

A5.53: Seagrass beds (other than Posidonia) on Mediterranean infralittoral sand

Summary

Seagrass habitats made by monospecific and mixed meadows of *Zostera* sp., *Cymodosea nodosa* and/or *Ruppia* sp. are widely distributed in the Mediterranean with a patchy distribution from a few meters to several kilometers wide. They provide habitat for a many organisms. The leaf canopy and the network of rhizomes and roots provide substratum for attachment, and refuges from predators. As a result, the abundance and diversity of the fauna and flora living in seagrass meadows are consistently higher than those of adjacent unvegetated areas. Seagrass meadows are act as spawning grounds for several species of fishes and are wintering areas of several species of birds.

Detailed information in trends in quantity are unknown besides few locations where have been well studied but it is thought that there is a small decline in quality in some locations. Anthropogenic disturbances from fishing activities (eg. benthic trawling, shellfish digging or boat anchoring) and deterioration of water quality (eg. eutrophication) and competition from invasive species are the main threats to this habitat and fragmentation of the meadows has been observed in some sites as a result of impacts by human activities. To prevent physical damage caused by trawling on the meadows, different measures should be considered such as placing artificial reefs along certain stretches of the coast, developing effective surveillance programmes and enforcing existing regulations to prevent illegal trawling. Awareness programmes with different sectors such as recreational boats and local councils will help to manage better coastal activities and identify areas where cost-effective schemes for threats reduction could be implemented.

Synthesis

The habitat is known to occur along most of the Mediterranean coast. It has a large EOO >50,000km² and AOO >50, which exceeds the thresholds for a threatened category on the basis of restricted geographic distribution. There is increasing anthropogenic pressure on this habitat from pollution, aquaculture and fishing gear and some declines in quality have been reported but trends in quantity are currently unknown. This habitat displays adaptive plasticity and successful colonisation after periods of pressure and can recover naturally in relatively short time periods. Based on the above and the knowledge of experts, this habitat assessed as Least Concern for both the EU 28 and EU 28+.

Overall Category & Criteria			
EU 28		EU 28+	
Red List Category	Red List Criteria	Red List Category	Red List Criteria
Least Concern	-	Least Concern	-

Sub-habitat types that may require further examination

The association with *Zostera marina* in euryhaline and eurythermal environment is rare in the Mediterranean, mostly found as small isolated stands, but dense eelgrass beds do occur, especially, in lagoons. Some significant regressions have been reported, particularly along the eastern Mediterranean and the Alboran sea and long term monitoring data are in need to assess its conservation status and trends.

Habitat Type

Code and name

A5.53: Seagrass beds (other than *Posidonia*) on Mediterranean infralittoral sand



Cymodocea meadows along the Libyan coast (© G. Pergent).



Zostera noltei meadows in a coastal lagoon (© M. Foulquie).

Habitat description

Mediterranean seagrasses form dense and highly productive meadows or beds, between the surface to 15 m depth in coastal lagoons and down to 50 m depth in the open-sea, in clear water conditions. Besides the seagrass *Posidonia oceanica*, these meadows are built by several submerged magnoliophytes, such as: *Cymodocea nodosa*, *Zostera marina*, *Zostera noltei* or the introduced species *Halophila stipulacea*, and, in transitional waters and coastal lagoons by *Ruppia* sp. All these species can be found alone or combined among them to form mixed meadows. The basic physical requirements of seagrass meadows habitats are sufficient light, a suitable substratum (muddy or sandy bottom) and moderate levels of wave exposure. Their tolerance to variation of environmental factors (e.g. salinity, temperature, nutrient concentration) and their geographical distribution differ depending on the dominant seagrass species.

Seagrasses provide habitat for a large set of organisms. The leaf canopy and the network of rhizomes and roots provide substratum for attachment, and creates hiding places to avoid predation. As a result, the abundance and diversity of the fauna and flora living in seagrass meadows are consistently higher than those of adjacent unvegetated areas. In addition seagrass meadows play an important role as spawning zone and hatchery for several species of fishes and are wintering areas of several species of birds

Several sub-habitat can be distinguished. *Cymodocea nodosa* beds are widely distributed throughout the Mediterranean, and outside, around the Canary Islands and down the North African coast, and are usually frequent in areas with salinity fluctuations from 26 to 44%. These meadows are observed in coastal lagoons and in the open-sea. Eelgrass beds (*Z. marina*) are rare in the Mediterranean and it is found mostly as small isolated stands, down to 10-15 meters depth depending on water clarity. Dense meadows can however occur, especially, in coastal lagoons and transitional waters. They are distributed from the Arctic waters until the Mediterranean and are very abundant in the Baltic Sea, the North Sea and along the Atlantic coasts down to northern Spain. *Ruppia* beds grow in brackish waters, in permanent pools of mud or sand flats, as well as in inlets or estuaries. Mixed beds of *Zostera* and *Ruppia* can be observed in shallow sublittoral sediments. These communities are generally found in extremely sheltered bays and coastal lagoons, with very weak tidal currents.

Indicators of quality:

Extended seagrass beds with a good penetration to deep waters are characteristic of coastal waters with minimal anthropogenic impact. Since seagrasses are mostly perennial organisms, they reflect the temporally integrated environmental conditions, and, therefore, seagrasses are very good indicator on which environmental monitoring and management of coastal waters can focus. *Cymodocea nodosa* is considered at the Mediterranean level, as a biological quality element for the implementation of the Water Framework Directive and several indicators have been proposed for this assessment.

Characteristic species:

The leaf canopy hosts epiphytes community, made up of Rhodobiontes (e.g. *Acrochaetium daviesii*, *Chondria mairei*, *Laurencia obtusa*) and filamentous Phaeophyceae (e.g. *Castagnea cylindrica*, *Myriactula gracilis*, *Myrionema orbiculare*), small calcified incrusting rhodobiontes (few millimeters in general, like *Hydrolithon*...) (a few millimeters in general), Rhodobiontes calcified encrusting (e.g. *Hydrolithon farinosum*, *Pneophyllum fragile* by Bacillariophyceae (mainly Pennales) and by Dinobiontes (*Prorocentrum lima*, *Ostreopsis siamensis* and *Coolia monotis*). Several species of polychaetes (*Sigalion mathildae*, *Onuphis eremita*, *Diopatra neapolitana*, molluscs among them bivalves (*Acanthocardia tuberculata*, *Macra stultorum*, *Tellina fabula*, *Donax venustus* and gastropods (*Acteon tornatilis*, *Nassarius mutabilis*, *Nassarius pygmaeus*, *Neverita josephina*, crustacean (*Ampelisca brevicornis*, *Hippomedon massiliensis*, *Pariambus typicus*, *Idothea linearis* and echinoderms (*Astropecten* sp., *Echinocardium cordatum*, *Paracentrotus lividus*) are observed between the rhizomes or inside the sediment.

Teleost occupy all available habitats, from the sediment to the water column overcoming beds. Characteristic species are closely associated with the phyllosphere through a ventral sucker (*Opeatogenys gracilis*, *Apletodon dentatus*, or by hanging them by their tails (*Hippocampus* sp., *Nerophis* sp., *Syngnathus* sp.). Inside the canopy several species can be observed as *Atherina boyeri*, *Pomatoschistus marmoratus*, *Liza aurata*, *Liza saliens* or *Aphanius iberus*. Despite geographical differences, it is always the same families that dominate in number of species and individuals: Labridae (*Coris julis*, *Symphodus* sp., *Labrus* sp., *Xyrichtys novacula*), Sparidae (*Diplodus* sp., *Sarpa salpa*, *SpondylIOSoma cantharus*, *Sparus aurata*, *Dentex dentex*, Scorpaenidae, Serranidae, Mullidae (*Mullus surmuletus*). Planktivorous species (*Boops boops*, *Spicara* sp., *Chromis chromis*) present in the water column during the day, find refuge in the beds at night.

Classification

EUNIS (v1405):

Level 4: A subhabitat of 'Sublittoral macrophyte dominated sediment' (A5.5).

Annex 1:

1110 Sandbanks which are slightly covered by seawater all the time

1120 Posidonia beds

MAES:

Marine - Marine inlets and transitional waters

Marine - Coastal

MSFD:

Shallow sublittoral sediment (coarse, sand, mud, mixed)

EUSEaMap:

Seagrass meadows

IUCN:

9.9 Seagrass submerged

Barcelona convention (RAC/SPA):

III. 1. 1. 1. Association with *Ruppia cirrhosa* and/or *Ruppia maritima*

III. 1. 1. 4. Association with *Zostera noltei* in euryhaline and eurythermal environment

III. 1. 1. 5. Association with *Zostera marina* in euryhaline and eurythermal environment

III. 2. 2. 1. Association with *Cymodocea nodosa* on well sorted fine sands

III. 2. 2. 2. Association with *Halophila stipulacea*

III. 2. 3. 4. Association with *Cymodocea nodosa* on superficial muddy sands in sheltered waters

III. 2. 3. 5. Association with *Zostera noltei* on superficial muddy sands in sheltered waters

Does the habitat type present an outstanding example of typical characteristics of one or more biogeographic regions?

Yes

Regions

Mediterranean

Justification

Seagrass beds are a common feature in the Mediterranean and form an important ecosystem and nursery ground for many juvenile fish. This habitat is widespread across the Mediterranean.

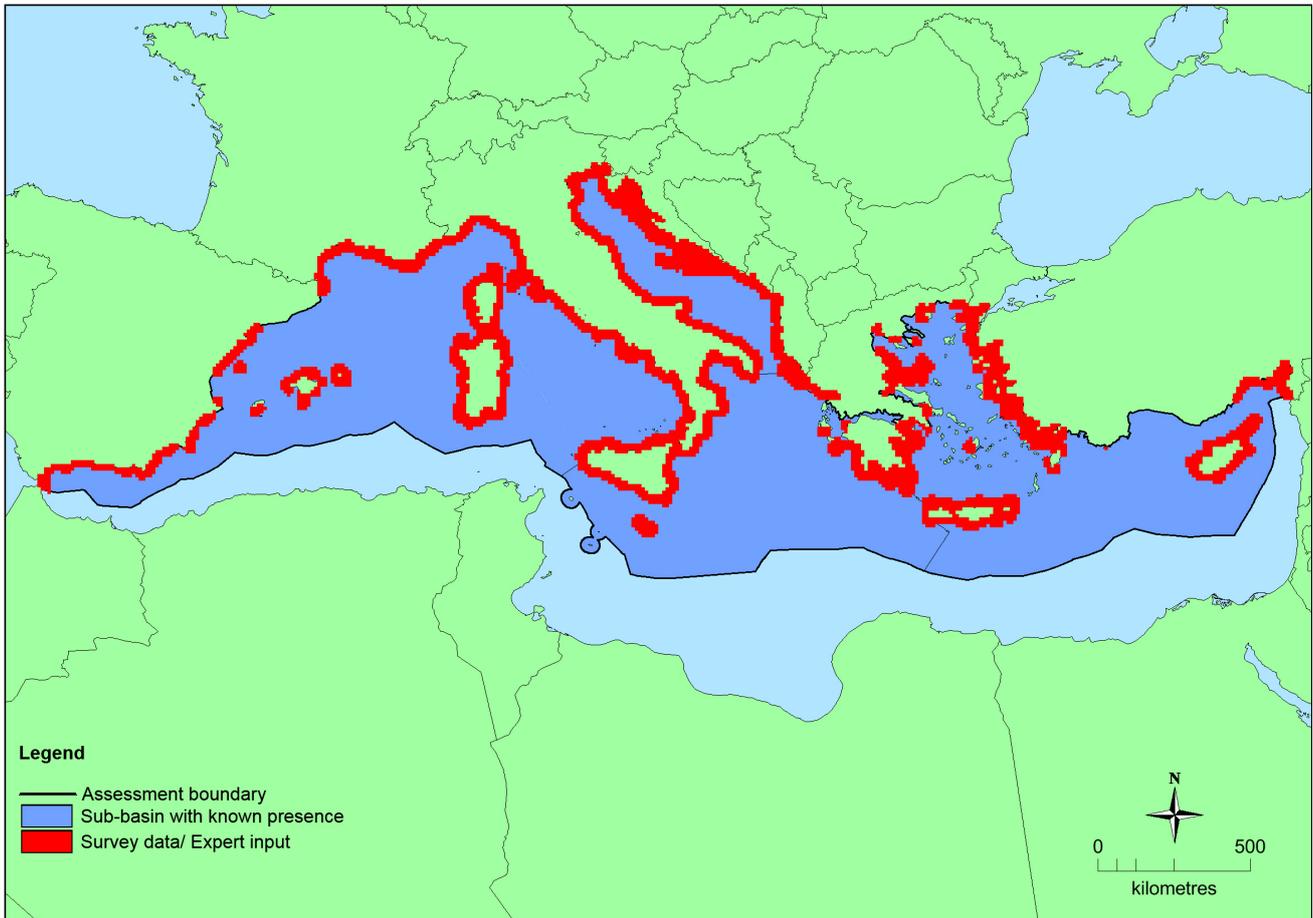
Geographic occurrence and trends

Region	Present or Presence Uncertain	Current area of habitat	Recent trend in quantity (last 50 yrs)	Recent trend in quality (last 50 yrs)
<i>Mediterranean Sea</i>	Adriatic Sea: Present Aegian-Levantine Sea: Present Ionian Sea and the Central Mediterranean Sea: Present Western Mediterranean Sea: Present	274000 Km ²	Stable	Decreasing

Extent of Occurrence, Area of Occupancy and habitat area

	Extent of Occurrence (EOO)	Area of Occupancy (AOO)	Current estimated Total Area	Comment
EU 28	2,528,443 Km ²	3,701	195,700 Km ²	
EU 28+	2,719,699 Km ²	4,082	>195,700 Km ²	

Distribution map



There are insufficient data to provide a comprehensive and accurate map of the distribution of this habitat. This map has been generated using EMODnet data from modelled/surveyed records from the Mediterranean (and supplemented with expert opinion where applicable) (EMODnet, 2015 and IUCN database 2015). EOO and AOO have been calculated on the available data presented in this map however these should be treated with caution as expert opinion is that this is not the full distribution of the habitat.

How much of the current distribution of the habitat type lies within the EU 28?

The habitat is well distributed along EU countries and varies depending which is the dominant seagrass species and its ecological characteristics. It can colonise different types of environment, such as open coastal waters, coastal lagoons and estuaries, and form both monospecific and mixed stands with a patch distribution. This habitat occurs in the EU 28+. The percentage hosted by the EU 28 is therefore less than 100% but there is insufficient information to establish the proportion.

Trends in quantity

Information regarding the habitat cover is known from some regions around the Mediterranean. At few sites, a decrease on the habitat has been observed such as the Venice lagoon (Italy) for example where the subhabitat of *Cymodocea nodosa* beds had greatly declined since the beginning of the 20th century. Isolated patches of the subhabitat type with *Zostera marina* beds have also been reported to have almost disappeared along the Spanish coast and more than 50% of loss of habitat has been estimated in Montenegro over the last 36 years. Overall, trends in the quantity of this habitat are unreported because the variability of methods used and the lack of long term monitoring programmes in place. Nevertheless, when pressures do not persist, recovery have been registered in multiple sites suggesting that this habitat is stable at present.

- Average current trend in quantity (extent)
EU 28: Stable

EU 28+: Stable

- Does the habitat type have a small natural range following regression?

No

Justification

This habitat does not have a small natural range. It is widespread, being found as far the Levantine Sea and as far west to the Gibraltar Strait.

- Does the habitat have a small natural range by reason of its intrinsically restricted area?

No

Justification

This habitat does not have a small natural range and can be found in different types of environment, such as open coastal waters and coastal lagoons.

Trends in quality

Not much information seems available about the trends on quality of these seagrass beds. At few sites, a decrease on the quality has been observed such as those observed along the Catalan coast (Spain) with an estimated 36% of meadows affected. Isolated patches of the subhabitat of *Zostera marina* beds have also been reported to have almost disappeared along the Spanish coast and a general regression on the quality of the subhabitat of *Cymodocea nodosa* meadows in Spain has been observed. Overall, expert opinion is that there is a decline in quality for this habitat in the EU 28 but it cannot be quantified.

- Average current trend in quality

EU 28: Decreasing

EU 28+: Unknown

Pressures and threats

Seagrass beds occur in coastal regions where there is a high level of human disturbance. The habitat is threatened locally by mechanical damage from trawling and anchoring from boats as well as coastal development. Eutrophication, competition from alien macroalgae species like *Caulerpa taxifolia* and *Caulerpa cylindracea*, urban and industrial waste dumping, modification of lagoon environments and coastal development such as building and maintenance of ports, sea walls and artificial platforms.

List of pressures and threats

Urbanisation, residential and commercial development

Urbanised areas, human habitation

Discharges

Biological resource use other than agriculture & forestry

Fishing and harvesting aquatic resources

Professional active fishing

Benthic or demersal trawling

Pollution

Pollution to surface waters (limnic, terrestrial, marine & brackish)

Marine water pollution

Invasive, other problematic species and genes

Invasive non-native species

Conservation and management

Cymodocea nodosa is considered at the Mediterranean level, as a biological quality element for the implementation of the Water Framework Directive and several indicators have been proposed for this assessment. Both *Zosteras* and *Cymodocea* are included in the Annex II of the Barcelona Conventions and some national legislations. Besides, the habitat formed by these seagrasses is also protected in various marine protected areas in the countries along the Mediterranean Sea.

To prevent physical damage caused by fishing trawling on the meadows, different measures should be considered such as placing artificial reefs along certain stretches of the coast, develop effective surveillance programmes and enforcing existint regulations to prevent illegal trawling. Awareness programmes with different sectors such as recreational boats and local councils will help to manage better coastal activities and identify areas where cost-effective schemes for threats reduction could be implemented.

Mapping and monitoring efforts are still much needed for most of its range of distribution.

List of conservation and management needs

Measures related to marine habitats

Restoring marine habitats

Measures related to spatial planning

Establish protected areas/sites

Measures related to hunting, taking and fishing and species management

Regulation/Management of fishery in marine and brackish systems

Conservation status

Annex 1:

1110: MMED XX

1120: MMED U1

At Mediterranean level, *Zostera noltei*, *Z. marina* and *Cymodocea nodosa* species are included in the Annex II, List of endangered or threatened species of the Barcelona Convention.

When severely damaged, does the habitat retain the capacity to recover its typical character and functionality?

The predicted recovery times is particularly short for fast-recovering species (e.g. *Cymodocea nodosa* - within 1 year) however the capacity for the habitat to recover its functionality would be longer.

Effort required

10 years
Naturally

Red List Assessment

Criterion A: Reduction in quantity

Criterion A	A1	A2a	A2b	A3
EU 28	unknown %	unknown %	unknown %	unknown %

Criterion A	A1	A2a	A2b	A3
EU 28+	unknown %	unknown %	unknown %	unknown %

There are no precise figures of the extent of this habitat therefore it is not possible to estimate any changes in quantity over the last 50 years. No future estimates of extent have been made. Therefore the habitat type is assessed as Data Deficient under Criterion A.

Criterion B: Restricted geographic distribution

Criterion B	B1				B2				B3
	EOO	a	b	c	AOO	a	b	c	
EU 28	>50,000 Km ²	Yes	Yes	no	>50	Yes	Yes	no	no
EU 28+	>50,000 Km ²	Yes	Yes	no	>50	Yes	Yes	no	no

The habitat is known to occur along most of the Mediterranean coast. It has a large EOO >50,000km² and AOO >50, which exceeds the thresholds for a threatened category on the basis of restricted geographic distribution. There are some reported declines in quality for this habitat but the distribution of the habitat is such that the identified threats are unlikely to affect all localities at once. The habitat type is assessed as Least Concern under Criterion B.

Criterion C and D: Reduction in abiotic and/or biotic quality

Criteria C/D	C/D1		C/D2		C/D3	
	Extent affected	Relative severity	Extent affected	Relative severity	Extent affected	Relative severity
EU 28	15 %	slight %	unknown %	Unknown %	unknown %	unknown %
EU 28+	15 %	slight %	unknown %	Unknown %	unknown %	unknown %

Criterion C	C1		C2		C3	
	Extent affected	Relative severity	Extent affected	Relative severity	Extent affected	Relative severity
EU 28	unknown %	unknown %	unknown %	unknown %	unknown %	unknown %
EU 28+	unknown %	unknown %	unknown %	unknown %	unknown %	unknown %

Criterion D	D1		D2		D3	
	Extent affected	Relative severity	Extent affected	Relative severity	Extent affected	Relative severity
EU 28	unknown %	unknown%	unknown %	unknown%	unknown %	unknown%
EU 28+	unknown %	unknown%	unknown %	unknown%	unknown %	unknown%

Experts report that there has been slight or moderate declines in the quality of this habitat in few countries (Spain, Italy and Montenegro). Nonetheless there is a lack of quantitative data to calculate percentage change in abiotic and/or biotic quality even if substantial reductions in quality have occurred in at least some parts of this habitat. Moreover, the adaptive plasticity and successful colonisation of the different structural species that form meadows and beds, has made possible the partial or full recovery of damaged habitats.

Based on this information and expert opinion, the habitat type is assessed as Least Concern under Criterion C/D.

Criterion E: Quantitative analysis to evaluate risk of habitat collapse

Criterion E	Probability of collapse
EU 28	unknown
EU 28+	unknown

There is no quantitative analysis available to estimate the probability of collapse of this habitat type. Therefore, it is assessed as Data Deficient under Criterion E.

Overall assessment "Balance sheet" for EU 28 and EU 28+

	A1	A2a	A2b	A3	B1	B2	B3	C/D1	C/D2	C/D3	C1	C2	C3	D1	D2	D3	E
EU28	DD	DD	DD	DD	LC	LC	LC	LC	DD	DD	DD	DD	DD	DD	DD	DD	DD
EU28+	DD	DD	DD	DD	LC	LC	LC	LC	DD	DD	DD	DD	DD	DD	DD	DD	DD

Overall Category & Criteria			
EU 28		EU 28+	
Red List Category	Red List Criteria	Red List Category	Red List Criteria
Least Concern	-	Least Concern	-

Confidence in the assessment

Low (mainly based on uncertain or indirect information, inferred and suspected data values, and/or limited expert knowledge)

Assessors

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References

Borum, J., Duarte, C.M., Krause-Jensen, D. and Greve, T.M. (Eds) 2004. *European Seagrasses: An introduction to monitoring and management*. The M&MS project. ISBN: 87-89143-21-3.

Boudouresque, C.F., Bernard, G., Pergent, G., Shili, A. and Verlaque, M. 2009. Regression of Mediterranean seagrasses caused by natural processes and anthropogenic disturbances and stress: a critical review. *Botanica Marina* 52, 395 e 418.

Espinosa, F., Navarro-Barranco, C., González, A.R., Maestre, M.J.C., García-Gómez, J.C., Benhoussa, A., Limam, A. and Bazairi, H. 2014. A combined approach to assessing the conservation status of Cap des Trois Fourches as a potential MPA: is there a shortage of MPAs in the southern Mediterranean? *Mediterranean Marine Science* 654-666.

- González-García, J.A., García-Peña, H. and Bueno del Campo, I. 2005. *Especies singulares y protegidas de la flora y fauna de Melilla y las Islas Chafarinas*, 264. Fundación Municipal Sociocultural. Excmo. Ayuntamiento de Melilla, Melilla.
- González-García, J.A. 1994. *La flora marina de Melilla*. Colección Ensayos Melillenses. 212 Fundación Municipal Sociocultural. Excmo. Ayuntamiento de Melilla, Melilla.
- Luque, A. and Templado, M. (Ed). 2004. *Praderas y bosques marinos de Andalucía*. Junta de Andalucía. Consejería de Medio Ambiente, 2004.
- Orfanidis, S., Papathanasiou, V., Gounaris, S. and Theodosiou, T.H. 2010. Size distribution approaches for monitoring and conservation of coastal Cymodocea habitats. *Aquatic Conservation: Marine and Freshwater Ecosystems* 20,177 e 188.
- Pergent, G., Bazairi, H., Bianchi, C.N., Boudouresque, C.F., Buia, M.C., Clabaut, P., Harmelin-Vivien, M., Mateo, M.A., Montefalcone, M., Morri, C., Orfanidis, S., PergentMartini, C., Semroud, R., Serrano, O. and Verlaque, M. 2012. *Mediterranean Seagrass Meadows: Las praderas de Magnoliofitas marinas del mar Mediterráneo: resiliencia y contribución a la mitigación del cambio climático, Resumen / Mediterranean Seagrass Meadows : Resilience and Contribution to Climate Change Mitigation, A Short Summary*. Gland, Suiza y Málaga, España: IUCN. 40 páginas.
- Pergent, G., Djellouli, A.A., Hamza, A.A., Ettayeb, K.S., El Mansouri, A.A., Talha, F.M., Hamza, M.A., Pergent-Martini, C. and Platini, F. 2002. Characterization of the benthic vegetation in the Farwa Lagoon (Libya). *Journal of Coastal Conservation* 8: 119-126.
- Pergent-Martini, C., Alami, S., Bonacorsi, M., Clabaut, P. and Pergent, G. 2014. *Cartographie des peuplements benthiques du littoral de la Corse*. Rapport CoralCorse, 79 AAMP, Université de Corse & GIS Posidonie Report.
- Pergent, G., Djellouli, A., Hamza, A.A., Ettayeb, K.S., El Mansouri, A.A., Talha, F.M., Hamza, M.A., Pergent-Martini, C. and Platini, F. 2001. *The benthic vegetation in the Farwà Lagoon (Libya) 567-578*. MEDCOAST. Proceeding of the 5th International Conference on the Mediterranean Coastal Environment, MEDCOAST 01.
- Pergent, G., Djellouli, A., Hamza, A., Ettayeb, K., Alkekli, A., Talha, M. and Alkunti, E. 2006. *Etude des communautés végétales benthiques dans les lagunes côtières d'Ain Al-Ghazala et de Farwa* (Libye). 64 CAR/ASP, Report.
- PNUE-PAM-CAR/ASP. 2013. *Le Cap des Trois Fourches (Méditerranée, Maroc): caractérisation écologique et orientations de gestion*. 113 RAC/SPA
- Mačić, V. 2014. Regresia naselja morskih trava u risanskom zalivu (Crna Gora) (Serbian language) *Voda* 337-341. Voda association Serbia . Congress paper
- Ruiz, J.M., Guillén, J.E., Ramos Segura, A. and Otero, M.M. (Eds.). 2015. *Atlas de las praderas marinas de España*. IEO/IEL/ UICN, Murcia-Alicante-Málaga, 681 pp.
- Sghaier, Y.R., Limam, A., Samah, L., Bitar, G., Khalaf, G., Samaha, Z., El-Shaer, H., Forcada, A., Ocaña, O., Valle, C. and Ramos Esplá, A.A. 2014. *Cymodocea nodosa distribution along the lebanese coast*. Proceedings of the 5th Mediterranean 248-249 RAC/SPA Proceedings of the 5th Mediterranean Symposium on Marine Vegetation (Portorož, Slovenia, 27-28 October 2014).
- Shabaka, S.H. 2004. *Ecological study of the benthic marine phanerogames meadows of Alexandria, coast, Egypt*. M.Sc. Alexandria University, 210 pp.
- Scarton, F., Curiel, D. and Rismondo, A. 1995. *Aspetti della dinamica temporale di praterie a fanerogame*

marine in Laguna di Venezia", *Lav. Soc. Ven. Sc. Nat.*, 20, 95-102.

Stjepčević, J. and Parenzan, P. 1980. *Il Golfo delle Bocche di Cattaro - condizioni generali e biocenosi bentoniche con carta ecologica delle sue due baie interne: di Kotor (Cattaro) e di Risan (Risano) Studia marina* : 3-148 Institute of marine biology Kotor.

Tagliapietra, D., Cornello M., Pessa G. and Zitelli, A. 1999. Changes in seagrass beds distribution at the Lido outlet of the Venetian Lagoon (Italy), *Biol. Mar. Medit* 6, 448-451.

Vela, A., Pasqualini, V., Leoni, V. Djelouli, A., Langar, H., Pergent, G., Pergent-Martini, C., Ferrat, L., Ridha, M. and Djabou, H. 2008. Use of SPOT 5 and IKONOS imagery for mapping biocenoses in a Tunisian Coastal Lagoon (Mediterranean Sea). *Estuarine Coastal and Shelf Science*, 79 (4), 591-598.