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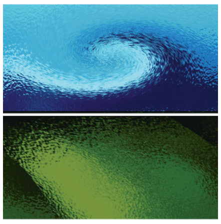

RESEARCH ARTICLE

Recent advances in coastal lagoons ecology: evolving old ideas and assumptions.

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Abstract

1 - Coastal lagoons are among the most productive ecosystems in the world. Their particular features, which include shallowness, relative isolation and protection from the sea, together with the presence of boundaries with strong physical and ecological gradients, make them especially interesting for human use. They provide goods and services for humans by supporting important fisheries, and intensive and extensive aquaculture exploitations. At the same time, they are suitable for other activities such as nautical sports, swimming or health care.

2 - However, their close relation with terrestrial ecosystem boundaries and the pressures derived from human activities, make these environments especially vulnerable to human impact and terrestrial and freshwater inputs. Because of their importance for human interests and their vulnerability, there is increasing social concern on the necessity for protecting and managing coastal lagoons.

3 - To manage a system we need to understand how it works and this implies that we need to know the components of the system, their links, the processes involved in their functioning and the cause-effect relationships between human activities and the alteration of ecological processes, as a prior step to building bio-economic models and decision support tools.

4 - Our knowledge and related conceptual bases of the ecological processes at work in coastal lagoons developed between the 1960s and 1990s, a period of intense activity in the study of these transitional ecosystems, including estuaries and brackish waters, in general, of the Mediterranean and Europe. However, after an apparent decline in concern and scientific production on these ecosystems, recent years have seen fresh interest in their study, both in Europe and the rest of the world, with the number of publications appearing in high impact journals increasing significantly. Knowledge and assumptions concerning coastal lagoon processes and functioning have evolved very quickly during these last decades.

5 - In this contribution, we analyze recent developments and findings on lagoon ecology concepts and the consequences for lagoon management, as well as the importance of constituting lagoon research networks and common data bases to boost future developments and to improve our management and decision making capabilities.

Keywords: coastal lagoon, transitional waters, coastal zone management, ecological processes.

Introduction

Coastal lagoons are found throughout the world, occupying 13% of the world coastline (Barnes, 1980; Nixon, 1982). Their particular features, such as shallowness, the intense interaction between terrestrial and marine ecosystems, the relative isolation and protection from the sea and the presence of boundaries with strong physical and ecological gradients, make them one of the most productive ecosystems in the world (Nixon, 1982; Alongi, 1998), and especially interesting for humans, whom they provide with a wide variety of societal benefits. They support important fisheries, with a mean yield of fish of 92.8 kg*ha^{-1}*year^{-1} (information obtained from 37 Atlanto-Mediterranean coastal lagoons), reaching 400 kg*ha-1*year-1 in some case (Nixon, 1982; Pérez-Ruzafa *et al.*, 2011), intensive and extensive aquacultural exploitations, and, at the same time, they are suitable for nautical sports, swimming or health care, among other uses. However, this close relation with the boundary of terrestrial ecosystems and the pressures derived from human uses, make these environments especially vulnerable to human impact and terrestrial and freshwater inputs.

Because of their importance for human interests and their vulnerability, social concern is growing about the need to protect and manage coastal lagoons in an integrated and sustainable manner. However, to manage a system it is necessary to understand how it works and this implies that we need to know the components of the system, how these components are linked, the processes involved in their functioning and the cause-effect relationships between human activities and the alteration of ecological processes. Only when we have such knowledge will it be possible to construct bio-economic models and develop decision support tools.

Although there are some interesting early studies (e.g. Cavinato, 1950; Hartmann, 1952; Lozano Cabo, 1953, 1959; Petit, 1953, 1962; Feldmann, 1954; Anonymous, 1959; D'Ancona, 1959; Mars, 1966; Margalef, 1969), most of our current knowledge about the functioning of coastal lagoons stems from studies conducted in the 1970s and 1980s (see Carrada & Fresi, 1988, the works of the Committee of "Ètangs salés et lagunes" of the Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée (CIESM), the FAO reports on coastal lagoon fisheries management (Kapetsky and Lasserre, 1984), or the UNESCO reports and symposia organized in these years (UNESCO, 1979, 1980, 1981, 1982, 1986; Lasserre and Postma, 1982)) (Pérez-Ruzafa *et al.*, 2011). From 1972 to 1992, the last period in which the Committee of "Ètangs salés et lagunes" was active, around 500 scientific papers appeared in CIESM reports on different aspects of the hydrography, sedimentology and biological assemblages of Mediterranean coastal lagoons.

After an apparent decrease in the interest of the scientific community in the study of coastal lagoons, and the disappearance of specific Committees such as this one of the CIESM, the number of publications appearing in high impact journals has increased significantly in the last two decades, and now covers ecosystems throughout the world (Pérez-Ruzafa *et al.*, 2011). Meanwhile, to establish the basic principles of sustainable water policy and to improve the sustainability of water management, the European Union has adopted the Water Framework Directive (Directive 2000/60/EC) which directly affects coastal lagoons and so-called transitional waters, making it necessary to establish typologies and reference conditions and to determine the biological quality and ecological status of these water bodies.

This has prompted intense and interesting discussions on the meaning of the transitional waters concept, the definition of coastal lagoons and their position between estuaries and the sea (Tagliapietra and Ghirardini, 2006; McLusky and Elliott, 2007; Tagliapietra *et al.*, 2009; Pérez-Ruzafa *et al.*, 2011; Potter *et al.*, 2010). But, to meet this challenge and to face up to such a complex task, it is important to keep in mind the old aphorism that says: "Every problem has a solution and if a problem has no solution it is ill-posed". If the starting assumptions are wrong, it will be difficult to find solutions to the many problems involved in the proper management of lagoon ecosystems.

Although the fundamentals of lagoon ecology were firmly established by pioneering works, the new generation of researchers has available modern techniques and more precise methodologies, together with new approaches derived from the advances made in ecological science, so that our knowledge on coastal lagoon processes and functioning has evolved very quickly during recent decades.

In this work, we review some of the old ideas and assumptions on coastal lagoon ecology in the light of new information and the implications of current knowledge for the management of these unique ecosystems.

The old assumptions

Coastal lagoons are dynamic ecosystems dominated and subsidized by physical energies. Traditionally, among lagoon characteristics are recognized their high productivity, ecological complexity, ecological stability and multiple interfaces (Carrada and Fresi, 1988). Intuitively, the high number of boundaries they have with the land, the open sea, air and sediment, and the intensity of the gradients that are established (with large differences in the values of any given parameter in a small space) endow these systems with a great ability to perform work in the physical sense of the term. That is, on the basis of their high biological productivity. But, at the same time, also leads to the old assumption that these systems undergo frequent physical and chemical disturbances and fluctuations (Unesco, 1981, Nienhuis, 1992), so that they are usually considered as naturally stressed habitats (Barnes, 1980; Kjerfve, 1994), and physically controlled ecosystems (sensu Sanders, 1968) (Michel, 1979) with low specific diversity and dominance of few species (Margalef, 1969; Carrada and Fresi, 1988; Reizopoulou and Nicolaidou, 2004). These features mean that estuarine benthic communities have many of the same characteristics as areas suffering from human-induced stress (Elliott and Quintino, 2007).

Such kinds of ecosystem are expected to be characterized by some of the following features:

1) As there are few species that can tolerate high doses of environmental stress, these ecosystems should be simple and relatively uniform in space and time, with a unique type of community.

2) The distribution of species in a lagoon would be determined by the gradients established from the sea to the inner part of the lagoon, with increasing physical-chemical stress acting as the limiting factor for the physiology of the species. Therefore, these areas are expected to be impoverished in species.

3) Being naturally stressed habitats, the system would be physically regulated, bottom-up controlled and exposed to eutrophication processes and dystrophic crises.

4) Based on the above statements, the ecosystem would be dominated by opportunistic species. Therefore, the main inhabitants of lagoon ecosystems are expected to be r strategists, while K strategists are marine migrant species which exploit the lagoon resources temporarily.

Are coastal lagoons simple and relatively uniform ecosystems, maintaining homogeneous and simplified assemblages and with a unique type of community?

Pérès and Picard (1964), in their now classic "*Manuel de bionomie benthique*", reviewed the concept of biocenosis and classified Mediterranean marine benthic communities. They considered Mediterranean lagoons and estuarine areas as a well differentiated and unique homogeneous community, the so-called euryhaline and eurythermal biocenoses (*Biocoenose lagunaire euryhaline et eurytherme* (LEE)):

"*Dans les étangs littoraux salés et dans les zones estuariennes, la biocoenose la plus fréquemment représentée s'accommode particulièrement bien des conditions d'euryhalinité et d'eurythermie fréquentes dans un tel biotope. Il est intéressant de constater que le peuplement de ces sables vaseux ou vases sableuses reste sensiblement le même, aussi bien lorsque l'eau est constamment moins salée que l'eau de mer du large que lorsqu'elle est constamment plus salée que l'eau de mer du large, ou bien enfin qu'elle présente des variations de salinité très importantes en cours d'année.*"

This consideration was supported by Guelorget and Michel (1979a, 1979b) and maintained later by Augier (1982) in his inventory and classification of Mediterranean marine benthic biocenoses. Carrada and Fresi (1988), also considered lagoon communities "*substantially homogeneous in space and time and relatively stable*", and we can find this assumption in many habitat lists of conservation agreements, including OSPAR, Barcelona or Eunis. Based on this assumption numerous studies have been carried out by different authors such as Chassany de Casabianca (1979), Nagy (1979), Guelorget and Perthuisot (1983, 1992), Skolka and Tiganus (1985), Bachelet *et al.* (2000), or Mouillot *et al.* (2005). Even works that accept the variation of species distribution or biomass along environmental gradients, such as those determined by confinement, salinity or trophic conditions (Palacin *et al.*, 1991; Koutsoubas *et al.*, 2000; Sfriso *et al.*, 2003; Curiel *et al.*, 2004; Garnerot *et al.*, 2004; Lin and Hung, 2004; Reizopoulou and Nicolaidou, 2004; Benhissoune *et al.*, 2005; Chaouti and Bayed, 2005; Marzano *et al.*, 2010; Ponti *et al.*, 2011), do not consider the existence of different communities, or the existence of a vertical zoning similar to those existing in coastal marine habitats. This constriction prevents appropriate sampling designs, limiting the possibility of detecting significant differences, or seriously affects the interpretation of the variability found by the authors mixing the effects of different factors.

All the above has had negative consequences, not only for interpreting the patterns and ecological processes in coastal lagoons, but also because such habitats tend to be managed as a unit, with decisions adopted at lagoon scale, when different areas of a given lagoon might require different management options (De Biasi *et al.*, 2003; Pérez-Ruzafa *et al.*, 2011) or different reference conditions in the context of the European Water Framework Directive.

However, different assemblages, characterized by well-defined groups of species, can be described in a coastal lagoon according to their isolation from the open sea, the type of substrate and depth, with a vertical zonation pattern for sessile organisms similar to that found in all marine communities but more compressed (Occhipinti Ambrogi *et al.*, 1988; Pérez-Ruzafa, 1989; Pérez-Ruzafa *et al.*, 2007b). Some studies have also characterized different communities according to the water characteristics or type of substratum, in one or several lagoons, for phytocenosis (Lovric, 1979; Zouali, 1979; Chassany de Casabianca, 1980; Pérez-Ruzafa *et al*., 2008), macroinvertebrates (Amanieu *et al*., 1981; Quintino *et al*., 1987), fishes (Franco *et al*., 2006; Pérez-Ruzafa *et al*., 2006) or for the overall assemblage (de Casabianca *et al*., 1972).

A single factor to explain inter and intra-lagoon variability?

Coastal lagoons are complex systems. They share many characteristics that differentiate them from other transitional and coastal waters (Pérez-Ruzafa *et al*. 2011b) but they are not homogeneous. Against the generalized assumption of lagoon biocenosis homogeneity, coastal lagoons show a wide range of geomorphological and hydrographic variability and internal environmental heterogeneity, including gradients, depending on the marine or fresh water influence. Here, it is important to distinguish the variability between different coastal lagoons and the spatiotemporal heterogeneity within each lagoon. For many ecological features, the factors that determine inter and intra-lagoon variability may be the same, and most of the numerous proposals for classifying these water bodies (D'Ancona, 1959; Petit and Schachter, 1959; Zenkevitch, 1959; see Segerstrale, 1959 for a historical survey) did not differentiate these aspects. Now, in the context of the Water Framework Directive, the need to typify these ecosystems and to characterize water bodies has gained new interest, as any evaluation of the ecological status of aquatic systems must refer to the adequate reference conditions, and natural variability must be controlled to distinguish it from changes produced by human impact (Underwood, 2000; Benedetti-Cecchi *et al*., 2001; Pérez-Ruzafa *et al*., 2007b).

Salinity has been considered the key factor that governs both the physiology and ecology of the organisms inhabiting brackish water biotopes (Arndt, 1989) and numerous studies from the 1980's and 1990's on brackish water environments focus on physiological studies of the effects of this parameter on estuarine species (McLusky, 1999). Therefore, it is not surprising that among the above mentioned proposals, the most widely used consider salinity as the main parameter (Petit, 1953; Aguesse, 1957; D'Ancona, 1959; Remane in McLusky, 1999). The Venice symposium on the classification of brackish waters unified criteria and defined the zones of an estuary, or brackish waters, in terms of salinity zones (Venice System, Anonymous, 1959). Later, Por (1972, 1980) combined salinity with biological criteria to classify hypersaline waters.

But lagoons also show great differences in size, morphology or trophic status, and not only in salinity, and these, too, condition biological assemblages structure, species composition and fishing yield (Joyeux and Ward, 1998; Pérez-Ruzafa *et al*. 2007a).

In an analysis of the main factors determining fish species composition, species richness and fishing yield in 40 Atlanto-Mediterranean coastal lagoons, Pérez-Ruzafa *et al*. (2007a) found that geomorphological factors such as openness (the potential influence of the sea on general lagoon hydrology) and shoreline development are the main factors determining species richness and fishing yield, respectively, in the lagoons. Trophic (mainly chlorophyll concentration) and hydrographic factors (mainly salinity) are mutually influenced and mainly conditioned by geomorphological features. The covariation of hydrographic, trophic and geomorphological factors explains 74.6% of the fish assemblage composition in coastal lagoons, while hydrographic and trophic factors by themselves explain only 3%, and geomorphological features explain 22% (figure 1).

When these three groups of factors are analyzed separately in relation to fish species composition, salinity versus the difference in salinity between the lagoon and adjacent sea determines the classical differentiation

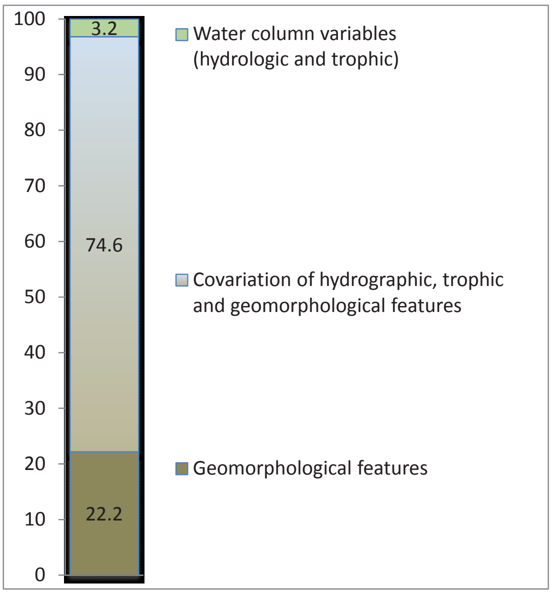


Figure 1. Results of the partitioning of the variance for analyzing the relative contribution of hydrographic (salinity, temperature and their ranges of variation and differences with the open sea), trophic (chlorophyll a and nutrients concentration) and geomorphological (twenty-four variables including surface, depth, volume, openness, perimeter, coastal development, etc.) variables on the fish assemblage species composition in 40 coastal lagoons in the Atlanto-Mediterranean area. See Pérez-Ruzafa et al. 2007a for details.

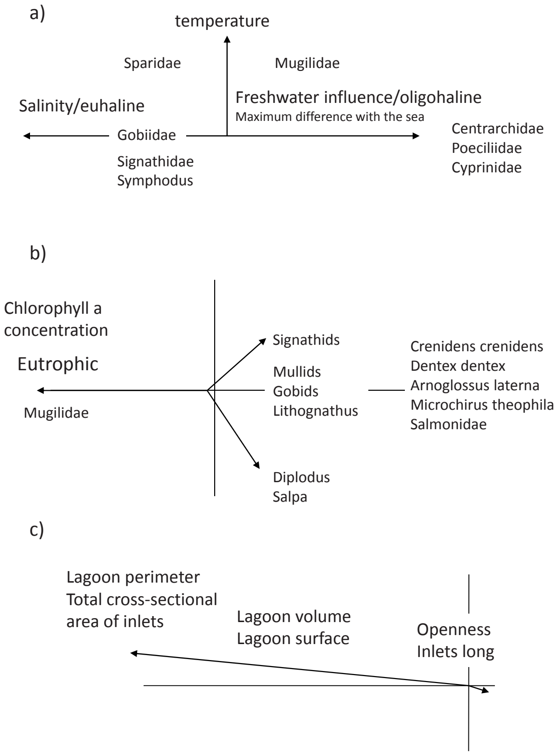


Figure 2. Representation of the main factors determining the fish assemblage composition of Atlanto-Mediterranean coastal lagoons when hydrographic (a), trophic (b) and geomorphological (c) variables are analyzed separately, according to the analyses performed in Pérez-Ruzafa et al. (2007a).

between euhaline, polyhaline, mesohaline and oligohaline lagoons, depending on freshwater influence, with Gobiidae, Signathidae and *Symphodus* species in the euhaline extreme, and Centrarchidae, Poeciliidae and Cyprinidae in the oligohaline. Water temperature explained only latitudinal differences in species composition (figure 2a). On the other hand, Chlorophyll a concentration determines a trophic gradient, ranging from eutrophic to oligotrophic, and segregates fish feeding strategies (figure 2b). Finally, the main geomorphological features determining lagoon assemblages are the size (lagoon volume), the openness, or potential influence of the sea on the lagoon's general hydrology, and shoreline development (see Chubarenko *et al*. (2005) for a detailed description of these parameters) (figure 2c). The size of the lagoon and openness explain species richness in lagoons both as regard fish (Pérez-Ruzafa *et al*., 2007a) and invertebrates (Basset *et al*., 2006). Shore development (measured as the ratio of the length of shoreline, the lagoon perimeter, to the circumference of the circle whose area is equivalent to that of the lagoon) is the main factor, along with chlorophyll concentration, that explains the fishing yield of lagoons. Joyeux and Ward (1998) did not measure shore development, but did find that fishing yield was mainly related with the interaction between the lagoon and land (positive relationship with runoff and with wetland area).

At the same time, as mentioned by Guelorget and Perthuisot (1983) and Guelorget *et al.* (1983), internally, each coastal lagoon shows biological gradients in species richness, abundance and productivity that are not explained by salinity. These authors proposed a new parameter, confinement, which represents the turnover time of marine water and the impoverishment in some oligo-elements of marine origin:

"*Par leur position intermédiaire entre mer et continent, les milieux lagunaires (ou paraliques) se caractérisent par l'existence de gradients hydrochimiques, biologiques et sédimentologiques. La salinité, presque fatalement "anormale", est considérée généralement comme un paramètre écologique essentiel et sert de base à la classification de ces milieux. Nos travaux sur plusieurs lagunes méditerranéennes (et d'autres régions) nous conduisent à remettre en cause cette conception et à proposer une autre dynamique des milieux paraliques par des facteurs internes (morphologie, hydrologie) qui commandent les temps que mettent les éléments venus de la mer pour atteindre chaque point du bassin considéré ou encore le temps de renouvellement du milieu en chaque point: nous appelons ce paramètre complexe le confinement.*"

The importance of the marine influence as the main parameter to explain lagoon functioning was also defended by Kjerfve (1994), who subdivided coastal lagoons into three geomorphic types: choked, restricted and leaky, as three points along a spectrum reflecting the exchange of water with the coastal sea. The rate and magnitude of oceanic exchange reflect both the dominant forcing functions and the time-scale of hydrological variability. Numerous studies have confirmed that salinity is not the main parameter to explain species distribution in coastal lagoons (Barnes, 1994; Lardici *et al.*, 1997), and many authors relate the distribution of organisms in coastal lagoons with confinement gradients (Pérez-Ruzafa and Marcos, 1993; Mariani, 2001, Garnerot *et al.*, 2004; Pérez-Ruzafa *et al.*, 2004, 2007a; Benhissoune *et al.*, 2005; Chaouti and Bayed, 2005; Bouchereau *et al.*, 2008).

However, Barnes (1989) questioned the existence of a specific brackish water fauna considering that lagoon assemblages are composed of marine species that are favored by lagoon environmental conditions, and rejected the applicability of the concept of confinement in north-east Atlantic macrotidal coastal lagoons (Barnes, 1994) in light of the species distribution observed inside them and the lack of zonation gradients in large enclosed lagoons. This agrees with the observations of Benedetti-Cecchi *et al.* (2001) and De Biassi *et al.* (2003) for the Orbetello lagoon. In fact, neither confinement nor salinity is the sole factor determining the distribution of lagoon organisms. Ionic composition (limnogenic vs. thalassogenic; Ca/Mg ratio), the nature of the substrate, wave exposure, food availability, temperature, oxygen concentration or depth also play an important role (Margalef, 1969; Arndt, 1989), which frequently overlaps and even neutralizes the effect of confinement. There are numerous exceptions to the distribution of species into the six zones proposed by Guelorget and Perthuisot (1983) in their theory. Barnes (1994) cites several examples, including *Hydrobia ulvae*, *Scrobicularia plana*, *Macoma balthica*, *Nereis diversicolor*, *Corophium volutator*, among others, all of which are typically estuarine, and some of them considered typical from Zone IV (a zone from which marine elements are absent according to Guelorget and Perthuisot, 1983), but which can also live in marine habitats wherever shallow-water soft sediments occur.

That is also the case of *Ruppia cirrhosa*, a species also considered characteristic of Zone IV, but which, in the Mar Menor lagoon, appears in shallow muddy areas with low hydrodynamics near the entrance of the inlets and under the direct influence of the sea (Zone I). Probably, the limiting factor here is not so much confinement as wave exposure and depth and, perhaps, sediment granulometry (Pérez-Ruzafa and Marcos, 1993). On the other hand, *Paracentrotus lividus*, a sea urchin considered by Guelorget and Perthuisot (1983) to be exclusive to Zones I and II (regions near the mouths in which coastal marine species dominate), can be found as large stable populations in the inner parts of Urbino lagoon in Corsica, where the nature of the substrata is the main factor determining their abundance (Fernández *et al*., 2002). Twenty years ago, Pérez-Ruzafa and Marcos (1992, 1993) already suggested that lagoon species might respond to multifactorial influences, in which confinement would be among the most relevant but sharing its influence with many other factors. Furthermore, these authors suggested that, rather than the recycling of vitamins and oligo-elements, the main factor explaining the structure of lagoon assemblages along a confinement gradient would be the rates of colonization by marine species. The species composition of each lagoon site will be the result of equilibrium, in the context of interspecific competition, between marine and lagoon species, taking into account that low competition coefficients of allochthonous species may be compensated by high immigration rates from outer habitats (Fenchel, 1975; Levinton, 1982).

In fact, coastal lagoons, and in general brackish, paralic or transitional aquatic coastal ecosystems, are inhabited by a wide variety of species with different habitat uses or biological strategies. McLusky (1981) considered five categories in the fish fauna of an estuary: oligohaline, true estuarine, euryhaline marine, stenohaline marine and migratory. He recognized that marine components are the dominant contributors to the diversity of estuarine species, while true estuarine and migratory components contribute with fewer species. Barnes (1994) differentiated three main components in the fauna of north-west European lagoonal environments: specific lagoonal species of marine ancestry, lagoonal species of freshwater ancestry, some of them also occurring in freshwater habitats, and species that also characterize adjacent marine and esturarine habitats. More recently, Franco *et al*. (2008), following Elliot and Dewailly (1995) and Elliot *et al*. (2007) proposed six functional guilds for fish assemblages: estuarine, marine migrant, marine stragglers, fresh water, anadromous and catadromous.

In the confinement model based on colonization rates (figure 3), allochthonous species can be classified in three classes (Pérez-Ruzafa and Marcos, 1992; Gamito *et al*., 2005): 1) Occasional visitors (marine stragglers): species which colonize the lagoon but cannot survive in lagoon conditions. These species are rare and often limited to the mouth of the inlets, and so have little influence on lagoon assemblages. 2) Species that colonize more or less regularly the lagoon and can survive as juveniles or adults, but are unable to reproduce in the lagoon environment. These include the typical marine migrants. This group is composed of many fish that help support important fisheries, and is a characteristic component of lagoon assemblages that is shared by most lagoons and estuaries over a wide geographical range (Pérez-Ruzafa *et al*., 2007a, 2011). 3) Species which colonize the lagoon (generally after some modification in inlet morphology leading to a change in the hydrographic conditions) and which are able to reproduce in the lagoon environment under the new conditions. These species will establish themselves in the lagoon

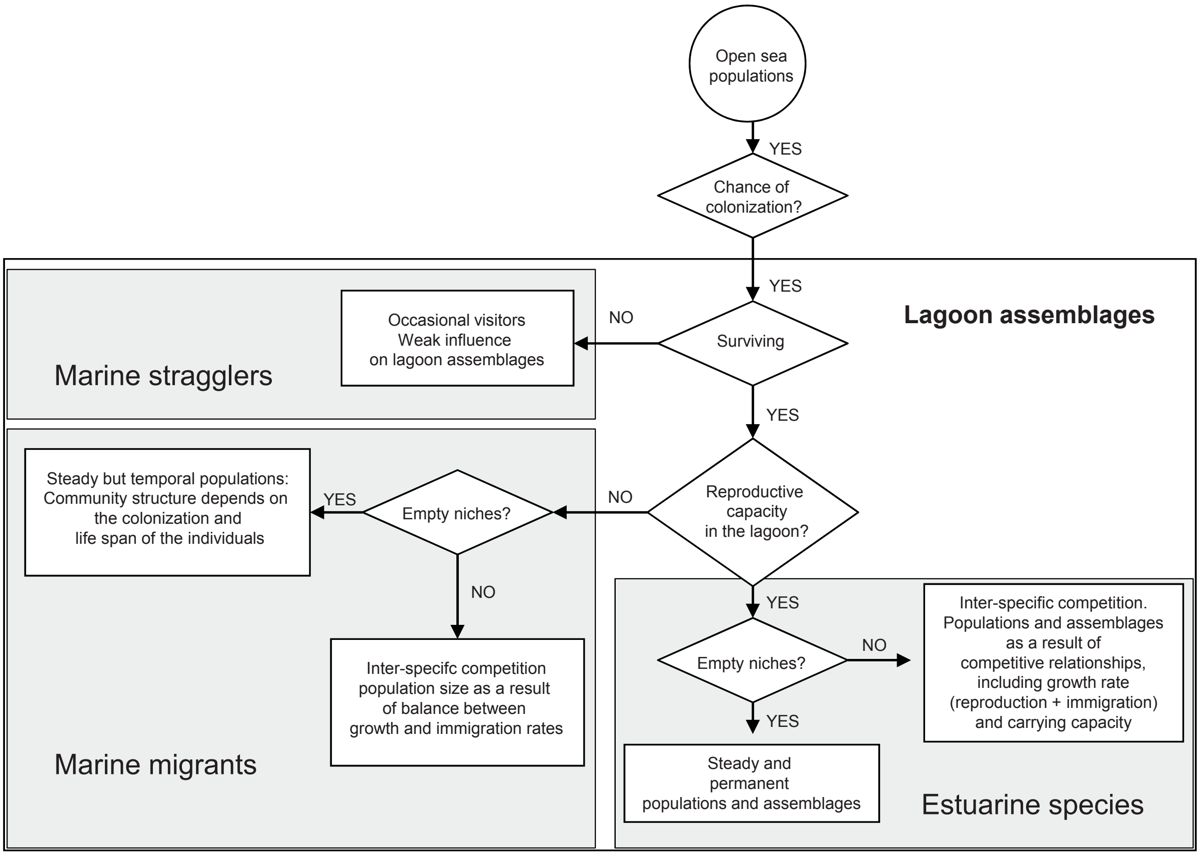


Figure 3. Conceptual model of the influence of marine species on lagoon assemblage structure and composition. Modified from the confinement model based on colonization rates in Pérez-Ruzafa and Marcos (1992).

ecosystems, where their permanence and relative abundance will depend on the results of competition with already established species which are adapted to the variability of the lagoon environment (paralic species). The gradients associated with confinement tend to be temporary and may disappear after several years, when individuals of these species reach the inner areas of the lagoon.

This model has an important stochastic component and introduces a degree of randomness in the configuration of the lagoon assemblages. As Cognetti and Maltagliati (2000) say, although euryhaline species predominate in these environments, it is not uncommon, depending on the various biotopes, to find typically stenohaline species. The specificity of the brackish biocoenosis should be addressed not so as much at species level as at population level. Both, random and periodical colonizers, in the context of the conceptual model of figure 3, would be subject to selective pressures by lagoon variability and extreme conditions, especially when colonization takes place during larval phases or as juveniles, leading to the development of populations adapted to these environments. Natural selection would act preserving specific alleles that could be rare in the marine environment but that become more frequent in the lagoon populations of a species. The randomness of the colonization process is consistent with the fact that, of the 179 fish species inventoried in Atlanto-Mediterranean coastal lagoons, only 98 were shared by at least 2 lagoons, and 121 species were present in less than 15 % of the cases studied (Pérez-Ruzafa *et al*., 2007a). In the same way, of the 944 taxonomic units of macroinvertebrate taxa recorded by Basset *et al*. (2006), 75% were observed in less than three of the twenty-six lagoons considered, and of the 621 species of macrophytes present in estuarine and lagoon waters, only 45 species (7.3% of the total) were shared by more than 10 lagoons (Pérez-Ruzafa *et al*., 2011). Using this colonization model to explain lagoon assemblage composition and structure also means that any confinement gradient in species richness would mainly be evident in groups with swimming behavior but limited competitiveness or with moderate dispersal as eggs or in larval phases. It also agrees with the fact that completely closed lagoons, as stated by Barnes (1994), do not show clear horizontal patterns associated to confinement. According to this, lagoon macrophyte assemblages, for example, would not follow clear gradients. This agrees with the work in the Orbetello lagoon performed by Benedetti-Cecchi *et al*. (2001), who underlined the absence of any gradient from the sea in the macroalgae recolonizing the hard substrata. Pérez-Ruzafa *et al*. (2008) also found that macrophyte species richness and diversity were highest in the most confined localities and, in each locality, in the infralittoral rocky assemblage compared with midlittoral assemblage. They suggested that the substratum type and environmental stability are probably more important in structuring algal assemblages than colonization rates and dispersal linked to confinement. At the same time, the depth, which is associated with vertical gradients of light radiation, hydrodynamics and also environmental stability, determines a vertical zonation that overlaps, on a smaller spatial scale, the horizontal patterns determined by the above mentioned variables.

Are coastal lagoons bottom-up controlled and sensitive to eutrophication?

Brackish water biotopes are usually considered to be naturally stressed and physically regulated systems because of their highly variable physico-chemical elements, including salinity, temperature and nutrients (Elliott and Quintino, 2007). Furthermore, the intense relation of coastal lagoon ecosystems with the terrestrial boundary, the long residence time of the water mass and the prevailing sedimentation, make these environments especially vulnerable to terrestrial and freshwater inputs and human impact, and more specifically, to eutrophication (Nienhuis, 1992).

It is assumed that typical estuarine species are tolerant of such stress. As in anthropogenically stressed communities and in the early successional stages of an ecosystem (Odum, 1969; 1985), estuarine benthic infaunal communities are expected to be characterized by small organisms, the high abundance of few species, low diversity, *r*-strategists and the replacement of *K*-strategists, accompanied by organisms of low individual biomass which have the potential to produce a high biomass. This implies that the community will have a high turnover and biological productivity as reflected in a high production to average biomass ratio (P/B) (Margalef, 1969; Elliott and Quintino, 2007). In these transitional waters bodies, which naturally receive large nutrient inputs which are retained, the vegetation also includes large concentrations of ephemeral green filamentous algae such as *Chaetomorpha linum* (O.F. Müller) Kützing, *Cladophora dalmatica* Kützing, *Cladophora vagabunda* (Linnaeus) Hoek, *Ceramium diaphanum* (Lightfoot) Roth, or thin tubular and sheet like (foliose) as *Ulva compressa* Linnaeus, *U. intestinalis* Linnaeus, *U. prolifera* O.F. Müller or

U. rigida C. Agardh, etc. (Wilkinson *et al*., 1995; Pérez-Ruzafa *et al*. 2011). These kinds of community are tolerant to adverse environmental conditions and, since estuarine benthic communities have many of the characteristics of areas suffering from human-induced stress, it is difficult to detect the effects of human activities leading to the so called 'Estuarine Quality Paradox' (Dauvin, 2007; Elliot and Quintino, 2007; Dauvin and Ruellet, 2009).

Species of these physically controlled communities must adapt their behaviour and physiology to a broad spectrum of physical fluctuations and so, in this kind of ecosystem, interspecies relationships do not develop to any great extent and are not expected to play a decisive role (Sanders, 1968).

Coastal lagoons and esturaries are considered particularly susceptible to the effects of nutrient over-enrichment (European Environment Agency, 1999; Taylor *et al*., 1999; NRC, 2000). As a result of the relatively low freshwater runoff into coastal lagoons, nutrient inputs into these systems are probably lower than those of river mouths (Nixon 1982). Nevertheless, nutrient loading estimates indicate that the levels of enrichment of lagoons can be as great as for bays and estuaries, reaching up to 7 and 12 mmol m^{-2} d^{-1} of dissolved inorganic nitrogen (DIN) (Taylor *et al*., 1999).

Eutrophication is a process, not a trophic state, involving an increase in the rate of supply of organic matter to an ecosystem (Likens, 1972; Nixon, 1995; Gamito *et al*., 2005). The process is mainly identified with an increase in the input of inorganic nutrients, which enhance primary production of the ecosystem (European Environment Agency, 2001). This leads to the progressive replacement of seagrasses and slow-growing macroalgae by fast-growing macroalgae and phytoplankton, with the final dominance of the latter at high nutrient loads (Gamito *et al*., 2005). In coastal lagoons this process has been widely described (Reyes and Merino, 1991; Boynton *et al*., 1996; Taylor *et al*., 1999, Newton *et al*., 2003; Solidoro *et al*., 2010) and modelled (Giusti *et al*., 2010). When eutrophication is chronic, the effects include anaerobiosis, toxic algal blooms, the massive killing of benthic and epibenthic animals and changes in species patterns, and, once the negative effects of eutrophication emerge, the process is very difficult to stop. The subsequent delivery of nutrients from underwater sediments may prolong the process for many years (Nienhuis, 1992).

As a result of the relatively low freshwater runoff into some coastal lagoons, nutrient inputs into these systems are generally lower than those of estuaries but, despite the oligotrophy of the water column, they still maintain important fisheries supported by benthic production (Nixon 1982; Joyeux and Ward, 1998; Pérez-Ruzafa *et al*., 2005b). Systems like these coastal lagoons whose ecological structures make them productive despite low nutrient inputs are considered to be more adversely affected by nutrient enrichment than other more nutrient-replete estuarine systems (Boynton *et al*., 1996).

In fact, altered nutrient cycles have been recognised as one of the main causes of mass blooms of nuisance seaweeds, which seem to be particularly stimulated by nitrogen availability (Valiela *et al*., 1997; Taylor *et al*., 1999), leading in some coastal lagoons to frequent dystrophic crises (Amanieu *et al*., 1975; Boutiere *et al*., 1982; Reyes and Merino, 1991; Ferrari *et al*., 1993; Sfriso *et al*., 1995; Viaroli *et al*., 1996; Gianmarco *et al*., 1997; Guyoneaud *et al*., 1998; Bachelet *et al*., 2000; Sakka Hlaili *et al*., 2007; Specchiulli *et al*., 2009; Giusti *et al*., 2010). The occurrence of ephemeral seaweed and, to a lesser extent, of other primary producers, may cause a strong imbalance of the oxygen metabolism, since periods of high photoautotrophic activity coupled to labile organic matter accumulation are followed by predominantly heterotrophic phases, leading to large and pulsed oxygen variations, ranging from supersaturation to complete anoxia on both seasonal and diurnal time scales (D'Avanzo *et al.*, 1996; Viaroli *et al.*, 2001; Viaroli and Christian, 2003)

However, despite this assumed vulnerability, the structural properties of coastal lagoons also suggest that their responses to enrichment might be more complex than the responses of bays and estuaries (Taylor *et al.*, 1999) due to the fact that they tend to be smaller, shallower, and possess narrower connections with the adjacent sea (Kjerfve and Magill, 1989). They also exhibit closer coupling between the sediments and water column than bays or estuaries (Nixon, 1982). In addition to the phytoplankton that dominate primary production in many bays and estuaries (Oviatt *et al.*, 1986), lagoons also support complex assemblages of seagrasses and drift and epiphytic macroalgae (Taylor, 1983; Thorne-Miller *et al.*, 1983). In the Venice lagoon, nutrient excess is controlled by blooms of *Ulva*, which probably prevent the dominance of phytoplankton (Sfriso *et al.*, 1992). At the same time, in shallow coastal areas, grazing by herbivores can buffer moderate eutrophication effects (Havens *et al.*, 2001). In mesocosm experiments Taylor *et al.* (1999) showed that the efficiency of drawdown of added DIN was larger in lagoon mesocosms than in an open bay and, the increased standing stocks of phytoplankton after dissolved nitrogen enrichment were less regular in the lagoon than in the bay studied. Furthermore, in the lagoon mesocosms, an effect of enrichment on standing stocks of phytoplankton could be detected only at very high loadings.

Cloern (2001) also found fundamental differences in the system-level responses to nutrient enrichment in lakes compared to estuarine and coastal ecosystems, suggesting that the old models and assumptions on system response to nutrient inputs should be reviewed.

In aquatic ecosystems, there is expected to be a very close correlation between changes in the availability of P (the most limiting factor in freshwater) and some measures of change in the productivity or biomass of phytoplankton. This forms the basis of conceptual models and of possible nutrient management. However, such kinds of relationships are difficult to find in coastal marine waters, and nutrient input alone is considered a poor predictor of algal blooms (Cloern, 2001).

In agreement with this, Pérez-Ruzafa *et al.* (2002) showed that, in the Mar Menor lagoon, despite the changes in nutrient input that occurred between 1988 and 1997 and the increase in nitrate concentrations in the water column from lower than 1 μmol N l^{-1} throughout the year to concentrations of up to 8 μmol N l^{-1}, thus stimulating the growth of larger phytoplankton cells, no significant differences were found in the pelagic size-spectrum slope due to top-down control by two allochthonous jellyfish species (*Rhyzostoma pulmo* and *Cotylorhiza tuberculata*) which have colonized the lagoon during the last two decades. Regression models showed that chlorophyll *a* concentration maintained a negative relationship with nutrient concentration and a strong positive relation with ichthyoplankton abundance, suggesting that phytoplankton controls nutrient concentrations, while herbivores are controlled by fish larvae, reinforcing the evidence of top-down control of the trophic web (Pérez-Ruzafa *et al.*, 2005b) (figure 4). Furthermore, the variation observed in the relationship between fish larva density and chlorophyll *a* concentrations pointed to a well-defined seasonal dynamics with a limit cycle.

As stated by Scheffer (1998), the oscillations and spatial differences in the amplitude on this limit cycles can be biologically explained as being the result of overshoots due to a delayed response in the population density of

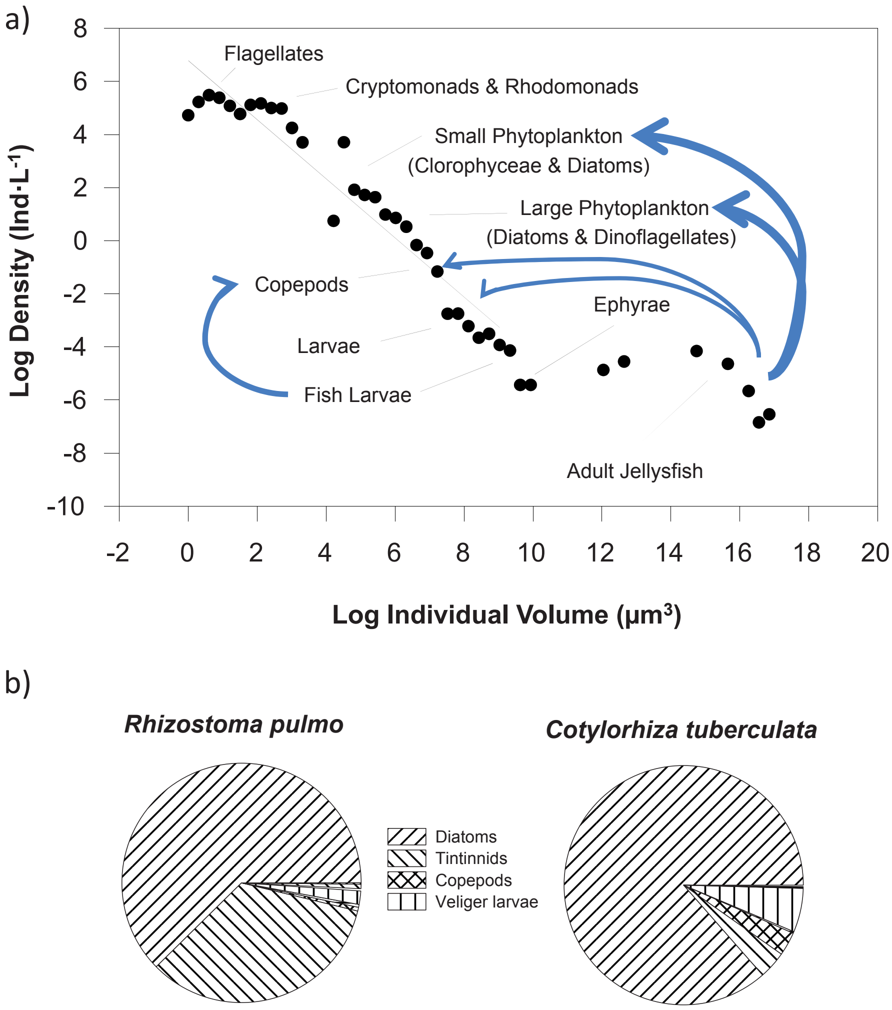


Figure 4. a) Example of pelagic biomass size-spectrum in the Mar Menor lagoon ranking from small flagellates (2 µm diameter) to adult jellyfish (up to 40 cm diameter), showing the top-down control exerted by jellyfish and icththyoplankton on the different compartments, according to Pérez-Ruzafa et al. (2002; 2005b). b) Main dietary components (%) in the gut contents of jellyfish *Rhizostoma pulmo* and *Cotylorhiza tuberculata* in the Mar Menor lagoon (from Pérez-Ruzafa et al., 2002).

herbivores to the amount of available food, or differences in the assemblage structure and life cycles, which would introduce homeorhetic controls (sensu Odum, 2000) and time lags in the responses of the successive trophic levels. Homeorhesis at community and ecosystem level is a laxer regulatory mechanism than homeostasis at individual level, acting by alternating positive and negative feedbacks with more pulsing and chaotic behaviour, leading to pulsing balances rather than equilibriums or steady states (Odum and Barret, 2006). The temporal stability in regulatory mechanisms would be provided by seasonal gaps in the reproduction of the different estuarine species (Pérez-Ruzafa *et al.*, 2004) (figure 5) and in the migration of marine species and in plankton-benthos coupling. Top-down control of phytoplankton by bivalve filter feeders has been described in different coastal bays and embayments (Newell *et al.*, 2007;

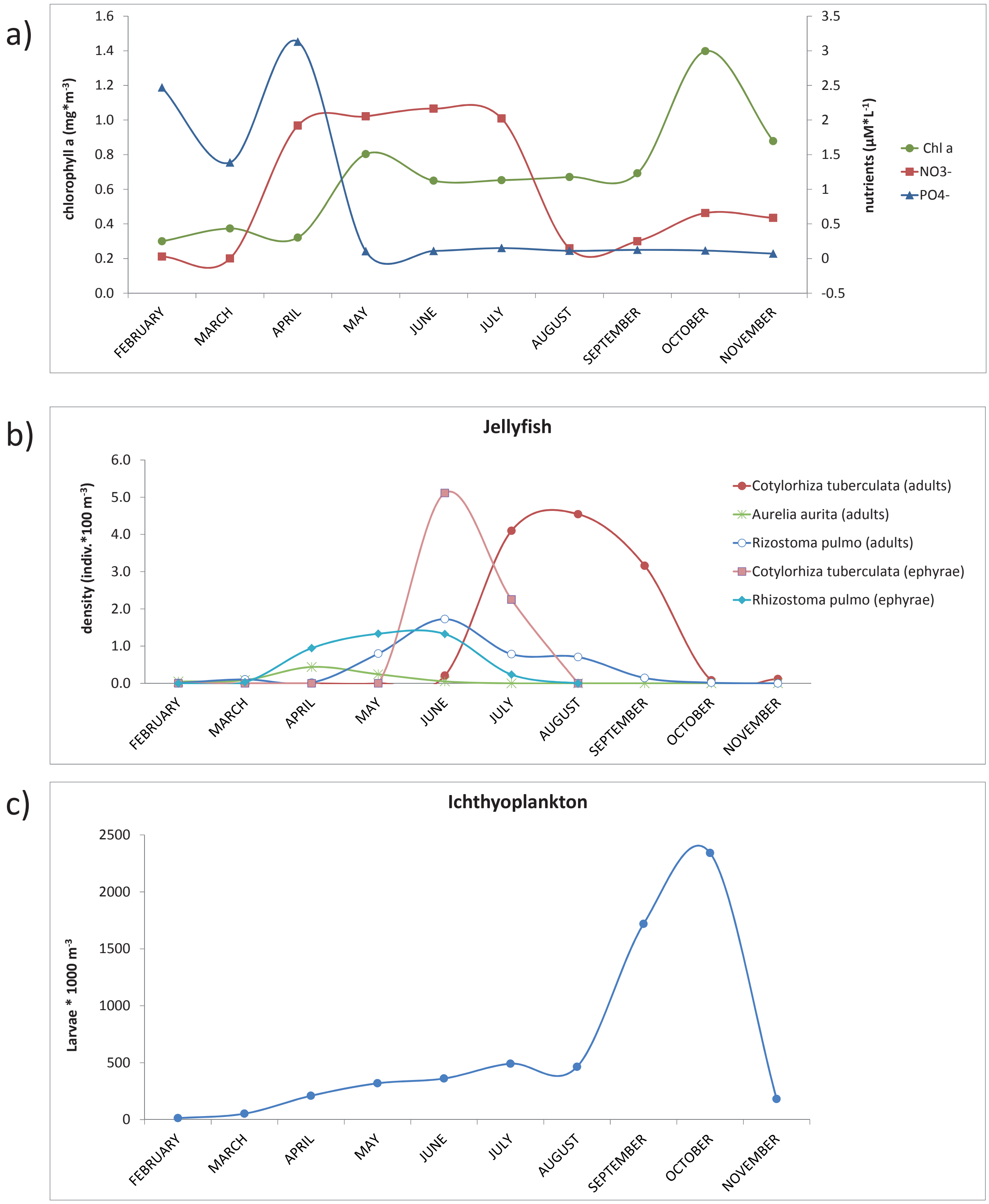


Figure 5. Monthly variation in a) nutrients (NO3- and PO4-) and chlorophyll a concentration; b) jellyfish density (including ephyra and adult phases of Rhizostoma pulmo and Cotylorhiza tuberculata, and adults of Aurelia aurita) and c) ichthyoplankton density.

Lonsdale *et al*., 2009) and is now considered the primary mechanism in controlling coastal benthic ecosystem structure and function (Heck and Valentine, 2007).

Therefore, the problem of coastal eutrophication must involve the consideration of several processes and factors, and, probably, different time scales for responses throughout the trophic web, which would constitute a filter or homeorhetic mechanism, modulating the response to the signal of change in nutrient loading in estuarine and coastal marine ecosystems (Cloern, 2001).

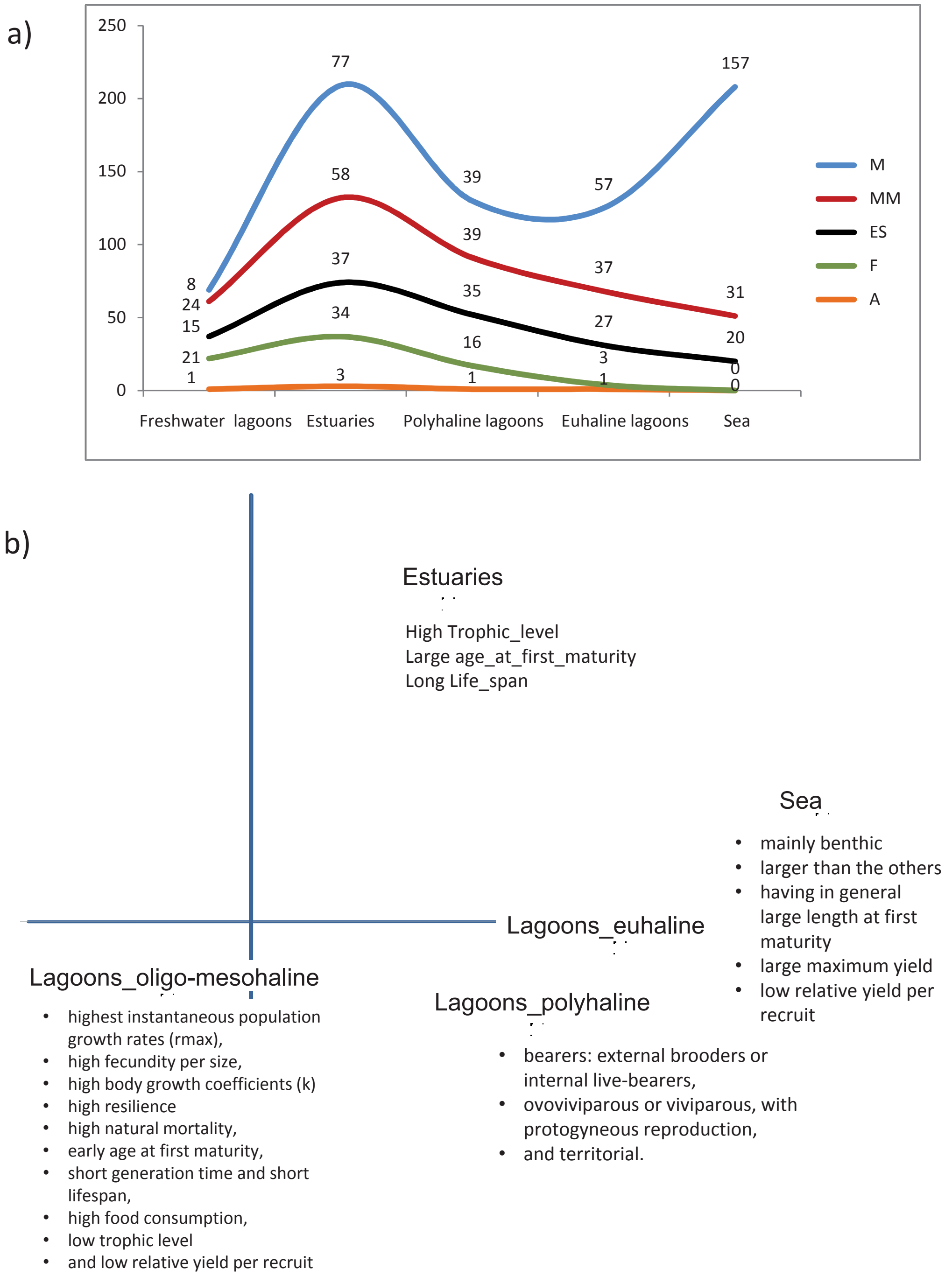
Are *r* strategists the main inhabitants of lagoon ecosystems, while *K* strategists are marine migrant species which exploit the lagoon resources temporarily?

Species respond to variability in environmental conditions through a wide spectrum in life-history traits. At the extremes of the gradient we can find two main types of strategy, *r* vs. *K* (Pianka, 1970; Margalef, 1974; Heip 1995; Gamito *et al*., 2005). The *r*-strategy species are characterized by high reproductive effort through early reproduction, small and numerous offspring with a large dispersive capability, short life-span and small body size of adults. These characteristics provide a selective advantage in unpredictable environments. At the other extreme, stable and predictable environments are dominated by *K*-strategy species, which are usually larger, long living, less abundant and show higher biomass/production ratios, spending more energy on homeostatic mechanisms and offspring care than on fecundity.

Although life history data are not always easy to interpret and do not clearly fit either deterministic or stochastic prediction models for *r*- and *K*- selection (Stearns, 1977), it is traditionally assumed that coastal lagoon environments are selective towards euryhaline and opportunistic, stress-tolerant species (*r*-strategy species) (Margalef, 1969; Lardicci *et al*., 1997; Gamito *et al*., 2005; Munari *et al*., 2009; Ponti *et al*., 2011), which would be the only ones able to reproduce in these habitats. Furthermore, lagoon habitats are used as a refuge, nursery area and feeding grounds by many marine migrant species which exploit the surplus production of coastal lagoons (Margalef, 1969; Yáñez-Arancibia and Nugent, 1977). It is also assumed that a transient physiological capability to cope with the lagoon conditions will give immigrants (*K*-strategists mostly) a competitive advantage over the *r*-strategists, at least for a limited time (UNESCO, 1981).

However, when analyzing biological strategies of fish species in coastal lagoons, these assumptions do not stand (Perez-Ruzafa *et al*., in press). The biological traits of the species inhabiting coastal lagoons and estuaries are diverse and cover a wide range of possibilities in the *r*/*K*- selection gradient. However, there are, in fact, significant differences between oligohaline lagoons and estuaries, which are dominated by *r*-strategists in the range of studied species, and polyhaline and euhaline coastal lagoons, which share the *K*-strategist part of the gradient with the sea assemblages. This differentiation is related, in part, to the relative abundance of functional guilds in each ecosystem type (figure 6a): oligohaline lagoons and estuaries have an important component of fresh water species at the expense of the marine origin species which predominate in poly- and euhaline lagoons.

On average, fish assemblages inhabiting freshwater lagoons tend to show the highest instantaneous population growth rates (r_{max}), high fecundity per size, high body growth coefficients, and therefore, high resilience, high natural mortality, early age at first maturity, short generation time and short lifespan, high food consumption, low trophic level and low relative yield per recruit (figure 6b). On the other hand, assemblages inhabiting polyhaline and euhaline coastal lagoons tend to be characterized by being bearers:



Estuaries

High Trophic_level
Large age_at_first_maturity
Long Life_span

Sea

- mainly benthic
- larger than the others
- having in general large length at first maturity
- large maximum yield
- low relative yield per recruit

Lagoons_euhaline

Lagoons_oligo-mesohaline

- highest instantaneous population growth rates (rmax),
- high fecundity per size,
- high body growth coefficients (k)
- high resilience
- high natural mortality,
- early age at first maturity,
- short generation time and short lifespan,
- high food consumption,
- low trophic level
- and low relative yield per recruit

Lagoons_polyhaline

- bearers: external brooders or internal live-bearers,
- ovoviviparous or viviparous, with protogyneous reproduction,
- and territorial.

Figure 6. a) Biological guild composition of fish assemblages in estuaries, coastal lagoons (oligo-, poly- and euhaline) and marine shallow coastal habitats in the Atlanto-Mediterranean region. Figures represent the number of species of each category and lines the cumulative number of species. M: marine species, MM: marine migrants, ES: estuarine especies, F: fresh water species, A: anadromous species (data from Pérez-Ruzafa et al, 2011b dataset). b) Mean characteristics of the fish assemblages inhabiting coastal lagoons, estuaries and shallow coastal sea according to the plot of the results of the non-metric multi-dimensional scaling (MDS) performed by Pérez-Ruzafa et al. (2011b) on the biological traits of the species inhabiting each type of ecosystem.

external brooders (as *Symphodus* spp, gobiids and blennies) or internal live-bearers (as syngnathids), ovoviviparous or viviparous, with protogyneous reproduction and territorial behaviour.

Species shared by euhaline lagoons and marine environments are mainly benthic, show great length at first maturity, a large length of maximum yield and low relative yield per recruit. They are also characterized by being larger than species characteristic of estuaries and oligohaline lagoons.

Typical estuarine and lagoon residents which make up the estuarine guild show a wider spectrum of responses in the *r*/*K*-selection gradient and greater heterogeneity in their ecological strategies to cope with the environmental heterogeneity and fluctuations characteristic of transitional environments. In general, few species can be identified as mainly *r*- or *K*-strategists and the majority are not completely *r*-selected or *K*-selected (Pérez-Ruzafa *et al.*, in press). On the one hand, estuarine species, compared with freshwater, marine or marine migrant species, show some traits characteristic of *r*-strategists, including higher values of body growth rate, higher natural mortality, higher r_{max}, higher resilience, higher food consumption, smaller size, early age at first maturity, smaller size at maturity, shorter generation time, and smaller length of maximum yield. On the other hand, they also contain many species which are external brooders or internal live-bearers, and most of the species have benthic eggs or are brooders with ovoviviparous or viviparous development. Estuarine species also show a lower mean reproductive effort (fecundity/size). All these features are characteristics of *K*-strategies.

Furthermore, estuarine fish reach the age of first maturity before the other species inhabiting brackish waters, but they also show the highest growth rates. The result is that they also show a larger average size for life spans than fresh water, marine or marine migrant species, giving them an advantage as regards reproductive effort. That is, estuarine fish take advantage of productivity and environmental lagoon conditions to grow quickly, to reach the age of first maturity early, to have the largest possible lifespan and maximum fecundity, at the same time optimizing their reproductive effort (low fecundity/size) by investing energy in the parental care of eggs, including egg brooding. In contrast, marine migrants probably constitute the guild located at the *r*-extreme of the gradient characterized by non-guarder species, most of them with pelagic eggs and larvae and high reproductive effort (high fecundity per size). Furthermore, marine migrants and freshwater species show the shorter lifespan for age at maturity. This slightly changes the scheme proposed by UNESCO (1981). They are not marine migrants but estuarine species that adopt *K*-strategies to cope with environmental constrains to reproduction (Pérez-Ruzafa *et al.*, in press). Marine migrants take transient advantage of the trophic opportunities offered by lagoon environments. Stenohaline species, which are typical of marine or freshwater habitats, can appear in coastal lagoons as migrants or stragglers. Lagoon environments shape and conform locally adapted populations, which gives rise to euryhaline populations that reach their maximum development in an optimal site (Cognetti and Maltagliati, 2000). As mentioned above, the stochastic nature of this process would explain the low frequency of occurrence of most of the species inhabiting these environments. Lagoonal selection would not necessarily act on all the biological traits of a species but only on some of them, improving the adaptation of local populations to the lagoon environment but breaking the coherence of all biological traits in an *r*/*K* context. This would explain why, in estuarine and lagoon ecosystems, species showing traits apparently corresponding to opposite strategies (like *Gambusia affinis* Baird et Girard, 1853), a viviparous species with very high population growth rate (r_{max}=11.72) or, at the other extreme, Acipenser species which are egg scatterers with a very low population growth rate (r_{max}=0.17-0.33) (Pérez-Ruzafa *et al.*, in press). The main conclusion reached by Pérez-Ruzafa *et al.* (in press) is that, besides the selective role of coastal lagoon environments on local populations, adaptation to variable and heterogeneous environments is not only a matter of species but of assemblages and communities. Probably partly as a result of the selective pressure of lagoon environments, species enjoy a wide range of possibilities in a continuum and the trade-off between biological traits is not always clear. It is at assemblage level that the heterogeneity in biological strategies and traits shown by each species allows them to cope with environmental stress and to develop homeostatic mechanisms. And it is mainly at this level that we can affirm that estuarine and coastal lagoon assemblages are far from being physically controlled but are biologically adapted sensu Sanders (1968). As Pérez-Ruzafa *et al.* (in press) pointed out, future research could be focused on the questions raised by Pianka (1980) on the cause-effect relationships between guild structure and community diversity and the consequences for ecosystem stability. Answering these questions would contribute to our understanding of the homeostatic mechanisms with which coastal lagoons and estuarine communities confront environmental fluctuations and the stress inherent in these ecosystems and, by extension, the impact of human activity.

Final remarks

Coastal lagoons are extremely dynamic, heterogeneous and complex ecosystems at the boundary between land and sea domains. For their species composition and ecological features they are transitional ecosystems between transitional and marine waters. Similarly to trade, culture or history, life and evolutionary processes are built at borders and are particularly active at transition points. Because of this, coastal lagoons are excellent laboratories, with spatially defined boundary conditions, for studying and validating models on a multiplicity of biological and ecological processes related to the organization of communities, their productivity, the impact of human activities or climate change on ecosystems, the processes involved in species adaptations (genetic drift and phenotypic expression), the development of homeostatic mechanisms in individuals, species and, in general, complex systems, to mention only a few. However, most interesting questions are difficult to answer if only a single ecosystem is put under the microscope. There is no doubt that many of the past or present assumptions about the ecology of coastal lagoons are inevitably influenced by the experience and knowledge of the scientists who propose them by reference to a limited number of lagoons with particular characteristics. Because of this, to answer the above questions or envisage new ones, it is essential to understand the whole range of ecological conditions that coastal lagoons offer. Hence, the importance of constituting networks of lagoon research and common data bases to boost future development and to improve our management and decision-making capabilities. The development of local observatories linked in networks, providing long term observations on hydrographic and biodiversity parameters from coastal lagoons and coastal ecosystems at local level that can be integrated to generate knowledge at Mediterranean basin and worldwide scale, is one of the challenges we face today. The present moment could be particularly favorable, exploiting the possibilities offered by laws, such as those of the Water Framework Directive, which requires regular monitoring of a set of biological and environmental parameters in the water bodies of Europe.

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