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Ascendency as an ecological indicator: a case study of estuarine pulse eutrophication

J. Patrício^{a,*}, R. Ulanowicz^b, M.A. Pardal^a, J.C. Marques^a

^aIMAR-Institute of Marine Research, c/o Department of Zoology, Faculty of Sciences and Technology, University of Coimbra, 3004-517 Coimbra, Portugal ^bChesapeake Biological Laboratory, Center for Environmental and Estuarine Studies, University of Maryland,

Solomons, MD 20688-0038, USA

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Abstract

Increasingly, management agencies require that the remediation of eutrophic waters be addressed at the level of the whole ecosystem. One whole-system approach to quantify ecosystems is called ecological network analysis. Ascendency theory, the branch of the field that deals with the quantification of whole-system status, specifically addresses the definition of eutrophication. This definition has been applied to data taken over a gradient of eutrophication. Three separate areas were observed: a non-eutrophic area (with *Zostera noltii* meadows), an intermediate eutrophic area (*Z. noltii* absent and macroalgae abundant at times) and a strongly eutrophic area (where *Enteromorpha* spp. blooms occur with regularity). Pulse eutrophication was considered as the major driving force behind a gradual shift in primary producers from a community dominated by rooted macrophytes (*Z. noltii*) to a community dominated by green macroalgae. The measures associated with the intermediate eutrophic region turned out not to be intermediate to those at the gradient extremes. The most likely explanation appears to be the highly unstable nature of this area. Conditions along the spatial gradient are discussed as representing various stages in the temporal evolution of the system, and analysed in the framework of the Intermediate Disturbance Hypothesis, Bifurcation, Chaos, and Catastrophe theories. © 2004 Elsevier Ltd. All rights reserved.

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1. Introduction

Most European and North American estuaries are affected to some degree by organic pollution and nutrient discharges, often to an extent that gives rise to eutrophication with linked effects upon resident biota (Diaz and Rosenberg, 1995; Norkko and Bonsdorff, 1996; Flindt et al., 1997; Marques et al., 1997; Weaver et al., 1997; Rafaelli et al., 1998; Cloern, 2001). It has been observed that benthic eutrophication in estuaries and coastal lagoons can induce a shift from rooted plant communities, dominated by slow-growing species, like the eelgrass *Zostera*, towards free-floating (or partially freefloating), faster-growing macroalgae, like *Enteromorpha*

* Corresponding author.

E-mail address: imar@ci.uc.pt (J. Patrício).

or *Ulva* (Hartog, 1994; Duarte, 1995; Borum, 1996; Marques et al., 1997; Lillebø et al., 1999; Pardal et al., 2000; Cardoso et al., 2002).

During the past two decades, the emphasis in ecology has shifted somewhat toward a vision of the ecosystem as a system of interactions (Fasham, 1984; Frontier and Pichod-Viale, 1995). That is, the center of interest has become less the state of the biomass of the different groups of organisms, than the status of the interactions between them, as quantified by flows of matter or energy (Niquil et al., 1999). In particular, there have been attempts to define quantitatively the process of eutrophication (Cloern, 2001). Any index used in such attempts must combine the attributes of system activity level and community structure. One such measure derives from the analysis of networks of trophic exchanges and is called the system "ascendency". Ulanowicz (1980) defines ascendency as an index that quantifies both the

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level of system activity and the degree of its organization whereby it processes material in autocatalytic fashion.

Ascendency is a rather abstract concept that reveals manifold attributes when viewed from a variety of aspects. This richness makes the measure useful in a number of practical circumstances. Ascendency was originally created to quantify the developmental status of an ecosystem. If the manager suspects that a particular disturbance has negatively impacted his/her ecosystem, ascendency can be invoked to test that hypothesis quantitatively, provided sufficient data are available to construct networks of exchanges before and after the impact. Not only can before and after comparisons be made, but the developmental stages of disparate ecosystems can also be compared with one another (e.g. Ulanowicz and Wulff, 1991).

Using ascendency, it is possible to determine quantitatively whether a system has grown or shrunk, developed or regressed. Furthermore, particular patterns of changes in the information variables can be used to identify processes that hitherto had been described only verbally (Ulanowicz, 2000). The process of eutrophication, for example, can be described in terms of network attributes as any increase in system ascendency (due to a nutrient enrichment) that causes a rise in total system throughput that more than compensates for a concomitant fall in the mutual information (Ulanowicz, 1986). This particular combination of changes in variables allows one to distinguish between instances of simple enrichment and cases of undesirable eutrophication.

The aim of this study, therefore, is to test whether the network formulation of eutrophication properly tracks changes in community structure along a known gradient of eutrophication in the south arm of Mondego estuary (Portugal), a well described small temperate intertidal estuary (e.g. Marques et al., 1997; Pardal et al., 2000; Cardoso et al., 2002).

2. Material and methods

2.1. Study area

The Mondego estuary, western coast of Portugal (Fig. 1), consists of two arms, north and south, with very different hydrological characteristics. The northern arm is deeper, while the southern arm is silted up, especially in upstream areas, which causes most of the freshwater discharge to flow through the northern arm. Consequently, the water circulation in the southern arm is dependent mainly on tidal activity and on the (usually small) freshwater input of a tributary, the Pranto river, which is controlled by a sluice.

Although, a large part of the southern arm intertidal area remains relatively unimpacted, consisting of sand/ mud bottoms covered by *Spartina maritima* marshes and



Fig. 1. Mondego estuary: location of the sampling stations along a spatial gradient of eutrophication.

Zostera noltii meadows, macroalgal blooms of Enteromorpha spp. have been regularly observed the last 20 years (Flindt et al., 1997; Marques et al., 1997; Lillebø et al., 1999; Pardal et al., 2000; Martins et al., 2001; Cardoso et al., 2002). In general, Enteromorpha spp. biomass increases from early winter until July, when an algal crash usually occurs (Fig. 2). These macroalgal blooms may not occur in exceptionally rainy years, due to long intervals of low salinity coupled to strong currents occasioned by discharge from the Pranto (Martins et al., 2001).

Three sampling stations representative of a spatial gradient in eutrophication were chosen along the south arm of the Mondego estuary (Marques et al., 1997; Lillebø et al., 1999; Pardal et al., 2000; Cardoso et al., 2002) (Fig. 1): a non-eutrophic area (*Zostera noltii* beds still present), an intermediate eutrophic area (*Z. noltii* mostly absent, although residual roots can still be found in the sediment and macroalgae is sometimes abundant) and a strongly eutrophic area (macrophyte community totally absent for a decade and *Enteromorpha* spp. blooms are regularly observed).



Fig. 2. Inter-annual changes in macroalgae (*Enteromorpha* spp. and *Ulva* spp.) biomass along the eutrophication gradient.

2.2. Methods

Estuarine food webs were constructed at the three sites and these quantified food webs were examined using network analysis, which quantifies input-output relationships (Leontief, 1951), cycling (Finn, 1976), through-flows, storage, information-theoretic indices of whole-system status (Ulanowicz, 1986) and indirect diet relationships.

In order to estimate the magnitudes of the links in the network (the trophic exchanges), an estimate of the biomass of each component (living and non-living) is needed. Information on the diets of all feeding species is also required, as are some estimates of the physiological requirements of each compartment (consumption:biomass, respiration:biomass, excretion:biomass, etc.) and of the intensities of flows between compartments and their external surroundings. These data for each of the three networks were collected from different sources (e.g. Marques et al., 1997; Pardal et al., 2000, 2002; Cardoso et al., 2002).

A complete network analysis requires estimates of the rates of export from the system, including the harvests of economically important species. In the south arm of the Mondego estuary the harvest of *Scrobicularia plana* and *Nereis diversicolor* was considered so small as to be negligible.

The annual average biomass of each compartment was reported in gAFDW m⁻² and fluxes were in gAFDW m⁻² y⁻¹. Energy budgets for each of the three stations were developed using "Ecopath with Ecosim" software (http://www.ecopath.org), which calculates a balanced budget for each trophic group, according to the linear equation $C_i = P_i + R_i + E_i$, where $C_i =$ consumption, $P_i =$ production, $R_i =$ respiration, and $E_i =$ egestion by *i*. Estimates of consumption, production

Table 1

Network analysis ecosystem in	ndices f	for the	three	area
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and respiration generated by Ecopath with Ecosim were imported into NETWRK 4.2a software (Ulanowicz, 1999) to calculate annual AFDW budgets for each heterotrophic compartment during one year. The structures of trophic levels and cycling for each network were analyzed and the system properties were calculated using algorithms described by Ulanowicz (1986), Kay et al. (1989) and Monaco and Ulanowicz (1997).

2.2.1. Whole system indices

2.2.1.1. Total system throughput (TST). The differences in system activity are gauged by the relative values of the TST (Table 1). The total system throughput is simply the sum of all transfer processes occurring in the system. That is $TST = \sum_{p,q} T_{pq}$ for all possible transfers T_{pq} , where p and q can represent either an arbitrary system component or the environment.

2.2.1.2. Ascendency. This is a key property of a network of flows that quantifies both the level of system activity and the degree of organization (constraint) with which the material is being processed in autocatalytic systems such as ecosystems. The ascendency, A, expressed in terms of trophic exchanges, T_{ij} , from taxon *i* to taxon *j* is calculated as,

$$A = \sum_{i} \sum_{j} T_{ij} \log \left[\frac{T_{ij} T_{\cdot}}{T_{j} T_{i\cdot}} \right]$$

where a dot as a subscript indicates summation over that index.

2.2.1.3. Development capacity. This index is a surrogate for the complexity of the food web (Monaco and

Information indices	Non-eutrophic area	Intermediate eutrophic area	Strongly eutrophic area 2612		
Total system throughput (g AFDW $m^{-2} y^{-1}$)	10852	1155			
Development capacity (g AFDW $m^{-2} y^{-1}$; bits)	39126	5695	10831		
Ascendency (%)	42.3	30.4	36.7		
Overhead on imports (%)	12.3	8.2	6.2		
Overhead on exports (%)	1.3	1.5	2.5		
Dissipative overhead (%)	17.7	22.1	19.9		
Redundancy (%)	26.4	37.8	34.6		
Average mutual information (bits)	1.52	1.50	1.52		
Φ/TST	2.08	3.43	2.62		
Connectance indices					
Overall connectance	1.67	2.43	2.1		
Intercompartmental connectance	2.41	3.57	2.63		
Finn cycling index	5.75E-02	0.2045	0.1946		
Total number of cycles	74 517	15009	9164		

Ulanowicz, 1997). In other words, it is the diversity of the system flows scaled by the total system throughput. Quantitatively, it takes the form

$$C = \sum_{i,j} T_{ij} \log \left[\frac{T_{ij}}{T_{\cdot \cdot}} \right]$$

2.2.1.4. Average mutual information (AMI). This measures the average amount of constraint exerted upon an arbitrary quantum of currency as it is channelled from any one compartment to the next (Ulanowicz, 1997). It is the unscaled form of the ascendency and is written as

$$AMI = \sum_{i,j} \frac{T_{ij}}{T_{..}} \log \left[\frac{T_{ij}T_{..}}{T_{i.}T_{.j}} \right]$$

2.2.1.5. Redundancy. This is the degree to which pathways parallel each other in a network. It can be calculated in an isolated system as the (non-negative) difference by which the system capacity exceeds the ascendency. In terms of flows it is

$$R = -\sum_{i,j=0}^{n} \frac{T_{ij}}{T_{\cdot \cdot}} \log \left[\frac{T_{ij}^2}{T_{i \cdot} T_{\cdot j}} \right]$$

where n is the number of components in the system (for more details see Ulanowicz and Norden, 1990; Ulanowicz and Wulff, 1991).

2.2.1.6. Specific overhead of the system (Φ/TST) . It measures the total flexibility of the system on a perunit-flow basis. The overhead of a system is the amount by which the capacity of a non-isolated system exceeds the ascendency. It consists mostly of redundancy, but in open systems it is also augmented by multiplicities in the external inputs and outputs. In terms of the flows it resembles the redundancy, only it also includes the transfers with the external world,

$$\Phi/\mathrm{TST} = -\sum_{i,j=0}^{n+2} \frac{T_{ij}}{T_{\cdots}} \log\left[\frac{T_{ij}^2}{T_i \cdot T_{\cdot j}}\right]$$

where the index (n+1) signifies an import and (n+2) an export or dissipation.

2.2.2. Trophic analysis

Food webs that are qualitatively very different can be mapped into a standard straight-chain network topology. This standard form allows comparison of corresponding trophic efficiencies between different estuaries (Baird et al., 1991). The trophic efficiency between any two levels is defined as the amount a given level passes on to the next one, divided by how much it received from the previous level (Ulanowicz and Wulff, 1991). The energy flow networks pertaining to the noneutrophic and the strongly eutrophic areas were aggregated into their canonical trophic forms (Fig. 3), called the "Lindeman spine" (Ulanowicz, 1997). The connectance indices (Table 1) are estimates of the effective number of links both into and out of each compartment of a weighted network.

2.2.3. Cycle analysis

The Finn Cycling Index (FCI) reveals the proportion of total system throughput that is devoted to the recycling of carbon (Finn, 1976). Thus, $FCI = T_c/TST$,



Fig. 3. Linear food chains: (a) *Zostera* meadows and (b) strongly eutrophic area. Flows out of compartment boxes represent exports $(g \text{AFDW m}^{-2} \text{y}^{-1})$, flows arriving to compartment boxes represent outside system inputs $(g \text{AFDW m}^{-2} \text{y}^{-1})$ and flows out of the bottom represent respiration $(g \text{AFDW m}^{-2} \text{y}^{-1})$. Level I+D corresponds to the association of autotrophs (level I) and Detritus (non-living compartment). The heterotrophic compartments are divided into levels II–IX (in a) or levels II–VIII (in b), according to their diet.

where T_c is the amount of system activity involved in cycling.

3. Results

The energy flow networks of each community are depicted in Fig. 4. Taken together with Table 1 and Fig. 3 these provide the measures that were used to characterize the trophic status of the three estuarine ecosystems. Fig. 5 characterizes the magnitude and structure of carbon cycling at the two endpoints of the eutrophication gradient.

Following Monaco and Ulanowicz (1997), no test of statistical significance was applied to the differences between the values of the indices pertaining to the different areas, due to the complexity of comparing information-theoretic combinations. When the results of network trophic structure and estuarine ecosystem properties were ordered according to magnitude, definitive patterns emerged, providing insights into the trophic structures, complexities and relative stresses exhibited by each community (Monaco and Ulanowicz, 1997).

3.1. Whole system indices

The current study was designed to test how the network formulation of eutrophication could be applied to the differences in trophic status among the trophic structures of three neighbouring communities along an eutrophication gradient. Although the three habitats are clearly distinct in physical appearance, network analyses revealed both differences and similarities among their trophic structures that had not been apparent at first glance.

It was possible to observe (Table 1) that the Zosteradominated community had the highest total system throughput, followed (unexpectedly) by the strongly eutrophic system and finally by the intermediate eutrophic area. The development capacity was highest in the Zostera beds and lowest in the intermediate eutrophic area. The index differed significantly among the three areas. Due to the logarithmic nature of this index, small differences can represent appreciable disparities in structure. The average mutual information was slightly higher in the non-eutrophic area, followed closely by the eutrophic area and was lowest in the intermediate eutrophic area. Concerning ascendency, it increased in order from the intermediate eutrophic to the heavily eutrophic zone to the Zostera meadows. Regarding redundancy, the intermediate eutrophic community had the highest value, followed by strongly eutrophic area and was least in the *Zostera* beds. The rankings in $\Phi/$ TST mirrored those in redundancy, which comprises the largest component of Φ/TST .

3.2. Trophic analysis

The Lindeman spine for the non-eutrophic area possesses an additional trophic level beyond those apparent in the strongly eutrophic chain (Fig. 3). Although both areas exhibited their highest transfer efficiencies at the first trophic level (*Zostera* beds with 14.8% and the strongly eutrophic with 47.2%), the intermediate eutrophic area was most effective in transferring material (8.9%) at the second trophic level.

In the Mondego system, connectance indices (Table 1) are relatively low, being modest in the intermediate eutrophic area, and decreasing yet further in the strongly eutrophic and *Zostera* community.

3.3. Cycle analysis

The Finn Cycling Index percentage (Table 1) was greatest in the intermediate eutrophic area (20.45%), decreased in the strongly eutrophic zone (19.46%) and then markedly in the Zostera-dominated system (5.75%). This would seem to indicate that the overall percentage of cycled matter increases as the degree of eutrophication rises. The structure of cycling changes dramatically between the pristine and eutrophic systems, however. The total number of cycles (Table 1) is highest in the Zostera beds (74517), followed by the intermediate eutrophic area (15009) and the fewest are counted in the strongly eutrophic community (9164). This is due to the fact that a larger number of cycles tend to be found among systems with more compartments at higher trophic levels. The preponderance of cycling occurs in both systems over cycles of length 2, and the major routes for recycle are shown in Fig. 5. From this figure it is evident that less material is flowing over the more complicated web of cycles in the Zostera community (Fig. 5a), while far more medium cycles flow over fewer pathways in the strongly eutrophic system (Fig. 5b). This is a common signature of a stressed ecosystem (Ulanowicz, 1986).

4. Discussion

Eutrophication as a state of an ecosystem is difficult to define quantitatively and little consensus has been reached (Christian et al., 1996; Cloern, 2001). Nevertheless, there are points upon which most investigators agree. The process of eutrophication, for example, is commonly considered to be an increase in the rate of supply of organic matter to an ecosystem (Nixon, 1995). The dystrophy attendant to over-enrichment is usually manifested as the loss of important species along with the system functions they help to maintain. That is, although nutrients tend to stimulate a system's growth, the organization of the system is degraded, despite its



Fig. 4. Energy flow diagrams: (a) Zostera meadows, (b) intermediate eutrophic area and (c) strongly eutrophic area. Biomass is given in gAFDW $m^{-2} y^{-1}$.





Fig. 4 (continued)



Fig. 5. Cycling diagrams: (a) *Zostera* meadows cycling diagram, representing the compartments involved in 91% of the cycled flow (g AFDW m⁻² y⁻¹) and (b) strongly eutrophic area cycling diagram, representing the compartments involved in 92% of the cycled flow (g AFDW m⁻² y⁻¹).

augmented activity. Almost all studies stress nutrient enrichment as well as its negative consequences for the system.

The long-term study in the Mondego estuary indicated that years of low precipitation tended to be associated with reductions in turnover rates and increases in water column stability, temperature, salinity and light penetration (Martins et al., 2001). These changes in habitat conditions encouraged blooms of macroalgae that gradually replaced the resident macrophytes (Marques et al., 1997; Martins et al., 2001). In the intermediate and strongly eutrophic areas primary production is largely the result of these macroalgal blooms (Marques et al., 1997). Production appears as a strong pulse during this specific time, but remains at very low levels during the rest of the year (Fig. 2). This limited temporal interval of primary production results in a significantly lower figure for the cumulative annual primary production and total system throughput (TST) in these areas as compared with the corresponding measures in the Zostera beds. Comparing the average mutual information values of the flow structure for the three areas, it is possible to discern a very small decrease in the measure among the three zones, suggesting that, as regards trophic structure, these areas are indeed different. The three zones appear nevertheless much more distinct by eye than is illustrated by the average mutual information values.

In the light of these results, the network definition of eutrophication appears to be inappropriate for the Mondego estuarine ecosystem. It would be more accurate to describe the enrichment processes occurring in this ecosystem as "pulse eutrophication". This process could be characterized as a disturbance to system ascendency in the form of an intermittent supply of excess nutrients that, when coupled with a combination of physical factors (e.g. salinity, precipitation, temperature, etc.), causes both a decrease in system activity and a drop in the mutual information of the flow structure. Even though a significant rise in the total system throughput does occur during the period of the algal bloom and at that time does give rise to a strong increase of the system ascendency (as per the network definition of press eutrophication), the annual picture nevertheless suggests that the other components of the intermediate and strongly eutrophic communities were unable to accommodate the pulse in production. The overall result was a decrease in the annual value of the system TST and, as a consequence, of the annual ascendency as well.

Regarding the results of the trophic analysis, the *Zostera* community has one more trophic level than those counted in the strongly eutrophic chain, implying that this community possesses a more complex web with additional top consumers. At the same time, the *Zostera* community exhibits lower transfer efficiency at the first trophic level, probably because the production of *Z. noltii* meadows usually cannot be eaten directly, but needs to be decomposed first (Lillebø et al., 1999).

Concerning the analysis of cycled materials, the overall percentage of cycled matter, as indicated by the FCI, increases as the degree of eutrophication rises. Odum (1969) suggested that mature ecosystems recycle a greater percentage of their constituent material and energy than do pioneer or disturbed communities. Hence, according to Odum, the progressive increase in the FCI would suggest the maturation of the ecosystem. It has been observed, however, that disturbed systems also often exhibit greater degrees of recycling. The speculation is that such an increase in cycling in disturbed systems is the homeostatic response that maintains in circulation resources, which before the perturbation had been stored as biomass in the higher organisms (Ulanowicz and Wulff, 1991). This latter scenario seems consistent with the present results.

When the whole-system properties of the three areas were compared, the measures associated with the system considered to lie between the two extremes in nutrient loading did not plot intermediate to the other two. Rather, the intermediate eutrophic area exhibited the lowest ascendency, AMI, TST and development capacity values and the highest figures for redundancy, Φ/TST and FCI, so to say it appears to be the most disturbed of the three areas. In a previous study (Marques et al., 1997) it was suggested that the most likely explanation appears to be in the highly labile nature of the intermediate system. In fact, observations using other ecological indicators have indicated that the communities built around both the Zostera and Enteromorpha populations represent more stabilised communities at the ends of the eutrophication gradient. Regarding the intermediate eutrophic area, since it always exhibited the lowest values of total biomass and the highest species heterogeneity (as measured by the Shannon-Wiener index), a preliminary interpretation of the results suggested that the Intermediate Disturbance Hypothesis (IDH) (Connel, 1978) was applicable to explain the observations (Margues et al., 1997). Nevertheless, the same database was also utilised to test other ecological indicators (the Exergy index and Specific Exergy, thermodynamically oriented), which allowed the conclusion that: (a) both indicators were consistently higher in the non-eutrophic area, followed by the most eutrophic and intermediate eutrophic areas; (b) their range of variation through time was smaller in the non-eutrophic area, expressing a more stable situation, while the magnitude of the variations was stronger in the other two areas, but especially in the intermediate eutrophic area (Margues et al., 2003). As a whole, by contrast with the other two areas, the intermediate eutrophic one clearly appeared too disturbed to allow for the establishment of a coherent community built around either mode of primary production.

Observations on the intermediate eutrophic area were not satisfactorily consistent with the IDH, which is thought to be realised in systems with a certain capacity to absorb changing environmental conditions at a larger time scale. The story would be not so simple had the system already lost or exploited most of the possibilities to react properly, either due to natural succession or long-term stress.

Qualitative observations carried out in the Mondego estuary since the early 1980s (Marques et al., 1984) provide a general idea regarding how the system was at the time. Since then, the most evident feature has been the increase of eutrophication symptoms and its impact on the biological communities, of which the most visible effect was the occurrence of green macroalgae blooms and a concomitant decrease of the area occupied by Zostera noltii beds. Twenty years ago, Z. noltii beds covered a large part of the intertidal area, extending to the upstream section of the south arm. Moreover, its disappearance first took place in the inner areas of the south arm of the estuary, what is now the most eutrophic area, and went forward to the downstream section, where it is presently restricted. In the intermediate eutrophic area, although Z. noltii disappeared some time ago, it is still possible to find the remains of its rhizomes in the sediment.

The way macroalgae extended from upstream to downstream sections in the south arm of the estuary, competing with *Zostera noltii* and the way this process influenced faunal assemblages have been fully described in the previous works, illustrating how a shift in primary producers may determine changes at other trophic levels (Marques et al., 1997; Marques et al., 2003). Additionally, a tentative interpretation of the recent biological changes in the system has been proposed (Marques et al., 2003), starting from a basic assumption: Since Z. noltii's disappearance in the south arm of the estuary commenced in the inner areas and progressed downstream, spatial changes in the system may be taken as representing temporal changes. The non-eutrophic area, with Z. noltii beds, may thus represent what the system was two decades ago, the intermediate eutrophic area may represent the changing areas during the process, and the most eutrophic area may represent the most advanced stage in the observed shift of primary producers, where macroalgae have totally ousted macrophytes.

Once this assumption is accepted, the recent modification in primary producers and its related food web may be seen as a dynamic shift in the ecosystem network structure, of the catastrophic type, described for instance by Scheffer et al. (2001). In the prevailing conditions two decades ago, rooted macrophytes, Zostera noltii and related epiphytic grazers dominated by Hydrobia ulvae were selected, and an important detrital food web was also present. As eutrophication affected an increasing area of the estuary, green macroalgae, like Enteromorpha spp. and Ulva spp. replaced the rooted macrophytes. As a consequence, the high turnover of these macroalgae, and the alternation between periods dominated by the occurrence of extensive algal mats and periods with bare bottom organically enriched sediments caused an increasing importance of the detrital pathway (Marques et al., 2003). How can this shift be theoretically understood?

The possible long-term development and modification, of an ecosystem exposed to various degrees of disturbances, natural as well as those caused by humans, may be illustrated by Fig. 6a. On the left part of the curve, at a relatively low level of stress corresponding to normal fluctuations in environmental conditions, a normal succession towards an increase and finally stabilization of the biomass and complexity of the system is represented. During this period, the system will follow traditional developmental patterns (see for instance the 24 principles of E.P. Odum) such as development from r- to K-strategists, increased cycling, and importance of the network, etc. (Odum, 1971).

For a given increase in stress, literature exists that reports an additional stimulation of biomass and diversity, illustrated by a "hump" on the curve (Fig. 6a), what is usually referred to as the IDH (Connel, 1978). Nevertheless, this developmental pattern is only thought to be realised in systems that possess a cache in diversity that enable them to react, buffering the disturbances at



Fig. 6. Ecosystem development as a function of succession and environmental stress: (a) relation between possible ways of ecosystem development and concepts from ecological theory and (b) possible interpretation of changes on going in the Mondego estuary in the frame of ecological theories.

a larger time scale, which is not always the case. If a system has lost or exploited most of its overhead already, either due to natural succession or long-term stress, such capability may be limited or not exist at all. If this is the case, higher stress forces will lead to "real" macroscopic modification, which takes place through other mechanisms. First of all, continuous adaptation and finetuning of parameters lead to a system of highly fitted and specialised organisms, which in turn will reduce an organism's adaptability in relation to changes in environmental conditions. As a result, it is believed that the system as a whole becomes very unstable and brittle (Jørgensen and Johnsen, 1989). This phase may be expected to correspond to large short-term fluctuations of the ecological indicators we may use to capture the state of the system (Fig. 6a), which corresponds to the observations by Marques et al. (2003). Second, adaptation of the network leads to a development where the ecosystem has decreased as much as possible its conditional entropy, or overhead in the sense of Ulanowicz (1986, 1997), i.e. maximizing the utilisation of the available resources (energy) through a more and more specialised (efficient) species composition. Such specialisation also means a decrease in the possibility of the system to cope with environmental changes, which eventually leads to change through a type of Holling cycle (Holling, 1986; Ulanowicz, 1997).

Moreover, the modification of systems is non-linear, and as time passes instability gives rise to a bifurcation to new stability points (Glansdorf and Prigogine, 1971) (Fig. 6a,b). In other words, the instability of the system will thus lead it to a breakdown-a catastrophe-with possibilities of new organisms and combinations to take over and be selected because the new constellation is better able to meet the prevailing conditions. Catastrophe is not necessarily used here in its narrow mathematical sense and may also not be mathematically as such (Zeeman, 1976). Beyond the point of bifurcation, whatever interpretation is preferred, several possibilities are allowed: (a) a total recovery of the system to an almost identical state can take place, which would correspond to a "normal" understanding and interpretation of the Holling cycle. This of course provided that the perturbation somehow has been stopped, and sufficient biodiversity has been conserved during the stress period to allow the system to return to a quasioriginal state; (b) in case these conditions are not fulfilled, the system will evolve to one or more stability points, or maybe even continuous instability. The shift to other stability points may also be viewed as if the system is leaving one Holling cycle (Holling, 1986) and entering into another.

Plausibly, several of these "states" of development can be identified in time and space along the south arm of the Mondego estuary. The following descriptions allow an understanding of the present state of each studied area along the south arm and interpret the situation in accordance with a broader theoretical frame, as previously suggested by Marques et al. (2003):

- (a) The Zostera noltii beds may be considered as corresponding to the more or less original state of the system, identical to the climax society (Fig. 6b). Meanwhile, these areas are in regression, showing that they are highly vulnerable to the present conditions.
- (b) The most eutrophic area has undergone a transition and, through a bifurcation, found another stability point (Fig. 6b).
- (c) In the intermediate eutrophic area changes exceed the natural variation to a degree where the system is never able to find a new stability point, and the scenario may be described as a chaotic regime (Fig. 6b), which will be followed by a catastrophic shift (Zeeman, 1976; Scheffer et al., 2001).

This interpretation is consistent with the fact that, through time, even in the short run, the highest variations of the ecological indicators estimated are found in this area (Marques et al., 2003). As a whole, the present results and conclusions appear to suggest that a possible recovery of the system should occur at different critical conditions than the shift to the scenario of macroalgal dominance, which is known as hysteresis (Scheffer et al., 2001), but at the present stage the data do not allow elucidation of this point and further work will be necessary.

Ecology thus deals with some of the most complex phenomena encountered in modern science. Ecosystem analyses must encompass several disciplines in a coordinated fashion to answer specific questions concerning how large, multidimensional systems work (Livingston et al., 2000; Jørgensen and Marques, 2001). Such research entails the integration of diverse studies, usually over a significant spatial area for intervals of time long enough to account for both seasonal and inter-annual variability of basic physical-chemical and biological factors. Such difficulties notwithstanding, network analysis appears to provide a systematic approach to understanding what is happening at the whole-system level. The current study on the Mondego estuarine ecosystem seems to have provided an example of how the measures coming out of network analysis can lead to an improved understanding of eutrophication process itself. Despite the considerable time and labour needed to collect all the data necessary to perform network analysis, the insights the method provided seem to demonstrate its promise as a very useful tool for ecosystem theory.

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