

## Guest introduction

# Mediterranean seagrasses

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## Seagrass ecosystems and Mediterranean seagrasses

Seagrass communities are considered one of the most productive and complex marine ecosystems; they have received increasing interest from marine scientists and ecologists over at least the last five decades. Seagrasses are a small group of 66 species (including Ruppiaceae and Zannichelliaceae) of marine flowering and rhizomatous plants classified in the monocotyledonous order Alismatidae, which has been able to form extensive meadows in all coastal systems worldwide except Antarctica (Green and Short 2003, den Hartog and Kuo 2006). They inhabit both sublittoral and mid-littoral environments, growing on sediments and rocky substrata, from coastal lagoons and estuaries to open oceanic waters. Their success in colonizing marine habitats is explained by a variety of physiological and morphological adaptations to life completely submerged in seawater and rooted in unstable and anoxic sediments (den Hartog 1977, Pettitt et al. 1980). In this sense, seagrass meadows represent distinct and unique plant-based marine ecosystems whose structure and dynamics give rise to ecosystem engineering functions (Duarte 2000a). Net primary production of seagrasses may be extremely high (300–1500 g C m<sup>-2</sup> year<sup>-1</sup>), making them among the most productive marine and terrestrial ecosystems (Margalef 1974, Duarte and Chiscano 1999). As in other well-known marine ecosystems based upon ecosystem engineers such as corals, kelps and mangroves, this high production drives multiple processes and functions of fundamental impact and relevance for the whole coastal ecosystem (Phillips and Durako 2000, Kenworthy et al. 2006):

- Primary and secondary production
- Food webs
- Structure (substratum and shelter for organisms)
- Biogeochemical processes and cycles
- Sediment accumulation and stabilisation
- Hydrodynamics and water quality.

Ecological goods and benefits provided by seagrasses in coastal environments have been repeatedly acknowledged by marine scientists and ecologists over the last century (Petersen and Boysen-Jensen 1911, Margalef 1974, McRoy and Helferich 1977; Rasmussen 1977) and have been extensively reviewed in an excellent research synthesis recently published (Larkum et al. 2006). They operate at a wide range of spatio-temporal scales (from daily cycles of photosynthetic O<sub>2</sub> production to C sinks at geological time scales) and some of them have been recognised as services of high socio-economical value for the community (e.g., nutrient cycling, Costanza et al. 1997). Seagrass functions are the basis of high species diversity due to the large number of organisms that use them as substratum, shelter, foraging, spawning or nurseries (Duarte 2000b, Williams and Heck 2001, Kenworthy et al. 2006). Many species inhabiting seagrass meadows are to some degree of great commercial importance and, hence, seagrass beds have a recognised role as fisheries habitats (Gillanders 2006). Further to these functions and services, an important fraction of the seagrass production is exported directly through currents or indirectly through animals (invertebrates, fishes and large herbivores), establishing links with other adjacent marine and terrestrial habitats over large spatial scales. The importance of seagrass functions and services is mirrored in the cumulative scientific evidence linking seagrass habitat losses with declines in habitat quality, disruption of coastal ecological processes and loss of biodiversity and fisheries (e.g., Valiela and Cole 2002). The increasing human development of coastal zones has accelerated seagrass losses during recent decades and it has largely driven the growing interest of marine ecologists in developing an understanding of seagrass functioning and the ecological consequences of an already acknowledged global seagrass ecosystem crisis (Orth et al. 2006, Waycott et al. 2009). Nowadays, seagrass conservation is one of the most important challenges for marine science and an increasing concern for coastal managers.

This concern has been particularly noteworthy in temperate areas, such as the Mediterranean Sea, where primary production of seagrasses and its associated algal assemblages (epiphytes and benthic algae) represents a major driving force of ecological processes in the coastal system. In tropical areas, this role is shared with two other major marine habitats of the coral system, coral reefs and mangrove communities, which have traditionally received more attention from scientists, managers and

public awareness (Orth et al. 2006). By contrast, in the Mediterranean Sea and other temperate warm and cold coastal systems, public awareness is mostly focused on seagrass communities since they represent the main component of the sublittoral marine environment of a wide range of singular coastal habitats (including estuaries and coastal lagoons) and, therefore, the most relevant ecosystem in terms of abundance and biological value. In the Mediterranean Sea, seagrass meadows are present throughout a 46,000 km coastline shared by 20 countries and 2 territories (Palestine and Montenegro) of Europe, Africa and Asia. Along this long coastline, seagrasses form a more or less continuous narrow band, directly in the path of the environmental pressures of a growing population of 70 million humans concentrated in coastal cities (which receive 175 million tourists every year; Benoit and Comeau 2005). As documented for a large number of seagrass communities worldwide (e.g., Short and Wyllie-Echeverria 1996), Mediterranean seagrasses have been susceptible to the drastic change in the marine environment caused by the rapid growth of this dense population, the rapid industrial development and the marked changes in land use experienced by the Mediterranean countries, especially on its northern side. Seagrass loss has been reported everywhere in the Mediterranean Sea where seagrass research has been intense (mainly Spain, France and Italy, see below) and it is mainly caused by the impact of human activities. The Mediterranean countries have experienced population growth since the 1950s, implying an increasing pressure from human activities, such as trawling, mining and agricultural wastes, urban and industrial sewage, coastal constructions, beach replenishment, aquaculture loads, etc. On geological time scales, seagrass meadows of the Mediterranean Sea have overcome dramatic episodes close to extinction [e.g., Messinian “salinity crisis” 6–5 million years (Ma) ago] and long-term climatic and eustatic fluctuations during Quaternary glaciations (Maldonado 1989, Pérès 1989). From this perspective it might seem unbelievable that human impacts represent a survival threat for Mediterranean seagrass meadows. However, human disturbances do not operate on evolutionary time scales. A human-induced perturbation on seagrass meadows, and subsequent habitat transformation, occurs at a rate that overcomes the capacity of the main seagrass ecosystem engineers to respond and adapt to a changing environment. This change has taken place in the last 50 years, a micro-instant in the evolutionary history of seagrasses that spans about 100 Ma (den Hartog 1970, Orth et al. 2006). As this response and adaptive capacity is species-specific, the threat of an extensive seagrass decline takes a particular dimension in the Mediterranean Sea, considering the extension of seagrass meadows constituted by a single species, *Posidonia oceanica* (Linnaeus) Delile (Procaccini et al. 2003). This species requires centuries to recover to its original state after a disturbance, due to its slow capacity to colonise denuded substrata. It is, probably, one of the slowest seagrass species in colonizing new substrata, in contrast to other species able to reach complete recovery in a few months or years (Duarte 1995, Duarte et al. 2006).

A total of six seagrass species are present in the warm temperate waters of this important biogeographic area: *Posidonia oceanica*, *Cymodocea nodosa* (Ucria) Ascherson, *Zostera noltii* Hornemann [= *Nanozostera noltii* (Hornemann) Tomlinson et Posluzni], *Zostera marina* Linnaeus and *Halophila stipulacea* (Forskål) Ascherson. The only endemic species is *P. oceanica*, while the others have a wider temperate distribution, except *H. stipulacea*, which is a Lessepsian migrant present since the late 19th century (Lipkin 1975). Detailed taxonomy and descriptions of the morphology, biology, ecology and actual distribution of these species can be found in Phillips and Meñez (1988), Green and Short (2003), Gobert et al. (2006) and Kuo and den Hartog (2006), as well as in Boudouresque et al. (2009; this issue, pp. 395–418). Their abundance and preferred environments depend on their respective biological characteristics and ecological requirements. *P. oceanica* is the largest and the most abundant species found on sandy and rocky substrata of oceanic waters between 0.5 and 40 m depth. Rough estimates of surface area colonised by this species in the whole Mediterranean Basin lie between 25,000 and 50,000 km<sup>2</sup> (Pasqualini et al. 1998, Boudouresque et al. 2006a, but see Boudouresque et al. 2009; this issue, pp. 395–418). *C. nodosa* is less abundant, but dense monospecific meadows of this species are common in shallow marine environments and coastal lagoons. It can also form shallow mixed meadows with *Z. noltii* (Marbà et al. 1996, Enríquez et al. 2004). In sites not colonised by *P. oceanica*, *C. nodosa* can extend down to more than 30 m depth. *Z. noltii* and *Z. marina* are much less abundant species restricted to very shallow and sheltered marine and lagoon environments characterised by extreme fluctuations in environmental conditions. In the Eastern Mediterranean Basin, the smaller *H. stipulacea* has spread over marine sediments of oceanic coastal environments down to 60 m depth (Lipkin et al. 2003). In the Mediterranean Sea, species of the genus *Ruppia* [i.e., *Ruppia cirrhosa* (Petagna) Grande and *R. maritima* Linnaeus] are often restricted to brackish lagoons and salt-marshes and, hence, they are not usually considered as true seagrass species. However, we believe that they deserve to be mentioned here since they can also occur in very shallow and sheltered environments of the inner parts of some semi-closed oceanic embayments, coexisting with some of the other seagrass species.

## Historical background

Early workers at the end of the 19th and first half of the 20th centuries reported the first descriptive studies of Mediterranean seagrass communities, providing first insights into their importance (e.g., Marion 1883). Research on seagrass ecology was launched between the 1950s and 1960s by scientists from US and European countries working on tropical (*Thalassia* spp.) and cold-temperate (*Zostera* spp.) species (see McRoy and Helfferich 1977 and references therein), but it was not until the 1970s that marine scientists started to study Mediterranean seagrass communities as complex ecological systems. It is important to realise that some work

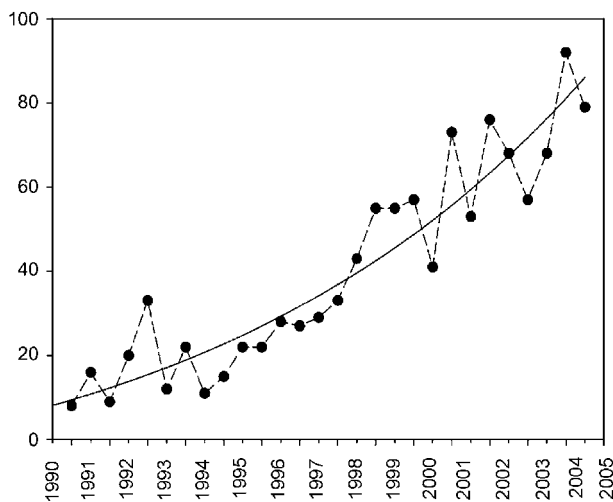
in the previous 20 years was also relevant (e.g., Molinier and Picard 1952, Aleem 1955, Augier 1955, Molinier and Zevaco 1962, Harmelin 1964). During the 1970s, descriptive studies predominated, although first contributions on important issues concerning seagrass ecological functions also appeared: growth and primary production (Molinier and Zevaco 1962, Ott 1979), vegetative structure and sexual reproduction (Giraud 1977a,b), epiphytic assemblages (van der Ben 1971), herbivory (Traer 1979), secondary metabolites (Cariello and Zanetti 1979a,b), photosynthesis (Drew 1978, Beer and Waiser 1979) and the interaction between seagrass meadows and sediment dynamics (Blanc 1974, Jeudy de Grissac 1975). Special mention is deserved by the classic review of Pérès and Picard (1975) *Causes of decrease and disappearance of Posidonia oceanica beds*, which showed for the first time the complex interactions between seagrass decline and disturbances of natural and/or human origin. Just at this time, the Mediterranean coast was undergoing a huge and irreversible transformational pathway due to the growth of urban populations (untreated urban wastes), the parallel development of industry (chemistry, mining), the industrialisation of agriculture and cattle farming (fertilisers, pesticides and organic wastes), overfishing, and the development of tourist infrastructures (marinas and artificial beaches). These circumstances motivated an increasing interest in the effects of human activities on the health of seagrass meadows and the potential losses of vitality and biomass (Maggi et al. 1977, Meinesz and Lefèvre 1978). First studies suggesting the use of *P. oceanica* and *Cymodocea nodosa* as pollution bioindicators (i.e., heavy metals and organic compounds) also date from this decade (Augier et al. 1977, 1979, Maggi et al. 1977, Eugene 1979), as well as the first attempts at seagrass transplants using *P. oceanica* (Cooper 1982). This increase in seagrass studies in the Mediterranean Sea coincided with the celebration of the First International Seagrass Symposium, held in Leiden, The Netherlands, in 1973, in which contributions were published in the first synthetic text on seagrass ecology (McRoy and Helfferich 1977); research done in different parts of the world, including the Western and Eastern Mediterranean Basins, was collated to provide an up-to-date presentation of the status of seagrass ecology.

Obviously, the emergence of Mediterranean seagrass science was not an independent and spontaneous event. From an historical perspective, this geographic area has been intimately linked to the development of modern marine biology (see Hofrichter 2004 for a detailed historical review). In the second half of the 19th century, numerous Marine Biology Centres were created in the Mediterranean, in part motivated by the publication of the *Origin of species* by Charles Darwin in 1859. Some of them persist today and they have played a crucial role in the course of marine biology, and hence in the further development of Mediterranean seagrass ecology. Clear examples are: the Stazione Zoologica Anton Dohrn of Naples, founded in 1872 by the German scientist Anton Felix Dohrn; the Marine Laboratory of Trieste, founded in 1875 by the Austrian zoologist Claus Carl from the University of Vienna; and the Laboratoire Arago of

Banyuls-sur-Mer, founded in 1882 by the French zoologist Henri de Lacaze-Duthiers. The Mediterranean Sea was home to the advent of the SCUBA-diving regulator (demand valve) developed in 1943 by Emile Gagnan and Jacques-Yves Cousteau; this was the technological prerequisite for the start of a new era not only in seagrass ecology, but also in many disciplines of marine biology and ecology worldwide. Nevertheless, the academic “seeds” of incipient Mediterranean seagrass ecology must be attributed to discrete, but very relevant works that took place both in Mediterranean and worldwide contexts:

1. Early works (late 1880s to the 1910s) of the Danish scientist C.G.J. Petersen dealing with *Zostera marina* in North Atlantic coasts, showing for the first time the importance of this plant for the marine ecosystem;
2. Numerous oceanographic expeditions realised in the first half of the 20th century, which contributed to the knowledge of the benthic marine flora and fauna and allowed the identification of Mediterranean biocoenoses, including seagrass communities (e.g., Dosil-Mancilla 2007);
3. The classic and seminal work of Roger Molinier and Jacques Picard (Molinier and Picard 1951, 1952) describing the dynamics and succession of Mediterranean seagrass communities from the pioneer stages to the final stage or climax, represented by the “*Posidonia oceanica* Association”;
4. The work of Cornelis den Hartog who published his famous book *Seagrasses of the world* (den Hartog 1970), which not only presented the first seagrass taxonomy but also stressed seagrass functional importance. This author encouraged the description and understanding of seagrass communities from multidisciplinary approaches combining “intensive site studies” with laboratory research (den Hartog 1977).

During the 1980s, two significant events stimulated descriptive and functional research on Mediterranean seagrass ecosystems and consolidated the initial efforts in the 1970s: the 1st and 2nd International Workshops on *Posidonia oceanica* Beds (1983, 1985), gathered by scientific institutions with a large tradition in marine biology and ecology in the Mediterranean Sea, the Groupeement d’Interêt Scientifique Posidonie (GIS Posidonie, Marseille, France) and the above-mentioned Stazione Zoologica di Napoli in Italy (Boudouresque et al. 1984, 1989). During this decade, more in-depth research was focused primarily on basic topics, such as (1) primary production (e.g., Bay 1984, Libes 1986, Romero 1989) and its fate [first studies using stable isotopes to disentangle seagrass food webs were done by Dauby (1989)]; (2) the uptake and long-distance transport of carbon (Libes and Boudouresque 1987); (3) biomass partitioning and meadow structure (e.g., Panayotidis et al. 1981); (4) structure and dynamics of the associated community (e.g., Romero Martinengo 1984, Ballesteros 1987); (5) biochemical and elemental composition of seagrass tissues (e.g., Pirc and Wollenweber 1988); (6) photosynthesis and nutrient physiology (e.g., Pirc 1986, Jiménez et al. 1987); (7) herbivory (e.g., Kirkman and Young 1981);



**Figure 1** Total number of publications each year on Mediterranean seagrass species (*Ruppia* included) in the period 1980–2007.

The search was conducted in three data bases: ASFA, ISI Web of Knowledge and Science Direct.

and (8) seagrass declines and the understanding of possible driving mechanisms (see Boudouresque et al. 1984, 1989, and the review by Mazzella et al. 1992 and references therein). However, despite this unprecedented research effort, scientific production remained in a modest steady state as only ca. 150 papers were published in this decade. It was necessary to wait until the second half of the 1990s to see a significant increment in the scientific production of seagrass research (Figure 1). In this decade, most of the topics mentioned above were pursued further (e.g., Pérez-Llorens et al. 1993, Pérez and Romero 1994, Pérez et al. 1994, Pergent et al. 1994, Alcoverro et al. 1995, Invers et al. 1995, Alcoverro et al. 1997a,b, Terrados et al. 1997a,b), but with occasional increases in comparative scope (i.e., descriptions of species-specific seasonal patterns in seagrass production, such as Marbà et al. 1996, Sfriso and Ghetti 1998; description of seasonal and age-dependent variability of leaf photosynthesis, Alcoverro et al. 1998; analyses of interspecific variability in biomass production, Duarte and Chiscano 1999, in herbivory, Cebrián et al. 1996a,b, Cebrián and Duarte 1998, and in biomass fate, Duarte and Cebrián 1996, Cebrián et al. 1997). Other important issues also emerged, such as the description of bacterial activity in the sediment (López et al. 1995, Danovaro 1996), detritus dynamics (including millenary organic deposits of *P. oceanica* which has been demonstrated to have an important role in biogeochemical cycles; Romero et al. 1994, Mateo and Romero 1996, 1997, Mateo et al. 1997), and the application of the demographic approach (Sarukan and Harper 1973, Sarukan 1978) for the study of community structure and dynamics of seagrass shoot population (see Duarte et al. 1994). This approach, which has been extensively developed for tropical trees but not yet fully developed for seagrasses, is an important contribution of this decade from a Mediterranean research group to worldwide seagrass ecology. Its utility is not limited to improving our knowledge of seagrass population

dynamics, but also to furthering use of seagrasses as tracers of coastal dynamics (e.g., Marbà et al. 1994a,b). Duarte and co-workers also provided in this decade the first allometric patterns for seagrasses (e.g., depth distribution, Duarte 1991a; tissue composition, Duarte 1990; form and productivity, Duarte 1991b; herbivory, Cebrián and Duarte 1998; and light absorption by leaves, Enriquez et al. 1992). This increasing scientific effort started in the 1980s led to an enormous impact on scientific and public awareness of the Mediterranean Sea, and of the importance of seagrass communities. The 1980s and 1990s served to define and consolidate many of the paradigms and challenges that have stimulated seagrass research in the following decades, but overall, for the first time in the 1980s, Mediterranean seagrasses were considered as prime target coastal ecosystems for conservation by coastal managers (see Foreword of the Second International Workshop on *Posidonia* Beds; Boudouresque 1989). One of the main interests of this increasing concern and scientific effort was the understanding of rapid seagrass losses induced by human impacts, particularly those concerning the endemic *Posidonia oceanica*, the most abundant and emblematic Mediterranean species. Thus, in France, these efforts resulted in the creation of the first “*Posidonia* Monitoring Network” in 1984 (Boudouresque et al. 1990, Nieri et al. 1993, Boudouresque et al. 2000) and *ad hoc* legislation to protect *P. oceanica* meadows in 1988 (Pergent 1991, Boudouresque et al. 1994). It was also during this decade that authorities started to implement protection policies to restrict the use of destructive fishing gears (trawling), which had caused extensive losses of *P. oceanica* meadows in the Western Mediterranean Basin (e.g., Ramos-Espla 1984, Ragonese et al. 1989). This can be considered as the embryo or start-point of an increasing effort to preserve Mediterranean seagrass ecosystems. In the course of the last 20 years, *P. oceanica* meadows and other seagrass species have been protected in several Mediterranean countries, the numbers of marine protected areas including seagrass meadows have considerably increased, and seagrass conservation is a priority target in international environmental directives both at the Mediterranean level (Action Plan for the Conservation of Marine Vegetation in the Mediterranean, UNEP-RAC/SPA 2000 – formerly the 1995 Barcelona Convention) and European level (1992 Habitat Directive, and 2000 Water Framework Directive, WFD 2000/60/CE; see below), and also in other more specific legislation concerning fisheries aimed at an ecosystem approach for resources exploitation (García et al. 2003).

## Present knowledge and motivation

Any conservation effort must be supported by a better understanding of the contribution of seagrasses to coastal ecosystems and the mechanisms that regulate their functioning, while providing the scientific basis and reliable tools to develop accurate management policies (Erftemeijer et al. 2006). In the last two decades, this scientific knowledge has been specifically requested by managers in order to implement the European Union (EU)

Habitat and Water Framework Directives. In the Council Directive of 1992 on the conservation of natural habitats and wild fauna and flora (known as the “Habitat Directive”), *Posidonia oceanica* beds are the only Mediterranean habitat specifically mentioned in Annex I (i.e., natural habitat types of community interest whose conservation require the designation of special areas of conservation). These Directives constitute the main basis for the implementation of the so-called “Natura 2000 areas”. In the later Water Framework Directive (WFD 2000/60/CE) established in 2000 for water protection and management, seagrasses are selected as one of the major groups of biological indicators for the evaluation of the ecological state and condition of coastal ecosystems in European countries. Marine scientists seemed to respond to this challenge, as shown in the spectacular increase in seagrass research on Mediterranean species during the last two decades (Figure 1). This growth has occurred at an annual mean rate (12.8 papers per year in the 1990s and 8.6 in the 2000s) that is very close to that reported for seagrass publications worldwide during the same period (Duarte 1999, Orth et al. 2006). Seagrass research on Mediterranean species represents, on average, about 40% of the total number of seagrass papers published annually in international journals, based on values of total scientific production in 1996 and 2006 reported in Duarte (1999) and Orth et al. (2006), respectively. Since world seagrass distribution has been classified in nine seagrass bioregions (Hemminga and Duarte 2000), these numbers indicate that the Mediterranean Sea is one of the “hot spots” of seagrass research in the world, together with other geographic areas where seagrass research has been particularly intense, such as the North Atlantic coasts of Europe, the USA and Australia (Duarte 1999). As discussed above, this development is in accordance with the importance of Mediterranean seagrass communities for the biodiversity of this particularly vulnerable bioregion, and the large tradition of marine biology in some Mediterranean countries. Many factors are responsible for this growing trend. More than 70 institutions are dedicated to marine biology, ecology and oceanography in the Mediterranean (Hofrichter 2004). Many of them have a group or department dedicated specifically to seagrass research. An increasing internationalisation of research groups and programmes has undoubtedly favoured this growing scientific production, which also contributed to the 4th International Seagrass Biology Workshop (Pergent et al. 2000, 2002) held in Corsica in 2000, and the Mediterranean Seagrass Workshop held in Malta in 2006 (Gambi et al. 2006).

Nevertheless, in accordance with the analysis made by Duarte in 1999 for global world seagrass research, scientific knowledge about the biology and ecology of Mediterranean species is still rather unbalanced and incomplete in many aspects. Geographically, most of scientific research done has been produced in a few countries within which 80% of marine biology research institutions are located (mainly Spain, France, Italy, Croatia and Greece). Information from a large part of the eastern Mediterranean Sea and North Africa is still very scarce or absent (Lipkin et al. 2003). Research has been concentrated on a single species, *Posidonia oceanica*

(87% of all published papers in the period 1980–2007), probably because conservation efforts are mainly focused on the most abundant species, which is also the main ecosystem engineer in the Mediterranean Sea. Most of the ecological paradigms and paradoxes attributed to this singular seagrass species have probably stimulated a large number of the studies produced by Mediterranean marine scientists (Boudouresque et al. 2006a). It is important to mention that there is a marked and worrying paucity of comparative studies between seagrass species. Experimental approaches are also limited, although increasingly used. Correlational studies predominate due to difficulties in performing experiments in the field or the difficulty in maintaining plants under laboratory conditions, particularly for the large species *P. oceanica*. Physiological experimental approaches either in the laboratory or “*in situ*” using submersible devices (i.e., light sensors and radiometers, diving PAM fluorometers, submersible respirometers, etc) need to be stimulated, as knowledge of basic information related to photosynthesis of Mediterranean species is far below the information available for other areas.

In contrast, studies on seagrass distribution, status and trends have considerably increased, although the information produced is still insufficient, unevenly distributed, highly fragmented or not available in scientific or end-user formats. Research efforts focused on different issues are also rather unequally distributed (Table 1), with descriptive studies on fauna at the level of both species and community the most abundant (253 published studies), followed by studies on contaminants (heavy metals and hydrocarbons) and human impacts. Analyses of anthropogenic effects sum to a total of 169 published studies. These data reflect two aspects that have motivated public awareness and scientific research since early times, viz., the great species diversity supported by seagrass communities and the ecological consequences of their loss through human impact. Other fundamental

**Table 1** Cumulative number of papers published between 1980 and 2007 for a number of identifiable selected issues on seagrass biology and ecology of Mediterranean species (including *Ruppia* spp.), which represent 80% of the total number of papers published on Mediterranean seagrasses in this period.

Issue	Number of papers (1980–2007)
1. Fauna	253
2. Contaminants (metals and Hydrocarbons)	87
3. Human impact	82
4. Habitat and taxonomy	81
5. Biogeochemistry and nutrients	80
6. Herbivory	71
7. Habitat conservation	50
8. Food web	47
9. Genetic	42
10. Primary production, growth and fates	35
11. Epiphytes	34
12. Sexual reproduction	27
13. Light and photosynthesis	23
14. Environmental factors (except light)	15
15. Transplanting	14
16. Population dynamics and demography	13

ecological processes and functions such as biogeochemistry, nutrient limitation, uptake and use efficiency, and herbivory have also received substantial attention (between 70 and 82 published papers). The microbiological approach, however, which analyses the activity of micro-organisms (Bacteria, Archaea, unicellular Eucaryota, Fungi, Labyrinthulomycota and Oomycota) involved in the biogeochemical cycles, is poorly developed, as are other relevant issues, such as food webs, population genetics, primary production (and its fate), epiphytes and sexual reproduction, where the number of published papers is also modest (25–50).

It is also important to recognise that the larger research effort invested in some topics has not resulted in a proportionately improved understanding of fundamental questions or paradigms. Thus, for example, a large number of studies on accumulation of metallic and organic pollution speculate on the potential of Mediterranean seagrass species as bioindicators of these sources of marine pollution. However, the mechanisms by which these pollutants operate and result in plant stress or injury at the subcellular, tissue or ecosystem level remain unclear (e.g., Schoendorf et al. 2001, Ferrat et al. 2002, Bucalossi et al. 2006). Studies analysing the nature and extent of human impacts on seagrass meadows are mainly descriptive and restricted to upper levels of seagrass organisation (meadow, shoots), but physiological responses to environmental stress are still poorly understood (e.g., Pérez et al. 2008).

Finally, the scarcity of studies (<25 published papers) on fundamental processes such as photosynthesis or the role of key environmental factors in controlling seagrass abundance and dynamics are issues of special concern. Little is known about photosynthetic regulation or photoacclimation plasticity and efficiency of the photosynthetic apparatus of Mediterranean species. Seagrasses are taxonomically closely related to terrestrial plants, but they are “adapted” (in the Darwinian sense) to highly diffuse light fields in the aquatic environment. Little is known about the intra- and interspecific variation in the capacity and efficiency of light absorption by Mediterranean seagrass leaves and canopies. General descriptions of light absorption at the 680 nm peak have already been reported (e.g., Enríquez et al. 1992, 1994, Olesen et al. 2002, Enríquez et al. 2004), but not a single light absorption spectrum and/or estimations of the specific absorption coefficient for the leaves of the Mediterranean species have yet been published. Similarly, little information is available on intra-specific variability (i.e., species plasticity) of leaves and/or canopies in the capacity and efficiency of light absorption and the associated variation in the photosynthetic rates at subsaturating and saturating irradiances, which determine species abilities to respond to variable light environments. Information about the variation in leaf photosynthetic light use efficiency supporting seagrass growth is also very limited.

There is speculation that light penetration is the main factor determining depth distribution of Mediterranean seagrasses, and hence depth limits are very sensitive to changes in light availability. However, the physiological bases of light limitation are not yet understood, as it requires the estimation of the minimum quantum require-

ments of photosynthesis ( $1/\Phi_{\max}$ ) and the minimum quantum requirements for growth (MQR; see Cayabyab and Enríquez 2007). Only two estimations of the minimum quantum requirements of photosynthesis,  $1/\Phi_{\max}$ , have been provided for seagrasses (see Cayabyab and Enríquez 2007) but neither of them in the Mediterranean Sea, although one of these estimations was reported for *Zostera marina*. The characterisation of MQR (not yet done for any species) requires empirical determinations of leaf photosynthetic rates, whole-plant respiration rates, and the description of the light fields within seagrass canopy. Little attention has been given in the Mediterranean Sea to the study of variation of the light fields within seagrass canopies, understanding of variation of whole-plant respiratory demands, and understanding of spatio- and age-dependent variability in leaf photosynthesis. Considering that the effects of other environmental parameters, such as water temperature, pH and hydrodynamics, on leaf photosynthesis are not yet fully understood (e.g., Invers et al. 1999) and that comparative studies are almost absent, we must admit that mechanistic understanding of the sensitivity or tolerance of Mediterranean seagrasses to shading (e.g., Ruíz and Romero 2001) is still a pending task. In the same manner, evaluation of the possible negative impact of invasive species on Mediterranean seagrasses, which is a growing concern, cannot be addressed by using only descriptive “*in situ*” observations. Understanding of physiological competition processes will help us predict seagrass responses and evaluate the effect of invasive species on seagrass ecosystems, which is currently impossible (see, e.g., Pergent et al. 2008).

During the last 30 years, significant advances have been made in the study of seagrasses in general and Mediterranean seagrass communities in particular. However, our understanding of the complexity of processes and mechanisms that affect seagrass growth and survival is far from acceptable, and remains at a low, predominantly descriptive level when compared to understanding of terrestrial plants (e.g., Lambers et al. 2006) or algae (e.g., Larkum et al. 2003). Although there is a growing concern requiring evaluation of anthropogenic impacts on seagrass ecosystems and the possible negative impact of invasive species on Mediterranean seagrasses, our capacity to predict seagrass responses to future scenarios where local or global environmental threats may strongly impact seagrass ecosystems is still very limited. Duarte (1999) strongly promoted a concept for progress from descriptive to synthetic stages through large-scale comparative analyses, and the need to develop general models. Undoubtedly, this kind of analysis is necessary, and the allometric comparative approach has produced interesting insights into key ecological traits of seagrass communities (e.g., productivity, herbivory or nutrient requirements). However, this comparative approach does not provide any knowledge of the mechanisms that regulate seagrass responses. More research efforts need to be invested in understanding the intrinsic mechanisms governing general processes in seagrasses. The mechanistic approach allows integration of system functions at all levels of biological organisation, from the biochemical processes to the leaf and whole-plant func-

tion. In this sense, multidisciplinary and experimental approaches incorporating scientific and technological advances achieved in other fields of plant science (i.e., biochemistry, spectroscopy, molecular biology, molecular genetics, physiology, growth analysis, productivity, modelling, remote sensing, etc.) are essential to progress knowledge of the biology and ecology of seagrasses.

### Presentation of this special issue

At this point, identification of the most important gaps and emergent challenges is essential for resolving specific questions in seagrass research, to shift to new paradigms and, in summary, to advance understanding of seagrass ecosystems. In this context, the contributions presented in this special issue of *Botanica Marina* are modest, but the interest of this selection was to give a general view of the current state-of-the-art in Mediterranean seagrass research. Our aim was also to substantially stimulate new scientific effort focussed on the relevant gaps and challenges identified. The traditional descriptive approach is still necessary, as natural variability of seagrass communities has not been yet fully documented, nor have the main factors that regulate this variability. Better knowledge of the ecological requirements of seagrass meadows and the recognition of natural patterns of variation in seagrass distribution, abundance and biomass dynamics will continue to be primary objectives in seagrass research. In this issue, Infantes et al. (pp. 419–427) present an interdisciplinary study to describe for the first time a quantitative relationship between wave energy and the upper depth limit of *Posidonia oceanica* meadows. Up to now, it has been widely assumed that the abundance of this Mediterranean seagrass at its upper depth limit is determined by exposure to wave action and the magnitude of its energy; however, no empirical quantitative evidence has been provided yet to support this assumption. The study of Infantes et al. provides new methodology to obtain testable estimates of the threshold level of tolerance of *P. oceanica* to wave energy, which represents a valuable predictive tool for identifying natural or anthropogenic impacts of temporal or permanent changes in the position of the upper meadow edge. It also allows identification of important changes in landscape configurations (i.e., meadow fragmentation). In fact, the distinction between human impacts and natural events in explaining the origin of spatio-temporal variability of seagrass meadows has been invoked as one of the major challenges in Mediterranean seagrass ecology (Erftemeijer et al. 2006). Similarly, the analysis of temporal and spatial variability of seagrass traits across different scales is another crucial issue in seagrass research (Bell et al. 2006). Recent studies have shown the importance of analysing spatial variability of different *P. oceanica* traits at multiple spatial scales (Balestri et al. 2003, Gobert et al. 2003, Pardi et al. 2006, Martínez-Grego et al. 2008) and to a lesser extent, this has been demonstrated for *Cymodocea nodosa* (Barberá et al. 2005). These studies offer advice on the possibility of masking or confounding additional variability associated with human distur-

bances. They also indicate the inadequacy of extrapolating observations from small spatial scales (seagrass patches or single locations) to larger ones (beds across regions or biogeographical regions). These types of descriptive studies are critical in assessing the range of natural variation in ecologically relevant seagrass attributes and gaining insight into the processes that govern this natural variation, as illustrated in the work of Mascaró et al. (with *C. nodosa* meadows) (this issue, pp. 429–438), who studied different meadows across a significant distributional range from the Western Mediterranean to the Eastern Atlantic coast.

The review of Vizzini (this issue, pp. 383–393) is a synthesis of the present knowledge of trophic ecology of Mediterranean seagrass communities, a topic that has received special attention since early times (e.g., Ott and Maurer 1977), but that has experienced substantial progress in the last decades due to the use of stable isotope techniques available since the end of the 1980s (e.g., Fry et al. 1987, Dauby 1989). Accumulated evidence supports the paradigm that most of seagrass primary production is channeled through the detritic pathway (e.g., Pergent et al. 1994), while direct consumption by herbivores has been considered a marginal process (Thayer et al. 1984, Cebrián and Duarte 1998). Indirect estimates of seagrass consumption by the main macrograzer species of *Posidonia oceanica* meadows [i.e., the purple sea-urchin *Paracentrotus lividus* (Lamarck) and the spard fish *Sarpa salpa* (Linnaeus, 1758)] had supported this contention in *P. oceanica* meadows (Cebrián et al. 1996a), in which herbivores were estimated to consume only 2% of the annual leaf production. These authors concluded that seagrass productivity exerts a bottom-up control in the ecosystem and is regulated by limiting factors, such as light and nutrients. As formulated for terrestrial counterparts (White 1993, Baraza et al. 2007), the low herbivory rates observed in seagrass communities are attributed to the apparent paucity of seagrass herbivores and the limited quality of seagrass leaves as food sources: high C/N ratios, structural carbon and secondary metabolites (Zapata and McMillan 1979, Duarte 1990, Agostini et al. 1998). However, during the last two decades, direct estimates of macrograzer consumption have provided increasing evidence that overgrazing on seagrass communities is more frequent than previously thought (Heck and Valentine 2006, Valentine and Duffy 2006) and it has questioned the validity of this established paradigm, even for the Mediterranean Sea (Tomas et al. 2005a, Prado et al. 2007). Seagrass-herbivore-interaction depends not only upon food quality of seagrass leaves, but also on the “quality” of the biomass of the epiphytic community associated with seagrass leaves, the growth and dynamics of the seagrass community, and species-specific herbivory patterns and feeding efficiencies. Epiphytes on *P. oceanica* leaves are significant contributors to the primary production of seagrass meadows (Mazzella et al. 1992). There is solid evidence for the key role of these epiphytes in the feeding behaviour of Mediterranean macrograzers (Lepoint et al. 2000, Tomas et al. 2005b). Epiphyte biomass of seagrass leaves is also controlled by an abundant and diverse mesograzers community of small gastropods and crus-

taceans, which in turn is controlled by predators (Orth et al. 1984, Mazzella et al. 1992, Williams and Heck 2001). The importance of this transfer pathway to higher trophic levels and its effect on seagrass ecosystems has not yet been evaluated in Mediterranean seagrass communities. In this issue, Gacia et al. (pp. 439–447) use an experimental approach to examine the potential control of seagrass epiphyte biomass by mesograzers in *P. oceanica* meadows. This study provides new insights in the role of epiphytes in the complex network of seagrass-epiphyte-herbivore interactions. A current issue of special concern is analysis of the effect of human impacts on plant-herbivore interactions as a potential cause of sudden changes in ecosystem functioning (Valentine and Duffy 2006). Historical overfishing or hunting has decimated the populations of some large herbivores, such as turtles and dugongs, and this has been suggested as the cause of the present limited importance of herbivory in some tropical seagrass communities, relative to the herbivore pressure they likely had in the past (Jackson et al. 2001). Overfishing can also induce overgrazing in seagrass communities by removal of the largest predators (Rose et al. 1999). Whether the direct or indirect impact of overfishing has an influence on herbivory patterns of Mediterranean seagrass communities is a question that has not been yet evaluated, but some evidence suggests that eutrophication resulting from human activities (sewage wastes, aquaculture) is also involved in the few overgrazing events documented in the Mediterranean Sea (Kirkman and Young 1981, Ruíz et al. 2001). In this issue, Ruíz et al. (pp. 449–458) provide experimental evidence that overgrazing is one of the major causes of seagrass decline in a *P. oceanica* meadow exposed to the influence of aquaculture wastes. These authors speculate on the possibility that feeding activity of grazers could be enhanced by nutrient loads through cascading effects triggered by changes in the quality and/or quantity of herbivore food sources (i.e., seagrass leaves, epiphytes and macroalgae). The validity of this explanation still needs to be tested, as does the understanding of mechanisms involved, which requires further experimental work in future research.

Turning to seagrass decline, the review of Boudourisque et al. (this issue, pp. 395–418) is a critical analysis of the magnitude of real losses of Mediterranean species and potential causes that may explain them on the basis of published documented cases. These authors show that the available quantitative data are very local and absent for a large part of the Mediterranean, that some data are of dubious value, and that the total surface area of Mediterranean seagrass meadows is still unknown. Therefore, they conclude that the hypothesis of a general seagrass decline in the Mediterranean Sea remains unclear, as a global estimation of the extent of seagrass losses in the Mediterranean Sea and the prediction of future trends can only be made by projection from this partial information. In spite of this fact, and considering the fact that some documented cases of seagrass decline have probably been confounded with natural processes, the bulk of available evidence suggests that most of the reported losses are accounted for by disturbances of an anthropogenic nature. Human activities that

potentially affect Mediterranean seagrasses are similar to those reported in other seagrass ecosystems worldwide (e.g., Short and Wyllie-Echeverria 1996, Orth et al. 2006): coastal development, mechanical damage by dredging, trawling or mooring, industrial and urban pollution, aquaculture, alteration of terrigenous inputs, brine discharges, biological invasions and global warming. The mechanisms by which such actions affect seagrass vitality, abundance and survival are still poorly understood. Present knowledge on causal relationships between these factors (and their interactions) and seagrass responses by Mediterranean species is very scarce or even absent. This is also the case for understanding the effect of increasing salinity on *P. oceanica* meadows, which has received the attention of scientists only in the last five years (Fernández-Torquemada and Sánchez-Lizaso 2005, Gacia et al. 2007, Ruíz et al., this issue, pp. 459–470) due to the recent development of a desalination industry to respond to water deficiencies in the arid and semi-arid climates characteristic of many Mediterranean coastal areas. At the moment, studies on *P. oceanica* tolerance of salinity do not exist, probably because salinity has not been considered a relevant ecological factor for this oceanic species inhabiting environments with constant salinity conditions. However, this information is also lacking for other Mediterranean species that occur in oceanic, estuarine or coastal lagoon environments, e.g., *Cymodocea nodosa* and *Zostera noltii*. Osmoregulatory mechanisms described in terrestrial plants, algae and some aquatic vascular plants (including some seagrass species) have never been investigated in Mediterranean seagrass species, even though they represent a fundamental issue for understanding species-specific sensitivity in terms of tolerance and acclimation to natural and anthropogenic changes in salinity. The limited knowledge of the mechanisms by which this and other more frequently cited factors (e.g., oversedimentation, light limitation, sediment anoxia and, in a lesser extent, nutrient loads) trigger seagrass decline obviously diminishes our capacity to predict the magnitude of the impact of human activities on Mediterranean seagrass ecosystems and to provide objective and reliable tools for coastal managers. A clear example is the set of predictions about responses of seagrass meadows to global climate change, which are of qualitative nature up to now (Duarte 2002), mainly due to our limited knowledge of the physiological mechanisms involved in the regulation of seagrass photosynthesis and productivity. This information, as indicated previously, requires a better understanding of basic plant functions, such as light absorption by leaves and canopies, leaf photosynthetic rates (P vs. E curves), carbon metabolism and its dependence on carbon concentration mechanisms (CCM) and on water pH, and whole-plant respiratory demand and its variation as a function of temperature and plant morphology. Although it is clear that knowledge of mechanisms that modulate seagrass responses to the environment still requires a large scientific effort and the integration of multidisciplinary approaches, the seagrass scientific community has to open its vision to other fields of research such as coral and terrestrial plant ecophysiology and incorporate important technical and



conceptual advances already achieved by them. Mechanistic knowledge of the different processes that affect seagrass growth will allow the development of more reliable predictions and the characterisation of future working scenarios. However, before this occurs, alternative management actions must be adopted right away to balance coastal development and ecosystem conservation. The protection of marine areas has been demonstrated as an efficient tool to preserve seagrass meadows and their functions from human impacts (Balestri and Cinelli 2003, González-Correa et al. 2007; but see Prado et al. 2008), but also to recover degraded meadows (González-Correa et al. 2005). Transplanting techniques have been proposed to accelerate recovery of degraded meadows and restore seagrass losses, but they are ineffective and even not viable tools as success is still unpredictable and without a scientific basis, and its implementation is too costly (Duarte 2002, Boudouresque et al. 2006b), even at small spatial scales. Major practical and economical problems arise when considering large, slow-growing species such as *P. oceanica*. A practical example is illustrated by Sánchez-Lizaso et al. (this issue, pp. 471–476) through a case study off the southeastern coast of Spain where seagrass transplanting is being offered as a measure to compensate seagrass losses caused by marina expansions, in spite of the lack of consensus reached in the scientific community about the viability of these actions. Regardless of the action taken, conservation of seagrass meadows will not be effective until public awareness is enhanced through educational programmes and scientific research aimed to illustrate and evaluate the socio-economic value of ecosystem services and functions and the responsibility that present society has on the preservation of these valuable environments for future generations.

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