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COMPARING CATEGORICAL AND CONTINUOUS ECOLOGICAL ANALYSES: EFFECTS OF "WAVE EXPOSURE" ON ROCKY SHORES

MATS LINDEGARTH[1] AND LARS GAMFELDT

Department of Marine Ecology, Göteborg University, Tjärnö Marine Biological Laboratory, S-452 96 Strömstad, Sweden

Abstract. Development of general theories and subsequent empirical testing are fundamental ingredients in ecological science. The progress of such efforts is determined by the logical coherence among central concepts, theories, and predictions on one hand, and experimental design, statistical analyses, and interpretation of results on the other. Here, we specifically explore an example of how differences in the way ecological concepts are defined lead to differences in the formulation and statistical testing of hypotheses and ultimately to differences in conclusions about the relative importance of ecological processes.

In marine intertidal habitats, the notion that wave exposure has an important structuring role is widely agreed upon. Nevertheless, generalizations about its effects and use for accurate prediction of assemblages are often limited. This may partly be explained by the frequent use of categorical rather than quantitative definitions of wave exposure. We compared the conclusions about the importance of wave exposure from (1) analyses of variance based on relative classification of wave exposure and geographic location to those of (2) regression analyses based on continuous measures from 16 locations on the Swedish west coast.

Variability in richness was substantially better explained by the regression analyses, while for the cover of individual taxa there was no consistent difference between the two analytical approaches in terms of explained variability. The two approaches detected significant spatial patterns for the same taxa, but conclusions about the nature of these patterns were often divergent. Categorical analyses of relative measures of wave exposure and geographic location indicated that interactive effects and differences between geographic areas were predominant. Regression analyses of absolute, continuous measures suggested that mean significant wave height was a better predictor than geographic location and interactive terms. Thus, the choice of definition of wave exposure has important consequences for how causes of spatial patterns of intertidal assemblages are perceived. Categorical analyses appear to provide clearer indications as to which factors are important while the use of continuous predictors sometimes provides a better fit to the data. The consequences of these findings are discussed in the context of rocky shore ecology as well as in a general perspective of ecological models, hypotheses, experimentation, and analysis.

Key words: environmental factors; experimental design; spatial patterns; statistical analysis; wave exposure.

INTRODUCTION

Contemporary ecological research embraces a large diversity of methodologies and philosophical frameworks (e.g., Loehle 1983, Peters 1991, Hilborn and Mangel 1997, Underwood 1997). Despite the diversity of approaches, the development of general theories (or models) is a common theme for ecological research within any such framework (Lawton 1999, Ford 2000, Colyvan and Ginzburg 2003), and the importance of testing hypotheses (predictions, deductions) derived from theories is widely agreed upon (Platt 1964, Peters 1991, Hilborn and Mangel 1997, Underwood 1997). Such tests require (1) that the components of the theory can be operationalized, i.e., unambiguously identified and quantified (e.g., Loehle 1987, Peters 1991) and (2) that its predictions are tested using one of many available techniques for statistical inference, accounting for the ever-present natural variability and sampling-error typical of ecological systems and data (e.g., Hilborn and Mangel 1997, Underwood 1997, Legendre and Legendre 1998).

In marine intertidal habitats, the importance of wave exposure as a structuring agent is intuitive and uncontested among researchers. Nevertheless, it does not follow that its apparent ecological significance can easily be transformed into general scientific models, from which precise, testable predictions can be derived (e.g., Dayton 1971, Underwood and Denley 1984, Denny 1995). This seeming paradox stems partly from the fact that wave exposure is a physically complex concept (but see accessible accounts in Denny 1988 and Massel

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[1] E-mail: mats.lindegarth@tmbl.gu.se

1999). Wave exposure affects organisms directly through mechanisms such as physical disturbance (e.g., Vadas et al. 1990), fluxes of propagules and nutrients (e.g., Bertness et al. 1992), sedimentation (e.g., Airoldi and Cinelli 1997) and indirectly by modifying behavior, importance of biotic interactions, and thermal and desiccation stress (Connel 1972, Menge 1976). However, the problem is further augmented by the frequent lack of continuous definitions and measurement of the term "wave exposure." A survey of papers in two leading marine ecological journals (*Journal of Experimental Marine Biology and Ecology* and *Marine Ecology Progress Series*) during the last 10 years suggest that approximately 50% of the studies involving tests of hypotheses about effects of wave exposure on the composition and abundance of assemblages, morphology and behavior of organisms use categorical definitions, such as "sheltered," "moderately exposed" or "semi-exposed," or "exposed" (M. Lindegarth, *personal observation*). These characterizations are often based on physical or biological proxies such as wave heights, momentum flux, orientation, composition of benthic assemblages or organismal morphology (Dalby et al. 1978, Bustamante and Branch 1996, McQuaid et al. 2000, Arsenault et al. 2001, Scrosati and Mudge 2004).

The frequent lack of quantitative definitions is surprising given the obstacles it may present for the development of general theories based on wave exposure. For example, it is possible that locations of similar exposure may be classified differently in different studies or that broadly defined categories may mask much variability because the physical mechanisms of exposure are in fact continuous. These problems can be alleviated if quantitative measures are used in combination with appropriate methods of analysis (e.g., Palumbi 1984, Denny 1995, Harley and Helmuth 2003). The most important force components experienced by benthic organisms, drag and lift, are functions of flow velocity (Denny 1988, 1995). Mean and maximum flow velocities can sometimes be measured directly using sophisticated techniques (e.g., Gaylord 1999); however, simultaneous measurement using such techniques at a large number of locations is usually not feasible. Therefore indirect estimates of flow are sometimes obtained from calibration curves and measurements using devices for measurement of maximum force on a standardized object (Jones and Demetropoulos 1968, Palumbi 1984, Carrington-Bell and Denny 1994) or rates of dissolution of plaster (e.g., Doty 1971, Porter et al. 2000). Although these methods are only approximate, they do provide an objective way to quantify individual or collective aspects of exposure. Another possible index of exposure is the wave height, which can be used to derive flow velocities using various versions of wave theory (Denny 1988). In ecological studies, estimates of wave heights are sometimes obtained by direct measurement (e.g., Denny 1995, Milligan and DeWreede 2000), but more commonly indirect measures of wave heights are obtained by measurement of local coastal morphology and information on wind speed and direction (e.g., Thomas 1986, Persson and Håkanson 1995, Ruuskanen et al. 1999). These and more sophisticated measures, available in the oceanographic and engineering literature (see also in Denny 1988 and Massel 1999), can be used as quantitative definitions of wave exposure and reasons for the frequent failure to provide such definitions must be sought elsewhere.

The choice between continuous or categorical definitions of environmental conditions has fundamental consequences for the study of ecological patterns and their causes. This is because this choice affects the way in which ecological hypotheses are formulated. More explicitly, it determines which statistical methods can be used to evaluate hypotheses (Hilborn and Mangel 1997, Underwood 1997, Legendre and Legendre 1998). Differences among categories of a predictor, such as "low" or "high" levels of wave exposure, are typically evaluated statistically using uni- or multivariate analyses of variance. These analyses are very useful for estimating effects and testing hypotheses about effects of individual levels of a factor and their interactive effects at different temporal and spatial scales (e.g., Underwood and Denley 1984). The interpretation does not require any prior knowledge about the nature of relationships between predictors and response (i.e., whether it is linear or curvilinear) and proper experimental and sampling design ensures that such analyses provide independent estimates and tests of individual sources of variation in the model. Alternatively, quantitative measures of continuous predictors may be used in combination with one of many available techniques for regression to test hypotheses about quantitative relationships (e.g., Neter et al. 1990, Hilborn and Mangel 1997, Legendre and Legendre 1998). Depending on the degree of correlation among predictor variables, however, it may be difficult to estimate the effects of individual predictor variables independently using these types of analyses (e.g., Neter et al. 1990, Mac Nally 2000). One particularly useful aspect of these analyses is that the estimated parameters can readily be used to make quantitative predictions about new observations of assemblages. In summary, the way in which environmental factors, such as wave exposure, are defined constrains the types of analyses and therefore the types of inferences that can be made about their effects.

The aim of this study was to test the hypothesis that explanatory power and relative effects of environmental factors differ depending on whether models and hypotheses are based on qualitative, categorical or continuous definitions of environmental variables. This was done through a series of analyses on the effects of wave exposure and position in an archipelago on abundance and diversity of intertidal assemblages of algae and animals on the Swedish west coast. Comparisons were made between conclusions from analyses using two types of linear models with identical numbers of

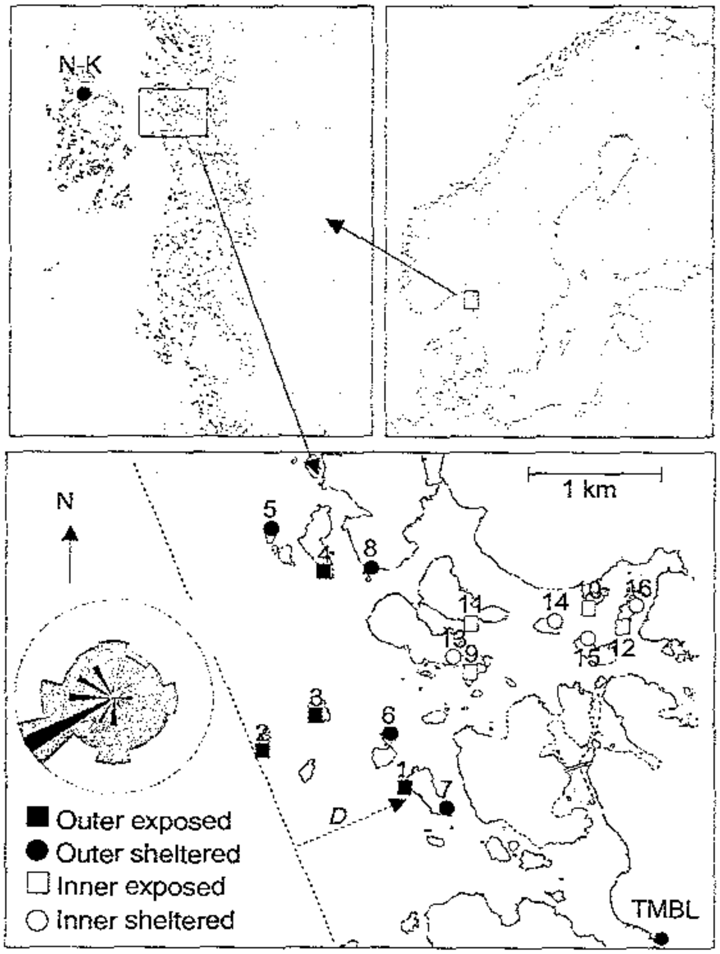

FIG. 1. Maps of regional and local coastal morphology and positions of exposed and sheltered locations in the inner and outer parts of the archipelago, Skagerrak, Sweden. Position in the archipelago, *D*, is measured as the distance from the outer location parallel to the dominant wind direction (see ***Materials and methods: Sampling and experimental design*** for further details). TMBL indicates the location of Tjärnö Marine Biological Laboratory and N-K (Nord-Koster) location of wind measurements. The length of gray wedges in the wind rose indicate frequencies of observations from that direction, and black wedges are an index of energy (mean velocities cubed multipled by their frequencies).

parameters. This allowed direct comparison of the conclusions about (1) proportion of variance explained and (2) relative importance of environmental factors for each type of model. Recognizing that the two types of analyses partly have unique purposes, common and distinctive features are further discussed and illustrated.

MATERIALS AND METHODS

Sampling and experimental design

The study was done in the Swedish part of Skagerrak, a semi-enclosed coastal sea connected to the North Sea (Fig. 1). The tidal range is 0.3 m, but, due to differences in atmospheric pressure and winds, the amplitude of fluctuations is up to 1 m in the area. Fluctuations in temperature and salinity (9.5° ± 6.2°C and 25.2‰ ± 3.8‰ [mean ± 1 SD]) exist and are largely driven by seasonal factors but there are no obvious gradients within the range of the investigated area. Sixteen locations situated on rocky islands in the archipelago close to Tjärnö Marine Biological Laboratory (TMBL; 58°54′ N, 11°7′ W) were sampled during two weeks in May 2001 (Fig. 1). Due to regional and local topographic characteristics, the wave climate around these islands is completely dominated by locally generated waves and not by swell from the North Sea (M. Lindegarth, *personal observation*). The sampled locations were defined as stretches of rocky shores (10–30 m) with slopes of 5–20° around mean water level. Subtidally, however, the slopes of the bottom at these sites were considerably steeper (45–70°) and energy dissipation due to shoaling is therefore minimal. Three 0.5 × 0.5 m quadrates with 7 × 7 (=49) regularly spaced points were randomly located and sampled at each location. Quadrates were placed 0.3 m vertically below mean water level (standardized against tidal gauge data at TMBL). Cover of macroalgae and sessile fauna was estimated by noting the type of organism under each of the 49 points. Abundances of mobile fauna were estimated by counting the number of animals in the quadrates. Algae and animals were identified to the lowest possible taxonomic level, usually species.

Locations were classified according to two factors: Exposure and Area (Table 1). In this region, the dominant wind direction is southwest. Therefore, within each of the "inner" and "outer" parts of the archipelago (the two levels of the factor Area), locations

Table 1. Categorical and continuous descriptors of positions and degrees of exposure for each of the 16 locations.

	Categorical		Continuous			
Location	Area	Exposure	Distance (km)	Mean H_{m0} (m)	SD H_{m0} (m)	Max H_{m0} (m)
1	outer	exposed	0.94	0.13	0.15	0.91
2	outer	exposed	0.00	0.14	0.16	1.00
3	outer	exposed	0.47	0.12	0.14	1.11
4	outer	exposed	0.94	0.19	0.24	1.69
5	outer	sheltered	0.65	0.07	0.14	1.52
6	outer	sheltered	1.00	0.06	0.11	1.27
7	outer	sheltered	1.24	0.02	0.02	0.16
8	outer	sheltered	1.18	0.02	0.03	0.16
9	inner	exposed	1.71	0.04	0.05	0.26
10	inner	exposed	2.71	0.05	0.05	0.30
11	inner	exposed	1.82	0.04	0.03	0.19
12	inner	exposed	2.94	0.03	0.03	0.19
13	inner	sheltered	1.65	0.02	0.02	0.23
14	inner	sheltered	2.53	0.02	0.03	0.19
15	inner	sheltered	2.47	0.02	0.03	0.19
16	inner	sheltered	3.12	0.02	0.02	0.17

were defined as exposed if facing westerly with more than 100 m of open water, and sheltered if facing east. This relative classification of locations was used for analyses of exposure using analysis of variance (ANOVA).

For each location, quantitative, continuous analogues to the categorical factors Exposure and Area were also developed (Table 1). First, to estimate wave exposure we calculated the energy based significant wave height, H_{m0}, according to the following empirical formula (modified from equations II-2–36 in Resio et al. 2003):

$$H_{m0} = 0.0132 \times \sqrt{X} \times u_*$$

where X is the straight line fetch distance over which the wind blows and u_* is the friction velocity in the water. The latter was calculated from

$$u_* = \sqrt{U_{10}^2 \times C_D}$$

$$C_D = 0.001 \times (1.1 + 0.035 \times U_{10}^2)$$

where U_{10} is the wind speed at 10 m elevation and C_D is the drag coefficient (Resio et al. 2003). Data on wind speed (U_{10}) and direction were obtained for eight times of day for 18 months at the station Nord-Koster (located a few km west of the study area) from the Swedish Meteorological and Hydrological Institute. At each location, the straight-line fetch was estimated at 10° intervals using digitally scanned maps and GPS software (GPSy Pro v1.18; Global Mapping Systems, Brooklyn, New York, USA). These equations were combined with data on winds and fetch to calculate mean (MW), standard deviation, and maximum of significant wave height for the 18 months at each location. These three parameters were all strongly correlated ($r > 0.83$, $P < 0.0001$) and mean significant wave heights were selected for further analyses. Second, a quantitative measure of the position in the archipelago was obtained by measuring the distance (D, in kilometers) from the outermost location parallel to the dominant wind direction (Fig. 1). Thus, these two measures of exposure and position were used as quantitative analogues to Exposure and Area and their effects were evaluated in statistical analyses involving continuous predictor variables, i.e., multiple regressions.

Physical basis for estimates of exposure

The perceived importance of categorical and quantitative measures of wave exposure was tested in an experiment measuring the rates of plaster dissolution. Blocks of plaster (with iron attachment hooks) were cast in 100-mL plastic cups and left to dry for two days at room temperature and then in an oven, starting at 45°C and finishing at 65°C (for 12 d). On 30 May, two blocks of plaster were attached to the rock 0.3 m below mean water level at each of the 16 sites. The blocks were left in the field for 24 h, after which they were collected, left to dry for 12 d at 65°C, and the loss of mass per hour exposure was calculated.

Statistical analyses

Patterns of species richness and abundance of individual taxa were estimated and tested using univariate techniques for analyses of categorical and continuous predictor variables, i.e., analysis of variance and multiple regression respectively (using SuperANOVA; Abacus Systems, Berkeley, California, USA). As a consequence of the sampling design, the linear model for analysis of categorical predictor variables ANOVA (hereafter referred to as the categorical model) was

$$Y_{ijk} = \mu + A_i + E_j + AE_{ij} + \varepsilon_{ijk}$$

where Y_{ijk} is the value at the kth location with level j

and i of factors Exposure and Area respectively, μ is the overall population mean, A_i is the effect of the ith level within factor A, E_j is the effect of the jth level within factor E, AE_{ij} is the effect of the effect of the ijth combination of A and E, and ε_{ijk} is the unexplained deviation associated with each value of Y. The corresponding linear model for analysis of the quantitative predictors (hereafter referred to as the continuous model) of the analyses was

$$Y_i = \beta_0 + \beta_D X_{iD} + \beta_{\mathrm{MW}} X_{i\mathrm{MW}} + \beta_{D\times\mathrm{MW}} X_{iD} X_{i\mathrm{MW}} + \varepsilon_i$$

where X_{iD} and $X_{i\mathrm{MW}}$ are the distances and mean significant wave heights at location i, β_0 is the population intercept, β_D is the slope for Y on the distances, β_{MW} is the slope for Y on mean significant wave heights, and $\beta_{D\times\mathrm{MW}}$ is the slope for Y on the product of distance and mean significant wave heights. Prior to all analyses, measures of diversity and abundance were transformed as $\ln(Y)$ and $\ln(Y + 1)$, respectively.

Both types of models had identical number of degrees of freedom, enabling direct comparison between the models with respect to the proportion of variance explained (R^2) for individual response variables (here R^2 denotes coefficient of multiple determination while r^2 is used for coefficient of simple determination [Neter et al. 1990]). Detailed interpretation of results of ANOVA followed standard procedures as described in Underwood (1997). Despite error in the measurement of X and Y variables, regressions were done using ordinary least-squares (OLS) procedures (model I regression). This was justified (instead of model II regression) because the error associated with measurement of X was small ($\sigma^2_X/X < 0.1$) in comparison to that of Y ($\sigma^2_Y/Y > 1$) (e.g., Legendre and Legendre 1998, Quinn and Keough 2002). The interpretation of multiple regressions did not involve any procedures for inclusion or exclusion of predictor variables (e.g., stepwise selection or criteria for selection of best model). Rather, the main purpose of these analyses was to test the fit of the whole model and compare it to that of the full categorical model. Nevertheless, coefficients of the regression model (β's) were also estimated and tested for statistical significance (using t tests). This was done to allow assessment of the importance of individual variables and to illustrate the potential use of these coefficients in empirical, predictive models. While the latter is unaffected by issues to do with correlation among predictor variables, inferences about the significance of individual variables need to be made with caution (Mac Nally 2000, 2002). To assess such problems, tolerance was calculated for the different predictor variables. As a rule of thumb, a value of tolerance >0.1 are considered to be unproblematic (Quinn and Keough 2002). Furthermore, the importance of individual predictor variables was assessed using hierarchical partitioning (Chevan and Sutherland 1991, Mac Nally 2000, 2002). This allows partitioning of the contributions of individual predictor variables to the overall correlation (R^2).

RESULTS

Patterns of plaster dissolution

Analyses of the patterns of plaster dissolution using categorical and continuous models revealed significant spatial patterns (Fig. 2). The proportion of explained variance by the categorical ANOVA model was 77%, while the corresponding value for the continuous model was 93%. The categorical model showed that the rate of dissolution was significantly higher in the outer area compared to the inner. Although the estimated mean rates were higher at the exposed compared to sheltered locations in the inner and outer parts of the archipelago (Fig. 2a), effects of exposure were not significant. The bivariate quantitative relationships between position, D, mean significant wave height, ln(MW), and their interaction, $D \times \ln(\mathrm{MW})$, with the rate of dissolution were remarkably strong ($r^2 = 0.83$, 0.70, and 0.85 respectively; Fig. 2b and c). Not surprisingly, there were significant correlations among all predictors in the model. Tolerances for D, ln(MW), and $D \times \ln(\mathrm{MW})$ were 0.015, 0.22, and 0.02, respectively. This indicates significant collinearity and interpretation of individual coefficients may therefore be difficult.

Patterns of species richness

The proportion of the total variance in species richness, richness of algae, and animals explained by the continuous model were all statistically significant (Table 2). Between 67% and 80% of the variation in the different measures of richness was accounted for in the regression models, while models based on categories explained only 23–46% (Fig. 3). Initial analysis of the coefficients estimated by the continuous model indicated that there was decreasing total, algal, and animal richness with increasing distance, i.e., further into the archipelago, while there were positive relationships with mean significant wave height (Table 3). The interpretation of these patterns was complex because of a substantial contribution of the interactive term for the total number of species and the number of algal species (Table 3). Categorical analyses showed significant patterns only for richness of animals (i.e., $P_{A\times E} < 0.05$ in Table 2). There were smaller numbers of animal taxa in the outer exposed locations compared to the sheltered (Fig. 3). Otherwise, few patterns were revealed by the categorical models.

Comparison of explained variance

Differences in the proportion of variance explained between continuous and categorical models were less evident for abundances of individual taxa compared to the different aspects of species richness (Table 2). In fact, the number of taxa for which the fit of the continuous model was better was only 16 out of 41

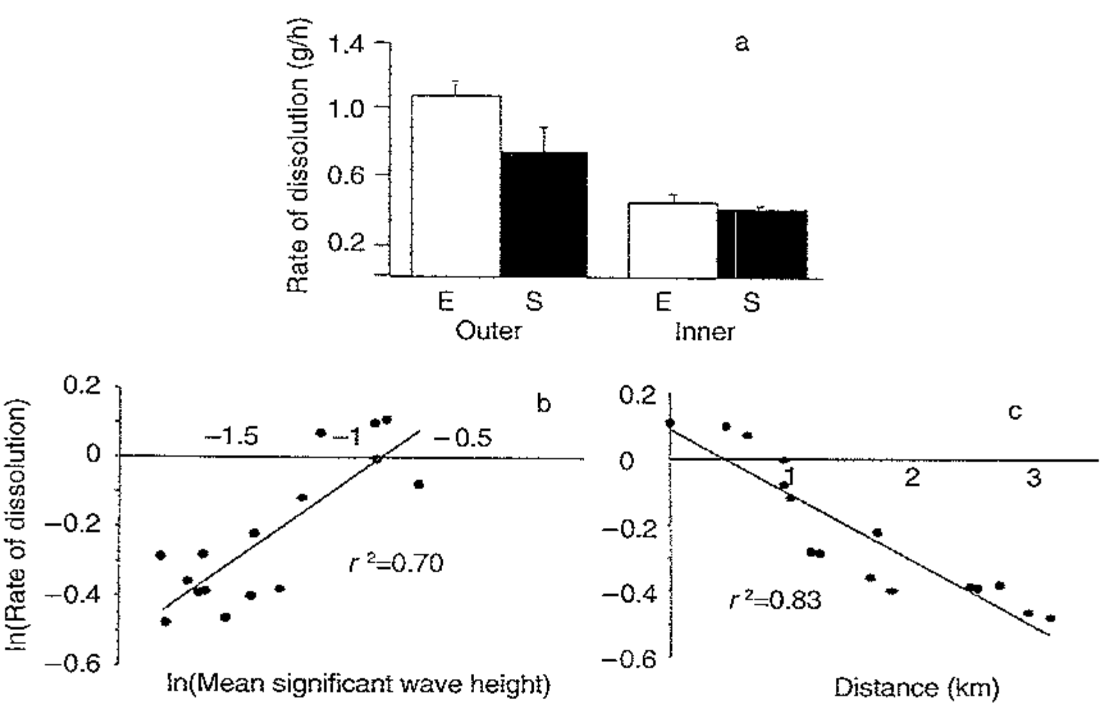

FIG. 2. (a) Rates of plaster dissolution (mean + 1 SE), by categories of locations. (b,c) Regression of mean dissolution rates at individual locations (b) on ln(mean significant wave height) and (c) on distance from outer islands.

(<40%). In general, there was a positive relationship between the proportion of variance explained by the continuous and categorical models (Fig. 4). Both types of models explained a significant proportion of the variability for 13 taxa (i.e., $R^2 > 0.466$ and $P < 0.05$). All taxa for which a significant proportion of variability was explained by the categorical model, were also detected by the continuous model. Additionally, significant proportions of variability were explained by the continuous model for three more taxa, compared to the categorical.

Patterns of individual taxa using categorical analyses

Significant outcomes were obtained for 16 algal or animal taxa using categorical analyses (Table 2). Of the observed patterns, nine instances were examples of interactive effects, one was a consistent effect of Exposure, and six were examples of consistent differences between the inner and outer areas (Table 2).

The interactive effects can be divided into two different types. First, there were species, for example *Corallina officinalis* and *Acrosiphonia* sp., which appeared only in exposed locations in the outer area (Fig. 5). This type of interactive effect indicates that the sampled area is in the periphery of the environmental range of these particular species. Second, there were some algae (e.g., *Fucus serratus* and *Chondrus crispus*) and animals (e.g., *Dynamena pumilla* and *Littorina fabalis*) that were more abundant at exposed locations in the inner area, while in the outer area they were more abundant at sheltered locations (Fig. 5). Such patterns clearly illustrate the relativity of the term "Exposure" used in the categorical formulation.

Only for one species, *Fucus vesiculosus*, was the percent cover significantly affected by exposure similarly way in both inner and outer parts of the archipelago (Fig. 5). In contrast, the cover of many species of algae and the abundance of one species of animal were consistently different between inner and outer areas, irrespective of whether the locations were categorized as sheltered or exposed (Table 2). Examples of such species were *Hildenbrandia rubra*, *Ascophyllum nodosum*, and the anthozoan *Sagartiogeton vidatus* (Fig. 5).

Patterns of individual taxa using continuous analyses

Further analyses were done on taxa for which significant proportions of variability were explained by the continuous models. Regression coefficients using the complete model were calculated for each predictor and response variable (Table 3). Of the 14 taxa analyzed this way, six taxa had $\beta_{\mathrm{MW}\times D} \neq 0$, nine had $\beta_{\mathrm{MW}} \neq 0$, and six had $\beta_D \neq 0$. Although the taxa showing significant interactions ($\beta_{\mathrm{MW}\times D}$) were slightly fewer, they were generally the same as those in the categorical analyses. This indicates that, for individual taxa, the two types of analyses often tended to detect similar

TABLE 2. Proportion of explained variance (r^2) and statistical significance (P) for continuous and categorical models fit to species richness and abundance of individual taxa.

Variable	$r^2_{\mathrm{continuous}}$	P_{model}	$r^2_{\mathrm{categorical}}$	P_{A}	P_{E}	$P_{\mathrm{A \times E}}$
Total no. species	0.80	0.00	0.23	0.17	0.94	0.27
No. algal species	0.71	0.00	0.31	0.06	0.43	0.56
No. animal species	0.67	0.00	0.46	0.32	0.08	0.04
Algae						
Corallina officinalis	0.80	0.00	0.93	0.00	0.00	0.00
Acrosiphonia spp.	0.74	0.00	0.97	0.00	0.00	0.00
Protomonostroma undulatum	0.63	0.00	0.81	0.00	0.00	0.00
Rhodomela confervoides	0.47	0.10	0.65	0.02	0.02	0.02
Fucus serratus	0.73	0.00	0.60	0.52	0.07	0.00
Chondrus crispus	0.73	0.00	0.47	0.84	0.77	0.01
Fucus vesiculosus	0.61	0.07	0.45	0.09	0.03	0.64
Hildenbrandia rubra	0.82	0.00	0.77	0.00	0.07	0.07
Ascophyllum nodosum	0.56	0.01	0.70	0.00	0.81	0.27
Ahnfeltia plicata	0.58	0.00	0.46	0.01	0.83	0.36
Polysiphonia stricta	0.56	0.09	0.56	0.01	0.10	0.10
Cladophora rupestris	0.29	0.33	0.31	0.05	0.56	0.56
Scytosiphon lomentaria	0.26	0.19	0.39	0.06	0.12	0.44
Laminaria saccharina	0.20	0.15	0.43	0.11	0.11	0.11
Pilayella littoralis	0.24	0.27	0.15	0.19	0.82	0.82
Laminaria digitata	0.07	0.80	0.20	0.34	0.34	0.34
Sphacelaria cirrosa	0.34	0.04	0.20	0.34	0.34	0.34
Chorda tomentosa	0.13	0.47	0.20	0.34	0.34	0.34
Polysiphonia fucoides	0.13	0.47	0.20	0.34	0.34	0.34
Ceramium nodulosum	0.06	0.33	0.20	0.34	0.34	0.34
Enteromorpha sp.	0.08	0.62	0.20	0.34	0.34	0.34
Ulva sp.	0.08	0.62	0.20	0.34	0.34	0.34
Furcellaria lumbricalis	0.26	0.01	0.09	0.44	0.88	0.49
Dumontia contorta	0.41	0.01	0.08	0.61	0.48	0.65
Spongonema sp./*Elachista* sp.	0.07	0.33	0.15	0.84	0.84	0.19
Phymatolithon sp.	0.42	0.00	0.28	0.85	0.28	0.09
Cystoclonium purpureum	0.37	0.01	0.14	1.00	0.18	1.00
Animals						
Dynamena pumilla	0.73	0.00	0.80	0.02	0.02	0.00
Littorina littorea	0.81	0.00	0.89	0.00	0.00	0.00
Litorina fabalis	0.47	0.00	0.41	0.33	0.15	0.05
Sargartiogeton viduatus	0.29	0.06	0.32	0.04	0.92	0.44
Halichondria panicea	0.29	0.01	0.30	0.07	0.44	0.44
Semibalanus balanoides	0.45	0.12	0.34	0.14	0.12	0.37
Littorina saxatilis	0.14	0.17	0.22	0.23	0.23	0.66
Hinia nitida	0.11	0.36	0.20	0.34	0.34	0.34
Nudibranchia sp.	0.11	0.36	0.20	0.34	0.34	0.34
Psammechinus miliaris	0.40	0.00	0.20	0.34	0.34	0.34
Metridium senile	0.20	0.09	0.20	0.34	0.34	0.34
Bryozoa sp.	0.20	0.09	0.20	0.34	0.34	0.34
Tectura sp.	0.20	0.09	0.20	0.34	0.34	0.34
Obelia/*Laomeda*	0.38	0.05	0.08	0.65	0.60	0.48
Mytilus edulis	0.10	0.41	0.03	0.95	0.69	0.64

Notes: The proportion of variance explained by continuous and categorical models are $r^2_{\mathrm{continuous}}$ and $r^2_{\mathrm{categorical}}$, respectively; P_{model}, P_{A}, P_{E}, and $P_{\mathrm{A \times E}}$ are values of statistical significance for the full regression model and for sources of variation "Area," "Exposure," and "Area × Exposure," respectively.

interactive patterns. It appears, however, that the independent contribution of the interaction to the correlation in hierarchical partitioning, was generally less important than those of the main effects (Table 3).

The effects of distance (β_D) were less frequent (six taxa) than those of the corresponding factor, Area, in the categorical analyses. Except for *Fucus serratus* and *Chondrus crispus*, the taxa showing significant patterns were consistent among the two analyses. Furthermore, the independent contribution of distance to the overall correlation was the most important only for two species, *Hildenbrandia rubra* and *Ascophyllum nodosum*. In contrast, the independent contribution of exposure measured as mean significant wave height to the overall correlation was generally the most important (11 of 14 taxa). For many taxa, its contribution was twice as large as those provided by the two other predictor variables. The importance of the effects of exposure was further underlined by the fact that a larger number of taxa showed significant effects of exposure (i.e., $\beta_{\mathrm{MW}} \neq 0$) than in the preceding, categorical analyses.

DISCUSSION

The aim of this study was to assess differences in the way ecological patterns and processes are perceived

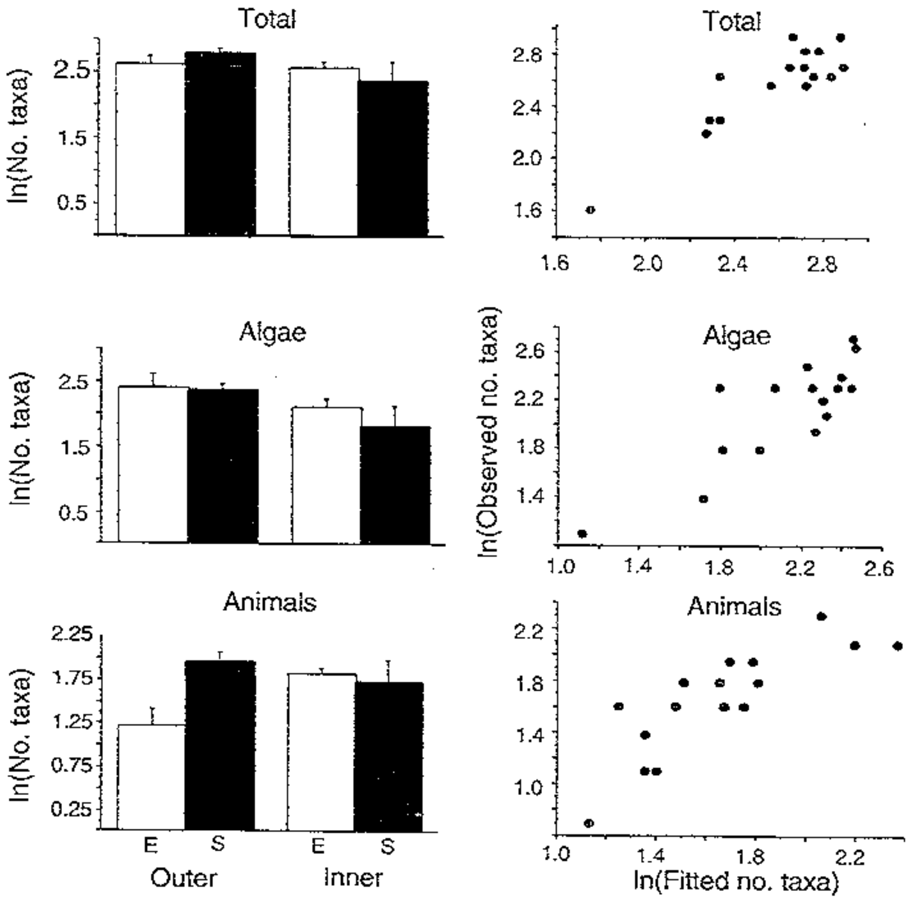

FIG. 3. Log-transformed number of total taxa, algae, and animal taxa in quadrats (mean + 1 SE). Left-hand panels show means of each category in each location. Right-hand panels show the observed mean vs. the mean predicted by continuous models.

TABLE 3. Coefficients (β), significance (P), and hierarchical partitioning of the independent contributions to the total R^2 of individual predictor variables in significant continuous models (shown in Table 2).

Variable	Coefficients							Independent contribution		
	β_0	β_D	P_D	β_{MW}	P_{MW}	$\beta_{MW\times D}$	$P_{MW\times D}$	D	MW	MW × D
Total richness	1.17	−0.59	**0.00**	1.28	**0.00**	0.46	**0.00**	0.24	0.19	**0.36**
Algal richness	1.10	−0.46	**0.02**	1.49	**0.00**	0.51	**0.00**	0.23	0.13	**0.34**
Animal richness	−0.32	−0.79	**0.00**	0.58	0.21	0.26	0.06	0.07	**0.48**	0.11
Corallina officinalis	4.62	−1.87	**0.02**	1.30	**0.00**	−0.52	**0.02**	0.18	**0.43**	0.19
Acrosiphonia spp.	9.27	−2.51	0.17	2.64	**0.00**	−0.73	0.17	0.14	**0.44**	0.17
Protomonostroma undulatum	4.25	−1.31	0.22	1.20	**0.01**	−0.37	0.23	0.12	**0.36**	0.15
Rhodomela confervoides	4.67	0.69	0.75	1.38	0.15	0.13	0.83	0.08	**0.28**	0.12
Fucus serratus	−10.48	8.46	**0.00**	−5.26	**0.00**	3.04	**0.00**	0.15	**0.35**	0.23
Chondrus crispus	−6.76	6.93	**0.00**	−3.40	**0.00**	2.27	**0.00**	0.18	**0.30**	0.25
Fucus vesiculosus	−1.79	−1.97	0.39	−1.18	0.22	−0.59	0.38	0.12	**0.30**	0.19
Hildenbrandia rubra	−1.34	3.26	**0.01**	−1.02	0.05	0.63	0.08	**0.35**	0.18	0.29
Ascophyllum nodosum	−6.09	6.23	0.06	−2.00	0.14	1.41	0.14	**0.24**	0.13	0.19
Ahnfeltia plicata	−0.98	2.48	0.14	−1.48	**0.04**	1.06	**0.04**	0.20	0.11	**0.26**
Polysiphonia stricta	5.33	0.19	0.93	1.39	0.12	0.07	0.91	0.10	**0.30**	0.15
Dynamena pumilla	−10.53	8.63	**0.00**	−4.67	**0.00**	2.65	**0.00**	0.16	**0.39**	0.17
Littorina littorea	−8.32	5.97	**0.00**	−3.76	**0.00**	1.78	**0.00**	0.17	**0.46**	0.18
Litorina fabalis	−3.70	2.37	0.29	−2.59	**0.01**	1.11	0.10	0.10	**0.24**	0.13

Notes: Variables are MW (ln[mean significant wave height]). D (distance from outer location [km]), and MW × D (interaction term). Coefficients that are significantly different from zero and are the largest independent contribution for each species are shown in bold.

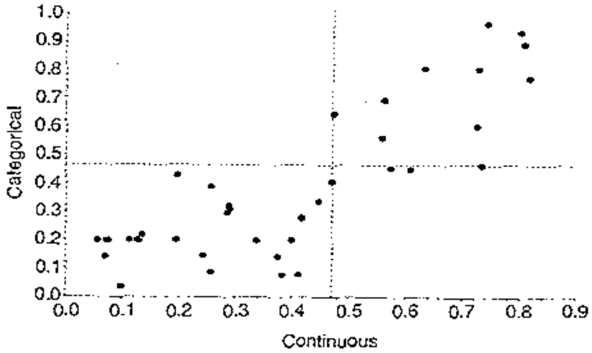

FIG. 4. Proportion of variance explained (R^2) by analyses of continuous and categorical models. Dashed lines indicate critical level to reject H_0 of no correlation.

depending on whether ecological models are formulated and tested within a categorical or continuous framework. This was done by a series of analyses of data on relationships between diversity and abundance of rocky-shore assemblages and two contrasting definitions of wave exposure. Clearly, the two approaches for analysis differ slightly in purpose and philosophical basis. Nevertheless, choosing whether to design experiments and observations for factorial or regression analyses is essential before testing predictions derived from any ecological model (e.g., Underwood 1997, Legendre and Legendre 1998, Quinn and Keough 2002). Chances are that differences among approaches limit the progress of science because they (1) lead to differences in interpretation of results within a particular study and (2) confound consistency of patterns among studies and thereby prevent the identification of general patterns.

Comparisons of results from ANOVA and regression analyses in this study suggest that some aspects of patterns may be consistent, while others may differ between the two types of approaches. The most striking difference in conclusions between the two types of analyses was that observed for species richness. The variability in total, algal, and faunal richness was explained substantially more successfully by the continuous than by the categorical models. For example, the regression model explained 80% of the variability in total species richness, while only 20% was explained by the ANOVA. In contrast, the two types of analyses generally tended to detect significant spatial patterns

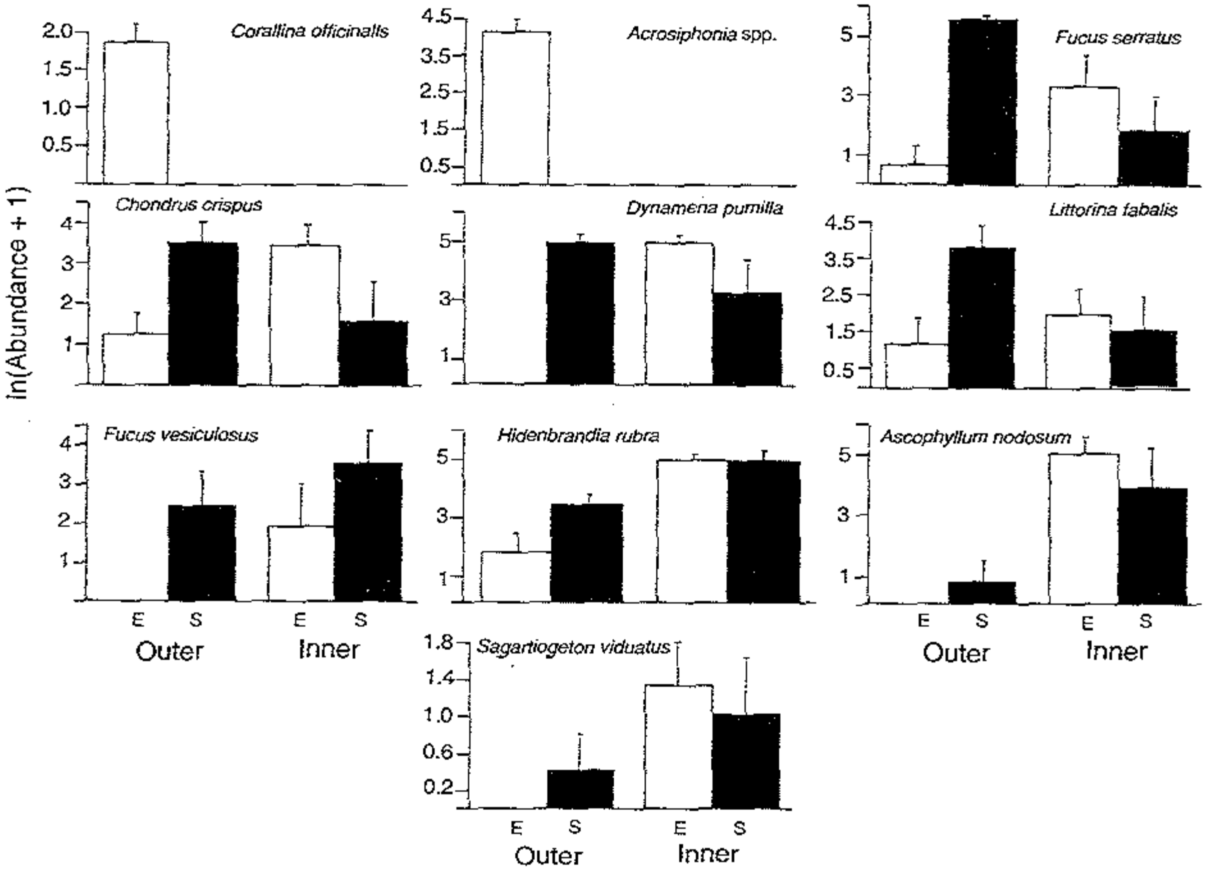

FIG. 5. Mean percent cover (ln-transformed) of sessile organisms (no./m^2 for *Littorina fabalis*) for each category and location (mean + 1 SE).

of variability for the same taxa and proportions of explained variability for individual taxa were generally similar. Examination of the relative importance of different predictors were, however, quite different. Categorical analyses suggested that consistent differences between the inner and outer parts or interactive patterns, i.e., differential effects of exposure between the inner and outer areas, were more important than simple effects of Exposure. Continuous regression analyses and hierarchical partitioning, however, suggested that patterns associated with exposure, defined as mean significant wave height, were largest and most frequent. Thus, for individual species, it appears that the power to detect significant patterns and the proportion variance explained is similar for both types of analyses, but the nature and interpretation of these patterns may be quite different.

The fact that the choice between categorical or continuous models for analyses appears to have a substantial impact on how we interpret the results of a study is frustrating. Not only does it mean that this choice affects our immediate views on the importance of different ecological processes, but if these results are used as the basis for further experimentation in a coherent research program, its consequences may be even greater. For example, based on the prevalence of interactive variability in the categorical analyses observed here, it would be perfectly logical for a researcher to propose the hypothesis that the effects of an experimental manipulation decreasing wave exposure at an exposed location will be very different in the inner compared to the outer parts of the archipelago. In contrast, because of the dominating influence of the mean significant wave height concluded from continuous analyses, another researcher might propose the hypothesis that there will be no difference in the effects of the same manipulation between the inner and outer areas. Thus, the choice of method for statistical analysis might to a large degree affect the emphasis and formulation of new hypotheses within the research program, even though both approaches are perfectly valid and carefully executed. To judge which of these particular hypotheses would be most likely supported is impossible from these data. It might, however, be suggested that whenever possible, identification of contrasting results by performing both types of analyses, could be useful for increasing our confidence in the observed patterns or for deriving multiple working hypotheses (e.g., Platt 1964, Chamberlin 1965, Underwood 1997).

One important aim of benthic ecology is to integrate existing empirical and theoretical sources of information into general models of dominating processes in natural systems. To be able to assess whether effects of disturbances are consistent among different physicochemical environments (e.g., temperature, salinity, and depths) and at different intensities of biological interactions (e.g., competition for space or nutrients, predation, grazing, and recruitment) using formal methods for meta-analysis (e.g., Gurevitch and Hedges 1999, Osenberg et al. 1999), it is imperative that the level of disturbances can be quantified and compared in common units. These analyses show that frequent use of relative measures of wave exposure may lead to failure to detect existing patterns and thus prevent development of general models of how wave exposure affect benthic assemblages. The prevalence of interactive effects resulting from the categorical analyses, i.e., the differences in effects of exposure between inner and outer areas, demonstrate clearly that differences in levels of disturbance may lead to failure to establish general patterns among different studies on the importance of wave exposure (e.g., Palumbi 1984, Denny 1995).

The classification of variables into mathematical types (categorical vs. continuous, qualitative vs. quantitative, absolute vs. relative, etc.; see Legendre and Legendre 1998) is fundamental in ecological science. Decisions about how to operationalize components of a theory to allow tests of its hypotheses must be made in all types of studies of environmental factors (e.g., moisture, soil and sediment grain size, temperature and altitude) and in studies of effects of fundamental biotic interactions such as predation, competition and grazing. The need for quantitative descriptions and explicit analysis of experimental treatments is obvious in manipulative studies. In mensurative studies, however, levels of important factors cannot be controlled and sometimes they are difficult or expensive to measure. As a response to such problems, levels of different factors are often defined in terms of broad classes and analyses are done using categorical analytical frameworks. In other instances, classification into categories is done regularly even where quantitative data are available (e.g., Wentworth scale in work on sediments and various versions of habitat classification schemes). This is presumably done in order to reduce complexity of analysis and interpretation of results. While there may be valid reasons for such simplification, the analyses presented here indicate that failure to define predictors continuously may reduce explanatory power within studies and present substantial obstacles for the development of general theories by integrating results from many studies.

Difficulties in generalizing and synthesizing results from different studies also arise because differences in the way hypotheses are formulated lead to differences in the way that data are analyzed. Within this study, conclusions about the generality and importance of wave exposure differed between regression and ANOVA. Clearly, these two approaches are not mutually exclusive and it would have been possible to use more elaborate and complex versions of linear models than those evaluated here, to make patterns more obvious and to reduce residual variation. For example, analyses using categorical predictors could have involved specific contrasts or included additional covariables to improve statistical power, while analyses of continuous predictors could have involved polynomial expansions (e.g., Rosenthal and Rosnow 1985, Legendre and Legendre 1998, Quinn and Keough 2002). This was, however, not attempted here because it would have made comparisons among approaches less straightforward and detracted focus from general issues by emphasizing those to do with characteristics of this particularly system. Nevertheless, the differences between the results of the two methods for analysis highlight how the choice of technique may influence the outcome of a single experiment and ultimately general models of exposure.

Apart from potential problems with operationalization and inconsistencies among techniques for analysis, any failure to make accurate, general predictions about effects of different types of environmental factors may obviously also be caused by an actual lack of consistent effects. Evidence of how effects of ecological processes are modified by other known or unknown processes are abundant in general as well as in marine ecological literature (e.g., Dayton 1984, Underwood 1985, Wootton 1994, Morin 1995, Leonard 2000). Identification of regularities and generally applicable laws in this complexity represents one of the greatest and most fundamental challenges in ecological science (e.g., Peters 1991, Lawton 1999, Colyvan and Ginzburg 2003, Hansson 2003). Unambiguous definitions of central concepts, formulation of logical hypotheses, and appropriate procedures for statistical testing are essential components in this context.

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