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 indicat-
ed, 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 ctenophore *Mnemiopsis* (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 leidyi* 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
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 out-
breaks. 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 between 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 WP II 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 (Bentfield et al., 1996; Davis et al., 1996), which visualizes and quantifies small-size zooplankton. The Underwater Video Profiler constructed by the Laboratoire d'Oceanographie 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.

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 physconet 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 faunistic 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.