

## Ecological Indicators

January 2005; 5(1) : 1-17

<http://dx.doi.org/10.1016/j.ecolind.2004.04.004>

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# Ability of taxonomic diversity indices to discriminate coastal lagoon environments based on macrophyte communities

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**Abstract:** Lagoons are highly productive areas representing more than 50% of the coastline area in Languedoc-Roussillon (South of France, Mediterranean sea). These lagoons are very different in their environmental conditions, human influences, eutrophication levels and aquaculture intensity. Based on macrophyte communities associated with soft substrates, two indices of taxonomic diversity (the "average taxonomic distinctness" ( $\Delta+$ ) and the "variation in taxonomic distinctness" ( $\Lambda+$ )) were used to discriminate four of these lagoons (Thau, Salse-Leucate, Bages-Sigean and Mauguio). Bages-Sigean presented a significant higher average taxonomic distinctness ( $p < 0.05$ ) and Salse-Leucate had a significant higher variation in taxonomic distinctness ( $p < 0.05$ ) without considering exotic species. The index values were neither influenced by sample size nor by presence of exotic species. Thus, the "average taxonomic distinctness" was related to human activities and eutrophication level whereas the "variation in taxonomic distinctness" was more related to the environmental variability, associated with the prime stressor of salinity in brackish coastal lagoons.

**Keywords:** Biodiversity; Eutrophication; Human impact; Exotic species; Languedoc-Roussillon

## Introduction

Worldwide, lagoon systems represent 13 % of the coastal line (Knoppers 1994) and with the other coastal ecosystems constitute a large part of the ecological richness of the biosphere (Costanza *et al.* 1997). Due to their location between the continent and the sea (interface area with freshwater inputs from the watershed and marine influence from the sea through the channel), and their shallow depths, lagoons are very productive ecosystems (on average of  $300 \text{ g C m}^{-2} \text{ y}^{-1}$ , Knoppers 1994), but also very sensitive to both climatic and human activities. Lagoons are distributed all over the world coastline, but are not equally widespread on the different coastal areas. In the northwestern part of the Mediterranean Sea, lagoons are numerous. In the Languedoc-Roussillon area, they constitute 50 % of the coastal line. They are subjected to many anthropogenic impacts, mainly due to permanent and seasonal population density increases, tourism activities expansion, aquaculture and agriculture. One of the urgent needs is to evaluate human influences on the structure and functioning of coastal lagoons, which was one of the goals of the “National Research Programme on Coastal Environment” (PNEC). In the context of this program, specific site studies were initiated in 1993 with a special interest in the macrophytic community, the composition and structure of which are known to be good indicators of environmental changes (Bachelet *et al.* 2000, Kunii & Minamoto 2000, Sfriso *et al.* 2001). Moreover, numerous studies highlighted the functional impact of macrophytes on lagoon ecosystems by its effect on epifaunal assemblages (Parker *et al.* 2001), sediment microbial processes (Hansen *et al.* 2000), or on benthic fluxes of oxygen, sulphide and nutrients (Viaroli *et al.* 1996, Plante-Cuny *et al.* 1998, Dhargalkar & Shaikh 2000).

To summarize a community composition, the more widely used parameter is the number of species or the specific diversity measured in samples ( $\alpha$ -diversity) (Magurran 1988, Gaston 1996). However, this observed taxonomic richness is an underestimation of the true taxonomic richness (the real number of species living on the studied site) and the error involved will depend on sampling effort (Gaston 1996, Griffiths 1997). Furthermore, this specific diversity or richness is difficult to relate to the ecosystem productivity or disturbance because the diversity-productivity relationship remains controversial and is not always monotonic (Grace 1999, Waide *et al.* 1999, Mackey & Currie 2001, Mittelbach *et al.* 2001). For these reasons, the community richness does not seem to be a useful indicator of disturbance in applied ecology (Drobner *et al.* 1998).

As early as 1949, Simpson suggested that the number of species only represented an aspect of species diversity, noting that the diversity of a given community also depends on the quantitative equilibrium between the species, which we term the evenness. To take into account the structure of the community, numerous diversity or evenness indices have been proposed such as the Shannon-Weaver (1949) index and its associated evenness or the Simpson (1949) index, for the most famous ones. These diversity indices are classically used in ecology to assess the environmental impacts on ecosystems (Coleman *et al.* 1997, Cusson & Bourget 1997, McRae *et al.* 1998, Chiarucci *et al.* 1999, Weiher & Keddy 1999, Pires *et al.* 2000). Nevertheless, some authors criticized the limited ability of these indices to discriminate between communities or to detect change within a given community (Cairns *et al.* 1993, Cao *et al.* 1996, Burel *et al.* 1998, Gray 2000, Lydy *et al.* 2000, Rice 2000). Moreover,

these indices do not take into account functional or taxonomic differences between species whereas some authors pointed out the necessity of including these differences between species to assess diversity (Purvis & Hector 2000, Shimatani 2001).

Since 1995, Warwick and Clarke (1995, 1998) and Clarke and Warwick (1998, 1999, 2001) proposed four indices of taxonomic diversity that take into account the “weighted” taxonomic differences between species. The first two, termed taxonomic diversity ( $\Delta$ ) and taxonomic distinctness ( $\Delta^*$ ), are natural extensions of Simpson diversity and use abundance of species. The two last ones measure average and variation in taxonomic distinctness ( $\Delta^+$  and  $\Lambda^+$ , respectively) with presence/absence data. Thus, the combination of the two last indices is supposed to provide a statistically robust summary of taxonomic relatedness patterns within an assemblage (Warwick & Clarke 2001). These four indices are intended to be independent of sample size, unbiased, related to functional diversity and to environmental impact (Clarke & Warwick 1998, Rogers *et al.* 1999, Clarke & Warwick 2001, Warwick & Clarke 2001, Warwick *et al.* 2002, Warwick & Light 2002). Nevertheless, using  $\Delta$  and  $\Delta^*$ , Somerfield *et al.* (1997) found no consistent pattern of decreasing taxonomic diversity of marine macrofaunal assemblages with increasing environmental impact and, following Hall & Greenstreet (1998), indices incorporating taxonomic distinctness showed identical time trends to conventional diversity measures with fish communities.

Undeniably, these indices need further investigation concerning their ability to assess environmental impact. Moreover, they have not been widely used in ecology because one must know all the members of the community theoretically present on each site, and these methods are heavily dependent upon calculations, especially for the associated randomisation test.

In this study, we focus on the ability of two new weighted taxonomic diversity indices ( $\Delta^+$  and  $\Lambda^+$ ), based on presence/absence data, to discriminate coastal lagoon environments. To this aim, we use a database on macrophytic communities sampled in four coastal lagoons of the Languedoc-Roussillon (France, Mediterranean Sea) with high contrast in their environmental conditions such as eutrophication level. Then we discuss a lagoon classification based on taxonomic diversity of macrophytic communities.

## **Material and methods**

### **Study areas**

During the “National Research Program on Coastal Environment” (PNEC), four coastal lagoons located in the Languedoc-Roussillon area were sampled between 1998 and 1999: Bages-Sigean, Mauguio, Salse-Leucate and Thau Lagoon (Figure 1). Two of them, Salse-Leucate and Thau Lagoon, harbour shellfish aquaculture activities (mainly oyster aquaculture). As the breeding of oysters is not of a level to allow the collection of larva in the Mediterranean Sea, production is wholly dependent on the importation of adults or spat. Since 1961, professionals have imported Portuguese oysters and, from 1976, Japanese oysters (*Crassostrea gigas*). These importations caused numerous accidental marine species introductions.

Main chemical and physical characteristics and the eutrophication level of each lagoon are summarized in Table 1 (RSL 2001). Eutrophication levels are estimated using parameters from the water column such as oxygen, turbidity, chlorophyll, pheopigments and some chemicals (P, N,  $\text{NH}_4^+$  and  $\text{NO}_2^-/\text{NO}_3^-$ ) (RSL 2001). Environmental features and human activities differ according to the lagoon:

**Table 1.** Environmental characteristics of the four studied lagoons. Mean values are given  $\pm$  standard deviation; organic matter is given as a percentage of dry sediment. Eutrophication level is estimated using parameters from the water column (RSL 2001) and varies between 1 (lowest eutrophication) and 5 (highest eutrophication).

Lagoon	Surface (ha)	Eutrophication level	Salinity (PSU)	Organic matter (%)	Watershed surface (ha)
Bages-Sigean	3 800	2	32.4 ( $\pm 2.6$ )	4 ( $\pm 1.7$ )	3800
Mauguio	3 170	5	17.3 ( $\pm 3.7$ )	7.7 ( $\pm 2$ )	31 300
Salse-Leucate	6 500	1	33.8 ( $\pm 1.5$ )	5.4 ( $\pm 4$ )	3170
Thau	7 000	2	35.3 ( $\pm 0.7$ )	7.2 ( $\pm 4.8$ )	35 000

- Bages-Sigean. This lagoon is the least influenced by human activities because of a low population density on the watershed. Water exchanges with the sea take place in the middle and south of the lagoon.
- Mauguio. All around this lagoon, human activities and urbanization have rapidly increased during the last thirty years because of development and the vicinity of the largest city of the region (Montpellier, 400 000 inhabitants within agglomeration in 2001). Industrial and commercial buildings are built along this lagoon and agricultural activities occupy a part of the watershed. Communication with the sea takes place through a channel (“*grau*”), but several gates hamper the water exchanges, increasing eutrophication processes.
- Salse-Leucate. This lagoon is not highly impacted by human activities or by eutrophication. However, aquaculture activities are present (1000 tons of shellfish per year), and constitute an important source of accidental species introduction (RSL 2001, Sauriau 1991).
- Thau lagoon. This lagoon is usually lightly impacted by eutrophication (RSL 2001) but it is the leading site of shellfish aquaculture in the Mediterranean Sea (about 15 000 tonnes of shellfish of which 12-13 000 tonnes of oysters are produced per year). These activities influence the biochemical composition of the water column (Souchu *et al.* 2001). Thau lagoon is one of the major hot spots of accidental marine species introduction, especially of marine algae (Verlaque 2001).

Figure 1. Lagoons location (Languedoc-Roussillon region, France)

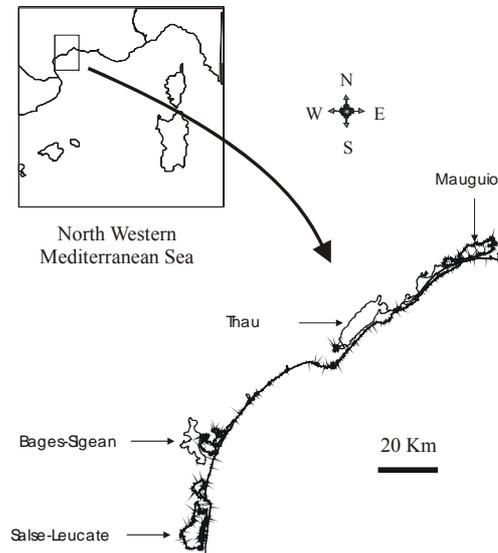


FIGURE 1

### Sampling

Macrophytic communities on soft substrates were sampled using a regular grid for each lagoon in the spring period depending on the studied community. Each sample represented a randomly distributed 2500 cm<sup>2</sup> to 1 m<sup>2</sup> quadrat in which the macrophytes were sampled by hand. Material was directly analysed or preserved in 4 % Formalin/seawater before identification to the laboratory. The number of quadrats was proportional to the surface area of the lagoon and we obtained respectively 57, 52, 32 and 32 samples for Thau, Salse-Leucate, Bages-Sigean and Mauguio lagoons.

A bibliographical analysis on the four Languedoc-Roussillon lagoons yielded 202 species of aquatic macrophytes, of which 43 are introduced (Verlaque 2000, 2001) (see Appendix). These 202 species were assumed to represent the list of species potentially present in the region. The hierarchical tree was constructed partially based on the taxonomic classification found in the world-wide web electronic publication: <http://www.algaebase.com/> (Guiry & Nic Dhonncha 2003).

### Taxonomic diversity indices

The first diversity index based on the taxonomic relationship between species proposed by Warwick and Clarke (1995), the taxonomic diversity index ( $\Delta$ ), can be

seen as a generalization of the Simpson diversity index incorporating an element of taxonomic relatedness whereas the second is a measure of taxonomic distinctness ( $\Delta^*$ ). Both can include abundances of species.

When data are only presence/absence of species,  $\Delta$  and  $\Delta^*$  converge to the average taxonomic distinctness ( $\Delta^+$ ) (Clarke & Warwick 1998, Warwick & Clarke 2001) with the formula:

$$\Delta^+ = 2 \frac{\sum \sum_{i < j} \omega_{ij}}{S(S-1)}$$

where  $S$  is the species richness and  $\omega_{ij}$  is the « distinctness weight » given to the path length linking species  $i$  and  $j$  in the hierarchical classification.

Recently, Clarke and Warwick (2001) proposed a new index based on the evenness of the distribution of taxa across the hierarchical taxonomic tree. This “variation in taxonomic distinctness” can be expressed by:

$$\Lambda^+ = 2 \frac{\sum \sum_{i < j} (\omega_{ij} - \bar{\omega})^2}{S(S-1)} = 2 \frac{\sum \sum_{i < j} \omega_{ij}^2}{S(S-1)} - \bar{\omega}^2 \quad \text{where } \bar{\omega} = 2 \frac{\sum \sum_{i < j} \omega_{ij}}{S(S-1)}$$

When species are placed within a taxonomic hierarchy, based on the Linnean classification into phylum, class, order, family, genus and species (Appendix), the average taxonomic distinctness,  $\Delta^+$ , is simply the mean number of steps up the hierarchy that must be taken to reach a taxonomic rank common to two species, computed across all possible pairs of species in an assemblage (Clarke & Warwick 1998, 1999, Warwick & Clarke 2001). Thus, if two species are congeneric, one step (species-to-genus) is necessary to reach a common node in the taxonomic tree; if the two species belong to different genera but the same family, two steps will be necessary (species-to-genus, and genus-to-family); and so on, with these numbers of steps averaged across all species pairs. Step lengths are standardized so that the distinctness of two species connected at the highest taxonomic level is set equal to 100 (Clarke & Warwick 1999);  $\Delta^+$  being between 0 and 100 and  $\Lambda^+$  being positive. If  $\Delta^+$  is the mean path length through the taxonomic tree connecting each pair of species,  $\Lambda^+$  is simply the variance of these pairwise path lengths and could be seen as an index of the “complexity” of the hierarchical tree.

These two last indices  $\Delta^+$  and  $\Lambda^+$ , used in our study, are explained in more detail in the synthesis of Warwick and Clarke (2001) and in Figure 2.

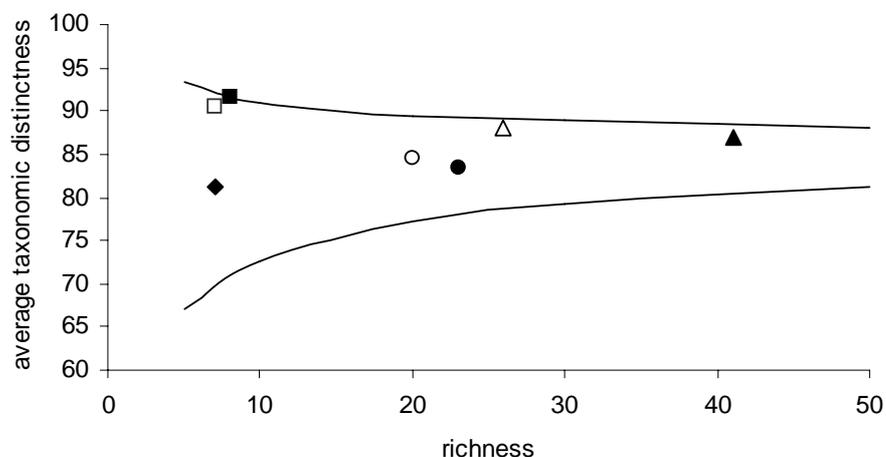


## Results

Species richness of soft substrate macrophytic communities is respectively 41, 23, 8 and 7 for Thau, Salse-Leucate, Bages-Sigean and Mauguio Lagoons. 15 species for Thau, 3 for Salse-Leucate and 1 for Bages-Sigean are exotic taxa from Asia (Appendix).

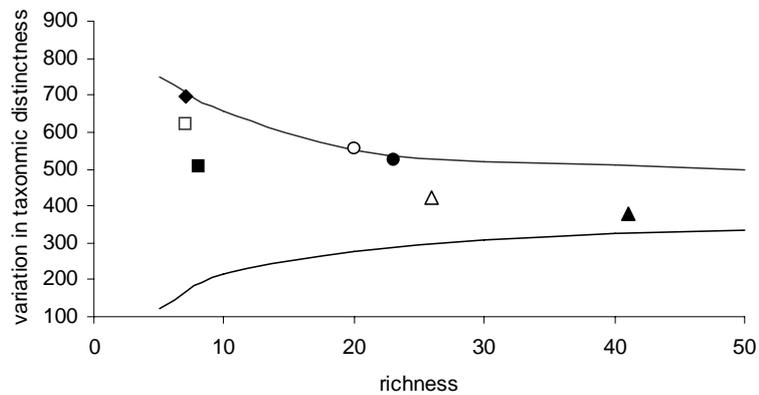
Taxonomic diversity indices are given in Table 2 for each lagoon, for the whole species list and for only exotic species or non-exotic species of this list. The 95 % confidence funnel was constructed for  $\Delta^+$  (Figure 3). We can notice that Thau, Salse-Leucate and Mauguio lagoons show no departure from the expected  $\Delta^+$  under the null hypothesis, *i.e.*, each lagoon is a random subsample of the whole macrophytic flora. Bages-Sigean presents a significant higher average taxonomic distinctness ( $p < 0.05$ ). Even though few species were observed (8), 4 different phyla with 2 species each were represented in this lagoon (see Appendix): Magnoliophyta (*Zostera marina* and *Z. noltii*), Rhodophyta (*Gracilaria bursa-pastoris* and *G. gracilis*), Chlorophyta (*Ulva rigida* and *Cladophora sp.*) and Heterokontophyta (*Sargassum muticum* and *Cladostephus spongiosus*). This pattern suggests high path length between species through the tree and a high  $\Delta^+$ . Without the exotic species *S. muticum* the significant higher average taxonomic distinctness for Bages-Sigean lagoon disappears. The lowest  $\Delta^+$  value is obtained for Mauguio lagoon with only two phyla, two families having 4 species (total of 7) leading to one relative low path length between species (Table 2, Fig. 2 and Appendix).

Figure 3. Values of the Average Taxonomic Diversity ( $\Delta^+$ ) for the macrophyte communities in Thau, Salse-Leucate, Bages-Sigean and Mauguio lagoons, plotted against the number of species on the 95% confidence funnel (see Estimation and randomisation test). Triangles, circles, squares and diamonds are for Thau, Salse-Leucate, Bages-Sigean and Mauguio lagoons, open marks are for macrophyte communities without exotic species, respectively.



Results for  $\Lambda^+$  are shown in Fig. 4 and Table 2. Thau, Bages-Sigean, Mauguio and Salse-Leucate lagoon show no significant values for variation in taxonomic distinctness ( $p > 0.05$ ). If exotic species are removed from Salse-Leucate, Bages-Sigean and Thau lagoons,  $\Lambda^+$  remains not significant for Thau and Bages-Sigean lagoons whereas  $\Lambda^+$  becomes significant for Salse-Leucate (Table 2). For this last lagoon 9 out of 12 orders sampled have only one species and, at the same time, 3 families (Cladophoraceae, Ceramiaceae, Rhodomelaceae) represent 11 species (about half of the total) leading to a high variation in the taxonomic tree (see Appendix).

Figure 4. Values of the Variation in Taxonomic Diversity ( $\Lambda^+$ ) for the macrophyte communities in Thau, Salse-Leucate, Bages-Sigean and Mauguio lagoons, plotted against the number of species on the 95% confidence funnel (see Estimation and randomisation test). Triangles, circles, squares and diamonds are for Thau, Salse-Leucate, Bages-Sigean and Mauguio lagoons, open marks are for macrophyte communities without exotic species, respectively.



## Discussion

First of all, by simulating various sample sizes or species richness from the whole species list, we can assess whether both indices are independent of sample size (Figs 3-4) as indicated by the authors in previous studies (Clarke & Warwick 1998, Warwick & Clarke 2001). When diversity indices are used to assess impact on communities, the major problems are the dependence on sample size (number of species sampled) and the ability to detect environmental influences. For the usual diversity indices and species richness, the relationship between diversity values and sample size was emphasized in the literature (Rice 2000). This kind of relation prevents any comparison between communities with different species richness. This is not the case with the indices used in the present paper.

Secondly, it appears that taxonomic diversity indices are weakly influenced by the presence of exotic species. Indeed, values of these indices vary little whether we consider the presence of exotic species, of non-exotic species or both (Table 2). This result is surprising because exotic species are supposed to add taxonomic diversity with new phyla, but the taxonomic diversity of macrophyte assemblages seems very robust. For example, Thau has been shown to be a “hot spot” for the accidental introduction of exotic species because of aquaculture activities (Verlaque 2001). In this lagoon, the 15 exotic species present in the samples add 5 new families (Rhodymeniaceae, Areschougiaceae, Dasyaceae, Chordaceae, Monostromataceae) and one new order (Laminariales), but the taxonomic index and the variance are not significantly different from the null hypothesis for this lagoon. This result could be related to the index values for the whole community of macrophytes in Languedoc-Roussillon lagoons. When we consider only exotic species or only non-exotic species in Table 2, we observe that  $\Delta^+$  and  $\Lambda^+$  are very similar to the whole community values. For the Salse-Leucate lagoon, we have the same evidence:  $\Lambda^+$  is not positively influenced by exotic species (Fig. 4). This result is in total accordance with the study of Enquist *et al.* (2002) suggesting that the processes which structure the taxonomic diversity of woody plant communities, operate in a regular manner over millions of years and across broad geographical gradients. Diversity might be more strongly regulated by local ecological and evolutionary rules, and only weakly influenced by environmental or historical factors such as dispersal barriers or speciation (Gotelli 2002). In other words, the taxonomic diversity or the structure of the taxonomic tree is about the same for exotic or non-exotic species (results for the whole community in table 2).

In many studies, diversity indices failed to assess environmental impact. For example Cao *et al.* (1996), Karydis and Tsirtsis (1996) or Lydy *et al.* (2000) showed the inefficiency of diversity indices in detecting polluted communities. According to Danilov and Ekelund (1999), all of the diversity indices calculated (Hurlbert's, Margalefs, Menhinick's, Shannon's, Simpson's, McNaughton's and Species Number) failed to distinguish between different levels of eutrophication. Likewise, Fortin *et al.* (1999) were unable to discriminate between post-fire successional gradient sites using only Simpson and Shannon diversity indices. Using taxonomic diversity as indicators, Somerfield *et al.* (1997) did not detect any influence of pollution impact when these indices are supposed to assess environmental changes (Warwick & Clarke 1998, Rogers *et al.* 1999). In the present study, even if the four lagoons considered are very different in their environmental conditions, we observed only

two weak significant results, *i.e.* departure from the null hypothesis (table 2). We observe a narrow range for  $\Delta^+$  values (81.11-91.67) and a range of 378.10-698.77 for  $\Lambda^+$  values.

Mauguio lagoon, the most depressed one in our study, presents the lowest  $\Delta^+$  value (81.11) whereas the highest  $\Delta^+$  value was observed for the less human impacted lagoon (low eutrophication, no aquaculture, low agriculture activity and low population density on the watershed) (table 1). A significant highest  $\Delta^+$  value for Bages-Sigean suggests large ecological niches are available with low environmental stress allowing macrophyte species with a high taxonomic diversity and different biological requirements to be established. For example, we found two Heterokontophyta species in Bages-Sigean (*Sargassum muticum* and *Cladostephus spongiosus*) whereas this phylum is absent from Salse-Leucate and Mauguio lagoons (appendix). We noted the presence of *Sargassum muticum* in Bages-Sigean lagoon, which is an invasive species in Europe (Rueness 1989), where no aquaculture activity is present. In contrast, we can hypothesize that environmental constraints in the Mauguio lagoon limit the taxonomic diversity of macrophyte community. For example, more than half of the species are from two families (Gracilariaceae and Ulvaceae) with species able to live in such impacted environments. Salse-Leucate and Thau lagoons with low eutrophication level but human impact through aquaculture (Souchu *et al.* 2001) were not discriminated from the regional pool with medium  $\Delta^+$  values.

The only significant result for  $\Lambda^+$  was obtained for the Salse-Leucate macrophyte community when exotic species were not considered. In this case the taxonomic tree is more irregular than the ones obtained under the null model. The highest level of  $\Delta^+$ , *i.e.* the most irregular observed taxonomic tree, was found for Mauguio lagoon (Figure 4, table 2) which had the highest eutrophication level and the lowest salinity level compared to the other three lagoons considered (Table 1). Nevertheless this trend was not observed when we consider the four lagoons of the study. More sampled lagoons are thus necessary to recommend  $\Lambda^+$  as a good indicator for the eutrophication level.  $\Lambda^+$  seems more related to the salinity coefficient of variation (ratio of the standard deviation to the mean) in our study. This coefficient varies from 2 % for Thau lagoon to 21 % for Mauguio with medium values for Bages-Sigean (8 %) and Salse-Leucate (4.5 %) lagoons. The relationship between the salinity coefficient of variation (environmental variability) and  $\Lambda^+$  is significant and positive ( $p < 0.05$ ). The distribution of organisms and diversity within estuaries had already been supposed to be influenced more highly by variation than by absolute salinity regimes (Attrill 2002). The environmental variability, associated with the prime stressor of salinity in brackish coastal lagoons, would therefore seem to influence the variation in taxonomic distinctness of macrophyte communities. We summarize all these tendencies in Figure 5 and speculate about a classification for coastal lagoon environments based on macrophyte communities, a classification independent of sample size, species richness or exotic invasion. We need certainly more lagoons to validate this classification more particularly those with high environmental variability but low human impact.

**Table 2.** Taxonomic diversity indices and species richness for the whole potential community of macrophytes (regional pool) in Languedoc-Roussillon lagoons and for the four sampled lagoons. When one index is significantly higher (5 % type I error) than expected (null hypothesis of random sample in the whole community) the sign + is added.

community	species considered	number of species	average taxonomic distinctness	variation in taxonomic distinctness
			$\Delta^+$	$\Delta^+$
Regional pool	all	202	85.10	408.97
	exotic	43	82.37	445.66
	without exotic	159	85.74	409.51
Thau	all	41	87.05	378.10
	without exotic	26	88.15	421.21
Salse-Leucate	all	23	83.4	525.91
	without exotic	20	84.56	556.97 (+)
Bages-Sigean	all	8	91.67 (+)	505.95
	without exotic	7	90.48	623.58
Mauguio	all	7	81.11	698.77

Research on summarizing information from a community is still useful in applied ecology, even if “biodiversity can never be fully captured by a single number” (Purvis & Hector 2000). Here, we applied for the first time, two new taxonomic indices based on presence/absence data to macrophyte communities sampled from four Mediterranean lagoons. A significant highest average taxonomic distinctness was estimated for the less human impacted lagoon (low eutrophication and no aquaculture) whereas other lagoons were not discriminated from the regional pool. Thus, proposing diversity indices that include differences between species is certainly an important step in ecology. These differences could be estimated through genetic data to obtain a phylogenetic diversity (Clarke & Warwick 2001) but interpretation of these differences is still unclear. These differences could be functional. Recently, Petchey and Gaston (2002) used a new functional diversity estimation based on morphological characters of species. We can expect some advances on this topic because functional diversity indices could be more relevant in environmental impact assessment or in ecosystem functioning studies.

## Acknowledgments

This study was granted by Thema-based Research Project # 4 “Numerical methods to study the influence of hydroclimatic/anthropic factors on the spatio-temporal variability of coastal ecosystems” (coordinators B Beliaeff and JP Durbec) from the “National Research Programme on Coastal Environment” (PNEC). We would like to thank JM Deslous-Paoli for his participation in diving operations and fieldwork and the Station of IFREMER (Sète) for the facilities provided during the fieldwork. We wish to thank BJ Anderson, N Mason, JB Wilson and an anonymous reviewer for helpful comments and language corrections.

Figure 5. Classification of Languedoc-Roussillon lagoons based on taxonomic diversity indices. Environmental variability is related to the variation of environmental factors such as salinity or temperature.

		Average taxonomic distinctness		
		Low	Medium	High
Variation in taxonomic distinctness	Low	Low environmental variability Human impact Eutrophication	Low environmental variability Medium human impact No eutrophication (Thau)	Low environmental variability No human impact No eutrophication
	Medium		Medium environmental variability Medium human impact No eutrophication (Salse-Leucate)	Medium environmental variability No human impact No eutrophication (Bages-Sigean)
	High	High environmental variability Human impact Eutrophication (Maugu)		High environmental variability No human impact No eutrophication

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## Appendix

Taxonomic tree for macrophyte community in Languedoc-Roussillon lagoons (Verlaque 2000, 2001; Guiry & Nic Dhonncha 2002), exotic species having a star. In the last column, the names of the lagoon where they were sampled: B, M, S and T for respectively, Bages-Sigean, Mauguio, Salse-Leucate and Thau lagoons

Phylum	Class	Order	Family	Genus	Species	Lagoon	
Magnoliophyta	Liliopsida	Najadales	Ruppiceae	Ruppia	cirrhusa	S	
		Potamogetonales	Potamogetonaceae	Potamogeton	pectinatus	M	
			Zosteraceae	Zostera	marina	BST	
Charophyta	Charophyceae	Charales	Characeae	Lamprothamnium	papulosum	BST	
				Chara	aspera	S	
Chlorophyta	Chlorophyceae	Bryopsidales	Bryopsidaceae	Bryopsis	plumosa	T	
			Chaetosiphonaceae	Blastophysa	rhizopus		
				Chaetosiphon	moniliformis		
			Codiaceae	Codium	bursa	T	
			Derbesiaceae	Derbesia	rhizophora		
				Bolbocoleon	pliferum		
		Chaetophorales	Chaetophoraceae	Entocladia	leptochaete		
				viridis			
		Chroolepidaceae	Piliinia	sp.			
				aerea		S	
		Cladophorales	Cladophoraceae	Chaetomorpha	linum		MST
					mediterranea		
				Cladophora	sp.	BST	
				Rhizoclonium	riparium		
		Dasycladales	Polyphysaceae	Acetabularia	acetabulum	T	
		Phaeophilales	Phaeophilaceae	Phaeophila	dendroides	S	
		Siphonocladales	Valoniaceae	Valonia	aegagropila	S	
		Ulotrichales	Ulotrichaceae	Eugomontia	sacculata		
				Ulothrix	sp.		
		Ulvales	Ulvaaceae	Monostromataceae	Monostroma	obscurum	T
clathrata							
Enteromorpha	compressa				MT		
	flexuosa						
	intestinalis						
	prolifera						
	fasciata						
	lactuca						
Ulvellaceae	Acrochaete			rigida	BMT		
	irifata						
Heterokontophyta	Phaeophyceae	Cutleriales	Cutleriaceae	Aglaozonia	parvula	T	
				Cutleria	multifida		
		Desmarestiales	Desmarestiaceae	Desmarestia	viridis	T	
				dichotoma			
		Dictyotales	Dictyotaceae	Dictyota	fasciola		
					linearis		
				Padina	pavonica		
		Ectocarpales	Ectocarpaceae	Acinetospora	crinita		
				Feldmannia	sp.		
				Streblonema	sp.		
				Hinksia	fuscata		
					granulosa		
					mitchellae		
					sandriana		
				Ectocarpus	fasciculatus		
				siliculosus			
				Kuetzingiella	sp.		
		Kuckuckia	spinosa				
		Chordariales	Pylaiellaceae	Pilayella	littoralis		
				cylindricus			
Chordariaceae	Cladosiphon		mediterraneus	T			
	zosteriae						
Sphaerotrichia	divaricata		T				
Corynophlaeaceae	Myriactula		sp.				
	Leathesia		difformis				
	Cylindrocarpus		microscopicus				
	Acrotrichaceae		Acrotrich	gracilis			
Elachistaceae	Elachista		stellaris				
		Halothrix	lumbicalis				
Myrionemataceae	Myrionema	orbiculare					
		strangulans					
Spermatochneaceae	Stilophora	rhizodes					
Punctariaceae	Punctaria	latifolia					
		tenuissima					
Dictyosiphonales	Giraudiaceae	Giraudia	sphacelarioides				

Rhodophyta	Rhodophyceae	Acrochaetiales	Acrochaetiaceae	Acrochaetium	daviesii leptonema mediterraneum reductum savianum secundatum virgatulum				
		Bangiiales	Bangiaceae	Bangia	atropurpurea				
				Porphyra	leucosticta yezoensis				
				Aglaothamnion	byssoides				
		Ceramiales	Ceramiaceae	Antithamnion	cruciatum nipponicum				
				Callithamnion	corymbosum tetragonum				
				Centroceras	clavulatum ciliatum codii diaphanum flaccidum petitii secundatum siliquosum strictum tenerrimum				
						Griffithsia	corallinoides		
						Pterothamnion	plumula		
						Seirospora	giraudyi		
						Spyridia	filamentosa		
					Dasyaceae	Dasya	sessilis		
						Dasyisiphonia	sp.		
					Delesseriaceae	Acrosorium	verulosum		
						Nitophyllum	punctatum		
						Radicilingua	reptans thyzanorhizans		
					Rhodomelaceae	Alsidium	corallinum capillaris		
						Chondria	coerulescens dasyphylla		
						Halophyllum	incurva		
						Herposiphonia	parca		
						Laurencia	microcladia okamurae		
						Lophosiphonia	obscura		
						Osmundea	truncata		
							Polysiphonia	atlantica brodiei denudata elongata furcellata harveyi morrowii opaca paniculata sertularioides setigera subulata pennata	
							Pterosiphonia	tanakae	
							Rytiphloea	tinctoria	
				Corallinales		Corallinaceae	Corallina	elongata	
							Hydrolithon	farinosum rubens	
							Jania	yessoense	
							Lithophyllum	sp.	
							Phymatolithon	lenormandii	
					Pneophyllum		confervicola fragile		
					Titanoderma		pustulatum		
				Erythropeltidales	Erythropeltidaceae	Erythrotrichia	carnea investiens simplex		
						Sahlingia	subintegra		

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