

## ***Community shifts, alternative stable states, biogeochemical controls and feedbacks in eutrophic coastal lagoons: a brief overview***

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### ABSTRACT

(1) The succession of primary producer communities in coastal lagoons is analysed in the light of the regime shift theory. Pristine coastal lagoons are considered to be dominated by extensive meadows of seagrass species, which are assumed to take advantage of nutrient supply from sediments. An increasing nutrient input is thought to favour phytoplankton and/or epiphytic micro-, macroalgae as well as opportunistic ephemeral macroalgae that coexist with seagrasses. In the latest stages of this succession, the imbalance of phosphorus to nitrogen ratio can favour macroalgal, cyanobacteria and/or picoplankton blooms, often causing dystrophy.

(2) The primary causes of shifts and succession in the macrophyte community are nutrient loadings, mainly nitrogen, as well as changes in coastal hydrology or interactions between them. To some extent, in very shallow choked lagoons, benthic vegetation is mainly controlled by loading rates, while in open deep estuaries hydromorphological factors predominate.

(3) External stressors/perturbations cause an amplification in benthic biogeochemical processes, e.g. wide variations in primary productivity and dark respiration, with large oscillations in oxygen and sulphide concentrations. Altered biogeochemical processes can determine positive feedbacks inducing a shift from pristine to altered macrophyte communities, which in turn amplify the perturbation until the shift becomes irreversible.

(4) Macrophyte typology, organic matter composition and sedimentary geochemistry are primary factors in controlling feedbacks and shifts. For example, the sedimentary buffering capacity of iron controls sulphide and phosphates, while nitrogen cycling is mainly controlled by primary producers - microbial process interactions.

(5) The alternative states which occur through the transition from pristine to modified primary producer communities can also be viewed as a sequence of stable states with different degrees of embedded information and with different ecological functions.

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KEY WORDS: coastal lagoons; benthic vegetation; community shifts; biogeochemical controls; eutrophication

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## COASTAL LAGOONS: TRANSITIONAL ECOSYSTEMS WITH TRANSITIONAL STATES

Coastal lagoons are intrinsically unstable, owing to their location along the coastline and inherent morphodynamics. They have shallow waters, only a few metres deep, and salinity that varies from fresh water to hypersaline depending on their water balance (Kjerfve, 1994). The degree of confinement depends upon the number and width of connections with the adjacent sea and on freshwater inputs. In the Mediterranean Sea, coastal lagoons are restricted and often choked (for definition see Kjerfve, 1994), with the only exception being deltaic coastal lagoons which are open and highly dynamic (Bellan, 1987).

Coastal lagoons are subjected to natural disturbance which depends mainly on morphodynamics and on climatic factors; e.g. freshwater flooding and summer drought. Owing to their location and value, coastal lagoons suffer also from strong human pressures, as they receive organic and mineral nutrients and are exploited for aquaculture and tourism.

When defining the ecosystem properties and processes of coastal lagoons, it is important to recognize that they are transitional waterbodies. The transition from the continental to the marine domains determines a steep gradient of sedimentological, hydrological and biological conditions, which make the lagoon not a unique system per se, but rather a composite mosaic of habitats (Tagliapietra and Volpi-Ghirardini, 2006). Moreover, the influence of natural and human stressors can induce a wide variability in those conditions, leading to substantial changes of the ecosystem and associated communities. To some extent and within certain thresholds, transitional conditions could allow multiple alternative and/or stable states to coexist and persist over several generations after the cessation of perturbations (for definition and details see Knowlton, 2004). Increased perturbation intensity and/or abrupt changes in perturbations and stressors can induce persistent and radical changes in abundance or productivity of one or more components of the community leading to a dominance of one or few of them (Folke *et al.*, 2004).

The ecological theory of regime shifts acknowledges that most often, abrupt changes in the ecosystem features are determined by responses of biotic-dependent variables to abiotic control variables or stressors (Holling, 1973; May, 1977; Collie *et al.*, 2004; Steele, 2004). The relationships between dependent and control variables determine the strength of the shifts. When the relationship is linear the shift is smoothed and the ecosystem evolves through a continuum of stress-dependent equilibria. Non-linear relationships are the causal factor of sudden and abrupt changes, which amplify the effects of the control variable on the community component, determining a shift from a stable

equilibrium to another stable equilibrium from which recovery is not possible, even in the absence of cause, without the supply of external energy (Gunderson, 2000; Maler, 2000; de Wit *et al.*, 2001; Scheffer *et al.*, 2001). Such discontinuous and abrupt responses are facilitated through an unstable equilibrium (region of bistability) which can control the trajectory of the community response, e.g. thresholds of reversibility (Collie *et al.*, 2004; Suding *et al.*, 2004; Schröder *et al.*, 2005). Independently of the type of ecosystem responses to environmental conditions, the final state of the succession will differ in quality/properties from the initial one (Scheffer *et al.*, 2001; Orfanidis *et al.*, 2008a).

The succession of lake conditions from oligotrophy to hypertrophy has been described as a transition between two alternative stable states, namely oligotrophic and eutrophic (Nilssen, 1978; Scheffer *et al.*, 2001). Transitions are triggered by abiotic variables, but changes in the community composition are usually ascribed to biological controls (e.g. grazing of microalgae). Similarly, in coastal lagoons eutrophication processes have been represented as a transition of alternative states, from pristine seagrass meadows to macroalgal or phytoplankton communities (Sand-Jensen and Borum, 1991; Nienhuis, 1992; Viaroli *et al.*, 1996; Valiela *et al.*, 1997; Flindt *et al.*, 1999; Schramm, 1999; Orfanidis *et al.*, 2003; Dahlgren and Kautsky, 2004). However, the assumption that ecological systems may undergo alternative stable states should not be taken as a rule before any experimental validation (Scheffer and Carpenter, 2003; Schröder *et al.*, 2005).

### Ecological concepts and models for benthic vegetation and eutrophication in coastal lagoon

In shallow waters, benthic vegetation forms the basis of community structure and ecosystem functioning, which evolves through a succession of at least three main phases (Table 1). Pristine coastal lagoons are considered to be dominated by extensive meadows of perennial seagrass species, since in oligotrophic waters rhizophytes take advantage of nutrient supply from sediment (Sand-Jensen and Borum, 1991; Borum, 1996; Hemminga, 1998). An increasing nutrient input is thought to favour an initial phytoplankton and fast growing epiphytic microalgae phase, and later on floating ephemeral macroalgae which alternate with phytoplankton communities. Finally, the increased water turbidity is assumed to depress macroalgal growth leading to dominance of phytoplankton species (Figure 1).

The functional differences of benthic vegetation components related to life-cycle strategy (*r*-, *K*-selected species) also have been used to describe benthic vegetation succession along a nutrient gradient (Figure 2). Namely, the oligotrophic-pristine and the eutrophic-degraded conditions (Harlin, 1995; Valiela

Table 1. Conceptual representation of the succession of aquatic vegetation along an increasing eutrophication gradient according to 1: Nienhuis (1992), 2: Valiela *et al.* (1997), 3: Dahlgren and Kautsky (2004), 4: Schramm (1999)

Succession phases and conditions (pristine → altered)				Ref
Phanerogams	Phanerogams + epiphytes	Macroalgae + phytoplankton		1
Seagrasses		Macroalgae	Phytoplankton	2,3
Perennial benthic macrophytes	Macrophytes + fast growing epiphytes	Free floating macroalgae + phytoplankton	Phytoplankton	4

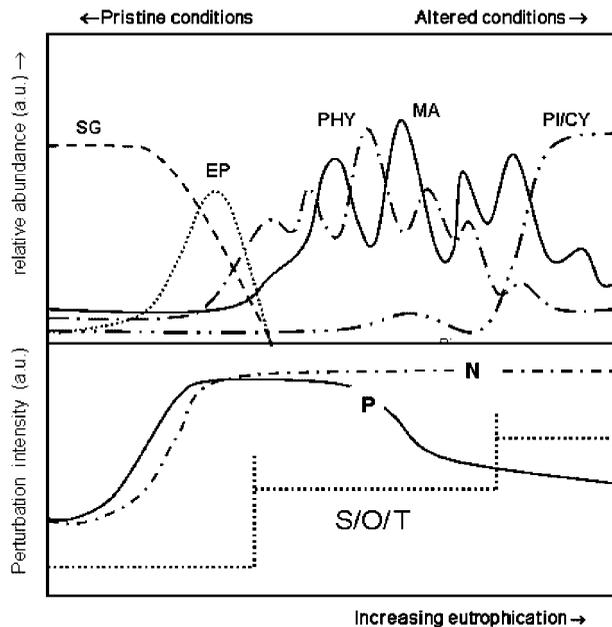


Figure 1. Conceptual representation of the succession of aquatic vegetation along an increasing eutrophication gradient [modified from Schramm (1999) and Nilssen (1978)]. Community shifts are accompanied by high-intensity perturbations. Smaller oscillations do not correspond to changes in the community structure. Legend - SG: seagrass; EP: epiphytes; PHY: phytoplankton; MA: macroalgae; PI/CY: picophytoplankton/cyanobacteria; P: phosphorus concentration; N: Nitrogen concentration; S: sulphide level, O: oxygen deficit, T: water turbidity.

*et al.*, 1997; Schramm 1999) have been assumed to represent two alternative stable states or attractors (*sensu* Scheffer *et al.*, 2001). Under low nutrient and clear water conditions of the pristine-oligotrophic state, the late-successional angiosperms *Ruppia* and *Zostera* spp. become dominant. By contrast, opportunistic seaweeds such as *Gracilaria*, *Ulva* and *Cladophora* spp. along with cyanobacteria indicate the degraded-eutrophic state, which is characterized by high nutrient conditions. Nutrient excess is considered to induce the shift between the two alternative states by favouring the rapid growth and/or the colonization ability of seaweeds to

exclude angiosperms (Valiela *et al.*, 1997; Schramm, 1999). The coexistence of macroalgae and angiosperms is a symptom of intermediate conditions. Both states are hypothesized to be resilient through feedback mechanisms (Carpenter *et al.*, 2001). For example, rooted plants tend to sustain clear water state through canopy and rhizomes by moderating water turbulence and stabilizing sediment. The distinction between late successional and opportunistic communities also has been used as a classification scheme to evaluate ecological status in transitional and coastal waters (see Orfanidis *et al.*, 2001, 2003 for details).

Overall, the conceptual models discussed here seem suited to representing the succession of primary producer communities at different phases of the eutrophication process, but mainly for very shallow and restricted or choked lagoons. Among the possible limiting factors, nitrogen rather than phosphorus is becoming the primary control of the shift in benthic vegetation (Ferdie and Fourqurean, 2004; Howarth and Marino, 2006; Orfanidis *et al.*, 2008b). Recent studies have added further evidence that in the latest stage of this succession small-sized cyanobacteria, nano- and picoplankton can prevail, with an increase of the heterotrophs to autotrophs ratio (Coppola *et al.*, 2007). However, the paradigm that increasing nutrient loadings cause an irreversible transition from seagrass to macroalgae or phytoplankton communities is still questioned, since it is not yet well supported by quantitative theories or models (Nixon *et al.*, 2001). Furthermore, less attention has been dedicated to microphytobenthic (MPB) communities, which often dominate in soft-muddy sediments, which can be favoured by wind-driven resuspension and out-competing other components of the benthic vegetation community (Sundback and McGlathery, 2005). The primary producer succession is often favoured or prevented also by hydrological and hydrodynamic conditions, namely by currents and flushing that disperse the phytoplankton community and/or floating macroalgal mats (Flindt *et al.*, 1997). However, given a certain water residence time, the succession from perennial benthic species to macroalgae and phytoplankton seems mainly caused by nutrient loadings (Valiela *et al.*, 1997; Dahlgren and Kautsky, 2004).

Although several studies have been made on the major factors controlling the community succession, it is rather difficult to find well defined and/or fixed boundaries for the

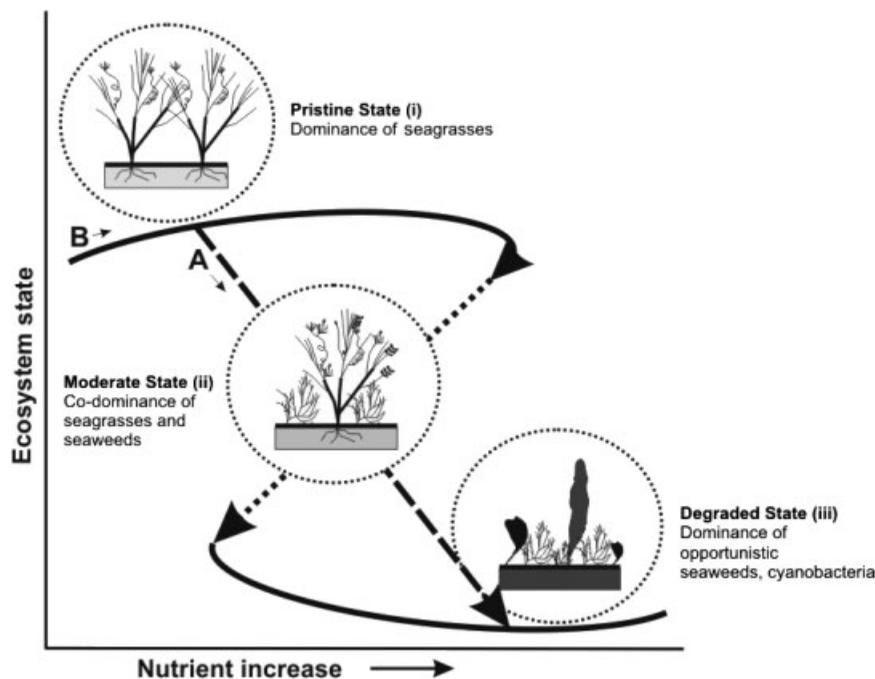


Figure 2. Conceptual model of two alternative stable states of marine benthic vegetation across a eutrophication (ecological status) gradient in lagoons. A conventional (A) and dynamic (B) view of vegetation changes in coastal lagoons is indicated (from Orfanidis *et al.*, 2005).

Table 2. Thresholds of regions of stability of the main components in the primary producer community

	Region of stability	
	DIN loading <sup>1</sup> (g m <sup>-2</sup> y <sup>-1</sup> )	DS in porewater <sup>2</sup> (µM)
Phanerogams	< 10	< 10 <sup>a</sup> –< 1000 <sup>b</sup>
Macroalgae	10–50	No effect
Phytoplankton	> 50	No effect

Data from Valiela *et al.* (1997)<sup>1</sup> and Dahlgren and Kautsky (2004)<sup>1</sup>, Calleja *et al.* (2007)<sup>2</sup> and Holmer *et al.* (2003)<sup>2</sup>.

<sup>a</sup>In carbonate rich (iron poor sediments).

<sup>b</sup>In iron rich (carbonate poor sediments).

region of stability of each community component. Nonetheless, tentative thresholds for hydrogen sulphide in pore-water and dissolved inorganic nitrogen (DIN) loading which are assumed to control mainly the persistence of benthic phanerogams were identified (Table 2). An example is given by Waquoit Bay, where 50% loss of the *Zostera marina* coverage was detected at ~6 g m<sup>-2</sup> y<sup>-1</sup> nitrogen loading rate, while only 10% coverage remained at ~15 g m<sup>-2</sup> y<sup>-1</sup> nitrogen loading rate (Hemminga and Duarte, 2000; Hauxwell and Valiela, 2004). Extended meadows of *Zostera noltii* are also persisting in the Etang de Thau (Southern France) which has been

Table 3. Dominant components in the primary producer community and associated net ecosystem metabolism (NEM, carbon units), dissolved inorganic nitrogen (DIN) loadings and water retention times (WRT) in 13 Mediterranean coastal lagoons

WRT (days)	DIN loading (g m <sup>-2</sup> y <sup>-1</sup> )	Primary producers	NEM (mol m <sup>-2</sup> y <sup>-1</sup> )
40–100	0.6–7.6	Phy + Pha	0.2 to 4.6
4–200	9.9–16.1	Phy + Pha + Ma	–1 to 11.9
3–25	8.7–70	Phy + Ma	–29.0 to 14

Phy: phytoplankton, Pha: Phanerogams, Ma: Macroalgae. Data from Giordani *et al.* (2005, 2007) and from the DITTY project database ([www.dittyproject.org](http://www.dittyproject.org)).

receiving less than 7 g m<sup>-2</sup> y<sup>-1</sup> nitrogen loading for a long time ([www.dittyproject.org](http://www.dittyproject.org)).

Experimental studies have demonstrated that abundance and distribution of the various primary producer forms are affected by a large variability, and that simple predictive relationships cannot be used for very shallow coastal lagoons (Taylor *et al.*, 1995; Nixon *et al.*, 2001). Although boundaries often overlap, broad relationships can be found between DIN loading and combinations of different primary producer components, and between DIN and the net ecosystem metabolism (Table 3, see also Giordani *et al.*, 2008).

The shift from pristine seagrass meadows to macroalgal blooms has been qualitatively demonstrated worldwide especially for well studied systems along the US coast, where benthic phanerogams persist under low nitrogen loadings, while they have disappeared in nutrient-rich waters (Valiela *et al.*, 1997; Bortone, 2000; Hemminga and Duarte, 2000; Hauxwell and Valiela, 2004). Similarly, until the mid-1970s in the Mediterranean region several shallow lagoons were covered by widespread meadows of *Ruppia* and/or *Zostera*, while in recent decades, increased nutrient inputs and other pressures associated with fishing and/or aquaculture have led to the rapid development of extended macroalgal blooms and displacement of perennial phanerogams (Table 4). In some lagoons, macroalgal blooms have disappeared, for example owing to canal dredging (e.g. Sacca di Goro, Viaroli *et al.*, 2006) and as a consequence of clam farming (e.g. Venice; Sfriso and Marcomini, 1996; Sfriso and Facca, 2007). In other lagoons, macroalgal blooms persist (e.g. Orbetello; Bombelli and Lenzi, 1996), although the relationship between macroalgae and rhizophyte often depends on meteorological conditions (Giusti and Marsili-Libelli, 2005). In the Valli di Comacchio lagoon, a clear succession was observed from pristine *Ruppia cirrhosa* and *Lamprothamnium papulosum* meadows, to an intermediate macroalgal bloom and, recently, to the development of a mixed community of nanoplanktonic green algae and cyanobacteria (Andreoli *et al.*, 1998; Piccoli, 1998). A similar pattern was observed in degraded sites of the Agiasma lagoon (Greece), where a seasonal alternation between summer *Ulva* and winter cyanobacteria blooms often occurs (Orfanidis *et al.*, 2008b).

### Biogeochemical switches and feedbacks: oxygen, iron and sulphide

The network of biogeochemical reactions related to primary production and microbial processes can be regarded as a system of feedbacks that regulate and control the transitions within the primary producer community, and ultimately within the lagoon ecosystem (de Wit *et al.*, 2001). The extent of oxygen production and consumption depends essentially on primary producer communities and microbial processes. Conversely, oxygen distribution and its concentration can modify microbial metabolism and can limit both distribution and persistence of primary producers (Crawford, 1992).

At certain biomass density, vegetation typology and morphology determine a physical partitioning of the water mass. For example, floating foliose thalli induce water lamination and stratification, with over-saturation in the superficial water mass above thalli and anoxia in the deeper layers beneath thalli (Krause-Jensen *et al.*, 1999; Brush and Nixon, 2003). Microphytobenthos is responsible for oxygen production at the water-sediment interface, thus allowing

Table 4. Recent evolution of benthic communities in selected coastal lagoons

	Pristine conditions	1975–1995	Present	Ref.
Sacca di Goro (Italy)	<i>Ruppia cirrhosa</i> , <i>Zostera noltii</i>	<i>Ulva</i> and <i>Gracilaria</i> blooms	Moderate growth of <i>Ulva</i> and <i>Gracilaria</i>	1, 2
Venice lagoon, central basin (Italy)	<i>Zostera noltii</i> , <i>Cymodocea nodosa</i>	<i>Ulva</i> blooms	Phytoplankton	3
Orbetello lagoon (Italy)	<i>Ruppia cirrhosa</i>	<i>Ulva</i> and <i>Gracilaria</i> blooms	<i>Gracilaria</i> blooms	4, 5
S'Ena Arrubia lagoon (Italy)	<i>Ruppia cirrhosa</i>	<i>Ulva</i> and <i>Gracilaria</i>	Filamentous macroalgae	4, 6
Valli di Comacchio (Italy)	<i>Ruppia cirrhosa</i> , <i>Lamprothamnium papulosum</i>	Filamentous macroalgae blooms	Nanoplankton, cyanobacteria	7, 8
Encanissada/Tancaada (Spain)	<i>Ruppia cirrhosa</i> , <i>Potamogeton crispus</i>	Moderate growth of <i>Chaetomorpha linum</i>	Patchy <i>Ruppia cirrhosa</i> , <i>Chaetomorpha linum</i> and <i>P. crispus</i>	9, 10
Etang du Prévost (France)	<i>Zostera noltii</i> , <i>Ruppia cirrhosa</i>	<i>Ulva</i> blooms	<i>Ulva</i> blooms	6, 11, 12,
Nestos lagoons, several basins (Greece)	<i>Ruppia cirrhosa</i>	n.a.	<i>Ruppia cirrhosa</i> , <i>Ulva</i> , <i>Gracilaria</i> and cyanobacteria	13
Tsopeli, Amvrakikos lagoons (Greece)	<i>Zostera noltii</i>	n.a.	<i>Ulva</i> blooms, <i>Zostera noltii</i>	14
Pappas lagoon (Greece)	<i>Cymodocea nodosa</i>	n.a.	<i>Ulva</i> , <i>Gracilaria</i> blooms	15
Aetoliko (Greece)	<i>Cymodocea nodosa</i>	<i>Ulva</i> and <i>Cladophora</i>	n.a.	16
Etang de Thau (France)	<i>Zostera noltii</i>	n.a.	<i>Zostera noltii</i> , moderate loss	17

Piccoli *et al.* (1991)<sup>1</sup>, Viaroli *et al.* (2006)<sup>2</sup>, Sfriso and Facca (2007)<sup>3</sup>, Bombelli and Lenzi (1996)<sup>4</sup>, Giusti and Marsili-Libelli (2005)<sup>5</sup>, Viaroli *et al.* (1999)<sup>6</sup>, Andreoli *et al.* (1998)<sup>7</sup>, Piccoli (1998)<sup>8</sup>, Menezes and Comin (1987)<sup>9</sup>, Menendez *et al.* (2002)<sup>10</sup>, Castel *et al.* (1996)<sup>11</sup>, Souchu *et al.* (2000)<sup>12</sup>, Orfanidis *et al.* (2001)<sup>13</sup>, Reizopoulou (pers. com.)<sup>4</sup>, Reizopoulou and Nicolaidou (2004)<sup>15</sup>, Bogdanos and Diapoulis (1984)<sup>6</sup>, www.dittyproject.org<sup>17</sup> n.a.: not available.

oxygen penetration in the superficial sediment horizon, as well as oxygen release through the whole water column. Similarly, rhizophytes and benthic sessile macroalgae deliver oxygen through the water column allowing its oxygenation. In healthy seagrass meadows, production and respiration rates are usually well balanced with smoothed fluctuations. Moreover, oxygen is released in the root system through radial oxygen loss (ROL), which fuels oxidation of reduced sediments allowing seagrass survival in a hostile environment (Hemminga, 1998; Pedersen *et al.*, 1998), where sulphate reduction rates associated with the rhizosphere can reach  $80 \text{ mmol m}^{-2} \text{ d}^{-1}$  (Isaksen and Finster, 1996; Welsh *et al.*, 1996; Holmer and Nielsen, 1997). When phytoplankton productivity and particulate matter concentrations are high, seagrasses act as traps enhancing sedimentation rates and making sediments more organic, thus greatly supporting bacterial sulphate reduction (Gacia *et al.*, 2002; Barron *et al.*, 2004). Shading by macroalgae and epiphytes further threatens the capacity of seagrasses to control the redox status and sulphide concentrations in the sediments (Heijs *et al.*, 2000; Azzoni *et al.*, 2001). Under increasingly low redox and high sulphide concentrations a positive-feedback loop in the root-sediment interactions can become established, which reduces root and rhizome elongation, inhibits cellular respiration and often has lethal effects (Touchette and Burkholder, 2000; Koch and Erskine, 2001; Calleja *et al.*, 2007). The inhibitory to lethal effects of sulphides further limit the degree of oxygen release to the sediments, thus enhancing sulphide accumulation. Overall, anoxia and sulphide production act as a positive feedback against seagrasses, resulting in their displacement.

Dissolved sulphides are buffered by the sedimentary labile iron pools which can precipitate sulphides as solid FeS and FeS<sub>2</sub> via a suite of redox reactions (de Wit *et al.*, 2001; Rickard and Morse, 2005). This mechanism, along with oxygen production and transport to the rhizosphere, could provide a feedback link between sediment and seagrasses, controlling the fate of benthic vegetation. Clearly, the shift in dominance within the primary producer community can potentially modify oxygen transport (decrease) and sulphide production (increase) and reinforce positive feedbacks which destabilize the community itself. Overall, oxygen and sulphides can act as switches amplifying the shift strength and determining the trajectory of the community response.

In shallow environments dominated by macroalgae, oxygen concentrations undergo much wider fluctuations than in seagrass meadows (Viaroli *et al.*, 2001; Viaroli and Christian, 2003 and references therein). The abnormal oxygen production is usually accompanied by the retention of labile organic matter (OM) within the water mass and at the sediment surface. Microbial decomposition of macroalgal detritus causes a strong and persistent oxygen deficit and the onset of

anoxia and anaerobic processes, with a strong dissolved sulphide release, which induce the shift from one state to another (Izzo and Hull, 1991; Castel *et al.*, 1996; Viaroli *et al.*, 1996; de Wit *et al.*, 2001). Therefore, the community does not respond solely to external stressors, but can also amplify responses through biomass build up, organic matter accumulation within the system and its decomposition (Nedergaard *et al.*, 2002; Banta *et al.*, 2004). Decomposition processes are regulated not only by OM quantity but depend also on its quality, which may control critical steps in the seasonal evolution of oxygen availability. In turn, OM quality and its recalcitrance depends on types, growth rates, life cycles and elemental and macromolecular composition of benthic vegetation (Enriquez *et al.*, 1993). Comparative studies demonstrate that under summer conditions *Ulva* sp. decomposes at an almost constant rate of 3% per day, which is three times greater than that of *Zostera marina* (Buchsbaum *et al.*, 1991). Decomposition modes and rates not only influence the extent of the oxygen deficit and sulphide release, but also modify nitrogen and phosphorus pathways and their fate (Amtoft Neubauer *et al.*, 2004; Lomstein *et al.*, 2006).

The extent of sulphide release is regulated by the sedimentary sulphide/iron-monosulphide/pyrite system, which represents a potential mechanism for the removal of toxic hydrogen sulphide (de Wit *et al.*, 2001; Rickard and Morse, 2005 and references therein). However, the iron buffer can easily be saturated allowing sulphides to move from solid phase to pore-water, where they interact with roots and rhizomes. Factors influencing iron availability have a great influence on iron-based buffers (Chambers *et al.*, 2001; Rozan *et al.*, 2002). For example, in carbonate-rich sediments, iron can be adsorbed and retained by carbonate particles, lowering sulphide buffering. Under these circumstances, dissolved sulphides released into pore-waters are toxic to vegetation at very low concentrations, while in carbonate-poor sediments the toxicity threshold rises by two orders of magnitudes (Table 2, see also Holmer *et al.*, 2003; Calleja *et al.*, 2007). An example of possible relationships among iron and sulphide pools and vegetation in coastal lagoons with different degrees of eutrophication is shown in Figure 3. In *Ruppia* meadows, dissolved sulphide concentrations in the water are related to both sedimentary iron and epiphyte colonization, while in *Ulva*-dominated lagoons, dissolved sulphides are mainly controlled by sedimentary iron. In the Prévost lagoon, where the reactive iron pool is very small, the buffering capacity of iron is readily saturated causing strong sulphide release in the water column. In the Sacca di Goro lagoon, under similar macroalgal biomass, dissolved sulphides concentration in the water column is approximately five-fold lower, probably as a consequence of the higher iron availability (Azzoni *et al.*, 2005). However, the sedimentary buffering capacity is not a

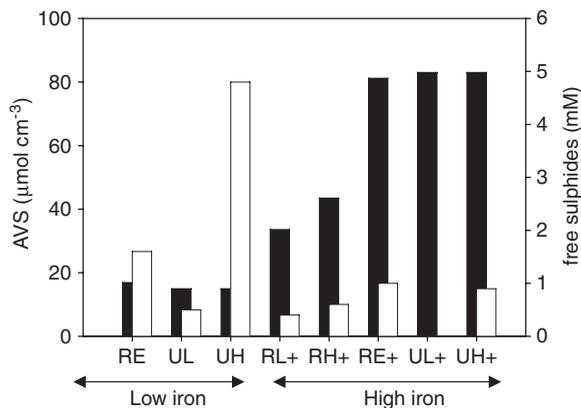


Figure 3. Acid volatile sulphides (AVS, dark bars) and dissolved sulphide (empty bars) concentrations in sediment and bottom water under low ( $<50 \mu\text{mol cm}^{-3}$ ) and high ( $150\text{--}300 \mu\text{mol cm}^{-3}$ ) sedimentary iron concentrations. RE: *Ruppia* with epiphytes; RL: *Ruppia* low density; RH: *Ruppia* high density; UL: *Ulva* low density; UH: *Ulva* high density (data from Viaroli *et al.*, 1996, 1997; Hejs *et al.*, 2000, and unpublished data).

simple function of the reactive iron concentration, since not all of the iron is available to react with sulphide; benthic fauna and microbial processes play also an important role in the sedimentary sulphur cycle (Meysman and Middelburg, 2005; Rickard and Morse, 2005). Nevertheless, reactions with iron remain of paramount importance in determining the sedimentary buffering capacity and providing a ready capacity for removing toxic hydrogen sulphide (Heijs and van Gernerden, 2000; de Wit *et al.*, 2001; Rozan *et al.*, 2002).

The biogeochemical reactions of iron and sulphide affect both availability and mobility of sedimentary phosphorus (Golterman, 1995; Giordani *et al.*, 1996; Roden and Edmonds, 1997; Heijs *et al.*, 2000; Rozan *et al.*, 2002). Among others, phosphorus speciation depends on geochemical reactions with calcium, carbonates, iron, aluminium and humic compounds (Golterman, 2001). Biogeochemical reactions can ultimately control phosphate availability to primary producers, with a negative feedback loop between sediment and macroalgae, yet potentially regulating growth rates and shifts within the community.

Overall, the suite of these biogeochemical reactions can act as a switch, controlling community shift and determining its trajectory. Presumably, at low iron availability the vegetation will evolve more quickly towards the macroalgae/phytoplankton phase, while at higher iron concentration it will oscillate maintaining a healthy to damaged seagrass community.

### Nitrogen cycling, nitrophilous macrophytes and coupled nitrification–denitrification

Conceptual models predict that increasing nutrient loading decreases benthic primary production with a possible seagrass die-off. Seagrass displacement seems to be induced mainly by nitrogen, rather than by phosphorus, through the stimulation of both phytoplankton and macroalgal growth (Hemminga and Duarte, 2000; Touchette and Burkholder, 2000; Hauxwell and Valiela, 2004). Furthermore, dissolved nitrogen loadings into coastal zones from different sources are rising much faster than phosphorus inputs (Howarth and Marino, 2006). Phosphorus limitation can establish in carbonate-rich coastal areas owing to the geochemical reactions between phosphate and carbonate (Chambers *et al.*, 2001; Ferdie and Furqurean, 2004; see also the previous section).

To a large extent, nitrogen cycling and transformations within coastal lagoons depend on the interactions between benthic vegetation and microbial processes (Risgaard-Petersen and Jensen, 1997; Eyre and Ferguson, 2002; Risgaard-Petersen, 2003) and between different primary producers groups (Sundback and McGlathery, 2005). During their growth phase, benthic phanerogams such as *Ruppia* and *Zostera* act as a nitrogen sink, keeping denitrification rates almost negligible and benthic fluxes of nitrate and ammonium mostly directed to the vegetation–sediment compartment (Risgaard-Petersen and Jensen, 1997; Welsh *et al.*, 2000; Bartoli *et al.*, 2001; Eyre and Ferguson, 2002). Bloom-forming ephemeral and nitrophilous macroalgae, like *Ulva* spp., induce large oscillations in nitrogen availability, with strong uptake periods followed by sudden release phases (Sand-Jensen and Nielsen, 2004). In nitrate-rich lagoons, macroalgae can control the transient nitrate availability with the cellular nitrate storage, but above certain thresholds cellular nitrate deposits depress nitrate uptake and can slow macroalgal growth (Naldi and Viaroli, 2002; Viaroli *et al.*, 2005). Macroalgae efficiently out-compete seagrasses, while they seem to have a lower impact on MPB, partially due to its colonization and recovery capacity (Sundback and McGlathery, 2005). MPB is also thought to favour the development of sharp gradients at the water–sediment interface, where in a very narrow sediment horizon, oxic to anoxic gradients can establish, which promote coupled bacterial nitrification–denitrification processes (Risgaard-Petersen, 2003). The stability of the MPB system depends on physical perturbation (e.g. turbulence and resuspension), as well as nitrification to denitrification coupling which is regulated by the autotrophy to heterotrophy ratio of the microphytobenthic system (Risgaard-Petersen, 2003).

The storage capacity of macrophytes coupled with the fast nutrient recycling at their growth peak clearly depresses microbial processes, namely the denitrification of water

Table 5. Denitrification, nitrogen uptake rates and nitrogen storage in different benthic communities

	Maximum denitrification rates ( $\mu\text{mol m}^{-2} \text{d}^{-1}$ )	Maximum nitrogen bulk at biomass peak ( $\text{mmol m}^{-2}$ )	Nitrogen uptake rates at biomass peak ( $\text{mmol m}^{-2} \text{d}^{-1}$ )	Reference
Seagrass	100–400	200–600	10–25	1, 2, 3, 4
Macroalgae	200	500–1250	6–25	5, 6, 7
MPB/BS	400–1600	—	2.5–5.0	4, 7

1: Welsh *et al.* (2000), 2: Risgaard-Petersen (2004), 3: Eyre and Ferguson (2002), 4: Bartoli *et al.* (2001), 5: Viaroli *et al.* (2005), 6: Sfriso and Marcomini (1996), 7: Sundback and McGlattery (2005). MPB: microphytobenthos; BS: bare sediments.

Table 6. Main community traits and biogeochemical features of the different alternative stable states determined by shifts in primary producer communities

	Seagrass meadow	Macroalgae (bloom forming)	Phytoplankton Microphytobenthos
Biomass bulk	High/persistent	High/ephemeral	Low/transient
Growth rate	Low	High/very High	High
Biomass degradability	Refractory	Labile	Labile/refractory
Oxygen	Balanced	Unbalanced/dystrophy	Variable
Sulphide in pore water/bottom water	Absent to low	High	Absent to low
Nitrogen	Retention low concentration	Pulsing; Low to high concentrations	Variable
Information ( $\beta$ -value)	High	Low	Very low

column nitrate as well as nitrification coupled with denitrification (Risgaard-Petersen, 2004). Great differences have been found for dissolved inorganic nitrogen assimilation, which peaks in macroalgal systems (Table 5). Overall, within certain thresholds the capacity of seagrass communities to store and retain nitrogen can be viewed as an internal control which keeps the nitrogen cycle balanced and counteracts the community shift to macroalgal or phytoplankton dominance. At low nitrogen loadings, seagrasses exploit pore-water nitrogen thus out-competing other primary producers and nitrifying/denitrifying bacteria. The imbalance in nitrogen cycling with nitrogen accumulation in the water mass is expected to stimulate the development of epiphytes and phytoplankton, which weaken seagrasses until the community switches towards a dominance of nitrophilous macroalgal species (Touchette and Burkholder, 2000). The endangered vegetation is also threatened by sulphide accumulation in the pore-water, which is toxic to roots and contrasts nutrient assimilation thus increasing the competition by phytoplankton and macroalgae.

Sudden development and outbreaks of macroalgal blooms can strongly modify nitrogen cycling, with the storage phase followed by a sudden release/dissipation. The latter is probably a result of both decomposition processes (Viaroli *et al.*, 2001) and organic matter export (Flindt *et al.*, 1997). Frequent growth-collapse cycles are thus expected to induce transient and unstable states to establish, through alternative macroalgal and phytoplankton dominance. Under these circumstances, organic enrichment can occur with persistent hypoxia and frequent anoxia, with concurrent sulphidic conditions. In a

highly reduced and sulphidic environment, nitrogen cycling becomes controlled by dissimilative nitrate reduction to ammonium (DNRA) instead of denitrification (Christensen *et al.*, 2000; Nizzoli *et al.*, 2006), while phosphorous buffers become ineffective. This allows a positive feedback loop to establish, and the system becomes self-perpetuating, also reinforcing the seaweed–phytoplankton loop.

## CONCLUSIONS AND PERSPECTIVES

Transitions from seagrass to seaweed and phytoplankton communities control and, in turn, are controlled by key biogeochemical factors/processes in a suite of reactions, switches and feedbacks. Benthic fauna and human activities themselves (e.g. fish farming, trawling, etc.) can further induce alterations of biogeochemical processes, amplifying feedbacks and community responses. Overall, community types can be viewed as alternative 'stable states', which are responsible for the ecosystem characteristics (Table 6).

Within certain thresholds, healthy seagrass meadows are able to buffer perturbations, maintaining oxygen balance, low turbidity and low nutrient concentrations. The ROL and inherent oxidative processes within the rhizosphere, can be viewed as the key functions controlling meadow persistence.

Massive macroalgal development can induce physical alteration in the water mass. Floating mats depress/prevent

light penetration and photosynthesis from occurring in the water mass, inducing water lamination with oxygen-rich surface waters and anoxia at the bottom. Sulphide release in the water column and pulsed assimilation and sudden release of nutrients act as stressors and positive feedbacks for seagrasses as well as for macroalgae themselves. In both macrophyte systems, nitrification and denitrification processes and their coupling are usually low, with potential nitrogen accumulation.

The trajectory of community changes, after macrophyte communities have been displaced, is less clear. A general statement is that the last phase of the transition from healthy to stressed ecosystems is dominated by phytoplankton. Picoplankton and small-sized protists and cyanobacteria have often been detected in heavily degraded lagoons. Microphytobenthic communities are also of paramount importance in sites with a high resuspension rate/frequency. Overall, these communities are unstable and fluctuating, mainly due to shallow depth and external perturbations (wind, currents, tides, etc.).

Shifts and transitions beyond thresholds in primary producer communities can also be analysed in terms of system complexity, taking into account the genetic information embedded ( $\beta$ -values, see Jørgensen *et al.*, 2005) in the biomass of each taxonomic group. At present,  $\beta$ -values for about 250 macrophyte species have been estimated, including the most common species of Mediterranean lagoons (Austoni *et al.*, 2007 and references therein). From these data, shifts from phanerogams to phytoplankton result in a marked loss of complexity, with  $\beta$ -values of 400–600 for seagrasses and perennial/sessile macroalgae (*K*-selection), 100–200 for bloom-forming macroalgae (*r*-selection) and less than 30 for phytoplankton. Since taxa with high  $\beta$ -values represent pristine conditions or, at least, less degraded conditions, one can conclude that the community shift results not only in a loss of ecosystem components, but rather it leads to an impoverishment of the ecosystem complexity and organization. Yet, the shift from phanerogams to macroalgae or phytoplankton dominated communities is also coupled with changes in benthic macrofaunal communities (Schramm, 1999). In turn, benthic fauna influences geochemical and microbial processes, e.g. through bioturbation, which has implications for benthic processes, and ultimately for benthic vegetation itself.

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