

Predicting *Pollicipes pollicipes* (Crustacea: Cirripedia) abundance on intertidal rocky shores of SW Portugal: a multi-scale approach based on a simple fetch-based wave exposure index

David Jacinto¹, Teresa Cruz^{1,2}

¹ MARE - Marine and Environmental Sciences Centre, Laboratório de Ciências do Mar, Universidade de Évora, Apartado 190, 7520-903 Sines, Portugal. E-mail: djacinto@uevora.pt

² Departamento de Biologia, Escola de Ciências e Tecnologia, Universidade de Évora, Portugal.

Summary: Understanding and predicting patterns of distribution and abundance of marine resources is important for conservation and management purposes in small-scale artisanal fisheries and industrial fisheries worldwide. The goose barnacle (*Pollicipes pollicipes*) is an important shellfish resource and its distribution is closely related to wave exposure at different spatial scales. We modelled the abundance (percent coverage) of *P. pollicipes* as a function of a simple wave exposure index based on fetch estimates from digitized coastlines at different spatial scales. The model accounted for 47.5% of the explained deviance and indicated that barnacle abundance increases non-linearly with wave exposure at both the smallest (metres) and largest (kilometres) spatial scales considered in this study. Distribution maps were predicted for the study region in SW Portugal. Our study suggests that the relationship between fetch-based exposure indices and *P. pollicipes* percent cover may be used as a simple tool for providing stakeholders with information on barnacle distribution patterns. This information may improve assessment of harvesting grounds and the dimension of exploitable areas, aiding management plans and supporting decision making on conservation, harvesting pressure and surveillance strategies for this highly appreciated and socio-economically important marine resource.

Keywords: *Pollicipes pollicipes*; abundance; wave exposure; GIS; SW Portugal.

Prediciendo la abundancia del percebe *Pollicipes pollicipes* (Crustacea: Cirripedia) en el intermareal rocoso del SW Portugal: un enfoque multi-escalar basado en un simple índice de exposición a las olas

Resumen: La comprensión y la predicción de los patrones de distribución y abundancia de los recursos marinos es importante para fines de conservación y la gestión, desde pesquerías artesanales a pequeña escala a la pesca industrial. El percebe (*Pollicipes pollicipes*) es un recurso marisquero importante y su distribución está estrechamente relacionada con la exposición al oleaje a diferentes escalas espaciales. Modelamos la abundancia (porcentaje de cobertura) de *P. pollicipes* en función de un simple índice de exposición al oleaje basado en estimaciones de fetch a partir de líneas de costa digitalizadas a diferentes escalas espaciales. El modelo explicó el 47.5 % de la varianza total; de acuerdo con el modelo, la abundancia de percebes aumenta de forma no lineal con la exposición al oleaje a escalas espaciales pequeñas (metros) y grandes (kilómetros). Obtuvimos mapas de distribución del percebe para la región de estudio en el suroeste de Portugal. Nuestro estudio sugiere que la relación entre los índices de exposición basados en fetch y el porcentaje de cobertura de *P. pollicipes* puede ser utilizada como una herramienta sencilla sobre los patrones de distribución de percebes de cara a la identificación de bancos marisqueros y la dimensión de las zonas explotables. Esto puede ayudar a mejorar los planes de gestión y apoyar la toma de decisiones en materia de conservación, presión pesquera y de estrategias de vigilancia para este importante recurso marino.

Palabras clave: *Pollicipes pollicipes*; abundancia; exposición a las olas; GIS; SW Portugal.

Citation/Como citar este artículo: Jacinto D., Cruz T. 2016. Predicting *Pollicipes pollicipes* (Crustacea: Cirripedia) abundance on intertidal rocky shores of SW Portugal: a multi-scale approach based on a simple fetch-based wave exposure index. Sci. Mar. 80(2): 229-236. doi: <http://dx.doi.org/10.3989/scimar.04330.27A>

Editor: J. Templado.

Received: August 1, 2015. **Accepted:** February 26, 2016. **Published:** May 28, 2015.

Copyright: © 2016 CSIC. This is an open-access article distributed under the Creative Commons Attribution-Non Commercial License (by-nc) Spain 3.0.

INTRODUCTION

Understanding and predicting patterns of distribution and abundance of marine resources is important for conservation and management in small-scale artisanal fisheries and industrial fisheries worldwide. Spatial planning and management of marine resources requires information on distribution patterns at relevant scales (Bekkby et al. 2009), which may be insufficient and/or difficult to obtain due to logistical constraints of biological sampling across large areas and/or in extreme habitats such as very exposed wave-swept rocky shores. When data are scarce, predicting distribution patterns using relationships between species abundance and physical variables may provide the required information and assist management and conservation decision making (Hill et al. 2010).

The role of wave exposure as a key process shaping the composition of coastal communities has long been acknowledged (Ballantine 1961, Kingsbury 1962, Lewis 1964). Wave exposure potentially affects both the organisms and their interactions directly by acting as a mechanical stressor (McQuaid and Branch 1985, Menge and Sutherland 1987, Denny 1988) and indirectly by affecting temperature (West and Salm 2003), sedimentation (Airoldi 2003, Schiel et al. 2006), nutrient intake (Hearn et al. 2001) and productivity (Hurd 2000), among other important ecological factors.

The goose barnacle *Pollicipes pollicipes* is an important shellfish resource on the northeast Atlantic coast from Brittany to Morocco and is intensively harvested on intertidal and shallow subtidal rocky shores (Boukaici et al. 2012, Parada et al. 2012, Sousa et al. 2013). In its distribution range, *P. pollicipes* occurs mostly at wave-exposed locations such as capes and headlands (Barnes 1996), but within these locations its abundance varies at small spatial scales (metres apart), depending on the orientation of the site to the prevailing incoming wave direction (Borja et al. 2006). On less exposed areas, *P. pollicipes* occurrence is rare and mainly restricted to a few individuals occupying small shelter areas such as cracks and crevices. Recent observations made on the SW coast of Portugal suggest that top-down control via predation is one of the main processes shaping *P. pollicipes* abundance patterns (unpublished results), and may vary along wave exposure gradients at a multitude of spatial and temporal scales.

Along the SW coast of Portugal, exposed rocky shores dominate the coastal landscape. Despite a few headlands, this coastline is roughly rectilinearly oriented from north to south and exposed to dominant NW and W swells (Instituto Hidrográfico 2006). At smaller spatial scales the topography of the coast often results in an intricate mesh of exposed and less exposed locations where goose barnacle abundance is highly variable at the scale of metres.

Borja et al. (2006) have shown that the distribution, coverage, and biomass of goose barnacles in the Gaztelugatxe Marine Reserve (Basque Country, Spain) are related to the wave regime and the energy received in each coastal sector. On this coast, these authors associated higher coverage and biomass of *P. pollicipes* with higher energy values. They suggest that the numerical

models used to simulate the energy produced by waves may be used as a tool in predicting potential biomass of goose barnacles along the Basque coasts.

Modelling wave energy reaching the coast often requires specialized software and elaborate datasets (e.g. detailed bathymetry, oceanographic and meteorological data) that are not readily available for most study regions worldwide. Existing methods range from cartographic solutions to complex numerical hydrodynamic simulations, and differ in the scale and spatial coverage of their outputs, performance and ecological relevance (Sundblad et al. 2014). Simple topographical indices based on the openness of the coastline combined with local wind data have been shown to be useful tools in the assessment of wave exposure variability at different spatial scales, depending on the resolution of the available cartography (Burrows et al. 2008). In recent years, several authors have developed computerized methods for deriving topographical indices of wave exposure based on digitized coastlines (Ekeboom et al. 2003, Lindegarth and Gamfeldt 2005, Hill et al. 2010). Such methods often consist in determining the wave fetch for a particular location as the distance to the nearest coastline in angular sectors, which, in combination with metrics from local wave and wind data, may be used to estimate different wave exposure indices.

Satellite imagery, cartographic and geographic information systems (GIS) resources, oceanographic and meteorological data and forecast models available online provide data that researchers worldwide can access and use for research purposes. Satellite imagery provided from online services and GIS software may be used to draw digitized coastlines of any specific location at an appropriate resolution for most coastal ecological studies. Online forecasting weather services, based on data produced by meteorological and oceanographic forecast models (e.g. the Global Forecast System [GFS], Weather Research and Forecasting [WRF] and the NOAA wave watch III model [NWW3]), provide model estimates for most coastal locations worldwide. These data, in combination with digitized coastlines, may then be used in cost effective GIS projects that provide researchers and stakeholders with the information they need to meet their management goals.

We modelled the abundance (estimated as percent coverage) of *P. pollicipes* as a function of a simple wave exposure index based on fetch estimates from digitized coastlines at different spatial resolutions and wave energy derived from oceanographic and meteorological data provided from nearby stations.

The aim of this study was to predict *P. pollicipes* abundance along a stretch of coast in SW Portugal and to discuss the potential use of this model as a simple and cost-effective management tool for the goose barnacle fishery in Portugal.

MATERIALS AND METHODS

Biological sampling

In the summer of 2010, *P. pollicipes* percent cover in the mid-intertidal of rocky shores in a 50-km study

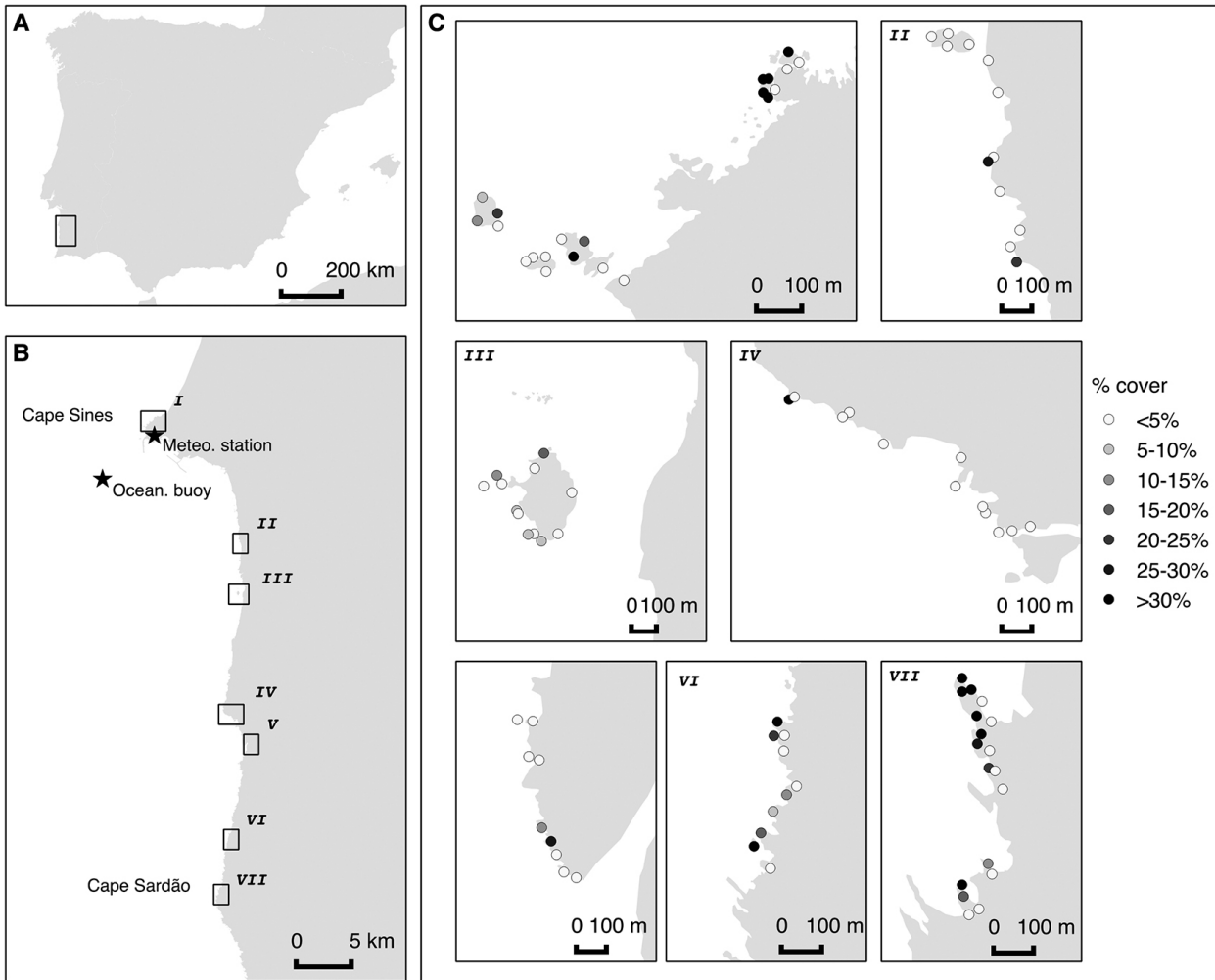


Fig. 1. – Study region in relation to the Iberian Peninsula (A) and location of sampling areas (I- VII) (B), meteorological station (Meteo. station) and oceanographic buoy (Ocean. buoy) in SW Portugal. Sampling site location and mid-intertidal *Pollicipes pollicipes* average percentage cover results from digital image analyses (C).

region in SW Portugal (a total of 94 sites tens of metres apart, sampled in seven areas kilometres apart, as shown in Fig. 1) was estimated by digital analysis of photo-quadrats (n=5) taken at each site. ImageJ software (Abràmoff et al. 2004) was used to superimpose an orthogonal 2.5-cm dotted grid on the digital images and to estimate the proportion of dots over goose barnacles in each image.

Digital coastline

Using QGIS geographical information systems software (www.qgis.org) with OpenLayers plugin, a high resolution digital coastline of SW Portugal was created based on satellite imagery (1:2000) provided by Google. Three spatial resolutions (10 m, 100 m and 1 km cell size) were used to create grid maps of the study area from digital coastline polygons.

Fetch estimates

Using the WAVE FETCH MODEL software (Burrows et al. 2008), wave fetch was determined as the

distance (m) to the nearest land cell in sixteen 22.5° angular sectors (N, NNE, NE, ..., NNW), by searching the surrounding cells up to a distance of 10 km for every coastal cell in the grid maps (at all spatial resolutions).

Wind energy

We used data from a five-year time series (2005-2010) provided by a meteo-station at a nearby location (8°52'43"W, 37°57'15"N) that sampled wind direction (16 angular sections: N, NNE, NE, ..., NNW) and speed (m s⁻¹) (among other variables) at a 10-min rate (incomplete data series with several gaps per year). Wind energy for each angular sector was estimated as the product of the square of the mean wind speed and the respective mean yearly relative frequency for the available data period.

Wave energy

We used data from a five-year time series (2005-2010) provided by an oceanographic buoy at a nearby

location (8°55'44"W 37°55'16"N) that sampled wave direction (16 angular sections: N, NNE, NE, ..., NNW) and significant height (m) (among other variables) at a 10-min rate (incomplete data series with several gaps per year). Wave energy for each angular sector was estimated as the product of the square of the mean significant wave height and the respective mean yearly relative frequency for the available data period.

Exposure indices

Three exposure indices based on fetch measurements and wind and wave energy were estimated for every coastal cell in the grid maps at all spatial resolutions (10 m, 100 m and 1 km): 1) $FeEx_{sum}$, the sum of fetch estimates for all angular sections; 2) $WaEx_{sum}$, the sum of the product of fetch and wave energy for all angular sections; and 3) $WiEx_{sum}$, the sum of the product of fetch and wind energy for all angular sections.

Data analysis

Using nearest point analyses in a GIS environment, each biological sampling site was assigned to the set of exposure indices from the nearest coastal cell in the grid maps at each spatial resolution considered (10 m, 100 m and 1 km).

Generalized additive models (GAM) were used to model the response variable, the percent cover of *P. pollicipes*, as a function of the explanatory variables,

i.e. each type of exposure index ($FeEx_{sum}$, $WaEx_{sum}$ or $WiEx_{sum}$) at different spatial resolutions (10 m, 100 m and 1 km). GAMs were constructed using the Poisson distribution family (corrected for over-dispersion) and the log-link function (Zuur et al. 2007). Thin plate regression spline smoothers with fixed degrees of freedom ($df=6$) were used for nested model comparison (Wood 2006). Of the data, 80% was used for model building and the remaining 20% was used for model validation, which was done by comparing (paired t-test) predicted model results with data from a new set of photo-quadrats ($n=18$ paired data points). All analyses were done using R statistical software (www.r-project.org)

RESULTS

In the study region (Fig. 1), barnacle abundance was highly variable at all spatial scales considered (10's m to 10's km). *P. pollicipes* mean percentage cover sampled in the mid-shore at the sampling sites ($n=94$) ranged from 0% to 64.6% (1.6% and 10.6%, median and mean, respectively). Both subsets of data used for model construction (80%) and model validation (20%) had similar distributions (Welch Two Sample t-test: $t=0.099$, $df=25.028$, $p=0.9219$).

Fetch estimates ($FeEx_{sum}$) were obtained for every coastal cell from grid maps at 1 km, 100 m and 10 m resolutions and an example of their variability is shown in Figure 2. $FeEx_{sum}$ varied between 35.1 and

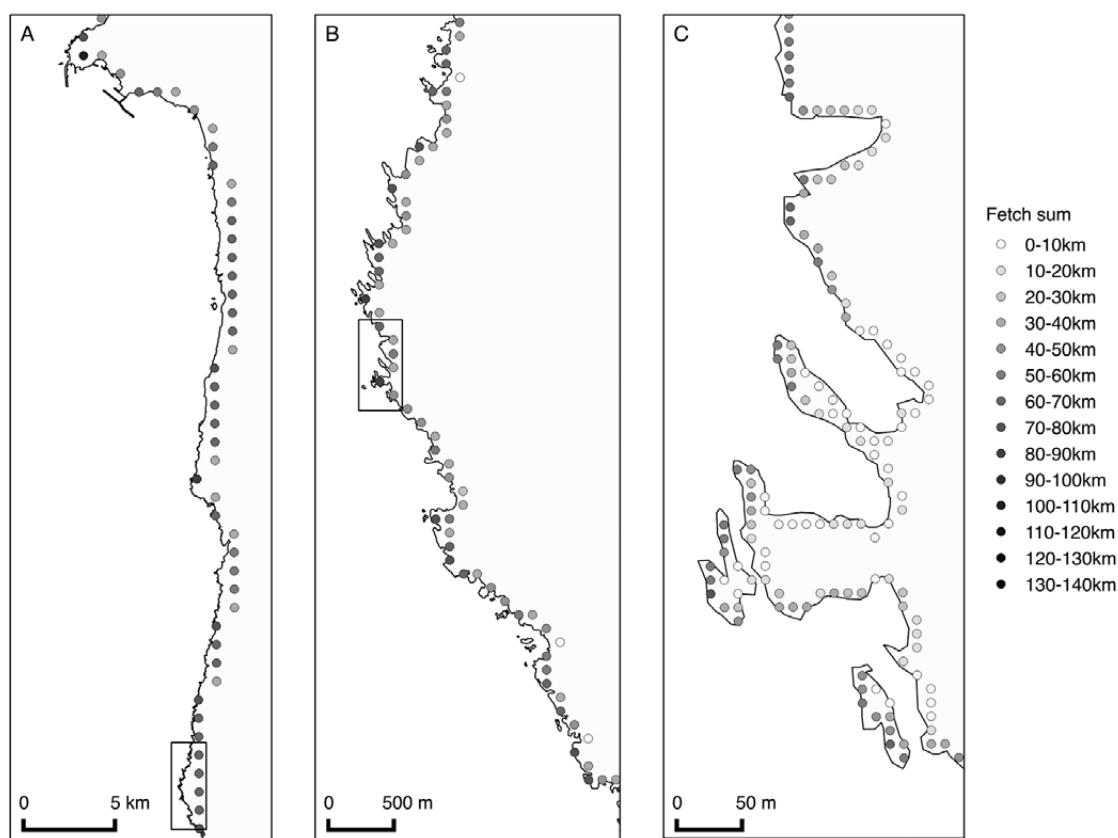


Fig. 2. – Examples of fetch estimates ($FeEx_{sum}$) for coastal cells at different spatial scales (A, B and C represent the 1 km, 100 m and 10 m resolutions, respectively; boxes in A and B represent the extents of B and C, respectively).

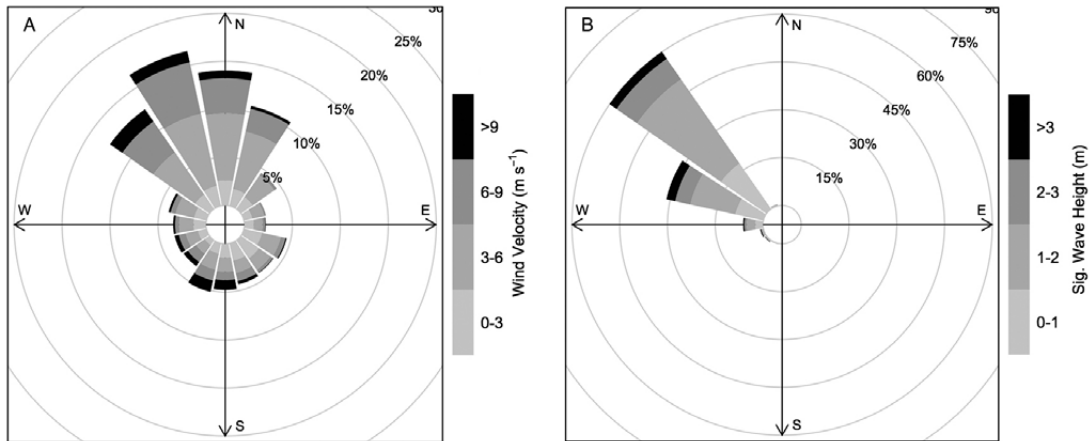


Fig. 3. – Wind and wave patterns from data collected at a meteorological station and an oceanographic buoy between 2005 and 2010 in the Sines region (SW Portugal). A) Wind velocity ($m s^{-1}$) and frequency (%) by coastal sector. B) Significant wave height (m) and frequency (%) by coastal sector.

84.2 km for every coastal cell along the SW coast of Portugal on the 1 km grid map; 0.3 km and 132.2 km on the 100 m grid map and 0.02 km and 90.0 km on the 10 m grid map.

Wind and wave data collected between 2005 and 2010 from a nearby meteorological station and an oceanographic buoy are summarized in Figure 3, and support the assumption that the study region is mainly exposed to northwesterly winds and waves. The estimated energy per coastal sector suggests that most

wind energy comes from the NW-ENE but there is also a strong component of wind energy that reaches the coast from the SSW-S. Wave energy, as estimated from local data, strikes the coast mainly from the WNW-NW. Exposure indices based on wind and wave energy were computed for each coastal cell at all spatial resolutions considered in the present study (results not shown).

The model that best and most parsimoniously described the relationship between barnacle abundance

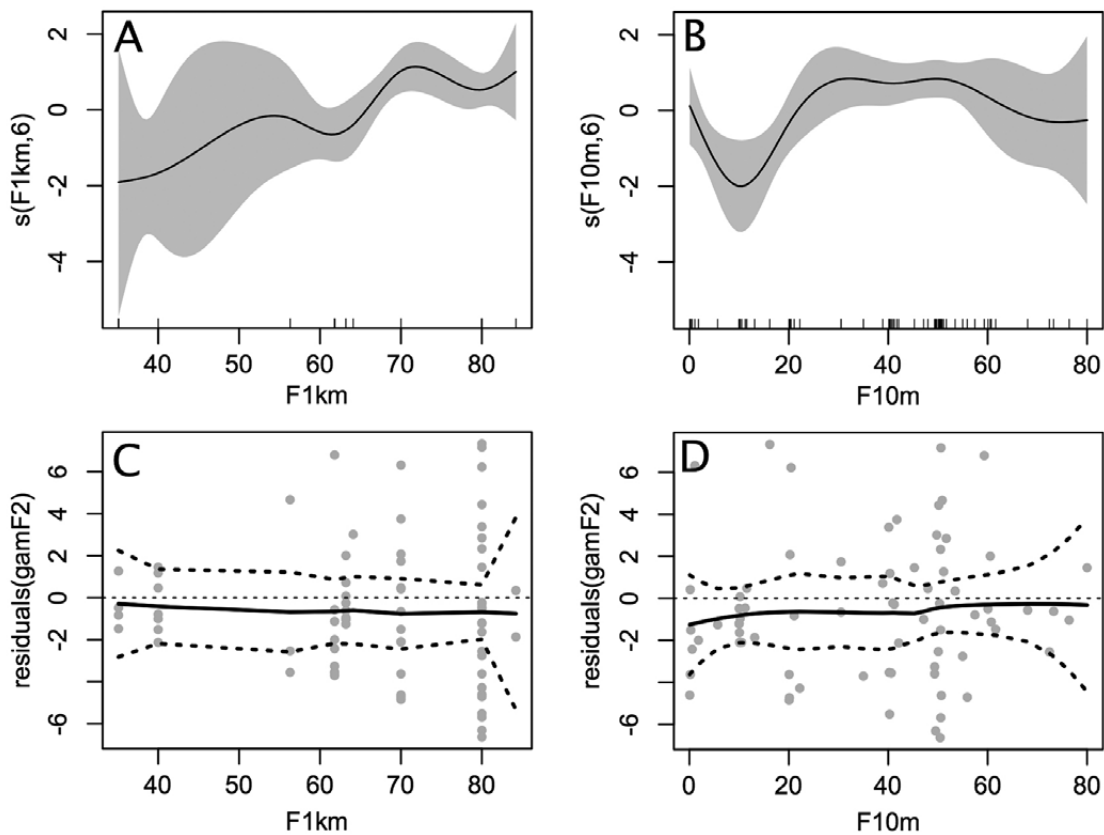


Fig. 4. – Generalized additive model (GAM) validation plots. Smoothing functions for the explanatory variables F1 km (A) and F10 m (B). Standardized residuals for the optimal GAM plotted against observations for each explanatory variable (C, D), with LOESS fit predictions for mean (span 0.65; solid black line) and 95% confidence intervals (dashed black lines) superimposed on the observed data (grey dots), showing no residual patterns.

Table 1. – Numerical output for a generalized additive model (GAM) using Poisson distribution corrected for over-dispersion and a log-link function. The model uses *P. pollicipes* percentage cover as a response variable and F1 km and F10 m as explanatory variables. A, estimated parameters and B, approximate significance of smooth terms. Bold type indicates significance ($p < 0.05$). Deviance explained=47.5%. N=74.

A, parametric coefficients	Estimate	SE	t-value	p-value
Intercept	1.764	0.233	7.572	<0.001
B, approximate significance of smooth terms	df	F	p-value	
s(F10 m)	6	3.065	0.0109	
s(F1 km)	6	2.846	0.0165	

(percent cover) and exposure indices included F1 km and F10 m as selected predictive variables. The GAM model explained 47.5% of the deviance and was of the following form: barnacle cover $\sim 1.76 + s(\text{F1 km}) + s(\text{F10 m})$.

Numerical output for the model is shown in Table 1, and smoothing functions and model validation plots are shown in Figure 4. The effects of the parametric intercept coefficient and the smoothing terms for both explanatory variables were significant ($p < 0.05$). For model validation purposes, deviance residuals were plotted against the explanatory variables, showing no discernible patterns (Fig. 4C and D). Again for model

validation purposes, a paired t-test on another set of data with both observed and predicted values was performed and the result was non-significant ($p = 0.87$), suggesting a good agreement between the observed and predicted values, and thus validating the model. According to the model, barnacle abundance increases non-linearly with wave exposure at both the smallest (metres) and largest (kilometres) spatial scales considered in this study.

The use of other exposure indices, accounting for wind and wave energy, to predict barnacle abundance in the study region did not increase the power or predictive value of the model (model outputs not shown) in comparison with a simpler, fetch-based exposure index model. Each of the three models performed similarly in predicting abundance of *P. pollicipes* for a subset of data (paired t-test: observations vs predictions; not significant; $p > 0.05$), and no significant differences were found between the predicted abundance values based on either model (paired t-test: not significant; $p > 0.05$).

A goose barnacle distribution map based on model predictions along natural the rocky coast of the study region is shown in Figure 5. Three areas with larger predicted barnacle abundance values ($>15\%$) are perceivable and are related to the three main headlands in the

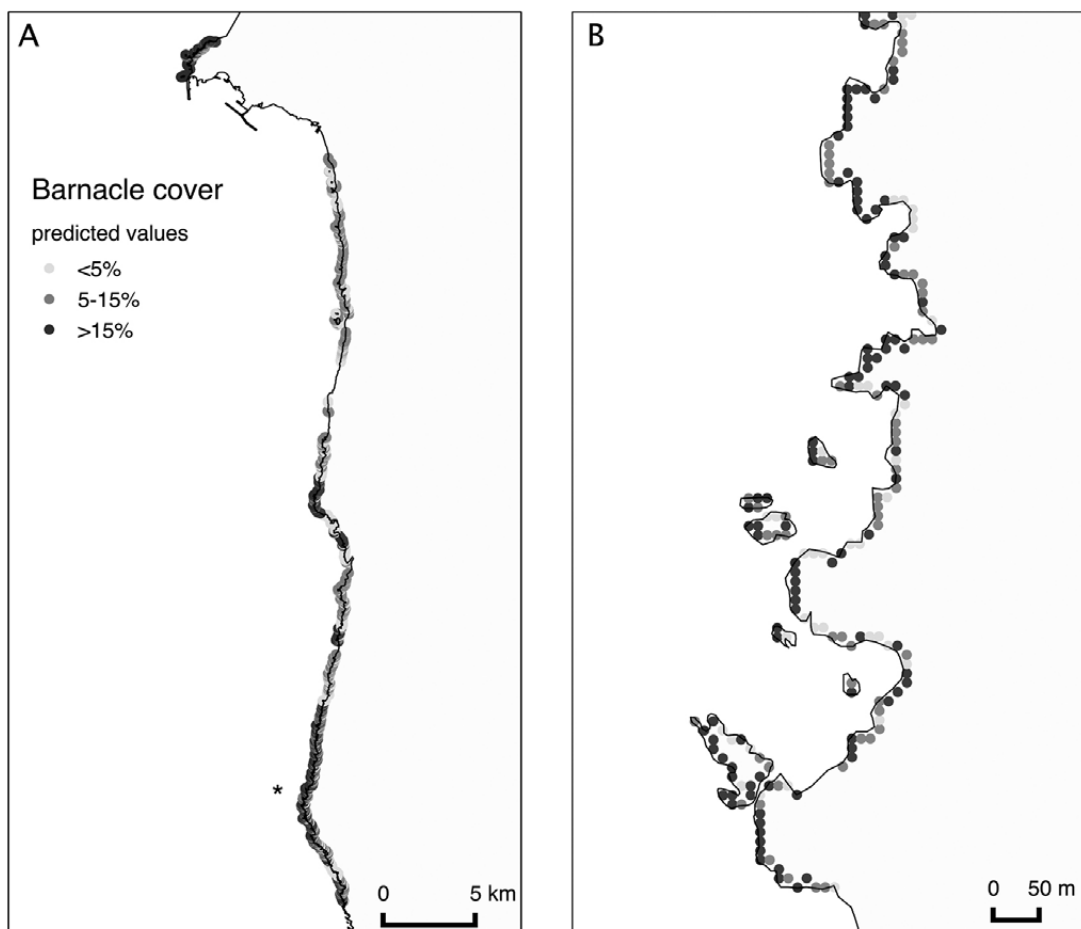


Fig. 5. – *Pollicipes pollicipes* predicted distribution in natural rocky shores of SW Portugal. A, larger scale map reveals main areas with higher predicted barnacle cover. B, smaller scale map (roughly centred around * in A) showing the high variability in barnacle cover associated with complex coastline configuration at smaller spatial scales.

study region. A total of 54.4 km of natural rocky shores was estimated in the study region, based on the sum of coastal cells from the small-scale grid map (10 m), excluding sandy beaches and artificial coastal structures. According to the model, goose barnacle abundances similar to those previously reported in harvesting areas (>15% of barnacle cover in the mid-shore; Sousa et al. 2013) were predicted to occur in about 17.0 km (31.3%) of rocky coast in the same region.

DISCUSSION

It has been long recognized that the distribution of the goose barnacle (*Pollicipes pollicipes*) along its geographical range is associated with heavy surf and strong water flows (Barnes 1996), and previous studies have shown that wave incident energy is one of the main environmental factors determining the absence or abundance of the goose barnacle (Borja et al. 2006). Therefore, the strong predictive power of the wave exposure indices used in the present study is not surprising. These simple wave exposure indices, the multi-scale approach and the accessible digital tools used in the present study may provide an effective framework for barnacle distribution modelling with direct application in the goose barnacle fishery and conservation.

In the present study we sampled for goose barnacles in a wide range of exposure conditions at different spatial scales along a stretch of coast in SW Portugal. Barnacle abundance data, from totally absent to high percentage covers, as observed in other studies in the same region (Sousa et al. 2013), were fed into predictive models in which wave exposure indices at different spatial scales were used as explanatory variables.

Three different wave exposure indices were used: a simple fetch-based index and two others based on the previous one but weighted with directional wind and wave data observed in the study region. Despite the added complexity, which could potentially give the model a higher level of realism by taking into account the regional meteorological and oceanographic conditions, the wind and wave energy weighted fetch-based indices did not increase the power or predictive value of the models in comparison with a simpler fetch-based model. Fetch, as a wave exposure index, was a fairly good predictor of barnacle abundance in rocky shores of SW Portugal, explaining a large amount of the variation observed in *P. pollicipes* distribution patterns in the study area. However, other factors acting on larger or smaller spatial scales, such as substrate type and inclination, biological interactions, harvesting pressure and others that were not addressed in this study, are also very important in shaping barnacle distribution patterns (Sousa et al. 2013).

It should be noted that more realistic oceanographic models on marine dynamics in coastal areas based on the available offshore wave energy and including the main physical processes affecting wave energy distribution along the coast, such as refraction and diffraction, and detailed bathymetry (Borja et al. 2006) could potentially explain a higher proportion of the data variability that our approach could not account for.

The present study suggests that the relationship between fetch-based exposure indices and *P. pollicipes* percent cover may be used as a simple tool to provide stakeholders with information on barnacle distribution patterns that may lead to better assessment of harvesting grounds and the dimension of exploitable areas, which may improve management plans and support decision making on conservation, harvesting pressure and surveillance strategies for this highly appreciated and socio-economically important marine resource. As an example, a total of 17.0 km of rocky coast with expected exploitable areas out of 54.4 km of rocky coast in the study region was predicted according to the model. The identification of these areas could now be used for management (e.g. spatial zoning and definition of number of harvesting licences) and surveillance purposes. It can also be useful for establishing a rotational moratorium in a number of areas likely to be exploited, and may permit the maintenance of a spawning pool of larvae that nourish and sustain the exploited areas, as suggested by Borja et al. (2000) and Bald et al. (2006).

As used in this study, free, open-source software in addition to simple biological monitoring strategies offers an attainable cost-effective management tool that may be implemented by stakeholders and resource users in areas where barnacle harvesting is an important socio-economic activity. Studies such as this one may serve to establish protected areas for conservation of certain commercially important sensitive species, such as the goose barnacle, and to prevent the subsequent damage of the associated communities.

ACKNOWLEDGEMENTS

We thank André Costa, Alina Marcelino and Nuno Mamede for help during the fieldwork. The Ports of Sines and the Algarve Authority (APS, S.A.) kindly provided oceanographic and meteorological data. This study is an output of the project “PERCEBES – Gestão, Ecologia e Conservação do Percebe em Portugal” (operação nº31-03-05-FEP-11), funded by PROMAR – Programa Operacional de Pescas 2007-2013 and the Portuguese State. This study had the support of Fundação para a Ciência e Tecnologia (FCT), through the strategic project UID/MAR/04292/2013 granted to MARE, and the grant awarded to DJ (SFRH/BD/28060/2006).

REFERENCES

- Abràmoff M.D., Magalhães P.J., Ram S.J. 2004. Image processing with Image. *J. Biophotonics Int.* 11: 36-42.
- Airoldi L. 2003. The effects of sedimentation on rocky coast assemblages. *Oceanogr. Mar. Biol. an Annu. Rev.* 41: 161-236.
- Bald J., Borja A., Muxika I. 2006. A system dynamics model for the management of the gooseneck barnacle (*Pollicipes pollicipes*) in the marine reserve of Gaztelugatxe (Northern Spain). *Ecol. Model.* 194: 306-315.
<http://dx.doi.org/10.1016/j.ecolmodel.2005.10.024>
- Ballantine W. 1961. A biologically-defined exposure scale for the comparative description of rocky shores. *F. Stud. J.* 1: 1-19.
- Barnes M. 1996. Pedunculate cirripedes of the genus *Pollicipes*. *Oceanogr. Mar. Biol. Annu. Rev.* 34: 303-394.
- Bekkby T., Rinde E., Erikstad L., et al. 2009. Spatial predictive distribution modelling of the kelp species *Laminaria hyperborea*.

- ICES J. Mar. Sci. 66: 2106-2115.
<http://dx.doi.org/10.1093/icesjms/fsp195>
- Borja A., Muxika I., Bald J. 2000. Protection of the goose barnacle *Pollicipes pollicipes* Gmelin, 1790 population: the Gaztelugatxe Marine Reserve (Basque Country, northern Spain). *Sci. Mar.* 70: 235-242.
- Borja A., Liria P., Muxika I., et al. 2006. Relationships between wave exposure and biomass of the goose barnacle (*Pollicipes pollicipes*, Gmelin, 1790) in the Gaztelugatxe Marine Reserve (Basque Country, northern Spain). *ICES J. Mar. Sci.* 63: 626-636.
<http://dx.doi.org/10.1016/j.icesjms.2005.12.008>
- Boukaici M., Bergayou H., Kaaya A., et al. 2012. *Pollicipes pollicipes* (Gmelin, 1789) (Cirripède, Lepadomorpe): étude de la croissance et de la dynamique des populations dans la région de Mirleft (sud ouest Marocain). *Crustaceana*. 85: 1073-1097.
<http://dx.doi.org/10.1163/156854012X651259>
- Burrows M., Harvey R., Robb L. 2008. Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. *Mar. Ecol. Prog. Ser.* 353: 1-12.
<http://dx.doi.org/10.3354/meps07284>
- Denny M. 1988. *Biology and the mechanics of the wave-swept environment*. Princeton University Press, Princeton, NJ.
<http://dx.doi.org/10.1515/9781400852888>
- Ekeboom J., Laihonon P., Suominen T. 2003. A GIS-based step-wise procedure for assessing physical exposure in fragmented archipelagos. *Estuar. Coast. Shelf Sci.* 57: 887-898.
[http://dx.doi.org/10.1016/S0272-7714\(02\)00419-5](http://dx.doi.org/10.1016/S0272-7714(02)00419-5)
- Hearn C., Atkinson M., Falter J. 2001. A physical derivation of nutrient-uptake rates in coral reefs: Effects of roughness and waves. *Coral Reefs*. 20: 347-356.
<http://dx.doi.org/10.1007/s00338-001-0185-6>
- Hill N.A., Pepper A.R., Puotinen M.L., et al. 2010. Quantifying wave exposure in shallow temperate reef systems: Applicability of fetch models for predicting algal biodiversity. *Mar. Ecol. Prog. Ser.* 417: 83-95.
<http://dx.doi.org/10.3354/meps08815>
- Hurd C.L. 2000. Water motion, marine macroalgal physiology, and production. *J. Phycol.* 36: 453-472.
<http://dx.doi.org/10.1046/j.1529-8817.2000.99139.x>
- Instituto Hidrográfico. 2006. Roteiros da Costa de Portugal - Portugal Continental - Do Cabo Carvoeiro ao Cabo de São Vicente. Instituto Hidrográfico, Lisboa.
- Kingsbury J.M. 1962. The effect of waves on the composition of a population of attached marine algae. *Bull. Torrey Bot. Club.* 89: 143-160.
<http://dx.doi.org/10.2307/2482562>
- Lewis J. 1964. *The ecology of rocky shores*. The English Universities Press, London.
- Lindgarth M., Gamfeldt L. 2005. Comparing Categorical and Continuous Ecological Analyses: Effects of "Wave Exposure" on Rocky Shores. *Ecology*. 86: 1346-1357.
<http://dx.doi.org/10.1890/04-1168>
- McQuaid C., Branch G. 1985. Trophic structure of rocky intertidal communities response to wave action and implications for energy flow. *Mar. Ecol. Prog. Ser.* 22: 153-161.
<http://dx.doi.org/10.3354/meps022153>
- Menge B., Sutherland J. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* 130: 730-757.
<http://dx.doi.org/10.1086/284741>
- Parada J.M., Outeiral R., Iglesias E., et al. 2012. Assessment of goose barnacle (*Pollicipes pollicipes* Gmelin, 1789) stocks in management plans: Design of a sampling program based on the harvesters' experience. *ICES J. Mar. Sci.* 69: 1840-1849.
<http://dx.doi.org/10.1093/icesjms/fss157>
- Schiel D.R., Wood S.A., Dunmore R.A., et al. 2006. Sediment on rocky intertidal reefs: Effects on early post-settlement stages of habitat-forming seaweeds. *J. Exp. Mar. Bio. Ecol.* 331: 158-172.
<http://dx.doi.org/10.1016/j.jembe.2005.10.015>
- Sousa A., Jacinto D., Penteado N., et al. 2013. Patterns of distribution and abundance of the stalked barnacle (*Pollicipes pollicipes*) in the central and southwest coast of continental Portugal. *J. Sea Res.* 83: 187-194.
<http://dx.doi.org/10.1016/j.seares.2013.04.005>
- Sundblad G., Bekkby T., Isæus M., et al. 2014. Comparing the ecological relevance of four wave exposure models. *Estuar. Coast. Shelf Sci.* 140: 7-13.
<http://dx.doi.org/10.1016/j.ecss.2014.01.008>
- West J.M., Salm R.V. 2003. Resistance and Resilience to Coral Bleaching: Implications for Coral Reef Conservation and Management. *Conserv. Biol.* 17: 956-967.
<http://dx.doi.org/10.1046/j.1523-1739.2003.02055.x>
- Wood S.N. 2006. *Generalized additive models: an introduction with R*. Chapman and Hall/CRC. Series: Chapman & Hall/CRC Texts in Statistical Science.
- Zuur A., Ieno E., Smith G. 2007. *Analysing ecological data*. Springer, New York.
<http://dx.doi.org/10.1007/978-0-387-45972-1>