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Implications of Liebig's law of the minimum for the use of ecological indicators based on abundance

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Many ecological responses to environmental variables or anthropogenic agents are difficult and expensive to measure. Therefore it is attractive to describe such responses in terms of indicators that are easier to measure. In ecosystem management, indicators can be used to monitor spatial and temporal changes in an environmental feature. The aim of this paper is to show that it is important to take Liebig's law of the minimum into consideration to understand when it is appropriate or inappropriate to use ecological indicators based on abundance. When developing indicators that relate the abundance of an organism to an environmental factor, it is likely that this relationship will be polygonal rather than a simple linear relationship. The upper boundary of the distribution describes how abundance is limited by this factor, while the variation below the upper boundary is explained by situations when factors other than the factor of interest limit abundance. The variation below the upper boundary of the distribution means that the use of indicators to examine spatial patterns in the response of abundance to an environmental factor can be problematic. Thus, while abundance-based indicators can identify sites that are in a good condition, they are less useful to detect those affected by environmental degradation. In contrast, abundance-based ecological indicators may enable temporal monitoring of the impact of environmental factors, as it is expected that limiting factors are less variable in time than in space. In conclusion, when multiple factors are limiting, a significant correlation between an indicator and a variable is not enough to validate the status of a factor as an indicator.

The current movement towards ecosystem based management has prompted a review of the range and suitability of system metrics that capture or represent the state of the ecosystem and its response to anthropogenic factors (Turner et al. 2000, Hall and Mainprize 2004, Nicholson and Jennings 2004). As a result, there is considerable interest in the identification and development of indicators of environmental quality for use in large-scale monitoring programs that fulfil the requirements of international and regional conventions (Anon. 2000, Bertiller et al. 2002, Llanso et al. 2003). For example, the International Council for the Exploration of the Sea (ICES) and the Oslo Paris Convention (OSPAR) either recommend or require the development

of appropriate ecological indicators (Ecological Quality Objectives, EcoQOs) against which to assess the achievement of wider management objectives (Kabuta and Laane 2003).

Many ecological responses (e.g. the relationship between plant production and nutrient levels) are difficult and expensive to measure on a repetitive basis, which has necessitated the description of such responses using indicators (e.g. plant biomass as a substitute for production) that are more easily quantified with adequate precision. In terms of ecosystem management, ecological indicators have been chosen to monitor spatial and temporal effects of changes in an environmental feature such as water quality, climate change, UV-levels or eutrophication (Kosmala et al. 1999, Gjerdrum et al. 2003). A good indicator should be sensitive to the underlying condition of interest, while insensitive to other unrelated conditions. In other words, the indicator value should only correlate tightly with the factor it is supposed to monitor, and does not covary with other factors. For ecological indicators to be of practical use they also must have properties that are amenable to measurement (e.g. biomass, density, colour) in relation to a specific change in the environment or human activity. To date, many of the proposed ecological indicators are derived from the measurement of the abundances of species. For example the abundance of seals and the density of the ocean quahog *Arctica islandica* (Kabuta and Laane 2003), the abundance of bird species in different functional categories (Bryce et al. 2002), abundance of breeding bird species (Browder et al. 2002) and epifaunal invertebrates living on hard substrata (Saiz-Salinas and Urkiaga-Alberdi 1999) have been proposed to examine environmental condition for governmental departments, environmental protection agencies and port-authorities.

However, here we demonstrate that the use of abundance as an indicator of ecological effects is problematic and prone to serious misinterpretation. The aim of this paper is to show that Liebig's law of the minimum, a fundamental ecological principle (Von Liebig 1840), must be used to understand when ecological indicators based on abundance may be used and when they are inappropriate and how potential pitfalls can be avoided if ecology is taken into account in development of the indicators.

Polygonal distributions and limiting factors

When using ecological indicators that relate the abundance of an organism to an environmental factor or anthropogenic activity, it is important to realise that abundance often is limited by a suite of environmental factors, including (but in addition to) the factor of interest. The relationship between biological indicators and an environmental variable, and the relationship between the abundance of an organism and habitat features, often are wedge or polygonal shaped and are not simple linear or curvi-linear functions (e.g. Fig. 1).

The observed pattern in the relationship between the environment and the abundance or biomass of organisms can be explained by Liebig's law of the minimum (1840). For example, when considering resources that limit growth or abundance. According to Liebig's law, the limiting factor is the one that is the least available at a particular time (e.g. prey or nutrients). Any factor can potentially limit growth or abundance, but at any time and location only one factor can act as the limiting constraint (Cade et al. 1999). For example, in the case of

Fig. 2A, abundance is likely to be limited by more than one factor across the different stations, e.g. by trawling intensity in some stations and natural physical disturbance in others (e.g. scouring by bottom currents). At high trawling intensities, trawling becomes the dominant or limiting factor in comparison with other environmental or biological factors, hence, biomass is likely to be limited by trawling. However, at low trawling intensity, biomass is as likely or more likely to be limited by the next limiting factor, e.g. natural sources of physical disturbance. In Fig. 2A, the effect of trawling on biomass is described by the upper bound of the measured biomass, while the remaining variation below this line may be explained by another environmental factor. The identity of limiting factors can interchange across seasons, for example food supply has been shown to constrain mussel population growth during the summer while predation becomes the dominant factor during the winter (Gascoigne pers. comm.).

We illustrate the theoretical patterns that are predicted according to Liebig's law of the minimum in a simple model, in which density was assumed to be limited by two factors, food resources and bottom trawling intensity (Fig. 1). Abundance of a theoretical predator (hereafter referred to as "abundance") was assumed to be positive and linear in relation to food abundance and negative and linear in relation to trawling intensity. A dataset of 100 locations were assigned a random food and trawling intensity value and from these values the resulting abundance was calculated. This gave two possible abundance values for each location. It was assumed that only one of the two factors was limiting. The limiting factor was identified as the factor that gave the lowest predicted abundance value, which was used as

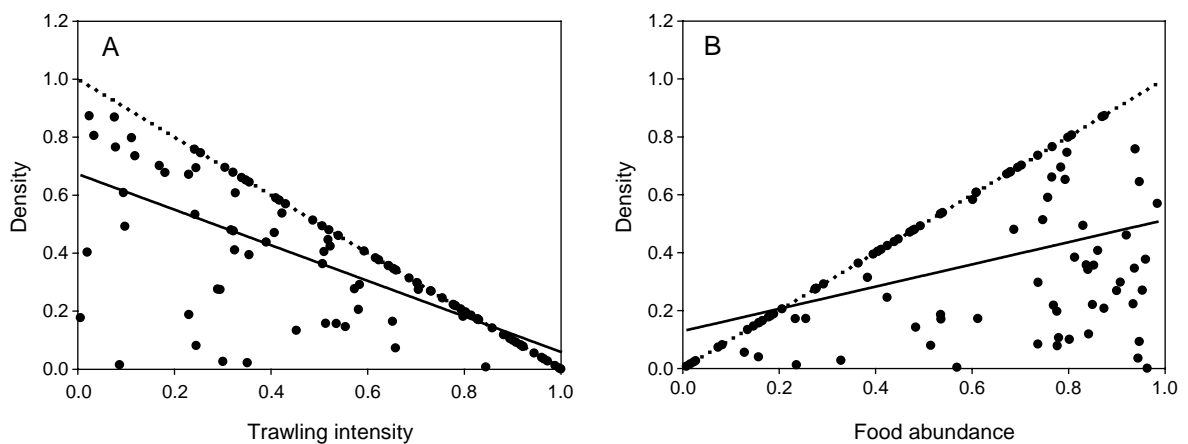


Fig. 1. Densities as predicted by a simple model showing interaction between two limiting factors. A simple one-on-one relation between trawling intensity and density (and food and density) was assumed. A) Trawling intensity, B) food abundance. The second factor food causes the variation below the upper bound of the distribution in (A). An ordinary least square regression (OLS, solid line) and the 99th quantile regression (dotted line) are drawn. If density would be used as an indicator for trawling intensity, it would wrongly predict trawling intensity in 50% of the cases if the quantile regression was used, and almost in 100% of cases if the OLS is used, even though trawling intensity does limit density in the model. Because 50% of the data points is on a straight line, all the high quantiles are the same and no data points are found above the 99th quantile regression.

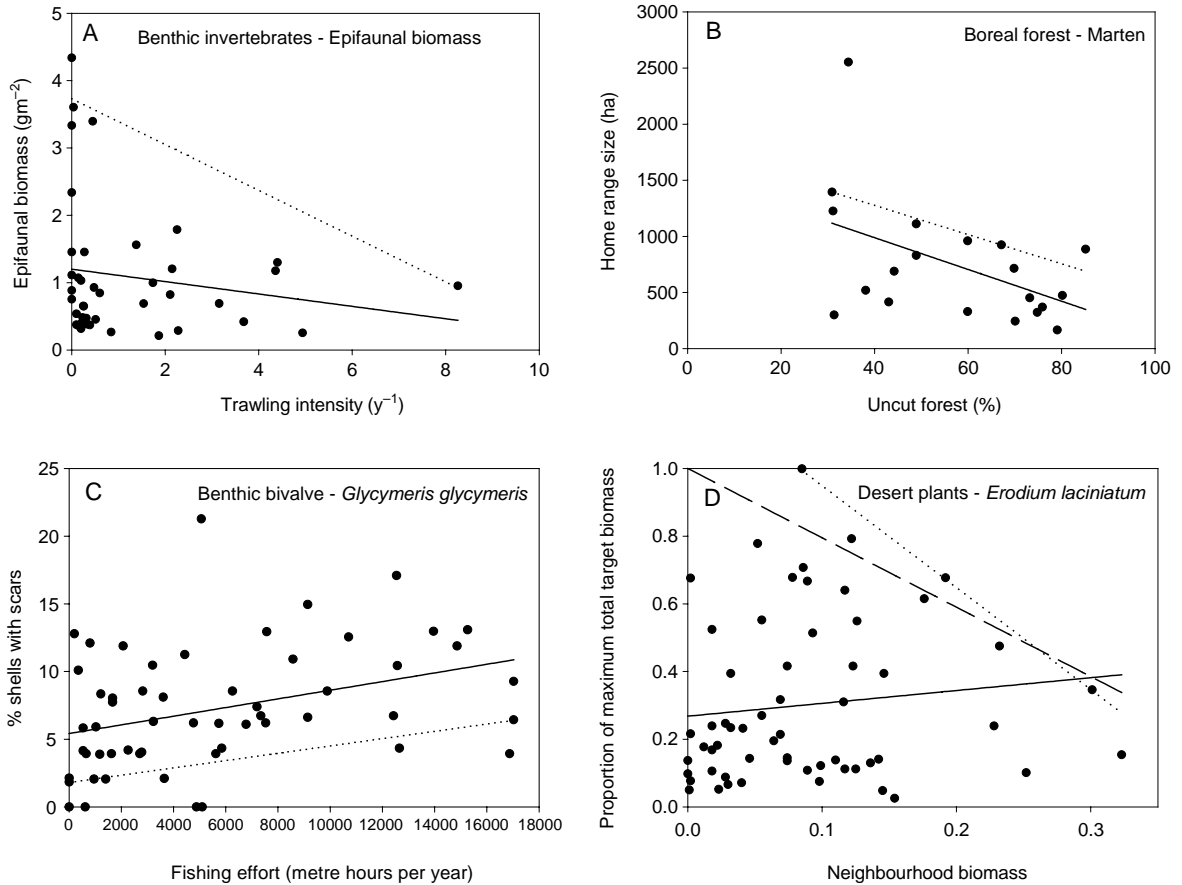


Fig. 2. Examples of abundance – environment relations where abundance is limited by the one environmental factor, while much variation remains unexplained. A) The relation between bottom trawling intensity and total epifaunal biomass on 3 locations in the North Sea. Biomass was sampled with a 2 m-beamtrawl and corrected for the distance trawled. Data from Hiddink et al. (unpubl.) and Jennings et al. (2001). B) Marten *Martes americana* home range size vs the proportion of uncut forest. Redrawn from Potvin et al. (2000). C) The relationship between fishing effort and frequency of scars on the shells of the bivalve *Glycymeris glycymeris* per year. Redrawn from Ramsay et al. (2000). D) The proportion of maximum mass against total neighbourhood mass of other species for the desert annual *Erodium laciniatum*. Redrawn from Lessin et al. (2001). Solid lines indicate fitted OLS, the dotted line indicate fitted quantile regressions, the dashed line in (D) shows the upper boundary analysis as drawn by Lessin et al. (2001) (see Table 1).

Table 1. Slope and intercept as predicted by the regressions as presented in the original papers, OLS and quantile regression for the examples used in the text.

Source	Regression method		Slope	Intercept
Hiddink et al. (unpubl.) and Jennings et al. (2001)	Original method	OLS, on Jennings et al. (2001)	-0.19 and -0.10**	0.47 and 1.74**
		OLS, on all data	-0.07	1.18
		95th quantile	-0.34	3.73
Potvin et al. (2000)	Original method	OLS	-14.2	1554
		85th quantile	-13.0	1795
Ramsay et al. (2000)	Original method	OLS	0.00032	5.42
		15th quantile	0.00027	1.80
Lessin et al. (2001)	Original method	Upper boundary analysis*	-2.05	1.00
		OLS	0.38	0.27
		99th quantile	-3.01	1.25

* Blackburn et al. (1992).

** Data sets from two locations were analysed separately.

the abundance that would be predicted by the model. In a situation in which both food and trawling intensity values were randomly distributed a plot of the predicted densities clearly has an upper boundary that is caused by the limiting effect of trawling (Fig. 1A). Nevertheless, there are many data points under this upper boundary that can be explained by the occasions when food abundance was more limiting than trawling disturbance (Fig. 1A and B). Even though trawling intensity had a limiting effect on the abundance of the predator, abundance cannot be used as a direct indicator of trawling intensity because of the additional limiting effect of the available food resource.

Additive versus limiting resources

Liebig's law of the minimum predicts that the growth rate of a species is determined by the most limiting resource. Liebig's law is open to criticism as it is known that resources may exhibit interactive effects. Huisman and Weissing (2002) gave a clear example of such an interaction between iron and nitrogen in phytoplankton ecophysiology. Iron is a component of the enzyme nitrate reductase, which is needed to reduce nitrate to ammonium. When available in the environment, ammonium can be taken up directly, in which case nitrate reductase would not be required. As a consequence, a deficiency of ammonium in the environment only has an effect on phytoplankton growth in the absence of iron. Thus, as iron and ammonium have interactive effects on phytoplankton growth they do not obey Liebig's law. Indeed, many resource combinations might have interactive effects. The importance of limiting resources relative to resources that cause interactive effects is unknown. It would appear that most large-scale studies indicate that resources limit abundance, while small-scale studies indicate that resources act interactively. At increasingly large scales (>1–100 km depending on organism habitat selectivity), there will always be an environmental factor that limits abundance, however suitable all other factors are. For example, a saltmarsh may contain suitable vegetation for consumption by rabbits, but the lack of a suitable soil for burrow construction limits their occurrence to areas with sandy soils (Kuijper 2004).

In smaller scale and experimental studies in which all factors are kept constant except those that are the subject of manipulation, additive and multiplicative effects between resources are often found. Returning to the rabbit example, on a smaller scale, within areas where it is possible to dig burrows, both vegetation and variation within the sandy soil type may affect rabbit abundance simultaneously, thus soil and vegetation may be additive at the smaller scale. However, the circumstances under which indicators are developed do not permit the control of known factors, given that most

applications are field based and occur at large-scale. Even when experimental data are amenable to statistical modelling assuming additive effects of factors (e.g. multiple regression or multi-factor ANOVA), which conflicts with Liebig's law, in some cases underlying patterns may actually be caused by multiple limiting factors. The model data in Fig. 1, which are generated under the assumption that both resources can be limiting, can be analysed using a multiple regression, relating abundance to food availability and trawling intensity. Both with, and without the interaction term, highly significant regressions were found. This shows that a successful analysis assuming additive factors, doesn't exclude the existence of limiting factors. Such an approach can however only be used successfully when all the factors that affect abundance are known. In cases where only one out of two or more factors that affect abundance is known, and in cases where abundance is to be used as an indicator of only one environmental factor, Liebig's law seems the most valid framework for analysis.

Statistical evaluation of limiting factors

If abundance is to be used as an indicator, the relationship between the environment and abundance has to be quantified. In the examples described above, a relationship fitted with an ordinary least squares regression (OLS) will pass through the mathematical centre of the data points (for an example see the solid lines in Fig. 1 and 2). The fitted line describes the response of abundance to the limiting factors that prevailed at the location at which each measurement was taken, and does not describe exclusively the response of abundance to the specific limiting environmental factor of interest. In other words, the response of a plant or animal is dependent on a range of variables both measured and unknown. Rather than modelling changes through the centre of the data distribution, responses that occur near the upper boundary might provide a better estimate of the changes expected when the measured environmental factor actively limits the response (Cade et al. 1999). Moreover, least-squares modelling techniques that estimate changes through the centre of the response will consistently underestimate the potential response to the habitat factors considered in the model, and provide only the general direction and shape of the response (Scharf et al. 1998), as illustrated in Fig. 1. To illustrate how these problems associated with OLS can be avoided when dealing with multiple limiting factors, we give two examples of statistical techniques that can correctly identify how factors are limiting, and illustrate this using the examples in Fig. 2.

Quantile regression is one of the statistical techniques that can be used to describe the relationship between abundance and a limiting factor, when other limiting

factors act simultaneously (for theory and concepts behind this approach see Cade et al. 1999). The 50th regression quantile is equivalent to a least absolute deviation (LAD) regression in which 50% of the observations are less than, and 50% are greater than, the fitted line. The 50th regression quantile will therefore generally be similar to the OLS. The higher quantiles, such as the 95th quantile describe the function in which 95% of the observations are less than the fitted line, and therefore can be used to examine how abundance is limited by a factor, regardless of the presence of other limiting factors (for an example see the dotted lines in Fig. 1 and 2). Another method to describe the upper boundary of a distribution was developed by Blackburn et al. (1992). Using this method, the slope of the upper boundary is measured by dividing the assemblage data into size classes, and using the highest abundance in each class to estimate the regression slope. The method accurately estimated slopes from simulated data with a known upper boundary. In the development of ecological indicators, it is important to use an appropriate statistical technique when describing the relationship between the indicator value and the environment. When using an OLS, the relationship between the indicator and the environmental factor of interest depends on which other environmental factors are limiting at the time and location where the indicator is developed. The relationship between indicator and environment as described by statistical techniques like quantile regression and upper boundary analysis, is not affected by other factors that are limiting, and should therefore be applicable under a wide range of conditions.

Case-studies

In the following section, we describe four separate studies in which abundance or biomass has been related to either environmental or anthropogenic factors, and then go on to demonstrate how it is possible to misinterpret these relationships without the consideration of limiting ecological, environmental or anthropogenic factors. These evaluations are not meant as criticisms on these papers, as most studies did not try to use abundance as an indicator of the environment or used a suitable analysis to identify limiting factors in the first place. We use these studies to try to establish if abundance data can dependably generate clear identification of environmental influences.

1) In two studies of the effects of chronic trawling on the biomass of marine epifaunal animals (e.g. crabs, starfish, anemones) (Jennings et al. 2001, Hiddink et al. unpubl.), the biomass of epifaunal animals was found to be low at high trawling intensities in line with expectations. However, at low trawling intensities the biomass of animals was found to be both high and low (Fig. 2A).

Jennings et al. (2001) used an OLS to describe the relationship between biomass and trawling intensity and concluded that there was no relationship between these two variables (Table 1). Given the distribution of the data, it seems likely that trawling limits biomass at some stations, but that at many other stations other factors must be limiting biomass. As such, the OLS underestimates the impact of trawling on biomass, and biomass gives a poor estimate of the trawling intensity.

2) In a study by Potvin et al. (2000), 20 marten *Martes americana* were equipped with radio collars to delineate their winter home range in an area where part of the forest in the area of study had been clearcut. The home ranges of the marten were relatively small in area with a low proportion of clearcut area, however, in areas where the clearcut fraction was high, home ranges were both small and large (Fig. 2B). The authors used an ordinary least squares regression (OLS) to describe the relationship between home range size and the fraction of uncut forest (Table 1). They concluded that on-average marten home range size was inversely related to the fraction of uncut forest. However, given the distribution of the data it seems very unlikely that the fraction of uncut forest is the only factor determining the home range, and it seems much more likely that the fraction of uncut forest is just one of the factors limiting home range size.

3) Ramsay et al. (2000) counted the number of scars that were incorporated into the shells of the dog cockle *Glycymeris glycymeris* (a bivalve) in the Irish Sea. These scars were hypothesised to occur as a consequence of physical contact with fishing gear that was trawled over the seabed, such that the numbers of scars recorded within the shell of *G. glycymeris* may differentiate heavily fished from lightly fished areas of seabed. The number of scars was always found to be high at sites with high trawling intensities, but high numbers of scars were also found at a proportion of sites with low trawling intensities (Fig. 2C). The authors used an OLS to describe the relationship between the number of scars and fishing intensity (Table 1). From this, they concluded that the number of scars could be used to examine spatial patterns in fishing intensity. They suggested that the high variation around the relationship could be explained by scars left by crab attacks on the bivalves, or by the patchy nature of fishing effort that was not represented in the resolution of their fishing effort data. Despite a realisation of the high variation around the fitted relationship, they argued that the data acted as independent corroboration of the distribution of fishing intensity. Figure 2C shows that it is not possible to identify high fishing intensity areas with absolute certainty based on an OLS, as a high fraction of shells with scars is not only found at high trawling intensities, but can also be found at low trawling intensities. Using a quantile regression, it was possible to identify the lower boundary of the distribution, instead of the upper

boundary, as trawling seemed to control the lowest possible levels of scar incidence (Table 1). The only areas where the number of shells with scars was an indicator trawling intensity, were the locations where <2.5% of the shells were scarred, which had a low trawling intensity. This would leave 84% of the locations with unidentified trawling intensity (Fig. 2C).

4) Lessin et al. (2001) examined the effect of competing plant species on the biomass of the annual species *Erodium laciniatum* in the Negev Desert of Israel (Fig. 2D). High biomass of *E. laciniatum* was only found in conjunction with low aboveground neighbour biomass of other species. However, low aboveground neighbour biomass of other species did not always co-occur with a high biomass of *E. laciniatum*. The authors used an upper boundary analysis (Blackburn et al. 1992) to delimit the upper boundary of the relationship between biomass of *E. laciniatum* and aboveground neighbour biomass of other species (Table 1). They concluded that the abundance of *E. laciniatum* can be limited by neighbourhood biomass and that competition may play a role in determining plant biomass in desert ecosystems. This study acknowledged that there are multiple limitations, ignored the interactions between these but suggested that the limiting effect of simple competition can be discerned.

All these four examples clearly illustrate that abundance can be limited by more than one factor. The slopes and intercepts predicted by quantile regression and upper boundary analysis for the four case-studies differed by a factor of up to 5 from the predictions of the OLS, and in one occasion the direction of the response was different (Table 1). Thus, because abundance can be limited by more than one factor, abundance data do not dependably generate clear identifications of environmental influences.

Indicators of ecological effects

Because of the law of limiting factors, the applicability of biological indicators that use measures such as the abundance or biomass of organisms may be limited. The case studies showed that low abundance values may occur at high impact sites, but also at low impact sites when another factor limits the response. Therefore, using abundance as an indicator to detect spatial differences in the ecological effects of an environmental factor will only give accurate predictions if the examined environmental factor is the sole limiting factor across the whole area under consideration. In the example of fishing impacts (Fig. 2A), high abundance values always coincide with low impact areas, but low abundance values may indicate low and high impact areas, as natural physical disturbance may alternatively limit abundance at sites with a low fishing impact. This makes indicators

that are based on abundance estimates unsuitable for the examination of spatial patterns in single environmental factors when other factors may be limiting. The only situation in which an indicator based on abundance or similar measure may be used to evaluate spatial variation in environmental impacts, occurs when the value of all other environmental factors are similar among locations. Such a situation may only occur at a small scale, often at a scale smaller than one would want to consider using the indicator given typical constraints on sampling resources. Thus, when considering the use of indicators to examine spatial variability, a consideration of the appropriate scale at which the indicator operates is imperative.

As we expect that the variation in limiting factors is more variable in space than in time, temporal patterns may be examined more reliably using indicators based on abundance, because the indicator is repeatedly evaluated at the scale of a single location. An indicator can be developed using a spatial lay-out, as described above, using a quantile regression to define the upper boundary of the relationship, and thus demonstrates how the factor of interest limits abundance. This relationship can then be used to evaluate temporal changes in the environmental factor using the indicator values (e.g. abundance or biomass) at these fixed stations. Any changes in the indicator value over time are likely to be related to the impact it is supposed to describe. Locations that have a low abundance, because they are limited by another factor, do not pose a problem in such a temporal comparison, because the indicator will rightly show that these stations are not affected by any changes in the environment. In contrast, these low abundance locations would have been labelled as having been affected by the environmental factor in spatial comparisons.

Beukema and Cadee (1997) illustrated that indicator values based on abundance cannot be used to indicate environmental effects in space but can be used to examine effects in time. They monitored macrobenthic infaunal biomass on a tidal flat area in the Dutch Wadden Sea, and related this biomass to the enhanced food supply due to eutrophication in the 1980s. Their data showed that in the 1970s, before the occurrence of mild eutrophication, infaunal biomass varied between 2 and 38 g ash free dry weight m^{-2} . During the period of eutrophication, in the 1980s, biomass remained roughly equal at all locations where the abiotic environment was unfavourable and on stations that were commercially fished for lugworms *Arenicola marina* (bait used by anglers) and cockles *Cerastoderma edule* (bivalve shellfish). On the remaining locations, biomass increased over this period. This suggested that the quantity of available food was limiting biomass at only 7 out of 15 locations studied. This meant that a spatial comparison of biomass to evaluate the ecological effects of eutro-

plication was invalid, because it would have indicated that some stations were affected by eutrophication in the 1970s, while there was no eutrophication at that time. In temporal comparisons of biomass at the individual locations, however, an increase in biomass between the 1970s and 1980s indicated which stations were affected by eutrophication. Thus, abundance cannot be used as a diagnostic indicator for spatial comparison and has to be used with care in temporal comparison. However, abundance may be used as an indicator to identify sites that need further study. Sites with good conditions are expected to always have high abundances, thus the indicator will have a low occurrence of false negative results. However, because other factors than the parameter of interest can be limiting, the occurrence of false positive results will be high. Thus, abundance can indicate sites that are potentially affected by an environmental factor and that need further study (Jope 2001). In such a use of abundance as an indicator, it has to be realized that according to Liebig's law the expected pristine abundance is the upper limit of the observed abundances, and not the mathematical average.

Conclusions

We have highlighted the importance of considering the role of limiting factors when developing indicators that are based on a biological parameter exhibited by organisms in response to environmental stressors. When developing indicators that relate biological parameters of an organism to an environmental factor, it is likely that no simple linear relationship will be found, because other environmental factors may be limiting simultaneously in the examined population. This consequence of Liebig's law of the minimum previously has not been linked in an explicit manner to the appropriateness of abundance based indicators. The development of ecological indicators may not be problematic when ecosystems are well understood, and limiting factors are known. For example, nobody will use the abundance of woodpeckers as a spatial indicator of management success in an area that includes meadow habitat because ecologists know that woodpeckers occur only in woods. However, in ecosystems that are less well understood, like the marine environment or rain forests, ecological knowledge is currently too limited to prevent this potential source of error. Thus the misuse of indicators may be overlooked, if the role of multiple limiting factors is not taken into account. When multiple factors are limiting, a significant regression between an indicator and an environmental variable does not necessarily describe the relationship between the abundance indicator and the environmental variable of interest. Consequently, the use of indicators to examine spatial patterns in the impact of an environmental factor can be

problematic. We expect that the variation in limiting factors is more variable in space than in time. Therefore, ecological indicators are more amenable for temporal site specific repeat sampling or monitoring, even when it is likely that multiple factors are limiting. Indices of biodiversity are often used as indicators of environmental change (Vandervalk et al. 1994, Trenkel and Rochet 2003) and abundance, biomass and biodiversity are often intricately linked. Therefore, the role of limiting factors on abundance is also an important consideration for the use of diversity indices as ecological indicators. Hence, the effect of limiting factors has much wider implications for the use of other standard "indicators".

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