

Kelp morphometric properties and the link to hydrodynamic modelling

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Background

Marine ecosystems are maintained by a variety of complex interactions between abiotic and biotic variables such as temperature, wave exposure, pH, competition, and processes such as top-down and bottom-up control, predator-prey relationships and phenology (Doney et al. 2012). These abiotic and biotic variables, the interactions between them, and the various ecological processes, ultimately determine the community composition and ecological functioning of all ecosystems. Climate directly and indirectly affects the way in which abiotic and biotic variables interact, but is often compounded by other impacts such as habitat destruction, pollution, and over-fishing (Blamey et al. 2015). Temperature and wave exposure have been recognised as important variables with regards to climate-driven changes within the ocean. In order to persist and survive within variable and changing environments, organisms must either migrate, adapt, or die.

Seaweeds are sessile organisms which are unable to migrate to new areas when local environmental conditions become unsuitable and therefore are forced to adapt to new conditions in order to avoid expiration. The main form of mortality for seaweeds is through mechanical dislodgment by wave action. Seaweeds, particularly brown seaweeds, are able to undergo rapid morphological adaptation to the hydrodynamic environment. This allows seaweeds to reduce mortality through mechanical dislodgement by inducing morphological changes which reduces overall drag. Seaweeds that are unable to avoid mechanical dislodgement either raft out to sea or wash up onto beaches, otherwise known as beach-cast. However, not all the beach-cast may have originated from a nearby kelp population and may have originated from other sites or regions of the coast through a combination of rafting and ocean currents. Therefore, because kelp morphology is specific to its local environment the morphological features may be able to indicate, within a certain amount of probability, what site or region it most likely originated from. In other words, beach-cast kelp may be used as proxy for investigating the flow of coastal currents. Using kelp as a proxy for determining its original location will be calibrated by means of a hydrodynamic model which will be designed from already existing SWAN and Delf3D models. This combined approach will allow investigation into flow regimes around the west and south-west coasts of South Africa and the role they play in sub-tidal and beach ecology. For instance, micro-plastics are recognised as a threat to marine life, however very little is known about how micro-plastics may be transported along the coast. The coupling of kelp morphology and the ability to simulate hydrodynamic processes can greatly improve our understanding of transport pathways and likely locations of accumulation.

The increased use of plastic in society over the past half century has resulted in large amounts of plastic litter in both the marine and terrestrial environment. The problems associated with large plastic debris have received attention for many decades, whereas those connected to marine micro-plastics comparatively received very little attention. However, today it has become a prioritized area among political organizations, agencies and NGOs around the world. The micro-plastic debris present in the ocean are derived from marine and terrestrial sources, however there is little understanding of how microplastics may be distributed with ocean currents. Therefore, the coupling of kelp morphology and the ability to simulate hydrodynamic processes can greatly improve our understanding of transport pathways and likely locations of accumulation. This in turn may inform management decisions with regards to eliminating and managing marine pollution in South Africa.

Rationale

Seaweeds, browns in particular, are capable of adapting morphological characteristics to persist in changing and variable ocean environments. Changes in morphology have been shown to increase photosynthetic ability, enhance nutrient uptake, and reduce drag with regards to changes in wave exposure. Wave exposure has been shown to be an important driver of seaweed morphology, as the main mechanism of seaweed mortality is through the mechanism of dislodgment. Changing morphology, such as decreasing frond area or strengthening through stipe circumference increase/reduces drag and increases the probability of survival. However, locally adapted seaweed may still be dislodged in pulse disturbance events such as storms, and may raft far distances and wash up on beaches. An example would be *Ecklonia maxima* which is a conspicuous brown seaweed along the coastline and beaches around South Africa. Therefore, the beach-cast may not always originate from

adjacent kelp populations but rather from other regions which the individual is adapted for. Therefore, the kelp morphology may act as a proxy for investigating coastal currents and changes thereof. The advances in ocean hydrodynamic modelling has made great progress and has been applied in a variety of ways. Therefore, this study will use advances in hydrodynamic modelling in combination with kelp morphological characteristics to investigate coastal currents. Once the model has been established it may be applied in other ways, such as investigating the transport of micorplastics along the South African coastline. The harms of microplastics to the marine environment has gained much traction in recent years, but research in South Africa is lacking. The coupling of kelp morphology and the ability to simulate hydrodynamic processes can greatly improve our understanding of transport pathways and likely locations of accumulation. This in turn may inform management decisions with regards to eliminating and managing marine pollution in South Africa.

Research problem

Pollution is a huge environmental problem that affects both terrestrial and marine ecosystems. Pollution from land enters the sea where it could harm or kill marine organisms or is transported by ocean currents to other coastal areas. In these areas the pollution could re-enter the ocean or be blown by wind into terrestrail ecoystems where it could once again be ingested by oragnsims causing harm or even death. Pollution is therefore a major threat to the environment and marine organisms. In recent years the affect of microplastics on the ocean has gained much traction with scientists and politictions alike. Microplastics cosiste of tiny particles of plastic and other pollution and are therefore are difficult to detect.

Currently there is no hydrodynamic model that is able to determine dispersion, source and accumulation of microplastics along the South African coastline. Given the significant detrimental affect microplastics play in the ocean, it is important that such a mechanism be developed that will aid in better management of marine pollution in South Africa. Furthermore, this project allows for a multidicisplinary approach to be taken by combining ecology and coastal oceanography.

Preliminary literature review

Wave exposure is also recognised as an important driver of the marine environment, and macroalgae are not exception. Wave exposure has been shown to play a role in determing distribution, abundance, diversity, composition, growth (Cousens 1982) and productivity (Pedersen and Nejrup 2012) of macroalgae communities. For example, the width, vertical zonation and diversity of algal communities often change predictably along gradients of wave exposure. Wave exposure may also drive macroalgae communities indirectly through the alteration in affect of another environmental driver. For instance, increasing degrees of exposure may positively influence the amount of area available to trap light on macroalgal fronds, as well as increasing nutrient uptake due to increased turbulence in the boundry layer around the frond (Pfeister 1995). The most important direct effect of wave exposure on macroalgal communities is through mechanical dislodgment, which ultimately leads to expiration. Mechanical forces generated by the hydrodynamic environment, in the form of sudden strong ocean currents or storms, between 10- 20 m s-1 with accelerations of 400 m s-2 (Friedland and Denny 1995) are the biggest threat to kelp survival. Kelps are able to rapidly adapt their morphological characteristics to reduce drag and avoid dislodgment (Blanchette 1997). For example a study by Koehl et al. (2008) showed that transplanted *Nereocystis luetkeana* plants from a wave sheltered site to a wave exposed site changed their morphology to flat blades and narrow laterals that are less prone to drag forces in 4-5 days. Another study by Fowler-Walker, Wernberg, and Connell (2006) tested for differences in morphology of *Ecklonia radiata* between wave-sheltered and wave-exposed sites and was a combination of *in situ* sampling and transplant of juvenile plants. The results showed that morphology differed between wave-sheltered and wave-exposed sites (thin thallus at sheltered sites and a narrow, thick thallus with a thick stipe at exposed sites), and was consistent with previous studies. Juveniles transplanted into wave exposed sites under went rapid morphological adaption, whilst the opposite was true for wave-sheltered sites which showed slower morphological adaption.

Wave exposure is a complex abiotic variable which varies spatially and temporarily in the marine environment (Sundblad et al. 2014; Bekkby et al. 2008). Furthermore, the degree to which a macroalgae community is exposed, is dependent on local site characteristics, such as bathymetry and local wind patterns (Sundblad et al. 2014; Bekkby et al. 2008). Despite this fact, macroalgae have been able to persist in often harsh and variable wave environments (Hatcher, Kirkman, and Wood 1987; Friedland and Denny 1995; Charrier, Le Bail, and De Reviers 2012; @ Blanchette 1997). Macroalgae are sessile organisms and incapable of migrating when local conditions become unsuitable. Therefore, macroalgae must adapt to the local wave climate in order to persist and survive, and achieve this through morphological adaptation (Charrier, Le Bail, and De Reviers 2012). The morphology of macroalgae are not fixed genetic traits. A study by @?? showed that *species name* was able to rapidly adapt to the local wave environment when transplanted from a low wave exposure site to a high wave exposure site. Advances in genetic techniques and taxonomy have revealed that species delimitation based on morphology has been inaccurate, and organisms that were once considered two separate species are actually one species. The morphological adaptation that macroalgae display are therefore mostly driven by local or site conditions, and therefore individuals must be morphologically flexible to persist in stochastic environments. This may be achieved through different strategies and are species-specific, which can be directly attributed the high diversity in morphological characters of algal communities. For example some algae have fronds and others are articulated coralline, and therefore these species would need to adapt their morphology differently in order to persist. Moss (1948) investigated the anatomy, chemical composition of *Fucus spiralis* at three sites that varied in wave exposure (sheltered, medium exposure and exposed). The authors found that individuals in exposed sites showed less branching of thalli as well as variation in organic nitrogen, mannitol, laminarian and alginic acid concentrations.

Advances in numerical modelling has gained much traction in recent years and has been applied in a variety of ways with regards to ecological studies. For example, a study by Wang and Xia (2009) used the Delft3D-Flow model to assess the hydraulic suitability of a stream as a spawning ground for the Chinese Sturgeon (*Acipenser sinensis*) in the Yangtze River. The authors calculated the horizontal mean vorticity which was used to assess the hydraulic environment of spawning ground. The flow field state was determined through model simulation and field-measured data used to validate the model. The results added to existing scientific database for spawning ground hydraulic environmental protection. Different numerical models can often be integrated to model across ecosystem levels. For example a study by Leon et al. (2003) used integrated physical (Delft3D hydrological model) and bio-chemical (Agricultural Non-point Source model) processes models to investigate the possible impact on the Lake Malawi water quality due to management actions performed at the watershed level. Traditional ecological measures of wave exposure usually incorporates integrative measures of hydrodynamic conditions at a particular site. More specifically, it is the integration of mechanical processes and the influence that it has on the ecology of nearshore communities.

Wave exposure may be modelled through various methods which range from simple cartographic to more advanced numerical wave models. Cartographical models can be qualitative or quantitative and were designed for the need of wave exposure measures to explain ecological distributions. A simple set of calculations on coastline and wind data, and relatively small input data sets are required. These are regarded as “fetch-based models”, which measure the length of open water associated with a site along a straight line. The output of such an approach is a simplified estimate of the potential wave energy for a specific set of sites. Advances in cartographical methods using fetch-based models has allowed for wave exposure measurements for larger areas, and has been suggested as a method for predicting macroalgal community structure (Burrows, Harvey, and Robb 2008). An example of such a model is the “BioEx model” which was developed by Baardseth and others (1970) to estimate wave exposure over large regions. BioEx requires frequency, strength and direction of winds, weighted by degree of exposure within various directions. BioEx is calculated as the sum of the index developed at different spatial scales (local, fjord and open).

Lindegarth and Gamfeldt (2005) criticized this approach, arguing that the choice of wave exposure method can influence ecological inference. The authors also highlighted the need for objective, reproducible and quantitative studies comparing exposure indices (Lindegarth and Gamfeldt 2005). Other authors, such as Hill et al. (2010), have argued that these simple measures can be improved upon by including bathymetry data which allows the incorporation of diffraction into the calculation. Diffraction is topographically induced variations in wave direction. A model incorporating this complexity was developed by M. Isæus (2004), and

is known as the “simplified wave model” (SWM). The model uses measurements of wind strength, fetch and empirically derived algorithms to mimic diffraction.

Advances in numerical modelling have been founded on physical wave theory on how a wave “behaves”. This approach is based on a theoretical perspective rather than the need to answer ecological questions. Besides diffraction, these models incorporate more complexity by including wind forcing, wave-to-wave interactions and loss of energy due to friction and wave breaking. Numerical models have a variety of applications and are often incorporated within hydrodynamic general circulation models and are used operationally for forecasting the sea state (Group 1988; Booij, Ris, and Holthuijsen 1999; Smith, Sherlock, and Resio 2001). The downside of advanced numerical models is that are computationally intensive which creates limitations for large scale simulations. Therefore, their application along long stretches of variable coastline, inshore environments and ocean-wide simulations are limited due to the poor spatial coverage. However, these models can be designed for local or site specific coverage, provided the correct data are available.

Since wave energy is an important driver in marine ecosystems, particularly kelp, the advances in hydrodynamic modelling offer a new opportunity for multifactoral and quantitative approach to research in marine ecosystems. The Delft3D and SWAN models have been used successfully in previous studies regarding brine plume discharge, impacts of storms, affects of climate change on the hydrological environment etc. The models have not been designed for shallow environments (<6m) and therefore may not be suitable to model coastal hydrological environments. However these models may be adjusted to suit coastal waters if they are combined with a new numerical model which can be calibrated to suit these needs. Numerical modelling for this study will be undertaken using the Delft3D suite of numerical models developed by Deltares. The suite of models allows for the simulation of flows, sediment transport, waves, water quality, morphological developments and ecology.

The Delft3D-WAVE module uses the SWAN (Simulating Waves Nearshore) numerical model developed at the Delft University of Technology to simulate the generation and propagation of wind-generated waves in coastal environments. The SWAN model is based on the discrete spectral action balance equation and is fully spectral (in all directions and frequencies). The latter implies that short-crested random wave fields propagating simultaneously from widely different directions can be accommodated (e.g. a wind sea with super-imposed swell). Delft3D-FLOW is a multi-dimensional (2D or 3D) hydrodynamic (and transport) simulation program which calculates non-steady flow and transport phenomena that result from tidal and meteorological forcing on a rectilinear or a curvilinear, boundary fitted grid. In 3D simulations, the vertical grid is defined following the sigma coordinate approach. The model solves the shallow water equations, consisting of the momentum and the continuity equations

In recent years there has been growing attention on plastic pollution, particularly the ocean. Plastic pollution can range from macroplastics to microplastics. Microplastics are tiny plastic granules used as scrubbers in cosmetics and air-blasting, and small plastic fragments that originate from larger pieces of plastic known as macroplastics. The potential harms of plastic was highlighted in the 1970’s and renewed interest has lead to research showing that plastics in the ocean are widespread. Plastic pollution is bio-available to biota in the food-web which may cause problems with an organisms physiological functioning. Therefore, this study not only enables research into the ecological affects of the hydrological environment on an important habitat-forming organism, it also offers the opportunity to improve on current hydrological numerical models to suit coastal environments. This in turn will allow investigation into the flow and accumulation of microplastics which are regarded as a major threat to marine life. Furthermore, the calibrated model could be applicable to other ecological studies such as dispersal of benthic flora and fauna, climate change studies, forecasting etc.

Aims of research

The aim of the project is to investigate coastal flow regimes along the west coast and south-west coast of South Africa and the role this may play in transport of kelp beach-cast and microplastics. This aim will be met through the following objectives:

- A) Determine if the hydrodynamic environment is the main driver of kelp morphology and if this is specific to a location

- B) Determine quantitative relationships with kelp morphology and the hydrodynamic environment to create a biological index.
- C) Use *in situ* morphological data to calibrate this to a specific area, or ideally site, within a reasonable amount of probability
- D) Simulate kelp rafting by means of a hydrodynamic modelling and calibrate this model with *in situ* beach-cast morphometric data.
- E) Use the calibrated hydrodynamic model to investigate dispersal of microplastics along the west coast and south-west coast of South Africa.

Research design and methodology

A combined quantitative ecology and oceanography approach will be used for this study. Morphological characteristics and their relation to the hydrodynamic environment must first be established and the findings will form the basis for the proceeding chapters. Once the relationship has been established it will be used to calibrate future hydrodynamic models developed during the course of the study. Once the hydrodynamic model has been established and calibrated it will be used to investigate the flow of microplastics along the South African coastline.

Morphology

Morphometrics collection Between October 2014 and April 2015, morphological measurements of *Laminaria pallida* and *Ecklonia maxima* were collected at 19 sites along the Western Cape coast of South Africa (Refer to morphology bar graphs). These varying morphometrics allowed measurements such as weight, length and thickness to be compared between sites. Because the macroalgae differ in construction, species-specific morphometrics were included. These sites span across the majority of the Western Cape coast, in varying thermal and wave energy regimes. Sites were chosen to represent an array of morphological differences seen within each *Ecklonia maxima* and *Laminaria*. Sites were also chosen to reflect locations that displayed variable wave and temperature regimes, to allow us to robustly test our hypothesis of environmental drivers influencing kelp morphology. St. Helena Bay and Betty’s Bay constituted the north western and south eastern boundary sites respectively. These sites are roughly 300km apart, and are confidently lie within separate marine provinces, as outlined above. Cape Peninsula provides an interesting topographical boundary that shelters the coast in False Bay. Sites were therefore chosen to represent an array of environments, from offshore reefs (Batsata Rock), to sheltered intertidal zones (Miller’s Point). West of Cape Point, a number of sites were chosen to highlight the presence of upwelling (Oudekraal, Kommetjie), as well as kelps growing in protected bays (Hout Bay).

Hydrodynamic model

The hydrodynamic model for coastal flow will be developed using already existing models that have been developed. These models will consist of the SWAN and Delf3D models and the approach is to use aspects of each model, that are related to coastal flow, from which further development will take place. Once the model has been developed it will be used to predict kelp morphology at random sites which will then be sampled. The *in situ* kelp morphology data collected at the predicted site will be used to calibrate the model. This process will be repeated until the model can predict coastal flow and kelp morphology within a certain degree of probability. Kelp morphology is driven by regional and local environmental factors, the spatial scales used will be dependent on the spatial patterns of the various abiotic variables being investigated. Fully nested hierarchical design at three spatial scales will be used: regions, locations (within regions) and sites (within locations).

Microplastics

The calibrated model developed in previous chapters will be used to determine flow, source and accumulation points along the South African coastline. Certain characteristics of microplastics such as buoyancy, flow rate, fluid dynamics etc. Which characteristics are important for modeling dispersion of microplastics will be achieved by investigating the literature and experimental simulations. Once the model has been established it will once again be calibrated through *in situ* sampling.

Outline of Chapters

Chapter and sections	Title
Chapter 1	Summary
Chapter 1.1	Background
Chapter 1.2	Kelp environmental drivers
Chapter 1.3	Ocean and coastal waves
Chapter 1.4	Hydrodynamic modelling
Chapter 1.5	Aims and objectives
References	Reference list for chapter
Chapter 2	Abiotic drivers of morphological adaption of <i>Ecklonia maxima</i> along the South African coastline
Chapter 2.1	Introduction
Chapter 2.1.2	Waves and kelp morphology
Chapter 2.1.3	The South African context
Chapter 2.2	Aims and objectives
Chapter 2.3	Methods
Chapter 2.4	Results
Chapter 2.5	Discussion
References	Reference list for chapter
Chapter 3	Using kelp morphology as an index for calibrating coastal-flow model
Chapter 3.1	Introduction
Chapter 3.1.2	The SWAN model design and application
Chapter 3.1.3	SWAN as a platform for further development
Chapter 3.2	Aims and objectives
Chapter 3.3	Methods
Chapter 3.4	Results
Chapter 3.5	Discussion
References	Reference list for chapter
Chapter 4	Application of modified coastal-flow model
Chapter 4.1	Introduction
Chapter 4.1.2	Plastic pollution in the marine environment
Chapter 4.1.3	Application of hydrodynamic modelling in dispersal of plastics
Chapter 4.1.4	Plastic pollution in South Africa
Chapter 4.2	Aims and objectives
Chapter 4.3	Methods
Chapter 4.4	Results
Chapter 4.5	Discussion
References	Reference list for chapter
Chapter 5	Synthesis
Chapter 5.1	Synthesis of Chapters
Chapter 5.2	Challenges and limitations
Chapter 5.3	Gaps and future research
Chapter 5.4	Concluding remarks

Time-frame

Months	Description
April 2018 - September 2018 September 2018 - December 2018	Develop and write proposal for submission to department Acceptable level of progress on literature review. The first data chapter should also be complete and submission of first paper
January 2019 - May 2019	Become competent in relevant software (Python). Data analyses for the 2nd data chapter should ideally be near completion. Substantial additions to literature review.
May 2019 - August 2019	Completion of 2nd data chapter and relevant paper should also be near completion.
August 2019 - December 2019	Complete analyses and write-up for final data chapter. Significant progress on the relevant paper. Literature review should be near completion.
January 2020 - June 2020 June 2020 - December 2020	Complete of final data chapter and final chapter. This time will be used to make final edits and complete thesis write-up

References

- Baardseth, Egil Morris, and others. 1970. "Square-Scanning, Two-Stage Sampling Method of Estimating Seaweed Quantities." Tapir.
- Bekkby, T, P E Isachsen, M Isæus, and V Bakkestuen. 2008. "GIS modeling of wave exposure at the seabed: A depth-attenuated wave exposure model." *Marine Geodesy* 31 (2): 117–27. doi:10.1080/01490410802053674.
- Blamey, L K, L J Shannon, J J Bolton, R Crawford, F Dufois, H Evers-king, C Griffiths, et al. 2015. "Ecosystem changes in the southern Benguela and the underlying processes." *Journal of Marine Systems* 144: 9–29. doi:10.1016/j.jmarsys.2014.11.006.
- Blanchette, C A. 1997. "Size and Survival of Intertidal Plants in Response to Wave Action : A Case Study with *Fucus Gardneri*." *Ecology* 78 (5): 1563–78. doi:10.1890/0012-9658(1997)078[1563:SASOIP]2.0.CO;2.
- Booij, NRRC, RC Ris, and Leo H Holthuijsen. 1999. "A Third-Generation Wave Model for Coastal Regions: 1. Model Description and Validation." *Journal of Geophysical Research: Oceans* 104 (C4). Wiley Online Library: 7649–66.
- Burrows, M T, R Harvey, and L Robb. 2008. "Wave exposure indices from digital coastlines and the prediction of rocky shore community Wave exposure indices from digital coastlines and the prediction of rocky shore community structure." *Marine Ecology Progress Series* 353: 1–12. doi:10.3354/meps07284.
- Charrier, B, A Le Bail, and B De Reviers. 2012. "Plant Proteus: Brown algal morphological plasticity and underlying developmental mechanisms." *Trends in Plant Science* 17 (8): 468–77. doi:10.1016/j.tplants.2012.03.003.
- Cousens, R. 1982. "The Effect of Exposure to Wave Action on the Morphology and Pigmentation of *Ascophyllum nodosum* (L.) Le Jolis in South-Eastern Canada." *Botanica Marina* XXV: 191–95.
- Doney, S C, M Ruckelshaus, J Emmett Duffy, J P Barry, F Chan, C English, H M Galindo, et al. 2012. "Climate Change Impacts on Marine Ecosystems." *Annual Review of Marine Science* 4 (1): 11–37. doi:10.1146/annurev-marine-041911-111611.
- Fowler-Walker, M J, T Wernberg, and S D Connell. 2006. "Differences in kelp morphology between wave sheltered and exposed localities: Morphologically plastic or fixed traits?" *Marine Biology* 148 (4): 755–67. doi:10.1007/s00227-005-0125-z.
- Friedland, M T, and M W Denny. 1995. "Surviving hydrodynamic forces in a wave-swept environment: consequences of morphology in the feather boa kelp, *Egregia menziesii* (Turner)." *Journal of Experimental Marine Biology and . . .* <http://www.sciencedirect.com/science/article/pii/002209819500038S>.
- Group, The Wamdi. 1988. "The Wam Model—A Third Generation Ocean Wave Prediction Model." *Journal of Physical Oceanography* 18 (12): 1775–1810.
- Hatcher, B G, H Kirkman, and W F Wood. 1987. "Growth of the kelp *Ecklonia radiata* near the northern limit of its range in Western Australia." *Marine Biology* 95: 63–73.
- Hill, Nicole A, Austen R Pepper, Marji L Puotinen, Michael G Hughes, Graham J Edgar, Neville S Barrett, Rick D Stuart-Smith, and Rebecca Leaper. 2010. "Quantifying Wave Exposure in Shallow Temperate Reef Systems: Applicability of Fetch Models for Predicting Algal Biodiversity." *Marine Ecology Progress Series* 417: 83–95.
- Isæus, Martin. 2004. "Factors Structuring *Fucus* Communities at Open and Complex Coastlines in the Baltic Sea." PhD thesis, Botaniska institutionen.
- Koehl, M A R, W K Silk, H Liang, and L Mahadevan. 2008. "How kelp produce blade shapes suited to different flow regimes: A new wrinkle." *Integrative and Comparative Biology* 48 (6): 834–51. doi:10.1093/icb/icn069.
- Leon, L F, D C Lam, C McCrimmon, and D A Swayne. 2003. "Watershed management modelling in Malawi: Application and technology transfer." *Environmental Modelling and Software* 18 (6): 531–39.

doi:10.1016/S1364-8152(03)00028-8.

Lindegarth, Mats, and Lars Gamfeldt. 2005. “Comparing Categorical and Continuous Ecological Analyses: Effects of ‘Wave Exposure’ on Rocky Shores.” *Ecology* 86 (5). Wiley Online Library: 1346–57.

Moss, B. 1948. “Studies in the genus *Fucus*: I. on the structure and chemical composition of *Fucus vesiculosus* from three Scottish localities.” *Annals of Botany* 12 (47): 267–79.

Pedersen, M F, and L B Nejrup. 2012. “Effects of wave exposure on population structure, demography, biomass and productivity of the kelp *Laminaria hyperborea*.” *Marine Ecology Progress Series* 451: 45–60. https://www.researchgate.net/profile/Morten-Pedersen3/publication/235938581_Effects_of_wave_exposure

Pfeister, Catherine A. 1995. “Seaweed Ecology and Physiology.” *Ecology* 76 (7). Ecological Society of America: 2341–2.

Smith, Jane M, Ann R Sherlock, and Donald T Resio. 2001. “STWAVE: Steady-State Spectral Wave Model User’s Manual for Stwave, Version 3.0.” ENGINEER RESEARCH AND DEVELOPMENT CENTER VICKSBURG MS COASTAL AND HYDRAULICSLAB.

Sundblad, G, T Bekkby, M Isæus, A Nikolopoulos, K M Norderhaug, and E Rinde. 2014. “Comparing the ecological relevance of four wave exposure models.” *Estuarine, Coastal and Shelf Science* 140. Elsevier Ltd: 7–13. doi:10.1016/j.ecss.2014.01.008.

Wang, Y, and Z Xia. 2009. “Assessing spawning ground hydraulic suitability for Chinese sturgeon (*Acipenser sinensis*) from horizontal mean vorticity in Yangtze River.” *Ecological Modelling* 220 (11): 1443–8. doi:10.1016/j.ecolmodel.2009.03.003.