Algal species diversity and dominance along gradients of stress and disturbance in marine environments

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Abstract

Data on algal species diversity from six areas along the Swedish coast, differing in salinity, length of growth period and grazing pressure were used to test two main predictions arising from the hump-backed model of species diversity (Grime 1973; Connell & Slatyer 1977; Tilman 1982; Fuentes & Jaksic 1988).

Total number of species per m², total biomass per m² and primary production values for each species were calculated for 175 samples. Wave exposure was used as a measure of disturbance. The results are discussed in relation to stress (salinity and light) and disturbance factors (wave effects, ice scouring and grazing).

A hump-backed model of species diversity, in relation to biomass per m² was found for all investigated areas. A similar response was also observed along local exposure gradients, with higher biomass and lower species numbers found at the sheltered sites compared to the more exposed ones. The most diverse communities were found at sites with intermediate wave exposure and in communities composed of species with intermediate primary production.

It is suggested that the frequency of physical disturbance and severeness of stress strongly affects algal diversity and competition by determining the time interval over which successional replacement of species can occur. This lends support to the non-equilibrium view of community structure giving rise to hump-backed species diversity curves.

Introduction

Several theories have been put forward to explain high or low species diversity (see Peet *et al.* 1983, for a botanical review). The importance of intermediate disturbance in maintaining high diversity was first suggested by Paine & Vadas (1969); this theory was later expanded by others (Connell 1978; Huston 1979; Grime 1979). These authors indicated a similar relation between species richness and disturbance, both physical disturbance, e.g. in temperate-zone marine communities (Dayton 1971) and in coral reefs subjected to storm damage (Connell 1978) and biological effects of disturbance on boulder fields (Osman 1977; Sousa 1980).

Coral reef communities have been described as non-equilibrium systems, where competitive ex-

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clusion is prevented by frequent disturbances, as predicted by the intermediate disturbance hypothesis (Connell 1978).

The basic assumption of the non-equilibrium paradigm is that competition for relevant resources such as space, light, nutrients etc. is intense and if competition interactions are allowed to proceed to their conclusion, they will usually result in the elimination of most species and the dominance by one or a few, with an associated reduction on diversity (Paine 1966; Tilman 1982).

A two-slope diversity response to grazing has been discussed by Harper (1969), Zeevalking & Fresco (1977), Grime (1973, 1979) and Naveh & Whittaker (1979) for terrestrial vegetation and by Lubchenco (1978) and Lubchenco & Gaines (1981) for algal communities. A model for herbivore effects on diversity within communities has been put forward by Lubchenco & Gaines (1981), where different grazing intensities produce a similar hump-backed species-richness curve as proposed by Grime (1979) and Tilman (1982).

Fuentes & Jaksic (1988) proposed that the hump-backed species diversity curve can be found only if three conditions are met: 1) that there is frequent and substantial release of resources; 2) that propagules originating from a large species pool are readily available for colonization of the resources released; and 3) that there is a strong interspecific competition between colonizers leading to rapid competitive exclusion of most colonies.

Two main predictions which arise from the hump-backed model will be tested in this paper. Firstly, the prediction that communities should remain species-poor in environments subjected to high intensities of stress and/or disturbance and under circumstances where one single species attains dominance. Secondly, species-rich communities ought to be found at intermediate stress and/or disturbance levels (Connell & Slatyer 1977) and should contain a majority of subordinate plants, which are neither capable of surviving in extreme habitats nor potential dominants.

The principal objective of this study was to investigate the effects of disturbance on algal species diversity along the Swedish coast and to test the hump-backed model together with Tilman's theory of plant competition for limiting nutrient and light resources (Tilman 1982). Tilman predicted that (1) the addition of nutrient resources would lead to decreased diversity, and (2) growth rate differences could be the major cause of changes in species number in a community, and (3) that species richness curves ought to have a maximum at intermediate resource conditions.

Study area

The gradient of decreasing algal species diversity from the Swedish coast of the North Sea into the innermost part of the Baltic was chosen as the object of study. Data from 6 areas (Fig. 1) along this salinity/stress gradient were used. A brief description of each locality is given below.
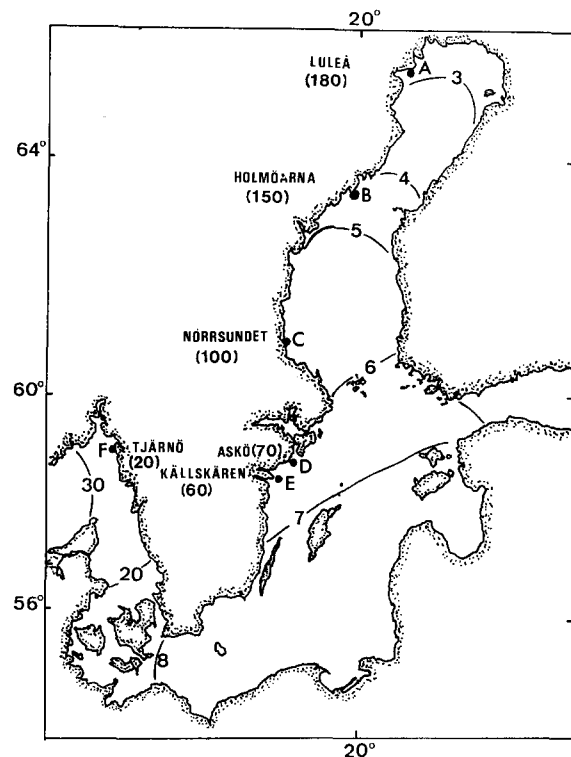

Fig. 1. Map of the investigated areas. Surface water isolines of salinity are indicated. Mean number of days with ice cover in brackets below the name of the area.

Area A

The Luleå archipelago, in the northern Bothnian Bay, is a very species-poor and fairly sheltered area. Samples from a depth of 0–0.5 m, where boulders are common, were dominated by two *Cladophora* species. The salinity is very low (0–3‰ S), which is partly due to the freshwater outflow from the Lule Älv River. The area is covered with ice for more than half of the year resulting in a short growth period. Data from Kautsky *et al.* (1981) are used for the present study.

Area B

The Islands of Holmö, on the sill between the Bothnian Bay and the Bothnian Sea, form an area with very mixed bottom types including rock, boulders and gravel, and with salinities varying from 3.5–4.5‰ S. In this area ice scouring may be severe during winter and spring. Data from Kautsky (1983) are used in this study.

Area C

The innermost shallow stations in the area outside the Norrsundet in the southern Bothnian Sea are influenced by effluents from a pulp mill and very few species are found. Salinity is around 5.1‰ S, but can occasionally be about 4‰ S at the innermost two stations included in this investigation. For this area data from Kautsky *et al.* (1989) are used.

Area D

In the archipelago of Askö, in the northern Baltic Sea proper, a great variety of both substrate and degree of wave exposure may be found. Surface salinity in the area is around 6.7‰ S but may occasionally be much lower due to outflow of freshwater or melting snow in shallow bays during spring. The bays are usually covered with ice for about three months and ice scouring affects the upper shores in winter. Data for the Askö archipelago from Jansson & Kautsky (1977) are used. Part of the material is original unpublished material.

Area E

The skerries of Källskären, just south of the Askö area, represent the outermost, extremely wave-exposed area in the northern Baltic Sea proper. This area has a salinity similar to the archipelago of Askö. Exposure effects are noticeable down to 3 m depth. Few species per m² are found, with a maximum at 1–4 m depth where there is a markedly patchy distribution caused by severe wave exposure. For this area data from Kautsky *et al.* (1983) are used.

Area F

The Tjärnö archipelago, is the only location from the Swedish North Sea coast included in this study. Species-rich marine algal communities from both sheltered and exposed stations were studied. The salinity in the area varies from about 17‰ to 32‰ S. The data used for this area represent original unpublished material sampled in the same way as in the other areas.

The tidal range in most of the Baltic Sea is negligible and about 0.2 m at the Swedish North Sea coast. However, meteorologically induced fluctuations in mean water level can deviate widely from the mean (over 1 m) over several weeks. Long periods of low water level generally occur in spring and of high water level in autumn.

Water level fluctuations, together with ice scouring in winter, are the main factors structuring the shallow communities. The Bothnian Bay is normally covered with ice for 180 days/yr, the Baltic Sea proper for 60 to 70 days/yr and the Swedish North Sea coast for only 20 days (Fig. 1). This directly influences the length of the growth period and the probability of ice abrasion.

Material and methods

The number of algal species in a sample of a given size, i.e. species density was used as a measure of diversity (Hurlbert 1971; Grime 1979). Disturbance (sensu Grime 1979), will refer to factors such as ice scouring, wave action, and grazing, which limit plant biomass by causing its partial or total destruction, while stress is used collectively for those external factors which limit the rate of dry-matter production by algae (i.e. light, nutrients etc.).

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Calculated biomass data per m² together with number of species per m² from the 6 localities described above with a total of 175 samples along the Swedish coast were used. Values of primary production for each species were compiled from the literature (Wallentinus 1979 and literature cited therein) and used together with actual species numbers per m² to calculate the mean primary production ability given as mg $C \cdot g$ dry wt$^{-1} \cdot h^{-1}$, for each sample.

Wave exposure was used as a measure of disturbance. An exposure index derived from the effective fetch (Håkanson 1981) and the sampling depth was used to calculate the degree of wave exposure at each sampling point. The reduction with depth of exposure, i.e. disturbance, was calculated according to the formula $E_z = E_0 \, e^{-z}$ where E_0 is the exposure at the surface and z is the depth in m and e is the basis of natural logarithm.

Results

In Fig. 2 clear decreases (except for Station E, which had a comparatively low total number of species per m²), both in total number of species and total biomass, were observed for the stretches between the Koster archipelago, area F (Fig. 2F), Area D (Fig. 2D), and up to the Luleå archipelago area A (Fig. 2A). Both effects are interpreted as due to increasing stress through decreasing salinity from the Swedish west Coast following the coast from south to north in the Baltic Sea. The low total number of species at station E was due to the extremely high exposure in this area. Only a suggestive line is drawn indicating the highest number of species for each biomass value. Values below this line, are interpreted as indicating communities which have not reached optimal species diversity or biomass for that particular site. The maximum species diversity found at intermediate biomass value sites can also be interpreted as being due to interactions between stress and disturbance, which would lower the number of species on the one hand and increase the dominance on the other. As can be seen in Fig. 2, the species diversity maximum shifts towards lower
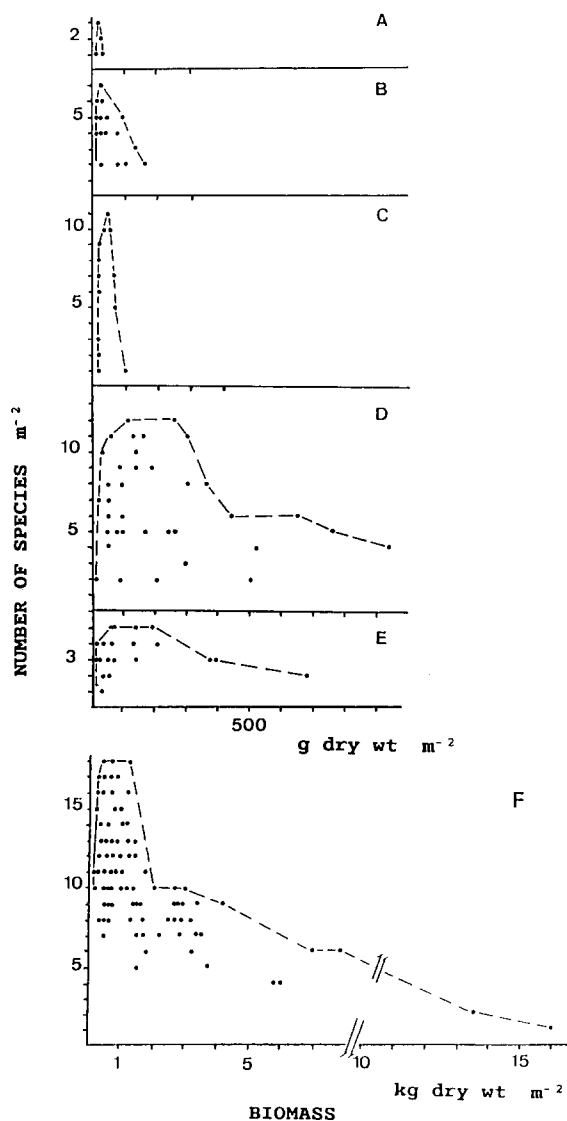

Fig. 2. Relationship between algal biomass and number of algal species in the areas of Luleå = A, Holmöarna = B, Norrsundet = C, Askö = D, Källskären = E, Tjärnö = F (cf. Fig. 1).

biomass values with increasing salinity stress. Together with salinity changes, the length of the growing season decreases as well, which will accentuate the stress gradient.

In all algal communities, species number per m² declined at both low and high biomass per m², with a specific corridor of diversity for each area. Al-Mufti et al. (1977) presented a biomass corridor of diversity for terrestrial vegetation (350–750 g/m²) and Day et al. (1988) reported
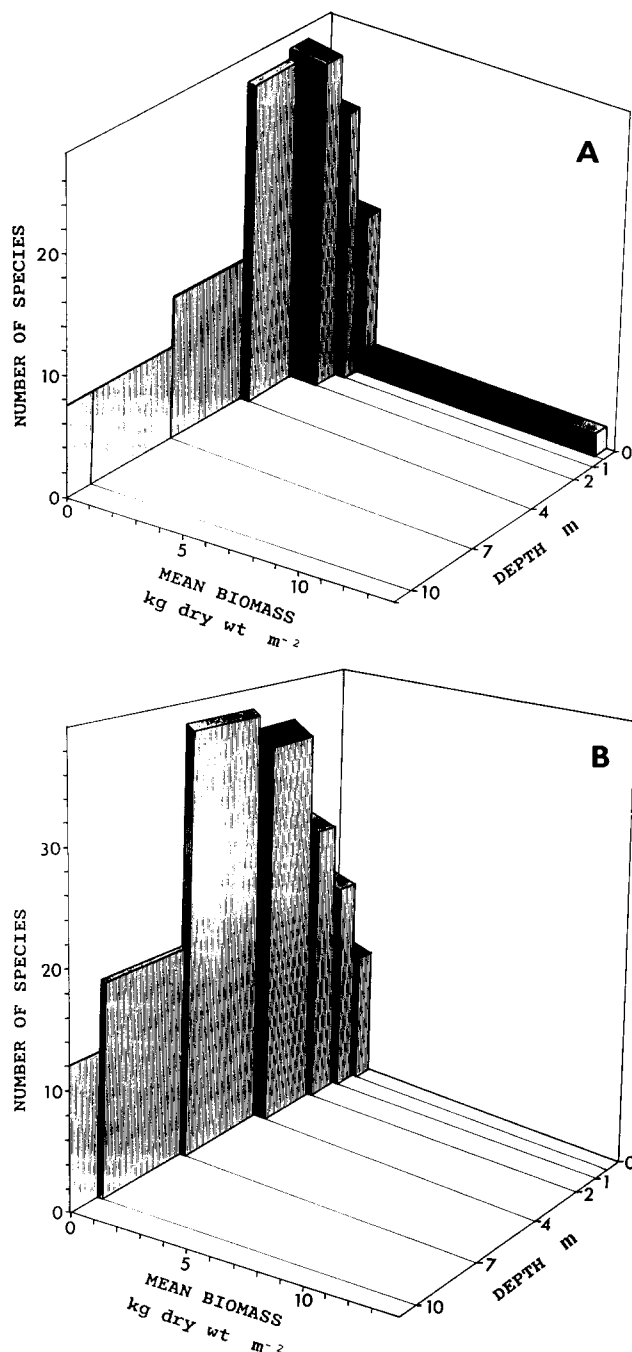
Fig. 3. A and B. Distribution of mean algal biomass m^{-2} and total species number m^{-2} in different depth intervals at a wave sheltered station (A) and an exposed station (B) from area F at the west coast of Sweden.

values well below this for riverine marsh vegetation. In this study, both much higher biomasses per m^2 were found at the Swedish North Sea
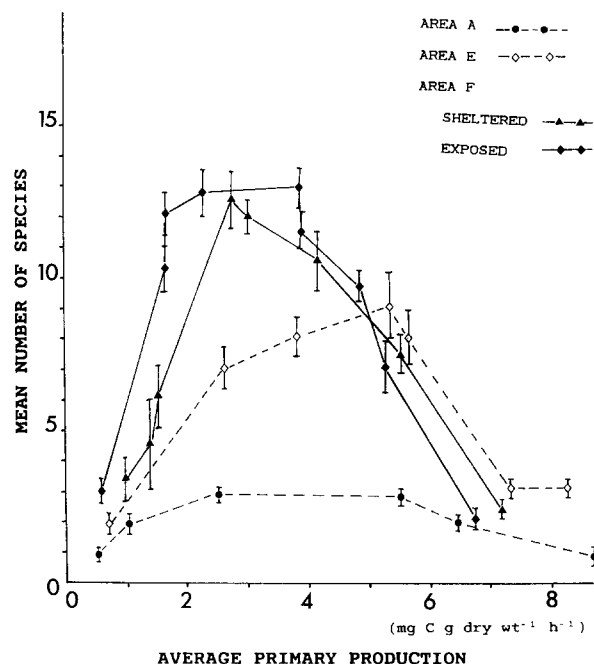

Fig. 4. Mean number of species and average primary production ability of the species calculated for different depth intervals in area A and E and for one sheltered and one exposed station in area F.

coast (500–1500 g dry wt · m^2) and much lower ones at the stations in the Bothnian Bay.

In Fig. 3 the total number of species and mean biomass values for area F are plotted for different depth intervals at two stations. At station A (Fig. 3A), the most sheltered site, biomass values are higher close to the surface as compared with the exposed station B (Fig. 3B). On the other hand the total number of species at intermediate biomass value sites is higher at the exposed station B, which results in a pattern of low species diversity near the surface and a maximum at intermediate depths.

Maximum species diversity was found in communities with intermediate primary production ability (Fig. 4). Lower diversity was found in communities composed of species with both low and high average primary production ability. These tendencies are even clearer at the species-rich Swedish North Sea coast (area F, station A and B and area E, respectively), than in the species-poor Bothnian Bay (area A). Maximum species diversity decreases in the communities with higher
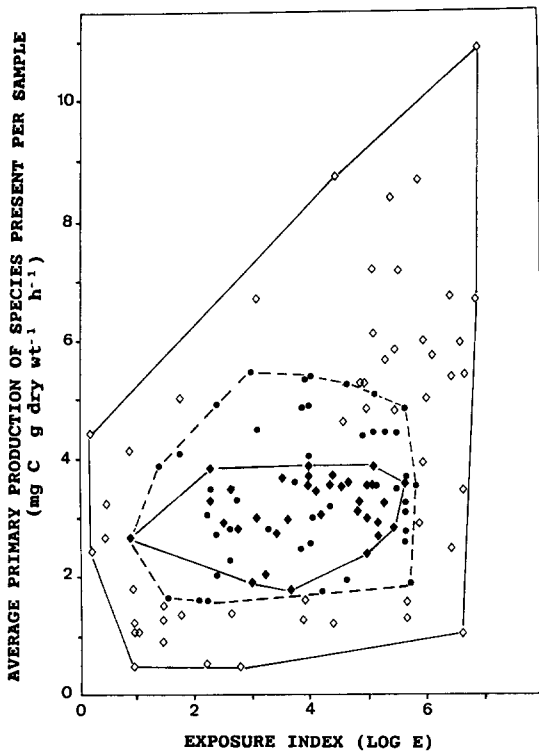
Fig. 5. Average primary production ability of species m^{-2} for all the samples from different areas plotted against degree of exposure. Species diversity is represented by contour lines. $\diamondsuit$ = 1–5 species, $\bullet$ = 6–10 species and $\blacklozenge$ = 11 or more species m^{-2}.

average production ability further north in the Baltic Sea.

In Fig. 5 the average primary production ability of algal species for all studied areas is plotted against the degree of exposure and with species diversity represented by contour lines. The most diverse communities were found at intermediate exposure sites between 5.4 and 1.5 log E, and with algal communities composed of species with intermediate primary production abilities i.e. between 1.2 and 4.5 mg $C \cdot g$ dry $wt^{-1} \cdot h^{-1}$. Most of the species-rich samples are concentrated in the middle range of both exposure and average primary production ability.

Discussion

The results suggest a non-equilibrium view of community structure (Paine 1966; Pickett 1980;

Agubov 1982), with maximum algal species diversity at intermediate exposure and in communities composed of species with intermediate primary production abilities. Thus the frequency of physical disturbance and amount of stress strongly affects algal diversity and competition by determining the time interval over which successional species replacement can occur. Similar results have been reported for shoreline vegetation with maximum species richness at intermediate levels of exposure (Keddy 1983).

The two main stress factors in the investigated algal communities are light and salinity, respectively. Light reduces production and sets the limit of algal growth at about 30 m depth at the Swedish North Sea coast and at ca 25 m depth in clear areas of the Baltic Sea. Salinity, on the other hand, influences the number of marine species able to colonize the Baltic Sea which results in a continuously decreasing number of species from the North Sea into the innermost parts of the Baltic Sea.

Abiotic disturbance events affecting algal communities are of two main types, (1) continual (e.g. wave slash and sedimentation) and (2) periodic e.g. ice scouring as stressed by Wethey (1985) and water level changes. These disturbance factors are most frequent and intense near the surface and decrease with depth. On the other hand, sedimentation has its main influence at sheltered sites and at greater depths.

In the Baltic Sea physical disturbance factors play a major role in structuring communities, both locally and regionally. On the Swedish North Sea coast the role of biotic interactions increases, and species competition and grazing are more important.

Hard-bottom algal communities are influenced by a variety of physical and biological processes each of which may have diverging effects on species diversity. The observed pattern of low diversity near the surface and maximum species diversity at intermediate depths, (Fig. 3) cannot be explained by one (simple) physical gradient but is rather a result of a complex combination of both abiotic and biotic factors.

In sheltered areas, high growth rates of algae in

shallow waters may lead to intense competition for space and reduced species diversity. In the central part of the zone reduced competition for space from fast-growing species under low-light conditions apparently allows the survival of slow-growing, stress-tolerant species that are unable to compete successfully in the low productive environment. In the upper part of the zone, the disturbance-tolerant species (ruderals) dominate, but stress-tolerant species are also a significant component of the community. A high rate of disturbance may, at the same time, reduce competitive species, preventing them from becoming dominant in the upper part of the zonation. As pointed out for shoreline vegetation by Wilson & Keddy (1986) there may be morphological explanations for disturbance in the selective removal of competitive algal dominants with a tall and flattened thallus. Conversely, the morphology types most resistant to wave damage, i.e. those of small size, with finely branched or crust-formed thallus, may be weak competitors since they are unable to shade larger species.

The importance of periodic mortality (as induced by disturbance) in preventing competitive dominance and thus maintaining high species diversity was stressed by Connell (1978). Factors that slow down the process of competitive exclusion, e.g. a higher degree of exposure such as in area A (Fig. 2) will result in highly diversified communities. Rapid growth rates, on the other hand, may speed up the process and thus the highest diversity is expected at intermediate to low growth rates which are still adequate to allow survival.

In the Baltic Sea, reduced competition for space between macroalgae enlarges their niches (Waern 1952; H. Kautsky in mscr.) as compared to true marine environments. On the other hand, dominance is attained by plants with predominantly stress-tolerant, biomass-storing traits (L. Kautsky 1988), through their capacity to utilize and retain resources and by shading other species. Canopy-forming species such as *Fucus* spp. and *Ascophyllum nodosum* often achieve complete dominance of the zone they occupy by their ability to elongate and concentrate biomass at the surface. Similar observations have also been made for many submersed aquatic phanerogams (Barko & Smart 1981). For the intertidal, Jernakoff (1985) reported that an absence of grazers initially led to an increase in the mean number of algal species when propagules recruited, which then declined, probably because the ulvoids overgrew and excluded other algae. Similar phenomena have been reported elsewhere by Paine & Vadas (1969), Dayton (1975), Lubchenco (1978), Lubchenco & Menge (1978), Sousa (1979, 1980) and Duggins (1980).

In the Baltic Sea the disturbance caused by grazers on macroalgae is generally low compared to marine environments, due to the low diversity of macrograzers such as marine molluscs and the absence of sea urchins.

Evidence from several studies of natural communities supports a non-equilibrium view of community structure giving rise to hump-backed species richness curves (Dayton 1971, 1975; Connell 1978; Sousa 1980; Paine & Levin 1981; Davis & Wilce 1987; Day et al. 1988). In agreement with these studies, the results presented here suggest that high diversity is maintained as predicted by the intermediate disturbance hypothesis, at intermediate wave exposure and in algal communities composed of species with intermediate primary production abilities.

All three important conditions required for the occurrence of the hump-backed species diversity curve (Fuentes & Jaksic 1988) were found in the investigated areas. First, a strong disturbance agent, i.e. wave and ice erosion, which is capable of frequent and substantial reduction of abundant species in the upper part of the zonation. Second, a rich pool of propagules of opportunistic species, readily available for colonization and use of the new space. Finally, strong competition between colonizing species, leading to a relatively quick competitive exclusion of some of the species. Along the studied salinity gradient all three of these factors are thought to influence species diversity and create different hump-backed species diversity curves depending on physical and biological structuring factors at each site. Thus it is suggested that the relationship between

species diversity and biomass varies from area to area creating a family of hump-backed curves of similar form. This emphasizes the broad generality of this conceptual model for both terrestrial and aquatic plant community ecology.

Acknowledgements

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