# Modelling spatial and temporal variability of intertidal *Zostera marina* on the Ems estuary, Dutch Wadden Sea

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Eelgrass and its habitats are protected under different environmental frameworks at global, European and national scales. Intertidal habitat forming species, such as the annual flexible type of *Zostera marina*, have a high year-to-year variability in extent and location, being local extinction and (re-)colonization part of their inherent dynamics. Thus, to achieve the conservation goals in this case, potentially suitable eelgrass habitats more than only existing eelgrass habitats should be protected. That would increase the population chances to yearly recover. Therefore, in this context it is extremely important to have an estimation of the total potential area of seagrass occurrence (Bos *et al*., 2005). Such estimation can be performed using Species Distribution Modelling (sensu Guisan and Zimmermann 2000; SDM hereafter). Nowadays, there is a large extent of techniques to build SDMs, some have been applied before to eelgrass in Northern Europe by van Katwijk *et al*. (2000), Bos *et al*. (2005) and Bekkby *et al*. (2008). An adequate selection of the modelling algorithm is critical for habitat distribution modelling (Elith *et al*., 2006), and variable selection is also an important step in the construction of a SDM (e.g. Guisan and Zimmerman, 2000; Valle *et al*. 2011).

Seagrass beds inhabiting the Ems estuary (Dutch Wadden Sea, Netherlands) have been monitored on a yearly basis since mid-1990s, by the Directorate-general for Public Works, under the framework of the biological monitoring program from the Dutch Government. Monitoring has been carried out on both, aerial and ground surveys. Hence, data on species presence from year 1995 to year 2009 (with year 1998 missing) were available and transformed into permanency year (number of years that one cell have been occupated). Data on different environmental variables which are known to affect the species distribution were also available and collected as GIS layers. Three different types of habitats were classified from the permanency data by linear discriminant analysis and under expert knowledge, 'core' habitat (from 10 to 13 years of permanency), 'moderately stable' habitat (from 6 to 9 years) and 'boundary' or 'dynamic' habitat (from 1 to 5 years) (Figure 1).

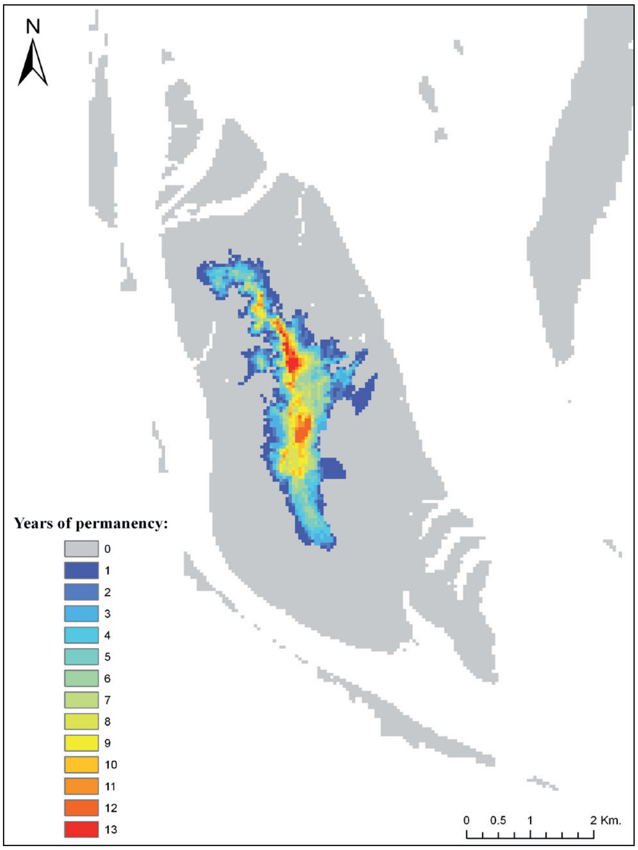

**Figure 1:** Map on species permanency. From 10 to 13 years: 'Core' habitat; from 6 to 9: 'Moderately stable' habitats; from 1 to 5: 'Boundary' or 'Dynamic' habitats.

Correlation between environmental predictors was assessed to avoid multicollinearity, setting the rejection threshold at 0.6 *Pearson* correlation index. SDMs were build using the following predictor variables: current velocity and wave exposure (regarding to water dynamics); depth and slope (regarding to topography); silt content of the sediment; ammonium load and salinity (regarding to sediment and water characteristics). Pseudo-absences were created for modelling purposes avoiding spatial overlap with the

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presences. The spatial aggregation of the presence data points was reduced by ensuring a minimal distance of 100 metres between consecutive points in order to avoid spatial autocorrelation.

Twelve different SDM algorithms were calibrated in order to find the best model for each type of the classified seagrass habitat. The used algorithms are implemented in, *R* packages (R development core team, 2012); *OpenModeller*, a niche modelling library (Muñoz *et al*., 2009), and *MaxEnt*, a software based on the maximum-entropy approach for species habitat modelling (Phillips *et al*., 2006). To achieve a more robust forecast, different ensembles of models were also produced by arithmetic average (Araújo and New, 2007; Marmion *et al*., 2009) (Table 1).

**Table 1.** Summary table of applied algorithms to model potential distribution of *Zostera marina* habitats. Id numbers are related to the numbers in AUC graphics from Figure 2.

| Group of SDMs | Id | Algorithm | Platform | References |
|---|---|---|---|---|
| Ecological distance | **1** | Chebyshev | Openmodeller | Muñoz et al., 2009 |
| | **2** | Euclidean | Openmodeller | |
| | **3** | Mahalanobis | Openmodeller | |
| | **4** | Manhattan | Openmodeller | |
| Emsenble forecasting | **5** | Enemble1: All models | Arithmetic mean in Quantum Gis | Elith et al., 2006 |
| | **6** | Ensemble2: MaxEnt+Boosted Regression Trees+ Generalized Additive Models + Generalized Linear Models Multivariate Adaptative Regression Splines | | |
| | **7** | Ensemble3: Distance based models | | |
| | **8** | Ensemble4: Machine learning based models | | |
| | **9** | Ensemble 5: Regression based models | | |
| Machine learning methods | **10** | Boosted Regression Tree | R package: dismo | Hijmans et al., 2012 |
| | **11** | MaxEnt | MaxEnt software | Phillips et al., 2006 |
| | **12** | Artificial Neural Networks | R package: nnet | Venables and Ripley, 2002 |
| | **13** | Random Forest | R package: randomForest | Liaw and Wiener, 2002 |
| | **14** | Support Vector Machines from Openmodeller | R package: kernlab | Karatzoglou et al., 2004 |
| Regression-based models | **15** | Generalized Additive Models | R package: gam | Hastie, 2011 |
| | **16** | Generalized Linear Models | R package: dismo | Hijmans et al., 2012 |
| | **17** | Multivariate Adaptative Regression Splines | R package: earth | Milborrow et al., 2012 |

Area Under the Curve (AUC) evaluation method (Fielding and Bell, 1997) was applied in order to select the best distribution model or ensemble of models for each type of habitat. Evaluation was performed by data-splitting and cross validation was undertaken with 5 groups with replacement using pseudo-absences, where 70% of the presence points were used to calibrate the model and 30% to evaluate it.

For 'core' habitat and 'moderately stable' habitat the modelling technique which performed better, regarding to the AUC index, was the ensemble 1, build averaging all the models (AUC values 0.977 and 0.970, respectively) (Figure 2, see Id number in Table 1 to identify the algorithms). In the case of the 'boundary or 'dynamic' habitats, it was the ensemble 5, build averaging the regression-based models, with an AUC value of 0.917 (Figure 2, see Id numbers in Table 1 to identify the algorithms).

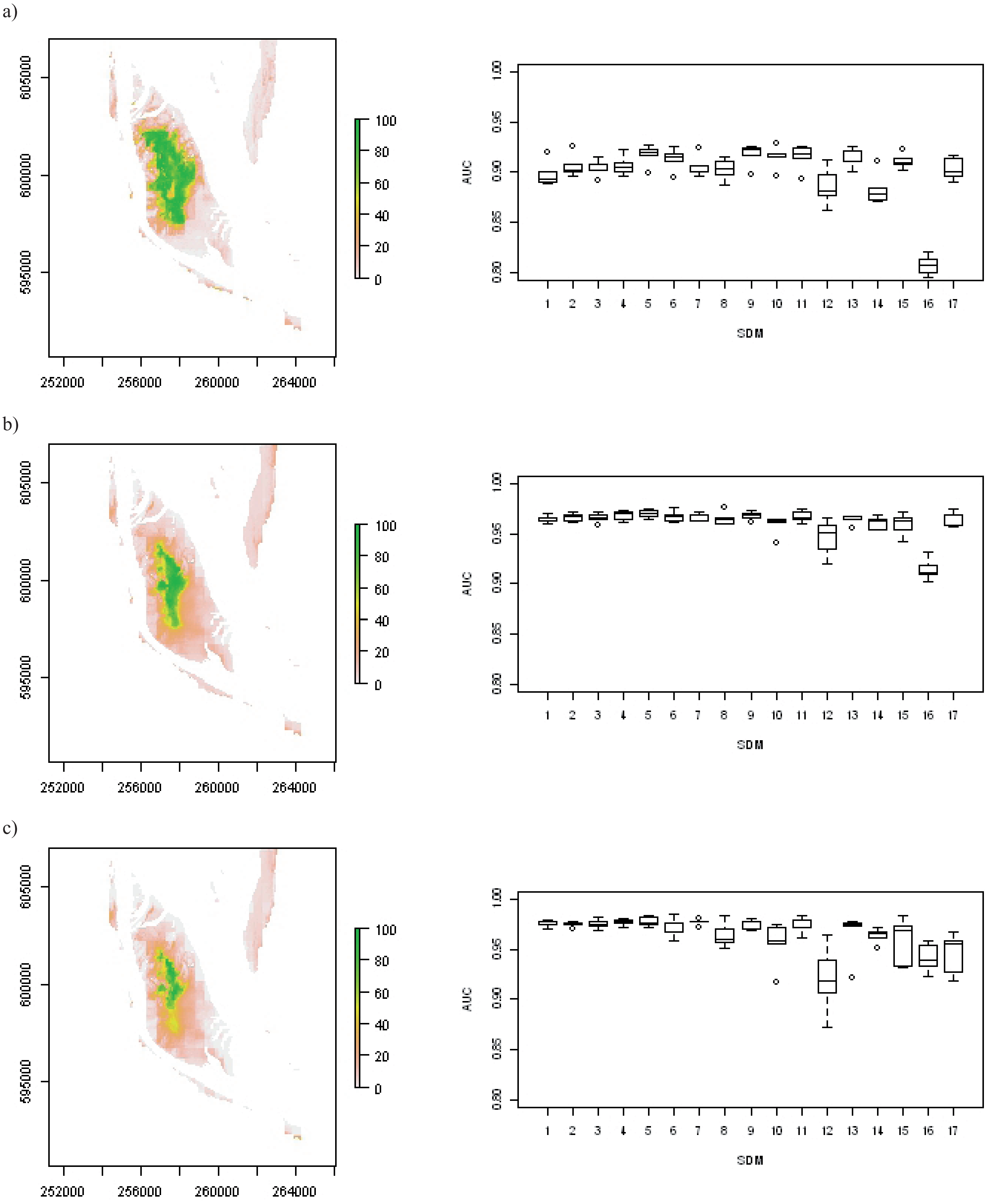

**Figure 2.** Geographic distribution probability maps and box plot graphics for Area Under the Curve (AUC) evaluations values. a) results for 'boundary' or 'dynamic' habitats; b) results for 'moderately stable' habitats; and c) results for 'core' habitats. See Id number in Table 1 to identify the algorithms.

Variable importance was tested for each model and differences were detected. For 'boundary' or 'dynamic' habitats variables such as wave exposure, depth, silt content of the sediment and current velocity were those which explained more the distribution (in order of importance), whereas, for 'stable' and 'core' habitats, the distribution was more explained by silt content of the sediment, wave exposure, current velocity and salinity.

Influence of water dynamics in seagrass distribution is well documented (e.g. Fonseca and Bell, 1998). The higher importance of wave exposure in the 'dynamic' habitat may be related to the severe effects that wave action has in those areas due to the continuously varying drag force on the leaves (Bos *et al*., 2005). The predominantly deeper distribution of this type of habitat, regarding to the distribution of 'moderately stable' and 'core' habitats, could yield to more water dynamics (namely wave dynamics). Those dynamics were found to directly determine the lower limit of *Zostera marina* in the Wadden Sea by van Katwijk and Hermus (2000). In addition, increased erosion and sedimentation was also found to negatively affect *Zostera marina* establishment (van Katwijk *et al*., 2000), which could be related to the low permanency of the 'dynamic' habitat. Silt content had more variability in the innermost areas than in outer areas, thus the higher importance of this variable in both habitat types, 'moderately stable' and 'core' could be explained. van Katwijk *et al*. (2000) accounted that areas with a diverse morphology were suitable for this species, as shelter and prevention of a rapid water runoff is provided.

Three different habitat distribution models have been selected for each habitat type ('core', 'moderately stable' and 'boundary' or 'dynamic' habitat); differences between models have been detected regarding to variable importance and geographical probability distribution. This study could help on the management and conservation of seagrass meadows. Ongoing research will analyse the distance to the 'core' habitat populations, as it seems to be a key factor for the occurrence of seagrass habitats. *Zostera marina* seed movement is limited to short distances (Orth *et al*., 1994) and therefore, proximity to a donor population is high relevant for the establishment of new colonizing specimens. A permanency time probability model will be built using that proximity as a predictor factor. As it has been mentioned previously, and considering our findings, the protection of an area surrounding the beds is highly recommended for an appropriate conservation of these dynamic populations. A combination of the models used here can be very helpful in determining how far such a surrounding area might stretch. The results from this analysis will be tested in the future in the seagrass beds inhabiting the Iberian Peninsula.

## References

Araújo, M. B. and New, M., 2007. Ensemble forecasting of species distributions. Trends in Ecology & Evolution. 22:42-47

Bekkby, T., Rinde, E., Erikstad, L., Bakkestuen, V., Longva, O., Christensen, O., Isæus, M. and Isachsen, P.E., 2008. Spatial probability modelling of eelgrass (*Zostera marina*) distribution on the west coast of Norway ICES Journal of Marine Science. 65(7):1093-1101

Bos, A.R., Dankers, N., Groeneweg, A.H., Carin, D., Hermus, R., Jager, Z., de Jong, D.J., Smit, T., de Vlas, J., van Wieringen, M., van Katwijk, M.M., 2005. Eelgrass (*Zostera marina* L.) in the western Wadden Sea: monitoring, habitat suitability model, transplantations and communication. In: Herrier, J.-L., Mees, J., Salman, A., Seys, J., Van Nieuwenhuyse, H., Dobbelaere, I. (Eds.), Proceedings 'Dunes and Estuaries 2005'- International Conference on Nature Restoration Practices in European Coastal Habitats. VLIZ Special Publication, 19, pp. 95-109, Koksijde, Belgium; xiv+685

Fielding, A. H. and Bell, J. F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation. 24:38-49

Fonseca, MS, Bell, SS, 1998 Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. Marine Ecology Progress Series. 171:109–121

Guisan, A., Zimmermann, N., 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147-186.

Hastie, T., 2011. gam: Generalized Additive Models. R package version 1.06.2. http://CRAN.R-project.org/package=gam

Hijmans, R.J., Phillips, S., Leathwick, J. and Elith, J., 2012. dismo: Species distribution modeling. R package version 0.7-17. http://CRAN.R-project.org/package=dismo

Karatzoglou, A., Smola, A., Hornik, K., Zeileis, A., 2004. kernlab - An S4 Package for Kernel Methods in R. Journal of Statistical Software 11(9), 1-20. URL http://www.jstatsoft.org/v11/i09/

Liaw. A. and Wiener, M.,2002. Classification and Regression by randomForest. R News 2(3):18-22.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K., Thuiller, W, 2009. Evaluation of consensus methods in predictive species distribution modelling. Diversity and Distributions. 15:59-69

Milborrow, S. Derived from mda:mars by Hastie, T. and Tibshirani, R., 2012. earth: Multivariate Adaptive Regression Spline Models. R package version 3.2-3. http://CRAN.R-project.org/package=earth

Muñoz, M.E.S., Giovanni, R., Siqueira, M.F., Sutton, T., Brewer, P., Pereira, R.S., Canhos, D.A.L. & Canhos, V.P., 2009. OpenModeller: a generic approach to species' potential distribution modelling. GeoInformatica. DOI: 10.1007/s10707-009-0090-7

Orth, R.J., Luckenbach, M. and Moore, K.A., 1994. Seed Dispersal in a Marine Macrophyte: Implications for Colonization and Restoration. Ecology .75(7): 1927-1939Phillips, J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231-259

R Development Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Valle, M., Borja, Á., Chust, G., Galparsoro, I., and Garmendia, J.M., 2011. Modelling suitable estuarine habitats for *Zostera noltii*, using Ecological Niche Factor Analysis and Bathymetric LiDAR. Estuarine, Coastal and Shelf Science 94:144-154

van Katwijk, M.M., Hermus, D.C.R., 2000. The effect of physical disturbance on *Zostera marina* L. transplantations in the Dutch Wadden Sea. Marine Ecology-Progress Series 208:107-118

van Katwijk, M.M., Hermus, D.C.R., de Jong, D.J., de Jonge, V.N., 2000. Habitat suitability of the Wadden Sea for *Zostera marina* restoration. Helgoland Marine Research 54:117-128

Venables, W.N., and Ripley, B.D., 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0

# Modelling sensitive elasmobranchs habitat

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## Introduction

Worldwide, there is an increasing concern over the exploitation of elasmobranchs because their biology makes them highly vulnerable to overexploitation and to environmental changes compared with the majority of teleosts species (Dell'Apa *et al*., 2012). Most elasmobranchs are predators at or near the top of marine food chains and thus play an important role in marine ecosystems, potentially regulating, through predation, the size and dynamics of their prey populations (Steven *et al*., 2000). Their removal could affect on the structure and function of marine ecosystems, inducing changes in the trophic interactions at the community level due to selection removal of predators or prey species, competitors and species replacement.

In the Mediterranean Sea, this is of particular concern since sharks and rays make up a important percentage of the by-catch (Carbonell *et al*., 2003) and their mobile nature makes them potentially accessible to several fisheries at various bathymetric ranges (Ferretti *et al*., 2009). Evidence of changes in the number of elasmobranchs and decreases in the abundance of some species (e.g. *Raja clavata* and *Dipturus batis*) throughout the last decade have been reported for all the Mediterranean Sea and in particular for the highly exploited area Gulf of Lions (Abdulla, 2004).

The European Commission adopted in 2009 the first Action Plan for the conservation and management of elasmobranchs with the aim rebuilds their stocks under threat, and to set down guidelines for the sustainable management of the fisheries concerned (Mendoza *et al*., submitted). Moreover, the implementation of the ecosystem approach to fisheries management contemplates the protection of vulnerable habitats, policy to reduce by-catches and the study of the current and expected impacts to prepare efficient strategies in order to preserve the marine environment and in particular its living marine resources (Katsanevakis *et al*., 2009). To this end, the needed requirement is a solid knowledge of species-environment relationships (*Massutí & Moranta, 2003*) in order to assess the ecological role, biology, distribution, and life-history stages of elasmobranchs.

The present study focused on understanding the spatial distribution of the three most captured species (*Scyliorhinus canicula*, *Galeus melastomus* and *Etmopterus spinax*) by trawl commercial vessels in relation to environmental, geological and geographical factors along the continental shelf and slope of the Western Mediterranean Sea. Our aim is to identify the sensitive habitat of elasmobranch species for their conservation and as a reference point for the monitoring of future trends in the same area and comparison with other Mediterranean areas. With this purpose we used a Bayesian hierarchical spatial modelling to estimate and predict the probabilities of occurrence of the studied elasmobranch species, incorporating the extrinsic factors of habitats as covariates. In addition, in order to verify if the same species-environment interactions also affect other elasmobranch species less fished, Cluster Analysis (CA) and Multi Dimensional Scaling (MDS) techniques have been applied to bottom trawl surveys analyzing the species assemblages.

## Material and methods

The study was carried out in the Western Mediterranean (FAO division 37.1.1). However, for practical purposes of the present study, this area is considered in its narrower sense including only the Gulf of Alicante, between 37º15.6'and 38º 30.0' N, and 1º 0.0' W and 0º 30.0' E (*Figure 1*). The Gulf of Alicante has a surface area of 3, 392 km$^2$ and an average shelf width of approximately 32 km.

The largest fleet is the bottom trawl, with 169 vessels landing an average of 8,000 t per year. Trawling seabed usually takes place on the shelf, yielding a multispecific catch, European hake *Merluccius merluccius* (Linnaeus, 1758) being one of the main target species. Other species commonly caught are red mullet *Mullus barbatus* (Linnaeus, 1758), striped red mullet M*ullus surmuletus* (Linnaeus, 1758), octopus (*Octopus vulgaris* Cuvier, 1797), angler fish (*Lophius* spp. Artedi, 1758) and blue whiting (*Micromesistius poutassou* Risso, 1826).

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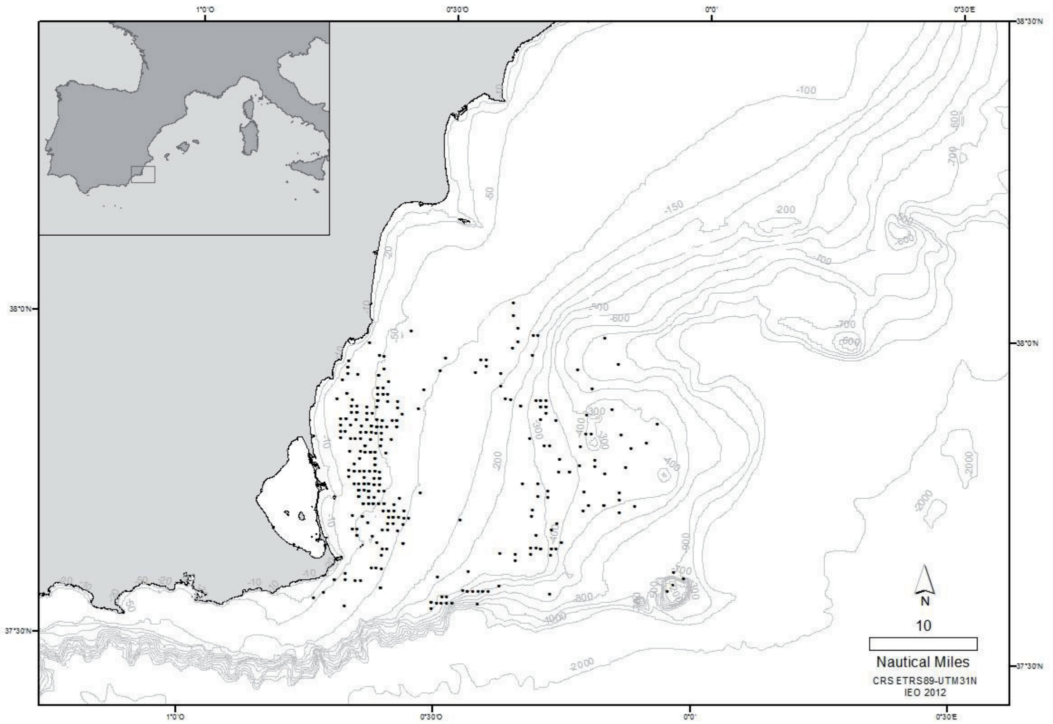

**Figure 1.** Map of the study area with the sampling locations indicated by black dots.

The data set includes 399 hauls of 25 different trawler vessels and has been provided by the Instituto Español de Oceanografía (IEO, Spanish Oceanographic Institute). The IEO provides the national input of the European Observers Programme for collecting fishery-dependent data. In particular, they collect samples from the commercial fleet with observers on board. This sampling has been carried from the 2003, usually involving about 2-3 observations every month. From this database we have used the geographical location and occurrence of the elasmobranch species for each haul. The fisheries were multispecies and none of the elasmobranchs were target species.

Extrinsic factors influencing the spatial distribution of elasmobranch species used are depth, which is often the main gradient along which faunal changes occur when analyzing shelf and upper slope assemblages (Kallianiotis *et al*., 2000), type of substratum (Demestre *et al*., 2000) and physical characteristics (such as Sea Surface Temperature (SST) and chlorophyll-*a*) of the water masses (Maravelias *et al.,* 2007). Bathymetry and type of substratum data was obtained from the IEO geo-viewer, accessible by the website of the Spanish Institute of Oceanography (http://www.ieo.es). The environmental satellite data, such as the monthly mean of chlorophyll-*a* and SST), has been extracted from the SeaWiFS (http://oceancolor.gsfc.nasa.gov).

Bayesian hierarchical spatial models were developed using occurrence data of the three most captured species (*Scyliorhinus canicula*, *Galeus melastomus* and *Etmopterus spinax*) as the response variable and a logit link function, to predict the mean presence probability of each of the species considered. In particular, assuming that the probability of catching a species is related to its presence, we model the occurrence of each species as a binary process, $Z_i \sim \mathrm{Bernoulli}(\pi_i)$, where $Z_i$ represents the occurrence (1 indicating presence; 0, absence) for each location *i*, and $\pi_i$ represents the probability of occurrence at location *i*. Then:

$Z_i$ ⍰ $\mathrm{Ber}(\pi_i)$,

$\mathrm{logit}(\pi_i) = X\beta + W_i$

where $X_i$ is the vector of covariates (logarithm of depth, the environmental variables and type of substratum) at location *i*, β is the vector of regression parameters, and $W_i$ are the components of the spatially structured random effect. This model assumes independence between the data. However, the geographical location introduces correlation since occurrence at nearby locations is influenced by similar environmental factors, so close locations should show similar occurrences for each species. The spatial effect, $W_i$, should collect this influence. The spatial effect was assumed to be temporarily independent because there was no evidence of consistent patterns over time.

Gaussian prior distributions for all the fixed effects in β are considered, while the prior distributions for *k* and τ, (representing respectively the range and scale parameter of the spatial effect, $W_i$), are assumed to be log-normal.

The inference has been performed using the R-INLA package (http://www.r-inla.org), which use *Integrated Nested Laplace Approximation* (INLA) (Rue *et al.,* 2009).

In order to predict the occurrence probability for elasmobranch species, especially in non-observed locations, we use the occurrence of the species at a new location as a random variable and compute, in addition to the estimation, a set of likely values together with their probabilities of being the true values at each of those new specific locations (Muñoz *et al.,* submitted).

Several models using different combinations of those covariates were fitted and the Deviance Information Criterion (DIC) introduced by Spiegelhalter *et al*. (2002) was used to compare competing models.

For the other elasmobranch species in which presence data were very limited, has not been possible to compute predictive models. In order to understand if the estimated species-environment interactions of the most fished species affect also other elasmobranch species less fished, multivariate analysis were applied.

Cluster Analysis (CA) and Multidimensional Scaling (MDS) were performed on a Euclidean similarity matrix with the average method, considering occurrence of each species to identify possible differences between the examined habitats. Multivariate analyses were carried out using the R software (R Development Core Team, 2009).

# Result

The main predictors of elasmobranch habitats in the western Mediterranean Sea were depth, type of substratum, followed by SST and chlorophyll-*a*.

Habitats associated with hard substrata and sandy beds, mainly from deeper waters, show greater probability of the presence of the studied species than those associated with mud from shallow waters (*Figure 2*). The temperature and chlorophyll-*a* concentration show a negative relationship with elasmobranchs occurrence.

The similarity dendrogram for the trawls hauls revealed the

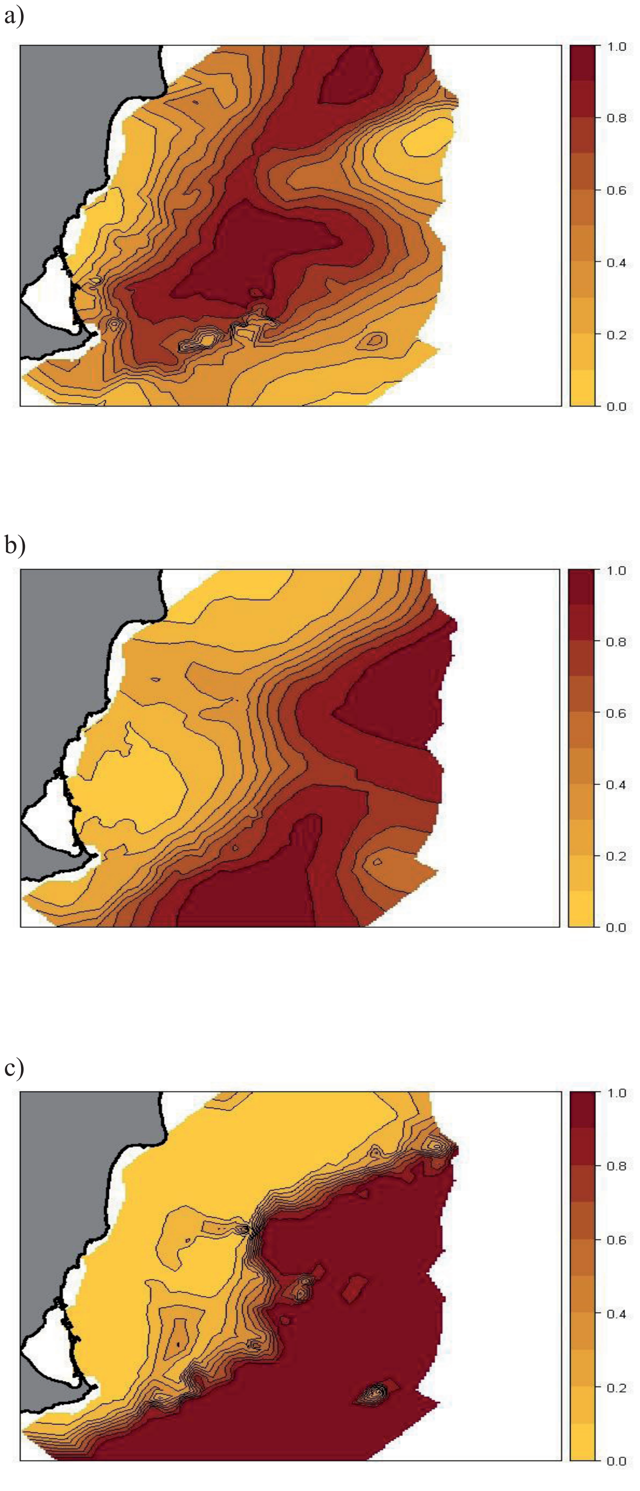

**Figure 2.** Median of the posterior probability of the presence of the *Scyliorhinus canicula* (A), *Galeus melastomus* (B) and *Etmopterus spinax* (C) in the Gulf of Alicante.

existence of three different assemblages for the elasmobranchs, which were confirmed by the MDS analysis (*Figure 3*). *Squalus acanthias* and *Myliobatis Aquila* form a separate group, *Pteromylaeus bovines* compose an individual group, and all the other elasmobranch species are included in a unique group.

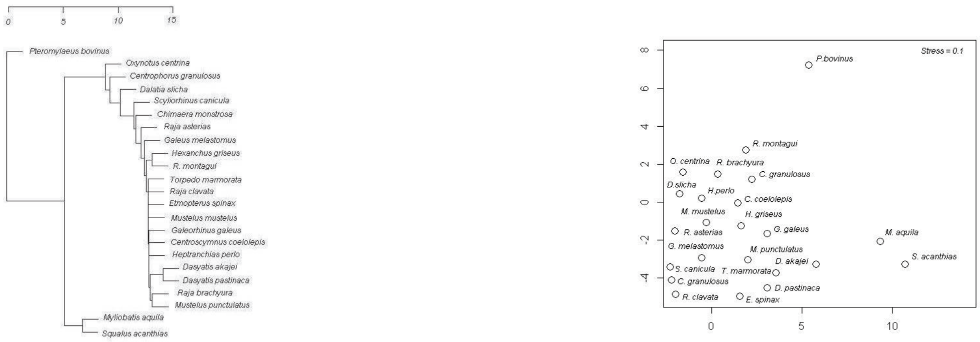

**Figure 3.** Dendrogram (A) and MDS ordination (B) of elasmobranch samples obtained during bottom trawl commercial hauls carried out in the Gulf of Alicante.

## Discussion

Fishery-dependent data were used to improve our understanding of habitat utilization by elasmobranchs in the western Mediterranean Sea, based on Bayesian spatial approach. Model parameters helped quantify habitat utilization and reveal important combinations of environmental variables for those species' habitat. The main predictors of elasmobranch habitats in the western Mediterranean were depth and type of substratum, followed by temperature and chlorophyll-*a*. These patterns were also consistent with those from other studies reporting on habitat utilization by the various species (e.g. *R. brachyura*, *R. montagui* and *S. stellaris* in Ellis *et al.,* 2005; *R. clavata* in Hunter *et al*., 2005; *S. canicula* in Vaz *et al.,* 2008).

Depth has been stated to be the main gradient along which fauna1 changes occur when analyzing shelf and upper slope assemblages (Demestre *et al*., 2000; Kallianiotis *et al*., 2000), and may be related to correlations with other important habitat variables like: productivity, prey and predator distributions, and sediment type. A good knowledge of bathymetric distribution of marketed fish is essential for fisheries management even though depth is not always a causal predictor of fish occurrence.

Our analyses show that the probability of the presence of all the elasmobranch species is greater in deeper waters compared with shallow waters. This also explains the negative relationship between the distribution of temperature, chlorophyll-*a* concentration and elasmobranchs. Shallow and sunlit waters above the continental shelf are usually areas of high productivity and SST mean values, while the deeper waters away from coastlines usually lack sun, nutrients and present low values of chlorophyll-*a* concentration and SST. Consequently, the presence of elasmobranchs is higher in deeper waters where the SST and concentration of chlorophyll-*a* is lower.

This study confirmed the importance of the type of substratum in the patterns of elasmobranchs spatial distribution, as substrate type was included in the best models of all species. Our analysis shows that elasmobranchs prefer hard and sandy substrates while muddy ones affect their occurrence negatively. This preference has already been documented (Skjæraasen & Bergstad, 2000) and probably it is partly attributed to the distribution of their preferred prey, as crustaceans are the most frequently occurring food items in their stomachs (Holden & Tucker, 1974).

There is a specific need to make sure that important habitats are of sufficient extent and quality to maintain available stock, taking into consideration any threats of habitat degradation (e.g. through dredging, aggregate extraction, pollution), from human exploitation (fisheries) and from environmental change. An improved knowledge of the habitat utilization of elasmobranchs is needed for the improved management of both commercial stocks and species of conservation interest and the present study highlighted some of the key areas for the main species in the western Mediterranean Sea. In terms of fisheries management, habitat maps could be used to select areas for improved regional management or technical measures (Wiegand *et al.,* 2011).

Although the present study was limited to three species, multivariate analysis show that of the 23 species of elasmobranchs caught in this area, 20 are fished always jointly with the species examined and share the same habitats. Our results may be helpful for the identification and mapping of marine habitats crucial for the conservation of the whole elasmobranch community.

# References

Carbonell, A., Azevedo, M., 2003. Application of non-equilibrium production models to the red shrimp (*Aristeus antennatus* Risso, 1816) fishery in the northwestern Mediterranean. Fishery Research, 65: 323-334.

Dell'Apa, A., Kimmel, D.G., Cló, S., 2012. Trends of fish and elasmobranch landings in Italy: associated management implications. ICES Journal of Marine Science, doi:10.1093/icesjms/fss067.

Demestre, M., Sánchez, P. & Abelló, P., 2000. Demersal fish assemblages and habitat characteristics on the continental shelf and upper slope of the north-western Mediterranean. Journal of Marine Biological Association UK, 80: 981-988.

Ellis, J.R., Cruz-Martinez, A., Rackham, B.D., Rogers, S.I., 2005. The distribution of chondrichthyan fishes around the British Isles and implications for conservation. Journal of Northwest Atlantic Fisheries Science, 35:195-213.

Farrell, E.D., Clarke, M.W., Mariani, S., 2009. A simple genetic identification method for Northeast Atlantic smoothhound sharks (Mustelus spp.). ICES Journal of Marine Science, 66: 561-565.

Holden, M.J., Tucker, R.N., 1974. The food of *Raja clavata* Linnaeus 1758, *Raja montagui* Fowler 1910, *Raja naevus* Müller and Henle 1841 and *Raja brachyura* Lafont 1873 in British waters. ICES Journal of Marine Science, 35: 189-19.

Hunter, E., Buckley, A.A., Stewart, C., Metcalfe, J.D., 2005. Migratory behaviour of the thornback ray, *Raja clavata* L., in the southern North Sea. Journal of Marine Biological Association UK, 85: 1095-1105.

Kallianiotis, A., Sophronidis, K., Vidoris, P. & Tselepides, A., 2000. Demersal fish and megafaunal assemblages on the Cretan continental shelf and slope (NE Mediterranean): seasonal variation in species density, biomass and diversity. Progress in Oceanography, 46: 429-455.

Katsanevakis, S., Maravelias, C.D., Damalas, D., Karageorgis, A.P., Tsitsika, T.E., Anagnostou, C., Papaconstantinou, C., 2009. Spatiotemporal distribution and habitat use of commercial demersal species in the eastern Mediterranean Sea. Fisheries Oceanography, 18:6, 439-457.

Maravelias, C.D., Tsitsika, E.V., Papaconstantinou, C., 2007. Environmental influences on the spatial distribution of European hake (*Merluccius merluccius*) and red mullet (*Mullus barbatus*) in the Mediterranean. Ecology Research, 22: 678-685.

Massutí, E., Moranta, J., 2003. Demersal assemblages and depth distribution of elasmobranches from the continental shelf and slope off the Balearic Islands (western Mediterranean). ICES Journal of Marine Science, 60: 753-766.

Muñoz, F., Pennino, M.G., Conesa, D., López-Quílez, A., Bellido, J.M. Estimation and prediction of the spatial occurrence of fish species using Bayesian latent Gaussian models. Submitted.

R Development Core Team, 2009. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna 3-900051-07-0, http://www.R-project.org.

Rue, H., Martino, S., Chopin, N., 2009. Approximate bayesian inference for latent gaussian models by using integrated nested laplace approximations. Journal of the Royal Statistical Society, 71: 319-392.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P., Van der Linde, A., 2002. Bayesian measures of model complexity and fit. Journal of the Royal Statistical Society, Series B, 64: 583-616.

Stevens, J.D., Bonfil, R., Dulvy, N.K., Walker, P., 2000. The effects of fishing on sharks, rays and chimaeras (chondrichthyans), and the implications for marine ecosystems. . ICES Journal of Marine Science, 57: 476-494.

Skjæraasen, J.E., Bergstad, O.A., 2000. Distribution and feeding ecology of *Raja radiata* in the northeastern North Sea and Skagerrak (Norwegian Deep). ICES Journal of Marine Science, 57: 1249-1260.

Vaz, S., Martin, C.S., Eastwood, P., Ernande, B., Carpentier, A., Meaden, G.J., Coppin, F., 2008. Modelling species distributions using regression quantiles. Journal of Applied Ecology, 45: 204-217.

Wiegand, J., Hunter, E., Dulvy, N.K., 2011. Are spatial closures better than size limits for halting the decline of the North Sea thornback ray, *Raja clavata*? Journal of Marine and Freshwater Research, 62: 722-733.

# Marine pelagic ecosystems in the vicinity of Gibraltar Strait: a physical-biogeochemical coupled model approach

**Catarina Guerreiro[a], Diego Macías[a], Álvaro Peliz[b], Temel Oguz[c], Laura Prieto[a], Javier Ruiz[a]**

The Gulf of Cadiz and the Alboran Sea enclose the unique connection between the Mediterranean Sea and the open ocean, the Strait of Gibraltar, which control the biogeochemical budget of the semi-enclosed Med Sea. In order to investigate the marine ecosystems of the region and also to being able of predicting changes in its biogeochemical characteristics, we present a primary study of an atmosphere-ocean-biology regional modeling system.

The simulations were performed using the Regional Ocean Modeling System (ROMS) with nesting capabilities (Shchepetkin and McWilliams, 2005; Penven *et al*., 2006) coupled to a Fasham type (Fasham *et al*., 1990) biological module. The single compartment (NPZD) ecosystem consists of four state variables: nitrate, phytoplankton, zooplankton and detritus. The model was forced with climatologic conditions and tested for different setups of the biological module in order to determine the biological parameters values and equations more adequated to represent the first trophic levels of the region. The setup validation was performed by comparing total chlorophyll output from the model with climatologic satellite data in eight control points at both sides of the strait by using Taylor's Diagrams (Taylor, 2001).

In a first approach, the higher correlation coefficient for the overall eight points (R=0.66) was obtained by using the standard Fasham's equations and only changing four parameters to site-specific values (Oguz *et al*., submitted): maximum grazing rate (0.6 d$_{-1}$), zooplankton mortality to detritus (0.05 d$_{-1}$), phytoplankton mortality to detritus rate (0.024 d$_{-1}$) and light attenuation by chlorophyll (0.03 (m$_2$.mg.Chla)$_{-1}$).

However, the individual analysis of the control points confirms that each modification in the biological module affects in a distinct way to each region. For instance a setup that yields maximum R values for the majority of the points, Cape of San Vincent, Huelva front, Western Alboran gyre and Estepona, involves changing (beside the above-mentioned parameters) the zooplankton grazing function (to a Holling type III, Holling, 1966) and scaling phytoplankton growth by 1/3.7 (Macías *et al*., 2012). However, this configuration is extremely bad for representing the Guadalquivir zone, which is a key point for the Gulf of Cadiz ecosystem dynamics, as R-values decreased below 0.01 in this coastal zone.

Therefore, our recommendation is to use the standard configuration with only the above four parameters changed for the single compartment application module. Our results clearly indicate that using a more complex biogeochemical code is a reasonable option to better represent the ecosystems in the vicinity of the Strait of Gibraltar. We propose using at least a N2P2Z2D2 model to take into account the very different food webs present in nutrient-rich coastal waters and in oligotrophic open-sea regions.

## References

Fasham, M.J.R. , Ducklow, H.W., McKelvie, D.S. , 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. Journal Marine Research, 48, pp. 591–639

Holling, C. S., 1966, The functional response of invertebrate predators to prey density. Memoirs of the Entomological Society of Canada 48: 1-86.

Macías, D., Franks, P.J.S, Ohman, M.D., Landry, M.R., 2012. Modelling the effects of coastal wind- and wind-stress curldriven upwellings on plankton dynamics in the Southern California Current system. Journal of Marine Systems 94, 107-119.

Oguz, T., Macías, D., Renault, L., Ruiz, J., Tintore, J., submitted. Controls of plankton production by pelagic fish predation and resource availability in the southwestern Mediterranean Sea. Progress Oecanography.

Penven, P., Debreu, L., Marchesiello, P., McWilliams, J.C., 2006. Evaluation and application of the ROMS 1-way embedding procedure to the central California upwelling system. Ocean Modelling, 12, 157-187.

Shchepetkin, A.F., McWilliams, J.C., 2005. The Regional Ocean Modeling System: A split-explicit, free-surface, topography following coordinates ocean model. Ocean Modelling, 9, 347-404.

Taylor, K.E., 2001. Summarizing multiple aspects of model performance in a single diagram. J. Geophys. Res., 106, 7183-7192.

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# “Restoring” marine biodiversity in an urbanized environment: a major challenge for the 21st century

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Urbanization, with its consequent loss of natural habitats, is widely recognized as a major environmental impact, so much so, that cities and their environments have been considered novel, emerging ecosustems. The effects of urban development on intertidal and inshore habitats have been less widely investigated, despite the fact that most of the world’s largest cities are coastal. Changes to intertidal habitats in and around cities mimic changes to terrestrial habitats and include fragmentation, loss and degradation of natural habitat and influx of invasive species. There is also growing awareness of the need to conserve species in areas where many people have access, largely prompted by the growing environmental movement. This has led to demands to restore or replace lost habitats, which is a challenge in areas which have been very altered by urban development and which are subjected to ongoing environmental disturbances. I will summarise some of the major changes to intertidal and inshore habitats due to urban development and associated activities. I will also describe examples of some of the recent research programmes that are investigating how to restore these damaged or lost marine habitats, or are developing techniques to create novel habitat for conservation of species when options to restore habitat have been lost.

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# A comparison of primary production models in an Antarctic mesoscale area

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## Introduction

In the last decades remote sensing models to estimate ocean primary production (PP) have been developed in order to monitor large areas of the global ocean (i.e. Eppley *et al*., 1985; Behrenfeld and Falkowsky 1997; Marra *et al*., 2003; Behrenfeld *et al*., 2005; Westberry *et al*., 2008) as well as specific sites like the Southern Ocean (Dierssen *et al*., 2000; Arrigo *et al*., 2008). Several papers have focused on the comparison of the results obtained by these models (Campbell *et al*., 2002; Carr *et al*., 2006) and controversial results, in relation to the algorithms used, have been presented, especially for the Southern Ocean (Campbell *et al*., 2002; Carr *et al*. 2006; Shang *et al*. 2010). This region is a well known High Nutrient Low Chlorophyll area (HNLC), and it is generally assumed to be controlled by the supply of micronutrients (especially iron) and light that are needed for photosynthesis by primary producers. This type of bottom-up control suggests that the ecosystem will be sensitive to changes in physical forcing that influence the light and nutrient environment experienced by phytoplankton (e.g. upwelling, mixed layer depth, sea ice) (Rintoul *et al*., 2012).

Three kind of remote-sensing models and one based in the Metabolic Theory of Ecology (MTE) were applied to real data obtained during *Coupling* cruise (January 2010) in a mesoscale area of the Southern Ocean around the South Shetland Islands (SSI). The results obtained were compared and discussed to discern why they differ. The previous knowledge of the study area has allowed us to implement improvements in the selected models to achieve realistic results of PP based on the limitation by light, mixed layer depth and nutrient concentration.

## Data collection and modelling

All the data used in this study were collected from *RV BIO-Hespérides* during *Coupling* cruise, 8th to 27 th January 2010, using a rosette system of 24 oceanographic 12-L Niskin bottles operated with a CTD Seabird 911plus. The survey was conducted around the SSI, with a main transect sampled from Drake Passage to Bransfield Strait (hereafter, Transect 1, Fig. 1). Sampling was performed at 6 depths (from 5 to 100 meters) including the depth of the fluorescence maximum (DFM). Chlorophyll a was measured fluorometrically following UNESCO (1994). Macronutrients concentration was measured by means of a Technicon TRAACS 800 System Autoanalyzers using standard protocols (Grasshoff *et al*., 1983). Phytoplankton composition and abundance was analysed by overlapping Flow cytometry and FlowCAM techniques to include the whole phytoplankton assemblage from 2 to 200 Em Equivalent spherical diameter (ESD). Plankton volume was then converted to carbon using Mender-Deuer *et al*. (2000) equations. PP was measured on board only at 11 stations at two sampling depths, including surface and DFM, using the $^{13}$C method. We used the Si* tracer (calculated as the concentration of silicate minus nitrate concentration) defined by Sarmiento *et al*. 2004 as a proxy for iron limitation in the sampling area. The irradiance at the sea surface was monitored on deck with a Kipp & Zonen CM11 sensor. The average daily irradiance just below the sea surface (Io) was estimated considering 0.8 as the transmittance at the air–sea interface (Figueiras *et al*., 1999).

Five models based on data surveyed during the cruise were used to calculate PP. They can be classified into 3 groups:

1. Models based on Chl a: VGPM (Behrenfeld and Falkowsky 1997) and that of Dierssen *et al*. (2000) for the Western Antarctic Peninsula. Both models are not vertically resolved, in the sense that they estimate vertically integrated values from surface data.

VGPM: Net PP (NPP) (mgC/m$^2$/d) = Chl$_0$ a x Zeu x f(Io) x DL x P$^B$opt ; f(Io) = 0.66125 x Io / (Io + 4.1) ; P$^B$opt = -3.27 x 10$^{-8}$ T$^7$ + 3.4132 x 10$^{-6}$ T$^6$ – 1.348 x 10$^{-4}$ T$^5$ + 2.462 x 10$^{-3}$ T$^4$ – 0.0205 x T$^3$ + 0.0617 x T$^2$ + 0.2749 x T + 1.2956

Dierssen's: NPP (mgC/m$^2$/d) = Chl$_0$ a x $Z_{eu}$ x F x DL x $P^{B}_{opt}$ ; F = $I_o$ / ($I_o$ + 11.77)

2. Models based on phytoplankton biomass: one based on Metabolic Theory of Ecology (MTE) developed by López-Urrutia *et al*., (2006) and that of Arrigo *et al*. (2008) for the whole Southern Ocean. As far as we know, this is the first time that a model based on the MTE is used for the calculation of PP in Antarctic waters. Arrigo *et al*. (2008) is in essence very similar to MTE, the main difference is that MTE calculates PP on an individual basis while

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Arrigo *et al*. (2008) uses the total biomass of the phytoplankton community.

López-Urrutia's: $\ln(\mathrm{NPP}\ (\mathrm{mmol\ O_2/cell/d}))_z = -13.18 + 1.02 \times \ln(M) - 0.28 \times (1/KT) + \ln(I_z/(I_z + 1.52))$ ; $I_z = I_o \times \exp(-K_d \times Z)$, using a Photosynthetic quotient (PQ) of 1.25 for carbon conversion and the cell abundance (cells/m3) in each depth to express NPP in mgC/m$^3$/d.

Arrigo's: $\mathrm{NPP}\ (\mathrm{mgC/m^3/d}) = \int C_{(z)} \times G_{(z,t)}\, dt$ ; $G_{(z,t)} = \mu\ \max_{(t)} \times L_{(z,t)}$ ; $\mu\ \max_{(t)} = \mu_0 \times \exp[r \times t_{(t)}]$ ; $L_{(z,t)} = 1 - \exp(-I_{(z,t)} / Ek'_{(z,t)})$

3. A model based on the Chl a/C ratio: CbPM (first described by Behrenfeld *et al*., 2005 and updated by Westberry *et al*., 2008). The primary processes which drive vertical changes in Chl a concentration in the CbPM are those associated with physiological, intracellular adjustments to ambient light and nutrient conditions:

$\mathrm{NPP}\ (\mathrm{mgC/m^3/d}) = \mu_{(z)} \times C(z)$ ; $\mu_{(z)} = \mu\ \max \times f(\mathrm{Nut}, T) \times f(I_g)$; $f(\mathrm{Nut}, T) = (\mathrm{Chl\ a/C})_{in\ situ} / (\mathrm{Chl\ a/C})_{max}$ ; $f(I_g) = 1 - \exp(-3 \times I_g)$. $(\mathrm{Chl\ a/C})_{max} = 0.022 + (0.045 - 0.022) \times \exp(-3 \times I_g)$, this expression represents Chl a/C in nutrient-replete, optimal growth conditions for a large sum of regions, so we re-parameterize this equation using quantile regression (enveloping 95% of our in situ data) and obtained specifically: $(\mathrm{Chl\ a/C})_{max} = 0.0091 + 0.00793 \times \exp(-3 \times I_g)$. µ max was calculated using Eppley's (1972) equation and the maximum temperature detected in the study area.

The integration depth for the two latter groups was that of the photic layer in the stations where the depth of 1% of light was deeper than the upper mixed layer (*Zml*) and was *Zml* in the stations where the photic layer was shallower than the upper mixed layer. *Zml* was calculated for each station following Kara *et al*., (2000). To calculate the irradiance term in each model we took into consideration the median mixed layer light level for those depths over the *Zml* ($I_{zml}$) and $I_z$ for deeper depths. To avoid the "fallacy of the averages" $I_{zml}$ was calculated as:

$$I_{zml} = \frac{\Sigma\,(I_o \times \exp(-K_d \times Z))}{Zml}$$

**Table 1.** Symbols and units used.

| Symbol | Units | Description |
|---|---|---|
| $P^B_{opt}$ | mgC/mgChl/h | Maximum chlorophyll-normalized C fixation rate within a water column |
| $I_o$ | mol photon/m$^2$/day | Surface daily photosynthetically available radiation (PAR) |
| $I_z$ | mol photon/m$^2$/day | Daily PAR at each depth |
| $Z_{eu}$ | m | Euphotic zone depth |
| $Z_{ml}$ | m | Mixed layer depth |
| $\mathrm{Chl}_0$ a | mg/m$^3$ | Surface Chlorophyll a concentration |
| Chl a | mg/m$^3$ | Chlorophyll a concentration |
| DL | hour | length of day time |
| $\mu_0$ | 0.59 d$^{-1}$ | Phytoplankton growth rate at 0ºC, as in Eppley 1972 |
| µ | d$^{-1}$ | Phytoplankton growth rate |
| M | pg C | Individual phytoplankton biomass |
| C | mg C/ m$^3$ | Phytoplankton biomass |
| T | ºK | Temperature |
| t | ºC | Temperature |
| $K_d$ | m$^{-1}$ | Diffusive attenuation coefficient |
| K | 8.62x10$^{-5}$ eV/k | Boltzman's factor |
| $Ek'_{(z,t)}$ | Emol photon/m$^2$/s | Spectral photoacclimation parameter |

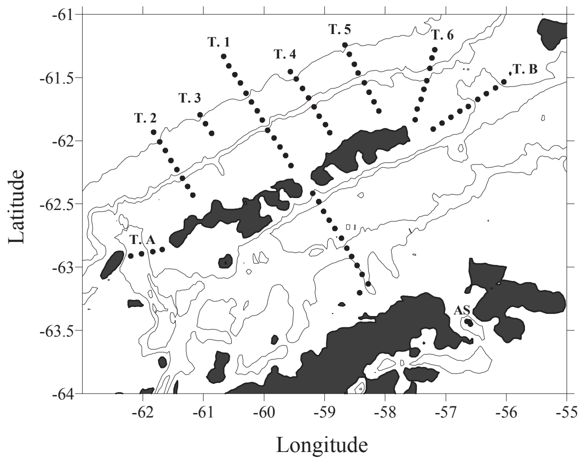

**Figure 1.** Map of the study area and stations locations.

# Results

The range of values for the input variables is roughly the range observed for our study period: for SST, -1.14 to 1.76 .C reaching the highest temperatures in the Drake area and the lowest in the stations close to the Antarctic Peninsula; for mixed-layer depth, 12–362 m, with the deepest layers related with hydrographical fronts and subduction points; for surface daily PAR, 8–50 mol photon/m2/day; for euphotic depth, 36-144 m; for chlorophyll concentration, 0.04–2.39 mg/m3 reaching the highest values in the southern area and the lowest in the Drake Passage, and for phytoplankton biomass in each sampling depth, 32.90-278.95 mg C/ m3. PP 13C values range from 0.52 to 19.32 (mg C/m3/d). For further details of physicochemical variables and water masses around the SSI see Hewes *et al*. (2009), SangraÅL *et al*. (2011). The results for discrete depths' and integrated NPP of the different models are presented in Tables 2 and 3.

**Table 2**. Mean and standard deviation (Std) of NPP (mg C/m3/d).

| | MTE | Arrigo's | CbPM |
|---|---|---|---|
| Mean | 37.97 | 29.29 | 11.46 |
| Std | 40.42 | 29.31 | 16.09 |

**Table 3.** Integrated mean and Std of NPP (mg C/m2/d)

| | VGPM | Dierssen's | MTE | Arrigo's | CbPM |
|---|---|---|---|---|---|
| Mean | 684.56 | 601.07 | 2753.25 | 2172.45 | 775.93 |
| Std | 300.92 | 300.58 | 1097.09 | 758.87 | 480.75 |

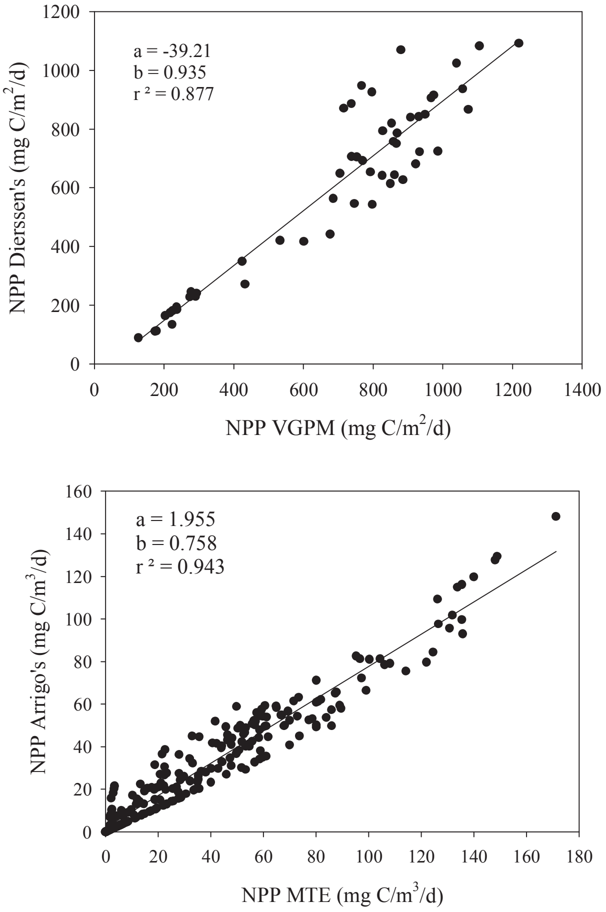

**Figure 2.** Linear regression between integrated models based on Chl a (VGPM vs Dierssen's) (on the left) and between discrete depths models based on phytoplankton biomass (MTE vs Arrigo's)

The production estimated from ocean-color algorithms (1st group) based on Chl a was found to be highly correlated between them when using in situ data as the inputs of the algorithms, with a slope close to a 1:1 relationship. Models from the second group gave also similar results between them with higher correlations ($R^2 = 0.943$) (Fig.2). Biomass-based models gave significant higher NPP results than Chl a-based models (p-valor < 0.05). In the case of the CbPM mean values were closer to group 1, but the overall trend in the study area was well defined between this 3rd group and the 2nd one with a power equation: $\ln Y = \ln a + b \ln X$ $Y = a X^b$: NPP Arrigo's = 4.145 x (NPP CbPM)$^{0.893}$ , $R^2 = 0.957$ (Fig. 3), CbPM vs MTE gave similar results (data not shown). There were no limitation for nitrate along the study area, neither phosphate but silicate distribution (Si* tracer) was selected as a reference for a possible iron limitation along the northern stations, as revealed by the strong silicate drawdown detected in the Drake Area (Fig. 4) summed to deep DFM and low Chl a values (Holm-Hansen *et al*., 2005).

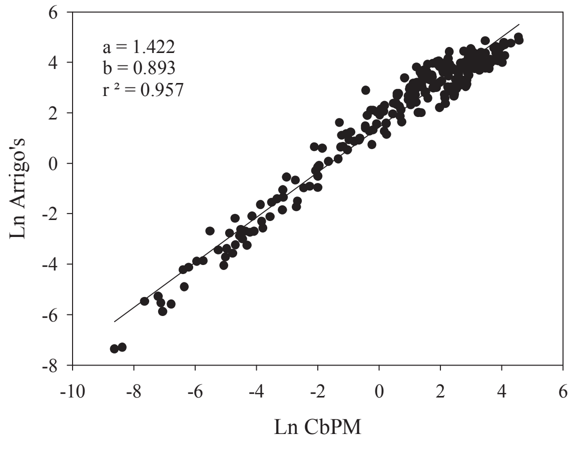

**Figure 3**. Linear regression between Ln-CbPM and Ln-Arrigo's.

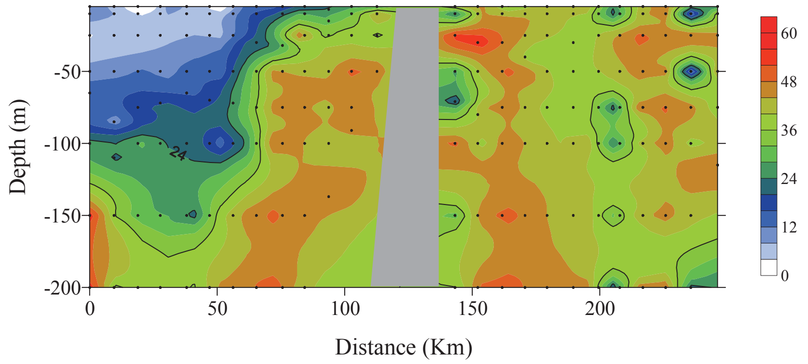

**Figure 4.** Silicate (EM) distribution along Transect 1, north (left) to south (right)

## Discussion

The overall conclusion obtained by those authors who estimate and compare PP using general models for areas as heterogeneous as the whole Southern Ocean, is the introduction of large errors (either overestimates or underestimates) due to the lack of punctual information (hydrographical fronts, subduction areas, eddies…). It is necessary to establish boundary conditions to obtain good results, especially at a mesoscale range. Carr *et al*. (2006) affirmed that the Southern Ocean is unquestionably the most challenging large basin, so it has been probed that the vertically integrated models such as those based just in surface Chl a (group 1, VGPM and derivatives) are too simple. Dierssen *et al*. (2000) comparing their results with data measured in situ, along Western Antarctic Peninsula (WAP), using $^{14}$C obtained high correlations explaining over 70% of the production variability. We must point out that they included few stations in the slope area underestimating the potential role of micro-nutrients (especially iron) in controlling the distribution, timing, and rates of primary production in this region (Seguret *et al*., 2012).

Although *Coupling* cruise was conducted at the end of the phytoplankton bloom, in some stations the biomass, specially nanophytoplankton, was still high. The use of 2$^{nd}$ group models seem to overestimate the NPP because the limitant terms do not include nutrients, they are based just in irradiance, temperature, vertical mixture limitations and body size of phytoplankton cells. In those stations situated in the Drake area, where the melting occurred much earlier in time and therefore the phytoplankton bloom, although a bulk of small size phytoplankton cells remained despite iron limitation, it did not achieve an optimal production yield. Arrigo's theoretical model is simple in some assumptions because it uses constant ratios of C:Chla for the whole Southern Ocean and assumes that Chl a concentration is constant from surface to *Zml*. Our input data do not confirm these assumptions, therefore it is necessary to introduce a variable C:Chl a ratio for each depth and station and study which physicochemical characteristics drive this variation. The high correlation found between MTE and Arrigo's models highlights the potential uses of MTE in the Southern Ocean, making suitable the 3/4 allometric scaling theory in this area with and activation energy for autotrophic processes close to the reference value of $E_a = 0.32$ eV.

Behrenfeld *et al*. (2005) state that, at a global scale, surface nutrients decrease with increasing Sea Surface Temperature (SST). As nutrients can not be directly measured from space, they used SST to infer nutrient limitation from the term: f(Nut, T) = $(\text{Chl a/C})_{in\ situ}$ / $(\text{Chl a/C})_{max}$ . When in situ nutrient data from our survey are used, not only a common trend of Behrenfeld's term, f(Nut, T), and SST is observed, but also a common trend with Si* tracer (Fig. 5, left). The power relationship found between CbPM and Arrigo's models (Fig. 3) showed that differences were more pronounced in values below 40 mg C/m$^3$/d which agree with our conclusion of the overestimation of 2$^{nd}$ group models in those stations limited by nutrients. Although few stations were sampled for $\text{PP}_{\text{in situ}}$ experiments, and the scarce values at discrete depths are not comparable to those of integrated models, a similar spatial trend with the Si* tracer was detected (Fig. 5, right).

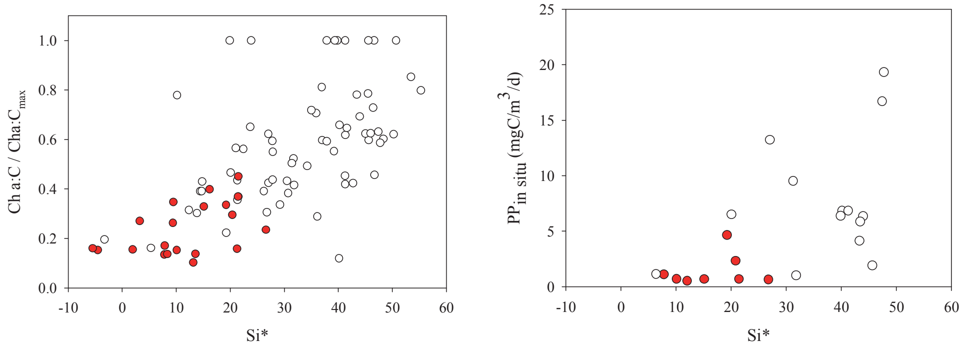

**Figure. 5.** Scatter plot between Si* tracer and f(Nut, T) (left). Scatter plot between Si* tracer and $\text{PP}_{\text{in situ}}$ (mg C/m$^3$/d) (right). Red dots are stations situated in the Drake Area.

We did not include Westberry's *et al*. (2008) nitracline depth consideration because nitrate was not limitant, taking constant values along the study area. Also we did not consider Chl/C = 0.0003 mg Chl/mg C when $\mu = 0$, since the variation is negligible. Finally the update introduced by Westberry *et al*. (2008) in the irradiance term (Ig) = 1 – exp (-5 x Ig), was rejected because it was less restrictive than Behrenfeld's one. Taking into account previous data of photosynthetic efficiency around the SSI, we observed photosaturation at surface layers in those stations sampled during sunny days. Only stations with deep *Zml*, or sampled in very cloudy days, may be experiencing light limitation. The improvements that we have introduced to CbPM have already been described in previous models as the original of Howard and Yoder (1997): the calculation of the maximum growth rate as a function of SST according to Eppley (1972) and the integration of NPP to the mixed-layer depth rather than to the euphotic depth.

In short, we consider that the results obtained with our updated version of CbPM (Fig. 6) fit with the real situation that was taking place during the austral summer of 2010. This conclusion could be extrapolated to other sites of the Southern Ocean, keeping in mind that each area of Antarctica is going to be limited by a specific variable. Shang *et al*. (2011) did not find good results using CbPM because they did not consider several aspects that we did.

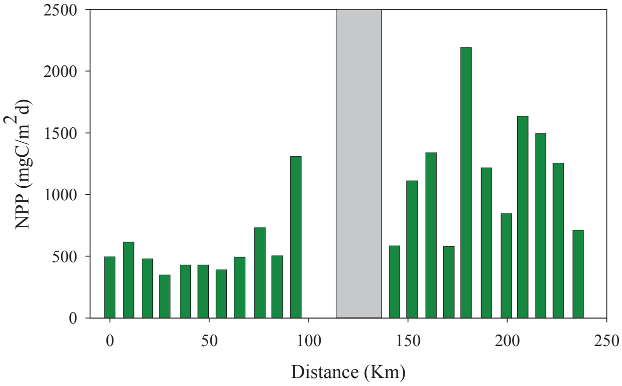

**Figure 6.** Net Primary Production (NPP) output from CbPM along Transect 1.

Prior knowledge of the study area is essential, especially for mesoscale studies, but in this paper we have highlighted the ability of models developed from remote sensing data to calculate PP with real input data. The calculation of PP can be performed with good results through these indirect methods and avoid the tedious, and non always precise (i.e. Richardson, K. 1991; Arístegui *et al*. 1996), $^{14}$C or $^{13}$C incubations on board.

# References

Arístegui, J., Montero, M. F., Ballesteros, S., Basterretxea, G., van Lenning, K. 1996. Planktonic primary production and microbial respiration measured by $^{14}$C assimilation and dissolved oxygen changes in coastal waters of the Antarctic Peninsula during austral summer: implications for carbon flux studies. *Mar. Ecol. Prog. Ser.* 132, 191-201.

Arrigo, K. R., van Dijken, G. L., Bushinsky, S. 2008. Primary production in the Southern Ocean, 1997-2006. *J. Geophys. Res.* **113**, 10.1029/2007JC004551.

Behrenfeld, M. J., Falkowski, P. G. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol.Oceanogr.* **42**, 1-20.

Behrenfeld, M. J., Boss, E., Siegel, D. A., Shea, D. M. 2005. Carbon-based ocean productivity and phytoplankton physiology from space. *Global biogeochem. cy.* **19**, 10.1029/2004GB002299.

Campbell, J. *et al*. 2002. Comparison of algorithms for estimating ocean primary production from surface chlorophyll, temperature, and irradiance. *Global Biogeochem. Cy.* **16**, 10.1029/2002GL015068.

Carr,M.-E. *et al*. 2006. A comparison of global estimates of marine primary production from ocean color. *Deep-Sea Res. II* **53**, 741-770.

Dierssen, H. M., Vernet, M., Smith, R. C. 2000. Optimizing models for remotely estimating primary production in Antarctic coastal Waters. *Antarct. Sci.* **12**, 20-32.

Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. *Fish. B.-NOAA* **70**, 1063-1085.

Eppley, R. W., Stewart, E., Abbott, M. R., Heyman, U. 1985. Estimating ocean primary production from satellite chlorophyll. Introduction to regional differences and statistics for the Southern California Bight. *J. Plankton Res.* **7**, 57-70.

Figueiras, F. G., Arbones, B., Estrada, M. 1999. Implications of bio-optical modelling of phytoplankton photosynthesis in Antarctic waters: Further evidence of no light limitation in the Bransfield Strait. *Limnol. Oceanogr.* **44**, 1599-1608.

Grasshoff, K., Ehrhardt, M., Kremling, K., (Eds) 1983. Methods of Seawater Analysis. Verlag Chemie, Weinheim. pp: 600.

Hewes, C. D., Reiss, C. S., Holm-Hansen, O. 2009. A quantitative analysis of sources for summertime phytoplankton variability over 18 years in the South Shetland Islands (Antarctica). *Deep-Sea Res. I* **56**, 1230-1241.

Holm-Hansen, O., Kahru, M., Hewes, C. D. 2005. Deep chlorophyll *a* maxima (DCMs) in pelagic Antarctic waters. II. Relation to bathymetric features and dissolved iron concentrations. *Mar. Ecol. Prog. Ser.* 297, 71-81.

Howard, K. L. and Yoder, J. A. 1997. Contribution of the subtropical oceans to global primary production. In: Liu, C.-T. (Ed.), Space Remote Sensing of Subtropical Oceans. COSPAR Colloquia Series, vol. 8. Proceedings of COSPAR Colloquium on Space Remote Sensing of Subtropical Oceans, Taiwan. Pergamon, New York, pp. 157–168.

Kara, A. B., Rochford, P. A., Hurlburt, H. E. 2000. An optimal definition for ocean mixed layer depth. *J. Geophys. Res.* **105**, 16803-16821.

López-Urrutia A., San Martín, E., Harris, R. P., Irigoien, X. 2006. Scaling the metabolic balance of the oceans. *PNAS* **103**, 8739-8744.

Marra, J., Ho, C., Trees, C. 2003. An alternative algorithm for the calculation of primary productivity from remote sensing data. LDEO Technical Report #LDEO-2003-1.

Menden-Deuer, S., Lessard, E. J. 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnol.Oceanogr.* **45**, 569-579.

Richardson, K. 1991. Comparison of 14C primary production determinations made by different laboratories. *Mar. Ecol. Prog. Ser.* 72, 189-201.

Rintoul, S. R., Sparrow, M. D., Meredith, M., Wadley, V., Speer, K., Hoffman, E., Summerhayes, C. P., Urban,E., Bellerby, R. 2012. The

Southern Ocean Observing System: Initial Science and Implementation Strategy. SCAR, Cambridge, 74 pp.

Sangrà, P., Gordo, C., Hernández-Arencibia, M., Marrero-Díaz, A., RodriÅLguez-Santana, A., Stegner, A., Martínez-Marrero, A., PelegriÅL, J. L., Pichon, T. 2011. The Bransfield current system. *Deep-Sea Res. I* **58**, 390-402.

Sarmiento, J.L, Gruber, N., Brzezinski, M. A., Dunne, J. P. 2004. High-latitude controls of thermoclines nutrients and low latitude biological productivity. *Nature* **427**, 56-60.

Shang, S. L., Behrenfeld, M. J., Lee, Z. P., O'Malley, R. T., Wei, G. M., Li, Y. H., Westberry, T. 2010. Comparison of primary productivity models in the Southern Ocean-preliminary results. *Proc. SPIE* **7678**, 10.1117/12.853631.

UNESCO 1994. Protocols for the Joint Global Ocean Flux Study (JGOFS) Core Measurements. Manual and Guide No 29. 179.

Westberry, T., Behrenfeld, M. J., Siegel, D. A., Boss, E. 2008. Carbon-based primary productivity modeling with vertically resolved photoacclimation. *Global biogeochem. cy.* **22**, 10.1029/2007GB003078.

# Vertical modelling of eggs distribution to improve assessment of anchovy (Engraulis encrasicolus) spawning biomass

**O. Erdaide[a,*] , G. Boyra[a], M. Santos[a], A.Uriarte[a], U. Cotano[a]**

European anchovy (Engraulis encrasicolus) is one of the most important commercial species in the Bay of Biscay. The economy of the Spanish purse seine fleets (principally from the Basque Country, Cantabria and Galicia) and the French fleet relies greatly on this resource. Anchovy is a short living species, and its biomass evaluation has to be conducted annually by direct methods. The Daily Egg Production Method (DEPM) has been applied since 1987 to monitor the biomass of this resource from the ratio of egg production concentration to the average fecundity of adults. The traditional method of sampling is to use vertical plankton tows (CalVET). However, nowadays, the use of other plankton samplers like the Underway Continuous Fish egg Sampler (CUFES), as an estimator of the total egg abundance, is a challenge for future estimates of fish egg biomass.

In this study different egg biological features and environmental factors were studied, such as permeability of the egg Chorion, density of the previtelline fluid relative to the seawater and vertical propagation of wind-induced turbulence, which affects the vertical distribution of anchovy eggs. Boyra«s model of vertical egg distribution was applied to the CUFES data collected from the 2011 DEPM survey. As a product, vertical egg distribution profiles were obtained, which allows inferring integrated egg abundances for the entire water column.

These results taken from the CUFES sampler were compared and combined with abundances obtained with Pairovet (type of CalVET net) through Statistical models. The combination of Pairovet samples with adjusted CUFES integrated egg abundances can provide a denser and reliable method of egg sampling that could reduce errors in the estimation of egg production from DEPM surveys.

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# Using habitat suitability modelling techniques on sedimentary and rocky communities on the Avilés Canyon´s system

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The case study presented here focused on the Avilés Canyon´s system, one of the areas included in the INDEMARES project "Inventory and designation of marine Natura 2000 areas in the Spanish sea". Due to the high complexity of this area and the difficulties of surveying it, modelling techniques to optimize the data were necessary to improve the understanding of this ecosystem and therefore develop appropriate conservation and management strategies. This study is based on multidisciplinary surveys carried out in the Avilés Canyon´s system during 2010, 2011 and 2012. The distribution data for the species studied were obtained from otter trawl and beam trawl to sample sedimentary areas and from photogrammetric sled, ROV and rocky dredge in complex and hard substrates. To characterize the benthic terrain multibeam data, high resolution seismic profiles (TOPAS system) and sedimentology data from the box-corer were used. These data produced a representative view of the area which was used to apply the Maximun Entropy technique (MAXENT) to create habitat suitability maps for three communities: *Madrepora oculata-Lophelia pertusa* community in rocky areas and two representative communities in sedimentary areas such as *Leptometra celtica* and *Funiculina quadrangularis* communities. The model used different environmental variables to identify the most suitable habitats for such species and indicates which environmental factors determine their distribution. These variables were depth and the derived quantitative descriptors of it such us rugosity, aspect, slope and Bathymetric Position Index (BPI) in fine and broad scale in the three communities. Then different variables were tested depending on rocky or sedimentary communities due to the different data available and the communities' preferences on these areas. Thus, organic content, and percentage of silt, medium and fine sand and coarse sand were used as environmental variables in sedimentary communities, while reflectivity was used in rocky communities. The Area Under the Curve (AUC) values were used to tested the performance in all cases and the Mann-Whitney test was applied to these AUC values to identify if the performance of the habitat suitability distribution was significantly better than random.

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# Primary productivity control by light availability in a temperate estuary (Guadalquivir river, SW Iberia): A modeling assessment

**Diego Macías[a], Catarina Guerreiro[a], Laura Prieto[a], M. A. Losada[b], Javier Ruiz[a]**

The Guadalquivir River (Fig. 1) is one of the most important forcing agent of hydrological and biogeochemical conditions of the Gulf of Cadiz basin (Ruiz *et al*., 2006; Navarro and Ruiz, 2006; Prieto *et al*., 2009). It provides fresh, warm and nutrient-rich waters to the nearby continental shelf creating suitable conditions for fish spawning (Catalán *et al*., 2006; Ruiz *et al*., 2006). At the same time, the estuary itself acts as nursery region for many commercially important species whose survivorship depends on the environmental quality of the estuary waters (Criado-Aldeanueva *et al*., 2006; García-Lafuente *et al*., 2006).

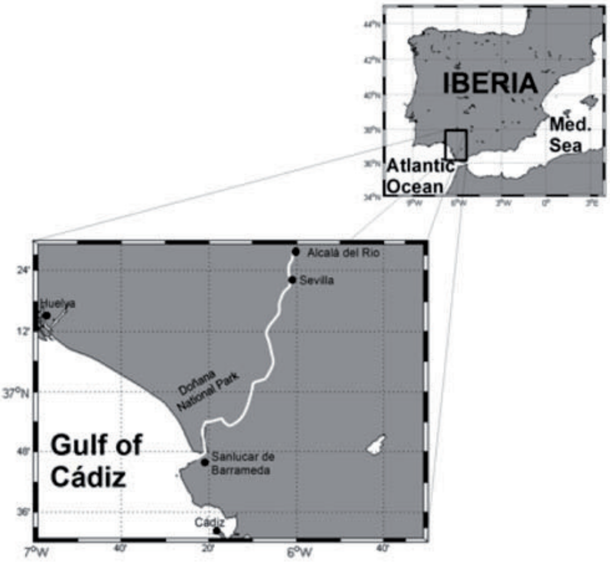

**Figure 1.** Area of study. Main cities along the Guadalquivir estuary are marked. The position of the Doñana National Park is also shown in the lower map.

Continental shelves and riverine/estuarine regions are highly variable as they are submitted to a wide variety of processes at different scales (Mann and Lazier, 1991); which made the dynamics of such ecosystems highly complicated and differentiated from the rest of the basins. Temporal and spatial scales of variability of environmental conditions in the estuaries are wide as they span from long-term climaticdriven fluctuations to sub-inertial (tides) and synoptic (meteorological) scales. Henceforth, numerical models are especially suitable to study these systems, as they could be resolved in time and space with sufficient detail to encompass all these scales of variability (e.g., Macías *et al*., 2010). In the present work we propose a mechanistic model of the Guadalquivir estuary water column (Fig. 2) built using previous ecosystems models of marine pelagic food webs but taking into account the special characteristics of the estuary.

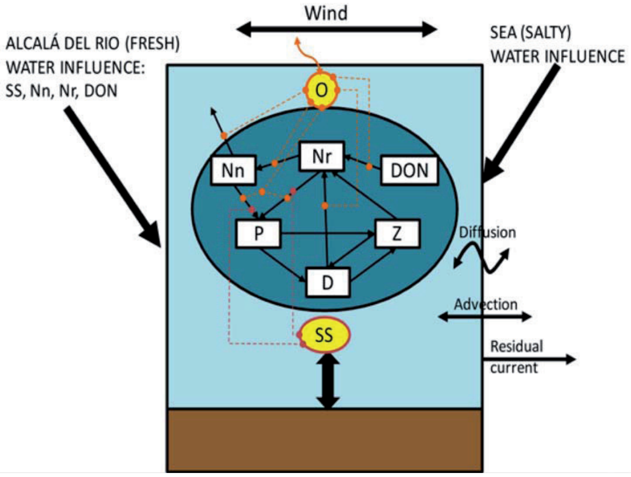

**Fig.ure 2.** Conceptual diagram of the biogeochemical-hydrodynamic coupled model. State variables; Nn (Nitrate), Nr (Ammonium), DON (Dissolved Organic Nitrogen); P (Phytoplankton), Z (Zooplankton) and D (Detritus) are shown in white boxes. Forcing variables; SS (Suspended Solids) and O (Oxygen) are shown in yellow ellipses. Black arrows are model fluxes and dotted lines mark those processes influenced by the forcing variables.

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Model results are compared with field data from a 3 annual monitoring program. We demonstrate that light availability (constrained by suspended material in the water column) severely limits biological productivity of the estuary, determining the hypoxic conditions of this system (Figs. 3 and 4).

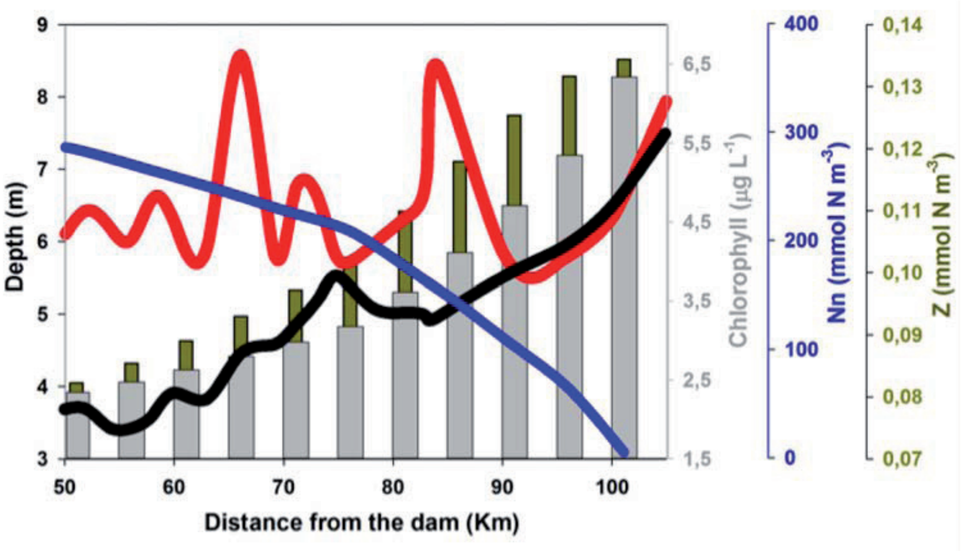

**Figure 3**. Mean water depth (H) (red line, m), compensation depth (Dc) (black line, m), nitrate (Nn) (blue line, mmol N m-3), Chlorophyll (grey bar, g L-1) and Zooplankton (green bar, mmol N m-3) at the 50 km of the estuary for the whole 2009, simulated by the coupled model.

The proposed model is useful to study any other estuary with similar biogeochemical characteristics and could also be used to assess expected changes in the environmental status of such systems by anthropogenic actions or by climatic changes.

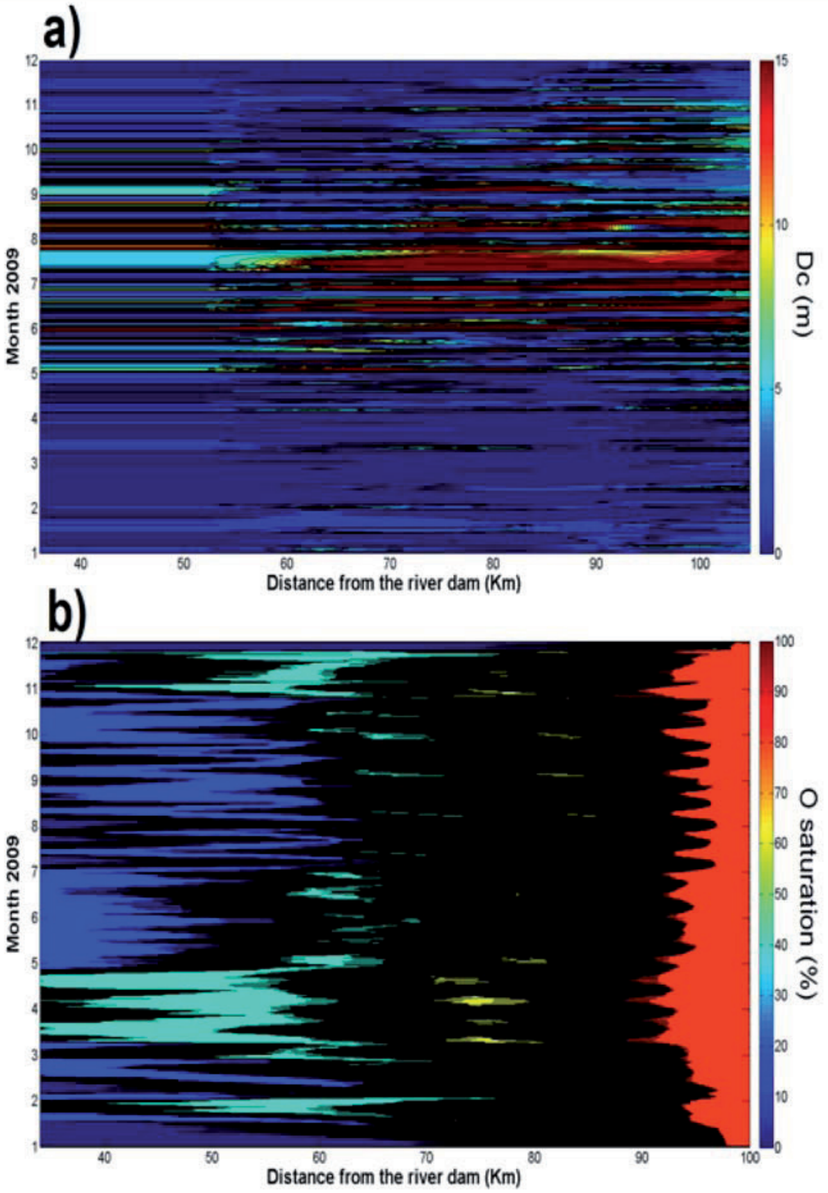

**Figure 4.** Hovmöller diagrams of a) critical depth ($m^{-1}$) and b) oxygen saturation (%) evolutions in the final 60 km of the estuary simulated during 2009.

## References

Catalán, I., Rubín, J.P., Navarro, G., Prieto. L., 2006. Larval fish distribution in two different hydrographic situations in the Gulf of Cádiz. Deep-Sea Research II 53, 1377-1390.

Criado-Aldeanueva, F., García-Lafuente, J.,Vargas, J.M., Del Río, J., Vázquez, A., Reul, A., Sánchez, A., 2006. Distribution and circulation of water masses in the Gulf of Cadiz from in situ observations. Deep-Sea Research II 53, 1144-1160.

García-Lafuente, J., Delgado, J.,Criado-Aldeanueva, F., Bruno, M., del Río, J., Vargas, J.M., 2006. Water mass circulation on the continental shelf of the Gulf of Cádiz. Deep-Sea Research II 53, 1183-1197.

Macías, D., Ramírez, E., García, C.M., 2010. Effect of nutrient input frequency on the structure and dynamics of the marine pelagic community. A modelling approach. Journal of Marine Research 69, 119-151.

Navarro, G., Ruiz, J., 2006. Spatial and temporal variability of phytoplankton in the Gulf of Cádiz through remote sensing images. Deep- Sea Research II 53.

Prieto, L., Navarro, G., Rodríguez-Galvez, S., Huertas, I.E., Naranjo, J.M., Ruiz, J., 2009. Oceanographic and meteorological forcing of the pelagic ecosystem on the Gulf of Cadiz shelf (SW Iberian Peninsula). Continental Shelf Research 29, 2122-2137.

Ruiz, J., García-Isarch, E., Huertas, I.E., Prieto, L., Juarez, A., Muñoz, J.L., Sánchez-Lamadrid, A., Rodríguez-Gálvez, S., Naranjo, J.M., Baldó, F., 2006. Meterological forcing and ocean dynamics controlling Engraulis encrasicolus early life stages and catches in the Gulf of Cádiz. Deep-Sea Research II 53, 1363-1376.

# Modelling the ecological niche of ‘El Banco de La Concepción” (Canary Islands) urchins. Which is the best model?

**José Manuel González-Irusta[a], Bruno Almón[b], Roberto Sarralde[b], Marcos González-Porto[b], Beatriz Arrese[c], Pablo Martín-Sosa[b]**

‘Banco de La Concepción’ seamount is located at northeastern Canary Islands, approximately 60 miles to the north of Lanzarote and 115 miles from the African coastline (Figure 1). This seamount is one of the ten study areas included in the LIFE + project *INDEMARES*. One of the main objectives of the *INDEMARES* project is to improve marine habitats knowledge to create a Spanish net of marine protected areas which include a good representation of the Spanish marine biodiversity (www.indemares.es).

Mapping marine biodiversity is still complex and expensive and the marine habitat distribution is unknown in most marine areas, including most of the marine protected areas (Halpern *et al*, 2008; Fraschetti *et al*, 2005). In this context, the species distribution models constitute a very useful tool to optimize information allowing to obtain habitats mapping on base of presence or absence/presence data and environmental layers (Fielding and Bell, 1997; Guisan and Thuiller, 2000; Bryan and Metaxas, 2007; Davies *et al*, 2008). Currently, there is a broad array of quantitative approaches available to model species distribution (Bedia *et al*, 2011) and researchers are faced with the difficulty of selecting between numerous modeling approaches. However, the use of these models in the management of the marine environment is relative recently (Monk *et al*, 2010) and the studies which have compared more than two methods in the marine environment are scarce (Mcleod *et al*, 2008; Tittensor *et al*, 2009; Monk *et al*, 2010). In this sense, the comparison between models based in only presence data and models based in absence/presence data is especially interesting.

This work compares four different statistical techniques to model the species distribution of four different urchins species present at ‘Banco de La Concepción’ seamount. The ecological niche factor analysis (ENFA, Hirzel, 2001) and the maximum entropy algorithms (MAXENT, Phillips *et al*, 2004) use only presence data, whereas the generalized linear models (GLMs) and the classification and regression trees (CARTs, Breiman *et al*, 1 984) use absence/presence data. Along 2010 and 2011, several multidisciplinary surveys have taken place at ‘Banco de La Concepción’ seamount. Benthic fauna was sampled using traps, beam trawls and benthic dredges. Moreover, multibeam data echosounder and very high reflexion seismic profiles (obtained with TOPAS) was used to make a geophysical study which provides a range of environmental factors (e.g. depth, reflectivity, slope, etc.). In these surveys until twelve different echinoid species have been identified but only four are enough abundant to model their distribution; *Stylocidaris affinis* (Philippi, 1845); *Coelopleurus floridanus* A. Agassiz, 1872; *Centrostephanus longispinus* (Philippi, 1845) and *Cidaris cidaris* (Linnaeus, 1758). The results showed that the four urchin’s species have different ecological niche, defined mainly by depth and sediment type. Differences between models are discussed.

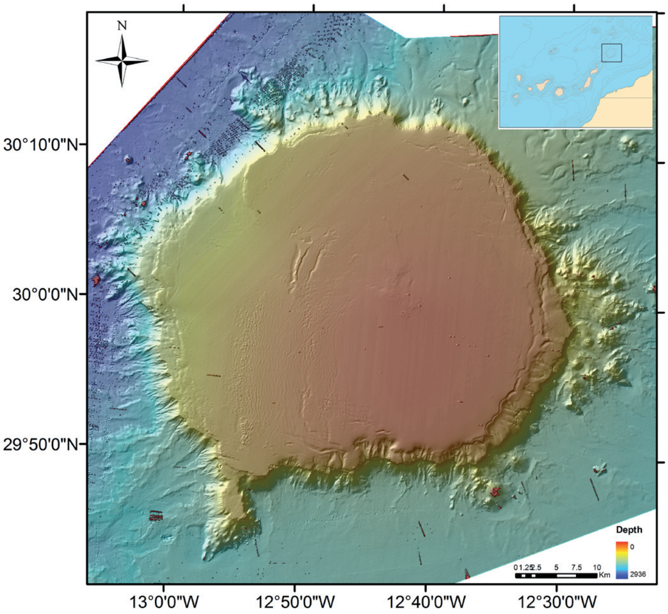

**Figure 1.** *Banco de la Concepción* seamount digital elevation model. The situation of the seamount is also showed.

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# References

Bedia, J.; Busquet, J. & Gutierrez, J. Predicting plant species distribution across an alpine rangeland in northern Spain. A comparison of probabilistic methods Applied Vegetation Science, Wiley Online Library, 2011

Breiman, L., Friedman, J., Olshen, R.A. & Stone, C.J. 1984. Classification and regression trees. Wadsworth Publishing Company, Belmont, CA, US.

Bryan, T. L. & Metaxas, A. Predicting suitable habitat for deep-water gorgonian corals on the Atlantic and Pacific Continental Margins of North America Mar Ecol Prog Ser, 2007, 330, 113-126

Davies, A. J.; Max Wisshak, J. C. O. & Roberts, M. Predicting suitable habitat for the cold-water coral Lophelia pertusa (Scleractinia) Deep-Sea Research I, 2008, 55, 1048– 1062

Fielding, A.H. & Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24: 38–49.

Fraschetti, S., Terlizzi, A., Bussotti, S., Guarnieri, G., D'Ambrosio, P., Boero, F., 2005. Conservation of Mediterranean seascapes: analyses of existing protection schemes. Marine Environmental Research 59, 309–332.

Guisan, A. & Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8: 993–1009.

Halpern, B.S.,Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. Science 319, 948–952.

Hirzel AH, Helfer W, Metral F (2001) Assessing habitat-suitability models with a virtual species. Ecol Model 145: 111–121

MacLeod CD, Mandleberg L, Schweder C, Bannon SM, Pierce GJ (2008) A comparison of approaches for modelling the occurrence of marine animals. Hydrobiologia 612: 21–32

Monk, J., Ierodiaconou, D., Vincent, L., Versace, A.B., Harvey E., Rattray, A., Laurenson, L., Quinn, G.P. (2010). Habitat suitability for marine fishes using presence-only modelling and multibeam sonar. Mar.Ecol. Prog.Ser., 420: 157-174.

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modelling of species geographic distributions. Ecol Model 190:231–259

Tittensor DP, Baco AR, Brewin PE, Clark MR and others (2009) Predicting global habitat suitability for stony corals on seamounts. J Biogeogr 36:1111–1128