Ecological indicators performance during a re-colonisation field experiment and its compliance with ecosystem theories

Joana Patrício [a,*], Fuensanta Salas [a], Miguel Ângelo Pardal [a],
Sven Erik Jørgensen [b], João Carlos Marques [a]

[a] *IMAR-Institute of Marine Research, c/o Department of Zoology, Faculty of Sciences and Technology,
University of Coimbra, 3004-517 Coimbra, Portugal*
[b] *Environmental Chemistry Section, Danish University of Pharmaceutical Sciences, Institute A,
Universitetsparken 2, DK-2100 Copenhagen, Denmark*

Abstract

Through a re-colonisation field experiment three main questions were approached: (1) How do different ecological indicators react during the process of recovery? (2) What does grow first during a community succession, biomass or complexity? (3) Can the chosen ecological indicators help in recognising the three proposed forms of growth: biomass, network and information, throughout re-colonisation?

The study was carried out in an intertidal rocky community dominated by the algae *Corallina elongata*. Experimental plots were cleared and macroalgae and fauna were removed. Multivariate analysis was performed to examine the convergence of the disturbed plots with the surrounding community during recovery. Shannon–Wiener Index, Margalef Index, Pielou evenness, Eco-Exergy and Specific Eco-Exergy were applied to characterise the state of the community during the process. Results show that the replacement of species over time happens both with the macroalgae and associated macrofauna community. Species richness increased rather rapidly and species composition was similar in disturbed and undisturbed areas. After 7 months, diversity was consistently higher in the community undertaking recovery. Eco-Exergy and Specific Eco-Exergy provided useful information about the structural development of the community but lacked discriminating power with regard to the informational status of the system. The observations appear to illustrate a case explainable by the Intermediate Disturbance Hypothesis (IDH). Overall, the characteristics of a systems' recovery after disturbance appear to be dependent on the spatial scale of the disturbance. If a disturbed area is small when compared to a contiguous non-disturbed one, complexity (information and network) will recover prior to biomass.

---

* Corresponding author.
  E-mail address: jpatricio@ci.uc.pt (J. Patrício).

1. Introduction

The concept of succession (Odum, 1969) has been broadly applied in marine systems as the process by which species settle and are replaced on new or disturbed surfaces. In a relatively undisturbed environment or at least in an environment that is imposing only a limited degree of disturbance, the communities will follow a succession adapted to meet the long-term environmental average condition. Often, it happens that ecosystems are exposed to disturbances other than the natural ones, which adds an extra stress on the top of the natural disturbance level. Such disturbances are often related to human activities and the ecosystem response may vary drastically in both space and time (Marques et al., 2003). Since the 1970s, many community ecologists have focused attention on the dynamics of assemblages in marine coastal ecosystems that are recovering from different types of disturbance (e.g. Connell and Slatyer, 1977; Sousa, 1979; Paine and Levin, 1981; Van Tamelen, 1996; Chapman and Underwood, 1998) and there is a rich literature describing such successional changes in detail in a wide variety of coastal marine ecosystems (e.g. rocky shores: Kim and DeWreede, 1996; Benedetti-Cecchi and Cinelli, 1996; Dye, 1998; Williams et al., 2000; Hutchinson and Williams, 2003; coral reefs: Connell et al., 1997; Diaz-Pulido and McCook, 2002; soft sediments: Levin and DiBacco, 1995; Rosenberg et al., 2002; estuaries: Nogueira et al., 2000; salt-marshes: Valiela, 1995; Levin et al., 1996; Craft and Sacco, 2003) from all over the world. These studies have demonstrated that succession is likely the composite result of several processes (depletion, tolerance, facilitation, inhibition, removal, allelopathy, etc.) that determine if replacement takes place (Connell and Slatyer, 1977) and at what rates it is accomplished (Valiela, 1995). Several of these mechanisms, probably co-occur in most communities.

To evaluate the status of communities' ongoing recovery, a panoply of ecological indicators has been used. Nevertheless, in most cases, ecological indicators either only take into consideration some components of the ecosystem or result from non-universal theoretical approaches. In general terms, a number of them are based on the presence/absence of indicator species, other take into account the different ecological strategies carried out by organisms, like, diversity, or the energy variation in the system through changes in species biomass. Another group of ecological indicators is either thermodynamically oriented or based on network analysis, looking to capture the information on the ecosystem from a more holistic perspective (Patrício et al., 2004). In fact, biology and ecology are, in many ways, still lacking universal laws and predictive theory, and many ecologists feel the need for a more general and integrative theoretical network that may help to explain their observations and experimental results. Simultaneously, a broad theoretical framework needs to be in straight connection with empiricism. With that purpose in mind, it would be appealing to perceive what type of information is capture by distinct ecological measures applied to the same recovery experiment.

Over the last two decades, ecology has changed from a largely qualitative discipline to a quantitative hypothesis-driven experimental science and manipulative field experiments have contributed greatly to ecological theory during this period (Hawkins, 1999). Rocky shores, in particular, have proved to be good testing ground for ideas of general ecological significance (e.g. Connell and Slatyer, 1977; Benedetti-Cecchi and Cinelli, 1996; Dye, 1998; Hawkins, 1999; Olobarria, 2002; Hutchinson and Williams, 2003).

The experiment carried out aimed to approach three working questions: (1) How do different ecological indicators elucidate the process of recovery? (2) What does grow first during a community succession, biomass or complexity? Regarding this second question, according to Odum (1969), the hypothesis advanced was that biomass would be the first ecosystem-attribute to recover. (3) Can the chosen ecological indicators help in recognising the three forms of growth proposed by Jørgensen et al. (2000): biomass, network and information, throughout the recovery process?

2. Materials and methods

2.1. Study site

The experiment was carried out from February 1999 to May 2000 in a small beach called "Portinho da Areia
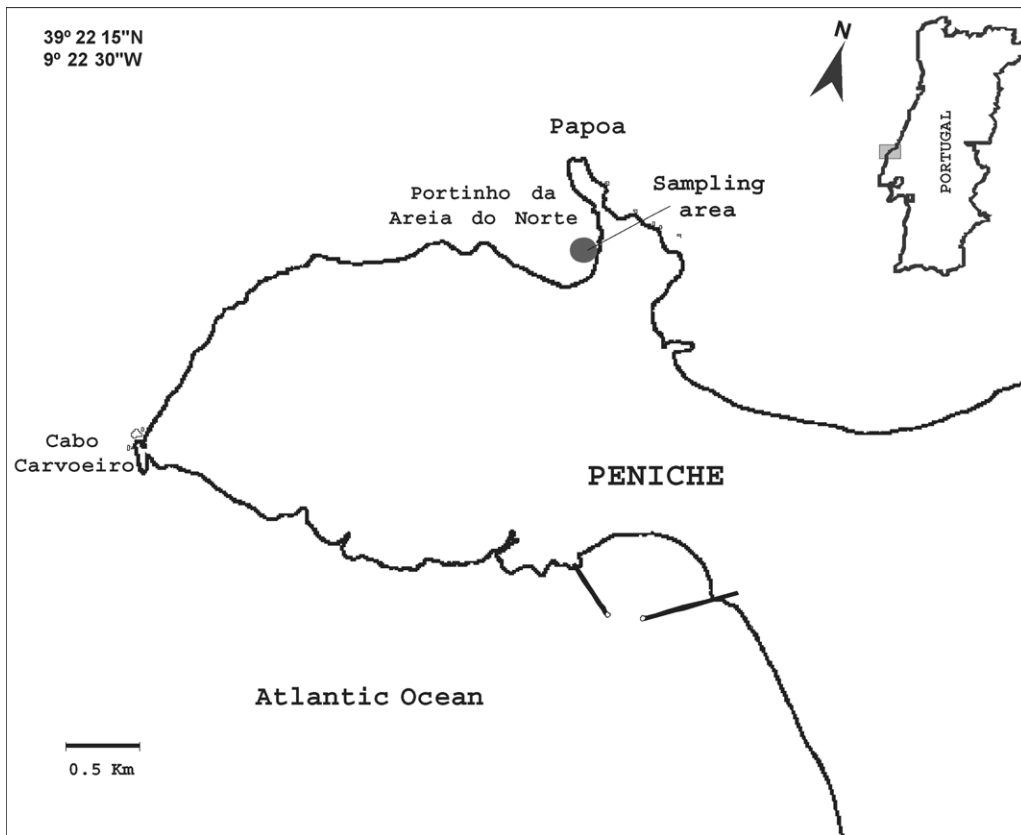
Fig. 1. Map of Peniche peninsula, Western Coast of Portugal, showing location of the study site.
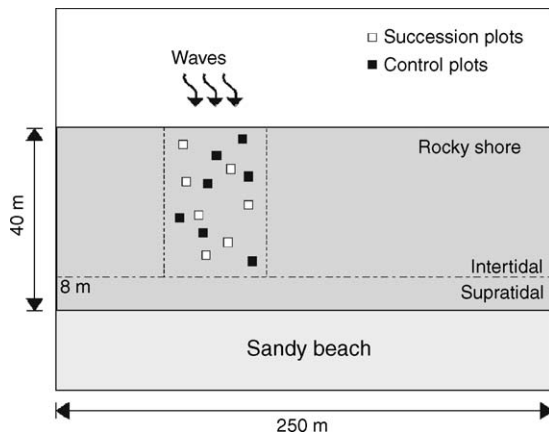

Fig. 2. Schematic diagram illustrating the 25 cm × 25 cm plots localization within the sampling area.

do Norte'' (39°22′15″N, 9°22′30″W) (Peniche), 70 km North from Lisbon, on the Western Coast of Portugal (Fig. 1). Slender calcareous layers alternate with marls structuring a nearly horizontal and homogeneous platform, with approximately 250 m in length and 40 m in width (Fig. 2). This intertidal rocky system is dominated by the turfing algae *Corallina elongata* Ellis and Solander, which forms a stiff matrix that held some sediment. Nevertheless, encrusting coralline *Lithophillum incrustans* Philippi, other red macroalgae (*Chondria caerulescencens* (Crouan) Falkenb., *Chondrachantus compressa* Grev., *Gigartina pistillata* (Gmelin) Stackh., *Asparagopsis armata* Harv., *Jania rubens* (L.) Lamouroux, *Lomentaria articulata* (Huds.) Lyngbye, *Gastroclonium ovale* (Huds.) Kütz., *Plocamium cartilagineum* (L.) Dixon, *Callithamnion tetricum* Agardh, *Ceramium* sp., *Nitophyllum punctatum* (Stackh.) Grev., *Laurencia pinnatifida* (Gmelin)

Lamouroux and *Calliblepharis jubata* (Gooden. Woodw.) Kütz., and green macroalgae (*Enteromorpha compressa* (L.) Grev., *Cladophora* sp. and *Ulva rigida* Agardh) also occur as epiphytes on the other plants or as early successional species.

2.2. Experimental design and sampling

For the present work, the broadly used concept of minimum area was applied. In February 1999, quadrats of 25 cm × 25 cm (625 cm^2) were randomly distributed across the study area (Fig. 2). The corners of each square plot were marked with casing nails for subsequent relocation. In this preparation phase, 27 discrete areas were created by totally removing macroalgae and the associated macrofauna with a chisel. Other plots were assigned as controls, being left undisturbed at this stage of the experiment. Subsequently, both experimental plots and control plots were sampled, during low tide, every 1 or 2 months, until May 2000. All experimental plots were replicated (three replicates); however, we were not able to replicate the control plots at all different dates.

Samples were preserved in 4% buffered formalin in seawater and sieved through a 500 μm mesh. Later, algae and associated macrofauna were separated, and identified. Both macroalgae and animals were subsequently dried at 70 °C for 72 h and weighted. Small individuals were pooled to obtain measurable values. Biomass, calculated as ash free dry weight (AFDW), was assessed after combustion of samples for 8 h at 450 °C.

2.3. Data analysis

Multivariate analyses were performed using the PRIMER 5 (Software package from Plymouth Marine Laboratory, UK) in order to examine for convergence of the recovering community with the surrounding area. Data (species abundance and biomass) were transformed by double square root. Bray Curtis similarity matrix was calculated and used to generate two-dimensional plot with the non-metric multidimensional scaling (nMDS) technique (Clarke, 1993; Clarke and Warwick, 1994). Stress values were shown for each MDS plot to indicate the goodness of representation of differences among samples.

On the other hand, the following ecological indices were applied: Shannon–Wiener Index (Eq. (1)), Margalef Index (Eq. (2)) and Pielou evenness (Eq. (3)):

$$H' = - \sum p_i \log_2 p_i \qquad (1)$$

$$D = \frac{S - 1}{\log(N)} \qquad (2)$$

$$J' = \frac{H'}{\log(S)} \qquad (3)$$

where p_i is the proportion of abundance of species i in a community were species proportions are p_i, p_2, p_3, ..., p_n, S the number of species found and N is the total number of individuals.

Moreover, we also applied Eco-Exergy (Eq. (4)), a concept derived from thermodynamics. Eco-Exergy (Jørgensen and Mejer, 1979) is one of the mathematical functions that have been proposed as holistic ecological indicators in the last two decades, intending (a) to express emergent properties of ecosystems arising from self-organization processes in the run of their development and (b) to act as orientors (goal functions) in models development. Such proposals resulted from a wider application of theoretical concepts, following the assumption that it is possible to develop a theoretical framework able to explain ecological observations, rules and correlations on basis of an accepted pattern of ecosystem theories. Eco-Exergy, which has been tested in several studies, can be seen as a measure of the maximum amount of work that the system can perform when it is brought into thermodynamic equilibrium with its environment.

If Eco-Exergy is calculated only from the chemical potentials, which are extremely dominant with regard to ecosystems, the following expression is valid with good approximation (Jørgensen, 2002):

$$EX = RT \times \sum C_i \times \beta_i \qquad (4)$$

where R is the gas constant, T the absolute temperature and C_i is the concentration in the ecosystem of component i (e.g. biomass of a given taxonomic group or functional group). β_i is a factor able to express roughly the quantity of information embedded in the biomass. β-Values have previously been calculated for several organisms based upon number of coding genes (see

Table 1
Values for the weighting factors to estimate Eco-Exergy related to organisms biomass for different groups of organisms (adapted from Fonseca et al., 2000)

Organisms	Weighting factor
Detritus	1
Minimal cell	2.7
Bacteria	2
Algae	25
Sponges	30
Jellyfish	30
Annelid worms	50
Insects	70
Crustaceans	230
Crustaceans (decapods)	230
Gastropods	450
Bivalves	760
Echinoderms	360

Jørgensen, 2002). The β-values used in estimating Eco-Exergy from biomass in the present paper are provided in Table 1.

Detritus was used as reference level, i.e. $\beta_i = 1$ and Eco-Exergy in biomass of different types of organisms is expressed in detritus energy equivalents. This formulation does not correspond to the strict thermodynamic definition, but provides nevertheless an approximation of Exergy values. In this sense, it was proposed to call it Eco-Exergy Index (Marques et al., 1997).

If the total biomass in the ecosystem remains constant Eco-Exergy variations will rely only upon its structural complexity, and thus a Specific Eco-Exergy of the system can be defined as Eco-Exergy/total biomass (Marques et al., 1997). Both Eco-Exergy and Specific Eco-Exergy have been tested as indicators in environmental assessment, being considered advisable to use them complementary (Marques et al., 1997, 2003; Jørgensen, 2002).

3. Results

3.1. Variation in algal structure

The algae community in the control plots (Fig. 3A) was, clearly, dominated by *C. elongata*, with a biomass peak in May 1999 (182 g m^{-2}) and a minimum in May 2000 (36 g m^{-2}) after a storm occurrence (April 2000)

that removed a significant part of the *Corallina*'s canopy. The other red macroalgae presented a biomass oscillation between 6.7 and 65 g m^{-2}. The green algae presented very low values through the study period, with an exception in May 2000 (12 g m^{-2}), after the storm occurrence, indicative of a partial restart of the re-colonisation process.

The succession plots were first re-colonised by the green algae *Enteromorpha compressa*, *Cladophora* sp. and *Ulva rigida*. Green algae biomass (Fig. 3B) increased from the beginning of re-colonisation until May 1999 (reaching 56 g m^{-2}), when an accentuated decrease occurred. Low values (1–5.5 g m^{-2}) were registered throughout until May 2000, when another biomass peak occurred (20 g m^{-2}), after a storm event. Inversely, the red algae *C. elongata* evidenced a slow biomass increase until June 1999, followed by a pronounced biomass increase which took place until May 2000. *Corallina* biomass peaks were observed in July 1999 (42 g m^{-2}), November 1999 (59 g m^{-2}) and March 2000 (65 g m^{-2}). The other red macroalgae showed only a slight increase throughout the study, although a pronounced biomass peak of these last ones occurred after the storm occurrence.

3.2. Variation in the macrofaunal community structure

A total of 2,637,979 individuals of 137 taxa (Table 2) were identified. In terms of abundance, the community in the control plots was dominated by different taxonomic groups according to the month considered (Fig. 3C). The main taxonomic groups were Gastropoda, Oligochaeta, Polychaeta, Enoploidea and Bivalvia. Considering the biomass estimates (Fig. 3E), Bivalvia and Polychaeta accounted between 72 and 92% of the total community biomass, showing inverse temporal trends. Bivalvia reached the highest biomass value in March 2000 and the minimum in June 1999 while, Polychaeta biomass presented a peak in June 2000 and rather low values in November 1999 and March 2000. Regarding the community abundance in the succession plots (Fig. 3D), during the first 3 months Gastropoda was the dominant taxonomic group, but subsequently its density decreased. In September 1999, a new peak of abundance occurred, declining afterwards until the end of the study period. Amphipoda,
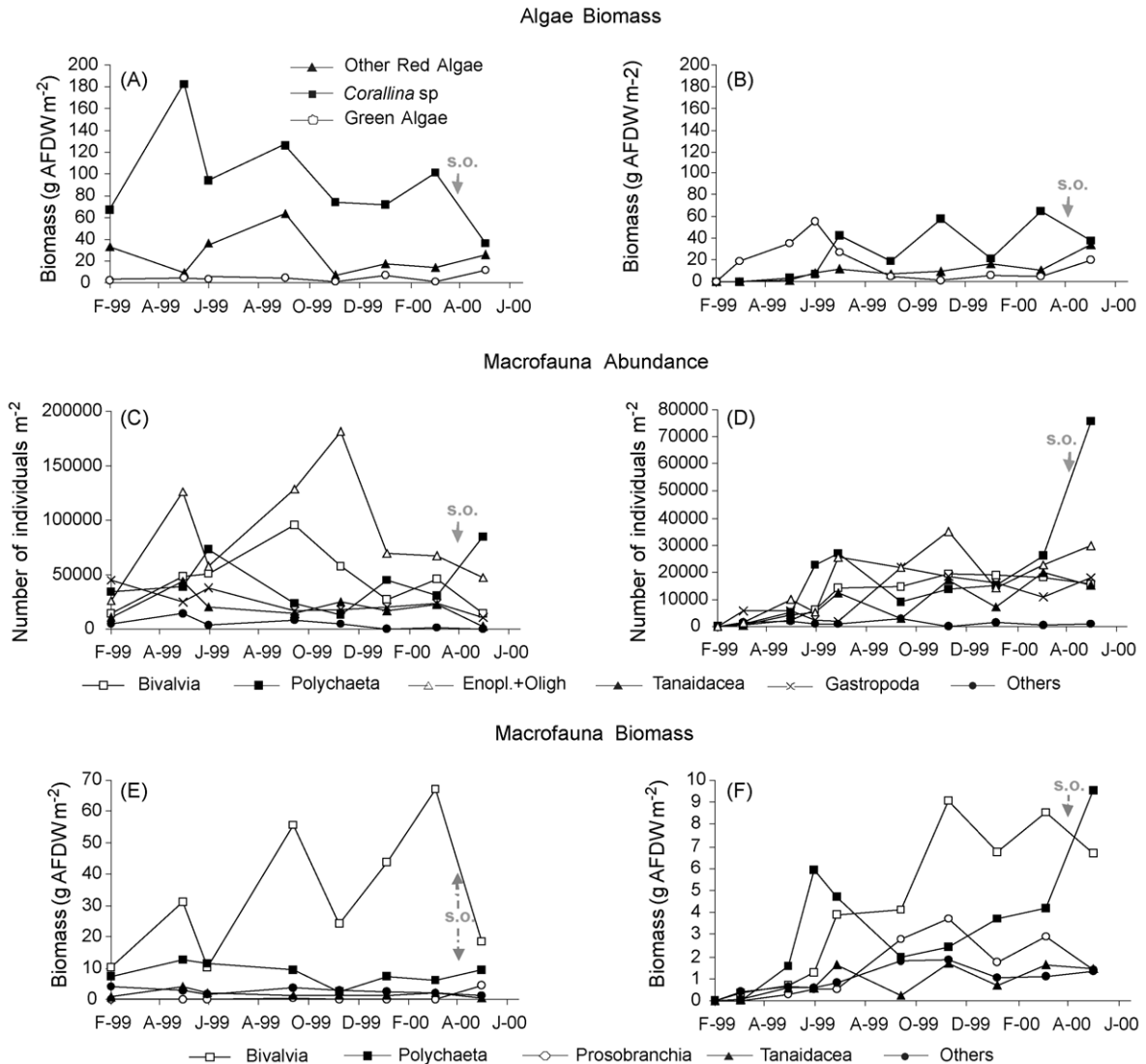
Fig. 3. (A–F) Changes of algae biomass, macrofauna abundance and macrofauna biomass in the control plots (left column) and succession plots (right column) along the studying period. s.o.: storm occurrence.

Diptera and Isopoda (included in the Others group) were also abundant at the very beginning of the community recovery (March 1999), but showed only residual values during the rest of the study period. Polychaeta was the prevailing group from June to July 1999 and from March 2000 to May 2000. Bivalvia, Enoploidea, Oligochaeta and Tanaidacea were also important groups in structuring the community during the whole recovery process. Regarding the biomass

estimation (Fig. 3F), Bivalvia was already leading during the first month of recovery. Although relatively less important in general, the Others, specifically, Amphipoda, Diptera and Isopoda presented the highest values during this period. The other taxonomic groups aggregated in the Others, such as Decapoda, Anthozoa and Polyplacophora occurred sporadically with values below 2% of the community biomass. Polychaeta was the dominant taxonomic group from May 1999 to July

Table 2
Taxonomic list of macrofauna species (or species groups) recorded

Anthozoa	Echinodermata
Actiniaria	*Asterina gibbosa* (Pennant)
Nematoda	*Amphipholis squamata* (DelleChiaje)
Enoploidea	*Paracentratus lividus* (Lamarck)
Diptera	Holothuroidea
Orthocladinae	Gastropoda
Tanytarsini	*Patella ulyssiponensis* Gmelin
Rhagionidae	*Tectura tessulata* (M?ller)
Psychodinae	*Tricolia pullus* (L.)
Tanaidacea	*Tricolia tingitana* Gofas
Tanais dulonguii (Audouin)	*Gibbula umbilicalis* (Da Costa)
Leptochelia savigny (Kroyer)	*Gibbula cineraria* (L.)
Isopoda	*Calliostoma zizyphinum* (L.)
Anthura gracilis (Montagu)	*Bittium simplex* (Jeffreys)
Paranthura costana Bate & Westwood	*Littorina neritoides* (L.)
Limnoria lignorum (Rathke)	*Littorina neglecta* (Bean)
Cymodoce truncate Leach	*Skeneopsis planorbis* (Fabricius)
Dynamene edwardsi Lucas	*Eatonina fulgida* (Adams)
Dynamene magnitorata Holdich	*Rissoa parva* (Da Costa)
Campecopea hirsuta (Montagu)	*Alvania semistriata* (Montagu)
Ischyromene lacazei Racovitza	*Setia pulcherrima* (Jeffreys)
Idotea pelagica (Leach)	*Barleeia unifasciata* (Montagu)
Idotea sp.	Eulimidae sp.
Amphipoda	*Ocinebrina edwardsii* (Payraudeau)
Caprella acanthifera Leach	Buccininae sp.
Caprella penantis Leach	*Rissoela glabra* (Alder)
Ampelisca rubella A. Costa	*Rissoela opalina* (Jeffreys)
Amphilochus brunneus Della Valle	*Rissoela globularis*
Ampithoe helleri Karaman	*Omalogyra atomus* (Philippi)
Lembos websteri Bate	*Ammonicera rota* (Forbes & Hanley)
Microdeutopus chelifer (Bate)	*Odostomia* sp.
Apherusa jurinei (Milne-Edwards)	*Odostomia eulimoides* Hanley
Dexamine spiniventris (A. Costa)	Gstropoda sp1
Guernea coalita (Norman)	Gastropoda sp2
Photis sp.	*Runcina coronata* Quatrefages
Melita obtusata (Montagu)	*Aplysia punctata* (Cuvier)
Podocerus variegatus Leach	Opistobranchia
Stenothoe monoculoides (Montagu)	Bivalvia
Hyale stebbingi Chevreux	*Mytilus galloprovincialis* Lamarck
Decapoda	*Musculus costulatus* Risso
Pachygrapsus marmoratus (Fabricius)	*Mytilaster minimus* (Poli)
Brachyura sp.	*Modiolaria sulcata* Deshayes
Pirimela denticulata (Montagu)	*Hiatella arctica* (L.)
Pantopoda	*Irus irus* (L.)
Callipallene emaciata (Dohrn)	*Venerupsis* sp.
Anoplodactylus virescens (Hodge)	*Turtonia minuta* (Fabricius)
Arachnida	*Parvicardium ovale* (Sowerby)
Arachnida sp1	*Lasaea rubra* (Montagu)
Arachnida sp2	*Cardita calyculata* (L.)
Halacaridae	Bivalvia sp1
Polyplacophora	Bivalvia sp2
Lepidochitona cinerea (L.)	Oligochaeta
Lepidochitona corrugata (Reeve)	Sipuncula
Acanthochitonia crinita (Pennant)	Nemertina
Polychaeta	*Protoaricia oerstedi* (Claparède)

Table 2 (*Continued*)

Eteone picta (Quatrefages)	*Boccardia polybranchia* (Haswell)
Eulalia viridis (L.)	*Polydora flava* Claparède
Eulalia mustela Pleijei	*Polydora hoplura* Claparède
Perinereis cultrifera (Grube)	*Pseudopolydora pulchra* (Carazzi)
Platynereis dumerilii (Audouin & Edwards)	*Caulleriella* spp.
Autolytus benazzi Cognetti	*Cirratulus cirratus* (M?ller)
Brania pusilla (Dujardin)	*Cirratulus chrysoderma* Claparède
Pseudobrania yraidae San Martin	*Cirriformia* sp.
Sphaerosyllis taylori Perkins	*Dodecaceria concharum* Oersted
Exogone naidina Oersted	Cirratulidae sp.
Ehlersia ferrugina Langerhans	*Capitella* spp.
Syllis garciai (Campoy)	*Arenicolides grubii* Langerhans
Syllis gracilis Grube	Maldanidae sp.
Syllis mediterranea (Bem–Eliahu)	*Sabellaria alveolata* (L.)
Syllis truncata criptica Bem- Eliahu	*Polycirrus* sp.
Odontosyllis ctenostoma Claparède	*Fabricia sabella* (Ehrenberg)
Syllides edentatus (Westheide)	Sabellidae spp.
Pholoe synophthalmica (Fauvel)	*Pomatoceros lamarcki* (Quatrefages)
Lysidice ninetta Audouin & Edwards	Polychaeta sp.
Lumbrineris latreilli Audouin & Edwards	Nematoda
Lumbrineris tetraura (Schmarda)	Enoploidea

1999, being replaced by Bivalvia from September 1999 to March 2000, when Polychaeta became dominant again.

3.3. Recovery of the community as a whole

Data on macrofauna total abundance (Fig. 4A) and total biomass (macrofauna and macroalgae) (Fig. 4B) of both communities tend to converge by the end of the study period. Both in terms of biomass and abundances, the convergence of the recovering community, with the surrounding community is illustrated in MDS plots (Fig. 5). In both cases, MDS bi-dimensional plots are associated with values of stress that fall into the categories of ''good'' and ''excellent'' representation or ordination, respectively (Clarke, 1993).

3.4. Ecological indicators performance

How did the different ecological indicators capture the recovery process? The variation of ecological indicators values in both communities over time is illustrated in Fig. 6. In general, the indicators based in species richness and evenness presented higher values in the control plots until September 1999, but a shift is then recognisable. In fact, from September 1999 up to
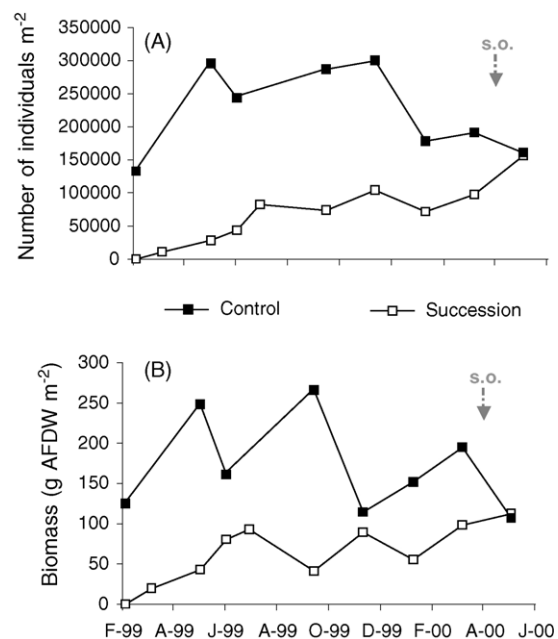

Fig. 4. Comparison of temporal changes between succession plots and control plots: (A) macrofauna abundance and (B) total biomass. s.o.: storm occurrence.
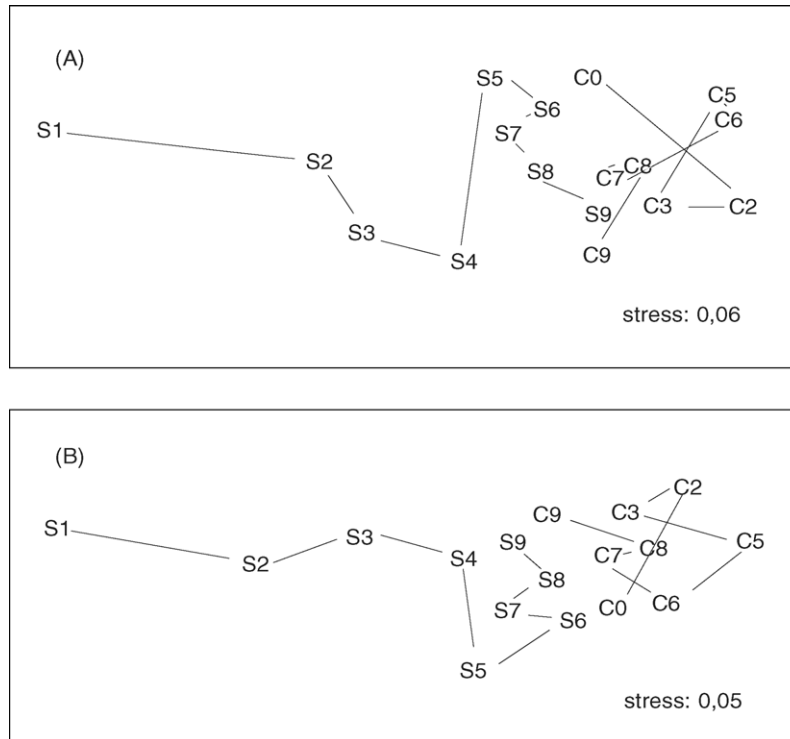
Fig. 5. Two-dimensional non-metric multidimensional scaling (nMDS) ordinations comparing communities: control plots (C) and succession plots (S), regarding (A) macrofauna abundance and (B) macrofauna + macroalgae biomass data.

the end of the study period, the experimental plots representing the recovering community presented higher values. A more detailed analysis shows that the control community presented higher values of Pielou's evenness in February 1999, June 1999 and March 2000 (Fig. 6B). Furthermore, the values of Margalef's Index (Fig. 6C) were always higher at the recovery community, except in the very beginning of the experiment, when the control assemblage, logically, exhibited higher values (7.42). Accordingly, the Shannon–Wiener Index (Fig. 6D) was higher at the recovering plots from September 1999. Nevertheless, these results must be examined cautiously, given that the differences between the control and the succession plots appear to be too small for being considered as significant.

With regard to the Eco-Exergy Index (Fig. 6E), values estimated for the experimental plots gradually increased, and converged towards those observed in the control community by the end of the study period. Finally, the Specific Eco-Exergy Index (Fig. 6F)

attained similar values both in the experimental and control communities after only 1 month of recovery, therefore expressing a more or less analogous structural complexity in both assemblages. Nevertheless, this index showed always slightly lower values in the community under recovery.

4. Discussion

What does grow first during the community recovery succession? At least in theory, all ecological indicators accounting for the composition and abundance of biological communities might be useful in detecting the environmental situation of an ecosystem. However, as many were in practice developed to approach the characteristics of a specific ecosystem, they often lack generality. Others have been criticised or rejected due to their dependence on specific environmental parameters, or because of their unpredictable behaviour depending on the type of
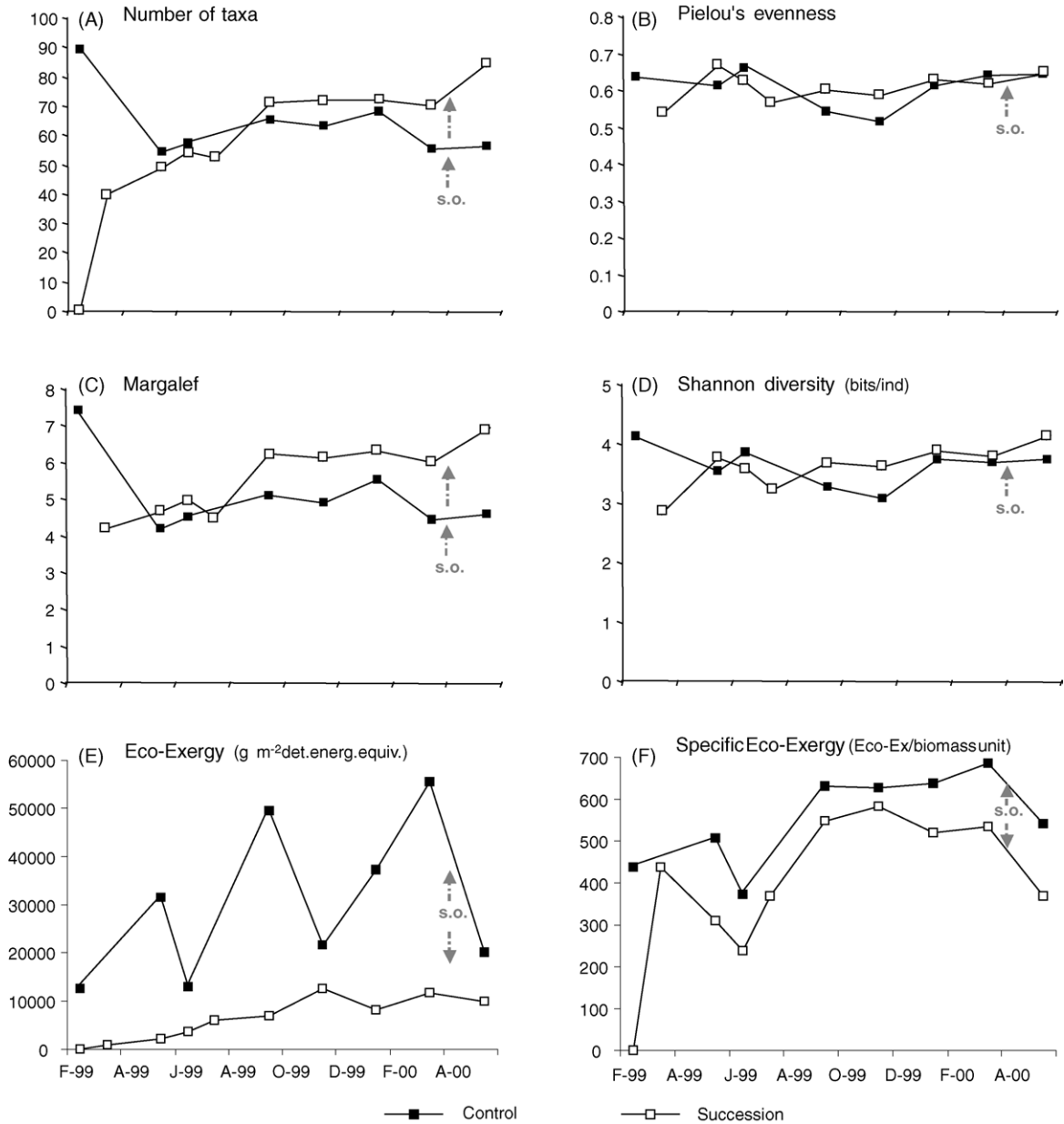
Fig. 6. Variation of (A) number of taxa, (B) Pielou's evenness, (C) Margalef, (D) Shannon diversity, (E) Eco-Exergy and (F) Specific Eco-Exergy in control and succession plots, from February 1999 to May 2000. s.o.: storm occurrence.

environmental stress. Therefore, it is not recommendable to use a single ecological indicator to assess something as complex as the recovery process of a system. Instead, different aspects must be taken into account and if possible combined.

It is commonly accepted that early colonisers tend to be rapid growing, opportunistic, r-selected species, and more palatable for consumers (Valiela, 1995). This pattern was in fact clearly recognisable at the beginning of the experiment when the bare surface

was firstly re-colonised by green algae. Then these early colonisers were replaced, firstly by red macro-algae, which also occur as early successional species, and finally by the turfing algae *C. elongata*. This shift in algal species in the community was also followed by changes in the associated macrofauna. Some groups as Amphipoda, Isopoda, Diptera and Gastro-poda presented high abundances only in the very beginning of the recovery process, being subsequently replaced by Bivalvia and Polychaeta.

In general, it is also known that as succession proceeds, the species, in most cases tend to be larger, grow more slowly, be less productive and have more complex morphology and special requirements. As time goes on, more species accrue, and diversity increases as a result of spatial heterogeneity. In fact, the species richness not only increased throughout the recovery period, but also became consistently higher than in the control community after September 1999. Not surpris-ingly, the Margalef's Index behaviour mirrored that of species number. Another category of diversity indexes combines the richness of species with a measure of their relative abundance, and includes the widely used Shannon–Wiener Index (*H'*). The Shannon Index was originally used in information theory, but it has been commonly employed to evaluate species diversity in ecological communities. Again not surprisingly, in our experiment, the Shannon–Wienner Index and Pielou's evenness presented a parallel behaviour.

Two attractive ideas emerge from these observa-tions. First, diversity increased rather rapidly. After approximately 6 months, succession plots came to resemble those of the surrounds concerning the information related to the number of species present. Additionally, species composition appeared also to be similar in both communities. This latter observation is also quite acceptable once patch size is known to exert influence on colonisation mechanisms (e.g. Kim and DeWreede, 1996). It has in fact been observed that after large-scale disturbances, plankton larvae are an important source of colonists, while after small disturbances, on the scale of cm or m, like in the present case, re-colonisation is often carried out by post-larvae and mobile adults from the adjacent assemblages (Levin et al., 1996).

Second, after September 1999, diversity was consistently higher in the community undertaking succession. Considering the plots clearance as a small-scale but harsh disturbance event, after the first algae settlement, re-colonisation was mainly achieved by invertebrates' post-larvae and adults from the undis-turbed community. Therefore, after 6–7 months, although effects of disturbance are still visible in the recovering communities, they are clearly becom-ing less evident.

On the other hand, our observations after Septem-ber 1999 appear to illustrate in very interesting and unexpected way a case explainable by the Inter-mediate Disturbance Hypothesis (Grime, 1973; Con-nell, 1978). This hypothesis predicts that highest diversity values will be found at intermediate levels of disturbance. If the disturbance is too mild or too rare, then patches will approach equilibrium and be dominated by a few species that are able to out-compete all others. If disturbance is too harsh or too frequent, then only a few species that are resistant to the disruption will persist.

In terms of biomass, the control community was, undoubtedly, dominated by Bivalvia (Mytilacea) (Fig. 3E). Moreover, the other species only showed a slight recovery, after a severe storm occurrence that removed large quantities of *Corallina enlongata* (late stage primary producer) and wash way loads of associated organisms, in April 2000. Paine and Levin (1981) had already mentioned that, particularly in rocky shores, potential sources of disturbance could be herbivores, waves and wave-driven rocks.

Furthermore, growth can be interpreted as an increase in the organisation of ordered structure or information (Marques and Jørgensen, 2002), although more commonly, in practical terms, growth is expressed as the increase of measurable quantities, most often biomass and diversity. Nevertheless, Jørgensen et al. (2000) considered three forms of growth, respectively, growth-to-storage (Form I), growth-to-throughflow (Form II) and growth-to-organisation (Form III), which when applied to our case can be considered as corresponding to biomass, network and information. Regarding these three forms of growth, Jørgensen et al. (2000) hypothesised that in ecological succession, energy storage in early stages is dominated by Form I growth which builds structure: the dominant mechanisms are increasing energy capture and low entropy production. In middle stages, growing interconnection of proliferating storage units (organisms) increases energy throughflow (Form II

growth) and, finally, in mature phases, cycling becomes a dominant feature of the internal network, reflecting advanced organisation (Form III growth).

Jørgensen and Mejer (1979) also proposed Eco-Exergy storage, mathematically defined by both conservative (energy and matter) and non-conservative (informational) terms, as a measure of complexity, hypothesising: (a) that complexity in ecosystems is associated to the presence of more complex organisms, corresponding to higher information content and (b) that ecosystems development drives them to optimise the Eco-Exergy storage levels under given environmental circumstances and with the available genetic pool. Stored Eco-Exergy expresses the distance from thermodynamic equilibrium, and reflects the size of the organised structure in terms of its content in thermodynamic information (Jørgensen, 2002).

The variation trend of the Eco-Exergy Index in experimental plots appeared to reflect, essentially, changes in biomass but not in information. Rates of convergence are known to vary from shore to shore and differ from time to time (Chapman and Underwood, 1998). In our experiment, although after 7–8 months the succession plots resembled the surrounds in terms of structure (Figs. 4B and 5B), even after 15 months biomass has not still reached the levels of the control plots. Particularly, the algae biomass was still at a considerable lower level in the recovering community. On the other hand, taking into account Specific Eco-Exergy, or average organism complexity (an average β-value), the community at the experimental plots has rapidly recovered in terms of information. In fact, Specific Eco-Exergy, after only 1 month of experiment, showed already comparable values in the succession and control plots, suggesting therefore an analogous structural complexity in both assemblages. Thus, the system information appears to have recovered much faster than biomass.

A problem in applying Eco-Exergy based indices is the obvious lack of discriminating power of the weighting factors used to estimate Eco-Exergy and Specific Eco-Exergy, because organisms are considered at very high taxonomic levels. A new updated set of β-values, resulting from a more refined calculation methodology, will soon be available (Jørgensen et al., 2005). Nevertheless, with regard to the forthcoming weighting factors, although values are different in absolute terms, the ratio between them is similar to the ratio between the β-values used in this study. On the other hand, despite significant methodological progress, in practical terms, an extensive work will still be necessary to improve the discriminating power at lower taxonomic levels. Therefore, the problem of estimating the β-values still constitutes a weak point, which will be gradually solved in the future as our knowledge about genes and their active expression increases (Fonseca et al., 2000; Marques and Jørgensen, 2002). Nevertheless, despite this problem, both thermodynamic oriented indices provided useful information about the structural development of the community.

The answer to the question, "What does grow first during the community succession: biomass, network or information?" was to a certain extent elucidated with the help of different ecological indicators. In our experiment, contrarily to what we hypothesised based on Odum (1969), the system information (expressed by Specific Eco-Exergy) recovered very quickly, closely followed by the network interactions (considering species diversity an indirect indicator of network complexity), while even by the end of the study period biomass remained lower than in the control community. Also, contrarily to what was hypothesised by Jørgensen et al. (2000), in our study growth-to-organisation and growth-to-throughflow dominated the early stages of the recovery process, while growth-to-storage increased in importance as maturity approaches. Nevertheless, it seems reasonable to assume that this result was related to the scale of the experiment. In fact, the cleared plots were very small in comparison with the surrounding *Corallina* algal community. Due to this fact, although the re-colonisation by primary producers followed the pattern usually described in the literature, the macrofauna found at each date probably consisted not only of the species usually found in the succession, but also of other ones proceeding from the undisturbed algal cover, that carried short incursions into the small experimental plots. In such case, biomass development was probably mostly dependent on the primary producers' growth, while complexity assessment was strongly affected by these invertebrates' incursions.

Consequently, a tentative generalisation of our experimental results could be the characteristics of a systems' recovery after disturbance appear to be dependent on of the spatial scale of the disturbance according to the following pattern: (a) if a disturbed

Numerical Example:

Assumptions:
Immigration rate: 1 org m^{-1} day^{-1}
Time period: 100 days
Openness=Periphery/Area

Situation A
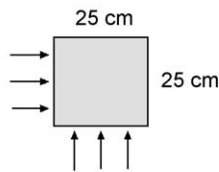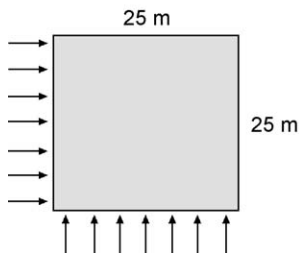
25 cm

25 cm

Area = 1/4 x 1/4 = 1/16 m^2

Periphery = 25 cm x 4 = 1 m

Openness = 1 / (1/16m^2) = 16 m^{-1}

N° of orgs/cm^2 = 100 orgs / (1/16m^2) = 1600 orgs cm^{-2}

Situation B

25 m

25 m

Area = 25 x 25 = 625 m^2

Periphery = 25 x 4 = 100 m

Openness = 100 / 625 = 0.16 m^{-1}

N° of orgs/cm^2 = 10000 orgs / (625 m^2) = 16 orgs cm^{-2}

Fig. 7. Numerical example: openness calculation in situation A (25 cm × 25 cm plots) and situation B (25 m × 25 m plots). orgs: organisms.

area is small when compared to a contiguous non-disturbed one, complexity (information and network) will recover prior to biomass. (b) If a disturbed area is large in comparison to a contiguous non-disturbed one, biomass will recover in first place, and complexity will gradually develop afterwards.

The above-mentioned considerations may be further explored if the concept of openness introduced by Jørgensen (2000) is considered. The initial premise that an ecosystem must be open or at least non-isolated to be able to import the energy needed for its maintenance, is easily accepted. Furthermore, *openness* is here expressed as the ratio of periphery (or perimeter) to area. Fig. 7 illustrates a numerical example where it is clearly demonstrated that small plots compared with big cleared areas present higher values of openness. As a consequence, these small areas express higher possibility to exchange energy or matter and increased chance for immigration of organisms. In this experiment, complexity (information and network) did, indeed, recover prior to biomass, fact that is reasonable since information

and network are more dependent of openness. Therefore, the higher the openness value the faster is information and network recovery. On the other hand, biomass is less dependent because the major biomass contribution is coming from slow growing species, leading this growth form to be the last one to recover. Although Debeljak (2002) examining managed and virgin forest in different development stages (e.g. pasture, gap, juvenile, optimum forest) has confirmed Jørgensen et al. (2000) development hypothesis, the present study results stressed how openness can shape and modify the sequence of ecosystem development.

Were the chosen ecological indicators able to help in recognizing the growth of biomass, network and information, throughout the recovery process? The answer to this question is obviously implicit in the discussion above: Yes, when applied in combination, almost not if used in isolation. In fact, diversity measures are obviously not suitable to capture the first form of growth (biomass), although they can provide useful hints regarding the other two (network and

information). On the other hand, Eco-Exergy and Specific Eco-Exergy provided useful information about the structural development of the community but lacked discriminating power with regard to the informational status of the system.

References

Benedetti-Cecchi, L., Cinelli, F., 1996. Patterns of disturbance and recovery in littoral rock pools: non-hierarchical competition and spatial variability in secondary succession. Mar. Ecol. Prog. Ser. 135, 145–161.

Chapman, M.G., Underwood, A.J., 1998. Inconsistency and variation in the development of rocky intertidal algal assemblages. J. Exp. Mar. Biol. Ecol. 224, 265–289.

Clarke, K.R., 1993. Non-parametric multivariate analysis of changes in community structures. Aust. J. Ecol. 18, 117–143.

Clarke, K.R., Warwick, R. (Eds.), 1994. Change in Marine Communities: an Approach to Statistical Analysis and Interpretation. Natural Environmental Research Council, Plymouth, UK, p. 144.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.

Connell, J.H., Slatyer, R.E., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111, 1119–1144.

Connell, J.H., Hughes, T.P., Wallace, C.C., 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales and time. Ecol. Monogr. 67, 461–488.

Craft, C., Sacco, J., 2003. Long-term succession of benthic infauna communities on constructed *Spartina alterniflora* marshes. Mar. Ecol. Prog. Ser. 257, 45–58.

Debeljak, M., 2002. Characteristics of Energetics of Managed and Virgin Forest. PhD Thesis, University of Ljubliana, 217 p.

Diaz-Pulido, G., McCook, L.J., 2002. The fate of bleached corals: patterns and dynamics of algal recruitment. Mar. Ecol. Prog. Ser. 232, 115–128.

Dye, A.H., 1998. Community-level analysis of long-term changes in rocky littoral fauna from South Africa. Mar. Ecol. Prog. Ser. 164, 47–57.

Fonseca, J.C., Marques, J.C., Paiva, A.A., Freitas, A.M., Madeira, V.M.C., Jørgensen, S.E., 2000. Nuclear DNA in the determination of weighting factors to estimate exergy from organism biomass. Ecol. Model. 126, 179–189.

Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. J. Environ. Manage. 1, 151–167.

Hawkins, S.J., 1999. Experimental ecology and coastal conservation: conflicts on rocky shores. Aquat. Conserv. Mar. Freshwater Ecosyst. 9, 565–572.

Hutchinson, N., Williams, G.A., 2003. Disturbance and subsequent recovery of mid-shore assemblages on seasonal tropical, rocky shores. Mar. Ecol. Prog. Ser. 249, 25–38.

Jørgensen, S.E. (Ed.), 2000. Principles of Pollution Abatement. Elsevier, Oxford, 520 p.

Jørgensen, S.E., Mejer, H., 1979. A holistic approach to ecological modelling. Ecol. Model. 7, 169–189.

Jørgensen, S.E., 2002. Integration of Ecosystem Theories: a Pattern, third ed. Kluwer Academic Publ. Co., Dordrecht, The Netherlands, 432 pp.

Jørgensen, S.E., Patten, B.C., Straškraba, M., 2000. Ecosystems emerging: 4. Growth Ecol. Model. 126, 249–284.

Jørgensen, S.E, Ladegaard, N., Debeljak, M., Marques, J.C., 2005. Calculations of Exergy for organisms. Ecol. Model., in press.

Kim, J.H., DeWreede, R.E., 1996. Effects of size and season of disturbance on algal patch recovery in a rocky intertidal community. Mar. Ecol. Prog. Ser. 133, 217–228.

Levin, L.A., DiBacco, C., 1995. Influence of sediment transport on short-term re-colonisation by seamounts infauna. Mar. Ecol. Prog. Ser. 123, 163–175.

Levin, L.A., Talley, D., Thayer, G., 1996. Succession of macrobenthos in a created salt marsh. Mar. Ecol. Prog. Ser. 141, 67–82.

Marques, J.C., Pardal, M.A., Nielsen, S.N., Jørgensen, S.E., 1997. Analysis of the properties of exergy and biodiversity along an estuarine gradient of eutrophication. Ecol. Model. 102, 155–167.

Marques, J.C., Jørgensen, S.E., 2002. Three selected ecological observations interpreted in terms of a thermodynamic hypothesis. Contribution to a general theoretical framework. Ecol. Model. 158, 213–221.

Marques, J.C., Nielsen, N.S., Pardal, M.A., Jørgensen, S.E., 2003. Impact of eutrophication and river management within a framework of ecosystem theories. Ecol. Model. 166, 147–168.

Nogueira, E., Ibanez, F., Figueiras, F.G., 2000. Effect of meteorological and hydrographic disturbances on the microplankton community structure in the Ría de Vigo (NW Spain). Mar. Ecol. Prog. Ser. 203, 23–45.

Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 267–270.

Olobarria, C., 2002. Role of colonization in spatio-temporal patchiness of microgastropods in coralline turf habitat. J. Exp. Mar. Biol. Ecol. 274, 121–140.

Paine, R.T., Levin, S.A., 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecol. Monogr. 51, 145–178.

Patrício, J., Ulanowicz, R., Pardal, M.A., Marques, J.C., 2004. Ascendency as an ecological indicator: a case study of estuarine pulse eutrophication. Estuar. Coast. Shelf. Sci. 60, 23–35.

Rosenberg, R., Agrenius, S., Hellman, B., Nilsson, H.C., Norling, K., 2002. Recovery of marine benthic habitats and fauna in a Swedish fjord following improved oxygen conditions. Mar. Ecol. Prog. Ser. 234, 43–53.

Sousa, W.P., 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol. Monogr. 49, 227–254.

Valiela, I., 1995. Development of structure in marine communities: colonization and succession. In: Valiela, I. (Ed.), Marine Ecological Processes. second ed. Springer-Verlag, New York, pp. 355–381.

Van Tamelen, P.G., 1996. Algal zonation in tidepools: experimental evaluation of the roles of physical disturbance, herbivory and competition. J. Exp. Mar. Biol. Ecol. 201, 197–231.

Williams, G.A., Davies, M.S., Nagarkar, S., 2000. Primary succession on a seasonal tropical rocky shore: the relative roles of spatial heterogeneity and herbivory. Mar. Ecol. Prog. Ser. 203, 81–94.