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

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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.