

# Long term changes in *Zostera* meadows in the Berre lagoon (Provence, Mediterranean Sea)

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## Abstract

The Berre lagoon (Provence, France), one of the largest Mediterranean brackish lagoons (155 km<sup>2</sup>), was occupied, at the turn of the 20th century, by extensive *Zostera* meadows (*Zostera marina* and probably *Zostera noltii*; perhaps over 6000 ha). Subsequently, the lagoon was disturbed by urban and industrial pollution and, from 1966, by the diversion of the Durance River. This resulted in a 10–49-fold and 8–31-fold increase of the freshwater and silt inputs, respectively. By means of digital analysis of aerial photographs for the years 1944, 1992, 1998 and 2004, coupled with ground truth for the last three dates, we mapped the *Zostera* meadows. The replacement of *Z. marina* by *Z. noltii*, the latter species being already dominant in the 1970s, was completed in 1990. In parallel to this substitution, the *Zostera* beds underwent a dramatic decline. Their depth limit, which was (6–9) m in the early 20th century, withdrew to 3.5, 3, 1 and less than 1 m by 1944, the 1970s, 1992 and 1998, respectively. Since 1998, *Zostera* must be considered as functionally extinct. The total surface area of *Zostera* meadows was of the order of 1.5 ha in 2004. In an attempt to alleviate disturbance, the input of freshwater and silt from the Durance River was significantly reduced from the early 1980s and 1990s respectively. Similarly, from the 1970s to the 1990s, urban and domestic pollution was drastically reduced. Despite these steps, *Zostera* meadows continued to shrink to near extinction. The lagoon has shifted from a system dominated by seagrass beds to a system with bare silt bottoms, which now occupy most of the lagoon. The reasons could be, in addition to continuing nutrient inputs, the resuspension of silt, no longer trapped under the seagrass canopy, during wind episodes, which are frequent in the area, and/or the release of nutrients from the bare silt habitat, which would constitute an indication of a possible hysteresis of the system. However, since 2000, the establishment of the mussel *Mytilus galloprovincialis*, a drop in turbidity and a slight, inconspicuous progression of *Z. noltii* could be the harbinger of a reverse shift of the system.

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## 1. Introduction

Coastal lagoons and estuaries have, since the early or middle 20th century, become among the most disturbed coastal ecosystems throughout the world. The initial causes for the disturbance

are usually more or less well identified: eutrophication and organic pollution through increasing agriculture and urbanisation in river catchments, port facilities, aquaculture, turbidity and over-sedimentation (Giesen et al., 1990; Valiela et al., 1997; Bowen and Valiela, 2001; Cardoso et al., 2004). In addition, seagrasses, which are common dwellers of these habitats, are declining throughout the world (Short and Wyllie-Echeverria, 1996). However, the subsequent dynamics of the ecosystems in response to further disturbances and/or to the improvement of water quality remains poorly understood in most habitats. The Berre brackish lagoon (Provence, Southern France,

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Mediterranean Sea) offers the opportunity of a time series of over one century, at least for some data. Furthermore, in addition to the above mentioned disturbances, the diversion of a river towards the lagoon resulted in a huge freshwater input.

In the late 19th and early 20th centuries, the Berre Lagoon, one of the largest Mediterranean coastal lagoons (155 km<sup>2</sup>), was occupied by very extensive *Zostera* meadows (Magnoliophyta, Plantae), from a few centimetres below the mean water level to 6 m depth, and sometimes even deeper (down to 9 m), close to the maximum depth of the lagoon (Marion, 1887; Gourret, 1907). Depth contours make it possible to estimate that their surface area was then over 6000 ha, a rather conservative figure. The *Zostera* species dwelling in the lagoon was *Zostera marina* Linnaeus, according to Gourret (1907). However, this author, after a good description of *Z. marina*, pointed out that some specimens exhibited narrow and 3-nerved leaves, which suggests that a second species also occurred at that time, *Zostera noltii* Hornemann (= *Nanozostera noltii* (Hornemann) Tomlinson and Posluszny).

In 1925, the 6 m deep channel which linked the Berre lagoon to the sea was deepened to 9 m (Mars, 1966). Subsequently, urban development and industrialisation (especially petrochemicals) of the lagoon region resulted in a steady increase in pollution (Mars, 1949; Schachter, 1954; Fèbvre, 1968). From 1966, the diversion of the Durance River towards the Saint Chamas hydroelectric power plant then into the Berre lagoon resulted in: (1) a heavy input of freshwater (up to seven times the volume of the lagoon per year); (2) the decline of surface water salinity from 24–36 to 1–22 (Riouall, unpublished data; Kim, 1985); (3) stratification with low salinity water down to 5 m and more salty water at depth (under calm conditions); and (4) eutrophication and unstable ecological conditions (Minas, 1974; Stora et al., 1995; Nérini et al., 2000, 2001). In the years following the putting into operation of the diversion of the Durance River to the lagoon, the decline of *Zostera marina* and *Zostera noltii* meadows was reported (Riouall, 1971, 1972; Huvé et al., 1973). Subsequently, this decline became more pronounced, and *Z. marina* disappeared from the lagoon (Pergent-Martini et al., 1995; Bernard et al., 2005).

To date, the only attempt to map the *Zostera* meadows of the Berre lagoon is a rough sketch (scale 1:100,000) published by Mars (1966). In addition, Pergent-Martini et al. (1995) mentioned the presence or absence of *Zostera* along the shoreline.

In the present study, by means of digital analysis of aerial photographs for the years 1944, 1992, 1998 and 2004, coupled with ground truth for the last three dates, we have mapped the *Zostera* meadows in 4 sectors of the Berre lagoon in an attempt to assess on the basis of factual and quantitative data the patterns of change over time and to connect them with the changes in the lagoon environment.

## 2. Materials and methods

### 2.1. Study sites and photograph acquisition

The whole shoreline of the Berre lagoon was explored in 1998 and 2004 (from a small boat and by snorkelling). The

study sites were chosen according to the occurrence of present day *Zostera* stands. The aerial photographs were selected within the archives of the National Geographic Institute (IGN) and the National Centre for Scientific Research (CNRS Centre Camille Julian) on the basis of the following criteria: (1) photographs must have been taken with no sun glint, no surface waves and optimum water transparency. Water transparency was considered sufficient when bottom details were perceptible down to 4 m depth, within or outside the limits of the mapped area (see below); (2) photographs must have been taken at the season of maximum seagrass leaf development, i.e. late spring–early summer; and (3) a site (east of the Pointe de Berre) commonly subject to accumulation of drift macroalgae (such as *Ulva* spp.) and/or seagrass leaves has been discarded since they may be confused with in situ seagrass in the image analysis. Four sites with a suite of aerial photographs fully matching these conditions were chosen on the western and eastern shores of the Berre lagoon (Fig. 1). A specific campaign was designed for aerial photograph acquisition in June 2004 (GIPREB-AERIAL) according to a standardized protocol (altitude, lens, time, angle, resolution, contrast; see McKenzie et al., 2001) optimising the quality of photographs for seagrass identification. The surface area of the study sites ranges from 48.9 to 283.5 ha (Table 1). All sites are shallow (less than 4 m depth).

### 2.2. Seagrass mapping from aerial photographs

The aerial photograph scale was 1:22,500 (1944), 1:20,000 (1992 and 1998) and 1:8000 (2004). The photographs were respectively scanned at 1143, 1016, and 406 dpi in order to get a pixel size of 0.5 m. Colour photos (1998 and 2004) were converted to B/W, in order to use the same mapping method. ArcGIS<sup>®</sup> georeferencing tool was used for rectification of the photographs, according to a single reference (IGN BDORTH0 1998, reported accuracy of 1 m). The rectification error, expressed as the RMS (root mean square) distance between original and modelled position of control points, varied from 1.11 to 5.48 m. Identification of seagrass beds was performed through published sources and maps (Huvé and Huvé, 1954; Mars, 1966; Pergent-Martini et al., 1995) and ground truth (observation by snorkelling: 1992, M. Brugeaille unpublished data, 1998, 2004). Depth, size and GPS position of each seagrass patch observed were recorded. At the study sites, the position of the depth lines (down to the 4 m one) was similar between 1955 (SHOM maps) and 2004 (GPS position).

The photographs were manually analysed and digitalised, through visual interpretation of different grey-tones corresponding to seagrasses, with GIS (ArcGis<sup>®</sup>). Contrast stretching was applied when necessary and seagrass was defined as pixel with grey tones up to a certain threshold value, to obtain the probable surface area of seagrass beds. The accuracy of the mapping process was determined by creating a maximum and minimum estimate of seagrass cover in addition to the normal mapping procedure as described by Frederiksen et al. (2004). In the maximum estimate, we decreased the grey tone threshold to include even sparse seagrass patches at the risk of including

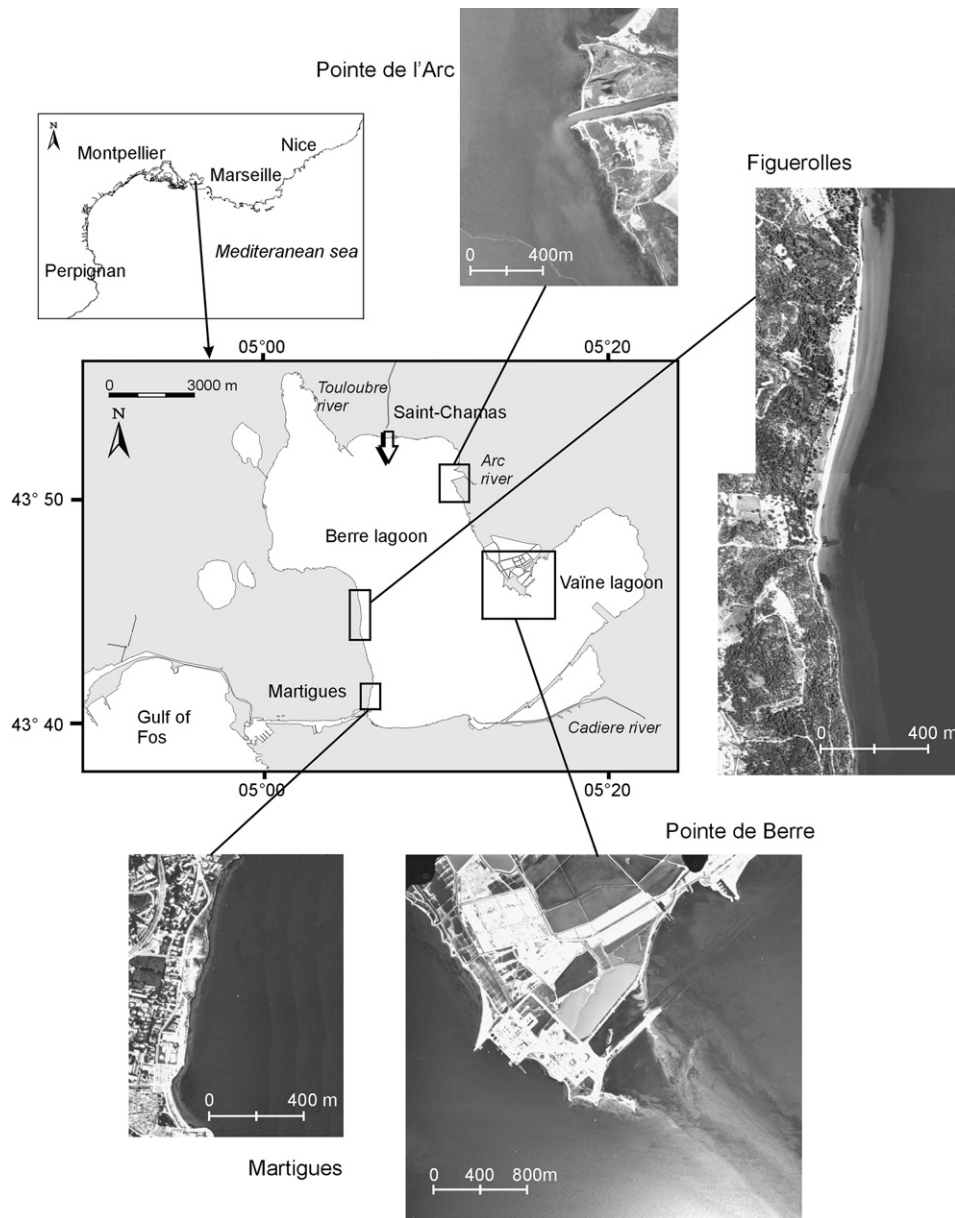


Fig. 1. Location of the study sites. Arrow: outfall of freshwater from the Durance River via the Saint Chamas power plant.

other features such as dark sand or macroalgal stands; the minimum estimate included only the darkest pixel values, representing the most distinct seagrass areas and therefore might underestimate seagrass surface area. The seagrass areas of the original mapping results ranged from  $-19.3$  to  $+4.7\%$  relative to the mean of the corresponding min-max interval.

### 2.3. Hydrological data

The data on inflow of fresh water and silt due to the diversion of the Durance River towards the Berre lagoon, via the Saint Chamas hydroelectric plant (1966–2004), has been provided by EDF (Electricité de France). Data on the inflow of fresh water due to rivers flowing into the lagoon, and on the inflow of

nutrients due to either the diversion of the Durance River or to rivers flowing into the lagoon, come from the literature (Minas, 1974; Arfi, 1989; Kim and Travers, 1997a,b), unpublished data (Romaña et al., Gosse et al.) and from the French Ministry of Environment databases (Banque HYDRO, 2006; Réseau

Table 1

Data on the study sites. Surface area only concerns bottoms between the mean sea level and the 4 m depth line

Study site	Surface area (ha)	Times series
Pointe de l'Arc	57.5	1992–1998–2004
Pointe de Berre	283.5	1944–1992–1998–2004
Martigues	48.9	1944–1992–2004
Figuerolles	55.6	1944–1998–2004

Table 2

Long-term changes in *Zostera* surface area at Pointe de l'Arc, Pointe de Berre, Figuerolles and Martigues. Above, the probable surface area in hectares. [ ] indicates the minimum and maximum estimates (see text). Below, the remaining surface area, as a percentage of the baseline value (i.e. 100%, in 1944 or 1992). md = missing data

	Pointe de l'Arc	Pointe de Berre	Martigues	Figuerolles
1944	md	84.17 [76.01–87.75] 100%	13.59 [12.28–14.17] 100%	22.43 [20.26–23.38] 100%
1992	6.32 [5.21–6.47] 100%	3.47 [2.86–3.56] 4.1%	0.24 [0.19–0.24] 1.7%	md
1998	0.10 [0.09–0.10] 1.6%	0.51 [0.47–0.53] 0.6%	md	0.00
2004	0.22 [0.18–0.22] 3.5%	0.81 [0.66–0.82] 0.9%	0.02 [0.01–0.02] 0.2%	0.02 [0.02–0.02] 0.1%

National de Bassin, 2006). Salinity (1994–2004) was measured with a CTD probe YSI<sup>®</sup>, every 50 cm down to 4 m.

#### 2.4. Statistics

Size-frequency distribution of patches was tested for normality using Shapiro–Wilk test. Statistical analyses (correlations and Kolmogorov–Smirnov) were conducted using STATISTICA<sup>®</sup>. Hydrological data were compared between years using a non-parametric Kruskal–Wallis test (normality

was rejected by a Shapiro–Wilk test), with post hoc comparisons using the Dunn method (Zar, 1999).

### 3. Results

#### 3.1. Changes in *Zostera* distribution

At all study sites, at least in 1992, 1998 and 2004, years for which ground observations were performed, only one species was present: *Zostera noltii*. *Zostera* meadows underwent

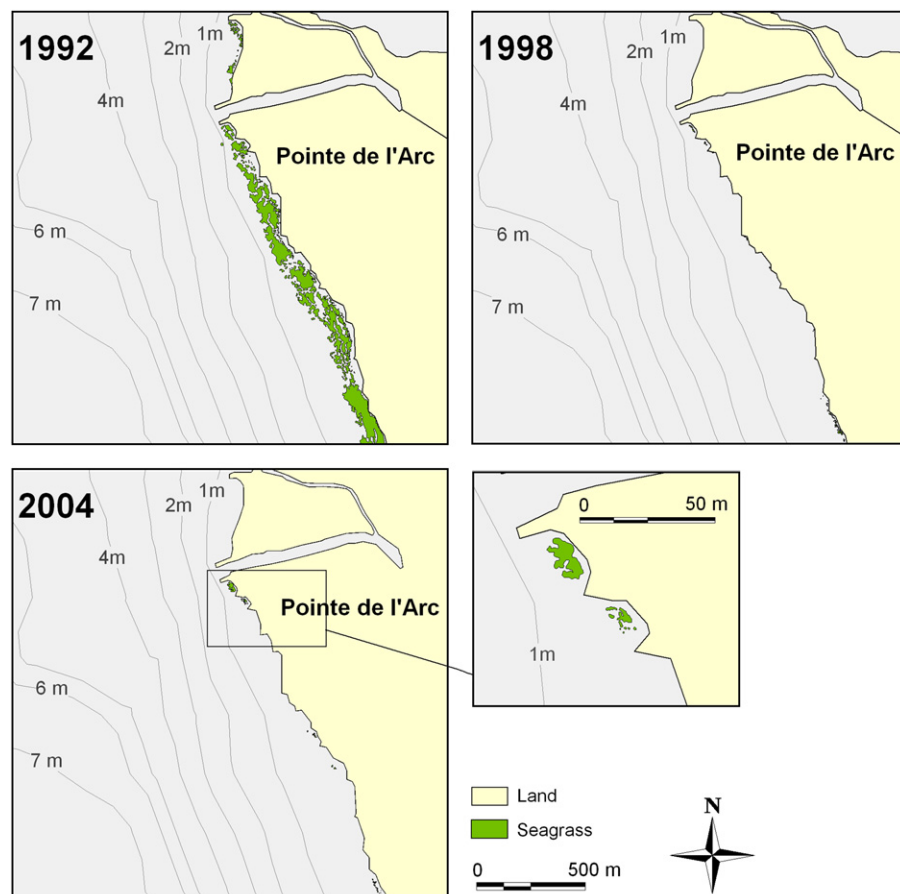


Fig. 2. *Zostera* distribution at Pointe de l'Arc study site in 1992, 1998 and 2004.



dramatic losses between 1944 and 1992 or 1998, with a reduction of covered areas of between 98 and 100%. This decline concerned the four sites studied (Table 2). It was less pronounced along the eastern shore (Pointe de l'Arc and Pointe de Berre; Figs. 2 and 3) than along the western shore of the Berre lagoon (Martigues and Figuerolles; Figs. 4 and 5).

In 2004 the *Zostera* meadows located at Pointe de l'Arc and Pointe de Berre exhibited a slight recovery. The increase is significant at the Pointe de Berre site (Kolmogorov–Smirnov test,  $p < 0.05$ ). At the Figuerolles site, where *Zostera* was absent in 1998, isolated patches were observed in 2004. The 2004 survey concerned almost all the sites where *Zostera noltii* is still present, with the exception of a site discarded due to drift macrophyte accumulation (see Section 2) and small patches located between Pointe de l'Arc and Pointe de Berre, and between Martigues and Figuerolles, not exceeding a few tens of square meters. Considering that the surface area of *Z. noltii* in the study areas represents 1.07 ha (Table 2), the total surface area of *Zostera* meadows of the Berre lagoon can therefore be considered as less than 1.5 ha, a very conservative figure.

The structure of the *Zostera* meadows also showed major changes since 1944 (Table 3). The decline of the covered area resulted from splitting of the largest stands together with the reduction of the mean size of the patches.

### 3.2. Hydrological data

The flow of fresh water from the tributary rivers into the Berre lagoon exhibits a high degree of inter-annual variability (Fig. 6a). The mean annual input into the Berre lagoon is  $0.2 \text{ Gm}^3 \text{ yr}^{-1}$  due to inflow from the rivers Arc, Cadière and Touloubre (69%, 19% and 12% respectively).

The inflow of fresh water from the Durance River diversion began in 1966 ( $2 \text{ Gm}^3 \text{ yr}^{-1}$ ) (Fig. 6b). It fluctuated between 3 and  $4 \text{ Gm}^3 \text{ yr}^{-1}$ , from the late 1960s to early 1990s, with a peak in 1977 ( $6.6 \text{ Gm}^3$ ) and a minimum in 1989 (the hydro-electric plant was out of order for several months). Finally, from the early 1990s to 2004, the mean flow was reduced to  $2 \text{ Gm}^3 \text{ yr}^{-1}$ , in an attempt to reduce its impact on the lagoon habitats. For the 1984–2004 period, the Durance fresh water input was 10–49-fold that of the tributary rivers, depending on the year. Salinity is homogeneous within the 4-m thick surface layer and has fluctuated, since 1994, from 6 to 27 (Fig. 7).

The silt input from the tributary rivers strongly fluctuated from one year to the next, depending upon rainfall and was on average  $25,000 \text{ t yr}^{-1}$  from 1966 to 1998 (data from Imbert et al., 1999).

Input of silt from the Durance River (Fig. 8) culminated in 1977 (1.6 Mt). A first decline occurred in late 1970s, after the setting up of a settling basin, and a second after 1994, when it

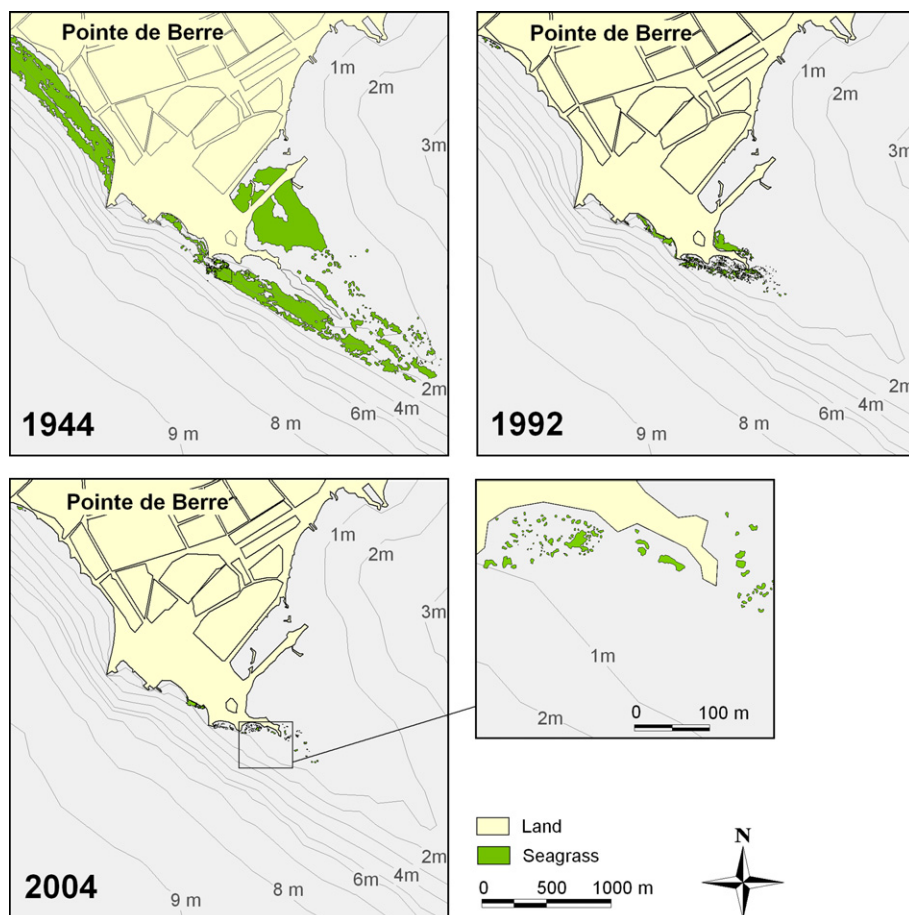


Fig. 3. *Zostera* distribution at Pointe de Berre study site in 1944, 1992 and 2004.

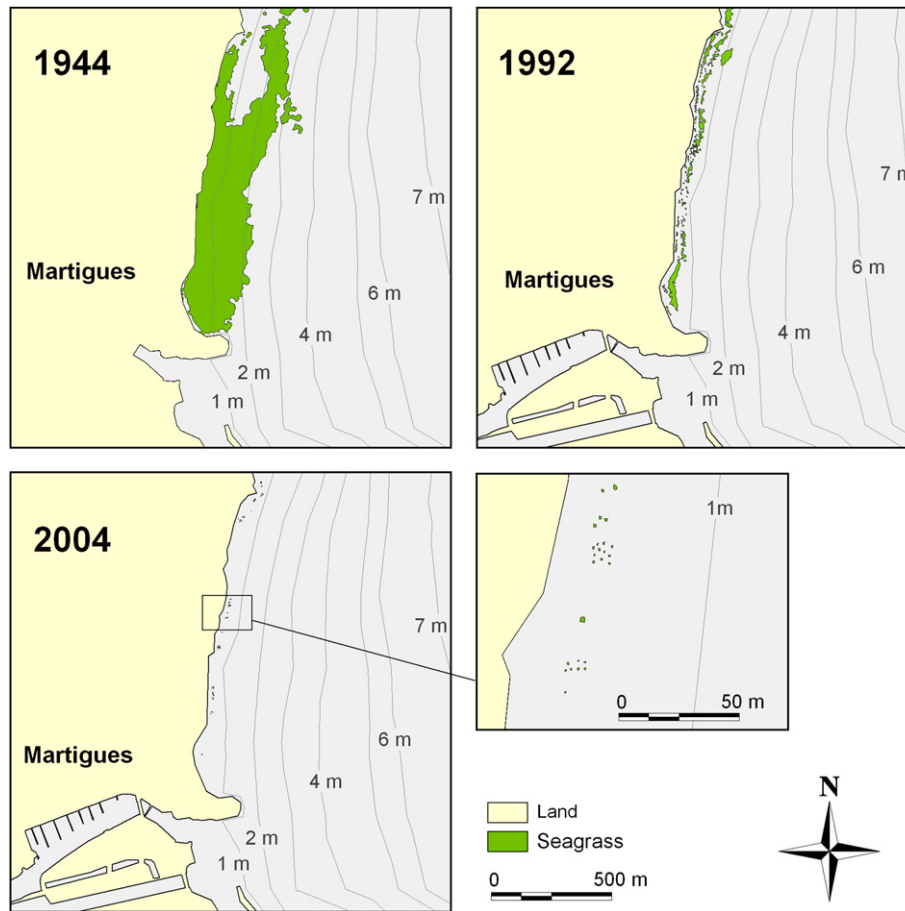


Fig. 4. *Zostera* distribution at Martigues study site in 1944, 1992 and 2004.

was decided to interrupt the diversion of the Durance River during high turbidity events (more than  $2 \text{ kg m}^{-3}$ ), which had previously resulted in high inputs of silt into the lagoon. The inflow of silt from the Durance River was on average 24, 31, 13, 8 and 2-fold that of the tributary rivers, for the 1966–1973, 1974–1980, 1981–1992, 1993–1998 and 1999–2004 periods, respectively.

#### 4. Discussion

There is no doubt that in the late 19th and early 20th century, *Zostera marina* was widespread and dominant in the Berre Lagoon, though a second species, *Zostera noltii*, probably also occurred (Gourret, 1907). A conservative figure of 6000 ha can be proposed, based upon the 6 m depth contour and the ancient literature. The fate of *Z. marina* from that time to the early 1960s, before the diversion of the Durance River towards the lagoon, is poorly known. Authors mentioned only generically the presence of *Zostera*, without specifying the species name (Chevallier, 1916; Mars, 1966). Of interest is the abrupt breakdown of *Zostera* meadows after an exceptionally warm summer (1911) and an exceptionally cold winter (1956) (Chevallier, 1916; Huvé, 1960). The replacement of *Z. marina* by *Z. noltii* may have been in progress as early as 1938, as Mars (1949) emphasized the more and more stunted

appearance of *Zostera* since then, possibly misidentifying *Z. noltii* as “stunted *Z. marina*”. Nevertheless, in the early 1960s, both species were still in more or less equal abundance (Ledoyer, 1966). After 1966, parallel to the overall dramatic decline of the *Zostera* beds, *Z. noltii* was clearly more abundant than *Z. marina* (Riouall, 1971; Huvé et al., 1973), the disappearance of the latter being completed in 1990 (Pergent-Martini et al., 1995; Bernard et al., 2005). Consequently, we cannot infer which of the species was (or were) present in 1944.

The ancient depth limit of *Zostera* meadows was said to be 6 m, sometimes even deeper (down to 9 m) (Marion, 1887; Gourret, 1907; Chevallier, 1916). In 1944, our interpretation of aerial photographs revealed an already shallow limit (3.5 m depth). In the absence of ground truth, the presence of deeper *Zostera* beneath the penetration depth of aerial photographs cannot be ruled out. However, the indented shape of the limit, together with visible patches beyond the limit, suggests that this is not the result of an artefact due to water transparency. This is consistent with the general trend of an upward withdrawal of this limit since at least 1938 (Mars, 1949): 3 m in the early 1970s (Riouall, unpublished data), 1 m in 1992, less than 1 m in 1998 and 2004 (this work).

Between 1992 and 2004, the decline of the *Zostera* meadows continued. This withdrawal can be considered as

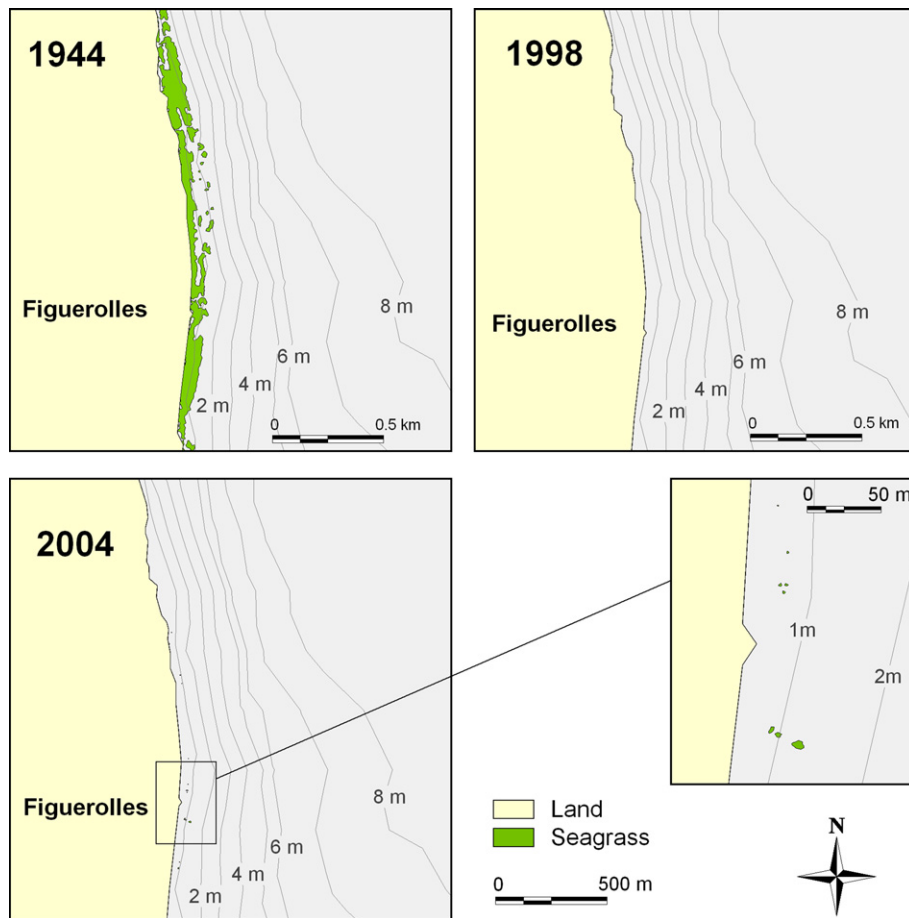


Fig. 5. *Zostera* distribution at Figuerolles study site in 1944, 1998 and 2004.

representative of the whole lagoon, since the present study concerns almost all the sites where *Zostera noltii* is still present. It therefore appears that the reduction of fresh water and silt input since early 1990s, the latter being conspicuous, had little effect on the *Zostera* beds, which became functionally extinct from 1998.

The year-to-year variations in the extent of *Zostera marina* and *Zostera noltii* beds may be considerable, due both to natural factors and human impact (e.g. Rasmussen, 1977; Rismondo et al., 2003; Frederiksen et al., 2004). The best known variation in the extent of the seagrass beds took place in the 1930s. It was known as the “wasting disease” and ravaged the seagrass beds on both sides of the North Atlantic. The Mediterranean seems to have been unaffected. Its cause remains controversial (*Labyrinthula zosterae*, a stramenopile parasite, or a climatic episode). Since then, more localized losses, often unexplained, have been recorded, e.g. Chesapeake Bay (USA), Helford River (Cornwall, UK), Terenez Bay (Brittany, France) (Rasmussen, 1977; Hartog den, 1994, 1996; Hartog den et al., 1996).

In contrast to these cases of decline followed (or not) by recovery, that of the Berre *Zostera* beds runs over at least six decades and possibly almost one century. Several hypotheses could account for this dramatic decline: the drop in

salinity, climate warming, competition with other macrophytes, pollution and turbidity.

As far as salinity is concerned, *Zostera noltii* is a euryhaline species which thrives from near freshwater to salinity over 30, including rapid changes of salinity (Hartog den, 1970; Hemminga and Duarte, 2000; Charpentier et al., 2005). In addition, surface water salinity increased since the early 1990s, while *Z. noltii* continued its decline.

Climate warming can hinder *Zostera marina*, a species with cold water affinities (Hartog den, 1970). However, this is not the case for *Zostera noltii*, whose temperature range is relatively wide (Hartog den, 1970). Climate warming cannot therefore account for its dramatic decline.

The habitat of *Zostera* has not been occupied by other macrophytes, such as *Potamogeton pectinatus* and *Ruppia* sp. Localized and shallow stands of these species occurred up to 1995 (Pergent-Martini et al., 1995; Soltan and Francour, 2000), but they disappeared between 1996 and 1998 (personal observation). So competition with newly established species occupying the habitat cannot be accepted as an explanation.

The concentrations of heavy metals in the Berre sediments (e.g. Cd, Hg, Cu, Pb, Zn) are similar to those observed in other Mediterranean coastal lagoons and even lower than values observed in Thau (France) and Venice (Italy) lagoons (A. Accornero,

Table 3  
Number and size (mean, median, 1st, 3rd quartile and skewness) over time of *Zostera* patches at the four study sites. md = missing data)

Sites	Year	Pointe de l'Arc	Pointe de Berre	Figuerolles	Martigues
Number of patches	1944	md	188	16	34
	1992	180	449	md	154
	1998	18	114	0	md
	2004	21	173	18	92
Mean size (m <sup>2</sup> )	1944	md	4477	14,018	3999
	1992	351	77	md	79
	1998	54	49	0	md
	2004	104	47	10	2
Median (m <sup>2</sup> )	1944	md	216	242	912
	1992	32	13	md	16
	1998	17	9	0	md
	2004	18	10	4	1
1st quartile (m <sup>2</sup> )	1944	md	78	131	252
	1992	13	6	md	10
	1998	7	5	0	md
	2004	6	4	2	1
3rd quartile (m <sup>2</sup> )	1944	md	735	940	1559
	1992	116	35	md	38
	1998	40	26	0	md
	2004	39	22	17	2
Skewness	1944	md	9	4	3
	1992	7	15	md	3
	1998	3	19	0	md
	2004	3	10	3	5

Università degli Studi di Napoli, pers. comm.), where extensive stands of *Zostera* occur.

The present day extent of the *Zostera noltii* meadows, restricted to very shallow waters, suggests light as the limiting factor (Valiela et al., 1997; Vermaat et al., 2000; Peralta et al., 2002; Brun et al., 2003; Charpentier et al., 2005). This is consistent with the shrinking of the euphotic zone, calculated from Secchi disk data by means of the Poole and Atkins relation (1929): mean depth 12.2 m, 10.9 m, 5.1 m and 3.5 m in 1912, 1965, 1966–1969 and 1978–1980, respectively (Chevallier, 1916; Minas, unpublished data; Kim, unpublished data) and the amount of suspended solids in the surface water (Table 4). *Zostera marina* is also very sensitive to light reduction, via the turbidity; shoots die after 3 weeks of light limitation (Giesen et al., 1990; Cabello-Pasini et al., 2002). Since silt input overwhelmingly decreased, light reduction could be due to either the silt input being still too high or to sediment resuspension. Once the major part of seagrass beds, prone to trapping sediment and to hindering its resuspension (see Gacia and Duarte, 2001; Charpentier et al., 2005) have disappeared, the wind easily resuspends them in shallow waters. It is worth noting that Provence is a very windy region, with a wind called the Mistral blowing southwards on average 142 days per year, up to 6 days running, 25–100 km h<sup>-1</sup>, in addition to frequent easterly winds (Fèbvre, 1968; Nérini et al., 2000, 2001). So the decline of *Zostera* could be a self-maintained process. It must be emphasized that most

of the Durance River diversion silt inputs, which were up to 31-fold those from the rivers, did not leave the lagoon towards the sea but on the contrary accumulated, mainly in the deepest areas of its northern part: the mean rate of sedimentation was 0.6–0.8 and 1.8–3.6 cm yr<sup>-1</sup> before and after the setting up of the diversion, respectively (Imbert et al., 1999). During the last period (2000–2004), suspended solids in the water column reverted to the pre-diversion mean values (Table 4). The explanation could lie in the establishment of dense cover of the mussel *Mytilus galloprovincialis* on the shallow (down to 4 m depth) sediment (GB, personal observations). Mussel beds have been suggested as a means to help restoration of lagoon habitats (Katwijk van, 2003).

Light reduction could also be related to eutrophication of the lagoon (Table 4), which started in the 1920s with the urbanisation of the lagoon shore and the setting up of petroleum refining and chemical plants. Eutrophication results in micro- and macro-phytoplankton (*Ulva* sp.) blooms together with high levels of colonization of *Zostera* leaves by epiphytes (Silberstein et al., 1986; De Casabianca et al., 2003): epiphyte biomass can be higher than leaf biomass (GB, personal observations). The suffocation by an enteromorph-like *Ulva* of a mixed meadow of *Zostera marina* and *Zostera noltii* (Hayling Island, Hampshire, UK) and its disappearance has been observed (Hartog den, 1994). Surprisingly, the nitrogen concentration did not clearly decline over time (Table 4), despite the reduction of the Durance River inflow (the nitrate input to the Berre lagoon due to the Durance River diversion is proportional to the water inflow;  $r^2 = 0.99$ ) and the improvement of the tributary river water quality from the 1970s to the 2000s (Agence de l'Eau Rhône Méditerranée Corse, 2006) with the setting up of sewage treatment plants; the percentage of urban sewage undergoing treatment was 10%, 18%, 40% and 95% in 1970, 1980, 1990 and 2000, respectively, while the population of the catchment area increased less than two fold (INSEE, 2006). In addition, between 2000 and 2004, all the sewage previously flowing directly into the lagoon has been diverted towards sewage treatment plants. Overall, the nitrogen input to the Berre Lagoon was 4665 t, 2514 t, 2021 t and 1338 t in 1977, 1983–84, 2000 and 2004, respectively (Kim and Travers, 1997a; Romana et al., unpublished data; Banque HYDRO, 2006; Réseau National de Bassin, 2006). The release of nutrients trapped within the lagoon sediments, as observed in Orbetello lagoon, Italy (Lardicci et al., 2001) and in the Greifswalder Bodden, a Baltic estuary (Munkes, 2005), could account for the concentration of nutrients which remains higher than that recorded before the diversion of the Durance River. During wind episodes, the vertical mixing of the water column provides a nutrient input in the photic zone inducing an extremely intense bloom of phytoplankton: up to 50 µg L<sup>-1</sup> chl *a* (Minas et al., 1976). Be that as it may, present day concentrations of nutrients are similar to those recorded in comparable Mediterranean lagoons, e.g. Venice lagoon, Italy (Sfriso and Marcomini, 1997) and Thau lagoon, France (Laugier et al., 1999). It is worth noting that both Venice and Thau lagoons, despite high levels of organic and nutrient load, still harbour extensive *Zostera* meadows (Laugier et al., 1999;



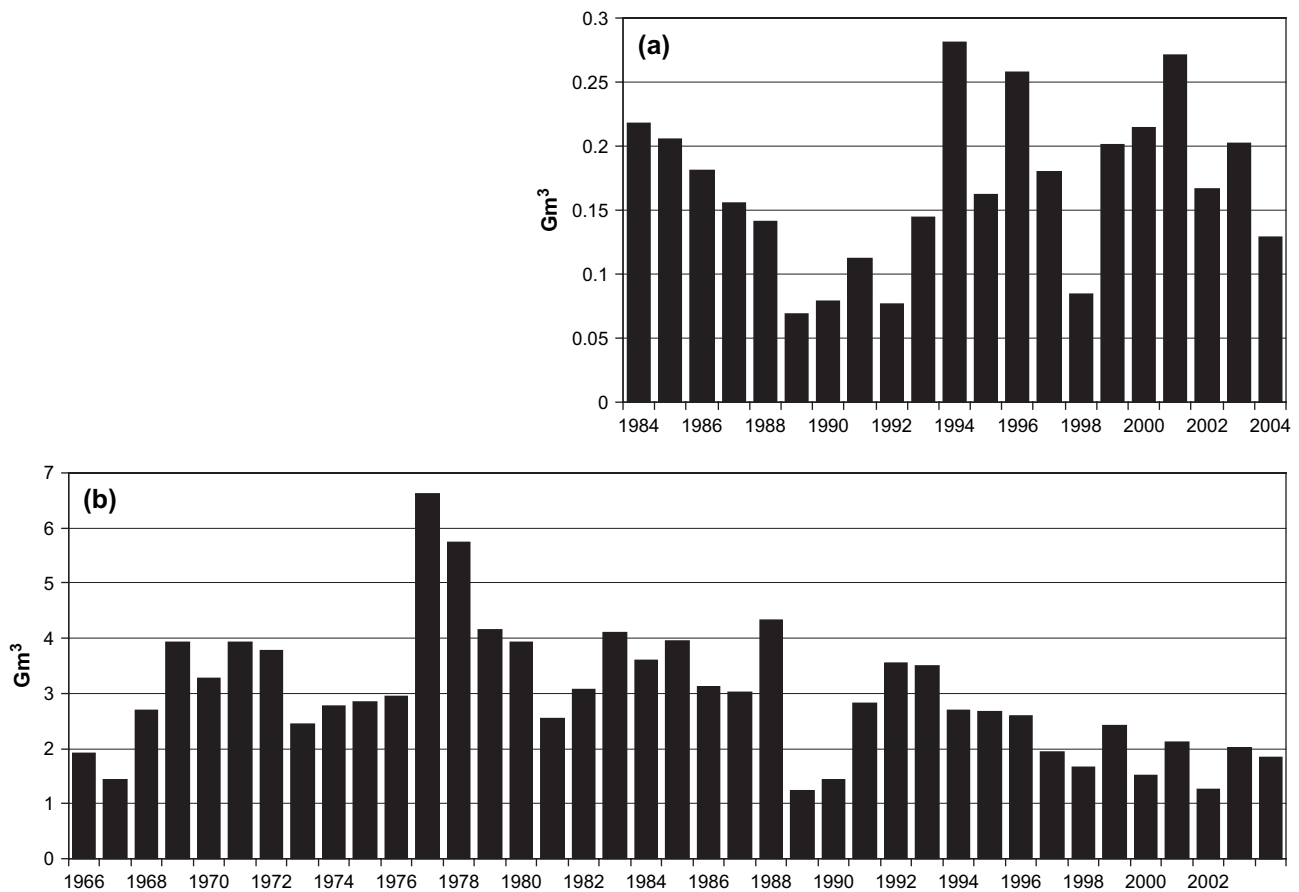


Fig. 6. Flow of freshwater (in  $\text{Gm}^3 \text{a}^{-1}$ ) from: (a) the rivers flowing into the Berre Lagoon, from 1984 to 2004; and (b) from the Durance River via the diversion of the Saint Chamas hydroelectric plant, from 1966 to 2004.

Rismondo et al., 2003). According to Bowen and Valiela (2001) and Hauxwell et al. (2003), substantial *Z. marina* loss occurs at loads of  $\sim 30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ , and total disappearance at loads  $\geq 60 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ; in the Berre Lagoon, the nitrogen load declined from 301 to  $86 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ , between 1977 and 2004, but still lies above the threshold of *Z. marina* disappearance, which accounts for the lack of recolonization. Several newly established patches of *Z. marina*, which were observed in 2001 in the southern part of the lagoon (Bernard et al., 2005), eventually disappeared. Unfortunately, no data on nitrogen sensitivity are available for *Z. noltii*, but its persistence during the period of highest nitrogen load suggests a far higher threshold.

Whatever the reason for light reduction (turbidity and/or eutrophication), *Zostera noltii* may prove to be more sensitive than other seagrasses. The length of time a seagrass species can survive below its minimum light requirement is related to its ability to store carbohydrates, especially in the rhizomes (Alcoverro et al., 1999; Cabello-Pasini et al., 2002). The storage capacity and the clonal integration (sensu Hartnett and Bazzaz, 1983) is largely seagrass size-dependent (Hemminga and Duarte, 2000). Small species like *Z. noltii* have presumably a lower capacity than those with thick and long-lived rhizomes, conferring a very limited tolerance to light deprivation episodes (Marbà and Duarte, 1998; Peralta et al., 2002).

The reduction of shoot density in response to decreased light availability is also a well-known response of seagrasses to reduce self-shading and therefore to enhance light harvesting efficiency (Hemminga and Duarte, 2000). Furthermore, a high ratio of above-ground/below-ground biomass would be favoured at low-light conditions (Hemminga, 1998). Low shoot-density and high above-ground/below-ground ratio observed for the *Zostera noltii* beds in the Berre Lagoon (GB, personal observations), compared to other Mediterranean lagoons (Laugier et al., 1999; Menéndez et al., 2002; Brun et al., 2003), support the hypothesis of light limitation.

The present day surviving *Zostera noltii* stands in the Berre lagoon mostly consist of small patches, with a skewed patch size distribution (Table 3) which is consistent with the distribution pattern usually reported for other species or populations (Duarte and Sand-Jensen, 1990; Olesen and Sand-Jensen, 1994; Vidondo et al., 1997; Ramage and Schiel, 1999). Skewness toward low values is indicative of fast patch formation (mostly through seedlings) and high mortality rates observed in seagrass populations depending largely on sexual reproduction (Duarte and Sand-Jensen, 1990). Such a high patch mortality rate is consistent with the poor environmental conditions in the Berre Lagoon.

Patch mortality is size-dependent. As patch growth proceeds, mortality rate decreases and heterogeneity (i.e. within

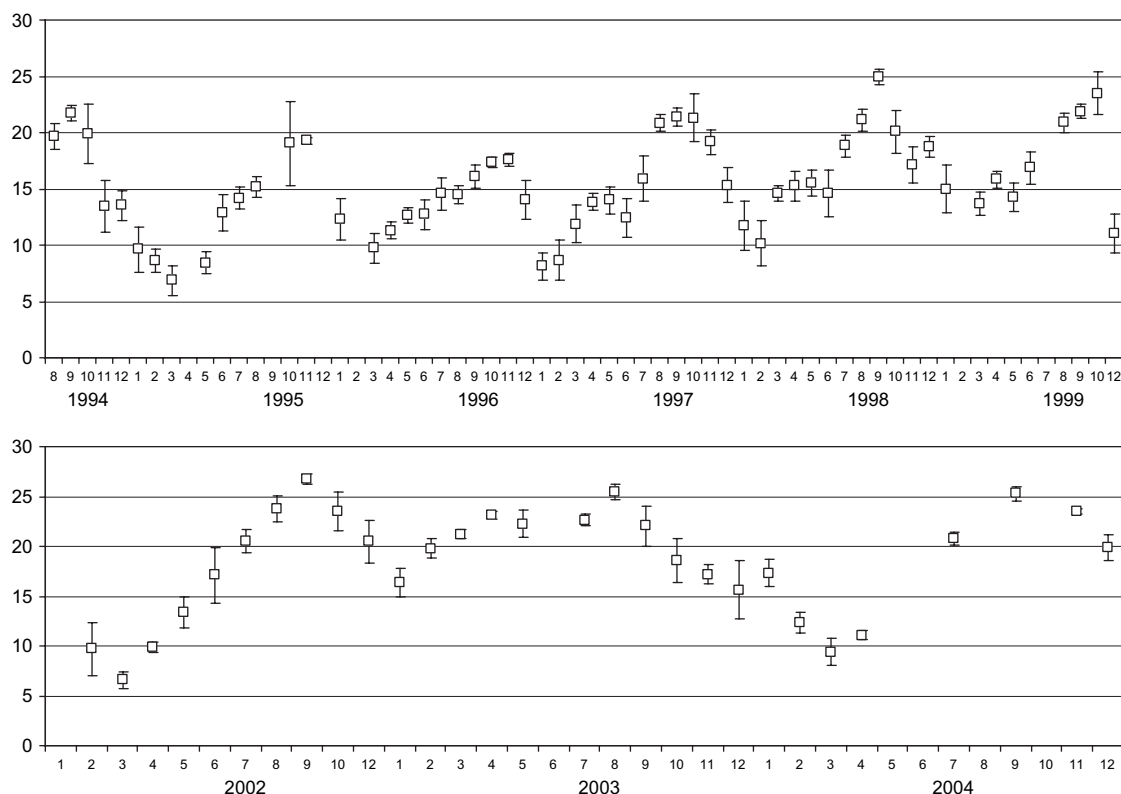


Fig. 7. Mean salinity of the surface layer down to 4 m depth from 1994 through 1999 and 2002 to 2004 in the Berre Lagoon.

patch variability) increases (Duarte and Sand-Jensen, 1990). Several studies support the notion of a minimum patch size above which the probability of patch mortality decreases (Duarte and Sand-Jensen, 1990; Olesen and Sand-Jensen, 1994) due to enhanced anchoring, mutual physical protection and physiological integration (“mutually sheltering structure”) (Thayer et al., 1984). For *Zostera novazelandica* Setchell, this minimum patch size is  $0.4 \text{ m}^2$  (Ramage and Schiel, 1999). Our results do not provide an adequate basis for suggesting a minimum patch size for *Zostera noltii*, though many patches disappeared from one map to the next, as factors

other than the mutually sheltering structure phenomenon can operate.

The present day near extinction of *Zostera* in the Berre lagoon probably results from several causes, operating over decades in synergy or successively, namely, pollution (including nutrients), low salinity and turbidity. There is no doubt that the decline of the *Zostera* beds began before the diversion of the Durance River towards the lagoon. However, the inrush of huge amounts of water and sediment was obviously the reason for the dramatic withdrawal of their lower limit and their eventual near extirpation. Overall, up to 2000, the lagoon

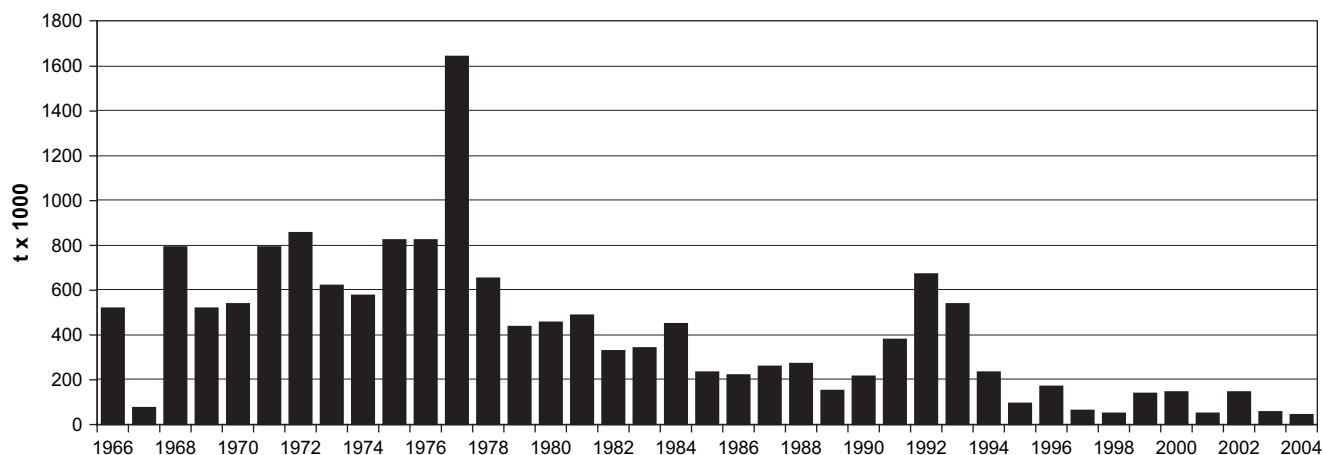


Fig. 8. Flow of silt (in  $10^3$  metric tons) from the Durance River via the diversion of Saint Chamas hydroelectric plant, into the Berre lagoon, from 1966 to 2004.

Table 4  
Mean (year round) content in  $\text{NO}_3$ ,  $\text{PO}_4$ , suspended solids and chlorophyll  $a$  of the surface water (less than 1 m depth) of the Berre lagoon, calculated from published and unpublished data. md = missing data. ( ) = SD, where available. Statistical analysis by Kruskal–Wallis with post hoc comparisons using a Dunn method. Periods with different letters below the SD were significantly different ( $p < 0.01$ )

Period	1955–56	1965	1966–69	1977–78	1978–80	1984–85	1994–99	2000–04
Data source	Nisbet and Schachter (1961)	Blanc et al. (1967), Minas (unpubl. data; 1974)	Minas (unpubl. data; 1974)	Kim (unpubl. data), Kim and Travers (1997a,b)	RNO* (unpubl. data)	M. Minas and R. Arfi (unpubl. data)	P. Raimbault (unpubl. data)	P. Raimbault (unpubl. data)
Number of sampled sites	16	5	5	5	2	2	10	10
Number of sampled months/year	10	12	11	12	12	12	12	12
$\text{NO}_3$ ( $\mu\text{mol L}^{-1}$ )	1.8 (3.5)a	1.8	6.6 (8.2)bc	17.6	10.7 (8.9)d	md	6.0 (8.8)b	9.9 (10.4)cd
$\text{PO}_4$ ( $\mu\text{mol L}^{-1}$ )	0.9 (0.9)a	0.6 (0.2)a	0.3 (0.2)b	0.5	0.6 (0.5)c	md	0.2 (0.3)d	0.3 (0.2)b
Suspended solids ( $\text{mg L}^{-1}$ )	md	8.5 (3.4)a	9.5 (16.4)b	8.3 (4.1)a	md	34.2 (39.0)c	16.3 (12.3)d	7.7 (2.7)a
Chlorophyll $a$ ( $\mu\text{g L}^{-1}$ )	md	5.2 (2.1)a	11.1 (6.9)b	12.6 (7.2)b	md	md	43.2 (46.1)c	12.8 (8.7)b

shifted from a system dominated by benthic primary producers (seagrasses) to a system with bare silt bottoms, no longer trapped under the seagrass canopy and therefore prone to resuspension, dominated by plankton primary producers. A similar shift has been described in a shallow lake in Denmark (McGowan et al., 2005) and in a Baltic Sea estuary (Munkes, 2005). The threshold level of the forcing variables allowing a natural shift back from the apparently “stable” bare silt habitats to the previous “stable” *Zostera* state remains unknown (see Knowlton, 2004; Schröder et al., 2005). Could the slight and inconspicuous progression of *Zostera noltii* since 2000, parallel to mussel development and turbidity reduction, be considered as the harbinger of a new shift towards a previous state? Or is it just a casual episode in the context of a phase which could be long-lasting, due to a possible hysteresis of the system in relation with silt resuspension (beyond the present-day interlude) or release of nutrient trapped within the sediments, or both?

## 5. Conclusion

The decline of the extensive *Zostera* meadows which occupied a large part (possibly over 6000 ha) of the Berre Lagoon in the early 20th century possibly began more than 60 years ago. It has been attributed to pollution and, from 1966, when the Saint Chamas power plant went into service, to the diversion of the Durance River, which resulted in a heavy input of freshwater, nitrogen and silt into the Berre Lagoon.

Subsequently, a significant reduction of silt (from the late 1970s) and freshwater (from the early 1990s) inputs occurred, in an attempt to reduce their impact on the lagoon habitats. Concomitantly, urban and industrial sewage outputs were drastically reduced, though the nitrogen concentration of the body water did not conspicuously change. As far as the *Zostera* meadows are concerned, their decline has continued steadily, to near extirpation from 1998 onward (less than 1.5 ha overall), despite a very slight recovery in 2004.

The present day localization of *Zostera noltii*, restricted to very shallow waters, suggests that light could be the limiting factor, either due to silt resuspension or eutrophication.

Our results suggest that freshwater, silt and nutrient inputs were the forcing variables responsible for the phase shift from seagrass meadows to bare silt habitats. However they do not provide a basis for forecasting whether we are on the brink of a reverse shift or in the context of a long-lasting alternative “stable” state.

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## References

- Agence de l'Eau Rhône Méditerranée Corse, 2006. <http://rdb.eaurmc.fr>.
- Alcoverro, T., Zimmerman, R.C., Kohrs, D.G., Alberte, R.S., 1999. Resource allocation and sucrose mobilization in light-limited eelgrass *Zostera marina*. *Marine Ecology Progress Series* 187, 121–131.
- Arfi, R., 1989. Annual cycles and budget of nutrients in Berre Lagoon (Mediterranean, France). *Internationale Revue der Gesamten Hydrobiologie* 74, 29–49.
- Banque HYDRO, 2006. <http://www.hydro.eaufrance.fr>.
- Bernard, G., Bonhomme, P., Boudouresque, C.F., 2005. Recovery of the seagrass *Zostera marina* in a disturbed Mediterranean lagoon (Etang de Berre, Bouches-du-Rhône, Southern France). *Hydrobiologia* 539, 157–161.
- Blanc, F., Coste, B., Minas, H.J., Szekielda, K.H., 1967. Distribution des principaux facteurs hydrobiologiques dans un milieu de forte production organique: l'étang de Berre. *Marine Biology* 1, 43–55.
- Bowen, J.L., Valiela, I., 2001. The ecological effects of urbanization of coastal watersheds: historical increases in nitrogen loads and eutrophication of Waquoit Bay estuaries. *Canadian Journal of Fisheries and Aquatic Sciences* 58, 1489–1500.
- Brun, F.G., Pérez-Lloréns, J.L., Hernández, I., Vergara, J.J., 2003. Patch distribution and within-patch dynamics of the seagrass *Zostera noltii* Hornem. in Los Toruños salt-marsh, Cádiz Bay, natural park, Spain. *Botanica Marina* 46, 513–524.
- Cabello-Pasini, A., Lara-Turrent, C., Zimmerman, R.C., 2002. Effect of storms on photosynthesis, carbohydrate content and survival of eelgrass populations from a coastal lagoon and the adjacent open ocean. *Aquatic Botany* 74, 149–164.
- Cardoso, P.G., Pardal, M.A., Lillebø, A.I., Ferreira, S.M., Raffaelli, D., Marques, J.C., 2004. Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. *Journal of Experimental Marine Biology and Ecology* 302, 233–248.
- Charpentier, A., Grillas, P., Lescuyer, F., Coulet, E., Auby, I., 2005. Spatio-temporal dynamics of a *Zostera noltii* dominated community over a period of fluctuating salinity in a shallow lagoon, Southern France. *Estuarine, Coastal and Shelf Sciences* 64, 307–315.
- Chevallier, A., 1916. L'étang de Berre. *Annales de l'Institut Océanographique* 7, 1–91.
- De Casabianca, M.L., Rabotin, M., Rigault, R., 2003. Preliminary results on eelgrass regression and red seaweed dominance under increasing eutrophication (Thau Lagoon, France). *Acta Adriatica* 44, 33–40.
- Duarte, C.M., Sand-Jensen, K., 1990. Seagrass colonisation: patch formation and patch growth in *Cymodocea nodosa*. *Marine Ecology Progress Series* 65, 193–200.
- Fèbvre, J., 1968. Etude bionomique des substrats meubles de l'étang de Berre. *Recueil des Travaux de la Station Marine d'Endoume* 44, 298–355.
- Frederiksen, M., Krause-Jensen, D., Holmer, M., Laursen, J.S., 2004. Long-term changes in area distribution of eelgrass (*Zostera marina*) in Danish coastal waters. *Aquatic Botany* 78, 167–181.
- Gacia, E., Duarte, C.M., 2001. Sediment retention by Mediterranean *Posidonia oceanica* meadow: the balance between deposition and resuspension. *Estuarine, Coastal and Shelf Sciences* 52, 505–514.
- Giesen, W.B.J.T., Katwijk van, M.M., Hartog den, C., 1990. Eelgrass condition and turbidity in the Dutch Wadden Sea. *Aquatic Botany* 37, 71–85.
- Gourret, P., 1907. Topographie zoologique des étangs de Caronte, de Labillon, de Berre et de Bolmon. Flore, faune, migrations, etc. *Annales du Muséum d'Histoire Naturelle de Marseille* 11, 1–166.
- Hartnett, D.C., Bazzaz, F.A., 1983. Physiological integration among intracolonial ramets in *Solidago canadensis*. *Ecology* 64, 779–788.
- Hartog den, C., 1970. The Seagrasses of the World. North Holland Publ. Co., Amsterdam, 275 pp.
- Hartog den, C., 1994. Suffocation of a littoral *Zostera* bed by *Enteromorpha radiata*. *Aquatic Botany* 47, 21–28.
- Hartog den, C., 1996. Sudden declines of seagrass beds: “wasting disease” and other disasters. In: Kuo, J., Phillips, R.C., Walker, D.I., Kirkman, H. (Eds.), *Seagrass Biology. Proceedings of an International Workshop*, Rottneest Island. Univ. of Western Australia Publ., Australia, pp. 307–314.
- Hartog den, C., Vergeer, L.H.T., Rismondo, A.F., 1996. Occurrence of *Labyrinthula zosterae* in *Zostera marina* from Venice Lagoon. *Botanica Marina* 39, 23–26.
- Hauxwell, J., Cebrián, J., Valiela, I., 2003. Eelgrass *Zostera marina* loss in temperate estuaries: relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Marine Ecology Progress Series* 247, 59–73.
- Hemminga, M.A., 1998. The root/rhizome system of seagrasses: an asset and a burden. *Journal of Sea Research* 39, 183–196.
- Hemminga, M.A., Duarte, C.M., 2000. *Seagrass Ecology*. Cambridge University Press, Cambridge, 298 pp.
- Huvé, H., 1960. Sur l'invasissement récent d'une portion de l'Etang de Berre (Etang de Vaine) par une Céramiacée du genre *Spermothamnion*. Rapport et Procès-verbaux des Réunions de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée 15, 141–145.
- Huvé, P., Huvé, H., 1954. Zonation superficielle des côtes rocheuses de l'Etang de Berre et comparaison avec celles du Golfe de Marseille (de Carry à Sausset). *Vie et Milieu* 5, 330–344.
- Huvé, H., Kiener, A., Riouall, R., 1973. Modifications de la flore et des populations ichtyologiques des étangs de Berre et de Vaine (Bouches-du-Rhône) en fonction des conditions hydrologiques créées par le déversement de la Durance. *Bulletin du Muséum d'Histoire Naturelle de Marseille* 33, 123–134. + Tables I–III.
- Imbert, G., Kerambrun, P., Degiovanni, C., 1999. Hydrodynamics and sedimentation linked to anthropogenic inputs in a Mediterranean littoral basin. *Comptes rendus de l'Académie des Sciences* 329, 205–209.
- INSEE, 2006. <http://www.insee.fr>.
- Katwijk van, M.M., 2003. Reintroduction of Eelgrass (*Zostera marina* L.) in the Dutch Wadden Sea: A Research Overview and Management Vision. *Proceedings of the 10th International Scientific Wadden Sea Symposium*, Groningen, 2000. Ministry of Agriculture, Nature Management and Fisheries/University of Groningen, Dept. of Marine Biology Publ., NL, pp. 173–196.
- Kim, K.T., 1985. La salinité et la densité des eaux des étangs de Berre et de Vaine (Méditerranée nord-occidentale). Relations avec les affluents et le milieu marin voisin. *Journal of Natural Sciences* 5, 221–246.
- Kim, K.T., Travers, M., 1997a. Les nutriments de l'Etang de Berre et des milieux aquatiques contigus (eaux douces, saumâtres et marines; Méditerranée NW). 2 Les nitrates. *Marine Nature* 5, 35–48.
- Kim, K.T., Travers, M., 1997b. Les nutriments de l'Etang de Berre et des milieux aquatiques contigus (eaux douces, saumâtres et marines; Méditerranée NW). 4 Les nitrites. *Marine Nature* 5, 65–78.
- Knowlton, N., 2004. Multiple “stable” states and the conservation of marine ecosystems. *Progress in Oceanography* 60, 387–396.
- Lardicci, C., Como, S., Corti, S., Rossi, F., 2001. Recovery of the macrozoobenthic community after severe dystrophic crises in a Mediterranean coastal lagoon (Orbetello, Italy). *Marine Pollution Bulletin* 42, 202–214.
- Laugier, T., Rigollet, V., De Casabianca, M.L., 1999. Seasonal dynamics in mixed eelgrass beds, *Zostera marina* L. and *Z. noltii* Hornem., in a Mediterranean coastal lagoon (Thau lagoon, France). *Aquatic Botany* 63, 51–69.
- Ledoyer, M., 1966. Ecologie de la faune vagile des biotopes méditerranéens accessibles en scaphandre autonome. II. Données analytiques sur les herbiers de Phanérogames. *Recueil des Travaux de la Station Marine d'Endoume* 41, 135–164.
- Marbà, N., Duarte, C.M., 1998. Rhizome elongation and seagrass clonal growth. *Marine Ecology Progress Series* 174, 269–280.
- Marion, A.F., 1887. Etude des étangs saumâtres de Berre (Bouches-du-Rhône). Faune ichtyologique. *Comptes Rendus de l'Académie des Sciences* 104, 1306–1308.



- Mars, P., 1949. Contribution à l'étude biologique des étangs méditerranéens. Quelques aspects de l'évolution de l'étang de Berre. Bulletin de la Société Linnéenne de Provence 17, 8–16.
- Mars, P., 1966. Recherches sur quelques étangs du littoral méditerranéen français et sur leurs faunes malacologiques. Vie et Milieu 20, 1–359.
- McGowan, S., Leavitt, P.R., Hall, R.L., Anderson, N.J., Jeppesen, E., Odgaard, B.V., 2005. Controls of algal abundance and community composition during ecosystem state change. Ecology 86, 2200–2211.
- McKenzie, L.J., Finkbeiner, M.A., Kirkman, H., 2001. Methods for mapping seagrass distribution. In: Short, F.T., Coles, R.G. (Eds.), Global Seagrass Research Methods. Elsevier Science B.V., Amsterdam, pp. 101–121.
- Menéndez, M., Hernandez, O., Comin, F.A., 2002. Spatial distribution and ecophysiological characteristics of macrophytes in a Mediterranean coastal lagoon. Estuarine, Coastal and Shelf Science 55, 403–413.
- Minas, M., 1974. Distribution, circulation et évolution des éléments nutritifs, en particulier du phosphore minéral, dans l'étang de Berre. Influence des eaux duranciennes. Internationale Revue der Gesamten Hydrobiologie 59, 509–542.
- Minas, M., Bonin, M.C., Coste, B., David, P., Minas, H.J., 1976. Caractère particulier du mécanisme de l'eutrophisation dans l'étang de Berre. Annales de l'Institut Océanographique 52, 153–161.
- Munkes, B., 2005. Eutrophication, phase shift, the delay and the potential return in the Greifswalder Bodden, Baltic Sea. Aquatic Sciences 67, 372–381.
- Nérini, D., Durbec, J.P., Manté, C., 2000. Analysis of oxygen rate time series in a strongly polluted lagoon using a regression tree method. Ecological Modelling 133, 95–105.
- Nérini, D., Manté, C., Durbec, J.P., Garcia, F., 2001. Une méthode statistique de détermination de séquences caractéristiques dans une série temporelle de plusieurs variables. Application à la physico-chimie des eaux de l'étang de Berre. Comptes-Rendus de l'Académie des Sciences 332, 457–464.
- Nisbet, M., Schachter, D., 1961. Contribution à l'étude écologique des étangs méditerranéens. Constituants chimiques des eaux de quelques étangs littoraux. Bulletin de l'Institut Océanographique de Monaco 1207, 4–46.
- Olesen, B., Sand-Jensen, K., 1994. Patch dynamic of eelgrass *Zostera marina*. Marine Ecology Progress Series 106, 147–156.
- Peralta, G., Pérez-Lloréns, J.L., Hernández, I., Vergara, J.J., 2002. Effects of light availability on growth, architecture and nutrient content of the seagrass *Zostera noltii* Hornem. Journal of Experimental Marine Biology and Ecology 269, 9–26.
- Pergent-Martini, C., Semroud, R., Rico-Raimondino, V., Pergent, G., 1995. Localisation et Évolution des Peuplements de Phanérogames Aquatiques de l'Étang de Berre (Bouches du Rhône – France). Proceedings of the 39th National Meeting of the Association Française de Limnologie. Université de Corse & Agence de l'Eau Rhône-Méditerranée-Corse Publ., France, pp. 169–179.
- Poole, H.H., Atkins, W.R.G., 1929. Photo electric measurements of submarine illumination throughout the year. Journal of Marine Biology Assessment 16, 297–324.
- Ramage, D.L., Schiel, D.R., 1999. Patch dynamic and response to disturbance of the seagrass *Zostera novazelandica* on intertidal platforms in southern New Zealand. Marine Ecology Progress Series 189, 275–288.
- Rasmussen, E., 1977. The wasting disease of eelgrass (*Zostera marina*) and its effects on environmental factors and fauna. In: McRoy, C.P., Helfferich, C. (Eds.), Seagrass Ecosystems. Dekker, pp. 1–51.
- Réseau National de Bassin, 2006. <http://sandre.eaufrance.fr>.
- Riouall, R., 1971. Inventaire floristique des étangs de Berre et de Vaïne (années 1970–1971). Bulletin de la Société des Sciences Naturelles et d'Archéologie de Toulon et du Var 23, 153–160.
- Riouall, R., 1972. A propos des Entéromorphes des étangs de Berre et de Vaïne. Bulletin du Muséum d'Histoire Naturelle de Marseille 32, 153–160.
- Rismondo, A., Curiel, D., Scarton, F., Mion, D., Caniglia, G., 2003. A New Seagrass Map for the Venice Lagoon. In: Özhan, E. (Ed.), Proceedings of the Sixth International Conference on the Mediterranean Coastal Environment (2). Ravenna, Italy. Medcoast 03. Middle East Technical University Publ., Ankara, Turkey, pp. 843–852.
- Schachter, D., 1954. A propos d'une pollution accidentelle de l'étang de Berre provoquée par un déversement massif d'hydrocarbures. Rapport et Procès-verbaux des Réunions de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée 12, 251–254.
- Schröder, A., Persson, L., De Roos, A.M., 2005. Direct experimental evidence for alternative stable states: a review. Oikos 110, 3–19.
- Sfriso, A., Marcomini, A., 1997. Macrophytes production in a Mediterranean coastal lagoon. Part I. Coupling with physico-chemical parameters and nutrients concentration in water. Marine Environmental Research 44, 351–375.
- Short, F.T., Wyllie-Echeverria, S., 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation 23, 17–27.
- Silberstein, K., Chiffings, A.W., McComb, A.J., 1986. The loss of seagrasses in cockburn sound, Western Australia. III. The effect of epiphytes on productivity of *Posidonia australis* Hook f. Aquatic Botany 24, 355–371.
- Soltan, D., Francour, P., 2000. Monitoring system of benthic macrophytes communities in Berre and Vaïne ponds: development of a new strategy. Journal de Recherche Océanographique 25, 53–57.
- Stora, G., Arnoux, A., Galas, M., 1995. Time and spatial dynamic of Mediterranean lagoon macrobenthos during an exceptionally prolonged interruption of freshwater inputs. Hydrobiologia 300–301, 123–132.
- Thayer, G.W., Kenworthy, W.J., Fonseca, M.S., 1984. The ecology of eelgrass meadows of the Atlantic Coast: a Community Profile. U.S. Fish Wildlife Service FWS/OBS-84/02, 1–147.
- Valiela, I., Collins, G., Kremer, J., Lajtha, M., Geist, M., Seely, B., Brawley, J., Sham, C.H., 1997. Nitrogen loading from coastal watersheds to receiving estuaries: review of methods and calculation of loading to Waquoit, Bay. Ecology Applications 7, 358–380.
- Vermaat, J.E., Verhagen, F.C.A., Lindenburg, D., 2000. Contrasting responses in two populations of *Zostera noltii* Hornem. to experimental photoperiod manipulation at two salinities. Aquatic Botany 67, 179–189.
- Vidondo, B., Duarte, C.M., Middelboe, A.L., Stefansen, K., Lützen, T., Nielsen, S.L., 1997. Dynamics of a landscape mosaic: size and age distributions, growth and demography of seagrass *Cymodocea nodosa* patches. Marine Ecology Progress Series 158, 131–138.
- Zar, J.H., 1999. Biostatistical Analysis, fourth ed. Prentice-Hall Inc., London, 663 pp.