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Aquatic Ecosystem Health and Management Society

Aquatic Ecosystem Health and Management 3 (2000) 419–430

Aquatic Ecosystem
Health & Management

www.elsevier.com/locate/aquech

Application of exergy and specific exergy as ecological indicators of coastal areas

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Abstract

Exergy and specific exergy have been found together with nine other ecological attributes for 12 coastal ecosystems. The correlation of the 11 attributes was examined, and the extent to which exergy and specific exergy can be applied as indicators to assess ecosystem health was discussed. The two concepts cover a range of important properties of ecosystems, but other indicators are also required to provide a sufficiently comprehensive assessment of ecosystem health. © 2000 Elsevier Science Ltd and AEHMS. All rights reserved.

Keywords: Ecosystem health; Marine systems

1. Introduction

An increasing number of environmental managers want to include ecological considerations in their management strategies, and they have therefore asked the following question to ecologists and system ecologists: how can we measure whether an ecosystem is ecologically sound and how can we express that health? The doctor of medicine attempts to express the health of a patient by the use of indicators such as blood pressure, body temperature, activities of various important enzymes, kidney function and so on. The environmental manager also searches for ecological indicators that can assess ecosystem health. Since an ecosystem is a very complex system, it is not surprising that it is not an easy task to find good ecological indicators to give appropriate information on ecosystem health. Nonetheless, many general and system ecologists are working on the problem.

Rapport (1995) adapted medical phrases, for example, ‘to take nature’s pulse’, ‘the problem of detecting diseases in nature’ and ‘clinical ecology’, to emphasize parallels to human pathology. Costanza (1992) summarized the definition of ecosystem health as follows: (1) homeostasis; (2) absence of disease; (3) diversity or complexity; (4) stability or resilience; (5) vigour or scope for growth, and (6) balance between system components. He emphasized that it is necessary to consider all or least most of these definitions simultaneously. Consequently, he proposed an overall system health index, $\mathrm{HI} = VOR$, where V is the system vigour, O the system organization index and R the resilience index. With this proposal, Costanza touches on the most crucial ecosystem properties to indicate ecosystem health. Kay (1991) used the term ‘ecosystem integrity’ to refer to the ability of an ecosystem to maintain its organization. Measures of integrity should therefore reflect the two aspects of the organizational state of an ecosystem: functional and structural. Function refers to the overall activities of the ecosystem and structure refers to the interconnections among the components

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PII: S1463-4988(00)00034-8

of the system. When function is measured, the amount of energy being captured by the system is measured. Function may be measured by measuring the exergy (the amount of work the system can perform when it is brought into thermodynamic equilibrium with its environment) captured by the system. Measures of structure indicate the way in which energy is moving through the system. Exergy stored in the ecosystem could therefore be a reasonable indicator of structure.

Goal functions are understood as functions that can describe the direction of ecosystem development. This should *not* be interpreted that ecosystems have predetermined goals, but rather that the self-organizational abilities of ecosystems make it possible to meet perturbations by directive reactions, which can be described by goal functions. At a recent system ecological workshop (at Salzau close to Kiel, Germany), the term 'goal function' was reserved for application to models, particularly structural dynamic models with variable parameters that are currently selected by optimization of a goal function. This is in contrast to ecological indicators, which are associated with the assessment of ecosystem health.

This paper presents the result of applying several ecological indicators including two recently proposed indicators, exergy and specific exergy, on 12 coastal ecosystems (Christensen and Pauly, 1993) in order to assess their health. As well, the extent to which the ecological indicators are correlated is examined. How these correlations may be explained is discussed.

2. Exergy and specific exergy

Exergy is strictly defined as the amount of work the system can perform when it is brought into thermodynamic equilibrium with its environment. As can be seen from the definition, exergy is dependent on both the environment and the system, and not entirely on the system. Exergy is therefore not a state variable, as for instance are free energy and entropy.

If we choose to define an ecosystem as a homogeneous 'inorganic soup' at the same temperature and pressure as the reference state (the environment), exergy will measure the thermodynamic distance of the ecosystem from the 'inorganic soup' in energy terms. Under these circumstances, we can calculate the exergy content of the system as coming entirely from biochemical energy and information embodied in system organisms. The exergy of the system measures the contrast, that is, the difference in work capacity, with the surrounding environment. If the system is in equilibrium with the surrounding environment, the exergy is zero. The only way to move systems away from thermodynamic equilibrium is to perform work on them, and the available work in a system is a measure of our ability to distinguish between the system and its environment or thermodynamic equilibrium (alias the 'inorganic soup').

Survival implies maintenance of biomass, and growth means increase of biomass. It costs exergy to construct biomass and obtain or store information. Survival and growth can therefore be measured by use of the thermodynamic concept, exergy. Darwin's theory can be reformulated in thermodynamic terms and expanded to the system level as follows: the prevailing conditions of an ecosystem steadily change and the system will continuously select the species that can contribute most to the maintenance or even growth of the exergy of the system.

Notice that the thermodynamic translation of Darwin's theory requires that populations have the properties of reproduction, inheritance and variation. The selection of the species that contribute most to the exergy of the system under the prevailing conditions requires that there are enough individuals with different properties that a selection can take place. This means that reproduction and variation must be high and that once a change has taken place due to a combination of properties giving better fitness, it can be conveyed to the next generation.

If we presume, as proposed above, a reference environment that represents the system (ecosystem) at thermodynamic equilibrium, we can calculate the approximate exergy content of the system as coming entirely from chemical energy: $\sum(\mu_c - \mu_{co})N_i$. Only what Szargut et al. (1988) and Szargut (1998) call chemical exergy is included in the computation of exergy. Physical exergy (Szargut, 1998) is omitted from these calculations since there are no temperature and pressure differences between the system and the reference system. We can calculate the exergy of the living system compared with the same system at the same temperature and pressure but in the form of an inorganic soup without any life, biological structure, information or organic molecules. As $(\mu_c - p-_{co})$ can be found from the definition of the chemical potential replacing activities by concentrations, we get the following expressions for exergy:

$$\mathrm{Ex} = \mathrm{R}T \sum_{i=0}^{i=n} c_i \ln c_i/c_{i\mathrm{eq}} \qquad [\mathrm{ML^2T^2}] \tag{1}$$

where R is the gas constant, T the temperature of the environment, c_i the concentration of the ith component expressed in a suitable unit (for example, for phytoplankton in a lake, c_i could be expressed as mg l^{-1} or as mg^{-1} of a focal nutrient), $c_{i\mathrm{eq}}$ is the concentration of the ith component at thermodynamic equilibrium and n the number of components. $c_{i\mathrm{eq}}$ is, of course, a very small concentration (except when $i = 0$, which is considered to cover the inorganic compounds), but it is not zero. This factor corresponds to the very low probability of forming complex organic compounds spontaneously in an inorganic soup at thermodynamic equilibrium.

The problem related to the assessment of $c_{i\mathrm{eq}}$ has been discussed and a possible solution proposed in Jørgensen et al. (1995), the most essential arguments of which should be repeated here. For dead organic matter, detritus, (index 1), $c_{i\mathrm{eq}}$ may be found from classical thermodynamics (see for instance, Russell and Adebiyi, 1993) as follows:

$$\mu_1 = \mu_{1\mathrm{eq}} + \mathrm{R}T \ln c_1/c_{1\mathrm{eq}} \qquad [\mathrm{ML^2T^2moles^{-1}}] \tag{2}$$

where μ indicates the chemical potential. The difference $\mu_1 - \mu_{1\mathrm{eq}}$ is known for organic matter, for example, detritus, which is a mixture of carbohydrates, fats and proteins. We find that detritus has approximately 18.7 kJ g^{-1} corresponding to the free energy of the mixture of carbohydrates, fats and proteins.

Generally, $c_{i\mathrm{eq}}$ can be calculated from the definition of the probability $P_{i\mathrm{eq}}$ to find component i at thermodynamic equilibrium:

$$P_{i\mathrm{eq}} = c_{i\mathrm{eq}}/\sum_{i=0}^{N} c_{i\mathrm{eq}} \qquad [\text{-}] \tag{3}$$

If we can find the probability P_i to produce the considered component i at thermodynamic equilibrium, we have determined the ratio of $c_{i\mathrm{eq}}$ to the total concentration. As the inorganic component c_0 is highly dominated by the thermodynamic equilibrium, Eq. (3) may be rewritten as:

$$P_{i\mathrm{eq}} = c_{i\mathrm{eq}}/c_{0\mathrm{eq}} \qquad [\text{-}] \tag{4}$$

By a combination of equations, we get:

$$P_{1\mathrm{eq}} = [c_1/c_{0\mathrm{eq}}]\exp[-(\mu_1 - \mu_{1\mathrm{eq}})/\mathrm{R}T] \qquad [\text{-}] \tag{5a}$$

For the biological components, 2,3,4,…,N, the probability $P_{i\mathrm{eq}}$, consists of the probability of producing the organic matter (detritus), that is, $P_{1\mathrm{eq}}$, and the probability $P_{i,a}$ of obtaining the information embodied in the genes, which determine the amino acid sequence. Living organisms use 20 different amino acids and each gene determines the sequence of about 700 amino acids (Li and Grauer, 1991). $P_{i,a}$ can be found from the number of permutations among which the characteristic amino acid sequence for the considered organism has been selected. We have the following two equations available to calculate P_i:

$$P_{i\mathrm{eq}} = P_{1\mathrm{eq}} P_{i,a} \tag{5b}$$

($i = 2$; 0 covers inorganic compounds and 1 detritus) and

$$P_{i,a} = 20^{-700g} \qquad [\text{-}] \tag{6}$$

where g is the number of genes.

Eq. (4) is reformulated to:

$$c_{i\mathrm{eq}} = P_{i\mathrm{eq}} c_{0\mathrm{eq}} \qquad [\mathrm{moles\ L^{-3}}] \tag{7}$$

Eqs. (7) and (2) are combined:

$$\mathrm{Ex} = \mathrm{R}T \sum_{i=0}^{N} [c_i \ln(c_i/(P_{i\mathrm{eq}}/c_{0\mathrm{eq}}))], \qquad [\mathrm{ML^2T^2}] \tag{8}$$

This equation may be simplified by the use of the following approximations (based upon $P_{i\mathrm{eq}} \ll c_i$, $Pi_{\mathrm{eq}} \ll P_0$ and $1/P_{i\mathrm{eq}} \ll c_i$, $1/P_{i\mathrm{eq}} \ll c_{0\mathrm{eq}}/c_i$) : $c_i/c_{0\mathrm{eq}} \simeq 1$, $c_i \simeq 0$, $P_i c_{0\mathrm{eq}} \simeq 0$ and the inorganic component can be omitted. The significant contribution comes from $1/P_{i\mathrm{eq}}$ (see Eq. (8)). We obtain:

$$\mathrm{Ex} = \mathrm{R}T \sum_{i=1}^{N} \ln(P_{i\mathrm{eq}}) \qquad [\mathrm{ML^2T^2}] \tag{9}$$

where the sum starts from 1, because $P_{0,\mathrm{eq}} = 1$.

Expressing $P_{i\mathrm{eq}}$ as in Eq. (5b) and $P_{1\mathrm{eq}}$ as in Eq. (5a), we obtain the following expression for the calculation of an exergy index:

$$\mathrm{Ex}/\mathrm{R}T = \sum_{i=1}^{N} c_i \ln(c_l/(c_{0\mathrm{eq}}))$$

$$-(\mu_1 - \mu_{1\mathrm{eq}})\sum_{i=1}^{N} c_i/\mathrm{R}T - \sum_{i=2}^{N} c_i \ln P_{i,a} \qquad [\text{moles L}^{-3}]$$

As the first sum is minor compared with the following two sums (use for instance $c_i/c_{0\mathrm{eq}} = 1$), we can write:

$$\mathrm{Ex}/\mathrm{R}T = (\mu_1 - \mu_{1\mathrm{eq}})\sum_{i=1}^{N} c_i/\mathrm{R}T - \sum_{i=2}^{N} c_i \ln P_{i,a} \qquad (10)$$

$[\text{moles L}^{-3}]$

This equation can now be applied to calculate contributions to the exergy index by important ecosystem components. If we consider only detritus, we know that the free energy released is about 18.7 kJ g^{-1} organic matter. R is 8.4 J mol^{-1} and the average molecular weight of detritus is assumed to be 100,000. We get the following contribution of exergy by detritus l^{-1} water, when we use the unit g detritus exergy equivalent l^{-1}:

$$\mathrm{Ex}_1 = 18.7c_i \qquad [\mathrm{kJ\,l}^{-1}] \text{ or}$$

$$\mathrm{Ex}_1/\mathrm{R}T = 7.34 \times 10^5 c_i \qquad [\mathrm{ML}^{-3}] \qquad (11)$$

A typical algal cell has on an average 850 genes. Previously, we used the number of genes and not the amount of DNA per cell, which would include unstructured and nonsense DNA. In addition, a clear correlation between the number of genes and the complexity has been shown (Li and Grauer, 1991). However, recently it has been proposed that nonsense genes may play an important role; for instance, they may be considered as spare parts, which are able to repair genes when they are damaged or be exposed to mutations. If it is assumed that only the informative genes contribute to the embodied information in organisms, an alga has 850 information genes in total, that is, they determine the sequence of $850 \times 700 = 595,000$ amino acids. The contribution of exergy l^{-1} water, using g detritus equivalent l^{-1} as the concentration unit, would be:

$$\mathrm{Ex}_{\mathrm{algae}}/\mathrm{R}T = 7.34 \times 10^5 c_i - c_i \ln 20^{595,000}$$

$$= 25.2 \times 10^5 c_i \qquad [\mathrm{g\,l}^{-1}] \qquad (12)$$

The contribution to exergy from a simple prokaryotic cell can be calculated similarly as:

$$\mathrm{Ex}_{\mathrm{prokar}}/\mathrm{R}T = 7.34 \times 10^5 c_i + c_i \ln 20^{329,000}$$

$$= 17.2 \times 10^5 c_i \qquad [\mathrm{g\,l}^{-1}] \qquad (13)$$

Organisms with more than one cell will have DNA in all cells determined by the first cell. The number of possible micro-states therefore becomes proportional to the number of cells. A zooplankton has approximately 100,000 cells and (see Table 1) 15,000 genes per cell, each determining the sequence of approximately 700 amino acids. ln P_{zoo} can therefore be found as:

$$-\ln P_{\mathrm{zoo}} = -\ln(20^{-15,000\times 700} \times 10^{-5}) = 315 \times 10^5 \qquad (14)$$

As shown, the contribution from the numbers of cells is insignificant. Similarly, P_{fish} and the P-values for other organisms can be found.

The contributions from phytoplankton, zooplankton and fish to the exergy of the entire ecosystem are significant and far more than simple correspondence to the biomass. Notice that the unit of Ex/RT is $\mathrm{g\,l}^{-1}$. Exergy can always be expressed in $\mathrm{J\,l}^{-1}$, provided that the right units for R and T are used. Eqs. (12)–(14) can be rewritten by converting $\mathrm{g\,l}^{-1}$ to g detritus l^{-1} by dividing by (7.34×10^5).

The exergy index can be found as the concentrations of the various components c_i multiplied by weighting factors, β_i, reflecting the exergy that the various components possess due to their chemical energy and to the information embodied in DNA:

$$\mathrm{Ex} = \sum_{i=0}^{n} \beta_i c_i \qquad (15)$$

β_i values based on exergy detritus equivalents have been found for various species. The unit exergy detritus equivalents expressed in $\mathrm{g\,l}^{-1}$ can be converted to $\mathrm{kJ\,l}^{-1}$ by multiplication by 18.7 corresponding to the approximate average energy content of 1 g detritus. Table 1 shows the number of information

Table 1
Approximate number of non repetitive genes in selected organisms

Organisms	Number of information genes	Conversion factor (β)
Detritus	0	1
Minimal cell (Morowitz, 1992)	470	2.7
Bacteria	600	3.0
Algae	850	3.9
Yeast	2000	6.4
Fungus	3000	10.2
Sponges	9000	30
Moulds	9500	32
Plants, trees	10,000–30,000	30–87
Worms	10,500	35
Insects	10,000–15,000	30–46
Jellyfish	10,000	30
Zooplankton	10,000–15,000	30–46
Fish	100,000–120,000	300–370
Birds	120,000	390
Amphibians	120,000	370
Reptiles	130,000	400
Mammals	140,000	430
Human	250,000	740

genes and the corresponding β-values calculated from the above presented equations.

The index 0 covers the inorganic components, which of course, in principle should be included in the calculations of exergy. However, in most cases they can be neglected, as the contributions from detritus and even to a higher extent from the biological components are much higher due to an extremely low concentration of these components in the reference system (the ecosystem converted to an inorganic dead system). The calculation of the exergy index accounts, by use of this equation, for the chemical energy in the organic matter as well as for the information embodied in the living organisms. It is measured by the extremely small probability that living components, for instance algae, zooplankton, fish, mammals and so on will form spontaneously from inorganic matter. The weighting factors may also be considered quality factors reflecting how developed the various groups are and to which extent they contribute to the exergy due to their content of information, which is considered in the computation. This follows Boltzmann (1905), who gave the following relationship for the work W that is embodied in the thermodynamic information:

$$W = \mathrm{R}T \ln N \qquad (\mathrm{ML}^2\mathrm{T}^{-2}) \tag{16}$$

where N is the number of possible states among which the information has been selected, N is, as seen for species, the inverse of the probability of obtaining the valid amino acid sequence spontaneously.

It is furthermore consistent with the following reformulation of Reeves (1991): ‘information appears in nature when a source of energy (exergy) becomes available but the corresponding (entire) entropy production is not emitted immediately, but is held back for some time (as exergy)’.

The total exergy of an ecosystem *cannot* be calculated exactly, as we cannot measure the concentrations of all the components or determine all possible contributions to exergy in an ecosystem. If we calculate the exergy of a fox, for instance, the above shown calculations will only give the contributions coming from the biomass and the information embodied in the genes. What are the contributions from the blood pressure, the sexual hormones and so on? These properties are at least partially covered by the genes but is that the entire story? We can calculate the contributions from the dominant components, for instance by the use of a model or measurements, which cover the most essential components for a focal problem.

Exergy as calculated by use of the above equations has some shortcomings. It is therefore proposed to consider the exergy found by these calculations as a *relative exergy index*: (1) We account only for the contributions from the biomass of the organisms and information in the genes. Although these contributions most probably are the most important ones, other important contributions may be omitted. (2) We do not account for the information embodied in the network, that is, in relationships between organisms. The information in the model network that we use to describe ecosystems is negligible compared with the information in the genes, but that the real, much more complex network may contribute considerably to the total exergy of a natural ecosystem cannot be excluded. (3) We have made approximations in our thermodynamic calculations. They are all indicated in the calculations and are in most cases negligible. (4) We can never know all the components in a natural (complex) ecosystem.

Therefore, we will only be able to utilize these calculations to determine exergy indices of our simplified images of ecosystems, for instance, of models. (5) The exergy indices are, however, useful, as they have been used successfully as goal functions (orientor) to develop structural dynamic models. The *difference* in exergy by *comparison* of two different possible structures (species composition) is decisive here. Moreover, exergy computations always give only relative values, because the exergy is calculated relative to the reference system.

As already emphasized, the presented calculations do not include the information embodied in the structure of the ecosystem, that is, in the relationships among the various components represented by the network. The information of the network encompasses the information of the components and the relationships of the components. The latter contribution is calculated by Ulanowicz (1986, 1991) as a part of the concept of ascendancy. In principle, the information embodied in the network should be included in the calculation of the exergy index of structural dynamic models, because the network also changes dynamically (Pahl-Wostl, 1995). However, it may often be omitted from most dynamic model calculations because the contributions from the network relationships of models (not from the components of the network, of course) are minor, compared with the contributions from the components. This is due to the extreme simplifications made in the models compared with networks in real ecosystems. Therefore, while networks of real ecosystems may contribute considerably to the total exergy of the ecosystems, for the type of models that we are using at present, we can probably omit the exergy of the information embodied in the network.

Specific exergy is defined as the exergy or rather exergy index divided by the biomass. Specific exergy expresses the dominance of the higher organisms because, per unit of biomass, they carry more information, that is, they have higher β-values. A very eutrophic ecosystem will have a very high exergy due to the large biomass, but the specific exergy will be low, as the biomass will be dominated by algae with low β-values.

The combination of the exergy index and the specific exergy index usually gives a more satisfactory description of the health of an ecosystem than the exergy index alone, because it considers diversity and life conditions for higher organisms (see also Jørgensen, 1997). The combination of exergy, specific exergy and buffer capacities, defined as the change in a forcing function relative to the corresponding change in a state variable, has been used as an ecological indicator for lakes. It can be shown that these three concepts together cover the six properties of ecosystem health proposed by Costanza (1992).

3. Results

The quantitative descriptions of the 12 marine ecosystems are taken from Christensen and Pauly (1993). Fig. 1 shows the steady state model for Tamaihua, a coastal lagoon in Mexico. These models are available for all 12 case studies. The 12 ecosystems are: (1) Tamaihua; (2) Celestun Lagoon on the southern Gulf of Mexico; (3) a coastal fish community of the southwestern Gulf of Mexico; (4) Campeche Bank, Mexico; (5) Maputo Bay, Mozambique; (6) a Mediterranean lagoon, Etang de Tahu, France; (7) Pangasinan Coral Reef, Philippines; (8) a Caribbean Coral Reef; (9) the Yucatan shelf ecosystem, Mexico; (10) the continental shelf ecosystem, Mexico; (11) a shelf ecosystem in Venezuela, and (12) Brunei Darassulak, South China Sea.

The following ecological indicators were determined for all 12 ecosystems: (a) biomass (g m^{-2} dry weight); (b) respiration (g dry weight $\mathrm{m}^{-2}\,\mathrm{y}^{-1}$); (c) exergy (kJ m^{-2}); (d) exergy dissipation (kJ $\mathrm{m}^{-2}\,\mathrm{y}^{-1}$); (e) diversity as the number of species included in the model (-); (f) connectivity as the number of connections relative to the total number of possible connections (-); (g) complexity expressed as ‘diversity’ times ‘connectivity’ (-), (h) respiration/biomass $= b/a$ (y^{-1}), (i) exergy dissipation/exergy$= d/c$ (y^{-1}), (j) exergy production (kJ $\mathrm{m}^{-2}\,\mathrm{y}^{-1}$); and (k) specific exergy (kJ g^{-1}).

A correlation matrix showed that only the following of the 11 indicators were correlated with a correlation coefficient >0.65: (1) exergy production to exergy, $r^2 = 0.93$ (see Fig. 2); (2) respiration to exergy, $r^2 = 0.98$ (see Fig. 3); (3) respiration to biomass, $r^2 = 0.68$ (see Fig. 4) (notice in this context that respiration is considerably better correlated to exergy than to biomass); (4) respiration to exergy

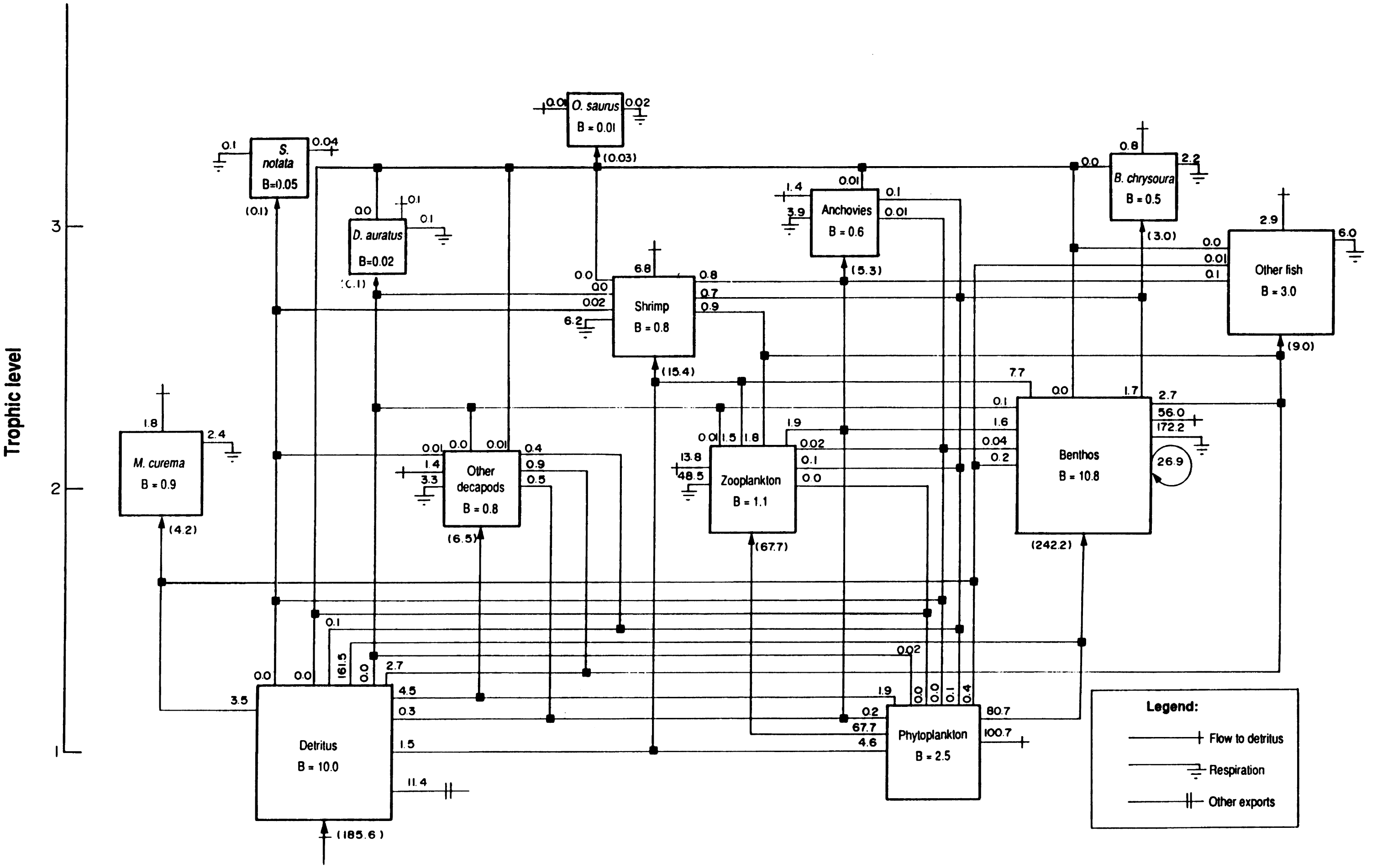

Fig. 1. Flow diagram of the fish community of Tamiahua Lagoon, Mexico. The diagram indicates the Results of use of ECOPATH II in g m^{-2} for biomasses and in g m^{-2} y^{-1} for rates.

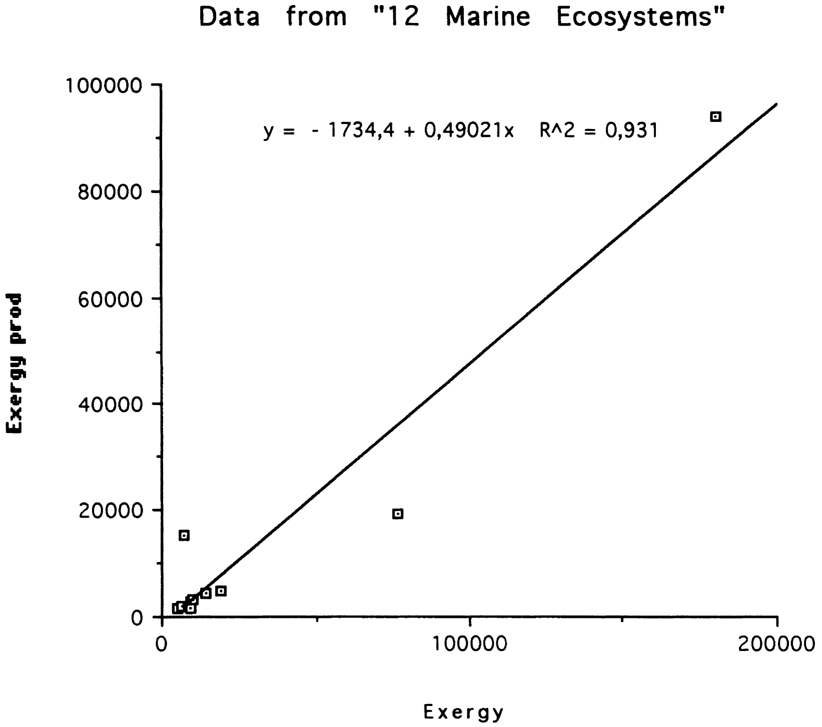

Fig. 2. Exergy production versus exergy.

production, $r^2 = 0.855$ (see Fig. 5); (5) exergy dissipation to respiration, $r^2 = 0.87$ (see Fig. 6); (6) respiration/biomass to specific exergy, $r^2 = 0.86$ (see Fig. 7).

4. Discussion

At least for the examined marine ecosystems, higher exergy levels are associated with higher rates of exergy production which is consistent with the translation of Darwin's theory to thermodynamics by use of exergy. The development of an ecosystem is toward increasing biomass, and when all the inorganic matter is used to build biomass, a reallocation of matter in the form of species with more information may take place. Increased information gives increased possibility that even more exergy (information) is available.

The respiration levels for the various examined ecosystems are considerably better correlated with exergy levels than with the amount of biomass in them, although, as shown in Fig. 3, there is a tendency to a decreasing slope of respiration/exergy with increasing exergy. However, for this tendency be shown to be statistically significant, more information from more marine ecosystems is required. Biomass includes plants (algae) which have relatively low exergy and also low respiration. This explains why exergy with high weighting factors for fish and other higher organisms is better correlated with respiration. The relationship is not surprising, as more stored exergy means that the ecosystem is more complex and more developed, which implies that it also requires more energy (exergy) for maintenance. Moreover, this is consistent with Fig. 5 where respiration is well correlated with exergy production. A high respiration level is associated with higher organisms with more information which gives the opportunity to increase the information further.

The correlation between the respiration level and the rate of exergy dissipation in Fig. 6 is not surprising, since the exergy dissipation is caused by respiration: two different measures of the same concept.

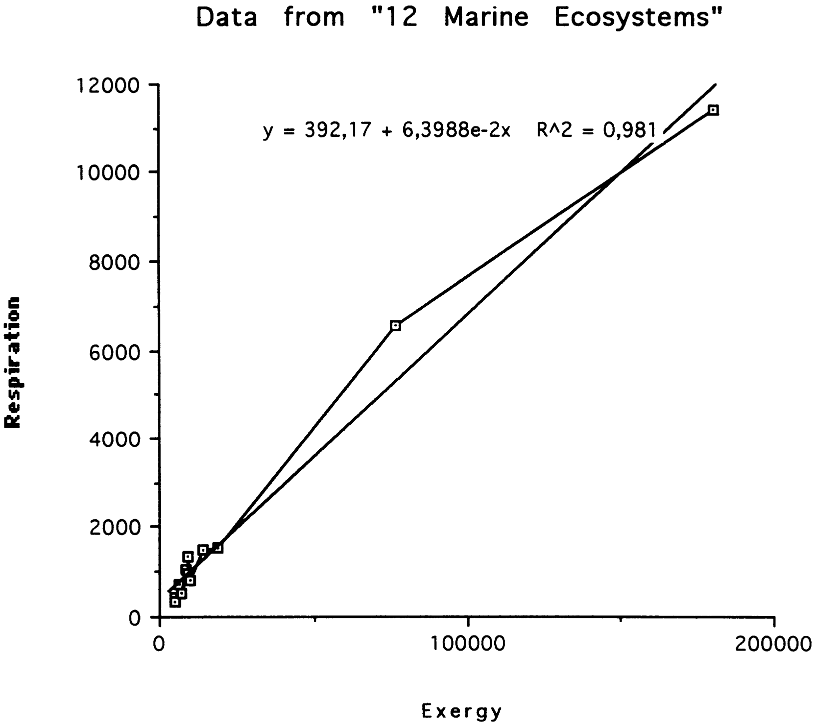

Fig. 3. Respiration versus exergy.

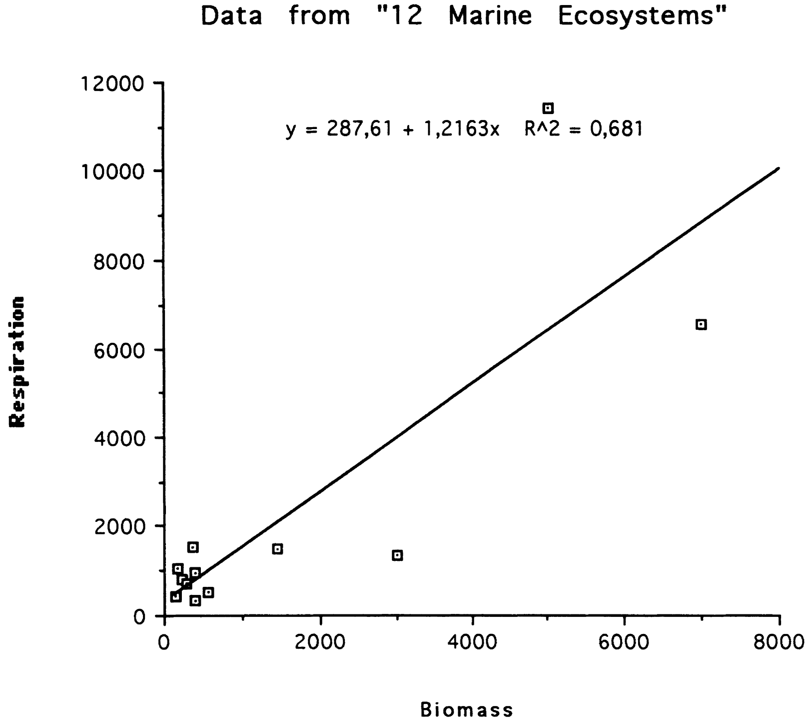

Fig. 4. Respiration versus biomass; notice that the correlation in Fig. 3 is considerably better than this correlation.

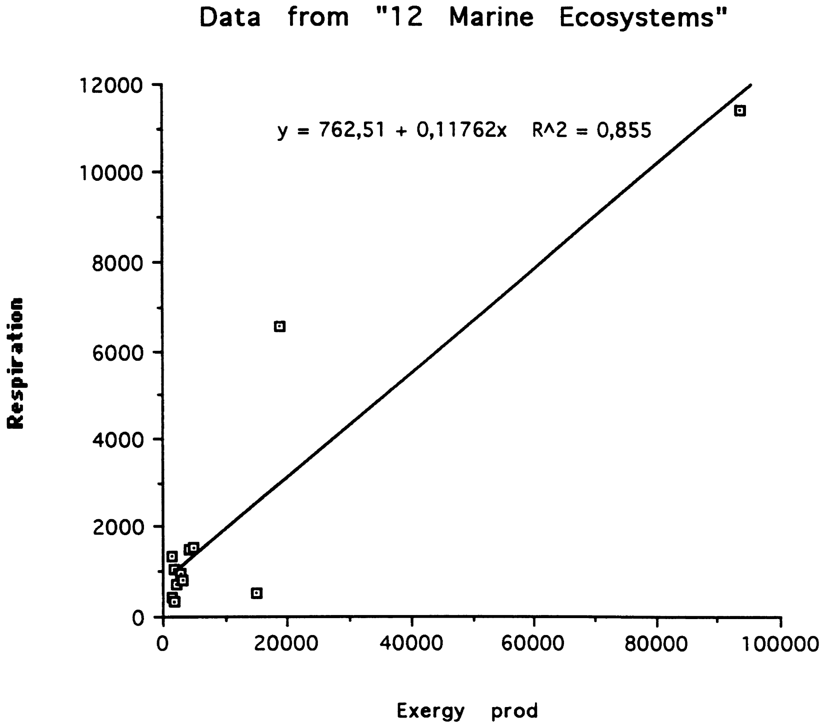

Fig. 5. Respiration versus exergy production (increase in exergy storage).

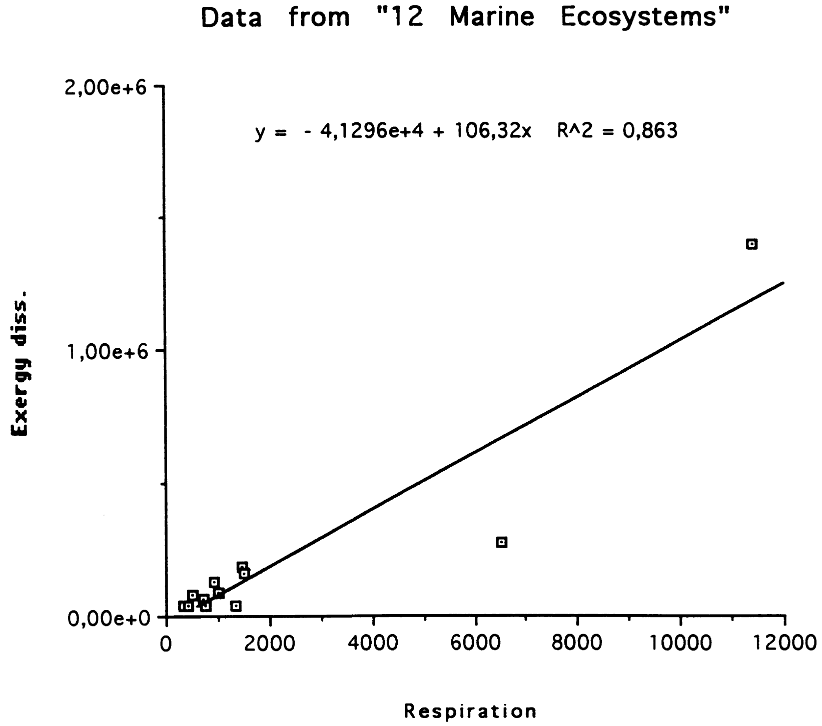

Fig. 6. Exergy dissipation versus respiration

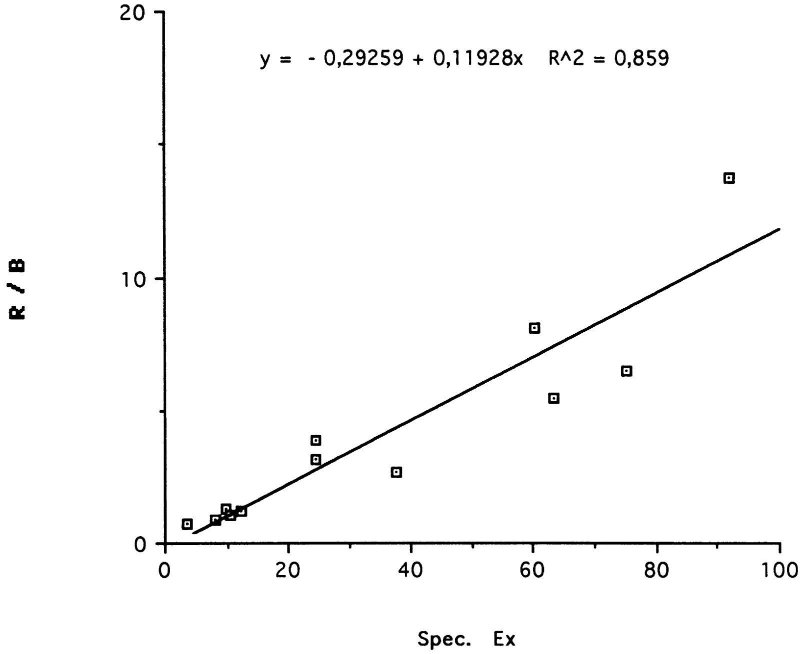

Fig. 7. Respiration/biomass versus specific exergy.

Fig. 7 indicates that the specific exergy for the examined ecosystems (higher specific exergy means more dominance of higher organisms) is well correlated to the ratio of respiration to biomass which is also consistent with the results presented in Fig. 5.

Exergy measures the distance from thermodynamic equilibrium. Svirezhev (1992) has shown that exergy measures the amount of energy needed to break down the ecosystem. Exergy is therefore a reasonably good measure of (compare with Costanza, 1992): (1) absence of disease; (2) stability or resilience; and (3) vigour or scope for growth (notice in this context that Fig. 2 shows a good correlation between exergy and exergy production (growth).

Specific exergy measures organization in the sense that more developed organisms correspond to higher specific exergy. More developed organisms usually represent higher trophic levels and imply a more complicated food web. Specific exergy is a therefore a reasonably good measure of: (1) homeostasis (more feedback is present in a more complicated food web); (2) diversity or complexity; and (3) balance between system components (the ecosystem is not dominated by the first trophic levels, as in ecosystems at an early stage).

5. Conclusions

Eleven ecological attributes were examined for 12 marine ecosystems with the results that good correlation could only be obtained for exergy/exergy production, exergy/respiration, biomass/respiration, exergy production/respiration, respiration/exergy dissipation, and specific exergy/R/B.

Exergy and specific exergy together cover the properties associated with ecosystem health according to Costanza (1992). On the other hand, is it probably not possible to assess the health of such a complex system as an ecosystem by means of two indicators only, which is also consistent with the lack of correlation between these two concepts and the other attributes included in this study. It can, however, be shown that exergy is a good measure of the ability of the ecosystem to grow (see Fig. 2). Exergy is also a better measure of the energy (exergy) required for maintenance than biomass, since more stored exergy and higher exergy production mean that more exergy is also needed for maintenance (see Figs. 3, 5 and 6). Exergy or specific exergy is not well correlated with diversity (expressed simply as the number of state variables in the model) or complexity (measured simply as the product of a number of state variables in the model and connectivity). On the other hand, specific exergy is a good expression for the presence of more developed organisms and thus a more complex ecosystem.

In all, these two concepts, exergy and specific exergy, cover a certain range of properties which we generally associate with ecosystem health. They should, however, be supplemented by other indicators in most practical management situations, as they are not strictly correlated to other important attributes.

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