Akademisk avhandling för Filosofie Doktorsexamen
Thesis for the degree of Doctor of Philosophy

Ecological disturbances:

The Good, the Bad and the Ugly

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Avhandlingen kommer att försvaras offentligt fredagen den 19 november 2010 kl 15.00, på institutionen för Marin ekologi, i lokalerna på stationen som helt oavsett namn ligger på Hättebäcksvägen, Tjärnö, Strömstad. Opponent är Professor Helmut Hillebrand från Institutionen för Marin kemi och biologi, Carl von Ossietzky Universitet, Tyskland.

The oral defence of this thesis will take place at 15.00 on Friday November 19th 2010 at the Department of Marine ecology, at the facilities of the laboratory on Tjärnö, Strömstad. The opponent is Professor Helmut Hillebrand from Institute for Chemistry and Biology of the Marine Environment, Carl von Ossietzky University, Germany.

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Abstract. This thesis focuses on the definitions, characterizations and quantifications of ecological disturbances, as well as hypotheses on their impacts on biological communities. The most prominent model on effects of disturbance on diversity is the Intermediate Disturbance Hypothesis (IDH), which is utilized in management of national reserves, has received over 3300 citations and has been corroborated by a multitude of studies from terrestrial and aquatic systems. According to the predictions of the IDH, diversity is high at intermediate levels of disturbance due to coexistence of competitors and colonizers. At low levels of disturbance diversity will be low due to competitive exclusion and few species can persist at high levels of disturbance. In an extension of the IDH, the Dynamic Equilibrium Model (DEM) predicts that the effects of disturbance depend on the productivity of communities, because at high growth rates a stronger disturbance is required to counteract increased rates of competitive exclusion. The IDH and the DEM were tested in a field experiment on effects of physical disturbance (scraping) and productivity (nutrient availability) on hard-substratum assemblages in paper **I**, where the patterns predicted by the IDH, but not the DEM, were observed. This outcome shows the importance of the nature of productivity alterations, as the productivity treatment had a general positive effect on growth rates but only marginal effects on the dominant species, thereby leaving rates of competitive exclusion unaffected.

In paper **II** I tested another extension of the IDH, which predicts that smaller, more frequent disturbances will have different effects on diversity compared to larger, less frequent disturbances. In this experiment I used two different regimes of disturbance, small and frequent vs. large and infrequent disturbances, while the overall rate (the product of area and frequency) was kept equal for both regimes. At the site where the IDH was supported, the regime with a large proportion of the area disturbed infrequently showed higher richness, due to a stronger decrease of dominants, compared to the regime with a small proportion disturbed frequently. In addition to these significant differences in diversity effects between different disturbance regimes, it may also matter what agent of disturbance that is causing the damage. In paper **III** I contrasted the effects of a physical disturbance (wave-action) to that of a biological disturbance (grazing), as well as their respective interactions with productivity in a multifactorial design tested on natural epilithic assemblages. The composition of assemblages and the total species richness was significantly affected by physical disturbance and interactively by biological disturbance and productivity. The algal richness was significantly affected by productivity and biological disturbance, whereas the invertebrate richness was affected by physical disturbance. The results show, for the first time, that biological disturbance and physical disturbance interact differently with productivity due to differences in the distribution and selectivity among disturbances.

In paper **IV** I investigate how the choice of diversity measure may impact the outcomes of tests of the IDH, which, surprisingly, has not previously been discussed. This was done by an extensive literature review and meta-analysis on published papers as well as by two different approaches to mathematical modelling. Both models support the IDH when biodiversity is measured as species richness, but not evenness. The meta-analysis showed that two-thirds of the published studies in the survey present different results for different diversity measures. Hence, the choice of diversity measure is vital for the outcome of tests of the IDH and related models.

Key words: competitive exclusion; DEM; disturbance; diversity; evenness; IDH; marine assemblages; productivity; rate of disturbance; regime; species richness; Tjärnö, Sweden.