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THE IMPACT OF WAVES ON THE DISTRIBUTION OF SUBMERGED MACROPHYTES IN KALVÖFJORD, SWEDEN – A STUDY OF "COMFORT ZONES"

Vindvågors Betydelse för Distributionen av Makrofyter i Kalvöfjorden, – En Studie av »Komfortzoner»

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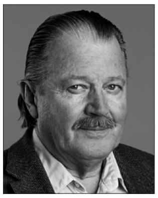

Abstract

A study of a shallow bay (Kalvöfjord) on the west coast of Sweden was conducted to determine the potential for wind waves to control the distribution of submerged macrophytes. A wave model was implemented, calculating the drag force exerted by the wave orbital motion. A new concept of "comfort zones" was introduced, ascribing an interval of survival to a certain species under the influence of a certain physical variable. A brief study of drought risk was also included. The model results showed that the Kalvöfjord most often is subject to low stresses, but with occasional intensifications associated with significant drag upon macrophytes. The observed zonation in the bay largely coincided with the different levels of stress, where *Zostera marina* was confined to parts with the lowest stresses, and without risk of drought (depth ≥ 1.2 m), whereas the fucoid algae were found exclusively in areas of moderate stress, although not shallower than circa 0.5 m. The locations of fucoid algae suggested that they inhabit an interval of drag stress, which is consistent with their requirement of some water movement to receive nutrients – at the same time having a structure vulnerable to drag. *Ruppia maritima* was found to be very resilient to both drag and drought, occurring sporadically at depths as shallow as 0.2 m.

Key words – modeling, wave exposure, drag, macrophytes, zonation, zostera marina, fucus, desiccation, comfort zones

Sammanfattning

För att undersöka vindvågors potential att kontrollera distributionen av makrofyter i marina habitat har en studie av den grunda viken Kalvöfjorden vid Sveriges västkust utförts. En vågmodell tillämpades som beräknar »drag force» till följd av vågens orbitalrörelse. Ett nytt koncept kallat »komfortzoner» introducerades, vilket är ett överlevnadsintervall som tillskrivs en specifik art under påverkan av någon specifik fysisk variabel. En översiktlig redogörelse för torrläggningsrisk inkluderades också. Resultatet av modelleringen visade att Kalvöfjorden oftast utsätts för låg vågstress, dock med enstaka intensifieringar associerade med kraftigt förhöjd »drag force» på makrofyter. Zoneringen i viken överensstämde till stor del med de olika nivåerna av stress. *Zostera marina* begränsades till att residera i områdena med lägst stress, samt med liten risk för torrläggning (djup ≥ 1.2 m), medan de fucoida algerna endast återfanns i områden med måttlig stress, dock inte grundare än cirka 0.5 m. De fucoida algernas utbredning indikerade att de lever inom ett intervall av vågstress, vilket är förenligt med deras behov av viss vattenrörelse för att tillgodogöra sig näring, samtidigt som de har en struktur som gör dem känsliga för »drag». *Ruppia maritima* påvisade avsevärd motståndskraft mot både vågstress och torka och förekom sporadiskt i områden så grunda som 0.2 m.

Introduction

This study is meant to demonstrate how wind waves may control the spatial distribution of marine macrophyte habitats in shallow semi-enclosed coastal waters. Here, the concept of "macrophyte" refers to all anchored multicellular organisms that protrude perpendicularly to the bottom, and includes some species of brown algae.

The traditional approach of studying coastal ecosystems is to focus the efforts on biochemical processes, competition and light conditions, and their significance for biological production (see eg. Valiela, 1984). This approach is not exhaustive enough to determine how the distribution and growth impairment of marine species will actually manifest themselves in the field; something which is dependent upon several additional factors. In this study, a modeling effort focusing on wave induced water movement constitutes a complement to the original approach, and a step further towards merging marine ecology with hydro dynamics. In contrast to many previous models which derive empirical statistical measures of physical exposure (see eg. Fonseca and Bell, 1998, Kelly et al., 2001), the current model incorporates a causal physical relationship between wind waves and water movement – hopefully leading to an enhancement in the current understanding of macrophyte extension in the littoral zone.

In addition, a brief study of the occurrence of drought due to low sea level has been included. Since wave exposure is likewise thought to largely coincide with depth, it was felt that the effects of the two would need to be treated separately.

The effort is based on a pilot project area off the west coast of Sweden called Kalvöfjord, which is a semi-enclosed, very shallow bay with only 0.3 m tidal range. This area is highly suitable for the study of wave-macrophyte interaction due to its shallow depth and high correlation between habitat extension and bathymetry, indicating a wave controlled ecological regime. In particular, it is the wave induced drag upon macrophytes that will be qualitatively described and quantified in relative terms by this article, along with the introduction of what could be a novel concept in marine ecosystem modeling – subsequently named the *comfort zone* by the authors. The comfort zone is the range of a specified physical variable in which a certain species of submerged macrophyte can sustain life.

Properties of the study area

At mean sea level, the Kalvöfjord has a horizontal surface area of ca. 12 km^2 and a total volume of roughly 21 680 000 m^3. The mean depth is 1.8 m with only few parts being deeper than 3 m. The deepest parts primarily belong to a narrow trench running north–south

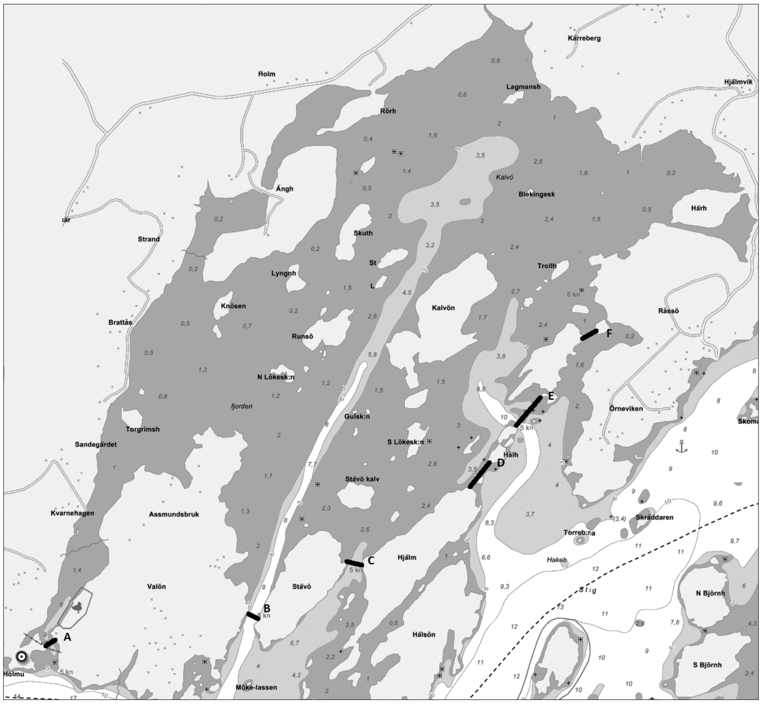

Figure 1. *Sea chart over Kalvöfjord and Stigfjord complete with depth measurements. The connecting straits and islet passages are marked with bars (A–F).*

across the bay, with depths up to 9 m. Kalvöfjord is connected to the larger Stigfjord basin through six narrow straits and islet passages in the southern and south-eastern parts (Figure 1). The combined vertical cross-sectional area of the outlets is ca. 4000 m^2, with about 50 % of the area above 2.5 m depth.

The sea level in Kalvöfjord varies in synchrony with the coastal waters of eastern Skagerrak (Figure 2). This fluctuation drives a barotropic in and out flow through the inlets connecting it to the adjacent Stigfjord basin. The calculated median batropic flow is in the range of +–130 m^3/s. Annual mean river discharge into the Kalvöfjord is modeled as 1.195 m^3/s, and is supplied by the three major rivers in the area; Hagaå, Stranne å, and Kärrebergså. The median residence time of the water in Kalvöfjord is roughly 3.5 days, when calculated based on the barotropic flow and river discharge. This is a conservative measure since it does not include the baroclinically driven exchange. This exchange is roughly +–70 m^3/s, i.e. around half that of the barotropic exchange, although its magnitude remains uncertain as sufficient data over density differences between Kalvöfjord and Stigfjord are lacking. Water exchange has been estimated using simple models in Stigebrandt (2001).

Fluctuations of sea level can have extensive consequences for a shallow region like the Kalvöfjord. When the sea level drops more than 0.2 m below the mean, significant areas of the fjord will drain and become exposed to the atmosphere. The frequency of occurrence and duration of exposure related to different sea levels are shown in Table 1.

An ecological mapping of Kalvöfjord has been carried out by Engström et al. (2012). The effort gives a brief overview of the biodiversity and zonation in the area, and constitutes the foundation for evaluating the present model (see Figure 5a). The shallow bay area is dominated by typical Swedish west coast flora and fauna found in the littoral zone. During the growth season, macro algae mats, micro algae mats and bacterial mats are especially predominant and constitute important ecological regimes. Also sea grass, most notably eelgrass (*Zostera marina*) grows in large meadows mainly distributed throughout the deeper parts of the bay, whereas some *Ruppia* (*Ruppia maritima*) grows in patches at shallower depths. Benthic mats extend throughout the smaller bays and coves and are primarily made up of cyanobacteria and diatom algae, whereas green algae are found in both deep and shallow parts as mats or clusters, or as epiphytes on taller structures. Brown algae (*Fucus vesiculosus*, *Fucus serratus* and *Chorda filum*) are generally found in the moderately shallow parts (0.5–1.5 m) attached to rocks or gravel.

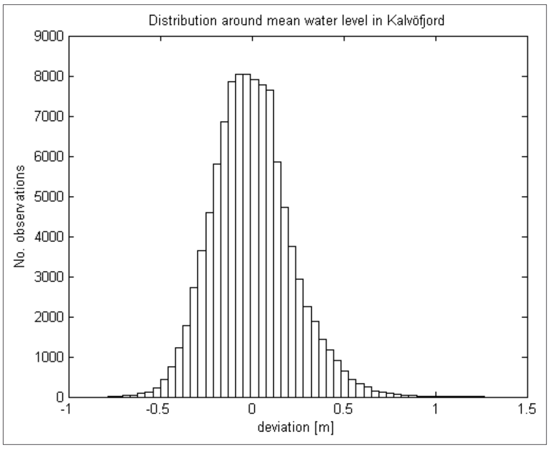

Figure 2. *Distribution of sea level around the mean sea level in Kalvöfjord (data from Smögen).*

Methods

Wave model description

To estimate the extent of benthic water movement caused by waves, a wind-wave model has been implemented. The model that is used was at least partly developed by Dr. Brian Sanderson of Newcastle University, Australia, Sanderson (2009). It is a basic grid model of two dimensional type, with a quadratic geographical

Table 1. *Percentage of exposed bottom (Exposure) at given reduction* Δh *in mean sea level, together with frequency of occurrence of said reduction, and the probability of duration of such an event, compressed to the first three hours along with the maximum duration (hours) from the data period.*

Reduction Δh [m]	Exposure [%]	Frequency [%]	Probability of duration (1,2,3 h) [%]	Maximum duration with probability [%]
≥0.2	≥13	16.6	16.7, 15.5, 13.6	156h = 0.0005
≥0.3	≥13	6.7	21, 18.9, 16	110h = 0.001
≥0.4	≥16	2.1	26.1, 22.2, 17.2	54h = 0.005
≥0.5	≥23	0.5	26.8, 23.3, 17.3	21h = 0.02
≥0.6	≥26	0.1	32.6, 29.2, 18.8	7h = 0.07
≥0.7	≥27	0.02	47, 35.3, 5.9	5h = 5.9

grid oriented north to south. The grid encloses the Kalvöfjord area with data entries represented by the nodes and with a spatial resolution of 48.2 m, resulting in a grid with about 10 000 nodes. The south western corner of the grid is located at latitude 58.09216, longitude 11.56082, and the north eastern corner at latitude 58.13721, longitude 11.65890 (WGS 1984).

The model works with three principal forcing parameters, or boundary conditions, comprised of depth, wind speed and wind direction. The depth is derived from the local bathymetrical mapping combined with progressive sea level data, and constitutes the vertical constraints and horizontal boundaries of the wave field. Evolution of the wave field is based on the theory of Young and Verhagen (1996), discretized to allow for variable depth. This theory derives expressions for total energy and peak frequency of the wave spectrum based on the empirical relationship between wave height and fetch at different wind speeds, measured in a field experiment. At each distance of fetch, the wave spectrum is analyzed for peak frequency, and integrated to derive the total energy. The experiment does not directly measure depth dependence of the wave spectrum, although it is indirectly inferred by noting the transformation of the spectrum as the waves grow larger and transition from short to long waves, thereby interacting increasingly with the sea floor. As a result the peak frequency f_p and total energy E, can both be described as functions of the three parameters; wind speed at 10 m above ground level U_{10}, the available length of fetch x, and the local depth d. The time parameter has been omitted since quasi stationary conditions are assumed. For the explicit expressions of the total enegrgy and peak frequency, see Young and Verhagen (1996).

As the aforementioned theory is discretized, it is only implemented for one grid point distance at a time. In every new spatial step, information from the previous grid point (total energy, peak frequency, depth, and fetch) is retained and combined with the depth and fetch from the next point to calculate the parameter values in that position. This procedure of stepwise interpolation builds up the wave field along wave rays parallel to the wind, accumulating fetch and adapting to variable bathymetry dynamics such as short and long wave transitions and shoaling effects. To deduce the effect of variable bathymetry on total energy, an energy conservation principle is applied where the energy flux (wave group velocity multiplied with total energy) is conserved. Thus, variations in total energy can, in addition to wind speed, only be affected by variations in group velocity resulting from variable bathymetry.

From the total wave energy, the significant wave height H_s can be derived

$$H_s = 4\sqrt{E} \text{ [m]} \tag{1}$$

The waves however, might become unstable and break as their wave height increase, thus losing energy mainly by dissipation. Breaking also marks the point where no further wind energy can be converted into wave energy, a condition known as "fully developed sea." A depth limited wave height criterion is put as a constraint on the significant wave height to represent this effect. The criterion is called the Miche criterion after Miche (1951) who empirically derived an expression for maximum wave height as a function of wave length and local depth. Battjes and Janssen (1978) determine the percentage of breaking waves at a given point by using the cumulative distribution function of wind wave heights, truncated at the depth limited wave height. They also give an expression for the associated dissipation, which is directly proportional to the percentage of breaking waves.

From the derived significant wave height, the horizontal orbital velocity,u, can be calculated.

$$u = \pi H_s / T\sinh(kz) \text{ [ms}^{-1}\text{]} \tag{2}$$

Where H_s is significant wave height, T is wave period, k is wave number (2π/L), L is wave length and z is depth. The orbital velocity is the velocity of water particles due to the wave motion. For short waves, water particles have a circular motion and the horizontal and vertical components are equally large and only phase shifted by 90°, whereas in the transition towards long waves, vertical motion is suppressed and the orbits become increasingly flattened, to only oscillate in the horizontal direction under pure long wave conditions. The magnitude of the orbital motion at the sea bed (z = d) can be obtained from Eq. (2). It is referred to as the maximum orbital velocity (MOV), since it is the highest orbital velocity reached at the bottom by any wave, long or short. The flow of water in the orbital wave motion will exert drag upon the submerged macrophytes. The major drag will be of two different types, pressure drag relating to body shape and area, and skin friction drag relating to surface area and surface roughness (Schutten et al., 2004). Together they represent the total drag, but combining them would require quantifying their relative importance which in turn requires specific knowledge about the size, shape, flexibility and surface characteristics of the treated organisms – parameters that are currently lacking. Therefore, this effort is content with using the potential for pressure drag as sole indicator of stress, as this type of drag is usually the dominating force upon protruding structures at current velocities higher than ca. 0.1 m/s (p. 97, Vogel, 1994).

The drag force, F, from pressure drag Eq. (3) scales as the MOV to the power of 2 multiplied with an area, A, usually defined as the maximum cross-sectional area presented by the body perpendicular to the line of flow. ρ is the density of the fluid (sea water) u is the MOV. C_D is the "drag coefficient" which is primarily dependent upon the streamlining of the submerged body, and secondarily is a function of the Reynolds number.

$$F = \tfrac{1}{2}\rho A u(z)^2 C_D \ [\mathrm{kgms^{-2}}] \qquad (3)$$

The potential for experiencing drag forces is simply taken as the MOV at the seabed (z = d) raised to the power of 2. All other parameters are aggregated into unity, and Reynolds number dependence of the drag coefficient is ignored. The highest calculated value of drag potential in each drag potential matrix will be referred to as the maximum drag potential (MDP). The model source code is available from the authors upon request.

Comfort zones

Conditions that allow for macorphytes to sustain life range over several different variables as mentioned in the introductory chapter. Such variables may include temperature, salinity, density, stratification, sea level (drainage), sediment composition, sediment cohesion, grazing, sea ice, wave currents and other currents. Each variable defines a habitable interval, or what may be termed a "comfort zone" for a given marine species but need not be independent, e.g. as with light intensity and water depth. The comfort zone is in other words a characteristic determined by the organism's capacity and approach in adapting to the physical environment.

In shallow areas where wind induced waves may propagate to interact with the bottom, a comfort zone of wave exposure is established for submerged macrophytes. In this type of comfort zone, the lower limit is marked by atrophy or suspended growth, whereas the upper limit is marked by a stressed and deleterious state. Starvation and atrophy occur as effects of vanishing nutrient diffusion when water movement becomes too low to replenish the diffusive boundary layer. This is an important factor for species absorbing nutrients directly from the water column such as brown algae. For sea grasses on the other hand, nutrients are primarily extracted from the sediment which will act as a buffer, making temporary stagnation less important.

The deleterious state is wholly related to mechanical damage resulting from wave induced forces. Schutten et al. (2005) has made an attempt to quantify what may be interpreted as this upper limit of the comfort zone. The report presents theoretically derived skin friction drag forces resulting from orbital wave motion acting on different species of macrophytes, put in relation to experimental data. The maximum resilience to drag is also a function of sediment cohesion and type of anchorage. Values of these characteristics are lacking for the species and sediment in Kalvöfjord, however each species is expected to receive its own interval and description – especially the algae that are pelagic feeders should have a clearly defined lower boundary.

A relative relationship of exposure to skin friction drag force can be established among the macrophytes in Kalvöfjord by ascribing properties of a similar type of macrophyte structure found in Schutten et al. (2005). The five types of anchored macrophytes in the fjord consist of *Zostera marina*, *Ruppia maritima*, *Fucus vesiculosus*, *Fucus serratus* and *Chorda filum*, depicted together in Figure 3.

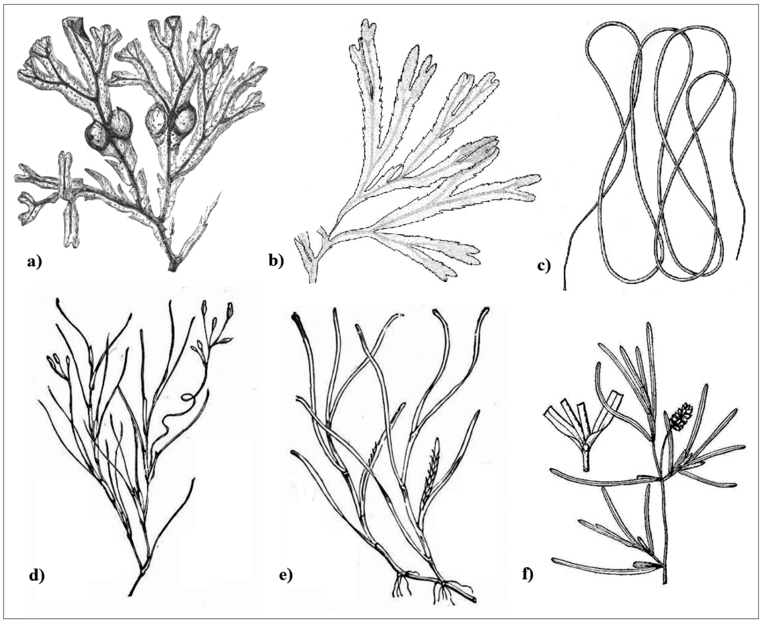

Figure 3. *A depiction of the species encountered in the Kalvöfjord (a–e) together with a species from Schutten et al. (2005) (f).* a) *Fucus vesiculosus*, b) *Fucus serratus*, c) *Chorda filum*, d) *Ruppia maritima*, e) *Zostera marina*, f) *Potamogeton obtusifolius.*

Of these, there exist reasonable approximations for *Zostera marina*, *Ruppia maritima*, *Fucus serratus* and *Fucus vesiculosus*, all three being somewhat well represented by *Potamogeton obtusifolius* (see Figure 3). This type of structure gives rise to a relatively high degree of skin friction drag as compared to less spreading types of marine vegetation, due to additional surface area (Schutten et al. 2005).

To represent the boundaries of the wave induced comfort zone, the 5th and 95th percentiles of the modeled drag potential have been extracted from the dataset, and the mean drag potential has been calculated as a reference. Neither boundary has been quantified, although the drag potential will be compared to the ecological mapping to reveal possible interdependence for each of the different species.

Drought resulting from low sea level establishes yet another comfort zone, wherein the habitat extension in theory should run parallel to the depth contours. Bottoms frequently exposed to the atmosphere will tend to lack drought sensitive species.

Forcing data

Forcing data is gathered from two different locations on the Swedish west coast. These locations have been chosen so as to be the most representative for the Kalvöfjord area among the ones available. Sea level data originates from Smögen, situated ca. 35km North West of Kalvöfjord, where sea level is assumed to be quite similar to that in the bay. Data is measured at hourly intervals starting at 00:00 and is provided by SMHI (Swedish Meteorological and Hydrological Institute) who also provide hourly wind speed and direction data from the station Måseskär situated some 16km west of Kalvöfjord at 10m above ground.

In combination, the two data sets give the model maximum temporal resolution of one hour. The available data set stretches from 2000 to 2011.

River runoff is provided by the SMHI models PULS and HYPE, which calculate weekly or monthly mean discharge from the streams Hagaå (PULS and HYPE), Stranne å and Kärrebergså (HYPE). Data from PULS starts at 1981 and proceeds until 2009, and data from HYPE starts 1990 and proceeds until 2010.

Bathymetry from the Kalvöfjord has been digitized manually from a sea chart produced by the Swedish maritime administration. The digitization was carried out by projecting a northerly oriented rectilinear quadratic grid with 48.2 m resolution onto the fjord area and subsequently reading and recording the depth in each grid intersection. The result is a depth matrix with 92x126 elements.

Results

Drag potential and habitat extension

The model run was executed over the years 2000–2011, with wind speed and sea level input four times a day to reduce computational time. The results are illustrated below in the form of a temporal distribution of maximum drag potential (MDP) (Figure 4) along with the drag potential matrix of the 95th percentile (Figure 5b).

The calculated drag potential is heavily concentrated towards lower values, meaning that most of the time, the area experiences low or no wave induced stress. The average MDP is 0.036 m^2s^{-2}, whereas the 5th percentile has a MDP of 0.00073 m^2s^{-2}, i.e. 1.9 % of the mean. The 95th percentile has a MDP of 0.18 m^2s^{-2}, which is circa 5 times larger than the mean, and 17 % of the size of the all-time high, which is 1.10 m^2s^{-2}. The wide spectrum concentrated on lower values supports the hypothesis that there exists an important stagnation regime, along with occasional but significant population decimations defining the habitat borders as the upper boundary is supposedly surpassed.

The general pattern of the 95th percentile drag potential coincides to a high degree with the bathymetry of the bay (see Figure 1). As the area is dominated by westerly winds, high drag potential is generally found in shallow water at west facing shores, as the energy builds up with available fetch.

Based on general structural shape and feeding mechanism, there can be distinctions made among the five macrophyte species included in the study – dividing them into three different classes. An additional fourth class is also included to represent the widespread presence of benthic cyano and diatom mats. A comparison

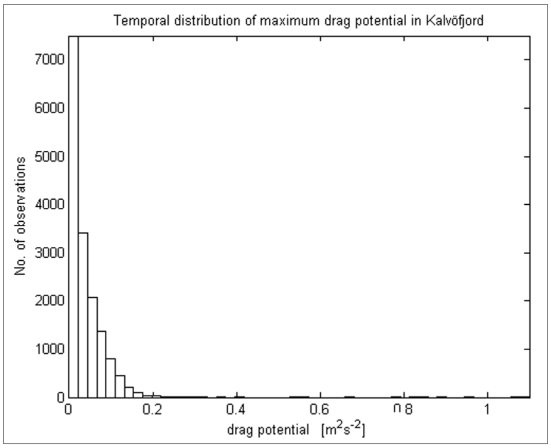

Figure 4. *Temporal distribution of modeled maximum drag potential (MDP) in Kalvöfjord.*

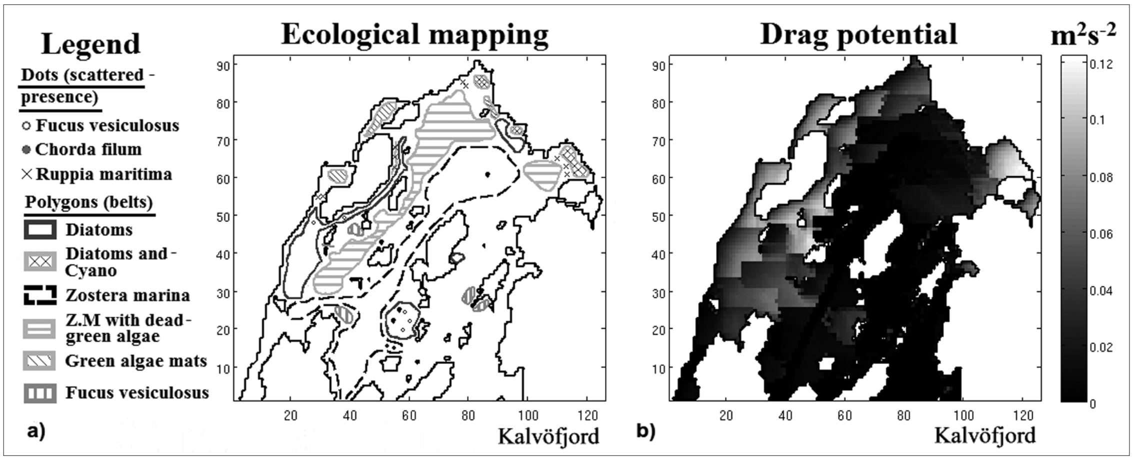

Figure 5. *Comparison between ecological mapping (a) and the 95th percentile of the modeled drag potential (b), in Kalvöfjord.*

between habitat extension and drag potential for the different classes is made below. Spatial reference to macrophyte occurrence within the matrices of Figure 5, is made by reading the matrix coordinates (x,y).

Spreading fucus (*Fucus vesiculosus*, *Fucus serratus*)

Spreading fucus is the only category of macrophytes found where the drag potential is elevated but not high. They are typically found at depths of 0.5–0.8 m, and never at low potentials. This is probably because of their nutrient uptake requirements which necessitates ample water movement. This would explain why the shallow (0.5 m) but relatively calm area at coordinates (25,45) in Fig 5 does not have any *Fucus*. At the same time, spreading fucus cannot withstand the higher stresses associated with most of the shallowest areas and must decrease their risk of demise by drag by inhabiting an appropriate interval. The depth interval is probably not an additional response to the risk of drought, as *Fucus* is fairly well adapted to dehydration (Schonbeck and Norton 1979 (II)). It can be assumed that spreading fucus would have inhabited the shallower plains, would there have been somewhat lower stresses together with suitable sediment. The limit in terms of drag potential seems to lie above the point of 0.02 m^2s^{-2} but below the point of 0.09 m^2s^{-2} in the 95th percentile map.

Sea grass (*Ruppia maritima*, *Zostera marina*)

The species included in this category differ significantly in their resilience to all types of treated stresses. The eelgrass is not found at depths shallower than ca. 1.2 m, and always below drag potentials of 0.05 m^2s^{-2}. The distribution is such that neither stress nor drought are high risk factors, and no lower boundary of the wave-related comfort zone can be recognized. Indeed, eelgrass inhabits the most tranquil areas of the Kalvöfjord. *Ruppia* on the other hand is readily found in areas as shallow as 0.2 m, even when exposed to high degrees of stress such as at coordinates (115,65) (Figure 5b). It is however not found in the deeper parts and seems to occur sporadically rather than in meadows. It is hard to establish its upper limits without more detailed information about the one site where it coincides with high stresses, but the limit should be well above 0.09 m^2s^{-2}. A lower limit is likewise hard to establish, although its absence from deeper parts is probably not an effect of starvation risk due to its nourishment from the sediment, but rather an effect of high light requirements.

A possible cause for the observed differences in drag resilience between the two species is the root anchorage strength in relation to macrophyte surface area. *Ruppia* has a leaner structure with smaller surface area compared to eelgrass – it is also shorter and thus inherently less exposed to drag. With a similar strength of anchorage, *Ruppia* would all in all be more adapted to withstand high drag potential. In addition, its resilience to drought could be an effect of its relatively small surface to volume ratio as compared to other sea grass, which would also support it having high light requirements.

Filament algae (*Chorda filum*)

This type of algae seems to be relatively sparsely distributed with only two reported observation around coordinates (50,15) (Figure 5a), embedded in a meadow of eelgrass. The local depth is 1.5 m and the drag potential is subsequently low. The alga probably coincides with eelgrass because it is likewise sensitive to drag and might be able to adhere to the eelgrass for support. At the same time, it does not take up nutrients from the sediment, but absorbs it directly from the water column, as is the case with the other algae, meaning it requires some degree of water movement. It should therefore not be found in the deepest parts along with eelgrass, but rather only in areas with a drag potential approximately between 0.01 m^2s^{-2} and 0.04 m^2s^{-2}.

Benthic mats (cyano bacteria, diatoms)

This class of organisms can inhabit areas where stresses are too high for most other species. In nearly all parts of the bay where depths are 0.2 m or less, cyano and diatom mats are found. This is probably an effect of the mats being anchored to sediment, and not having any protruding structures prone experiencing drag. Cyano mats are however not found any deeper than 0.2 m, and diatoms no deeper than 1 m, most likely due to light requirements. They are also resilient to draught which is relatively common at depths of 0.2 m (Table 1).

Drainage and dehydration

Drainage occurs when the mean sea level retreats more than 0.2 m which exposes at least 13% of the Kalvöfjord's bottom. This is a fairly regular event prevailing circa 17% of the time. The sea level can retreat as much as 0.8 m below the mean within a few days during a severe drainage event (see Figure 2), and drainage may last between a few hours to well over a hundred hours. Table 1 displays the percentage of exposed area, frequency and duration of drainage events, gathered from sea level data.

During the observed period, drainage has lasted for 156 h at most, but as indicated by Table 1, the probability for duration is concentrated to the first few hours. This short period of time may however be enough to cause serious dehydration in drought sensitive organisms such as eelgrass, and may very well be a factor limiting their migration to calm but shallow (≤0.5 m) areas.

Discussion

This study is meant to demonstrate what potentials lie in the new approach of comfort zones. Much more data about the studied area and its ecology is needed to draw any stronger conclusions regarding the level of predictability for marine vegetation. There are a few factors to address in particular for improving the current study. These are discussed below.

The lower boundary of the wave induced comfort zone has not been quantified. In order to do so, measures of drag potential and orbital velocity are insufficient, other nutrient transporting processes must also be included such as breaking waves and barotropic and baroclinic currents.

The wave model has been used to calculate the potential for drag forces at the seabed. To present the results, different statistical measures have been used. It is likely that these can be improved or augmented further to represent the two boundaries of the comfort zone more precisely. It is not clear that the 95th percentile is a good representative of the upper boundary of the comfort zone which enables the values in the 95th percentile matrix to causally and absolutely determine where macrophytes can and cannot live. This measure rests on the assumption that stresses are deleterious circa five percent of the time and even though the frequency of deleterious drag should certainly not be much higher – as that would leave most of the areas uninhabitable by anything but benthic mats – it is no more than an indication of the upper limit of the comfort zone. A reliable measure would need verification by conducting experimental studies, possibly at location in Kalvöfjord.

It would certainly be of benefit for this and similar studies if the drag characteristics of common west coast flora could be specified in a similar fashion to that of Schutten et al. (2004;2005). This is a necessary measure if absolute drag is to be calculated. Sediment samples from the treated area also need to be analyzed for cohesion strength, since the drag forces alone cannot determine whether the macrophyte becomes uprooted or not. In addition, a more detailed sea chart would increase the reliability of the model to predict drag. As of now, single depth measurements often stand to represent several hectares of bottom, possibly resulting in areas of interest being missed and discrepancies in habitat extension not being properly accounted for. Finally, the ecological mapping constituting the very standard against which the model and future models must be validated is much short of a reliable and complete picture. It is based on sporadic observations without a stringent spatial referencing system or exhaustive methodology for species inventory. Apart from lacking distinct ecological zonation, it has most likely missed several important occurrences of species that could give deeper insight of adaptation, and act as validation or falsification for the model. A suggested methodology for ecological surveying would be to cross the bay along several vertical and horizontal sections, making observations at a fixed interval of length, thus creating a grid net of data tied together with reliable coordinates. This could be a seasonal and annual undertaking in order to detect possible changes in the biodiversity and extension of habitats.

A factor that is easily ignored when treating organisms as something generic is the potential for species to vary their degree of adaptation in time. This is true for different morphotypes as well as for fully developed individuals. Studies support that, for instance, some species of brown algae can adopt different strategies depending on the availability of nutrients or exposure to drought during different seasons. Organisms living with one certain type of seasonal adaptation may not survive under the same circumstance as another individual of the same species with a different seasonal adaptation (Schonbeck and Norton, 1979 (I)). The importance of this factor must be known when proceeding with the approach of comfort zones.

As a note on the wind wave model and on modeling physical processes in general, the reader should be aware that a model is never more than an approximation of reality as it cannot encompass all physical processes involved, and often utilizes imperfect data. Thus the model should not be the basis for determining reality, but rather vice versa.

A final remark should be made about the good potential for importing data from this model into a GIS environment. It may even be possible that the whole model can be incorporated within a GIS structure, but at the very least, data over drag and other hydrodynamic variables should be able to serve as layers for determining or predicting ecological zonation as a result of comfort zones.

Conclusions

The Kalvöfjord area is heavily influenced by wave induced stress acting upon the submerged macrophytes in the form of pressure drag forces relating to their largest cross-sectional area and length. The temporal variation of drag potential is great, with a scaling factor of 260 between the 5^{th} and the 95^{th} percentile MDP.

The level of drag potential correlates significantly with habitat extension where more resilient organisms such as *Ruppia*, *Fucus*, and especially benthic diatoms and cyano mats, are found in areas with high drag potential, whereas sensitive structures such as eelgrass and *Chorda filum* are found in areas with low drag potential, most often coinciding with the deeper parts. Eelgrass in particular appears to be sensitive to both drag and drought and is never found at depths shallower than 1.2 m, but instead inhabits the calmest parts of the bay. Why the other species of sea grass studied, i.e. *Ruppia maritima*, seems to have such a high degree of drag tolerance is not clear, however it may be a consequence of a lean and short structure together with good anchorage in strong sediment.

Fucus is the only category of macrophyte for which a possible interval of the comfort zone can be discerned. *Fucus* is never found in areas with less than moderate drag potential, however also never in areas with very high drag. This is probably an effect of *Fucus* being pelagic feeders, requiring some degree of water movement to receive nutrients. The same seems to be true for *Chorda filum*, although too few observations are made of the species to draw any conclusions.

Drought sensitivity cannot be strictly inferred by simply observing the distribution of macrophytes; however some generalizations can be made for the most common types. Eelgrass is the only species that does not inhabit any areas where drought is at high or even moderate risk. Spreading fucus is similarly absent from areas which are at high risk from drought (0.2 m). However, their resilience to drought probably allows them to inhabit shallower areas than what is observed, as long as nutrient and sediment requirements are fulfilled.

The few instances of *Ruppia* seem to indicate that it is fairly well accustomed to drought as it resides in shallow areas not much deeper than 0.2 m, possibly due to a high volume to area ratio.

All in all there seem to be no significant exceptions to the principle that drag and drainage limit habitats, since no species is found across the whole spectrum of drag potential or depth. The results strengthen the hypothesis that the method of comfort zones is a valid and rewarding approach in determining habitat extension in shallow bays.

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List of words

Benthic – residing at the bottom.

Comfort zone – habitable interval for specific species under the impact of some physical variable.

Drag – the force acting upon a rigid body moving relative to a fluid.

Drag potential – the potential for any given macrophyte, or benthic structure, to experience wave induced drag at a certain location within a wave field.

Epiphyte – an organism that grows on another organism upon which it depends for mechanical support but not for nutrients.

GIS – geographical information system, a type of software.

Maximum drag potential (MDP) – the highest value of potential drag within a drag potential matrix over a geographical area.

Maximum orbital velocity (MOV) – the highest velocity reached by the wave orbital motion at a given depth, wave height and wave period.

Macrophyte – here meaning any anchored multicellular organism that protrudes perpendicularly to the bottom.

Morphotype – a phase in the growth of an organism that differs structurally from other phases or stages.

Orbital velocity – the sinusoidal velocity of water particles resulting from the wave form's propagation with depth.

Group velocity – the speed of the wave train, equivalent to the propagation speed of energy.

Zonation – the distribution of habitats exhibited by different species.