

Dispersal ecology and phylogeography of *Scyphomedusae* in the Mediterranean Sea

By Andreja Ramšak and Katja Stopar

Large jellyfish blooms have been recorded in the Adriatic Sea several times in the past. Different hypotheses have been proposed, such as relationships with eutrophication, anoxia, climatic factors and over-exploitation of pelagic fish, but no definitive conclusions regarding possible causes for their massive presence were widely accepted. Aggregations of large jellyfish in the northern Adriatic have significant impact on tourism and the artisanal fishery of Slovenia. There is a long tradition of jellyfish research at the institutions around the Adriatic. Nowadays, the scientific interest is also focused on the genetic diversity within and at species level.

Periodical swarms of scyphozoan jellyfish are not unusual in the Mediterranean Sea (Purcell, 1999; CIESM, 2001) but seem to have become more frequent in the last few years. The most notorious event was swarms of the mauve stinger *Pelagia noctiluca*, which inflicts a rather severe sting.

Pelagia blooms were recorded several times in the Mediterranean during the last two centuries and several factors were proposed which correlated with blooms, such as low rainfall, high temperatures and high atmospheric pressure (Goy *et al.*, 1989). High *Pelagia* densities have been observed with a periodicity of about 12 years in the western and central Mediterranean, while swarms in the Adriatic Sea have been less predictable. Three periods of high densities have been observed in the Adriatic Sea in the last 100 years: 1910-1914, 1976-1986 and the latest one, from 2004 to the present (Malej *et al.*, 2007). However, in the last few years blooms of the mauve stinger have been recorded all over the Mediterranean, from the western to the eastern part in Rhodes and in the Adriatic Sea.

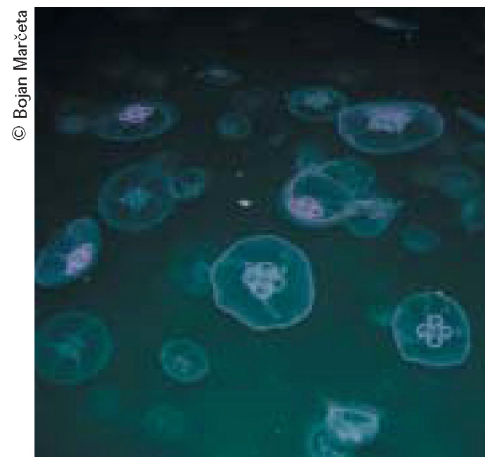
The moon jelly *Aurelia aurita* is usually present during the winter/spring in the Adriatic Sea, but in the last few years its blooms have become more evident and have also occurred in the coastal regions of the northern Adriatic. The moon jelly is not the only species that has caused blooms in the northern Adriatic: since 2003, massive blooms of white jellyfish *Rhizostoma pulmo* have occurred during the autumn/winter period in the northern Adriatic. Blooms of white jellyfish and moon jelly in the Gulf of Trieste resulted in economic losses in Slovenian artisanal fisheries, due to clogging of fishing nets. Blooms usually last several months, with jellyfish then dying out or becoming rare. Several hypotheses have been proposed to explain the more frequent blooms

around the world and these can also be applied to the Mediterranean Sea: for example, climatic fluctuations and trophic regime shifts, eutrophication, overfishing, translocation of jellyfish by maritime traffic, etc (Mills, 2001; Lynam *et al.*, 2004; Purcell *et al.*, 1999).

Aside from the plausible causes that can trigger blooms, *Scyphomedusae* have life-history traits that can result in rapid increases in numbers, growth and high dispersal rates. All mentioned jellyfish species that recurrently form blooms belong to the class *Scyphozoa*. Most of the Scyphozoan members have a typical bipartite life-cycle consisting of free-swimming medusae, representing the sexually reproducing animal, and an asexually-reproducing sessile polyp. Medusae have separate sexes, and the fertilized egg evolves into a planula that settles on substrate and develops into a scyphistoma (polyp). They



White jelly *Rhizostoma pulmo*.



Huge aggregations of moon jelly *Aurelia aurita* were recorded during April 2007 in the Gulf of Trieste.

asexually produce new polyps by budding and/or strobilate into ephyrae that grow into medusae. Polyps are important, since they sustain the benthic phase (they may also be dormant) and they enable rapid asexual reproduction of polyps or new medusae by the process of strobilation. Free-swimming medusae can live from a few months up to more than one year and are dispersed by currents. Usually we notice them on the shore as strandings due to currents and strong winds, or in water, as mentioned earlier. The question of what happens to the jellyfish population after the bloom is still open. Species such as *Pelagia* which are holopelagic may persist in smaller numbers, but the species with a benthic phase can become dormant in the polyp phase and wait for the stimulus that triggers strobilation.

In order to better understand jellyfish blooms, a more detailed characterisation of their populations is needed. In this regard, it is important to monitor the population dynamics and reveal genetic structure at temporal and spatial scales. Different polymorphic markers, from mitochondrial and nuclear genome, are useful in the indirect monitoring of spatial and temporal demographic changes.

Genetic diversity and geographic distribution of mitochondrial DNA haplotypes are currently being studied on the mentioned jellyfish (*Pelagia noctiluca*, *Aurelia aurita* and *Rhizostoma pulmo*) in the Mediterranean basin and further afield. The mitochondrial markers were amplified using standard oligonucleotide

The Mediterranean Sea

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Mauve stinger *Pelagia noctiluca*.

primers and using distance-based methods for evaluation of genetic distances within and between species. Phylogeography analysis provides a framework to explain and integrate patterns of species biodiversity at specific levels. Comparison of mitochondrial sequences of white jellyfish indicated substantial separation between samples from the northern Adriatic and eastern Black Sea (Ramšak *et al.*, 2007). According to the current classification, white jellyfish in the Mediterranean and adjacent seas belong to the species *R. pulmo*, but those found at the western and northern coasts of Europe are of a separate species, *R. octopus*. The life-cycle of white jellyfish has not been very well described, but the gap in knowledge has been supplemented recently by a study of the life-cycle of white jellyfish collected in the North Sea (Holst *et al.*, 2007; Holst and Jarms, 2007).

More studies have been devoted to the mauve stinger due to frequent blooms and detrimental effects on humans. Keeping this in mind, less predictive swarms of the mauve stinger and its potential transport routes were

studied using the Lagrangian tracking of water-mass in the climatic circulation of the Adriatic Sea (Malačič *et al.*, 2007). Because of more available data on the seasonal occurrences, size structure, patterns of growth, reproduction and mortality in the northern Adriatic, the dynamics of its population has been modelled by a modified Leslie matrix using size rather than age classes. The demographic parameters such as shrinkage and temporal changes for different seasons were incorporated into the model (Malej & Malej, 1992). The model was coupled to Lagrangian tracking of water parcels in order to trace transport pathways of mauve stinger within the Adriatic Sea. The results from tracing transport pathways suggest that the mauve stinger enters the Adriatic at the eastern side of the Otranto Strait and via the connection between the Adriatic and other Mediterranean metapopulations. Connectivity is also supported by phylogeographic analysis of mitochondrial markers. Analysis of genetic structure based on mitochondrial genome (COI gene sequences) in mauve stinger collected in different parts of the Adriatic and other Mediterranean biogeographic regions indicates a common pool of this jellyfish and rich haplotype diversity at the sampling sites in the Mediterranean Sea. The more detailed impact of the oceanographic and ecological characteristics of the Mediterranean basin on the dispersal ability of both species will be assessed in the future.

Andreja Ramšak & Katja Stopar

National Institute of Biology, Marine Biology Station, Fornače 41, 6330 Piran, Slovenia. Email: ramsak@mbss.org

Jellyfish research and GBIRM

The above work on jellyfish is part of Genetic Biodiversity Responsive Mode (GBIRM; leader: Jean-Pierre Féral, DIMAR). GBIRM links studies on selected species of invertebrates, fish and seaweed in order to promote study of genetic diversity in connection with ecological parameters and biological traits such as life history, reproductive mode and behaviour. Knowledge from studies of genetic diversity will help us to understand the causes of observed patterns of genetic variation within and among populations, testing the role of biogeographic transition zones, effects of various anthropological induced stresses (over-exploitation, contaminants), and so on.

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Moon jelly *Aurelia aurita*.

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During the winter months, blooms of white jellyfish caused economic losses in the artisanal fisheries in the Gulf of Trieste. Blooms were extensive and for some period the only catches in trawl were white jellyfish.