannot relate their occurrences to hormesis effects. But "restricted in space" are blooms of pluteus larvae and *Aurelia aurita* in the North Adriatic, and *Aurelia* sp. in Mljet lakes. Thus, stress response and hormesis could be major causes. Atrill and Thomas (1996) have shown explosive mass appearance of some estuarine invertebrates after 60 years. They have proposed a long-term decrease of freshwater flows in the estuary as a possible cause of invertebrate blooms. P. Kremer (this volume) states that: "*Additional experimental work* (Purcell *et al.*, 1999b) *showed that the rate of strobilation by the scyphistomae is strongly affected by both salinity and temperature. Due to the life cycle of this scyphozoan, the benthic phase determines the number of medusae in the subsequent pelagic phase*". We suggest that these statements could be an additional evidence of hormesis.

Erratic fluctutations in abundance of medusoid and ctenophore populations in two systems, Ligurian Sea and Benguela ecosystem : some examples

Emmanuelle Buecher

University of the Western Cape, Zoology Department, Bellville, South Africa
Email : ebuecher@mcm.wcape.gov.za

Gelatinous carnivores such as medusae, siphonophores, ctenophores and scyphomedusae exert a top-down control on the pelagic food web. They feed upon fish eggs and larvae and have the same prey (*e.g.* crustaceans, such as copepods) as zooplanktivorous fish, inducing some direct effects on fish populations. Massive appearances of gelatinous zooplankton have been reported world-wide: for example *Chrysaora quinquecirrha* in Chesapeake Bay (Purcell *et al.*, 1999a), *Mneniopsis leydii* in the Black Sea (Kideys, 2000), *Pelagia noctiluca* in the Mediterranean Sea (UNEP, 1994), *Aurelia aurita* in Danish fjords (Mills, 2000). These proliferations of gelatinous predators are causing economic problems such as losses of tourism and fisheries activities (*e.g.* clogging and bursting of trawl nets) and also public health risks (*e.g.* in the Mediterranean Sea with the stinging *Pelagia*). Over the last two decades the interest concerning the dynamics of these populations and their proliferations, described as new or recurrent depending on the area, has considerably increased. However, a lot of processes remain unknown.

In recent years, with the collaboration of many researchers, I have compared nine surveys to describe, with various time and space scales, the fluctuation of medusoid and ctenophore populations in two systems: the oligotrophic Ligurian Sea (NW Mediterranean) and the eutrophic Benguela Ecosystem (SE Atlantic). The data presented here illustrate two kinds of erratic fluctuations, some pluri-annual successions of presence/absence over 27 years and the massive appearance of two medusae over 30 years.

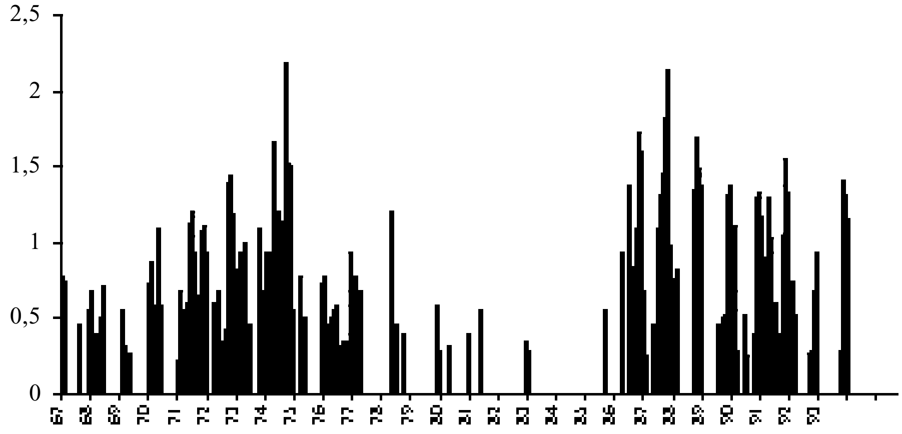
THE LIGURIAN SEA

The Bay of Villefranche is a sheltered embayment near Nice (France). It is typical of the inshore waters of the Ligurian Sea. An analysis of a 27-year survey conducted at a fixed station in the Bay between 1966 to 1993 (vertical tows between 75 m and the sea surface) showed irregular pluri-annual fluctuations of seven species of gelatinous carnivores. Cluster analyses were used to group the years in function of their similarities. Three groups were usually identified: years where the species was totally absent or very rare (called "poor years"), years with medium abundances (called "normal years") and years where the species was massively abundant or was presenting some variation in its seasonality (called "rich years").

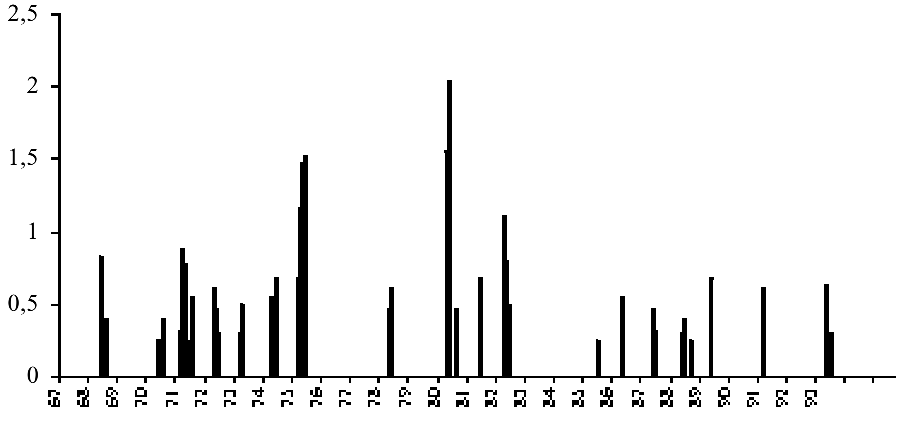
Two groups of species were distinguished :

- 1. Species presenting a cycle of high occurence/low abundance or absence (succesion of poor years → normal years → rich years → normal years → poor years). The duration of the different periods was irregular. *Liriope tetraphylla* displayed this kind of fluctuations (fig. 1a; Buecher *et al.*, 1997). Its population was denser when the environment was characterised by a warm temperature (temperature higher than the global average calculated over the 27 years between 1985 and 1992) and a high salinity (salinity higher than the average between 1981 and 1990).
- 2. Species, such as *Pelagia noctiluca* (ephyrae stage) or *Pleurobrachia rhodopis* (fig. 1b), occurring only for a few years in the Bay (3-4 years) with extremely high abundances (Buecher, 1997). In other years, these species were absent or occurred at low levels. The occurrence of these "rich years" was not following a regular cycle.

1a) *Liriope tetraphylla*



1b) *Pleurobrachia rhodopis*



Globally the gelatinous carnivores populations occurred in the Bay of Villefranche-sur-mer with high abundances between 1986 and 1992 but they were scarcer between 1974 and 1975 and between 1982 and 1984. Medusoid and ctenophore species, which have a similar ecological role, were altering during this 27-year survey. Their preferences for specific environmental parameters did obviously favour the blooming of one species rather than another. However, we are not capable of forecasting their abundances and other biotic and abiotic parameters (as life cycle, currents) should be taken into consideration.

THE BENGUELA ECOSYSTEM

This ecosystem (~15°S to ~35°S) is one of the most important upwelling areas in the world and supports very valuable industrial fisheries. Plankton studies conducted in the region in the 50's and 60's (Hart and Currie, 1960; Stander and De Decker, 1969) did not report the presence of the Hydromedusae *Aequorea aequorea* and the Scyphomedusae *Chrysaora hysoscella*. However, since the 70's, massive occurrences of these two species have been noted, especially in the northern Benguela (Venter, 1988; Fearon *et al.*, 1992). It is tempting to link these blooms of big medusae to the collapse, by more than a factor 10, of the pilchard fishery noticed in the same period (Crawford *et al.*, 1987). A survey was performed in September 1999 to study the spatial distribution of these two medusae.

There was a clear spatial segregation between the two species (Sparks *et al.*, in press). *A. aequorea* was more abundant offshore throughout the water column with high densities close to the surface. An average of 172 kg of *A. aequorea* was caught per minute at a bottom depth greater than 200 m, compared to 60 kg/min at a depth comprised between 100 and 200 m. *C. hysoscella* attained higher densities inshore (averages of 89 kg/min and 191 kg/min caught at bottom depths of < 100m and between 100 and 200m compared with 7 kg/min at depths deeper than 200 m). It was abundant mainly between the surface and 30m. The size and weight distribution of the medusae were also estimated (Table 1; Buecher *et al.*, in press).

Table 1: Weight and diameter of *Chrysaora hysoscella* and *Aequorea aequore*a caught off Namibia in September 1999. Owing to *Aequorea*'s fragile nature, only the remaining central disk of the umbrella was measured and weighted.

	Weight (kg)			Diameter (cm)		
	Average	Minimum	Maximum	Average	Minimum	Maximum
C. hysoscella	1.469 ± 1.521	0.030	11.200	27.8 ± 10.197	8.0	63.0
A. aequorea	0.062 ± 0.021	0.001	0.360	7.294 ± 0.951	1.5	18.0

These results were used to estimate, for the first time, the biomass of these two species in the northern Benguela, an area of 179 000 km^2, extending from 19°S to 29°S and covering the 500-m depth contour. The maximal biomasses calculated for the area were 13.1x10^6 tons for *C. hysoscell*a and 22.3x10^6 tons for *A. aequore*a. These values modify significantly the results of the locally done Ecopath model illustrating the functioning of the Northern Benguela ecosystem (Shannon and Jarre-Teichmann, 1999 and Shannon, pers. comm).

Multi-frequency acoustic data were collected in conjunction with pelagic trawl samplings in order to estimate the biomasses by an indirect method. The Target Strengths (TS) of *A. aequorea* and *C. hysoscella* were defined at frequencies used on fisheries surveys (Brierley *et al.*, 2001). The high numerical densities of these two species of medusae, combined with the substantial TS at frequencies used for fisheries surveys, imply that jellyfish could potentially bias acoustic estimates of fish abundance.

Long term studies have showed shifts in the structural composition of pelagic communities and the existence of global changes of the environment (*e.g.* Southward, 1980). The two surveys described here show different population dynamics for few species of gelatinous carnivores. The descriptions of the population fluctuations and the environmental changes, mainly the temperature, have suggested some hypothetical explanations. However, it remains difficult to predict precisely when these populations will bloom. On the other hand, the ecological and biological studies of the polyp stage done in parallel to those on the pelagic stage are critically missing. The polyp, for the meroplanktonic species, is the one which liberates the young medusae and can react differently to the environmental conditions than the pelagic medusae. It seems fundamental for an understanding of the ecology of these animals to link benthic and pelagic studies.

Are irregular plankton phenomena getting more frequent in the northern Adriatic Sea?

Alenka Malej

Marine Biology Station Piran, National Institute of Biology, Slovenia. Email: malej@nib.si

The issue of irregular massive plankton events is characterised by rather high scientific uncertainty mainly due to multiple linkages between causes and effects, but also to lack of evidence and to our inability to monitor these events at proper spatial and temporal scales. Many scales of variability that make definition of "regularity" rather difficult typify plankton dynamics. Irregular plankton events may be defined as those that show spatial and/or temporal patterns that deviate from those commonly observed. In many cases, even in marine systems where plankton have been studied for over a century like in the northern Adriatic, some important patterns are still dubious. Limited knowledge of plankton fluctuations and insufficient understanding of underlying processes make valuation of irregular and/or massive events troublesome. Irregularity of plankton events is in many cases judged from an anthropocentric point of view and public perception is that these phenomena are getting more frequent. Very often, especially in coastal marine environments, nutrient overload, i.e. eutrophication, is blamed not only for harmful algal blooms but also for other massive plankton events.

Exceptional events associated with phytoplankton like discoloured waters, toxic algae or mucilage accumulations (gelatinous masses) in the northern Adriatic are a matter of great environmental concern. These problems were among priority subjects in the national marine research programmes of the Adriatic countries and in major EU funded projects (Hopkins *et al.*, 1999). Zooplankton massive events have received limited research attention with the exception of the extraordinary abundance of stinging jellyfish *Pelagia noctiluca* (UNEP, 1991). Yet, massive presence of plankton organisms may have profound ecological impacts such as changes in community structure and functioning, and loss of biodiversity. Additionally, they may affect different human activities (fisheries, tourism) and pose serious health risk for humans.

A survey of massive plankton events, generated by larger zooplankton in the northern Adriatic during the last 30 years, is presented. Outbreaks of red tides caused by massive presence of heterotrophic dinoflagellate *Noctiluca miliaris* and mucilage accumulations were also included.

The survey is based on our own observations (published and unpublished) and those reported in scientific literature. An attempt was done to relate these irregular plankton events to shifts in the trophic status of the northern Adriatic ecosystem. In their analysis of long-term changes in the northern Adriatic ecosystem related to anthropogenic eutrophication, Degobbis *et al.* (2000) revealed a significant increase of eutrophication that occurred during the 70's, reaching maximum in the early 80's. They also indicated that eutrophication was diminishing since the late 80's. On the basis of these findings our data on massive plankton events for the last 30 years were grouped into three periods: 1971-1980, 1981-1990, 1991-2000.

Due to visible water discoloration, the massive presence of *Noctiluca miliaris* was easily recorded. Other most frequently reported massive plankton events in the northern Adriatic were outbreaks of large jellyfish. Species involved include mainly the scyphomedusae *Aurelia aurita*, *Chrysaora hysoscella*, *Cotylorhiza tuberculata*, *Pelagia noctiluca* and *Rhizostoma pulmo* although masses of hydromedusa *Aequarea forskalea* were mentioned several times.

Ctenophora were another plankton group that was recurrently reported as extremely abundant in the northern Adriatic. Unfortunately, in most zooplankton studies samples were collected using nets and only a small fraction of Ctenophora were preserved in recognizable condition. Enormous numbers of the pteropod *Creseis acicula* were recorded only twice during the whole period taken into consideration (1971-2000).

Events and organisms involved are presented in Table 1; shown are only events when organisms (and mucilage) were present in mass.

Table 1. Massive zooplankton events in the northern Adriatic and organisms involved in three periods during 1971-2000. Mucilage events are also listed. Periods (after Degobbis *et al.,* 2000) taken into consideration: 1971-1980; 1981-1990; and 1991-2000 (**+** event was observed once in the period; **++** event was observed several times in the period; **+++** event was observed every year in the period).

Organisms involved	**1971-1980**	**1981-1990**	**1991-2000**
Aequorea forskalea	+	+	++
Aurelia aurita	+	+	++
Chrysaora hysoscella		+	+
Cotylorhiza tuberculata	++	+	
Pelagia noctiluca	++	++	
Rhizostoma pulmo		+	+
Ctenophora	+	+	++
Noctiluca miliaris	++	++	++
Creseis acicula	+		+
Mucilage events		++	++

The majority of organisms causing irregular massive events during the last 30 years and listed in Table 1 were also described as bloom/swarm forming in earlier plankton studies in the northern Adriatic (Avian and Rottini, 1994; Car and Hadzi, 1914; Issel, 1922; Purcell *et al.*, 1999a), some already in the first decades of 20th century. Similarly, mucilage events were known to occur at irregular intervals in the northern Adriatic since the 18th century. The exception is *Noctiluca miliaris* that was recorded in the Gulf of Trieste in early plankton reports (Steuer, 1903) but not as a bloom forming species. It’s only since the late 70’s that this organism was present in such quantities that it caused red tides (Fonda Umani *et al.*, 1983; Malej, 1983).

From our observations and available data we may conclude that there are no clear indications of increased recurrence of massive plankton events neither of linkage with eutrophication. However, in future we should improve our ability to study these phenomena in relation to physical and biological factors, also including more work in situ using relevant methodology and laboratory experiments.

Past and present anthropogenic factors promoting the invasion, colonization and dominance by jellyfish of a Spanish coastal lagoon

Francesc Pagès

Institut de Ciències del Mar (CSIC), Barcelona, Catalunya, Spain. Email: fpages@icm.csic.es

Jellyfish blooms in coastal lagoons are an irregular massive plankton event that apparently is becoming more regular in some tropical and temperate coastal ecosystems. The blooms usually recorded in Central America and the Caribbean Sea are characterized by scyphomedusae with endosymbiotic dinoflagellates as *Cassiopea*, *Lychnorhiza*, *Stomolophus* and *Linuche* (Collado *et al.*, 1988; García and Durbin, 1993; Kremer *et al.*, 1990). More recently events are reported in north-Atlantic and Mediterranean waters involving other jellyfish species, not always with zooxanthellae associated (Kikinger, 1992; Ballard and Myers, 1996; Benovic *et al.*, 2000a). This phenomenon implies important socio-economic consequences in the regions where they occur, particularly on fisheries and tourism, as in Mar Menor (south-eastern Spain).

Mar Menor is a hypersaline coastal lagoon of 135 km^2 surface area, salinity 42.7-47.1 psu and 3.5 m mean bottom depth. It is separated from the Mediterranean Sea by a sandy barrier (20 km in length and 100-900 m wide) with five shallow inlets connecting both basins. It is a singular ecosystem that traditionally has supported important artisanal fisheries (grey mullets, sea breams and prawns). Jellyfish have been always present and a small population of *Aurelia aurita* is known from early last century. However, the scyphomedusae *Cotylorhiza tuberculata* (up to 35 cm in diameter) and *Rhizostoma pulmo* (up to 40 cm in diameter) were recorded for the first time about ten years ago and both species developed the first massive bloom in summer 1993, which has been recurrent every year up to date.

Now jellyfish are the most conspicuous organisms in the lagoon over the year and the peak abundances of the three species show a seasonal lag (up to 0.001 *Aurelia* m^{-3} in April-May, up to 0.02 *Rhizostoma* m^{-3} in May-July, up to 0.9 *Cotylorhiza* m^{-3} in July-September) (Mas, 1999).

The results and observations obtained up to date appear to indicate that the occurrence and proliferation of *Cotylorhiza* and *Rhizostoma* could be associated to the strong environmental changes suffered by this coastal ecosystem over the last century, starting in the 70's with the enlargement of some inlets for facilitating the pass of recreational boats together with the building of sport harbours (Pérez-Ruzafa *et al.*, 1991). The large inflow of Mediterranean waters caused a salinity decrease from 50-52 psu to the present levels, and doubtless the introduction of both scyphomedusae into the lagoon.

The anthropogenic activities made in and around the lagoon have been responsible for drastic changes in the water circulation that have altered the water properties, the sediment composition, and both the benthic and pelagic communities. These activities comprised saltworks, mining, dumping, sport harbours, human settlements and development of touristic activities from intensive building that affects 42% of the lagoon's perimeter.

Geomorphological changes, particularly since a 1987 policy of creating artificial beaches from dredging for sediment extraction and deposition of sand along the coast. These changes have caused the retreat of the *Zostera marina* and *Cymodocea nodosa* meadows and the expansion of *Caulerpa prolifera* that causes muddy bottoms. Dissolved oxygen in the water at the bottom decreases nearly to zero in muddy areas with dense plant cover.

Simultaneously there has been a significant fall in the fishery stocks of some of the more relevant species. Lagoon species as grey mullets and sea breams were progressively replaced by Mediterranean species as *Anguilla anguilla* after the 70's and the amount of grey mullets captured decreased (426.802 kg in 1888, 101.346 kg in 1973, 11.380 kg in 1981; Pérez-Ruzafa and Marcos, 1987).

In addition, agricultural activities in the region have been transformed and have increased much in the last thirty years after the transfer of waters from northern rivers and the intensive pumping of groundwater. Fertilizers are intensively used in the irrigated lands and they are channeled towards the lagoon. Urban dumping has dramatically increased, mainly in summer when sewage farms are insufficient. The general result is that the high input of nutrients in the lagoon (2000 nitrogen T/year and 60 phosphorus T/year; Martínez and Esteve, 2000) from the watershed, groundwater drainage, and saltworks is changing the original oligotrophy towards a progressive eutrophication, mostly from agriculture sewage and to a lesser extent from touristic development.

Purcell *et al.* (1999a) argued that jellyfish populations may be enhanced by nutrient enrichment due to the resulting increases in the availability of planktonic food, but that direct connections between human effects on estuarine systems and changes in jellyfish populations were difficult to make. They also noted that the lack of long-term data on nutrients and plankton populations prevents evaluation of possible connections of eutrophication to jellyfish population sizes. In general, this a correct argument but I support Pérez-Ruzafa (1997) in concluding that abundance of *Cotylorhiza* and *Rhizostoma* in the Mar Menor has increased as a result of the increase in the amount of nutrients entering the coastal lagoon. His study also suggested that the present populations of both scyphomedusae play an important role in regulating nutrient levels in Mar Menor because the sudden absence of both jellyfish would cause an increasing eutrophication by the development of algal blooms.

The introduction of the oyster *Ostrea edulis* in the 70s' originated a large population that reached maximun densities in the 80's. However, oysters did not adapt well to a new environment of muddy and anoxic bottoms. Encrusting esponges caused problems in shell formation, depriving oysters of any commercial value. In addition, high quantities of oyster larvae were found in the stomach content of *Aurelia aurita* (Franco and Gili, 1991). Now, most of the population is dead, the central basin is covered by millions of empty shells that appear to be the main substrate for *Cotylorhiza* and *Rhizostoma* polyps (Marhuenda *et al.*, 2000).

Why is *Cotylorhiza tuberculata* the main actor of these blooms? This species is the only scyphomedusan in Mediterranean waters with endosymbiotic dinoflagellates and it appears that zooxanthellae can play a key role in the proliferation of this scyphomedusan in assimilating the high content of nutrients dissolved in the water and traslocating the carbon fixed to the host. At sunrise, all *Cotylorhiza* aggregate in surface waters, they migrate downwards before noon and they re-appear on the surface before sunset. The horizontal distribution depends on winds and currents direction. On the contrary, *Rhizostoma* aggregates mostly in the south-western part of the lagoon, in front of the watershed mouths (Pérez-Ruzafa, 1997).

An important question is wether jellyfish populations have increased in direct proportion to dissolved nutrients concentrations, or if the latter have favoured micro- and mesozooplankton populations that are prey items of both jellyfish. The only other location where *Cotylorhiza* often occurs in high densities is Vlyho Bay, Lefkada Island, Greece. The population was investigated by Kikinger (1992) and the gut content analysis of *Cotylorhiza* specimens showed copepods, gastropod larvae and tintinids as the only prey, insufficient to meet the nutritional demands of the high growth rates observed, as happens in Mar Menor. Other studies on scyphomedusae with endosymbiotic dinoflagellates reached similar conclusions (García and Durbin, 1993; Kremer *et al.*, 1990).

Purcell *et al.* (1999a) noted that in the northern Adriatic only *Aurelia aurita* and *Pelagia noctiluca* have occurred in extremely large numbers in coastal waters, although *Cotylorhiza tuberculata* has been observed to cause swarms too. They also commented that qualitative observations of different jellyfish species in the northern Adriatic indicated that coastal aggregations were repeatedly formed by *A. aurita* in April-June, and *C. tuberculata* in August-October, which is the seasonal trend observed in Mar Menor by Pérez-Ruzafa (1997). It is also interesting to note that Malej (this volume) shows that during periods characterized by *A. aurita*, swarms of *C. tuberculata* were very rare, the latter being associated with rather high abundances of *Rhizostoma pulmo*, the same co-occurrence pattern observed in Mar Menor (Mas, 1999; Pérez-Ruzafa, 1997).

Tourism is the main economic activity in Mar Menor. More than 300,000 people live in the vicinities of the lagoon during summer. The regional authorities, alarmed by the conspicuous presence of jellyfish swarms that could cause a potential decrease of visitors, have financed some preventive measures (permanent nets set up off the main beaches, jellyfishing with pelagic nets) over the last four years with no incidence on jellyfish blooms. In summer 2001, the regional authorities have continued setting up nets offshore and paying fishermen for collecting jellyfish with a cost around 1,000,000 Euros (Salamanca, 2001). Most of the artisanal fleet has been involved in exchanging of the problems caused to them by the offshore nets. The regeneration of this environment implies drastic changes in the agricultural and town planning policy of the region, particularly the treatment of agricultural and urban sewage.

II - 4. Black Sea : *Mnemiopsis et al. ...*

Distribution of gelatinous macrozooplankton and ecosystem change in the Black Sea

Erhan Mutlu

Institute of Marine Sciences, Middle East Technical University, Erdemli, Içel, Turkey
Email: mutlu@ims.metu.edu.tr

The present study is a reevaluation of the database collected for the distribution of common gelatinous macrozooplankton in the Southern Black Sea during 1991-1999 by the Institute of Marine Sciences in Turkey (IMS-METU), and additionally, includes effects of anchovy overfishing on the ecosystem. Biological oceanography of the Black Sea has been studied extensively by the riparian countries. Optimization of concepts and hypotheses for the distribution pattern is difficult for them because of the lack of standardization in biomass measurements, due to the different techniques used by each country, even each investigator in Turkey. The intercalibration study on the biomass and abundance of gelatinous organisms by two different institutes best reveals these differences (Table 1; Niermann *et al.*, 1995).

Table 1. Average number (n) and wet weight (W) of *Mnemiopsis leidyi* and *Aurelia aurita* from 68 stations measured by the IMS-METU (Hensen Net) and by the Shirshov Institute (Bogorov Rass Net) in the southern Black Sea in August 1993 (Niermann *et al.*, 1995).

Sp/Net	**Hensen**	**Bogorov-Rass**	**Factor**
M. leidyi			
n m^{-2}	34	39	1.2
W (g m^{-2})	186	1077	5.8
A. aurita			
n m^{-2}	14	17	1.2
W (g m^{-2})	202	1322	6.5

These significant differences mainly emerged from the different methods used to estimate biomasses : simply, hand balance was used for the weight measurements by the IMS-METU whereas assessments of the weights were made from the length-weight regression equations applied for three different size classes by the Shirshov Institute.

Five gelatinous macrozooplankton inhabit the Black Sea and the Bosphorus Strait: *Aurelia aurita*, *Pleurobrachia pileus*, *Mnemiopsis leidyi*, *Beroe ovata*, and *Rhizostoma pulmo*. The first two have existed for a long time, the rest were introduced at the end of 1980s. Except *P. pileus*, these species were observed in the Sea of Marmara and Dardanelles Strait, whereas none of them were observed in the Aegean Sea exit of the Dardanelles to the south, during R/V *Bilims*' cruises between 1999 and 2001. Uysal and Mutlu (1993) reported the first time occurrence of *M. leidyi* in the Eastern Mediterranean Sea, in Mersin Bay. Specimens were recorded only in highly eutrophic shallow parts along the coast. *M. leidyi* and *Beroe* sp. were also observed recently in the Iskenderun Bay (Adana-Yumurtalık) in 2000 and 2001.

It is commonly admitted that *M. leidyi* was first introduced to the Black Sea in 1980s via the ballast waters of ships coming from the USA. However since the ships were also coming in and out the Black Sea before 1980s, outbreak of this species may be simply a consequence of the increasing eutrophication triggering the phytoplankton bloom and hence an increase in mesozooplankton during the period 1978-1988. Observation of *M. leidyi* only in the highly eutrophic coastal sectors of the Mediterranean Sea (Uysal and Mutlu, 1993; Kideys and Niermann, 1993) also supports this conclusion. All the species (*M. leidyi, P. pileus*, and *A. aurita*) formed patchy aggregations. The distributions were correlated with hydrodynamic features in the Black Sea with higher concentrations in the coastal anticyclonic eddies (Mutlu *et al.*, 1994). The two central main gyres had a low biomass of the species (Figure 1). Anticyclonic gyres, in which the water downwells, continuously accumulate planktonic individuals in the core of the eddies, resulting in high biomass (Mutlu, 1999, 2001). This association was quite true for *M. leidyi* and partly for *A. aurit*a that live in surface waters. In addition to the effect of the circulation on shaping patches of *P. pileus*, vertical distribution must be taken into consideration. In contrast to two

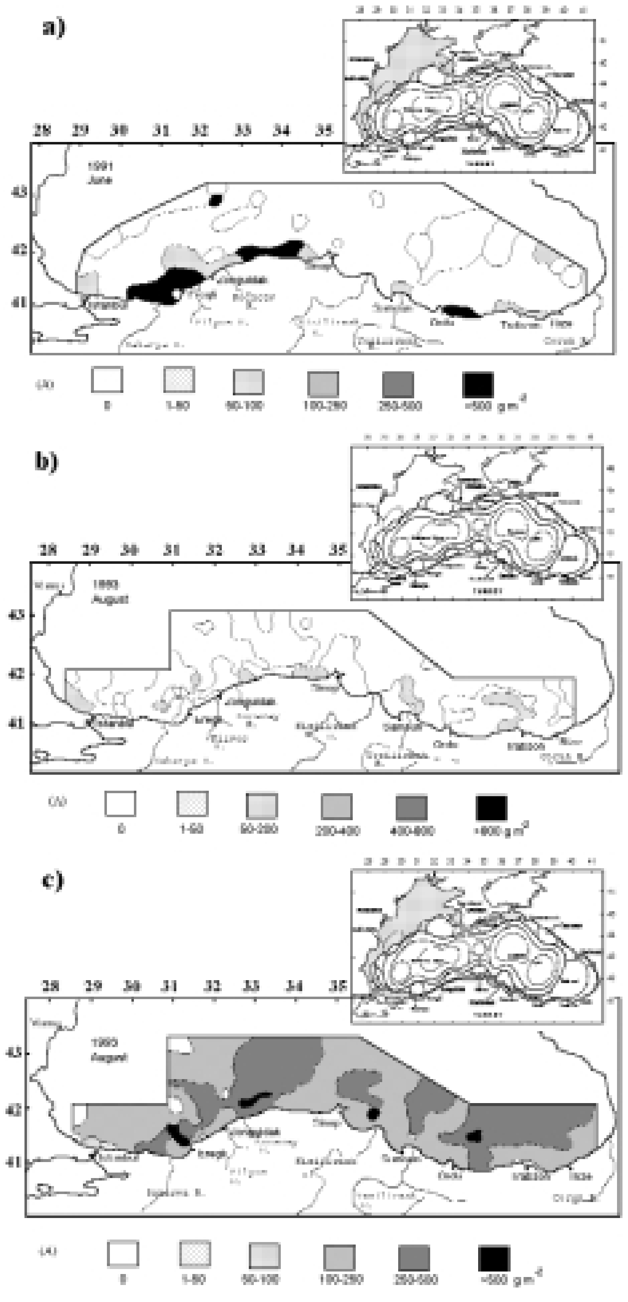


Figure 1. Spatial distribution of three common gelatinous macrozooplankton in summer.
a) *M. leidyi*
b) *A. aurita*
c) *P. pileus.*

other gelatinous species, *P. pileus* individuals live in a layer from the thermocline to the anoxic zone. Most individuals, especially larger ones which contribute much to the wet weight biomass, were found where the maximum density stratification (pycnocline) of anticyclonic eddies occurred (Mutlu and Bingel, 1999).

Coastal transportation of the gelatinous individuals occurred with the rim current meandering the longshore of the Black Sea basin. An average biomass of about 50-450 g m^{-2} was measured for all species. *Aurelia* was the least numerous (2-14 individuals m^{-2}), with highest numbers (55-523 individuals m^{-2}) belonging to *Pleurobrachia*. The abundance of *Mnemiopsis* varied from 11-160 m^{-2}. The biomass and abundance of *Mnemiopsis* peaked in winter when the quantity of *Pleurobrachia* and *Aurelia* dropped. In contrast, the abundance of *Aurelia* and *Pleurobrachia* peaked in summer. Maximum total biomasses estimated for the entire Black Sea were 205 million tons (March 1995), 109 (August 1993), and 98 (August 1993) for *M. leidyi*, *P. pileus* and *A. aurita*, respectively. If we divide the 800 million tons biomass of *M. leidyi* estimated by Vinogradov (1990) by a factor of 5.8 (Table 1), a biomass of 137 million tons is was recalculated for the entire Black Sea.

Overall, the gastrovascular cavities of 9709 *M. leidyi* individuals contained food items of copepods (50%), molluscs (40%), fish eggs and larvae (1%), cladocerans (1%) and others (8%, Mutlu, 1999). The stomachs of 862 *A. aurita* individuals contained food items of copepods (42%), molluscs (35%), fish eggs and larvae (3%), cladocerans (4%) and others (16%, Mutlu, 2001). The gastrovascular cavities of 27424 *P. pileus* individuals contained food items of copepods (90%), molluscs (1%), fish eggs and larvae (1%), cladocerans (1%) and others (7%, Mutlu and Bingel, 1999). Compared to the stomach content of *Mnemiopsis*, *Aurelia* consumed three times more fish eggs and larvae. As Kideys and Romanova (in press) repeatedly observed, the period 1995-1999 was low both in abundance and biomass of *A. aurita*. Similarly, *M. leidyi* was also low in centers of offshore cyclonic regions and in the coastal upwelling area. Generally, it was more abondant in coastal regions, along the rim current. Compared to the other two species, *P. pileus* showed a more homogeneous distribution, with somewhat higher number in deep offshore regions than in the coastal areas.

As Gucu (in press) emphasized, the Black Sea ecosystem has changed from oligotrophy in the 1960-1970’s period (Sorokin, 1983; Ivanov and Beverton, 1985; Balkas *et al.*, 1990). The most characteristic feature of this period was probably the low phytoplankton biomass whose average annual biomass fluctuated around 3.6 10^6 tons for the entire Black Sea (Greze, 1979). This value led to a considerably low annual average mesozooplankton biomass estimate at about 15.6 10^6 tons. The gelatinous organisms consisted only of thejellyfish *A. aurita*. Mironov (1971) reported 675 thousand tons (1.3 kg m^{-2}) of biomass of *A. aurita* for this period. The eutrophy phases (Sorokin, 1983; Tolmazin, 1985; Caddy and Griffiths, 1990; Mee, 1992; Zaika, 1992; Niermann *et al.*, 1994) was associated with such anthropogenic effects as river out-flows (Bondar, 1977), changes in nutrient loads (Bologa *et al.*, 1984; Gomoiu, 1990), introduction of exotic species (Vinogradov *et al.*, 1989a; Mutlu *et al.*, 1994) and excessive fishing (Figures 2a, b) Ivanov and Beverton, 1985; Stepnowski *et al.*, 1993; Gucu, 1997).

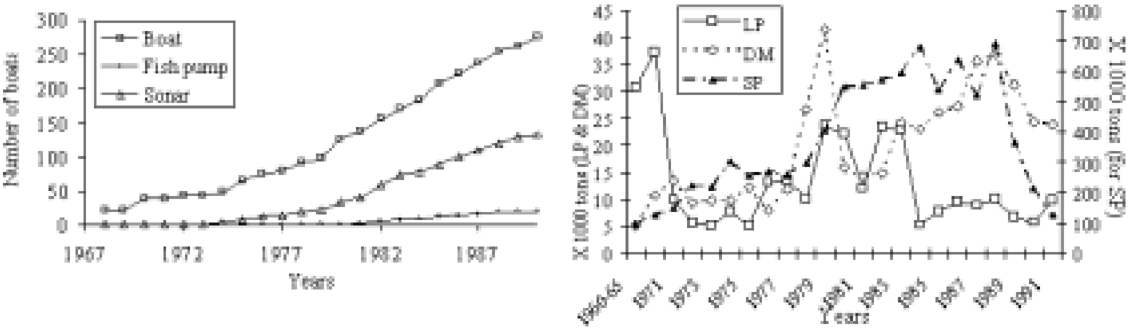


Figure 2. Number of Turkish purse seiners, boats with a sonar and boats with a fish pump in the Black Sea (Ano., 1992) and catch of the **LP** (= large pelagics), **SP** (=small pelagics), **DM** (=demersals) during the period between 1960-1991 (GFCM, 1991; 1993). From Gucu (in press).

Many anomalies were observed in the ecosystem due to eutrophication (ANON, 1993; GESAMP, 1994, 1995). Finally, in 1989 *M. leidyi*, which was a newly introduced species, appeared in the Black Sea in huge quantities. In the autumn of 1989 a biomass of about 800 million tons wet weight of *M. leidyi* was estimated for the entire Black Sea (Vinogradov, 1990). Its appearance has been synchronously followed by a sudden decline in various fish stocks, which many authors linked to possible predation by *M. leidyi* on pelagic eggs and larvae (Vinogradov, 1990; Zaika, 1992).

On the other hand, ecosystem modelling (Gucu and Oguz, 1998) suggests that neither carrying capacity, nor the trophodynamic structure of the Black Sea can support such a high biomass value of *M. leidyi* as the one reported in 1989. During this, period of eutrophy (1978-1988) marked increasing human population, developments in agriculture, and industrialization, resulted in increase of nutrient loads to the Black Sea via major European rivers which turned the Black Sea into one of the most eutrophic seas of the world (Zaitsev, 1991).

Towards the end of the decade, severe changes in the ecosystem took place. Now, the 1990's are considered as the "Collapse and Recovery" period in recent articles by many authors including Zaitsev and Alexandrov (1997). Gucu (in press) concluded that the combined analysis of ecological observations, fisheries data and mass balance model experiments indicate that overfishing did play a crucial role in the successful development of *M. leidyi*, by emptying ecological niches, which were occupied by small pelagic fishes and by allowing gelatinous competitors to re-inhabit (Figure 3a, b). The recovery of the ecosystem relies, to some extent, on management attempts to bring fisheries back to a sustainable level.

Besides overfishing (Figure 4) which drastically reduced small pelagic fish stocks in the Black Sea, hypoxia as a consequence of eutrophication, and increasing pollution in the spawning grounds on the northwestern shelf, are also influential. Some pelagic species like anchovy and horse mackerel are affected by hypoxia (Zaitsev, 1993). Negative effects of pollutants on fish eggs and larvae must be taken into consideration as well.

Oguz *et al.* (2001) described the role of *M. leidyi* in changing the ecosystem of the Black Sea. In the pre-*Mnemiopsis* phase of the ecosystem prior to 1988, mesozooplankton peaks occured toward the end of March following the early spring phytoplankton bloom. Thereafter, *Aurelia* bloom took place in April as they grazed the mesozooplankton. The absence of mesozooplankton grazing then allowed phytoplankton to produce a relatively weaker late spring bloom, which

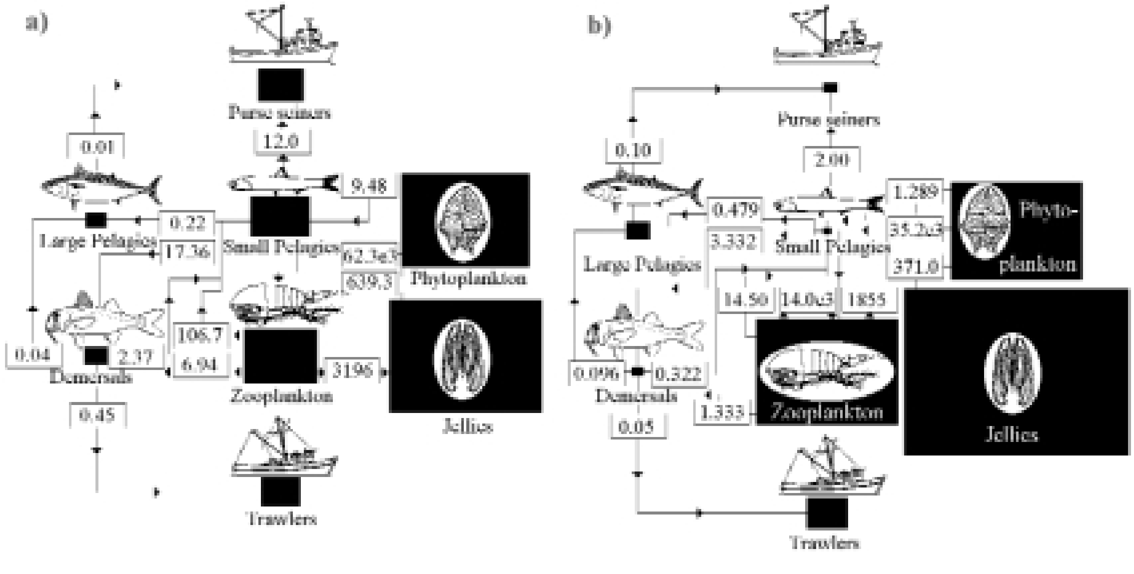


Figure 3. Food web of the Black Sea and the flows between different components in **a)** the eutrophication Period (1978-1988) and **b)** the period of "Collapse and Recovery" (1988-1995). The size of the boxes is kept equal to enable comparison of the changes taken place at the future periods. Number in box is in tons/km^2/year. From Gucu (in press).

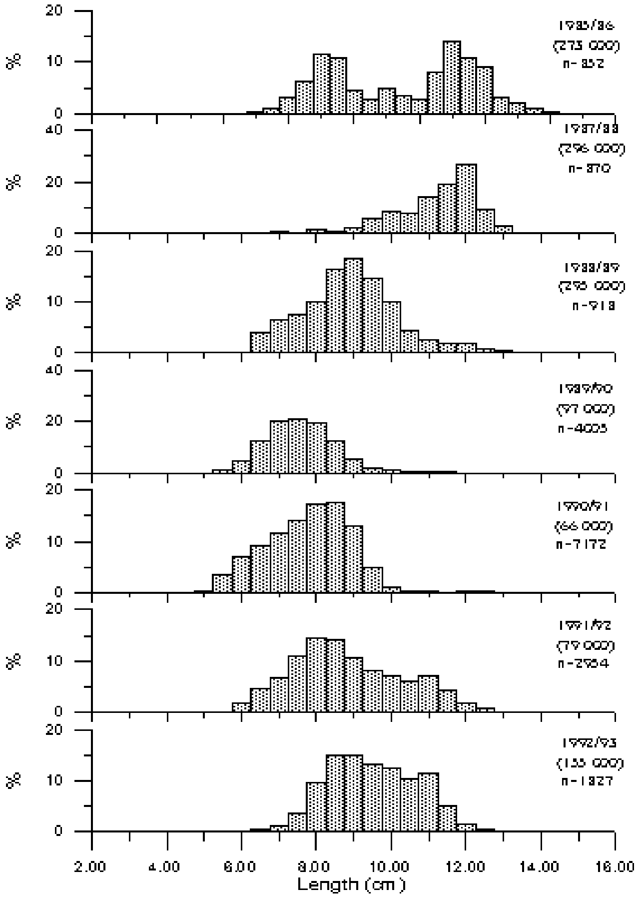


Figure 4. The first signs of over-fishing on the Small Pelagics were realized during the 1987/88 fishing season (Figure 2). Time series of the length composition of anchovy landed by the Turkish Black Sea fishing fleet (Data taken from Ozdamar *et al.*, 1991 and Bingel *et al.*, 1993). From Gucu (in press).

subsequently triggered a steady increase in *Noctiluca* biomass in mid-summer. The *Aurelia* population revealed a gradual decrease during this period. Finally, in August, the mesozooplankton first and phytoplankton and Aurelia later gave rise to successive blooms during the September-October period.

The same model simulations (Oguz *et al.*, 2001) pointed out that this annual structure of the plankton community had been subject to some changes at the time of *Mnemiopsis* outbreak during 1989-1991. The annual phytoplankton biomass structure was characterized by more pronounced and longer-duration three successive blooms. More importantly, the classical early spring phytoplankton bloom was initiated earlier in January, reaching a peak toward the end of February. This wass followed by a second peak in spring, and a third in the late summer. These blooms were stronger and longer-lasting too. There was no autumn bloom during the peak *Mnemiopsis* period. The rest of the plankton community has also been subject to somewhat different annual biomass structure. The primary reason was shown to be the different life cycle of *Mnemiopsis* compared to *Aurelia*. Although both of them had two peaks within a year, the former had these peaks about a month earlier. The winter phytoplankton bloom is a consequence of particular form of grazing pressure exerted by *Mnemiopsis*, which almost completely depleted the microzooplankton, mesozooplankton, and *Noctiluca* stocks toward the end of autumn season. The lack of grazing on the phytoplankton community then promoted earlier growth by the beginning of January. In the previous case of *Aurelia* dominance, the zooplankton community developed following phytoplankton growth.

CONCLUSION

The gelatinous organisms in the Black Sea drew the interests of many scientists only after *M. leidyi* became strikingly abundant (with remaining uncertainties in biomass estimates) and the anchovy population declined in 1989. It still remains uncertain that *M. leidy*i can consume so many of the eggs and larvae of the anchovy to cause a sharp decline in the stocks. It is also argued by some researchers that *Mnemiopsis* is the most efficient consumer of mesozooplankton. Biomass of *Mnemiopsis* peaked in 1989 as a consequence of increasing eutrophication and over-fishing during the period 1978-1988. During this period as more fish were taken from the environment there remained more food (mesozooplankton) for the rest of the consumers. Another factor was the pollution and hypoxia impacting the nursery and spawning grounds (the north-western shelf) of the anchovy. Invasion of *Beroe ovata* (main predator of *Mnemiopsis*) of the Black Sea resulted in the recent reduction of *Mnemiopsis* population.

Impact of the invaders ctenophores *Mnemiopsis leidyi* and *Beroe ovata* on the pelagic foodweb and biodiversity of the Black Sea

Tamara Shiganova

P.P. Shirshov Institute of oceanology Russian Academy of Sciences, Moscow, Russia
Email: shiganov@chip.sio.rssi.ru

The invasion of alien species has become a great problem for many seas of the world due to increasing international commerce combined with the use of ballast water on ships. The discharge of ballast water has resulted in the transfer of species to regions where they are not indigenous. As a rule the invasion of alien species has a damaging effect on ecosystems. For example, the introduction of the ctenophore *Mnemiopsis leidyi* with ballast water from ships from the northern American Atlantic areas at the beginning of the 1980s was a real catastrophe for the Black and Azov Seas (Vinogradov *et al.*, 1989b; Volovik *et al.*, 1993, Shiganova, 1998). These ecosystems were already damaged due to hydrological and hydrochemical changes resulting from decreased river discharge, euthrophication and overfishing (Caddy and Griffiths, 1990). The invasive *M. leidyi* demonstrated explosive development in 1989, when its total biomass reached 1 billion tons for the entire Black Sea. Co-incident with high ctenophore abundance, the biomass of trophic mesozooplankton, its main food, sharply declined. Species diversity of zooplankton and ichthyoplankton decreased (Shiganova *et al.*, 1998). The stocks of zooplanktivorous fish (anchovy, Mediterranean horse mackerel and sprat) dropped, presumably due to competition with *M. leidyi* for food and predation by *M. leidyi* on fish eggs and larvae. Decrease of stocks was recorded in all fish groups (Shiganova *et al.*, 1998; Shiganova and Bulgakova, 2000).

In 1997, *Beroe ovata* was recorded in the Black Sea for the first time. According to our studies it was also introduced with ballast waters from American coastal area (Seravin *et al.*, 2001). In late August-early September 1999 first bloom of *B. ovata* occurred in the whole Black Sea (Shiganova *et al.*, 2000). Our observations demonstrated that *B. ovata* consumes two other species of ctenophores in the Black Sea, *M. leidyi* and *Pleurobrachia pileus,* and feeds primarily on the more available *M. leidyi*. A sharp decrease in the density and biomass of *M. leidyi* in the Black Sea in September 1999, compared to September of previous years implicates *B. ovata* as a potentially important source of mortality.

The mean biomass of zooplankton greatly increased to reach about 11g m^{-2} in the open sea and about 13 g m^{-2} in the inshore waters in early September 1999. This biomass was several times higher than had been observed in the same season during all years since the *M. leidyi* invasion. Compared to 1998, biomasses of *C. euxinus* and *Pseudocalanus elongatus* remained approximately constant in 1999, but biomass of other copepods increased more than three-fold and reached 1.4 g m^{-2} and > 4 x 10^4 m^{-2} between these periods. The density of *Sagitta setosa* also increased substantially to 6-15 x 10^3 ind. m^{-2} and the density of meroplankton also went up. The most conspicuous increase in mesozooplankton concerned Cladocera, which increased up to 150-300 x10^3 ind. m^{-2}. The most abundant cladoceran species was *Penillia avirostris* .

After many years of absence from the Black Sea zooplankton samples, species such as *Pontella mediterranea* and *Centropages ponticus* appeared, and were found in the 1999 samples in large numbers (Fig. 1).

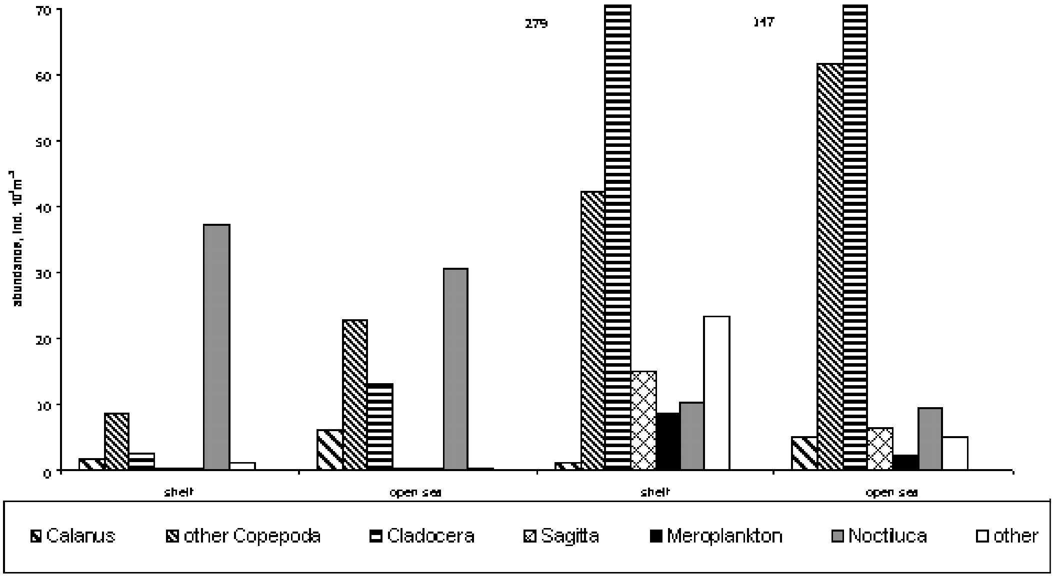


Figure 1. Abundance of zooplankton species in September 1998 and 1999.

In 1999, twenty-four species of fish eggs and larvae were selected as part of this study. The eggs of the anchovy *Engraulis encrasicolus ponticus* predominated (ave. 323 eggs m^{-2}), followed by the eggs of *Trachurus mediterraneus ponticus* (ave. 11.1 eggs.m^{-2}), and the eggs of *Mugil saliens* and *Diplodus annularis* (ave. 1.2 eggs m^{-2}). This marked the first time that such high densities of *E. encrasicolus* and *T. mediterraneus* eggs had been recorded since the *M. leidyi* invasion (Fig. 2). Planktivorous fish also began to recover.

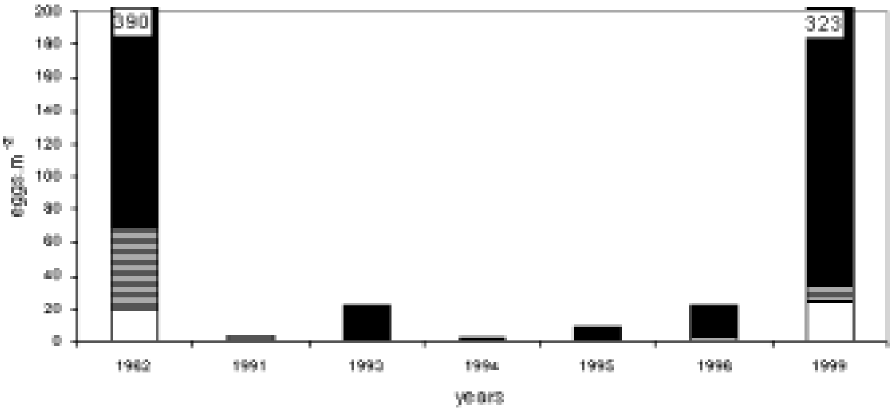


Figure 2. Long term variation of abundance of fish eggs in August.

Results of our investigation in 2000 showed that *M. leidyi* can reach very high biomass in favorable conditions (high temperature, high prey availability) in the seasonal absence of *B. ovata* (winter, spring, summer) with resulting drops in zooplankton and ichthyoplankton density. The renewed seasonal growth of *B. ovata* led to a sharp decrease of *M. leidyi* (Fig.3) and to a gradual recovery in zooplankton.

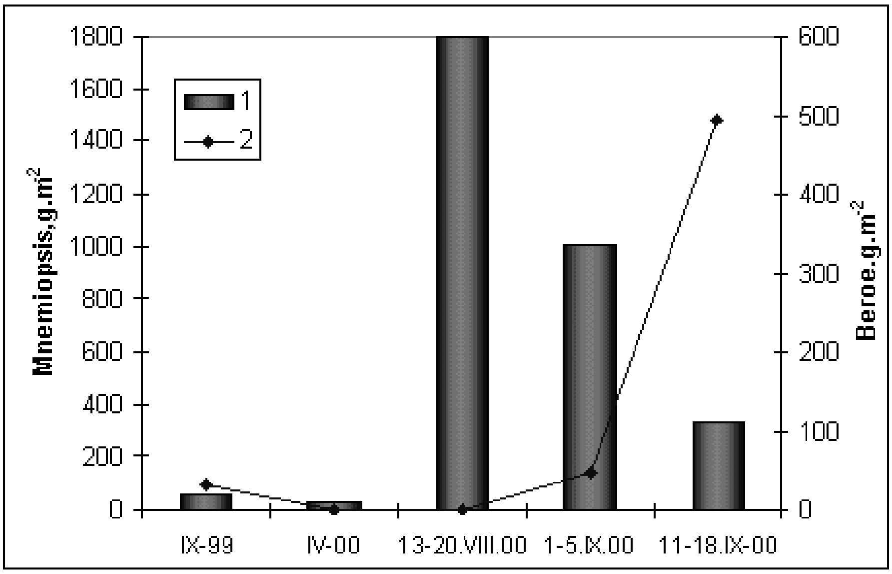


Figure 3. Biomass of *M. leidyi* (1) and *B. ovata* (2) in 1999-2000.

The last two decades have seen major changes in the Black Sea ecosystem following the introduction, likely via ballast waters of the ships, of two gelatinous invaders. The ecosystem was strongly degraded by the arrival of *Mnemiopsis leidyi*, and began to recover with the arrival of *Beroe ovata*. This provides a striking example of anthropogenic impact on the ecosystem, showing its sensitivity to invasion of gelatinous animals and how strict ballast water controls must be everywhere.

The catastrophic invasion of the Black Sea by *Mnemiopsis leidyi* : is it only doing what other ctenophores did long ago ?

G. Richard Harbison

Woods Hole Oceanographic Institution, Woods Hole, USA. Email: gharbison@whoi.edu

Mnemiopsis leidyi Agassiz, 1865 is a member of a small phylum of exclusively marine carnivores, the Ctenophora. A single polymorphic species was, until the 1980's, restricted to the eastern seaboard of the Americas, with a continuous range extending from Cape Cod, USA (41°N, 70°W) in the north to Peninsula Valdez, Argentina (43°S, 64°W) in the south (Harbison and Volovik, 1994). It is most common in bays and estuaries, and does not occur very far from shore, since it seems to do best in environments with high levels of food (Reeve and Baker, 1975). It forms massive blooms over its entire home range. It was apparently transported to the Black Sea in the ballast water of ships, and was first reported in 1982. In 1988, massive blooms of this animal captured the attention of fishermen and biologists. By 1989, pelagic fisheries in the Black Sea had dropped precipitously (GESAMP, 1997). The two fisheries that were most effected were those of the anchovy (*Engraulis encrasicolus*) and the Azov Sea kilka (*Clupeonella cultriventris*).

In hindsight, it is obvious that *Mnemiopsis leidyi* has the characteristics of an ideal invasive species :

1 - it is a simultaneous self-fertilizing hermaphrodite (*e.g.,* Martindale, 1987), which means that only a single animal is needed to establish a population;

2 - it is a feeding generalist, ingesting a wide spectrum of food, ranging from algae and microzooplankton to crustaceans, fish eggs and fish larvae;

3 - it tolerates a wide range of environments, with salinities ranging between 3.4 (Miller, 1974) and 75 (Simmons, 1957) and temperatures ranging between 1.3°C (Burrell and Van Engel, 1976) and 32°C (Baker, 1973);

4 - at optimal temperatures (above 20°C), it develops rapidly, reaching full sexual maturity in 12 days. Dissogony (precocious production of gametes) can occur as early as 6 days after hatching (Martindale, 1987);

5 - it releases copious quantities of eggs (up to 2 to 3 thousand per day), and sexual reproduction is only a minor component of its carbon budget (Reeve *et al.*, 1989);

6 - it responds to elevated food concentrations with rapid growth and reproduction (Reeve *et al.*, 1989).

Although *Mnemiopsis leidyi* needs high concentrations of food for optimal growth and reproduction, it can also live for weeks without feeding, by simply de-growing (Reeve *et al.*, 1989). Thus, it is difficult to imagine an organism that is better adapted to colonize new eutrophic marine environments (particularly through the vector of ships' ballast water) than *M. leidyi*.

In the 1990's another ctenophore from the Americas, *Beroe ovata sensu* Mayer (1912), was also introduced, also probably in ships' ballast water. This ctenophore is a specific and highly voracious predator on other ctenophores, and has most of the invasive characteristics listed above for *M. leidyi*. It is now functioning as a biological control agent there, appearing to be dramatically reducing populations of *M. leidyi* in the Black Sea (*e.g.*, Vostokov *et al.*, 2001), as predicted by Harbison and Volovik (1994).

In fact, when one looks at the phylum Ctenophora as a group, one finds that many of the more common species in the Mediterranean also share most of those invasive characteristics of *Mnemiopsis leidyi* listed above. Of the 17 species from the Gulf of Naples listed by Chun (1880), all (with the exception of the problematic species *Euchlora filigera*) are found over broad areas of the Atlantic and Pacific. Thirteen species form large aggregations under appropriate conditions. Extremely large blooms of the following “Mediterranean” species have been reported on numerous occasions in different regions of the world: *Pleurobrachia pileus, Euplokamis stationis, Bolinopsis vitrea, Eurhamphaea vexilligera, Leucothea multicornis, Cestum veneris, Velamen parallelum* and *Beroe ovata sensu* Chun (1880). One is forced to conclude that most ctenophores have the characteristics of highly invasive species, and that these worldwide invasions occurred long before there were marine biologists to document them.

It should be noted that, before the *Mnemiopsis leidyi* invasion, only a single species of ctenophore, *Pleurobrachia pileus*, inhabited the Black Sea. Now there are three. As the salinity of the Black Sea increases due to human activities, other Mediterranean species will enter, and ctenophore faunal diversity will increase.

Thus, it appears that the invasion of the Mediterranean, Black and Caspian seas by *Mnemiopsis leidyi* occurred through a combination of human activities and the evolutionary peculiarities of the species. In contrast to most other ctenophores, *M. leidyi* is apparently unable to reproduce in oligotrophic environments. In the Americas, it is mostly found close to shore in bays and estuaries, and is not found around coral reefs, for example, which frequently have blooms of *Bolinopsis vitrea* and *Eurhamphaea vexilligera* instead. Thus, before the use of ship’s ballast water, *M. leidyi* was unable to cross the Atlantic. It is interesting that *M. leidyi* is not found on the Pacific seaboard of the Americas. This indicates either that it evolved after the Isthmus of Panama was formed (about three million years BP), or that environmental conditions are unfavorable for its establishment along the western coasts of the Americas.

Since most of the Mediterranean is oligotrophic, it is unlikely that catastrophic blooms such as have occurred in the Black Sea will occur here. Although large concentrations of *Mnemiopsis leidyi* have been observed in the Sea of Marmara, the Aegean Sea and Mersin Bay (Kideys and Niermann, 1994), it is likely that its distribution in the Mediterranean will be restricted to eutrophic areas. Should *M. leidyi* become established in the Mediterranean, its distribution will probably resemble that of the American blue crab, *Callinectes sapidus* (Fischer *et al.*, 1987), which has environmental preferences similar to those of *M. leidyi*. Thus, one would expect to find blooms of *M. leidyi* in the Nile delta and in the upper Adriatic, for example. The situation in the Caspian Sea is quite different, since this sea has environmental conditions that more closely resemble the preferred habitats of *M. leidyi*. The potential for a catastrophic decline in endemic zooplankton and fishes is therefore much higher in the Caspian Sea.

Beroe ovata sensu Mayer (1912) may be more successful in the Mediterranean than *Mnemiopsis leidyi*. It appears to be better able to reproduce in oligotrophic conditions, and feeds on a wide variety of ctenophores (Swanberg, 1974). In contrast to *M. leidyi*, it is found on coral reefs. Although it is only rarely collected in the open ocean and is regarded as neritic (Harbison *et al.*, 1978), it will probably become more widespread and abundant in the Mediterranean than will *M. leidyi*. Mediterranean plankton biologists should be on the alert for both *M. leidyi* and this “new” species of *Beroe*. Whether or not *B. ovata sensu* Mayer (1912) will reach the Caspian Sea will depend on whether or not ballast water controls in the Volga-Don Canal are promptly put in place. Should it enter the Caspian, its long-term survival will depend on the success of *M. leidyi*, since this ctenophore will be its only source of food there.

Opportunistic lifestyles of the gelatinous and abundant: what gives a species “the right stuff” ?

Patricia Kremer

Department of Marine Sciences, University Connecticut, Groton, USA
Email: pkremer@uconnvm.uconn.edu

Intermittent high abundance characterizes a number of species of gelatinous zooplankton, including both primary consumers (pelagic tunicates) and secondary consumers (ctenophores and medusae). These gelatinous “blooms” are composed of species which are able to take advantage of favorable ecological conditions to increase their population rapidly. Although we presently do not thoroughly understand the population dynamics of these bloom formers, it is likely that at least three parameters must be simultaneously favorable to allow the population explosion of these animals:

a) optimum temperature;
b) suitable food - both in terms of quality and quantity for the various life stages;
c) and relatively low mortality from predators, parasites and disease (compared with the population growth rate of bloom former).

For example the ctenophore *Mnemiopsis*, coastally abundant in the Western North Atlantic, has demonstrated in both laboratory and field studies that egg production by these simultaneous hermaphrodites seems to exhibit a threshold at 8-12°C (Kremer, unpublished) and the timing of the increase in the abundance is linked with spring water temperatures. The ctenophores become abundant earlier in the summer the years when winter/spring temperatures are warmer (B. Sullivan *et al.*, in press). The food type necessary to fuel a population explosion of these ctenophores is somewhat different over their life cycle. Newly hatched *Mnemiopsis* are detrimentally affected by large copepods and require large concentrations of microzooplankton (Stanlaw *et al.*, 1981; L. Sullivan, unpublished), while ctenophores greater than about 2 mm in diameter thrive on copepods such as the neritic *Acartia tonsa*. Experimental work has further demonstrated a direct relationship between prey concentration and somatic/reproductive growth (Reeve *et al.*, 1989). Unlike many other taxa, these ctenophores do not appear to satiate, but consume greater and greater amounts of prey at higher food concentrations (Reeve *et al.*, 1978; Kremer, 1979), despite a decrease in their assimilation efficiency (Reeve *et al.*, 1989). Individual based models have shown that the specific growth rate is more strongly affected by food concentration than any of the other included parameters (Kremer and Reeve, 1989). Despite a mortality rate of greater than 99% prior to reproductive maturity, population changes of over four orders of magnitude were simulated to occur in less than three months due to the high somatic and reproductive growth rates (Kremer, 1976).

For “massive events” to occur, there must be a strong imbalance between population growth and mortality, suitable to result in large increases in abundance over a relatively short length of time. If these massive events are irregular in time and space, it is logical to infer that either the conditions favoring rapid population growth (such as food supply and temperature) do not occur regularly, or there is an irregularity in the factors that hold the population in check. We may gain insights into predicting these irregular massive events by comparing ecological conditions in these locations with locations where similar taxa form regular (*e.g.* annual) massive events, or where massive events do not occur at all. Also, there may be parallels we can draw with strong and weak year classes in dominant fish species. Favorable conditions can be controlled directly by the physical environment (temperature, salinity, water column stability, longevity of fronts) or in combination with the biological setting (food availability, potential for competitors, direct mortality and disease/parasites). For most taxa we currently know neither what constitute favorable conditions nor the causes of poor population growth. The complexity and subtly of the interaction of factors makes this task challenging, needing not only more field study, but more experimental investigations where single variables can be manipulated in a systematic and controlled manner. The importance of physical forcing functions can be strong, as it is translated through the biology, but the routing can be subtle.

A long-term data set of the relative abundance of the sea nettle medusae (*Chrysaora quinquecirrha*) in the Chesapeake Bay has showed an inverse correlation between jellyfish abundance and fresh water runoff (Cargo and King, 1990). Additional experimental work (Purcell *et al.*, 1999b) showed that the rate of strobilation by the scyphistomae is strongly affected by both salinity and temperature. Due to the life cycle of this scyphozoan, the benthic phase determines the number of medusae in the subsequent pelagic phase. Therefore, conditions that affect the scyphistomae either favorably or unfavorably have direct consequences on the number and impact of the stinging jellyfish.

In the Southern Ocean, krill and salps alternate their annual abundance in a complex and irregular way. As the importance of ice cover and ice algae to the over wintering and survival of krill has been better understood and appreciated, scientists realized that in order to have “good” krill years it was necessary to have at least two consecutive years of wide-spread cover of sea ice. When there is not sufficient ice cover to maintain a large over wintering population of krill, salps can become the dominant macrozooplankton in the austral summer, presumably due to their ability to grow and reproduce rapidly when conditions are favorable (Loeb *et al.*, 1997). When there are not a sufficient number of grazing krill that have overwintered, salps become dominant . What at first appeared to be an unpredictable phenomenon, makes sense with a greater understanding of krill ecology and a sufficiently long record of the relative abundance of krill, salps, and ice cover in the Southern Ocean (Loeb *et al.*, 1997).

One of the challenges in understanding the population dynamics of species capable of irregular massive events, is that their very irregularity and abundance make it difficult to determine the favorable conditions that trigger the rapid population growth. This is a problem particularly in open ocean habitats, where environmental and biological monitoring are not well developed. Once the massive event has occurred and there is a large biomass of animals, the conditions leading to the increase in abundance have undoubtedly changed. The consequence of abundance is a destruction of the favorable habitat. Ecosystems “out of balance” cannot continue indefinitely.

In the presence of salp swarms there are typically very low levels of particulates in the water. Salps are non-selective filter feeders that commonly can ingest any particles larger than 2 um that does not swim out of the way. Typically copepods are scare in salp blooms as the salps remove the food most desirable to the copepods, and can remove microzooplankton including copepod eggs and young weak-swimming nauplii.

Crustacean mortality due to large numbers of ctenophores and medusae is well documented in some coastal environments (Kremer, 1979; Purcell, 1992). Once the prey supply is low, ctenophore’s egg production is strong affected (Kremer 1976; Reeve *et al.*, 1989). For medusae that are not holoplanktonic, the results of reduced levels of prey are not as straightforward. Although egg production may be affected, it is not clear how important this rate is to strobilation of the scyphistomae and the production of ephyrae. Large numbers of gelatinous carnivores such as ctenophores and medusae have not only a direct effect on their dominant prey of crustacean zooplankton, but they may also adversely affect species that humans value. The jellies may ingest fish eggs and larvae directly (Purcell *et al.*, 1994), and/or may reduce the prey field available to fish to a point that fish growth is affected, making the small fish more vulnerable to piscovores.

Although the past thirty years have brought a much better understanding of a few of the most common coastal gelatinous plankton, and even fewer examples of more offshore forms, there is still much to be learned before most intermittent massive events can be at all predictable. Even our limited research has revealed that the detailed biology of the dominant species can be vital to understanding the underpinnings of the population dynamics. It is clear than simplistic N-P-Z models will not bring us any closer to understanding these outbreaks. What is needed is an understanding of the effect of changing environmental variables on critical life history parameters of the species that form the outbreaks: their prey, their predators, parasites and competitors. We may see massive events related to climate change, and the consequences of these events may be important to biogeochemical cycles and fisheries. Nevertheless, the key to understanding how these species form irregular massive events is likely to lie in an understanding of the quantitative natural history, specific characteristics and behaviors of these bloom-forming animals.

III – BIBLIOGRAPHIC REFERENCES

Acuña, J. L., 2001. Pelagic tunicates: why gelatinous? *Am. Nat.*, 158(1): 100-107.

Alexander, C., 1967. Notes on the Synthesis of Form (Harvard University Press) 137 p.

Allen J., PJ. Somerfield and J. Siddorn, 2001. Primary and bacterial production in the Mediterranean Sea : a modeling study. *Journal of Marine Systems*, (in press)

ANON, 1993: Ecosystem modelling as a management tool for the Black Sea: A regional progam of multi-institutional cooperation, NATO TU- Black Sea Project, IMS-METU, May 1993: 67 p.

Attrill M.J. and R.M. Thomas, 1996. Long-term distribution patterns of mobile estuarine invertebrates (Ctenophora, Cnidaria, Crustacea: Decapoda) in relation to hydrological parameters. *Mar. Ecol. Prog. Ser.*, 143: 25-36.

Avent S.R., S.M. Bollens, M. Butler, E. Horgan and R. Rountree, 2001. Planktonic hydroids on Georges Bank: ingestion and selection by predatory fishes. *Deep-Sea Reserach*, II. 48: 673-684.

Avian M. and Rottini L., 1994. History of scyphomedusae in the Adriatic Sea. *Boll. Soc. Adriat. Sci. Nat. Trieste*, 1: 5-12.

Baker L. D. 1973. The ecology of the ctenophore, *Mnemiopsis mccradyi* Mayer, in Biscayne Bay, Florida. Univ. Miami, Rosenstiel School Mar. Atmos. Sci. Tech. Rep. n°73-016, 131 pp.

Balkas T., Dechev G., Mihnea R., Serbanescu O. and Unluata, Ü., 1990. State of marine environment in the Black Sea Region. UNEP Regional Seas Reports and Studies, 124 p.

Ballard L. and Myers, A., 1996. Seasonal changes in the vertical distribution of five species of the family Bougainvillidae (Cnidaria:Anthomedusae) at Lough Hyne, south-west Ireland. *Sci. Mar.*, 60: 69-74.

Becacos-Kontos T., 1997. Primary production and environmental factors in an oligotrophic biome in the Aegean Sea. *Marine Biology,* 42: 93-98.

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

Benovic A, Justic D. and A. Bender, 1987. Enigmatic changes in hydromedusan fauna of the northern Adriatic Sea. *Nature*, 396: 597-599.

Benovic A., D. Lucic, V. Onofri, M. Peharda, M. Caric, N. Jasprica and S. Bobanovic-Colic, 2000a. Ecological characteristics of the Mljet Island sea water lakes (South Adriatic Sea) with special reference to their resident populations of medusae. *Sci.Mar.*, 64 (suppl. I): 196-206.

Benovic A., D. Lucic and V. Onofri, 2000b. Does Change in an Adriatic Hydromedusan Fauna Indicate an Early Phase of Marine Ecosystem Destruction? *P.S.Z.N. Marine Ecology*, 21: 221-231.

Berner L., 1967. Distributional atlas of Thaliacea in the California Current region. CalCOFI Atlas 8.

Bingel F., Kideys A.E., Ozsoy E., Tugrul S., Basturk O. and Oguz T., 1993. Stock assessment studies for the Turkish Black Sea coast. NATO-TU Fisheries Final Report. Institute of Marine Sciences. METU Içel, Turkey, 108p.

Blumberg A.F. and G.L. Mellor, 1987. A description of a three-dimensional coastal ocean circulation model, pp. 1-16, *In* : N.S. Heap (ed.), Three-dimensional coastal ocean models, AGU Publishers, Washington D.C.

Boero F., 1991. Contribution to the understanding of blooms in marine environments. UNEP, MAP Tech. Rep. Ser. 47: 72-76.

Boero F. 1994. Fluctuations and variations in coastal marine environments. *P.S.Z.N. I. Mar. Ecol.,*, 15: 3-25.

Boero F., 1996. Episodic events: their relevance in ecology and evolution. *P.S.Z.N. I. Mar. Ecol.*, 17: 237-250.

Boero F., 2001. Light after dark : the partnership for enhancing expertise in taxonomy. *Trends in Ecology and Evolution*, 16 (5): 266.

Boero F. and C.E. Mills. 1997. Agricultural *versus* ethological oceanography. *Trends in Ecology and Evolution*, 12 (6): 208-209.

Boero F., G. Belmonte, G. Fanelli, S. Piraino and F. Rubino, 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.

Bologa A.S., H.V. Skolka and Frangopol P.T., 1984. Annual cycle of planktonic primary productivity off the Romanian Black Sea coast. *Marine Ecology Progress Series*, 19:25-32.

Bondar C., 1977. Changes in hydrological pattern induced by engineering works on the lower Danube. *Hidrotecnica*, 22(7): 87-9 (in Romanian).

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

Bouillon J., F. Boero and S. Fraschetti, 1991. The life cycle of *Laodicea indica* Browne 1906 (Laodiceidae, Hydromedusae, Cnidaria). *Hydrobiologia* , 216/217: 151-157.

Braconnot J.C., Choe S.M., Nival P., 1988. La croissance et le développement de *Salpa fusiformis* Cuvier (Tunicata, Thaliacea). *Ann. Inst. Oceanogr*., 64: 101-114.

Braconnot J.-C., M. Etienne et M. Moitié, 1990. Distribution du tunicier pélagique *Salpa fusiformis* Cuvier à Villefranche: 13 années d’observations. *Rapp. Comm. int. Mer Médit.*, 32 (1): 225.

Brierley A.S., Axelsen B.E., Buecher E., Sparks C., Boyer H. and Gibbons M.J., 2001. Acoustic observations of jellyfish in the Namibian Benguela. *Mar. Ecol. Prog. Ser.*, 210: 55-66.

Buecher E., 1997. Distribution and abundance of *Pleurobrachia rhodopis* (Cydippid Ctenophore) in the bay of Villefranche-sur-Mer (North western Mediterranean) from three different planktonic time series. *Ann. Inst. océanogr.*, Paris, 73: 173-184.

Buecher E., Goy J., Planque B., Etienne M. and Dallot S., 1997. Long-term fluctuations of *Liriope tetraphylla* in Villefranche Bay between 1966 and 1993 compared to *Pelagia noctiluca* pullulations. *Oceanol. Acta*, 20: 145-158.

Buecher E., Sparks C., Brierley A.S., Boyer H. and Gibbons M.J. (in press). Biometry and size distribution of *Chrysaora hysoscella* (Cnidaria, Scyphozoa) and *Aequorea aequorea* (Cnidaria, Hydrozoa) off Namibia with some notes on their parasite *Hyperia medusarum*. *J. Plankton Res.*

Burns T.P., 1989. Lindeman’s contradiction and the trophic structure of ecosystems. *Ecology*, 77: 1351-1362.

Burrell V.G. and W.A. Van Engel. 1976. Predation by and distribution of a ctenophore, *Mnemiopsis leidy*i A. Agassiz, in the York River Estuary. *Estuarine Coastal Mar. Sci.*, 4: 235-242.

Caddy J. and Griffiths R., 1990. A perspective on recent fishery related events in the Black Sea. *Studies and Reviews. GFCM*, 63:43-71.

Caddy J. F.and R. C. Griffiths, 1990. A perspective on recent fishery-related events in the Black Sea. *Studies and Reviews. GFCM*, 63: 43-71.

Calbrese E.J. and L.A. Baldwin, 1998. Hormesis as a Biological Hypothesis. *Environ. Health Perspect*., 106 (Suppl., 1): 357-362.

Capitanio F.L., Pájaro M. and G.B. Esnal, 1997. Appendicularians (Cordata: Tunicata) in the diet of anchovy (*Engraulis anchoita*) in the Argentine Sea. *Sciencia Marina*, 61 (1): 9-15.

Car J. and Hadzi J., 1914. Biologijska opazanja. Izvestaji o 1. i 2. naucnom istrazivanju Jadranskog mora. Prir. Istraz. JAZU, 2: 9-20.

Cargo D.G. and D.R. King, 1990. Forcasting the abundance of the sea nettle, *Chrysaora quinquecirrha*, in the Chesapeake Bay. *Estuaries*, 13: 486-491.

Carré C., Carré D., 1991. A complete life cycle of the calycophoran siphonophore *Muggiaea kochi* (Will) in the laboratory, under different temperature conditions: ecological implications. *Phil. Trans. R. Soc. Lond. B*, 334: 27-32.

Chesson P.L. and R.R.Warner, 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist*, 117 6: 923-943.

Chun C., 1880. Ctenophoren des Golfes von Neapel. Fauna Flora Golf. Neapel. I: 313 pp., 16 pls.

CIESM, 2000. Fishing down the Mediterranean food webs ? CIESM Workshop Series n°12, 100 p., Monaco. <http://www.ciesm.org/Corfou.pdf>

Collado L., Segura L. and Merino M., 1988. Observaciones sobre dos escifomedusas del género Cassiopea en la laguna de Bojórquez, Quintana Roo, México. *Rev. Inv. Mar.*, 9: 21-27.

Crawford R.J.M., Shannon L.V. and Pollock D.E., 1987. The Benguela ecosystem. Part IV. The major fish and invertebrate resources. *Oceanogr. Mar. Biol. Ann. Rev*., 25: 353-505.

Dagg M. J., Green E. P., McKee B. A., and Ortner P. B.,1996. Biological removal of fine-grained lithogenic particles from a large river plume. *J. Mar. Res.*, 54(1): 149-160.

Davis C.S., Gallager S.M., Marra M. and W.K. Stewart, 1996. Rapid visualisation of plankton abundance and taxonomic composition using the Video Plankton Recorder. *Deep-Sea Research II*, 43: 1947-1970.

Degobbis D., S. Fonda-Umani, P. Franco, A. Malej, R. Precali and N. Smodlaka, 1995. Changes in the Northern Adriatic ecosystem and the hypertrophic appearance of gelatinous aggregates. *Sci. Total Envir.*, 165: 43-58.

Degobbis D., Precali R., Ivancic I., Smodlaka N., Fuks D., and Kveder S., 2000. Long-term changes in the northern Adriatic ecosystem related to anthropogenic eutrophication. *Int. J. Environm. Pollut.*, 13: 495-533.

Edwards M., John A.W.G., Hunt H.G. and Lindley J.A., 1999. Exceptional influx of oceanic species into the North Sea late 1997. *J. mar biol. Ass. UK*, 79: 737-739.

Fearon J.J., Boyd A.J. and Schulein F.H., 1992. Views on the biomass and distribution of *Chrysaora hysoscella* (Linne, 1766) and *Aequorea aequorea* (Forskal, 1775) off Namibia, 1982-1989. *Scientia Marina*, 56: 75-85.

Fernex F.E., Braconnot J.C., Dallot S., Boisson M., 1996. Is ammonification rate in marine sediment related to plankton composition and abundance ? A time series study in Villefranche Bay (NW Mediterranean). *Estuarine, Coastal and Shelf Science*, 43: 359:371.

Fernex F.E., Braconnot J-C., Dallot S. and Boisson M., 1996. Is ammonification rate in marine sediment related to plankton composition and abundance? A time-series study in Villefranche bay (NW Mediterranean). *Estuarine, Coastal and Shelf Science*, 43: 359-371.

Fischer W., M.-L. Bauchot and M. Schneider, eds. 1987. Fiches FAO d'identification des espèces pour les besoins de la pêche. (Révision 1). Méditerranée et mer Noire. Zone de pêche, 37. Volume I. Végétaux et Invertébrés. Rome, FAO, 760 p.

Fonda Umani S., Princi M., and Specchi M., 1983. Note ecologiche su *Noctiluca miliaris* Suriray del Golfo di Trieste (Alto Adriatico). *Atti del Museo Civico di Storia Naturale*, 35: 259-265

Franco I. and J-M. Gili, 1991. Some aspects of the biology of Aurelia aurita in the coastal lagoon mar menor (SE Spain). Proceedings of the 5th International Conference on Coelenterate Biology, Southampton.

Fraser J. H., 1962. The role of ctenophores and salps in zooplankton production and standing crop. *Rapp. Cons. perm. Int. Explor. Mer,* 153: 121-123.

Frid C.L.J., Newton L.C., Williams J.A., 1994. The feeding rates of *Pleurobrachia* (Ctenophora) and *Sagitta* (Chaetognatha), with notes on the potential seasonal role of planktonic predators in the dynamics of North Sea zooplankton communities. *Netherland J. of Aquatic Ecology,* 28: 181-191.

Frontier S. et Pichot-Viale D., 1991. Ecosystèmes - Structure, fonctionnement, évolution. 21 (Masson), 392 p.

Gacic M., V. Kovacevic, B.Manca, E. Papageorgiou, P.M.Poulain, P.Scarazzato and A.Vetrano, 1996. Thermohaline properties and circulation in the Otranto Strait. *In*: F. Briand (ed.), Dynamics of Mediterranean Straits and Channels, CIESM Science Series n°2, pp. 117-145.

Galil B.S., E. Spanier and W.W. Ferguson, 1990. The Scyphomedusae of the Mediterranean Coast of Israel, including two Lessepsian migrants new to the Mediterranean. *Zool. Med. Leiden,* 64 7: 95-105.

García J. and Durbin E., 1993. Zooplanktivorous predation by large scyphomedusae *Phyllorhiza punctata* (Cnidaria: Scyphozoa) in Laguna Joyuda. *J. Exp. Mar. Biol. Ecol.,* 173: 71-93.

General Fisheries Council for the Mediterranean, 1993. GFCM Statistical Bulletin, n° 9: 1979-1991. *FAO Bulletin. of Fishery Statistics,* 32(9): 237 p.

GESAMP (IMO/FAO/UNESCO-IOC/WMO/WHO/IAEA/UN/UNEP Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection), 1994. Opportunistic settlers and the problem of the ctenophore *Mnemiopsis leidyi* in the Black Sea. First meeting of the GESAMP. UNEP(OCA)/GES.WG., 35. 1/3: 63 p.

GESAMP (IMO/FAO/UNESCO-IOC/WMO/WHO/IAEA/UN/UNEP Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection), 1995. Opportunistic settlers and the problem of the ctenophore *Mnemiopsis leidyi* in the Black Sea. Second meeting of the GESAMP. UNEP(OCA)/GES.WG., Draft Report.

GESAMP (IMO/FAO/UNESCO-IOC/WMO/WHO/IAEA/UN/UNEP Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection), 1997. Opportunistic settlers and the problem of the ctenophore *Mnemiopsis leidyi* invasion in the Black Sea. Rep. Stud. GESAMP (58): 84 pp.

Gomoiu M.T., 1990. Marine eutrophication syndrome in the north-western part of the Black Sea. pp. 683-703. *In*: Vollenweider R.A., Marchetti R. and Viviani R. (eds.). Marine Coastal Eutrophication. Elsevier Publ.

Goy J., 1984a. Climatic fluctuations of the jellyfish, *Pelagia noctiluca. Comp. rend. Acad. Sci.* ser. III Sci. de la Vie, 299 (12): 507-510.

Goy J., 1984b. Les concentrations de méduses en mer Ligure. UNEP Workshop on jellyfish blooms in the Mediterranean, Athens, 31 October-4 November, pp. 109-120.

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

Goy. J., P. .Morand and S. Dallot, 1991. Dynamique d'une population de *Pelagia noctiluca* (Cnidaria, Scyphozoa) en Mer Ligure. UNEP, MAP Tech. Rep. Ser. 47: 112 – 118.

Greze V.N., 1979. On the bioproductive system of the Black Sea and its functional characteristics. *Gidrobiol. Zh*., 15(4): 3-9.

Gucu A.C., 1997. Role of fishing in the Black Sea ecosystem, pp. 149-16. *In*: E. Ozsoy and A. Mikaelyan (eds), Sensitivity to changes: Black Sea, Baltic Sea and North Sea, Kluwer Acad. Publ., The Netherlands.

Gucu A. (in press): Can overfishing be responsible for the successful establishment of *Mnemiopsis leidy*i in the Black Sea. *Estuarine, Coastal and Shelf Science*.

Gucu A. C. and Oguz T., 1998. Modeling trophic interrelationships in the Black Sea. pp. 359-371. *In*: L. Ivanov and T. Oguz (eds.), NATO TU-Black Sea Project: Ecosystem Modelling as a Management Tool for the Black Sea. Vol. 2. Kluwer Academic Publishers, Netherlands.

Harbison G.R. and S. P. Volovik. 1994. The ctenophore, *Mnemiopsis leidy*i, in the Black Sea: a holoplanktonic organism transported in the ballast of ships. *In*: Non-Indigenous Estuarine and Marine Organisms (NEMO) and Introduced Marine Species. Proceedings of the Conference and Workshop, NOAA Tech. Rep., U.S. Dept. Commerce. U.S. Govt. Print. Office, Washington, D.C.

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

Hart T.J. and Currie R.I., 1960. The Benguela Current. *Discovery Rep.*, 31: 123-298.

Haskell A.G.E., Hofmann E.E., Paffenhöfer G.A. and Verity P.G., 1999. Modelling the effects of doliolids on the plankton community structure of the southeastern US continental shelf. *Journal of plankton research*, vol 21 (9): 1725-1752

Herndl G. J., Karner M. and P. Peduzzi, 1992. Floating mucilage in the Northern Adriatic Sea: the potential of a microbial ecological approach to solve the “mystery”, pp. 525-538. *In:* Vollenweider R.A., Marchetti R. and Viviani R. (eds.), Marine coastal eutrophication, Elsevier Sci. Publ., Amsterdam.

Heron A. C., 1972. Population ecology of a colonizing species: the pelagic tunicate *Thalia democratica*. II. Population growth rate. *Oecologia* (Berl.), 10: 294-312.

Heron A. C., and Benham E.E., 1984. Individual growth rates of salps in three populations. *J. Plankton Res*., 7: 365-379.

Hopcroft R.R.and Roff. J. C., 1998. Production of tropical larvaceans in Kingston Harbour, Jamaica : are we ignoring an important secondary producer? *J. Plankton Res*., 20: 557-569.

Hopkins, T. S., Artegiani A., Cauwet G., Degobbis D., and Malej A. (eds.), 1999. The Adriatic Sea. Ecosystem research report N° 32 / EUR 18834.

Hoptcroft R.R. and J.C. Roff, 1995. Zooplankton growth rates: extraordinary production by the larvacean *Oikopleura dioica* in tropical waters. *Journal of Plankton Research*, 17: 205-221.

Hutchinson G. E., 1951. Copepodology for the ornithologist. *Ecology,* 32(3): 571-577.

Hutchinson G.E., 1961. The paradox of the plankton. *American Naturalist,* 95: 137-147.

Huxley T. H., 1859. The oceanic Hydrozoa; a description of the Calycophoridae and Physophoridae observed during the voyage of H.M.S. *Rattlesnake*, in the years 1846-50. Roy Society, London.

Ikeda T., 1970. Relationship between respiration rate and body size in marine plankton animals as a function of temperature of habitat. *Bull. Fac. Fish. Hokkaido Univ.*, 21: 91-112.

IMS-METU address: Institute of Marine Sciences (http://www.ims.metu.edu.tr) - Middle East Technical University (http://www.metu.edu.tr). POB, 28, Erdemli, 33731, Icel, Turkey

Issel R., 1922. Nuove indagini sul plankton nelle aquae di Rovigno. *Mem. R. Comit. Talass. Ital*., 102: 1-36.

Ivanov L. and Beverton R.J.H., 1985. The fisheries resources of the Mediterranean. Part Two: Black Sea. G.F.C.M. Studies and Reviews n°60, Rome, FAO, 135p.

Jordán F., 2001. Seasonal changes in the positional importance of components in the trophic flow network of the Chesapeake Bay. *Journal of Marine Systems*, 27: 289-300.

Kideys A. E. and U. Niermann, 1993. Intrusion of *Mnemiopsis mccradyi* into the Mediterranean Sea. *Senckenbergiana Maritima*, 23: 43-47.

Kideys A.E. and U. Niermann, 1994. Occurrence of *Mnemiopsis* along the Turkish coast. *ICES J. Mar. Sci*. 51: 423-427.

Kideys A.E., Kovalev A.V., Shulman G., Gordina A. and Bingel F., 2000. A review of zooplankton investigations of the Black Sea over the last decade. *J. Mar. Systems*, 24: 355-371.

Kideys A.E., and Romanova, Z., (in press): Distribution of gelatinous macrozooplankton in the southern Black Sea during 1996-1999. *Marine Biology*.

Kikinger R., 1992. *Cotylorhiza tuberculata* (Cnidaria:Scyphozoa) – life history of a stationary population. *P.S.Z.N.I. Mar Ecol*., 13: 333-362.

Kiorboe T., 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *Advances in Marine Biology*, 29: 1-71.

Kremer P., 1976. Population dynamics and ecological energetics of a pulsed zooplankton predator, the ctenophore *Mnemiopsis leidyi*, pp. 197-215. *In*: M.L. Wiley (ed.), Estuarine Processes, Vol. 1. Academic Press, NY.

Kremer P., 1979. Predation by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Estuaries*, 2:97-105.

Kremer P. and M.R. Reeve, 1989. Growth dynamics of a ctenophore (*Mnemiopsis*) in relation to variable food supply II: Carbon budgets and growth model. *J. Plankton Res*., 11: 553-574.

Kremer P., Costello J., Kremer J and Canino M., 1990. Significance of photosynthetic endosymbionts to the carbon budget of the scyphomedusa *Linuche unguiculata*. *Limnol. Oceanogr*., 35: 609-624.

Krom M.D., S. Brenner, N. Kress, A. Neori and L.I. Gordon, 1992. Nutrient dynamics and new production in a warm-core eddy from the Eastern Mediterranean Sea. *Deep Sea Research*, 39(3/4): 467-480.

Krsinic F. and J. Njire, 2001. An invasion by *Muggiaea atlantica* Cunningham 1892 in the northern Adriatic Sea in the summer of 1997 and the fate of small copepods. *Acta Adriat.*, 42 (1): 49-59.

Lacroix G., 2001. Ecosystem model (MODECOGeL) of the Ligurian Sea revisited. Seasonal variability and pluriannual simulation. Submitted to *J. Mar. Syst*.

Lacroix G. and Nival P., 1998. Influence of meteorological variability on primary production dynamics in the Ligurian Sea (NW Mediterranean Sea) with a 1D hydrodynamic/biological model, *J. Mar. Syst*., 16: 23–50.

Larson R.J., 1987. A note on the feeding, growth, and reproduction of the epipelagic scyphomedusa *Pelagia noctiluca* (Forskål). *Biol. Oceanogr*., 4 (4): 447-454.

Loeb V.V., Siegel O., Holm-Hansen R., Hewitt W., Fraser W., Trivelpiece and S. Trivelpiece, 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature*, 387: 897-900.

Luh H.-K., and Pimm S.L., 1993. The assembly of ecological communities: a minimalist approach. J*ournal of Animal Ecology*, 62: 749-765

McArthur R., 1955. Fluctuations of animal populations and a measure of community stability. *Ecology*, 36: 533-536

Madhupratap M., Devassy V.P., Sreekumaran Nair S.R., Rao T.S., 1980. Swarming of pelagic tunicates associated with phytoplankton bloom in the Bay of Bengal. *Indian J. Mar. Sci*., 9: 69-71.

Malej A., 1983. Observations on *Noctiluca miliaris* Suriray red tide in the Gulf of Trieste during 1980. *Thalassia Jugosl*., 19: 261-269.

Mann K.H. and Lazier J.R.N., 1991. Dynamics of marine ecosystems. Biological-physical interactions in the oceans. Boston, Blackwell Scientific Publications. 466 p.

Marchetti R., 1990. Algal blooms and gel production in the Adriatic, pp. 21-42. *In*: H. Barth and L. Fegan (eds.), Sea Water Pollution Research Reports, Proceedings of the Workshop: Eutrophication-related phenomena in the Adriatic Sea and in other Mediterranean coastal zones.

Marcus N. and F. Boero, 1998. Production and plankton community dynamics in coastal aquatic systems: the importance of benthic-pelagic coupling and the forgotten role of life cycles. *Limnology and Oceanography*, 43 (5): 763-768.

Margalef R., 1974. Ecologia, Ediciones Omega, Barcelona, 951 p.

Marhuend M., Pérez E., Sánchez M., and Gallego C., 2000. Asistencia técnica para la búsqueda de escifopólipos en el mar Menor (Murcia). Mediterráneo Servicios Marinos, 39 pp.

Martindale M.Q. 1987. Larval reproduction in the ctenophore *Mnemiopsis mccradyi* (order Lobata). *Mar. Biol*., 94: 409-414.

Martínez Fernández J. and M.A. Esteve Selma, 2000. Estimación de la entrada de nutrientes de orígen agrícola en el mar Menor mediante un modelo dinámico. *Mediterranea*, 17: 5-33 (University of Alicante).

Mas J., 1999. Estudio de la dinámica de poblaciones de las medusas *Cotylorhiza tuberculata, Rhizostoma pulmo* y *Aurelia aurita* en el mar Menor y de su problemática asociada. Instituto Español de Oceanografia, internal report, 101 pp.

Matsakis S., and Nival. P., 1989. Elemental composition and food intake of Phialidium hydromedusae in the laboratory. *J. Exp. Mar. Biol. Ecol.*, 130: 277-290.

Mayer A.G. 1912. Ctenophores of the Atlantic Coast of North America. Carnegie Inst., Washington, DC.

Mee L.D., 1992. The Black Sea in crisis: The need for concerted international action. *Ambio*, 21(3): 278-286.

Ménard F., Dallot S., Thomas G., Braconnot J.C., 1994. Temporal fluctuations of two mediterranean salp populations from 1967 to 1990. Analysis of the influence of environmental variables using a Markov chain model. *Mar. Ecol. Prog. Ser.*, 104 : 139-152.

Ménard F., Fromentin,J-M , Goy, J. and Dallot, S., 1997. Temporal fluctuations of doliolid abundance in the bay of Villefranche-sur-mer (Northwestern Mediterranean Sea) from 1967 to 1990. *Oceanologica Acta*, 20: 733-742

Miller R.J. 1974. Distribution and biomass of an estuarine ctenophore population, *Mnemiopsis leidyi* (A. Agassiz). *Chesapeake Sci*., 15: 1-8.

Mills C.E., 1995. Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. *ICES J. mar. Sci.*, 52: 575-581.

Mills C.E., 2000. Jellyfish and global change: population increases and decreases in response to changing conditions in the sea. Oral presentation, International conference on Jellyfish Blooms, Alabama, January 2000.

Mironov G.N., 1971. Biomass and distribution of medusa *Aurelia aurita* L. according to the catches with the bottom trawl in the Black Sea in the period 1942-1962. *Biol. Morja.*, 14:49-69 (In Russian).

Mutlu E., 1999: Distribution and abundance of ctenophores and their zooplankton food in the Black Sea. II. *Mnemiopsis leidyi. Marine Biology*, 135(4): 603-613.

Mutlu E., 2001: Distribution and abundance of moon jellyfish (*Aurelia aurita*) and its zooplankton food in the Black Sea. *Marine Biology*, 138(2): 329-339

Mutlu E. and Bıngel F., 1999: Distribution and abundance of ctenophores and their zooplankton food in the Black Sea. I. *Pleurobrachia pileus. Marine Biology*, 135(4): 589-601.

Mutlu E, Bingel F., Gucu A.C., Melnikov V.V. Niermann U., Ostr, N.A., and Zaika V.E., 1994. Distribution of the new invader *Mnemiopsis* sp. and the resident *Aurelia aurita* and *Pleurobrachia pileus* populations in the Black Sea in the years 1991-1993. *ICES J. Mar. Sci.*, 51: 407-421.

Nakamura Y., 1998. Blooms of tunicates *Oikopleura* spp. and *Dolioletta gegenbauri* in the Seto Inland Sea, Japan, during summer. *Hydrobiologia*, 385(1-3): 183-192.

Niermann U., F. Bingel, A. Gorban, A.D. Gordina, A.C. Gücü, A.E. Kideys, A. Konsulov, G. Radu, A.A. Subbotin and V.E. Zaika., 1994. Distribution of anchovy eggs and larvae (*Engraulis encrasicolus* Cuv.) in the Black Sea in 1991 and 1992 in comparison to former surveys. *ICES J. Mar. Sci.*, 51: 395-406

Niermann U., and Kideys A.E., Besiktepe S, Nicolae B., Goubanova A., Khoroshilov V., Mikaelyan A., Moncheva S., Mutlu E., Nezlin N., Petranu A., Senichkina L. and Shiganova T., 1995. An assessment of recent phyto- and zooplankton investigations in the Black Sea and planning for future, TU-Black Sea Project,NATO Science for Stability Program, Report on the meeting of Marine Biologist in Erdemli, Turkey, 20 Feb.-3 March 1995, Institute of Marine Sciences, Middle East Technical University, Erdemli, Turkey, 100 p.

Oguz T., Ducklow H., Purcell E., 2001. Modeling the response of top-down control exerted by gelatinous carnivores on the Black Sea pelagic food-web. *Journal of Geophysical Research*, 106 (C3), 4543-4564.

Oguz T., Ducklow, HW., Purcell, JE and Malanotte-Rizzoli, P., 2001: Modelling the response of top-down control exerted by gelatinous carnivores on the Black Sea pelagic food web. *Journal of Geophysical*, 106(C3): 4543-4564.

Omori M. and W.M. Hamner, 1982. Patchy distribution of zooplankton: behaviour, population assessment and sampling problems. *Marine Biology*, 72: 193-200.

Ott J. A. and G.J. Herndl, 1995. Marine snow, mucus aggregates and bottom anoxias: consequences for benthic-pelagic coupling. *Bulletin de l'Institut Océanographique*, Monaco. 15: 133-147.

Ozdamar E., Kihara K., and Koyuncu I., 1991. Some biological characteristics of European anchovy *Engraulis encrosicolus* L. in the Black Sea. *Journal of Tokyo University of Fisheries*, Vol, 78, N°1: 57-64.

Paffenhöfer G.-A., 1975. On the biology of Appendicularia of the southeastern North Sea. *Mar. Biol.*, 2: 437-455.

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

Pérez-Ruzafa A., 1997. Estudio de la dinámica de las poblaciones de medusas en el mar Menor, problemática asociada y búsqueda de soluciones. Informe final. Departamento de Ecología e Hidrología, Universidad de Murcia, 234 pp.

Pérez-Ruzafa A. and Marcos, C., 1987. Los sustratos arenosos y fangosos del mar Menor (Murcia), su cubierta vegetal y su posible relación con la disminución del mújol en la laguna. Cuad. Marisq. Publ. Téc., 11: 111-123.

Pérez-Ruzafa A., Marcos-Diego C., Ros J., 1991. Environmental and biological changes related to recent human activities in the Mar Menor (SE of Spain). *Mar. Poll. Bull.*, 23: 747-751.

Pimm S.L., 1991. The Balance of Nature? Ecological Issues in the Conservation of Species and Communities, University of Chicago Press, 434 p.

Platt T., Dickie, L.M. and W. Trites, 1970. Spatial heterogeneity of phytoplankton in a near-shore environment. *Journal of Fisheries Research Board of Canada*, 27: 1453-1473.

Psarra S., A. Tselepides and L. Ignatiades, 2000. Primary productivity in the oligotrophic Cretan Sea (NE Mediterranean): seasonal and interannual variability. *Progress in Oceanography*, 46: 187-204.

Purcell J.E., 1982. Feeding and growth of the siphonophore *Muggiaea atlantica* (Cunningham, 1893). *J. Exp. Mar. Biol. Ecol.*, 62: 39-54.

Purcell J.E., 1992. Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay, USA. *Mar. Ecol. Prog. Ser.*, 87: 65-76.

Purcell J.E., 1997. Pelagic cnidarians and ctenophores as predators: selective predation, feedingrates, and effects on prey populations. *Annales Institut Océanogr.,* 73: 125-137.

Purcell J.E., D.A. Nemazie, S.E. Dorsey, E.D. Houde and J.C. Gamble, 1994. Predation mortality of bay anchovy *Anchoa mitchilli* eggs and larve due to scyphomedusae and ctenophores in Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, 114: 47-58.

Purcell J. E., Malej A., and Benovic A., 1999a. Potential links of jellyfish to eutrophication and fisheries. *In:* Malone T. C., Malej A., Harding T. L., Smodlaka N., Turner R. E. (eds.), Ecosystems at the land-sea margin: Drainage basin to coastal sea. *Coastal and Estuarine Studies,* Vol. 55: 241-263.

Purcell J.E., J.R. White, D.A. Nemazie and D.A. Wright, 1999b. Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha*. *Mar. Ecol. Prog. Ser*, 180: 187-196.

Purcell J. E., W. M. Graham and H. J. Dumont (eds), 2001. Jellyfish blooms: ecological and societal importance. Developments in Hydrobiology 155. Kluwer Academic Publishers, Dordrecht: xviii + 334 pp. Reprinted from *Hydrobiologia*, 451.

Reeve M.R. and L.D. Baker. 1975. Production of two planktonic carnivores (chaetognath and ctenophore) in south Florida inshore waters. *Fish. Bull.,* 73(2): 238-248.

Reeve M.R., M.A. Walter and T. Ikeda, 1978. Laboratory studies of ingestion and food utilization in lobate and tentaculate ctenophores. *Limnol. Oceanogr.*, 23: 740-751.

Reeve M.R., M.A. Syms and P. Kremer, 1989. Growth dynamics of a ctenophore (Mnemiopsis) in relation to variable food supply I: Carbon biomass, feeding, egg production, growth and assimilation efficiency. *J. Plankton Res.*, 11: 535-552.

Russel F.S., 1970. The Medusae of the British Isles.II. Pelagic Scyphozoa. Cambridge University Press, Cambridge, pp. 284.

Salamanca J.M., 2001. Las medusas invaden las aguas del Mar Menor. *Mar*, 394: 68.

Seki H., 1973. Red tide of *Oikopleura* in Saanich inlet. *La mer. Bull. Soc. franco-japonaise d'océanographie*, 11(3):153-158.

Sélié H., 1950. Stress. Acta.Inc., Montreal, pp. 281.

Seravin L.N., Shiganova T.A. Lupova N.E., 2001. The history of study of ctenophore *Beroe ovata* (Ctenophora, Atentaculata, Beroida) and some peculiarities of morphology of the representative from the Black Sea. *Zoological Journal.*, T.80 in press

Shannon L.J. and Jarre-Teichmann A., 1999. A model of trophic flows in the northern Benguela system during the 1980s. *S. Afr. J. mar. Sci.,* 21: 349-366.

Sheldon R.W., Prakash A., and Sutcliffe W.H.R., 1972. The size distributions of particles in the Ocean. *Limnol. Oceanogr.,* 17: 327-339.

Shiganova T. A., 1998. Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. Fisheries Oceanography – GLOBEC Special Issue, pp. 305-310, Ed. Steeve Coombs.

Shiganova T.A., and Bulgakova Yu.V., 2000. Effect of gelatinous plankton on Black and Sea of Azov fish and their food resources. *ICES Jour. Mar. Sc.*, 57: 641-648.

Shiganova T.A., U. Niermann, A.C. Gugu, A. Kideys, and V.S. Khoroshilov, 1998. Changes of species diversity and their abundance in the main components of pelagic community after *Mnemiopsis leidyi* invasion. pp.171-188. *In* : L. Ivanov and T. T. Oguz (eds), Kluwer Academic Publishers, Dordrecht/Boston/London.

Shiganova T.A., Yu.V. Bulgakova, P.Yu. Sorokin and Yu.F. Lukashev, 2000. Investigations of new settler *Beroe ovata* in the Black Sea. *Biology Bulletin*, 2: 247-255.

Silguero JMB, and Robison BH, 2000. Seasonal abundance and vertical distribution of mesopelagic calycophoran siphonophores in Monterey Bay, CA. *J. Plankton Res.,* 22(6): 1139-1153

Simmons E.G. 1957. An ecological survey of the upper Laguna Madre of Texas. *Publ. Inst. Mar. Sci. Univ. Texas,* 4(2): 156-200.

Slobodkin L.B., 1989. The null case of the paradox of the plankton. pp 341-348. *In:* Cosper E.M., Carpenter E.J., and Bricelj M. (eds.), Novel phytoplankton blooms: causes and impacts of recurrent brown tide and other unusual blooms, Springer-Verlag, New York.

Smayda T.J., 1997. What is a bloom? A commentary. *Limnol. Oceanogr.*, 42: 1132-1136.

Sorokin Y.I., 1983. The Black Sea. Ecosystems of the world. *In:* P. H. Ketchum (ed.) Estuaries and enclosed seas, 26: 253-291. Elsevier, Amsterdam

Southward A.J., 1980. The western English Channel – an inconstant ecosystem. *Nature*, 185: 361-366.

Southward A.J., Boalch G.T. and Maddock L., 1988. Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th century. *J.mar biol. Ass. UK*, 6:, 423-445.

Southward A.J., Hawkins S.J. and Burrows M.T. 1995. Seventy years' observations of changes in the distribution and abundance of zooplankton and intertidal organisms in the western English channel in relation to rising sea temperature. *J. therm.biol*., 20: 127-155.

Sparks C., Buecher E., Brieley A.S., Axelsen B.E., Boyer H. and Gibbons M.J., (in press). Observations on the distribution, and relative-abundance of *Chrysaora hysoscella* (Cnidaria, Scyphozoa) and *Aequorea aequorea* (Cnidaria, Hydrozoa) in the northern Benguela Ecosystem. *Hydrobiologia*.

Sreekumaran-Nair S.R., Devassy V.P., Madhupratap M., 1992. Blooms of phytoplankton along the west coast of India associated with nutrient enrichment and the response of zooplankton. *Mar. Coastal Eutroph.* (Suppl.), 819-828.

Stachovitsch M., 1984. Mass mortality in the Gulf of Trieste: the course of community destruction. *P. S. Z. N. I, Mar. Ecol.,* 5: 243-264.

Stanlaw K.A., M.R. Reeve and M.A. Walter, 1981. Growth, food, and vulnerability to damage of the ctenophore *Mnemiopsis mccradyi* in its early life stages. *Limnol. Oceanogr.,* 26: 224-234.

Stander G.H. and De Decker A., 1969. Some physical and biological aspects of an oceanographic anomaly off South West Africa in 1963. Investl Rep. Div. Sea Fish. S. Africa 81: 1-46.

Stebbing A.R.D., 1981. Stress, Health and Homeostasis. *Mar. Pol. Bull.*, 12: 326-329.

Stebbing A.R.D., 1982. Hormesis – the stimulation of growth by low levels of inhibitors. *Sci. Tot. Environ.*, 22: 213-234.

Stebbing A.R.D., 1991. The stimulation of reproduction in coelenterates by low levels of toxic stress. *UNEP, MAP Tech. Rep. Ser.,* 47: 298-301.

Stepnowski A., Gücü A.C. and F. Bingel, 1993. Assessment of the pelagic fish resources in the southern Black Sea using echo integration and Dual-Beam processing. Archives of Acoustic, *Polish Academy of Science Journal*, 18 (1): 83-104.

Steuer A., 1903. Beobachtungen uber das Plankton des Golfes vom Triest im Jahre 1902. *Zool. Anz. Bd.,* 27: 369

Steuer A., 1910. Planktonkunde. Teubner, Leipzig-Berlin, pp. 723.

Sullivan B.K., K.D. Van Keuren, Michael Clancy, (in press). Duration and size of blooms of the Ctenophore *Mnemiopsis leidyi* in relation to temperature in Narragansett Bay, RI. *Hydrobiologica*.

Sumich J.L., 1988. An introduction to the Biology of Marine Life. WCB Publishers, College Division, pp. 434.

Sverdrup H.U., 1953. On conditions for the vernal blooming of phytoplankton. *J. Conseil Exp. Mer.,* 18: 287-295.

Swanberg N. 1974. The feeding behavior of *Beroe ovata*. *Mar. Biol*., 24: 69-74.

Theocharis A., D. Georgopoulos, A. Lascaratos and K. Nittis, 1993. Water masses and circulation in the central region of the Eastern Mediterranean : Eastern Ionian, South Aegean and Northwest Levantine. *Deep-Sea Research II*, 40(6): 1121-1142.

Tolmazin D., 1985. Economic impact of the riverine-estuarine environment of the USSR: The Black Sea basin. *Geo. Jl*, 11:137-152

Travizi A., 1998: Recovery of meiofauna after anoxic stress. II. Spatial distribution. *Periodicum Biologorum*, 100: 71-79.

UNEP, 1984. Proc. Workshop on jellyfish blooms in the Mediterranean. Athens, 31 October-4 November 1983, 221 p.

UNEP, 1991. Jellyfish blooms in the Mediterranean. MAP Technical Reports Series N° 47, 320 p.

Uye S.-I. and S. Ichino, 1995. Seasonal variations in abundance, size composition, biomass and production rate of *Oikopleura dioica* (Fol) (Tunicata: Appendicularia) in temperate eutrophic inlet. *Journal of Plankton Research*, 1-2: 1-13.

Uysal Z. and Mutlu, E., 1993: Preliminary note on the occurrence and biometry of Ctephoran *Mnemiopsis leidyi* finally invaded Mersin Bay, *Turkish J. of Zoology*, 17(2): 229-236.

Venter G.E., 1988. Occurrence of jellyfish on the west coast off South West Africa/Namibia. Rep. S. Afr. natn. scient. Progms., 157: 56-61.

Vinogradov M.Ye., 1990. Investigation of the pelagic ecosystem of the Black Sea (44th Cruise of the R/V *Dimitriy Mendeleyev*, 4 July - 17 September 1989. *Oceanology*, 30(2): 254-256.

Vinogradov M.YE., E.A. Shushkina, E.I. Musayeva and P. Yu Sorokin, 1989a. A newly acclimated species in the Black Sea: the ctenophore *Mnemiopsis leidyi* (Ctenophora: Lobata). *Oceanology*, 29(2): 220-224.

Vinogradov M.E., E.A. Shu shkina, E.I. Musaeva and P.Yu. Sorokin, 1989b. Ctenophore *Mnemiopsis leidyi* (A. Agassiz) (Ctenophora: Lobata) – new settlers in the Black Sea. *Oceanology*, 29: 293-298.

Vollenweider R. A., Rinaldi A. and G. Montanari, 1992. Eutrophication, structure and dynamics of a marine coastal system: results of ten-year monitoring along the Emilia-Romagna coast (Northwest Adriatic Sea). pp. 63-106. *In*: Vollenweider R.A., Marchetti R. and Viviani R. (eds.), Marine coastal eutrophication, Elsevier Sci. Publ., Amsterdam.

Volovik S. P., I.A. Mirzoyan and G.S. Volovik, 1993. *Mnemiopsis leidyi*: biology, population dynamics, impact to the ecosystem and fisheries. ICES. Statuary meeting: 1-12.

Vostokov S.V., E.G. Arashkevich, A.V. Dritz and Yu.F. Lukashev, 2001. Ecological and physiological characteristics of the ctenophore *Beroe ovata* in the coastal waters of the Black Sea: abundance, biomass, size distribution, behavior, feeding and metabolism. *Oceanol*., 41(1): 105-110.

Vucetic T., 1984. Some causes of the blooms and unusual distribution of the jellyfish *Pelagia noctiluca* in the Mediterranean (Adriatic). UNEP Workshop on jellyfish blooms in the Mediterranean, Athens, 31 October-4 November, pp. 167-176, Watt K.E.F., 1964. Comments on long-term fluctuations of animal populations and measures of community stability. *Canadian Entomologist*, 96: 1434-1442

Widder E.A., 1992. Mixed light imaging system for recording bioluminescence behaviors. *J. Mar. Biol. Assoc. U.K.*, 72: 131-138.

Wyatt T. and Jenkinson I.R., 1997. Notes on Alexandrium population dynamics. *J. Plankton. Res.*, 19: 551-576.

Yasuda T., 1970. Ecological Studies on the Jellyfish *Aurelia aurita* (l.), in Urazoko Bay, Fukui Prefecture – V. Vertical Distribution of the Medusa. *Ann. Rep. Noto Mar. Lab.*, 10: 15-22.

Yoon W.D., Marty J.C., Sylvain D. and Nival P., 1996. Degradation of faecal pellets in *Pegea confoederata* (Salpidae, Thaliacea) and its implication in the vertical flux of organic matter. *J. exp. mar. biol. ecol.*, 203: 147-177.

Zaika V.E., 1992. The ecosystem degradation is increasing. pp. 97-100. *In*: Problems of the Black Sea. International Conference on Problems of the Black Sea. International Conference. Sevastopol, Ukraine. November 10-15.

Zaitsev Yu.P. and Alexandrov B. G., 1997. Recent Man-made changes in the Black Sea ecosystem, pp. 25-32. *In*: E. Ozsoy and A. Mikaelyan (eds), Sensitivity to changes: Black Sea, Baltic Sea and north Sea, Kluwer Acad. Publ., The Netherlands.

Zaitsev Yu.P., 1991. Cultural eutrophication of the Black Sea and other South European Seas. *La mer* (Société franco-japonaise d’océanocraphie, Tokyo), 29: 1-7.

Zaitsev Yu.P., 1993. Fisheries and environment studies in the Black Sea system. Part 2: Impact of eutrophication on the Black Sea fauna. Studies and Reviews. General Fisheries Council for the Mediterranean. N°.64: 59-86. Rome, FAO.

Zeldis J.R.,Davis C.S., James M.R., Ballara S.L., Booth W.E. and Chang F.H., 1995. Salp grazing:effects on phytoplankton abundance, vertical distribution and taxonomic composition in a coastal habitat. *Mar. Ecol. Progr. Ser.*, 126: 267-283.

IV – LIST OF PARTICIPANTS

Jose Luis Acuña	Area de Ecologia Universidad de Oviedo 33071 Oviedo - Spain e-mail: acuna@sci.cpd.uniovi.es
Adam Benovic	Institute of Oceanography and Fisheries Laboratory of Dubrovnik P.O. Box 83, 20000 Dubrovnik - Croatia e-mail: benovic@labdu.izor.hr
Ferdinando Boero *(Workshop coordinator)*	Dipartimento di Biologia Università di Lecce Lecce - Italia e-mail: boero@unile.it
Quentin Bone	Plymouth Marine Laboratory Prospect Place, The Hoe Plymouth, PL1 3DH- England e-mail: qb@mba.ac.uk
Frédéric Briand *(Director General, CIESM)*	CIESM 16, Bd de Suisse MC 98000 - Monaco e-mail: fbriand@ciesm.org
Emmanuelle Buecher	University of the Western Cape Zoology Department Private Bag X17 Bellville 7535 - South Africa e-mail: ebuecher@mcm.wcape.gov.za
Gabriel Gorsky	Observatoire Océanologique, B.P. 28. 06230 Villefranche/mer - France e-mail: gorsky@obs-vlfr.fr
Richard Harbison	Woods Hole Oceanographic Institution Biology Department Woods Hole, MA 02543 - USA e-mail: gharbison@whoi.edu
Patricia Kremer	Dept. Marine Sciences University of Connecticut 1084 Shennecossett Rd Groton, CT 06340 - USA e-mail: pkremer@uconnvm.uconn.edu
Geneviève Lacroix	Geohydrodynamics and Envtal Research Université de Liège B5 Sart Tilman B-4000 Liège - Belgique e-mail: g.lacroix@ulg.ac.be
Alex Lascaratos	University of Athens Dept. of Applied Physics, Oceanography Group University Campus, Bld PHYS-V 15784 Athens - Greece e-mail: alasc@oc.phys.uoa.gr

Priscilla Licandro	Stazione Zoologica Anton Dohrn Villa Comunale, Punta S. Pietro 1 80121 Napoli - Italia e-mail: licandro@alpha.szn.it
Maria Mazzocchi	Stazione Zoologica Anton Dohrn Villa Comunale, Punta S. Pietro 1 80121 Napoli - Italia e-mail: grazia@alpha.szn.it
Alenka Malej	Marine Station of Piran National Institute of Biology 6330 Piran, Fornace 41 - Slovenia e-mail: malej@nib.si
Erhan Mutlu	Institute of Marine Sciences Marine Biology and Fisheries P.O. Box 28. 33731 Erdemli, Icel - Turkey e-mail: mutlu@ims.metu.edu.tr
Paul Nival	Station Zoologique Observatoire Océanologique BP 28. 06230 Villefranche/mer - France e-mail: nival@obs-vlfr.fr
Francesc Pagès	Institut de Ciències de Mar (CSIC) Plaça del Mar s/n 08039 Barcelona, Catalunya - Spain e-mail: fpages@icm.csic.es
Tamara Shiganova	P. P. Shirshov Institute of Oceanology Russian Academy of Sciences Moscow - Russia e-mail: shiganov@chip.sio.rssi.ru
Tim Wyatt	Instituto de Investigaciones Marinas Eduardo Cabello 6 36208 Vigo - Spain e-mail: twyatt@iim.csic.es

La Commission Internationale pour l'Exploration Scientifique de la mer Méditerranée :

Une organisation intergouvernementale - 22 Etats-membres - intervenant dans le domaine de la recherche océanographique et de la gestion côtière pour favoriser les coopérations entre scientifiques ainsi qu'entre chercheurs et décideurs. Avec le concours d'un vaste réseau pluridisciplinaire : plus de 500 instituts spécialisés et de 2000 chercheurs.

An intergovernmental organization - 22 State-members - aiming to facilitate cooperations among scientists as well as between researchers and decision makers in the fields of oceanographic research and coastal management. Supported by a large pluridisciplinary network: more than 500 institutes and 2000 researchers.

--

Fax : + 377 92 16 11 95
http:// www.ciesm.org

Déjà parus
Already published :

1
Mediterranean marine biodiversity
Nicosia (Cyprus), May 1997

2
Current issues in marine microbiology
Siena (Italy), August 1997

3
Role of ocean-atmosphere processes in the biogeochemistry of the Mediterranean Sea
Bologna (Italy), October 1997

4
Environnement littoral
Marseille (France), octobre 1997

5
Gaps in Mediterranean fishery science
Dubrovnik (Croatia), June 1998

6
Mediterranean scientific drilling prospectives
Granada (Spain), June 1999

7
Precautionary approach to local fisheries in the Mediterranean
Kerkenna Island (Tunisia), Sept. 1999

8
Scientific design and monitoring of Mediterranean marine protected areas
Porto Cesareo (Italy), October 1999

9
Role of sea surface microlayer processes in the biogeochemistry of the Mediterranean Sea
Paris (France), December 1999

10
The Eastern Mediterranean climatic transient : its origin, evolution and impact on the ecosystem
Trieste (Italy), March-April 2000

11
Investigating marine microbial loops: new tools and perspectives.
Zichron Yaakov (Israel), May 2000

12
Fishing down the Mediterranean food webs ?
Kerkyra (Greece), July 2000

13
African continental margins of the Mediterranean Sea
Djerba (Tunisia), November 2000

Conception : Dynactis - Nice