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Species distribution modelling to support marine conservation planning

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Species distribution modelling to support marine conservation planning

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Abstract

Species distribution modelling to support marine conservation planning

Charlotte Emily Marshall

This thesis explores some important practical considerations concerning the use of species distribution models in marine conservation planning. Using geo-referenced gorgonian distribution data, together with explanatory environmental variables, predictive models have been used to map the spatial distribution of suitable gorgonian (sea fan) habitat in two study sites; Hatton Bank, in the Northeast Atlantic, and Lyme Bay on the south coast of Devon. Generalized Linear Models (GLMs), Generalized Additive Models (GAMs) and a Maximum Entropy (Maxent) model have been used to support critical investigation into important model considerations that have received inadequate attention in the marine environment. The influence of environmental data resolution on model performance has been explored with specific reference to available datasets in the nearshore and offshore environments. The transferability of deep-sea models has been similarly appraised, with recommendations as to the appropriate use of transferred models. Investigating these practical issues will allow managers to make informed decisions with respect to the best and most appropriate use of existing data. This study has also used novel approaches and investigated their suitability for marine conservation planning, including the use of model classification error in the spatial prioritisation of monitoring sites, and the adaptation of an existing presence-only modelling method to include absence data. Together, these studies contribute both practical recommendations for marine conservation planning and novel applications within the wider species distribution modelling discipline, and consider the implications of these developments for managers, to ensure the ongoing improvement and development of models to support conservation planning.

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Several relevant scientific seminars and conferences were attended at which work was often presented. Two papers are also in preparation for publication.

Publications:

Work from Chapter 5 was included in the following book chapter: Plater, A. and Rice, J. (2011). Review of Existing International Approaches to Fisheries Management: The Role of Science in Underpinning the Ecosystem Approach and Marine Spatial Planning. In *The Ecosystem Approach to Marine Planning and Management. Kidd, S., Plater A, and Frid, C. (eds.)* Earthscan, London.

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Work from Chapter 7 is being prepared for submission to Ecological Applications. Working title: *Transferability of deep sea species distribution models.*

Work from Chapter 8 will also be prepared for submission to a suitable journal in due course.

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Posters and conference presentations:

2011
1st Marine Management Organisation conference, Plymouth, UK.
Poster presentation: *Species distribution modelling for offshore marine planning: data issues, challenges and recommendations.*

1st Marine and Coastal Policy Forum, Plymouth, UK.
Poster presentation: *Species distribution modelling for offshore marine planning: data issues, challenges and recommendations.* Prize awarded.

2010

45th European Marine Biology Symposium, Edinburgh, Scotland.
Oral presentation: *More bang for your buck? The use of 'proxy' areas for species distribution modelling in the deep sea.*

12th International Deep Sea Biology Symposium, Reykjavik, Iceland.
Oral presentation: *The devil* is *in the detail: ecological insight and management implications differ after modelling deep sea gorgonian distribution using different data resolutions.*

2009

1st International Marine Conservation Congress, Virginia, USA.
Poster presentation: *Joining the dots: can predictive species distribution models outline plans for marine nature conservation?*

Oral presentations have also been given at the University of Plymouth (Marine Planning course, 2011), Falmouth Marine School (2010), Marine Biological Association (2009) and at two Marine Institute conferences (2007 and 2009). See Appendix A for conference posters.

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Chapter 1

Introduction

1.1 Setting the scene

With deadlines upon governments worldwide for both regional and international legislative commitments to conservation mandates, we are now in a position where we must reconcile "the need to know versus the need to act" (Ardron et al. 2008). To this effect, species distribution models (SDMs) have great potential to support marine conservation planning.

The use of SDMs in the marine environment is a growing field, especially within marine conservation. However, there remain several aspects of species distribution modelling that are important to marine conservation planning that have received little attention, especially in deep-water areas.

Increasing pressure on the marine environment has put marine planning on the agenda in both coastal areas and on the high seas. With international requirements including the need to establish marine protected areas by 2012 (in line with the Convention on Biological Diversity), a renewable energy target of 20% of total energy generation within the EU by 2020 and a forecasted growth in coastal tourism, the spatial consideration of activity in the marine environment is now critical. Accordingly, marine spatial planning has been advocated at the local initiative level through to international strategic recommendations such as UNESCO's Marine Spatial Planning Initiative.

There is a recognised need, and political will, to establish a comprehensive marine spatial planning framework and, globally, legislative commitments to the same effect which require progress in the coming years. Within these planning frameworks, marine protected area (MPA) networks will be used to meet conservation targets and SDMs have the potential to make an important contribution.

Disparity in survey effort means that some areas lack detailed spatial information about species and habitat distributions, which in turn can impede the establishment of MPAs. Collection of field data can be time consuming and expensive, especially offshore. Species distribution modelling offers a viable compromise and makes the best use of available environmental data and species distribution records. SDMs identify relationships between known species distribution data and their environment. With any such relationships identified it is then possible to make informed predictions about the distribution of suitable habitat in areas lacking such information, providing relevant environmental data is available.

The application of these models in the marine environment to date is relatively limited compared to terrestrial systems, where their application to conservation management was developed, and the potential for using them to support marine conservation planning has not been adequately addressed.

1.2 Marine spatial planning

Ehler and Douvere (2007) describe marine spatial planning as "analysing and allocating parts of three-dimensional marine space to specific uses or non-use, to achieve ecological, economic, and social objectives that are usually specified through a political process".

Marine spatial planning is a method of looking at both current and possible future uses of a marine area and addressing them spatially in order to highlight potential conflicts and maximise the sustainable use of the space. Traditionally focussed on MPAs (as a mechanism to implement them), the remit of marine spatial planning is now the wider use of marine space (Douvere 2008). This refocus has been necessary due to mounting pressure on the marine environment which has led to increased conflict potential through, for example, the expansion of existing activities and nature conservation requirements (Maes 2008). Some uses of the marine environment are spatially and temporally demanding. Whilst this is not a problem *per se*, the fact that some activities can be incompatible results in a situation where different industries may compete for space, as was the case in Belgium when offshore wind developers and the aggregate industry both wanted to expand into the same area (Plasman 2008).

Certain uses can also exert pressure on the marine environment. Activities are termed pressures when they induce change in the environment. The environmental impacts of this change can in some circumstances be adverse. Considering commercial fishing and aquaculture as pressures, the Marine Strategy Framework Directive (European Union 2008) identified physical damage to the seabed and inputs of nitrogen respectively as impacts associated with these activities. Marine spatial planning can help to balance the cumulative effects of such impacts on the marine environment (Ehler 2008; Ardron et al. 2008). As such, marine spatial planning becomes much more than just a tool for managing potential conflict between certain human activities but will encompass what Douvere (2008) refers to as ‘user-environment’ conflicts; conflicts between human use (activities) and the marine environment. ‘Non-use’ activities such as marine nature conservation are valid competing uses of marine space (Stevens et al. 2006) and the subject of much targeted management effort worldwide.

Marine planning can facilitate integrated, forward-thinking and consistent decision making (Ardron et al. 2008). Additional potential benefits include the engagement of a wider group of stakeholders in the planning process and a better integration of ecosystem based objectives (Degnbol and Wilson 2008; Gilliland and Laffoley 2008). However, marine spatial planning is more than simply producing maps (Gilliland and Laffoley 2008). Products can include strategic plans or a 'vision' for the area in question (Douvere 2008; Maes 2008). In addition, if marine planning systems are adaptive, as is often recommended (e.g. Ehler and Douvere 2007), change can be incorporated into the plans in addition to feedback from evaluation of the plans' effectiveness (Day 2008). Hence there is also a temporal dimension to marine planning which is why this term is often used in preference to marine *spatial* planning, the latter suggesting a less temporally adaptable approach. In this study the term marine planning is used from hereon in, except where reference has been made to specific legislation that uses the term marine spatial planning.

The three dimensional nature of the marine environment has made the leap from research to practical solutions more difficult (Plasman 2008) which may explain the lag in developing and implementing marine planning systems in comparison to terrestrial environments. However, formal recommendations regarding its implementation in international and European legislation were made in the early years of this millennium (Vincent et al. 2004; Commission of the European Communities 2006). In 2002 at the 5th International Conference on the Protection of the North Sea (the Bergen Declaration), Ministers recognized a need for co-operation in the planning process among North Sea states and invited the OSPAR Commission for the Protection of the Marine Environment of the North East Atlantic to help further the marine planning process for the North Sea. In Europe, the Marine Strategy Framework Directive, adopted in June 2008, sets out further commitments to the ecosystem approach and sustainable use of the marine environment

(European Union 2008).

In the United Kingdom, plan-led management of the marine environment is still in its infancy, partly as a result of its sectoral management to date. The UK Government's first commitment to explore a system of marine planning was set out in the Marine Stewardship Report *Safeguarding Our Seas* (Defra 2002). In this report the Government stated that their vision of "clean, healthy, safe, productive and biologically diverse oceans and seas" could be achieved by adopting an ecosystem-based management approach, principles of which include the conservation of biological diversity and the precautionary principle. In the same year Natural England's (formerly English Nature) *State of Nature* report heralded both the Ecosystem and Precautionary Approaches to marine management, identifying them as fundamental pillars of marine spatial planning, and ultimately highlighting a clear requirement for change. Leading from this, the Marine and Coastal Access Bill White Paper (Defra 2007a) highlighted 'sustainable development' and 'forward-thinking' in its introduction to marine planning; themes which are mirrored in alternative definitions. The White Paper also set out its aim to create the first set of marine plans within five years of the assent of the Bill. Marine planning receives considerable attention in the Marine and Coastal Access Act 2009. This Act represents the first piece of nationwide legislation to take an integrated approach to the spatial management of marine resources in the UK. More recently, the Marine Policy Statement (HM Government 2011) sets out the framework within which marine plans will be developed by the UK administrations. The statement, provided for by the Marine and Coastal Access Act 2009, commits to ensuring that marine plans will be developed to allow the management of activities in a way that achieves sustainable development and reduces conflict.

Symes (2005) noted that marine planning was fostered by marine conservation interests by way of implementing the ecosystem approach at sea and that this is evident in its various definitions. Consequently, and guided by the Ecosystem Approach, a common objective of marine planning includes the implementation of a network of MPAs (Gilliland and Laffoley 2008). In the final conclusions of the UNESCO International Workshop on Marine Spatial Planning (UNESCO 2006), it was explained that protecting key ecosystem features, such as ecosystem structure and function and habitat integrity, as a fundamental part of planning was essential to realise ecosystem based management. Marine planning and MPAs are therefore intrinsically linked and recommendations pertaining to MPAs are now invariably seen nested within a wider marine planning context.

1.3 Marine protected areas

‘Marine protected area’ is an umbrella term used globally to describe an area of the sea or coast that is protected to some degree against disturbance in order to protect certain species, habitats and/or other important features e.g. wrecks. The IUCN define a protected area as follows:

“*an area of land and/or sea especially dedicated to the protection and maintenance of biological diversity, and of natural and associated cultural resources, and managed through legal or other effective means*” (IUCN 1994)

[See Table 1.1 for IUCN protected area categories]

MPAs vary greatly in characteristics including size, name (marine park, highly protected marine reserve, marine conservation zone etc.) and associated habitat type. However, among the key features that differ are the objectives of the protected area and the type of protection offered which are, justifiably, strongly related.

Goals are often varied and a protected area may have more than one stated objective although a common purpose is to reduce or prevent damage to, and destruction of, certain habitats and/or species. Other objectives include: replenishment of fisheries stock through, for example, the protection of nursery habitat; scientific monitoring; and public education, that is, having a protected area so that people can actively engage with the notion of marine conservation and benefit from knowledge of the area's existence (IUCN 1994).

MPAs can range from sites where few restrictions are placed on the type of activity that can occur within its boundaries to areas where all activities are excluded, including limits on human presence (Table 1.1).

Zoning, whereby certain activities are restricted to designated areas within the reserve, is common. The most elaborate zoning scheme can be seen within the Great Barrier Reef Marine Park in Australia (Day 2002) but even tiny protected areas such as Lundy Marine Nature Reserve in England (3.3 km^2) and Lamlash Bay in Scotland (9.27 km^2) encompass zoned areas.

Evidence from MPAs worldwide suggests that benefits can include increased spawning stock, biomass, size and abundance of protected animals, and habitat recovery (Bradshaw et al. 2001; Gell and Roberts 2003). However, much of the reported successes are based on sessile species and from marine reserves in the tropics (Kaiser 2005). Furthermore, the designation of protected areas is often met with much opposition and there are some reservations as to the realised benefits to fisheries (Sale et al. 2005). MPAs, as a standalone management measure, may offer insufficient protection and additional management measures are often recommended (Allison et al. 1998). When combined with reduced fishing effort outside the closure, for example, MPAs may provide more effective conservation of stock.

Concomitant with imminent marine planning obligations are several commitments, again from international to national level, relating to MPAs. In accordance

Table 1.1: Examples of the marine protected area categories as defined by IUCN. Objectives (italicised) and features of each category are summarised from Dudley (2008).

IUCN category and primary objective
Key features
Ia. Strict Nature Reserve e.g. Masinloc and Oyon Bay Marine Reserve, Philippines *'to conserve regionally, nationally or globally outstanding ecosystems, species and/or geodiversity features'*
• Features will be degraded or destroyed when subjected to all but very light human impact. • Human visitation, use and impacts is strictly controlled and limited to ensure protection of conservation values. • Such areas can provide indispensable reference areas for scientific research and monitoring.
Ib. Wilderness Area e.g. Alaska Maritime National Wildlife Refuge *'to protect long-term ecological integrity of natural areas that are undisturbed by significant human activity, free of modern infrastructure and where natural forces and processes predominate, so that current and future generations have the opportunity to experience such areas'*
• Unmodified or only slightly modified and without permanent or significant habitation. • Protected and managed to preserve its natural condition.
II. National park e.g. Mu Ko Ang Thong National Park, Thailand *'to protect natural biodiversity, its underlying ecological structure and supporting environmental processes, and promote education and recreation'*
• Large natural or near natural areas. • Protect large-scale ecological processes, along with the species and ecosystems characteristic of the area. • Provide basis for environmentally / culturally compatible spiritual, scientific, educational and recreational opportunity.

III. Natural monument or feature   e.g. Sugar Loaf Islands, New Zealand *'to protect specific outstanding natural features and their associated biodiversity and habitats'*
• Set aside to protect a specific natural monument (e.g. seamount), geological feature or living feature. • Generally quite small protected areas, often with a high visitor value.
IV. Habitat/species management area   e.g. Skomer Marine Nature Reserve, Wales *'to maintain, conserve and restore species and habitats'*
• Aim to protect particular species or habitats. • Many require regular, active interventions to address the requirements of particular species or to maintain habitats.
V. Protected landscape/Seascape   e.g. Scott Islands Park, Canada *'to protect and sustain important landscapes/ seascapes and associated nature conservation and other values created by interactions with humans through traditional management practices'*
• Areas where the interaction of people and nature over time has produced an area of distinct character with significant ecological, biological, cultural and scenic value. • Safeguarding the integrity of this interaction is vital to protecting and sustaining the area and its associated values.
VI: Protected area with sustainable use of natural resources   e.g. Archipielago de Revillagigedo, Mexico *'to protect natural ecosystems and use natural resources sustainably, when conservation and sustainable use can be mutually beneficial'*
• Areas conserving ecosystems and habitats and associated cultural values and traditional natural resource management. • Generally large, with most of the area in a natural condition, some under sustainable natural resource management and where low-level non-industrial use of natural resources is compatible with nature conservation.

with the World Summit on Sustainable Development, World Parks Congress and the Convention on Biological Diversity, commitments have been made to create a network of MPAs by 2012.

Contracting Parties to OSPAR agreed to have established an ecologically coherent network of MPAs by 2010 and the Bergen Declaration mirrors this commitment in the North Sea. OSPAR recognises the development of MPAs as a key process in achieving its overarching objective to protect and conserve ecosystems and the biological diversity of the maritime area, adopted in Annex V of the Convention (MASH 2005).

The conservation of marine ecosystems and sustainable use of the seas are key aims of the Marine Strategy Framework Directive (European Union 2008), within which Member States are required to implement 'spatial measures' to protect biodiversity and therefore contribute towards meeting Good Environmental Status (GES) in their waters by 2020 (European Union 2008). The continuing development of the Natura 2000 'network' of sites across Europe also makes a significant contribution to Europe's legislative commitments.

In the UK, the Working Group of the Review of Marine Nature Conservation (Defra 2004) also endorsed the identification and establishment of an ecologically-coherent, representative network of MPAs and Stevens et al. (2006) recommended that policy makers start to recognise "marine nature conservation as a valid and competing use for space and resources in UK coastal and marine areas". Marine Conservation Zones represent a significant element of the Marine and Coastal Access Act 2009. The term Marine Conservation Zone (MCZ) is new to UK legislation but in essence is an MPA which can be designated on the grounds of conserving "marine flora or fauna, marine habitats or types of marine habitat and/or features of geological or geomorphological interest" (Marine and Coastal

Access Act 2009). The terminology varies slightly across the UK administrations with Highly Protected MCZs being developed in Wales and ‘Marine Protected Areas’ as part of the Marine (Scotland) Act 2010. In Northern Ireland, they are also termed MCZs.

The development of MPAs in line with some existing or developing management framework has long been recommended. The IUCN, for example, recommended that protected areas be established within a co-ordinated and holistic management framework and that this integrated management is essential for achieving adequate conservation of the marine environment in the face of various potentially conflicting uses (Kelleher and Kenchington 1992).

Marine planning and marine protected areas share some keystone principles including long term commitment, inclusion of relevant stakeholders to ensure effective outcomes from the project, and transparent aims and objectives from the outset. But the integration of MPAs into a marine planning system will necessitate more than just similarities on paper and requires both political will, the motivation of disparate management organisations and industries etc to resolve existing conflicts regarding conservation and, above all, effective legislation.

It is likely that, within the wider remit of marine planning, MPAs are where the greatest potential for species distribution modelling exists. In a report by Gubbay (2004), MPAs and marine spatial planning were identified as ‘two specific management tools’ and the ways in which protected areas could be incorporated into a spatial plan are discussed. Whilst marine spatial planning, as Gubbay (2004) points out, has a wider remit, the development of future MPAs in many areas will now most likely fall into a wider spatial plan. MPAs will contribute towards marine plans reaching their ecologically relevant objectives therefore becoming an integral part of the evolution of ecosystem based marine planning.

Large-scale maps allow managers to visualise the spatial distribution of habitats which in turn aids the planning of MPA networks (Mumby and Harborne 1999). However, the designation of protected areas, especially in response to damaging activities, is often hampered by the lack of such detailed spatial information about species and habitats distribution, especially offshore (e.g. Davies et al. 2007; Leathwick et al. 2008). Rodriguez et al. (2007) acknowledge limited distribution data and access to data sets as common impediments to progress in conservation and lack of data was cited as an explanation behind the difficulty in identifying offshore Special Protection Areas (Johnston et al. 2002). The common disparity between the amount and/or resolution of data between nearshore and offshore environments needs to be addressed in the context of marine planning, specifically regarding MPAs.

Data collection, especially of primary data on species distribution, can be time consuming and expensive and this is particularly true in remote areas and in deep-sea environments (Day 2008; Ardron et al. 2008; Guinan et al. 2009a). Environmental data are generally easier to collect and have better coverage than biological data, and the associated difficulties and costs of subtidal survey work are one reason preventing widespread mapping of habitats at the local scale (Stevens and Connolly 2004). Yet comprehensive data coverage is often required so that management decisions can be made regarding the protection of species and habitats, the full extent of whose distribution is often unknown. The Marine Strategy Framework Directive (European Union 2008), for example, requires member states to undertake analysis of the ‘features’ and ‘characteristics’ of their marine waters which include special habitat types and invertebrate bottom fauna.

In the absence of such data, appropriate management action may be delayed or made in the absence of knowledge, despite recommendations that appropriate management action should not wait for all the answers (Day 2008).

However the timescale regarding international commitments to the conservation of the marine environment has fostered the advocacy of maximising the use of existing data as opposed to postponing decision making. OSPAR recommend using biological data “to their fullest” when considering representivity for the OSPAR MPA network and that ‘other approaches’ should be used in the absence of detailed survey data (MASH 2005). The Ecosystem Approach report (Laffoley et al. 2004) identified, as a priority for improving coherence in the management of the marine environment, the use of surrogate information in the absence of detailed biological information. The report acknowledges the costs and time constraints involved with data collation and also the potential for using physical information as a surrogate for biological information.

Species distribution modelling can therefore be appropriately adopted to underpin management decisions, especially with a conservation agenda, and has been recommended as a potential option in cases where data coverage is incomplete (Ardron et al. 2009).

1.4 Species distribution modelling

Species distribution models (SDMs, Elith and Graham 2009) offer great potential for inclusion into the toolbox of today’s marine environmental manager, especially with regard to marine conservation and planning. SDMs identify relationships between the geographical distribution of species, or communities, and characteristics of their present environment (Guisan and Zimmerman 2000). With any such relationship(s) identified, the models can then be applied to make informed predictions concerning suitable habitat for the species in areas lacking distribution data, providing that relevant environmental data is available. This is most commonly achieved through the combined efforts of a statistical package and Geographical Information Systems (GIS) software, the latter of which allows for the spatial mapping of predicted habitat suitability. These models are static and probabilistic due to the fact that the results are based on a snapshot of the relationship between the species and its environment (Guisan and Zimmerman 2000).

Species distribution modelling offers a viable compromise between the lack of comprehensive species distribution data and the expense of collecting additional data by maximising the potential use of existing distribution data sets. SDMs have been successfully applied at both a local and global scale and from the deep-sea to high mountain environments (e.g. Graf et al. 2006; Olivier and Wotherspoon 2006; Tittensor et al. 2009; Woodby et al. 2009). The use of such models is a thriving discipline (Rodriguez et al. 2007) with a wide remit including managing the spread of reintroduced or invasive species (Hirzel et al. 2002; Inglis et al. 2006), identifying areas of conservation priority (Bryan and Metaxas 2007; Pittman et al. 2007; Gavashelishvili and Lukarevskiy 2008), or highlighting the potential influence of a changing climate on communities (Gottfried et al. 1999; Tittensor et al. 2010). The application of SDMs in the marine environment over the past few years has also been varied although still relatively few in comparison with terrestrial application. The number of spatial modelling studies in deep-sea marine ecosystems is fewer again and Ardron et al. (2008) acknowledge that in deep-sea areas, gaps in data availability can hinder conventional management which would suggest that there is room for the development in application of these models in this area.

Guisan and Zimmerman's seminal review paper on species distribution modelling (Guisan and Zimmerman 2000) does not include marine studies in the list of previous applications. A more recent article presents an excellent case for the use of spatial distribution models in the conservation of biodiversity (Rodriguez et al.

2007). However whilst this article provides good reasoning for the use of SDMs and draws points that could be applied to a variety of scenarios, the examples given are again all terrestrial. Table 1.2 details a variety of recent species distribution modelling studies in the marine environment.

Concomitant with the growth in application of these models has been an increase in the range and availability of different modelling methods, especially the development of presence-only modelling methods including Ecological Niche Factor Analysis (Hirzel et al. 2002) and Maximum Entropy (Phillips et al. 2006) which have allowed the creation of predictive maps from museum collections, herbarium data and atlases (Elith et al. 2006).

The use of pseudo-absences has also developed. Pseudo-absences are 'absence' records randomly generated from the background environment where distribution is unknown. Also referred to as background samples (Ferrier et al. 2002; Elith et al. 2006), pseudo-absences can be user-generated in cases where absence data is unavailable so that traditional modelling methods requiring presence-absence data including regression based analyses can be used. Essentially, models fitted with presence-absence data have more information than presence-only models and should therefore results in a better calibrated model (Elith and Graham 2009).

Many of the commonly used modelling packages are freely available to download, either as part of modelling packages (e.g. Maxent, Biomapper) or as part of some other platform such as R which is a statistical program that has several available modelling libraries. This availability has increased the accessibility of these models to the wider scientific community. In addition, the fact that some packages have a user friendly front end, or 'graphical user interface' (GUI), means that people not necessarily from a statistical background can produce models relatively easily.

Table 1.2: Recent species distribution modelling studies in the marine environment. Shaded studies are deep-sea models.

Study: application	Response				Modelling method							
Modelling approach	P	PA	CPUE	SR	RT	ANN	MR	ENFA	GRASP	GAM	GLM	Maxent
Pittman et al. (2007) Improving ecosystem-based management of coral reefs				•	•	•	•					
Bryan & Metaxas (2007) Improving knowledge of deep-sea coral distribution for conservation	•							•				
Hazin & Erzini (2008) Improving management and efficiency in the swordfish fishery	•		•						•	•		
Dolan et al. (2008) Ground truthing of seabed features and use in models	•							•				
Willems et al. (2008) Identifying habitat preferences of a polychaete		•				•					•	
Tittensor et al. (2009) Predicting global distribution of stony corals on seamounts	•							•				•
Embling et al. (2010) Identifying areas of conservation importance for harbour porpoise		•								•		
Clark & Tittensor (2010) Identifying vulnerability using predicted coral distribution and fisheries data	•											•

P (presence data); PA (presence-absence data); CPUE (Catch Per Unit Effort); SR (Species Richness); RT (Regression Trees); ANN (Artificial Neural Networks); MR (Multiple Regression); ENFA (Ecological Niche Factor Analysis); GRASP (Generalized Regression Analysis and Spatial Prediction); GAM (Generalized Additive Model); GLM (Generalized Linear Model;) Maxent (Maximum Entropy).

1.5 Species distribution models for use in marine conservation planning

The application of predictive species modelling to support marine conservation planning has not been fully addressed and there remain some, as yet, unexplored practical considerations. Maxwell et al. (2009) refer to the usefulness of the modelling approaches set out in their paper to marine planning. However the main focus of the paper is the modelling approach adopted and although the potential benefit of habitat suitability maps to marine planning is stated it is not discussed in any detail.

By their very nature the outcomes of species distribution modelling studies will provide a spatial contribution to marine planning, but they can also be used to inform temporal aspects of marine plans, such as predicting spatial changes over time as a species responds to climate change, and can also be used adaptively, therefore ensuring that the application of the model is relevant through time. The inclusion of predicted species distribution maps into marine plans has several potential benefits, especially for those with a conservation agenda.

Firstly, and providing that access to relevant environmental variable data is not a concern, full advantage can be taken of existing distribution data by using it to produce maps covering the planning area in question. So instead of having pockets of distribution data a continuous layer of (predicted) suitable habitat could be used instead. Depending on the planning scenario it may then be possible to protect additionally those areas that the model has highlighted as suitable for that species, as opposed to simply protecting areas where distribution is known to occur, especially when the layers are used in concert with other layers including fisheries data or the locations of wrecks for example.

The development of increasingly sophisticated decision support tools such as Marxan (Ball and Possingham 2000), which can be used to facilitate the process of marine protected area site selection, means that predictive species modelling has the potential to assist in the decision making process for marine reserves. A continuous layer / surface is entirely preferable to point data with regard to Marxan input files (Jeff Ardron, pers. comm.) and species modelling can produce just that.

Secondly, species distribution models can be produced relatively quickly, notwithstanding data availability and familiarity with modelling techniques, meaning that organizations which have been given little time to respond to, for example, a planning application can represent their interests adequately in the time available. This is especially important for rare or scarce species for which little data may exist.

Additionally, spatial models calibrated in one area might be used (with prudence) to predict the distribution of suitable habitat in areas where no distribution data exists at all but where environmental variable data is available.

Whilst it is likely that SDMs will make the most direct contribution to the development of protected areas, it is discussed in the wider context of marine planning because this is the direction of current and future management development both within the UK and internationally. In other words, MPAs are no longer stand alone management tools in many cases but will contribute to the wider objectives of a marine plan.

In 2008, UNEP produced a step by step guide to marine spatial planning (Ehler and Douvere 2009), targeted especially at situations where “time, finances, information and other resources are limited”. The step-by-step guide has been adapted here to include a similar flow chart produced by Foley et al. (2010), and modified

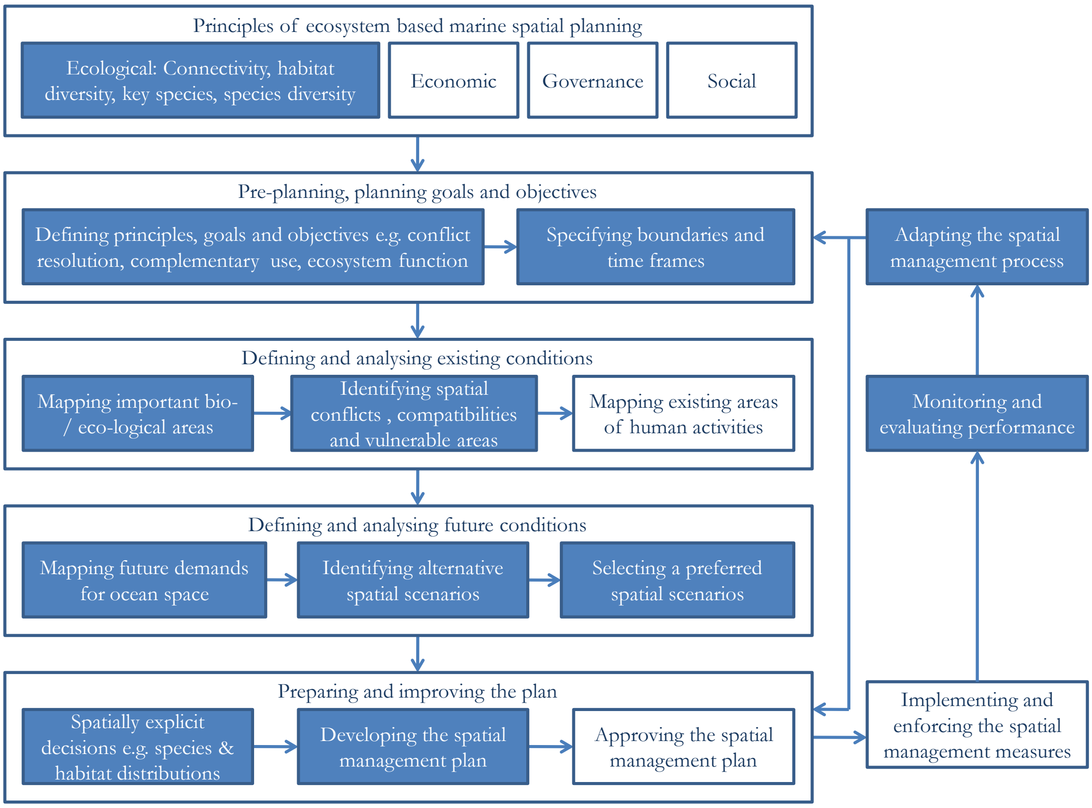


Figure 1.1: Step by step approach to marine spatial planning highlighting (in blue) the stages at which species distribution modelling could make a contribution and/or are relevant to species distribution modelling. The flowchart is an adapted amalgamation of the flowcharts in Ehler and Douvere (2009) and Foley et al. (2010).

to highlight the aspects of the marine planning approach that species distribution modelling could contribute to (Figure 1.1). Species distribution modelling outputs will support marine planning and do not represent part of the actual planning process, although the model outputs need to be transparent enough that people can understand the process and foster confidence in the results.

An early stage in the UNEP plan (not included in the figure) includes allocating resources. Those responsible for the development of the marine plan may allocate the majority of resources for stakeholder involvement, plan implementation, monitoring and enforcement etc, leaving limited funds for the preliminary stages that would enable the collection of new data to support the mapping of species and habitats. The inclusion of time frames in the pre-planning is similarly relevant because limited time might preclude the potential for additional survey effort, resulting in the use of existing data sets for mapping, however coarse. These factors have implications for species distribution modelling because if only coarse resolution environmental data exists, for example, it may influence model performance. Equally, if only presence records are available, managers may have a limited choice of modelling methods.

1.6 Thesis aim and objectives

The aim of the present study is to determine how species distribution modelling can best be used to support marine conservation planning based on several practical applications. The study will use different gorgonian species to trial the models and will focus on two areas:

- Lyme Bay, a shallow bay on the south coast of England, and
- the deep-water areas of Rockall Trough and surrounding seamounts in the Northeast Atlantic.

These two areas vary both in terms of scale and, potentially, the availability of environmental and species distribution data. To this effect, the study will address the issue of scale in addition to identifying factors influencing the distribution of sea fans in both areas. Objectives of the study are to:

1. identify the environmental factors primarily responsible for influencing the distribution of gorgonians in the Lyme Bay and Rockall Trough study areas through the use of species distribution models (Chapters 4-8);
2. critically appraise the potential for species distribution models to inform monitoring in a marine protected area (Chapter 5);

3. determine the effect of environmental data resolution on model performance (Chapter 6);
4. investigate the potential transferability of species distribution models between different areas in the deep-sea (Chapter 7), and
5. compare the performance of traditional, regression based Generalized Linear Models (GLMs) and Generalized Additive Models (GAMs) using presence-absence gorgonian distribution data with a new-generation 'off the shelf' modelling package Maxent (designed for presence-only data but adapted here to include presence-absence data) (Chapter 8).

Chapter 2

Gorgonians

2.1 Selection of a test group of species

The aim of this thesis is to explore several practical issues related to the application of SDMs to marine conservation planning, and it was therefore imperative to select a test group of species that would be robust to the methodologies involved and with respect to the data available for the study. Gorgonians were selected for a number of reasons but principally because they are conspicuous on video transects and therefore suitable for generating presence and absence data. In addition, due to the long lived and fragile nature of the majority of gorgonians, they can be indicative of the health of the wider ecosystem. Modelling the distribution of gorgonians is therefore potentially valuable as a proxy for the distribution of ecologically significant habitats.

2.2 Gorgonian taxonomy

Gorgonians form part of the Anthozoa: one of five classes of the phylum Cnidaria. The Anthozoa are further subdivided into two subclasses, namely the Hexacorallia and Octocorallia, the latter of which include more than 1400 species of gorgonians in the order Alcyonacea (Daly et al. 2007). Classification of gorgonians remains problematic (Daly et al. 2007). Two morphologically distinct suborders of gorgonians exist in the Alcyonacea (Calcaxonia and the Holaxonia) which between them contain the named species covered in this study (see Section 2.5).

2.3 Gorgonian ecology

2.3.1 Growth form

More commonly referred to as sea fans, gorgonians are permanently attached to the substratum in a whip-like, branched or crustose form. Their morphology and size are diverse (Grasshoff 1972; Mortensen and Buhl-Mortensen 2005). The colonies are often erect and sometimes fragile whose polyps shroud an underlying skeleton (Figure 2.1).

2.3.2 Habitat

Sea fans populate diverse habitats and have been recorded from abyssal depths in the deep-ocean (Cairns and Bayer 2009) to chart datum (Manuel 1981) and from cold Antarctic waters (e.g. Lopez-Gonzalez 2006) to the tropics (e.g. Hermanlimianto and van Ofwegen 2006). The majority of deep-water gorgonians are found between 200-1000 m (Mortensen and Buhl-Mortensen 2005).

On a smaller scale, gorgonians inhabit areas with varying levels of exposure to waves, silt, turbidity, and water current and from substrata including bedrock and cobbles to artificial materials including metal (Hiscock et al. 2010). Some gorgonians can also attach to soft bottoms including some deep-sea members of the families Isididae and Chrysogorgiidae (Buhl-Mortensen et al. 2010).

In shallow water, sea fans provide a conspicuous and often dominant member of many reef communities (e.g. Lasker 2005). In the deep-sea, communities of sea fans contribute to increasing habitat complexity (Watanabe et al. 2009), often providing an oasis of heterogeneous habitat in vast sediment plains which are, comparatively, structurally simple landscapes. Sea fans themselves can provide

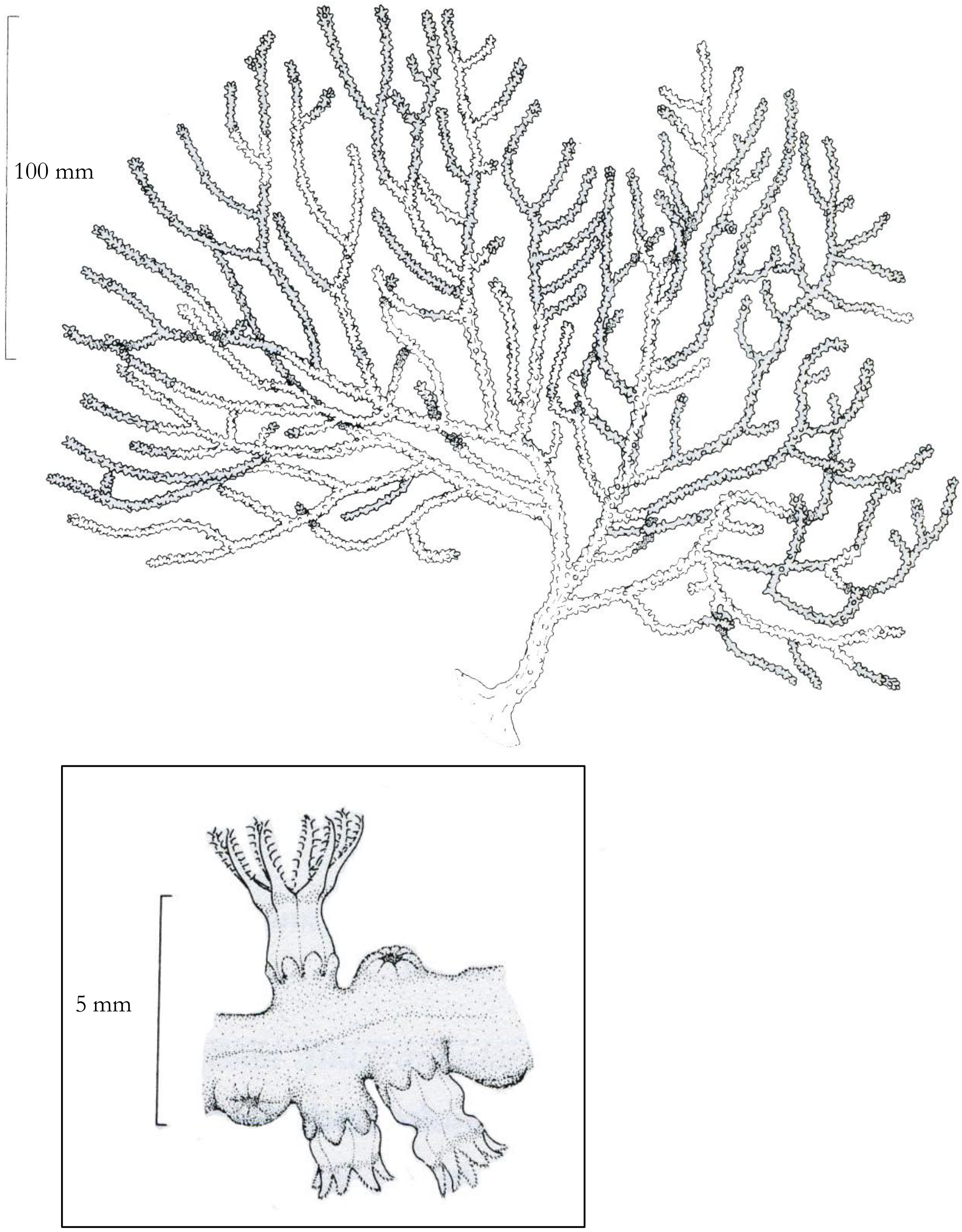


Figure 2.1: Drawing of the pink sea fan *Eunicella verrucosa* illustrating a whole colony with retracted polyps. Insert: branch, showing polyps and calyces. Reproduced with kind permission from the Linnean Society. From Manuel (1981), p.51.

habitat and protection from predators for other species in addition to the direct (their own tissue) and indirect (trapped detritus) provision of food (Gage 1986; Buhl-Mortensen et al. 2010). Such habitats are therefore often associated with high species richness (Buhl-Mortensen and Mortensen 2005; Rogers et al. 2007).

2.3.3 Diet

Gorgonian diet can be varied although feeding types can be crudely split into those species with symbiotic zooxanthellae (e.g. *Eunicella singularis*; Gori et al. 2007) and azooxanthellate species (e.g. *Eunicella caviolini*; Weinbauer and Velimirov 1995) which include all deep-sea colonies.

Those species without symbionts rely entirely on secondary production. Gorgonian diets can include zooplankton (Sanchez et al. 2009), invertebrate eggs (Coma et al. 1994), dissolved organic matter (DOM) and mucous (Coffroth 1984), nanoeukaryotes, phytoplankton and detrital particulate organic carbon (POC) (Ribes et al. 1999).

2.3.4 Growth

Growth rates in gorgonians are variable although many are slow growing (e.g. 3 mm per year, *Primnoa resedaeformis*; Mortensen and Buhl-Mortensen (2005) and 0.24 mm per year, *Primnoa pacifica*; Matsumoto (2007)). Following a mass mortality event in the Mediterranean, growth rates in *Paramuricea clavata* were shown to vary depending on the size of the colony; colonies less than 5 cm in height grew on average 1-3 cm per year during the recovery period whereas colonies over 10 cm were observed to lose over a third of their height as a result of branch fragmentation (Cerrano et al. 2005). An inverse relationship between age and growth rate has been reported for the deep-water gorgonian *P. resedaeformis* (Mortensen and Buhl-Mortensen 2005).

2.3.5 Reproduction

Gonochorism is the most frequently reported reproductive type in gorgonians, including in *Briareum asbestinum* (Brazeau and Lasker 1990), *Acanella arbuscula* (Lawson 1991), *Plexaura flexuosa* (Pakes and Woollacott 2008) and four Antarctic gorgonians (Orejas et al. 2007).

Both sexual and asexual reproductive strategies can be found among the gorgonians. In some species, vegetative reproduction is dominant and modes include fragmentation (e.g. *Plexaura kuna*; Coffroth and Lasker 1998) and autotomy (Walker and Bull 1983). In others, sexual reproduction is evident (e.g. *P. clavata*; Linares et al. 2008).

Although broadcast spawning has been observed (e.g. *P. flexuosa*; Pakes and Woollacott 2008), brooding appears to dominate. Brooding can be seen as analogous to broadcast spawning because egg fertilisation takes places in a parent colony, either on the colony surface or within polyps. Internal fertilisation is common (e.g. *Eunicella stricta* (Theodor 1967), *B. asbestinum* (Brazeau and Lasker 1990) and *A. arbuscula* (Lawson 1991)) and both internal (e.g. *E. singularis*; Gori et al. 2007) and external (e.g. *P. clavata*; Linares et al. 2008) brooding has been reported.

Spawning in gorgonians is frequently reported to be limited to a discrete period associated with increased or peak water temperature (e.g. *P. clavata* and *E. singularis*; Gori et al. 2007) or lunar activity (e.g. *B. asbestinum* (Brazeau and Lasker 1990), *P. kuna* (Lasker et al. 1998), and *P. clavata* (Linares et al. 2008)).

High variability in reproductive output between colonies has also been reported and is frequently associated with difference in age or size (e.g. *B. asbestinum* (Brazeau and Lasker 1990), *P. kuna* (Lasker et al. 1998) and *Pseudoplexaura* *porosa* (Kapela and Lasker 1999)).

Planulae have been noted to settle within the confines of parent colonies (e.g. *P. clavata*; Coma et al. 1995), in the vicinity of the parent colonies (e.g. *B. asbestinum*; Brazeau and Lasker 1990) or a short distance away after the planulae have drifted as is probably the case with *Eunicella verrucosa* (Hiscock 2007a).

Recruitment in gorgonians is often reported to be sporadic and/or low (Yoshioka 1996; Lasker et al. 1998; Coma et al. 2006).

2.4 Factors influencing the distribution of gorgonians

Of the factors primarily responsible for the distribution of gorgonians, water movement, substratum, depth and temperature are commonly listed (Barham and Davies 1968; Stoddart 1969; Kinzie 1973; Carpine and Grasshoff 1975; Bunker 1986; Gilbert 1988; Wood 2003; Bryan and Metaxas 2007). These factors are also important for deep-sea gorgonian distribution (Gage 1986; Genin et al. 1986; Frederiksen et al. 1992; Rogers 1994, 1999; Mortensen and Buhl-Mortensen 2004; Leverette and Metaxas 2005; Watanabe et al. 2009; Edinger et al. 2011).

Water motion was cited as the primary factor influencing the presence and absence of gorgonians in an early study in the Gulf of California (Barham and Davies 1968). Oscillatory water movement is also important for shallow water gorgonians (Kinzie 1973). The importance of water current is often attributed to its role in delivering food to sea fans (Carpine and Grasshoff 1975) yet it has also been argued that water movement is more essential for the removal of CO_2 and sediment than for supplying either food or oxygen to the colonies (Stoddart 1969). Colonies in areas without significant water movement may be starved of food and subject to the build up of silt which can lead to the death of tissue (Hiscock 2007a).

In contrast, strong currents have the potential to interfere with the dispersal and settlement of planulae larvae (Opresko 1973). Furthermore, sea fans may retract their polyps when current velocity is high enough that polyps are no longer able to retain food (Hiscock 2007a).

The availability of firm substrata has been cited as the primary factor limiting settlement (and hence distribution) of shallow water gorgonians in the West Indies (Kinzie 1973). Substratum is also one of several key factors influencing the settlement, growth and distribution of sea fans in the Mediterranean (Carpine and Grasshoff 1975). The suitability and stability of the habitat can also be influenced by the substrata (Grigg 1975). Some species of the deep-sea gorgonians families Isididae and Chrysogorgiidae can attach to soft bottoms (Buhl-Mortensen et al. 2010).

Unpublished work by Yoshioka & Yoshioka (cited in Yoshioka and Yoshioka (1989)) suggested that sediment transport was the overriding factor governing the regional distribution of sea fans around the coasts of Puerto Rico. Due to the delicate nature of the tissue covering the coral skeletons, coarse sediment in combination with strong current flows has the potential to scour the delicate colonies or clog the feeding apparatus. Alternatively, the newly settled gorgonian planulae larvae could be smothered by sediment (Opresko 1973) and periodic inundation of sand can lead to periods of elevated mortality and reduced recruitment (Grigg 1975).

Light is intrinsically linked with depth yet literature relating to light is also contradictory. Too much light can lead to enhanced epiphyte growth which can smother the gorgonians (Kinzie 1973; Hiscock 2007a), although Kinzie added that light is important where symbionts are relevant. In addition light might directly harm the colonies (Kinzie 1973). In contrast, Barham and Davies (1968) conclude that gorgonians flourish in shallower water because there is no competition from large algae.

Stoddart (1969) suggested that the changes in temperature and light with depth were more important in influencing the distribution of gorgonians than changes in current. In the deep-sea, bathymetric changes can lead to distinct variations in salinity, water temperature and dissolved oxygen (among other things) and these changes are reflected in deep-sea faunal distribution (Gage 1986). Temperature is known to have an important role in the reproductive cycle of gorgonians (Pakes and Woollacott 2008) and growth rates (Matsumoto 2007). Elevated sea temperature events have also been implicated in the mass mortality of gorgonians (Cerrano et al. 2005).

The drivers mentioned thus far are entirely physical and there has been little mention of chemical or biological factors in the early literature, other than indirectly e.g. the gaseous exchange and food delivery resulting from water movement. In relation to phytoplankton distribution however, Bryan and Metaxas (2007) found chlorophyll *a* concentration in surface waters to have an influential role in the distribution of gorgonians on the continental margins of North America.

2.5 Threats

Owing to their growth form, gorgonians are highly susceptible to damage from physical abrasion and substratum removal resulting from a variety of activities including benthic trawling and anchoring. The unfavourable effects of bottom trawling on sea fans have been well documented in both shallow and deep-water environments (Bavestrello et al. 1997; Mortensen et al. 2005).

Another recognized threat to gorgonians is disease. Necrosis, a condition in which the polyps are sloughed off the skeleton, has been documented from gorgonians worldwide including the Bristol and English Channels (Hiscock 2003; Hall-Spencer et al. 2007), the Mediterranean (Cerrano et al. 2000) and the Caribbean (Lasker 2005). During a thermal event in the Bahamas a prolonged period of high water temperature was implicated as the driving force in the rapid demise of numerous colonies although, unlike many other coral species (Glynn 1996), sea fan mortality during this thermal event was not associated with loss of pigmentation i.e. bleaching (Lasker 2005). Martin et al. (2002) also pinpointed temperature in the development of necrosis in gorgonians although the underlying causes of necrosis remain contentious (Hall-Spencer et al. 2007).

2.6 Gorgonians used in the present study

The gorgonians used in the present study include deep and shallow water species and are listed in Figure 2.2. Note that the figure includes only named gorgonian species as examples; other gorgonians have been included in the study based purely on their morphology (see Chapter 4). The shallow water species *Eunicella verrucosa* is one of only two species of shallow water sea fans found in the UK. The other, *Swiftia pallida*, is restricted to the northern reaches of the UK from where it extends northwards.

Eunicella verrucosa, commonly known as the pink sea fan, is protected through national legislation (the Wildlife and Countryside Act 1981) in addition to being listed as vulnerable on the International Union for Conservation of Nature and Natural Resources Red List of Threatened Species. It is a Biodiversity Action Plan (BAP) species meaning that it is one of a collection of species and habitats that have been identified as threatened and that therefore require targeted conservation effort.

Within the Northeast Atlantic study area there is a greater diversity of gorgonian species than for the UK's shallow water. Like much of the deep-sea benthos, none

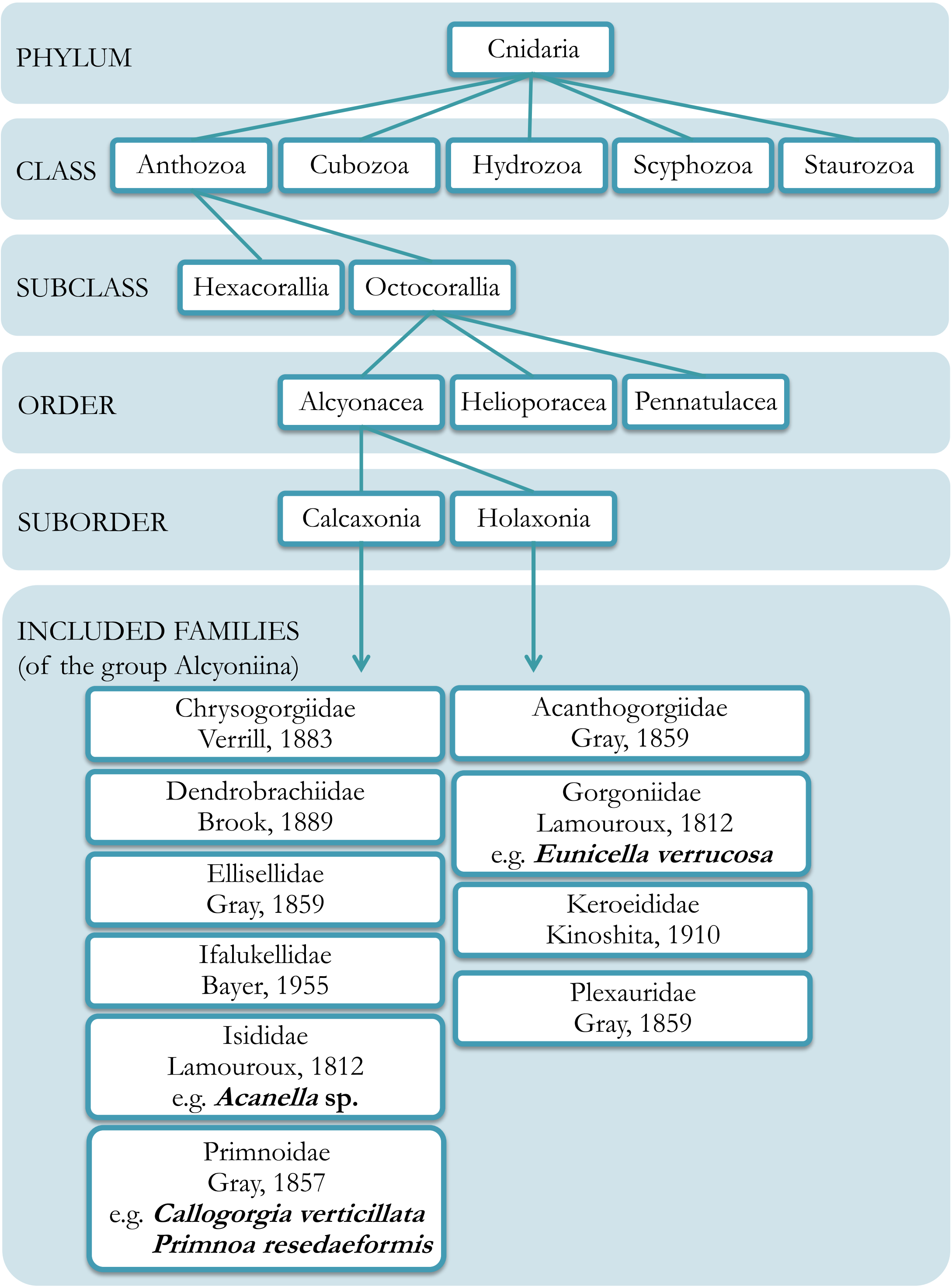


Figure 2.2: Gorgonian classification including named gorgonian species in this study (emboldened). Taxonomy based on Daly el al. 2007.

of the deep-sea gorgonians used in this study are specifically protected through legislation although ‘coral garden’ habitats, in which gorgonians are constituents, are protected under OSPAR (OSPAR Commission 2010).

2.7 Pink sea fan (*Eunicella verrucosa*); ecology and factors influencing its distribution

Eunicella verrucosa (Figure 2.3) has been recorded from southern and western areas of Britain and Ireland to the western Mediterranean and north-west Africa (Carpine and Grasshoff 1975; Manuel 1981; Hiscock 2007a). Importantly, the UK represents the northern limit of its distribution and the source of almost all of the available literature surrounding this species.

The depth range of the pink sea fan extends from low water, in the Channel Isles (Manuel, pers. comm., cited in Bunker (1986)) to 200m water depth in the Mediterranean (Carpine and Grasshoff 1975). In the UK, pink sea fans have been recorded in very shallow water (less than 10 m) (Wood 2003; Doyle 2005).

Although *Eunicella verrucosa* is reported to be found primarily on upward facing bedrock with moderately strong current (Hiscock, 2007a), a wider range of substratum use including cobbles, gravel and artificial substrata is also evident (Munro 1992; Doyle 2005; Black 2007; Hiscock et al. 2010).

Literature relating to water movement and the distribution of *Eunicella verrucosa* is conflicting. The pink sea fan has been recorded from very exposed sites with strong tidal streams (Bunker 1986; Doyle 2005) to very sheltered sites with very strong current (Doyle 2005) yet has also been reported as being rare in areas exposed to very strong or weak tidal streams and from very wave exposed sites (Bunker and Hiscock (1984, 1985), cited in Bunker (1986)).

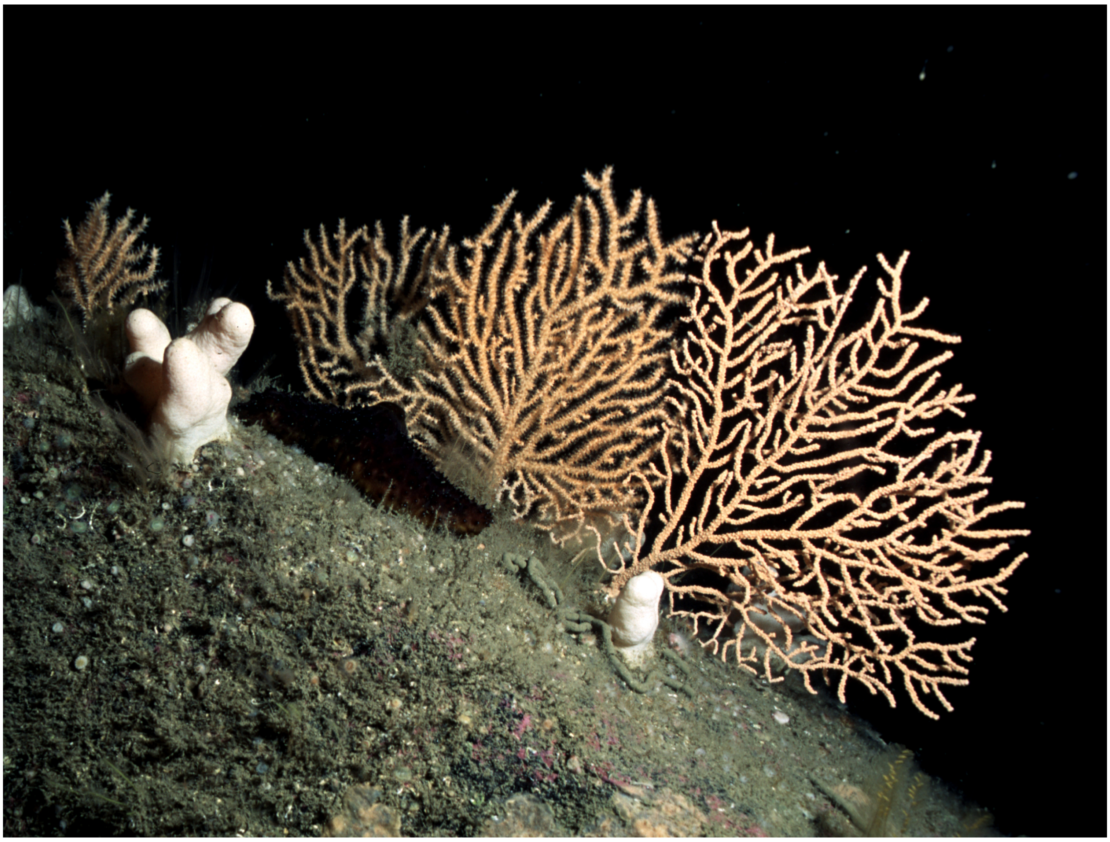


Figure 2.3: Photograph of the pink sea fan *Eunicella verrucosa* on bedrock with a cotton spinner *Holothuria forskali* and the soft coral *Alcyonium digitatum*. Photograph: Keith Hiscock, with permission.

The range of environmental conditions in which *Eunicella verrucosa* has been recorded is summarized below from Hiscock (1981); Manuel (1981); Bunker (1986); Bunker and Hiscock (1987); Doyle (2005) and K. Hiscock (pers. comm.):

- very little water movement to strong current movement;
- no silt to very silty including on very muddy boulders;
- wave sheltered to very wave exposed, and
- vertical and overhanging to horizontal.

Seawater temperature and wave and current exposure are reported as the factors primarily responsible for the presence and survival of *Eunicella* in the Skomer Marine Nature Reserve in Wales (Gilbert 1988). Bunker (1986) noted that there was no obvious reason why the pink sea fan was not more widely distributed around Skomer when there was plenty of seemingly suitable habitat available.

Therefore in summary it is likely that a complex combination of variables influence the distribution of the pink sea fan in addition to substratum, depth and water current.

Eunicella verrucosa typically feeds on suspended material including plankton (Hiscock 2007b).

Growth rate is thought to be highly variable with annual growth ranging from negligible to 6 cm increases in branch length reported in Lyme Bay colonies (C. Munro, pers. comm., cited in Hiscock (2007a)).

Little is known of the reproductive traits of *Eunicella verrucosa* although it is reported to be a broadcast spawner whose spawning may coincide with peak water temperature (Munro, 2004). However no evidence was found to suggest that a threshold water temperature triggers spawning Munro (2004). The production and settlement of the (probably) lecithotrophic larvae are only occasionally successful in south-west Britain (Hiscock 2007a).

Historically, divers used to collect pink sea fans as souvenirs and they were popular in the curio trade in the late 1960s (Hiscock 2007a). Following their designation as a protected species however, this threat is much reduced and it is likely that the biggest threat to their numbers in the UK at present is mobile benthic fishing gear, especially for pectinids, since their habitats can overlap (Bullimore 1985; Devon Wildlife Trust 1993). The slow growing nature of *Eunicella verrucosa*, like many other gorgonian species, combined with its sporadic recruitment, makes it especially sensitive to this activity.

2.8 Deep-water gorgonians; ecology and factors influencing their distribution

The 1873 HMS Challenger expedition saw the first study of deep-sea gorgonians (Lawson 1991). Deep-sea gorgonians form part of a group of species commonly referred to as 'cold-water corals' which also includes stony, black and hydro-corals (Roberts et al. 2006). Little specific information is available concerning the ecology of the named species in this study (*Callogorgia verticillata*; Figure 2.4, and *Primnoa resedaeformis*; Figure 2.5) and indeed the ecology is not well described for many deep-sea gorgonians, although the reader is referred to the more general section on gorgonian ecology above for details on diet, reproduction and growth rates where deep-sea examples are given.

The full extent of the distribution of *C. verticillata* is not known but *Primnoidae* sp. have a cosmopolitan distribution (OSPAR Commission 2010). *P. resedaeformis* is one of the largest deep sea gorgonians and one of the most abundant and widely distributed in the North Atlantic (Mortensen and Buhl-Mortensen 2004; Leverette and Metaxas 2005; Buhl-Mortensen et al. 2010). In addition to Hatton Bank and George Bligh Bank *C. verticillata* has also been recorded on le Danois Bank seamount in the Bay of Biscay at depths of around 550-570 m (Sanchez et al. 2009), on the Josefine Bank seamount to the west of Portugal, and in the Azores (OSPAR Commission 2010).

Like the majority of coral species, deep-sea gorgonians preferentially settle on rocky substrata. In a study on le Danois Bank a significantly higher number of *C. verticillata* were recorded on rocky areas, as opposed to mixed areas of sand and rock (Sanchez et al. 2009). The presence of rocky substrata is an important factor governing the distribution and abundance of *P. resedaeformis* too, along

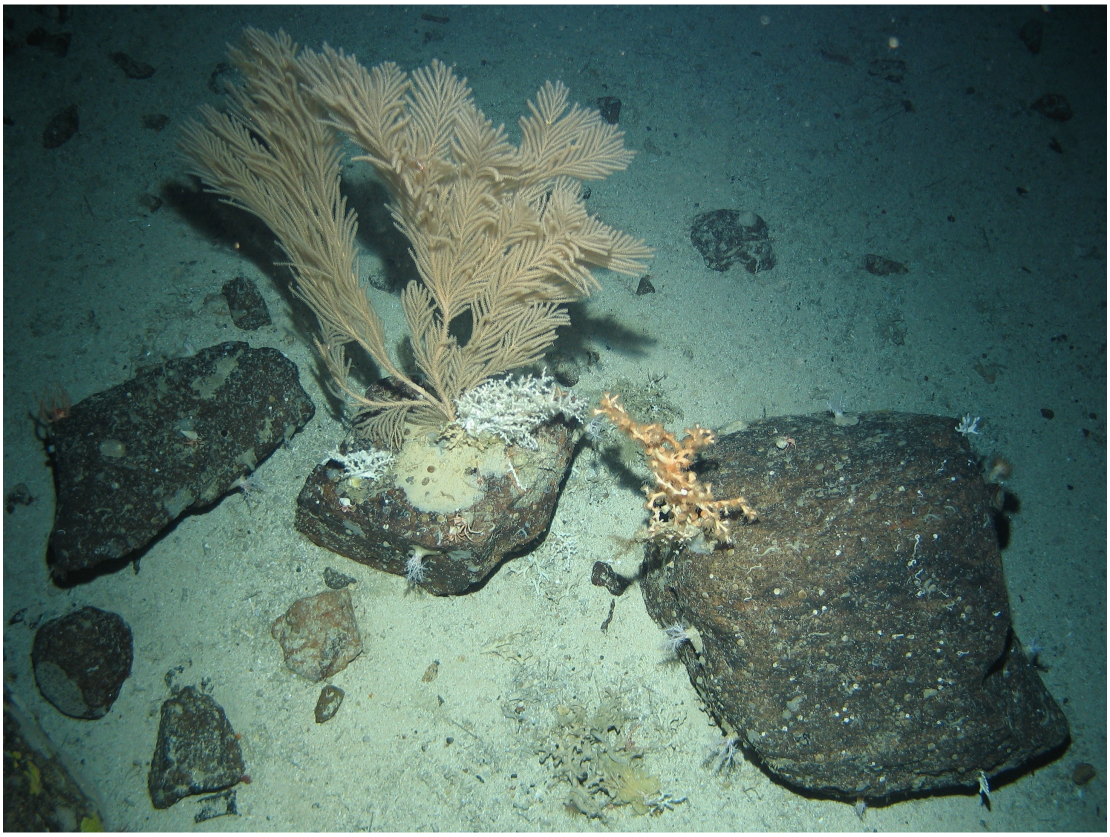


Figure 2.4: The deep-sea gorgonian *Callogorgia verticillata* on a boulder at 550 m on southern Hatton Bank. A diverse fauna is also shown and includes the reef forming cold water corals *Lophelia pertusa* and *Madrepora oculata*, hydrocorals, sponges, crustaceans and echinoderms. Photograph: Crown Copyright, 2006.

with depth, temperature and water current (Mortensen and Buhl-Mortensen 2004; Leverette and Metaxas 2005; Watanabe et al. 2009; Edinger et al. 2011).

Deep-sea gorgonians can be found in ‘coral gardens’; a highly biodiverse OSPAR habitat which can include a variety of species in addition to gorgonians including hard corals (Scleractinia), black corals (Antipatharia) and leather corals (Alcyonacea) (OSPAR Commission 2010). The extent of coral gardens in the Northeast Atlantic is presently unknown (OSPAR Commission 2010) although gorgonian dominated coral gardens were first recorded in UK waters in 2010 (Long et al. 2010). Deep-water gorgonians can provide habitat for numerous species and *P.*

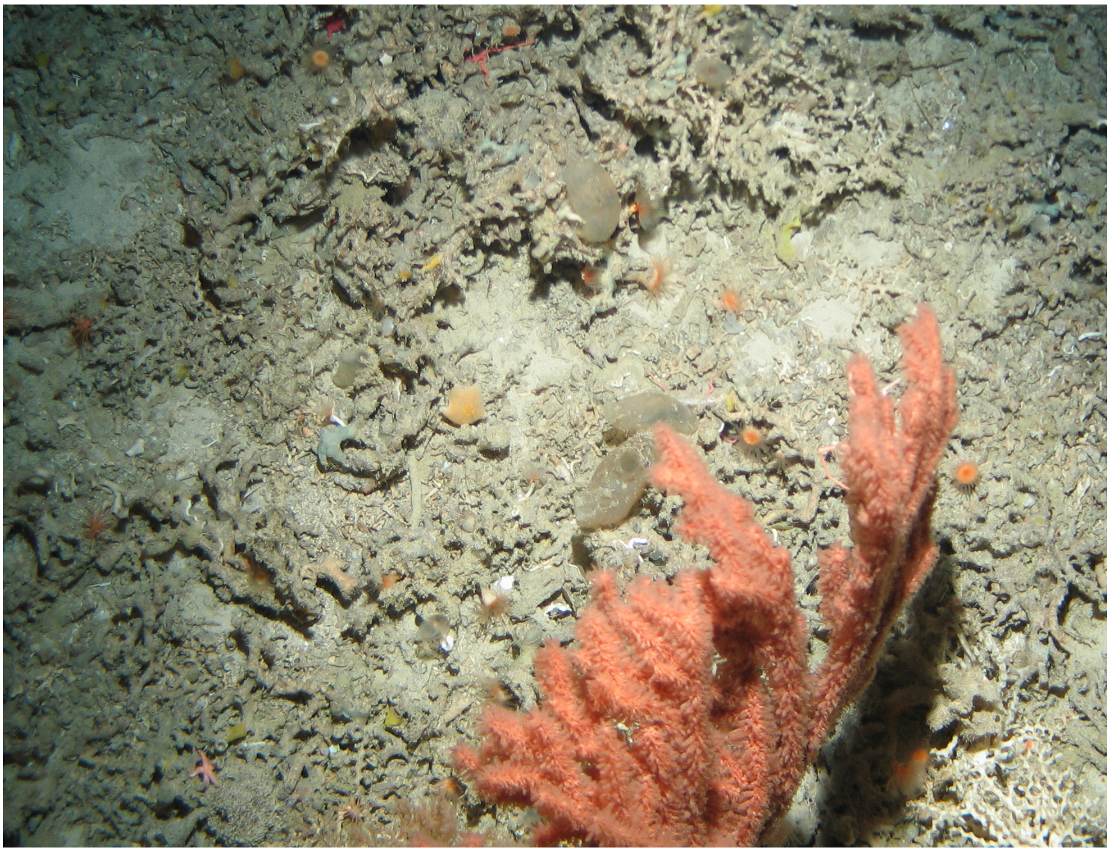


Figure 2.5: Primnoa resedaeformis at 830 m on southern Hatton Bank surrounded by a matrix of coral rubble and diverse associated epifauna. Photograph: Crown Copyright, 2006.

resedaeformis can host a rich, suspension feeder-dominated epifauna in addition to providing shelter for fish species, including commercial species such as rockfish (Buhl-Mortensen et al. 2010).

Both *C. verticillata* and *P. resedaeformis* can be described as 'bushy' gorgonians. The size and abundance of *P. resedaeformis* colonies can respectively exceed 1 m and 120 colonies per 100 m^2 (Mortensen and Buhl-Mortensen 2004; Buhl-Mortensen and Mortensen 2005; Watanabe et al. 2009).

The reproductive ecology for deep-water gorgonians is unknown for many species but seasonality has been recorded even though they are not subject to temperature or light cues like their shallow water counterparts. In the deep-water gorgonian *A. arbuscula*, Lawson (1991) observed internal fertilisation (in October) followed by a six month period of brooding prior to the release of planula larvae. Lawson (1991) proposed that fluxes of surface derived organic matter provided the cue for reproduction in this species, as is the case for many deep-sea species (George and Menzies 1967, 1968; Tyler 1988; Tyler et al. 1990; Gage and Tyler 1991). Mercier and Hamel (2011) studied the reproductive ecology of three deep-water octocorals from the Atlantic coast of Canada, including *P. resedaeformis* and the following summary is from their study: *P. resedaeformis* is a broadcast spawner and fertilisation occurs externally. An extended or continual period of oogenesis is likely. Based on the sampling regime in the study, no evidence of periodicity was found. An inverse relationship between depth and fecundity was found, with a potential colony fecundity of 100,000-250,000 oocytes reported, based on polyp density and for a colony of $\sim$ 30 cm and depending on depth.

Deep-water gorgonians are increasingly subject to threats from mobile benthic fishing gear as the development of technology permits fishing at greater depths (Davies et al. 2007; Hall-Spencer et al. 2007). The impact of benthic trawling on deep-water coral habitats (Rogers 1999) has resulted in the closure of several areas to fishing, including in the Northeast Atlantic.

2.9 Suitability of corals for species distribution modelling

The strength of predictive species distribution models lies in the relationship between the distribution of the target species and its environment and for this reason sessile species are especially desirable because it is possible to pinpoint their distribution at specific locations and, as a result, marry this distribution with relevant (and available) environmental data.

Among sessile marine fauna, corals represent a valid study group for several reasons. Many species are protected and often the subject of targeted surveys thereby boosting the distribution data set. Furthermore, some corals are considered to be indicative of the health and biodiversity of a wider ecosystem because the presence of long-lived and fragile epifauna suggests that the habitat is stable and has seen little natural or anthropogenically driven physical disturbance. Many coral species are unmistakable and this bestows confidence in their distribution (presence and absence) records and facilitates detection and identification by divers and video surveys alike. This is especially true of gorgonians which are often erect and conspicuous making them ideal to study within the context of species distribution modelling. Many gorgonians are slow growing, especially deep-sea species, and threats to fragile coral communities make them a worthy focus.

Chapter 3

Study sites

3.1 Selection of sites

The selection of sites was determined by the aim of this study, namely to investigate key issues surrounding the use of species distribution models to support marine conservation planning. Lyme Bay, on the south coast of England, and the Rockall Trough and surrounding seamounts in the Northeast Atlantic were selected on the basis that they have divergent needs and challenges regarding the implementation of marine planning and marine protected areas. The selection of these two sites has allowed for the investigation of the potential influences that differences in, for example, data availability, current protection, accessibility, pressures and management may have on both the model outputs themselves and/or the future application of species distribution models to conservation management in each area. Interestingly, the areas surrounding the Rockall Trough are among the world's best studied deep-sea areas (Howell et al. 2010), and Lyme Bay has similar claims in respect to nearshore environments in the UK (Stevens et al. 2006). That gorgonians are a conservation target in both areas further supports the selection of these corals to demonstrate the use of species distribution models for use in marine conservation.

3.2 Lyme Bay

3.2.1 Physical environment

Lyme Bay encompasses the area from Start Point in south Devon to Portland Bill in Dorset, and covers an area of approximately 2500 km^2 (Figure 3.1).

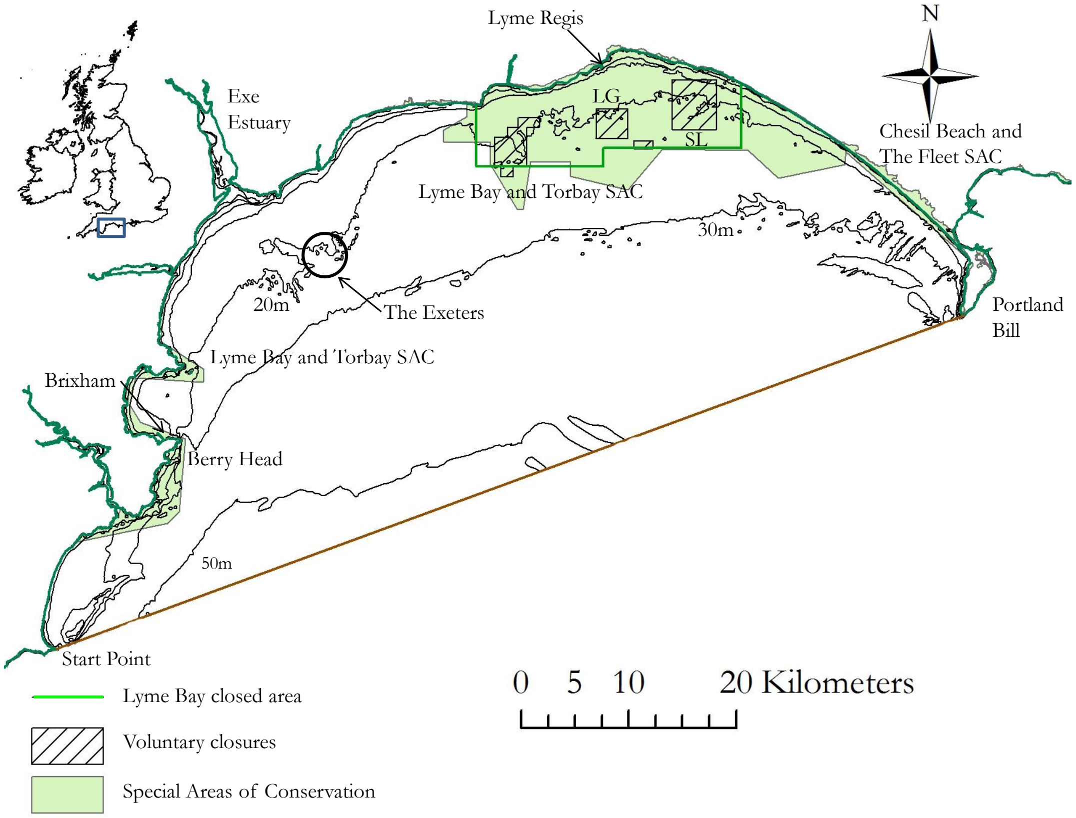


Figure 3.1: The extent of the study site is delimited by the Bay's closing line. The ports of Brixham and Lyme Regis are highlighted. The Lyme Bay statutory closed area is shown as the large boxed area in the north of the Bay. The four smaller shaded boxes highlight the four voluntary areas initially proposed by Defra, including Sawtooth Ledges (SL) and Lane's Ground (LG). The Jurassic coast runs from the Exe eastwards to Portland Bill (and extends eastwards beyond the study site).

Lyme Bay represents a physically diverse environment with a wide range of substrata from rocky reefs and cobbles to sand and mud. The water deepens gradually from the shore and much of the water around the closing line exceeds 50 m. Sites within the bay range from very wave sheltered to wave exposed sites and current flow also varies, with speeds exceeding 90 cm $^{s-1}$ recorded off Portland Bill (Nunny 1995a). Portland Bill is also associated with a marginal front which curves and extends south westerly from the Bill and which is associated with increased chlorophyll *a* concentration (Pingree et al. 1983). Lyme Bay has relatively turbid water and stratification is also evident at times (Pingree et al. 1983).

3.2.2 Ecology

The rocky and mudstone reef areas in the north of the bay provide a structurally complex environment with numerous microhabitats for species including rare or protected species such as the sunset cup coral *Leptopsammia pruvoti* and the pink sea fan *Eunicella verrucosa* (Hiscock 2007b). The reefs also support structurally important species including branching sponges (e.g. *Axinella* sp.) and ross 'coral' *Pentapora foliacea.* A recent report on UK marine biodiversity hotspots (Hiscock and Breckels 2007) identified areas of Lyme Bay as a hotspot for species richness and 'Nationally Important Marine Features species richness' (Vincent et al. 2004).

3.2.3 Management issues

The varied and biologically diverse underwater landscape has supported a productive fishing industry for generations and it is this industry that now provides a key focus of current management effort within the bay.

The reefs of Lyme Bay have attracted divers, anglers and fishermen for years but it was the Devon Wildlife Trust dives in 1991, 1992 and 1998 that publicised not only the diversity of the reef habitats and communities but also their vulnerability to scallop dredging (Devon Wildlife Trust 2007). The movement of the heavy scallop dredges across reef systems have the potential to damage both the reef communities themselves and the abiotic reef habitat, such as the soft mudstone reefs of Lyme Bay. Dredging for scallops was implicated in the almost total destruction of The Exeters, a reef area in the north of the bay, following the 1992 survey which failed to locate any of the Exeters reef features previously described (Devon Wildlife Trust 2007). In 2001 Devon Wildlife Trust and local scallop fishermen agreed to close voluntarily two areas to scallop dredging. These closures, centred on Lane's Ground and Sawtooth Ledges (Figure 3.1), resulted from mounting concern regarding the state of various reef areas in the bay and their associated communities following observations made by divers, including those on Devon Wildlife Trust dive surveys.

In response to socioeconomic drivers, principally the market value of scallops, the voluntary agreements supporting the two closed areas started to deteriorate in 2005 (Devon Wildlife Trust 2007) and the following year Devon Wildlife Trust requested that Natural England apply for a ministerial stop order to close 60 square miles of reef area in the northern part of the bay.

Defra responded by announcing a voluntary 12 square mile closure of four reef areas (Figure 3.1) that had been agreed with the South West Inshore Scallopers Association (Devon Wildlife Trust 2007). Devon Wildlife Trust threatened to take the Government to judicial review over this decision, citing major misconceptions surrounding data interpretation as reasoning behind the decision. In response, a Partial Regulatory Impact Assessment and Consultation was released by Defra on "measures to protect biodiversity in Lyme Bay from the impact of fishing with dredges and other towed gear" (Defra 2007b).

Results of this public consultation showed an overwhelming support for the statutory closure of 60 square miles of reef area and, in July 2008, Defra closed this area (approximately 8% of the bay) to scallop dredging and other mobile fishing gear (Defra 2008) (Figure 3.1). This closure is the first and so far only one within the UK set up explicitly for the purpose of biodiversity conservation, and was established to protect high diversity rocky reef assemblages from the effects of such fishing. The closure is in direct line with the aims of OSPAR to "protect, conserve and restore species, habitats and ecological processes which are adversely affected as a result of human activities" and "prevent degradation of and damage to species, habitats and ecological processes, following the precautionary principle".

Ongoing management within the Bay includes enforcement of the closed area restrictions and an ongoing benthic recovery monitoring programme that formed part of a wider three year Defra funded monitoring program *Lyme Bay - a case-study: measuring recovery of benthic species; assessing potential "spillover" effects and socio-economic changes with the closure of 60 square nautical miles to scallop dredging.* The monitoring project originally finished in March 2011 although the project has received some continuation funding.

Results from the comprehensive monitoring programme are diverse, but initial results from the socio-economic assessment include that: the impact of the closure on fishermen was dependent on gear type and area in the Bay; an increased conflict between static and mobile gear fishers was observed outside the closure; an increase in diving and angling activity in the two years following the closure was observed at several sites; dive businesses were generally unaffected by the closure, and that some mobile gear damage to previously good dive sites has been observed outside the closure (Mangi et al. 2011a,b).

The preliminary ecological results suggest some benthic recovery, albeit with lots of variation in the results (Attrill et al. 2011). For example, two years after the closure, assemblages in newly closed sites (previously fished) were significantly different from assemblages in some of the control sites that remain open to fishing. In addition, differences in assemblage structure between the newly closed sites and sites previously unfished by mobile gear under voluntary agreement (and still unfished) have decreased over time, suggesting that their overall similarity is increasing. A significant increase in the number of scallops in the new closure by 2010 was also observed (Attrill et al. 2011).

Consent for a lease underpinning the pilot development of an offshore mussel farm in Lyme Bay was recently granted (September 2010) to Offshore Shellfish Ltd by The Crown Estate and will require spatial consideration in light of commercial fishing and recreation activities within the Bay, adding complexity to its management.

Lyme Bay supports a diverse recreation industry, including diving, angling and wildlife watching (Rees et al. 2010). Earlier activities within Lyme Bay included exploratory drilling for oil and gas in the mid 1990s, Lyme Bay being licensed for hydrocarbons exploration (Nunny 1995b), and ship to ship oil transfer, with western parts of Lyme Bay providing a sheltered anchoring point from prevailing weather (Anon 1994). Such ship to ship transfer is now subject to regulation in the form of The Merchant Shipping (Ship-to-Ship Transfers) Regulations 2010 (Department for Transport 2010).

3.2.4 Designations

The Jurassic Coast, part of which extends from the mouth of the Exe to Portland Bill, forms a natural World Heritage Site; a World Heritage Coast. Chesil Beach and The Fleet, and the Exe Estuary are designated Ramsar Convention sites (an international designation) and Special Protection Areas (a European designation). There are more than 20 Sites of Special Scientific Interest (SSSI) along the coast of the bay and further designations include an Area of Special Protection (AoSP) at Berry Head and three Areas of Outstanding Natural Beauty (AONB); South Devon, East Devon and Dorset. Sensitive Marine Areas (SMAs), a non-statutory designation, cover a large proportion of Lyme Bay's coast and were identified by Natural England (formerly English Nature) for notable marine flora and fauna communities or sites which provide ecological support to adjacent sites protected by statute (Barne et al. 1996a,b).

Two years after the statutory closure of the northern reefs previously mentioned, parts of northern and eastern Lyme Bay, including the closed area, were submitted to Europe as a Candidate Special Area of Conservation (cSAC) in August 2010. This area, together with an area around Torbay in west Lyme Bay, make up the Lyme Bay and Torbay cSAC (Figure 3.1). Bedrock and stony reef habitats were included as conservation objectives in this submission. More recently (September 2011), eight sites within Lyme Bay have been recommended as part of the wider MCZ network, including three estuaries and two reference areas.

3.3 Rockall Trough and surrounding seamounts

3.3.1 Physical Environment

The Rockall Trough is a large area of the Northeast Atlantic deep-ocean just west of the continental shelf of Ireland and the United Kingdom (Figure 3.2). It is bordered on the west by Rockall Bank and, to the north, by the Wyville-Thomson ridge. The Rockall Trough gradually deepens with distance south, reaching its deepest (∼4000 m) at its mouth (Ellett et al. 1986; Bett 2000).

The Rockall Trough offers a diverse range of habitats from abyssal plains to steep sided canyons and gullies and a wide range of substrata including gravel, bedrock and boulders (Bett 2000). In addition, layers of phytodetrital material several centimetres thick derived from seasonal fluxes have been reported from the area (Bett 2001), resulting from the rapid settlement of surface-water derived primary production (Billett et al. 1983; Lampitt 1985). In excess of 800 seamounts have been recorded in the North Atlantic (Epp and Smoot 1989), including Rosemary Bank, George Bligh Bank and Anton Dohrn (Figure 3.2).

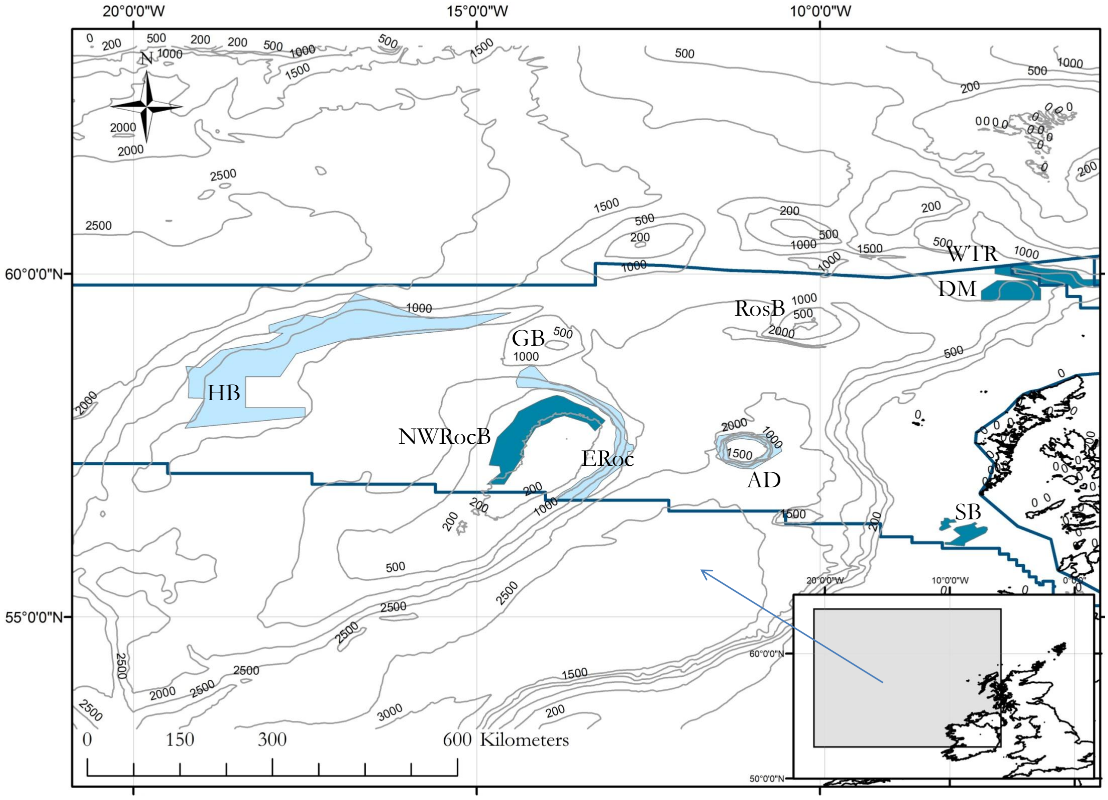


Figure 3.2: The Northeast Atlantic. Candidate Special Areas of Conservation (SACs) are shaded in dark blue and include, from left to right, the North West Rockall Bank (NWRocB), Stanton Banks (SB), Darwin Mounds (DM) and Wyville Thomson Ridge (WTR). Possible SACs are shaded in light blue and include, from left to right, Hatton Bank (HB), East Rockall (ERoc) and Anton Dohrn (AD). George Bligh Bank (GB) and Rosemary Bank (RosB) are also labelled. The UK Continental Shelf limit is marked by the bold line. Bathymetry is from The General Bathymetric Chart of the Oceans (GEBCO).

Rockall Trough and much of the Northeast Atlantic is bathymetrically and hydrographically complex with features operating at a variety of scales. The trough is characterised by two principal water masses: the Eastern North Atlantic Water (ENAW), which extends from the surface to about 1200 m depth, and the cooler Labrador Sea Water (LSW) beneath it (Ellett et al. 1986; Holliday et al. 2000).

Hatton Bank, upon which several of the chapters in this study focus, is an elongate, relatively shallow bathymetric high located to the west of the Rockall Bank and the Rockall Trough in the Northeast Atlantic (Figure 3.2). The Bank is ∼450 km in length and is orientated approximately southwest-northeast to the south of 59°N changing to a more west-east orientation north of 59°N. The Bank descends >2500 m below sea level into the Iceland Basin to the west and >1100 m below sea level into the Hatton Basin, sometimes referred to as the Hatton-Rockall Basin, to the east. At its shallowest its summit lies at ∼480m water depth.

3.3.2 Ecology

The ecology of the Northeast Atlantic is varied and diverse yet many ecologically significant deep-sea habitats were largely unknown until the 21^{st} century including the Darwin Mounds. These mounds, a series of low lying hummocks on the sea floor, are presumed to be carbonate mounds and were only discovered in 1998 (Bett 2000). Interest surrounding the mounds lies principally in their associated epifauna which includes the structurally complex cold-water coral *Lophelia pertusa*. *Lophelia pertusa* is a reef forming stony coral which is found elsewhere in the Rockall Trough and is widely distributed in the Northeast Atlantic (Wilson 1979). *Lophelia* and other cold-water corals provide a structurally complex habitat, often in relatively simple (structurally speaking) surrounding environments, and accordingly are associated with biodiverse communities (Roberts et al. 2006).

Apart from stony corals, black, hard, bamboo and leather corals are all found within the Northeast Atlantic. Combined, these species can form coral gardens

(OSPAR Commission 2010). The first record of gorgonian dominated coral gardens from UK waters was recently documented on the Anton Dohrn seamount (Long et al. 2010). The diverse benthic assemblages found in the study area have recently been described by Howell et al. (2010) as part of the development of a biological classification system to aid in habitat mapping efforts.

Several well described phenomena exist within deep-sea ecology including seasonality in the reproduction of some deep-sea species which is linked to the periodic, seasonal pulses of phytodetritus to the sea floor as previously mentioned (Tyler et al. 1990). The distribution of fauna has also been linked to depth via other physical and hydrographic parameters such as seasonal and permanent thermoclines, the depth of the extent of mixing of water masses, sediment type, phytodetrital food supply and currents (Rowe and Menzies 1969; Haedrich et al. 1975; Rex 1981; Gage 1986).

Depth related faunal patterns include changes in abundance with depth, reductions in diversity, distinct depth zones for certain species and bathymetric zones of pronounced change in the fauna (Rowe and Menzies 1969; Sanders and Hessler 1969; Haedrich et al. 1975; Carney et al. 1983; Gage 1986; Howell et al. 2002). Rex (1981), for example, described the continental shelf-slope boundary as an area of pronounced change in the fauna with peaks in the abundance of polychaete and fish species. Zonation in deep-ocean fauna has been described as a 'non-repeating sequential change with depth' (Carney et al. 1983). For the most part, the deep-water distribution records in this study are at mid-slope depths, in a transitional zone above the permanent thermocline (Rowe and Menzies 1969; Haedrich et al. 1975; Howell et al. 2002).

In addition to physical factors associated with depth, several hydrographic phenomena influence the distribution of fauna within the area including boundaries between different water masses, where temperature and salinity differences can occur, and current acceleration, such as that associated with the summits of seamounts (Gage 1986; Genin et al. 1986; Frederiksen et al. 1992). Higher currents have been recorded off coral mounds on the Rockall Bank with respect to surrounding gullies and plains (Duineveld et al. 2007). Seamounts and their effect on local and regional hydrography have been implicated in the dominance of suspension feeders on seamount summits because the increased currents serve to increase food availability (Genin et al. 1986; Rogers 1999).

With respect to the ecology of gorgonians and other suspension feeders, the availability of firm substrata and a strong current that help clear sediment and waste and deliver food, and in some cases the availability of phytodetrital material, all serve to influence the distribution of those fauna (Rowe and Menzies 1969; Rogers 1999; Bryan and Metaxas 2007). The number of suspension feeders decreases in the deep-sea, at the same time as an increase in the dominance of deposit feeders is observed, as a result of several factors in addition to availability of suitable substrata, including phytoplankton availability (Carney et al. 1983).

In addition to sessile benthos, the Northeast Atlantic supports a diverse demersal and pelagic fauna, including several important commercial species such as haddock and blue whiting.

3.3.3 Management issues

Investigative dredging in the Rockall Trough started in the late 19th century on HMS Porcupine although it was to be a century later before commercial trawling began (Gordon 2003). Bottom-trawling was found to be causing irreversible damage to fragile temperate coral communities and reefal substrata (Hall-Spencer et al. 2002).

Bottom trawling and long-lining are principle management concerns in the Hatton Bank area, with both activities known to have damaged vulnerable marine ecosystem (VME) indicators including fragile sponges and gorgonians (Benn et al. 2010; ICES 2011; Durán Muñoz et al. 2011). For example, Figure 3.3 illustrates the spatial distribution of fishing effort by the Spanish trawl fleet on Hatton Bank from 1996-2006 (ICES 2007).

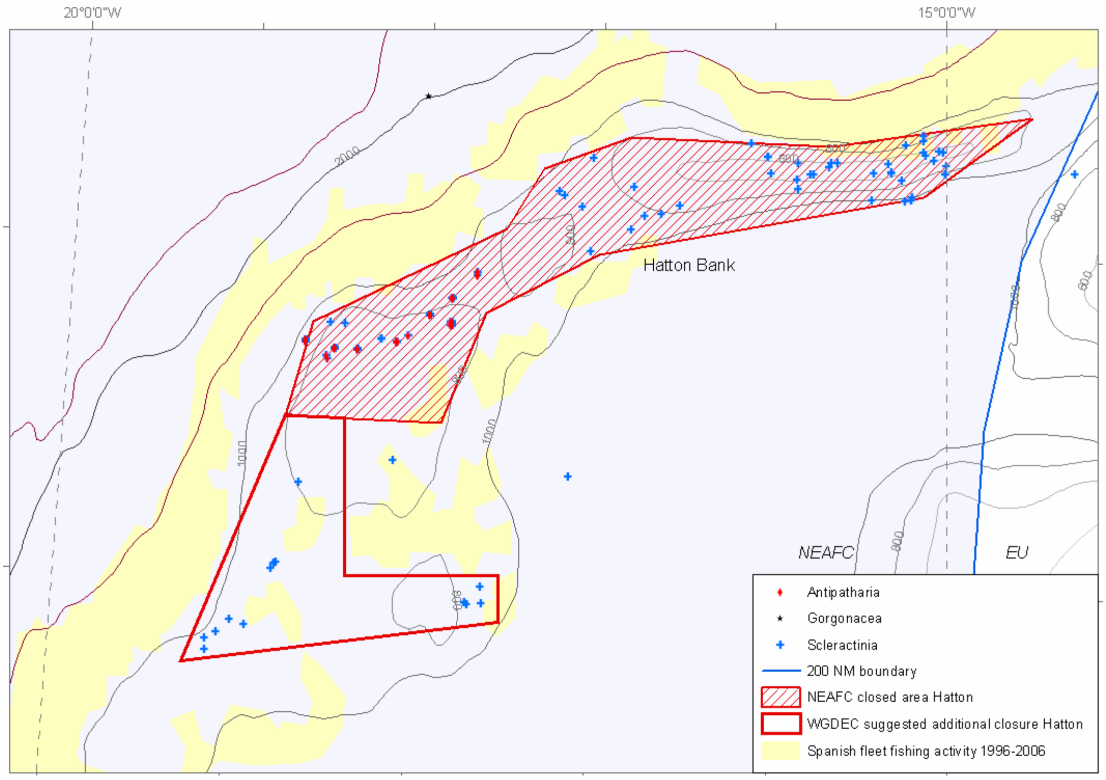


Figure 3.3: Spatial distribution of bottom trawling on Hatton Bank, based on observed Spanish trawling effort 1996-2006. The NEAFC closure is hatched in red. An area recommended for closure to protect sensitive habitats of cold-water coral is also shown. Map taken from the 2007 Working Group on Deep-water Ecology report (ICES 2007), p19. Used with the kind permission of the International Council for the Exploration of the Sea.

In 2007, the North East Atlantic Fisheries Commission (NEAFC) and Directorate-General for Maritime Affairs and Fisheries (DG MARE) closed four areas within the Rockall and Hatton Bank area to bottom contact trawling, explicitly to protect deep-coral habitats (NEAFC 2007). The ICES Joint Working Group on Deep-water Ecology (WGDEC) has recently (March 2011) recommended revisions to the boundary of the Northwest Rockall closure based on new data for cold-water VMEs (ICES 2011). WGDEC also put forward a proposal for a fisheries closure on Anton Dohrn seamount, based on recent survey work (the Joint Nature Conservation Committee 2009 Offshore Natura survey) and predictive modelling (K. Howell and J. Davies, unpublished) which suggests that the steep slopes of the seamount might be especially important for VMEs (ICES 2011).

Concern about the impact of human activities on vulnerable marine ecosystems, including cold water habitats and seamounts, has repeatedly been raised in United Nations General Assembly resolutions on the Oceans and the Law of the Sea, emphasizing the importance of implementing the precautionary approach and Part XII of the United Nations Convention of the Law of the Sea (UNCLOS), the latter of which calls for the protection of the marine environments from physical degradation.

Emerging threats to deep-sea ecosystems, including habitat forming ecosystems (as summarised by Davies et al. (2007), Benn et al. (2010) and Buhl-Mortensen et al. (2010)) include fisheries, oil and gas, carbon capture and storage, mining, waste disposal, petroleum exploration and ocean acidification. The OSPAR maritime area of the Northeast Atlantic is considered one of the most heavily impacted by human activities (Benn et al. 2010). Rockall, in August 2008, became the centre of an international struggle for sovereignty, seeing Denmark (for the Faroe Islands), Iceland, Ireland and the United Kingdom lay claim to the Rockall area in the hope of securing offshore oil and gas reserves. Whatever the outcome, this has potentially far reaching consequences for spatial planning in the area.

3.3.4 Designations

The coral communities found on the Darwin Mounds led to their designation as the UK's first offshore MPA. Deep-sea coral environments have been linked to increased fish catches, when compared to non-coral habitats (Husebø et al. 2000), and it was ultimately the impacts of commercial fishing that led to the protection of the Darwin Mounds.

Consideration for a precautionary approach in the Common Fisheries Policy, in addition to the inclusion of emergency measures, allowed the initial protection of the Darwin Mounds which was effected in August 2003 (De Santo and Jones 2007). The closure was made permanent in March 2004 and in August 2008 the Darwin Mounds was recommended as a candidate SAC.

Several other UK offshore areas have been submitted as candidate SACs (in two tranches). The first tranche, submitted alongside the Darwin Mounds, include the Stanton Banks (Figure 3.2). The second and most recent tranche, submitted in August 2010, includes North West Rockall Bank and the Wyville Thomson Ridge. In addition, Hatton Bank was formally recommended as a draft SAC (dSAC) in February 2009. However, the NEAFC and EU closures remain the dominant spatial management measure in the Rockall and Hatton area.

3.4 Suitability of selected study sites

Lyme Bay and the Rockall Trough and surrounding seamounts are suitable sites in which to investigate the use of species distribution models to support marine conservation planning because they offer divergent case studies yet are underpinned by some similarities in conservation and management effort (Table 3.1).

Lyme Bay is very accessible and has a diverse and well documented management history that has been brought to public attention through the campaigning efforts of several Non-Governmental Organisations, in addition to a government-led public consultation. Following the designation of the closed area in 2008, a large part of Lyme Bay is also a candidate SAC meaning that monitoring and continued conservation effort will be required by statute.

Areas of the Northeast Atlantic covered in this study include (proposed) SACs also but aside from the fact that they are geographically inaccessible to most people, not to mention psychologically inaccessible, the management of these high seas areas will require international agreement as opposed to national legislation and local byelaws. This is of course relevant to modelling because it will be necessary to identify the endpoint application of the models. Will the model outputs be used to give weight to existing conservation measures and inform monitoring, for example, or will the model outputs be used to inform new designations?

The selection of a large, offshore, deep-sea area in addition to a (relatively) small inshore site has allowed for the issue of scale and data availability to be addressed within the context of modelling and planning. Whilst this facet of species distribution modelling has been well explored in a terrestrial context (Scott et al. 2002), it has not been adequately addressed within the remit of marine conservation planning. In this context scale relates to data availability, both in terms of type of data and the quantity and quality, and data resolution between inshore and offshore areas and the potential for disparity between the two. Generally speaking, offshore data is frequently of a coarser resolution, if available at all.

Table 3.1: Comparative overview of Lyme Bay and Hatton Bank study site characteristics.

Comparative overview of study site characteristics		
Lyme Bay	**Study site**	**Hatton Bank**
•Diverse ecology resulting from broad range of habitats •Benthic fauna range from important sedimentary communities including *Zostera* beds, maerl beds and burrowing anemone communities, to structurally complex reef communities supporting rare branching sponges and protected corals	**Ecology**	•A broad range of species, again resulting from a broad range of habitats •Benthic fauna range from large and sparse echinoderm dominated sedimentary plains to complex rocky and carbonate reef systems containing mature cold water corals reef and sponge communities
•Majority of Lyme Bay <50m water depth •Deepest point ~70m •Wave exposure ranges from sheltered to exposed •Currents can exceed 90 cm $^{s-1}$ •Geomorphological diversity mostly provided by rocky and mudstone reef areas	**Physical**	•Significantly deeper than Lyme Bay, with the majority of Hatton Bank >1000m water depth •Shallowest point ~480m •Water currents much slower and include those driven by large scale geomorphological features such as seamounts •Geomorphologically highly diverse including depressions and furrows to pinnacles and ridges
•Lyme Bay supports a range of commercial fisheries including netting, potting, trawling and scallop dredging •2008 Statutory Instrument preventing mobile gear in reef area represents ongoing management concern •Productive recreation industry including diving, angling and wildlife watching •Potential development offshore mussel farm in Lyme Bay	**Management Issues**	•The principle management concerns on Hatton Bank are deep-sea trawling and long-lining
•MCZs: eight proposed, including two reference areas •Ramsar sites: Chesil Beach and The Fleet; Exe Estuary •SACs: Sidmouth to West Bay; Chesil Beach and The Fleet •Candidate SACs: Lyme Bay and Torbay •SPAs: Chesil Beach and The Fleet; Exe Estuary •Several SSSIs including Portland Harbour Shore, Dawlish Warren and Isle of Portland	**Statutory designations (marine features)**	•Possible SAC: Hatton Bank •NEAFC closure to bottom-trawling

Physical differences between the sites are also important. For example, the huge difference in depth will have implications for the relevance of difference environmental predictors which again links back to data requirements. Furthermore, data sources will vary between the study areas (volunteer dive survey data versus offshore video survey data for example) and this may in turn result in differences in data quality, data availability and, crucially, the spatial coverage of relevant data sets.

The pressures that exist in inshore and offshore environments can vary enormously. Inshore areas can have a relatively higher direct anthropogenic pressure than offshore which not only determines the type of data input required for spatial planning but also influences data availability. For example, coastal areas may benefit from ad hoc survey data whereas this is unlikely in offshore areas where data collection is invariably associated with high cost and considerable logistical consideration.

Nearshore environments and areas in the high seas will both require the coordination of marine plans in the future and it is essential to be aware of and understand any differences that may exist in the application of species distribution models in these areas so that future data collection may be targeted accordingly.

Chapter 4

General methodology

4.1 Methodology overview

This methodology chapter outlines the general methodological approach adopted throughout the course of the study. Broadly split into two halves, the first covering data and the second focusing on species distribution models, the chapter aims to avoid repetition among the four subsequent data chapters. The flowchart overleaf (Figure 4.1) forms the basis of the structure within this chapter, which includes details on topics from the source of distribution and environmental data, data acquisition and data preparation to the modelling methods adopted (including model choice) and the assessment of model performance. Methodological detail in this chapter is restricted to the methodology that applies to all four analysis chapters; method details specific to certain data chapters are provided in the relevant section of those chapters. With the assistance of Figure 4.1 this chapter runs in a logical progression through the various stages undertaken as part of this study and justifies the choices made with regards to data and model selection.

4.2 Video data

Due to the difficulty associated with sampling underwater environments, especially in the deep-sea, remote sampling techniques are often adopted for survey work. Traditional techniques such as grab sampling are not always possible due to the

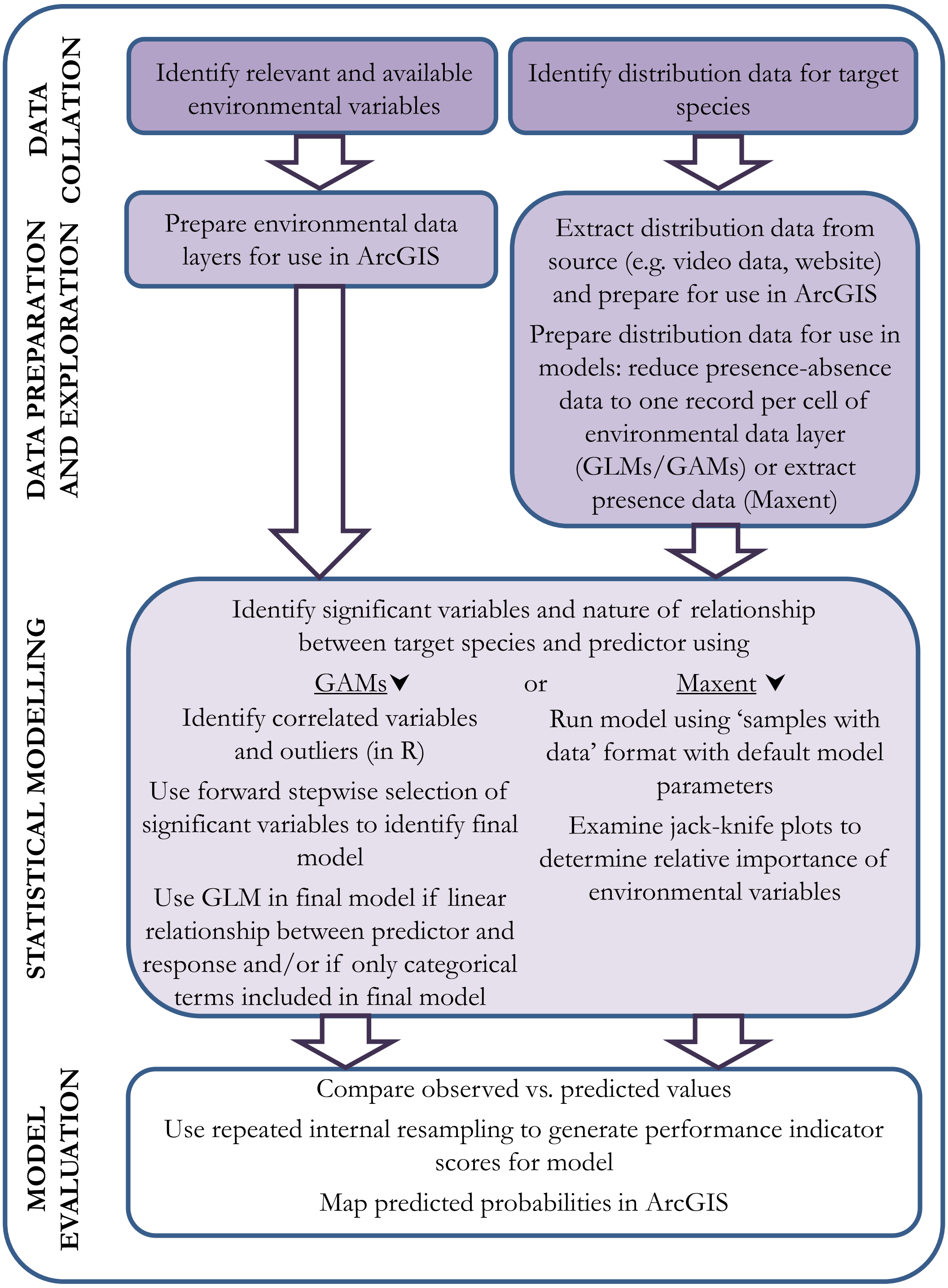


Figure 4.1: Flow diagram summarising species distribution model procedure undertaken. The majority of the individual steps in the Maxent modelling process have not been listed because the program performs them automatically.

nature of the substrata or because of the damaging impact this type of sampling might have on fragile benthic structures such as biogenic reefs. Dive surveys have many associated safety issues, are expensive and depth limited. Video surveys are now a popular, cost-effective method for marine habitat mapping and survey work (Stevens and Connolly 2005). In the deep-sea especially, video survey is of critical importance for informing conservation planning and management (Howell et al. 2010; Schlacher et al. 2010). Not only is video a non destructive form of surveying but it allows the distribution of sessile species to be analysed in the context of their specific habitat (Wilson et al. 2007) which may change along the course of the video transect; information which could be lost if the species were collected by trawling. In addition, video survey essentially provides a continuous sample along the length of the transect, therefore providing a larger spatial coverage than point sampling might.

However video surveys come with their own set of limitations regarding biological surveying, the main one being that the presence of the majority of infauna cannot be ascertained unless, for example, a diagnostic burrow or cast is observed. Furthermore, positive identification can often only be confirmed from physical samples. In addition, the quality of the stills or video footage can sometimes prevent the accurate identification of some species. However, the offshore study areas in this project are deep enough that remote video is the only viable option for survey.

With few exceptions (Woodby et al. 2009) species distribution modelling studies in the deep-sea have traditionally focused on presence-only modelling approaches (Bryan and Metaxas 2007; Guinan et al. 2009b; Tittensor et al. 2009) so in order to use the presence-absence algorithms adopted in this study it was imperative to select fauna that would be readily identified on video because presence-absence models rely on accurate presence and absence data. Species that are hard to spot such e.g. those that prefer the undersides of boulders, would be entirely unsuitable for generating presence-absence data from video transects. Uncertain absences can be dealt with by replacing absence records with pseudo absences (Gibson et al. 2007) but the selection of gorgonians as a test group was made in order that we may have confidence in the designation of absence records. Gorgonians lend themselves well to observation in video and stills photography and are usually conspicuous. Gorgonian distribution data was obtained from video footage in both study areas.

4.3 Gorgonian distribution data

4.3.1 Lyme Bay *Eunicella verrucosa* distribution records

Owing partly to its status as a protected species, the pink sea fan has been the subject of several targeted surveys. Distribution data were collected from several different sources, totalling over 220 records (including Black 2007; Munro 2007; Stevens et al. 2007).

In an attempt to reduce the potential variability of data quality from different sources, only data collected during two video survey programs were used to construct the models (see Black (2007) and Stevens et al. (2007) for details of video methodology), reducing the number of pink sea fan records for use in the models by over 60%. The first survey, undertaken by the Devon Biodiversity Records Centre, comprised nine separate survey dates from December 2006 to June 2007 and targeted the reef areas in the northern part of the Bay. Here, 2-5 minute videos of seabed communities were taken at 125 sites whilst allowing the boat to drift (Black 2007). The University of Plymouth carried out the second survey, targeting soft sediment areas in the rest of the bay (Stevens et al. 2007).

The Lyme Bay video data was appealing for two reasons. Firstly, all of the data had been collected in 2006 or later. Given the scallop dredging activity in the area up to the time of the closure (see section 3.2.3) and the potential damage caused to the reef community as a result, older *E. verrucosa* distribution records are more likely to be unrepresentative of recent conditions. Secondly, the majority of video data included a description of the site and could therefore be cross referenced (see Appendix B for details) with the Devon Wildlife Trust substratum layer (currently the best available substratum data for Lyme Bay), discarding records inconsistent with the substratum map. Despite comprising short transects, the video data were available as single points. The pink sea fan records that were used in the model building process are illustrated in Figure 4.2.

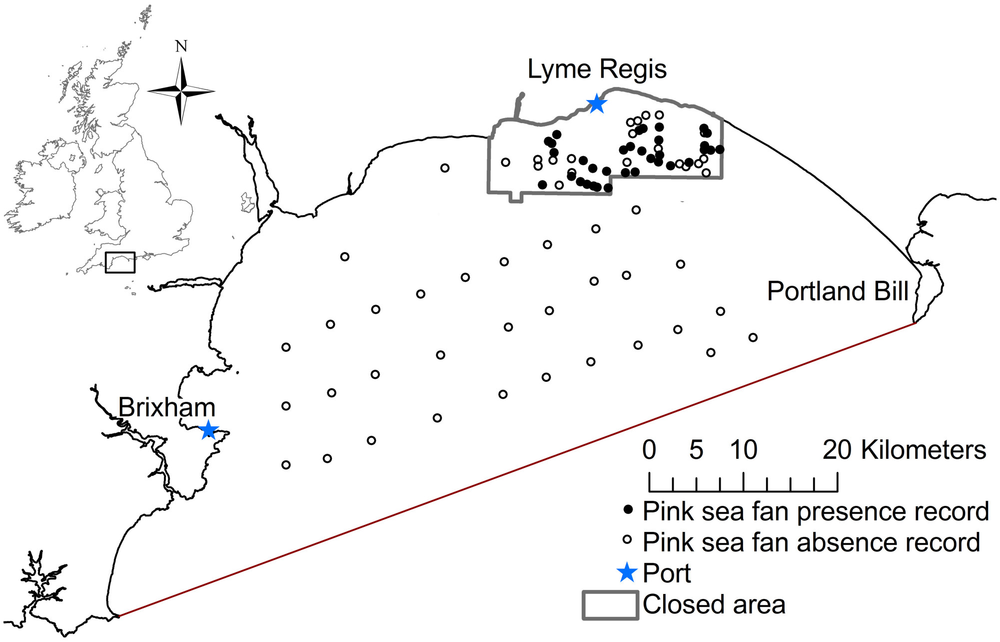


Figure 4.2: Dots represent *Eunicella verrucosa* presence-absence records used in the study. The Lyme Bay statutory closed area is the boxed area adjacent to Lyme Regis.

4.3.2 Hatton Bank gorgonian distribution records

Gorgonian distribution records for the Northeast Atlantic study site were obtained from the 2005 and 2006 Strategic Environmental Assessment (SEA) survey programs (Narayanaswamy et al. 2006; Howell et al. 2007) (Figure 4.3). In 2005 and 2006 large areas of the summit of Hatton Bank were surveyed using multibeam echosounder and video groundtruthing as part of the UK's SEA process (Jacobs 2006; Jacobs and Howell 2007; Stewart and Davies 2007). Collection of biological (video) data and medium resolution multibeam echosounder data (200m grids) were undertaken over a one month period (August-September) in 2005 using the commercial research vessel S/V Kommandor Jack. Further collection of biological (video) data and high resolution multibeam echosounder data (25m and 50m grids) were undertaken over a two month period (August - October) in 2006 using the commercial research vessel M/V Franklin. Video sampling stations were selected during operations using multibeam bathymetry and backscatter data. Video tows were selected to cover a range of geomorphology, substratum type and water depths. For full details of sampling strategy and details of the multibeam echosounder systems used see Howell et al. (2010, 2011).

A video log recorded for each transect was continually georeferenced by way of an Ultra Short Base Line (USBL) beacon attached to a drop frame, allowing the location of each species observation to be matched with a geographic reference point throughout. In addition to the (colour) video camera, the Seatronics drop frame was also equipped with a stills camera and sensors for depth, salinity and temperature (see Howell et al. (2010) for further details of the camera system and methodology). The videos were subsequently analysed and the presence of all taxa clearly visible on the video footage recorded in an Access database.

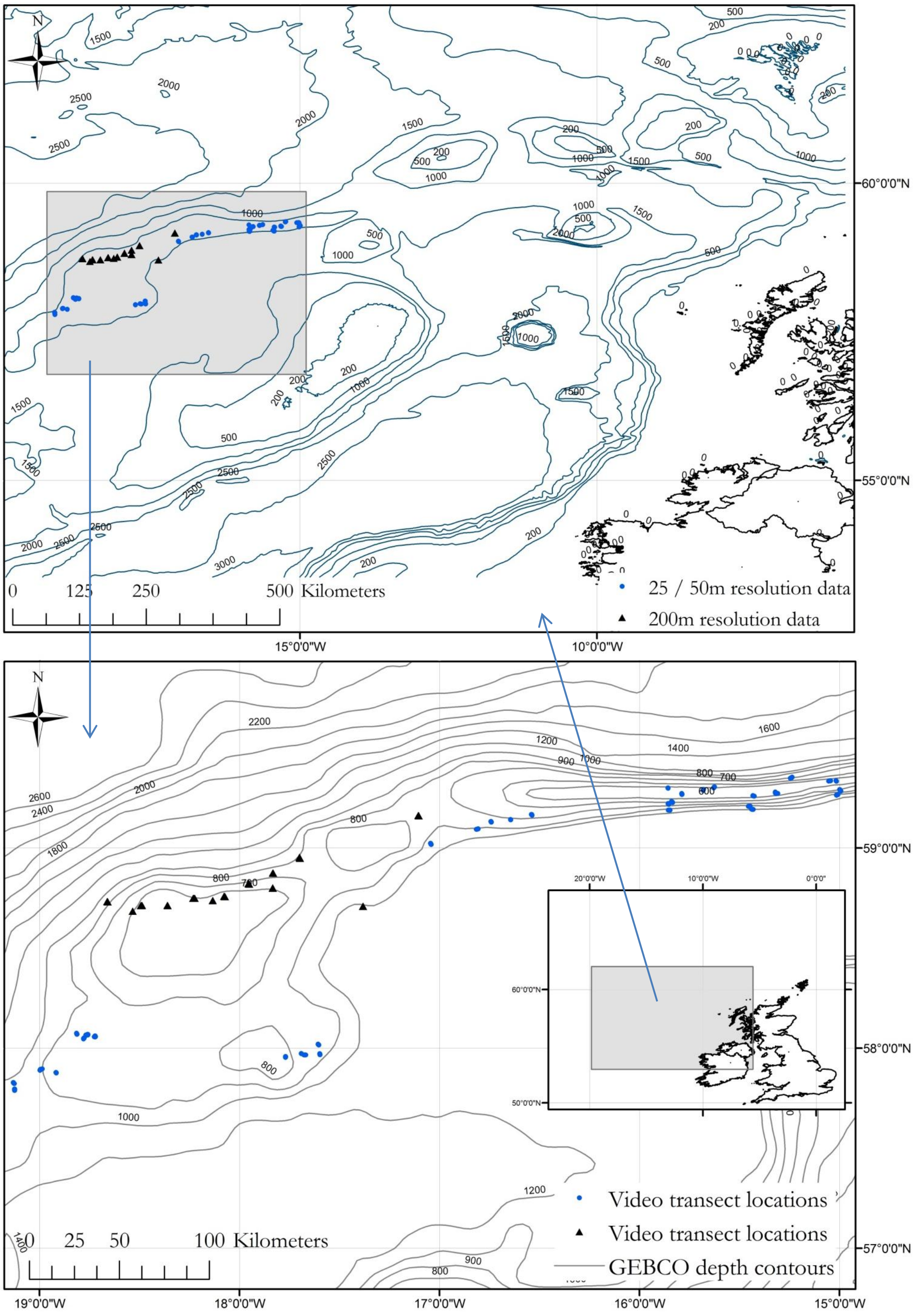


Figure 4.3: Video transect locations on Hatton Bank. Circles represent transects where high resolution gridded environmental data was available (see Chapter 6). Medium resolution environmental data was available for transects represented by the triangles. Low resolution environmental data was available for all transects. Bathymetry is from The General Bathymetric Chart of the Oceans (GEBCO).

Note that the video analysis was carried out by a consortium of scientists, including the author, as opposed to a single observer.

Due to the difficulty of identifying gorgonians to species level from towed video, a generic grouping of ‘gorgonian’ was used, with multiple species included in the grouping. This method was also adopted by Woodby et al. (2009); another modelling study using deep-water gorgonians. Absence data used in the model were any species observations that were not gorgonians. Sections of the video log where no species observations were documented were not used to infer absence, since this could have resulted from the camera being too far above the seabed at the time, for example. Gorgonian presence and absence data was extracted from the video logs and used to generate shapefiles in ArcGIS 9.2.

4.4 Environmental data

The environmental variables selected for use in the models were based on the available literature concerning factors which influence the distribution of gorgonians, but their inclusion in the model building was ultimately subject to availability. Table 4.1 lists the environmental variables used in the study along with their source and range of values across the study areas. All environmental data were prepared for use in the models using ArcGIS (ver. 9.2).

For both Lyme Bay and the Hatton Bank area, different resolutions of environmental data were available and were used to investigate the influence of resolution on model performance. However, the data referred to in this general methodology (in Table 4.1 for example) are the highest resolution data used for the majority of chapters; other (lower resolution) environmental data is detailed in Chapter 6.

4.4.1 Lyme Bay

The environmental data for Lyme Bay was obtained from various sources and, apart from the remotely sensed data from NEODAAS for which a peer-reviewed application is required, the layers are readily available.

The remotely sensed data, namely sea surface temperature (SST), suspended particulate matter (SPM) and chlorophyll *a* concentration (Chl. *a*), were obtained at a cell resolution of 1.1 x 1.1 km. The Geographic Co-ordinate System (GCS) of the remotely sensed data (based on the Clarke 1866 datum) was incompatible with the rest of the Lyme Bay data and no direct transformation was available. The GCS was subsequently removed from the remotely sensed data and it was manually georeferenced according to the Lyme Bay coast. Weekly composites of the three remotely sensed variables were used to calculate annual minimum, mean and maximum values for each grid square for the period July 2007 to June 2008 using the 'mosaic' tool in ArcGIS. However due to the fact that clouds can create 'blank' values within the composite, the mean and minimum figures obtained through this method are only an approximation of the true values. The minimum, mean and maximum values were modelled individually.

SeaZone gridded bathymetry data was available through the EDINA Marine Digimap service at a resolution of 0.0017 degrees. Modelled current data were downloaded as a polygon, with a resolution of 1.8 km.

Table 4.1: The Lyme Bay and Hatton Bank environmental variables, their source, and range. The remotely sensed data cover the year period July 2007-June 2008. The variable ranges / classes listed here are derived from the highest resolution data. Hatton Bank temperature and salinity are limited to those recorded with species observations.

Variable (units)	**Source**	**Data range in study site**	**Resolution**
Lyme Bay			
Substratum	Devon Wildlife Trust / Devon Biodiversity Records Centre	Rock; rock and mixed; mixed; mud and sand and mixed; gravel; sand; mud and sand; mud	See text (section 1.4.1)
Depth (m)	SeaZone Solutions Ltd	0 - 67.77	0.0017 degrees
Spring peak current velocity (m s^{-1})	Atlas of UK Marine Renewable Energy Resources	0.08 – 1.40	1.8 km
Sea surface temperature (°C)	NEODAAS (AVHRR sensor)	7.6 – 18.1	1.1 x 1.1 km
Suspended particulate matter (g m^{-3})	NEODAAS (MERIS sensor)	0.08 – 3.47	
Chlorophyll *a* concentration (mg m^{-3})	NEODAAS (MODIS sensor)	0.01 – 64.57	
Hatton Bank			
Depth (m)	Multibeam acoustic data	487-1073	25-50 m
Substratum	BGS interpreted multibeam acoustic data	Bedrock with carbonate veneer; bedrock; gravel; sandy gravel; gravelly sand; sand.	Interpreted from 25-50 m acoustic data
Geomorphology		Escarpment; flank; furrow; iceberg plough mark; pinnacle mound; ridge; ridge crest; relatively flat seabed	
Salinity (psu)	Video frame sensor	36.12-38.15	Recorded continually along video transect
Temperature (°C)		7.17-9.37	

In addition to the individual variables listed in Table 4.1, the interaction between water current and maximum suspended particulate matter concentration (hereafter referred to as the scour proxy) was investigated in order to represent the scouring potential of sediment-laden fast-flowing water. Data was also available for peak neap current speed although this was strongly correlated with spring currents. To avoid collinearity in the model, spring current was favoured because these stronger currents might be more influential in terms of preventing planulae larvae settlement or interfering with feeding potential of the colonies, for example.

The substratum layer is a composite derived from acoustic swath mapping, grab and drop video samples (pers. comm., Gavin Black, formerly Devon Wildlife Trust / Devon Biodiversity Records Centre). The majority of the underlying acoustic data was from a 1984 single beam survey with full sidescan sonar coverage. Survey line spacing was 62.5 m and 125 m in water depth of less than and deeper than 40 m respectively (pers. comm., Paul Hart, UK Hydrographic Office). Although the substratum layer used in the Lyme Bay models is based on the Devon Wildlife Trust / Devon Biodiversity Records Centre biotope map, substrata were merged into three classes (sediment, mixed and rock), in agreement with Black (2007), in order to increase the numbers of distribution records in each class (Table 4.2).

Table 4.2: Lyme Bay substratum layer classification.

New substratum class	**Original Lyme Bay substratum layer classes included**
Rock	Rock; rock and mixed
Mixed substrata	Mixed; mud and sand and mixed
Soft sediment	Mud; mud and sand; sand; gravel

4.4.2 Hatton Bank

Much of the Hatton Bank environmental data is derived from multibeam data. Depth data was derived from multibeam bathymetry grids at 25m and 50m resolution. Lower resolution data were available for other areas of Hatton Bank (see Chapter 6 for further details).

Depth *per se* has no direct influence on the distribution of deep-sea benthos but correlated parameters often do, including temperature and pressure (Howell et al. 2002; Harris and Whiteway 2009; Buhl-Mortensen et al. 2010; Howell et al. 2010). With depth more easily measured, it is more widely used in modelling studies. The real-time temperature and salinity data recorded with the species' observations on Hatton Bank were highly correlated with depth. Although temperature is known to influence deep-sea gorgonian distribution (Mortensen and Buhl-Mortensen 2004), depth was chosen for inclusion in the modelling over temperature and salinity for the simple reason that as far as predicting into new areas is concerned, depth layers are far more likely to be available than temperature and salinity which would most likely have to be interpolated from point data. Additionally, temperature and salinity varied little over the observed distribution records. In conclusion, although salinity and temperature data were available for many of the transects, they are not considered further. Remotely sensed variables such as chlorophyll and nutrients were not included in the deep water models principally because given the water depth at the Hatton Bank study site and the indirect nature of the link between surface derived parameters and deep water gorgonian distribution, terrain variables were considered much more relevant given their relationship to water current speeds and therefore food supply and substrate type, both are which are important to gorgonian distribution. In addition, these remotely sensed parameters are often only available at very coarse resolutions, e.g. 1 degree and thus would reduce the overall resolution of the model. Table 4.1 provides further details about the data range of environmental variables across the study site.

4.5 Model choice

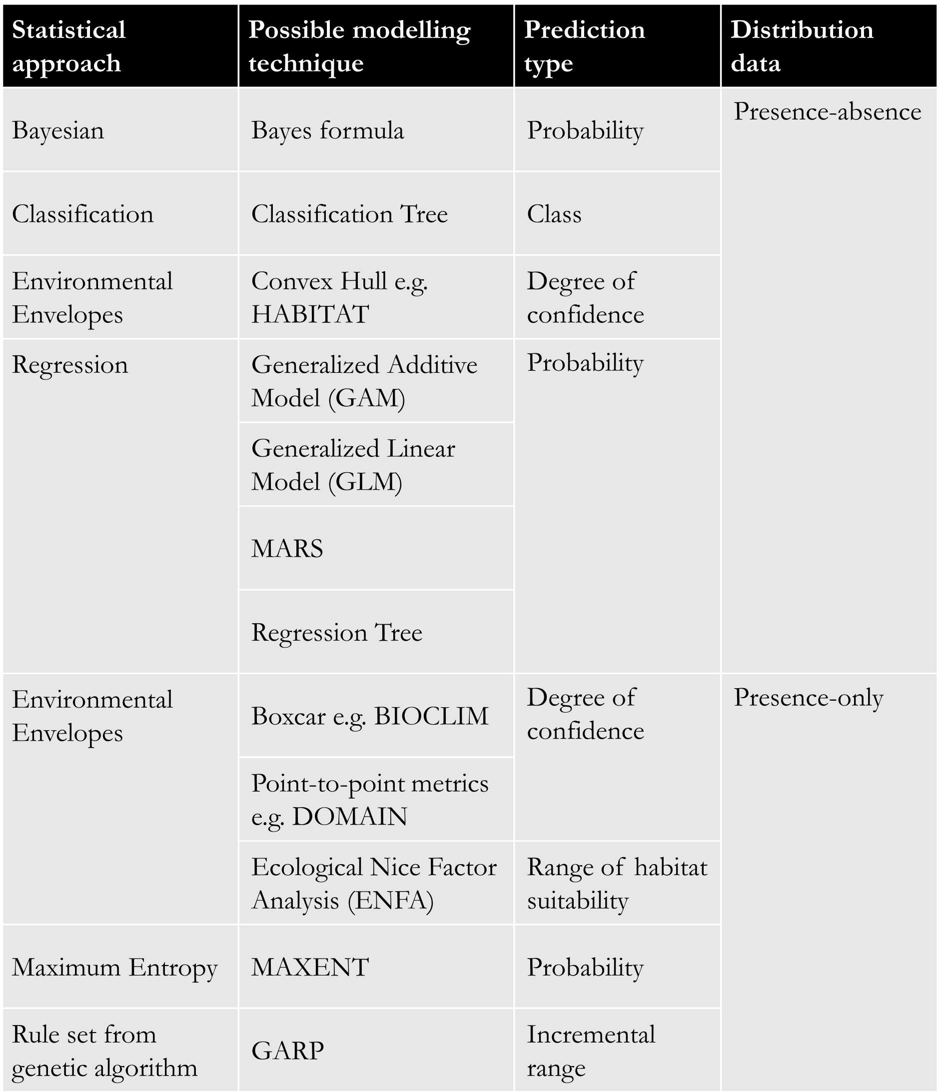
Numerous options exist for the species distribution modeller, both in terms of model choice and in subsequent options within the various modelling programs (Guisan and Zimmerman 2000; Elith et al. 2006). With regard to available data, the type of environmental data (predictor variables) and distribution data (response variable) are influential to model choice. In this study, a combination of categorical and continuous predictor variables, in addition to the availability of presence and absence (binomial) data influenced model choice and the fact that non-linear relationships existed between response and explanatory variables was also important. This considered, several options were available (see Table 4.3, adapted from Guisan and Zimmerman (2000); Elith et al. (2006); Wisz et al. (2008)).

One prerequisite of model choice was that the model(s) should be freely available and therefore accessible to anyone wishing to undertake exploratory predictive modelling, for example conservation managers in developing countries or NGOs who may not necessarily have access to the expensive licensed software available at many universities and scientific institutions.

4.5.1 Generalized Linear Models and Generalized Additive Models

Generalized Linear Models (GLMs, McCullagh and Nelder, 1989) and Generalized Additive Models (GAMs, Hastie and Tibshirani, 1990) were selected for use throughout this study because they are well established within the species distribution modelling literature, often outperforming several of the methods in

Table 4.3: Some of the modelling options available for presence-absence (PA) and presence-only (PO) data (from Guisan & Zimmerman (2000), Elith et al. (2006) and Wisz et al. (2008)).



Statistical approach	Possible modelling technique	Prediction type	Distribution data
Bayesian	Bayes formula	Probability	Presence-absence
Classification	Classification Tree	Class	
Environmental Envelopes	Convex Hull e.g. HABITAT	Degree of confidence	
Regression	Generalized Additive Model (GAM)	Probability	
	Generalized Linear Model (GLM)		
	MARS		
	Regression Tree		
Environmental Envelopes	Boxcar e.g. BIOCLIM	Degree of confidence	Presence-only
	Point-to-point metrics e.g. DOMAIN		
	Ecological Nice Factor Analysis (ENFA)	Range of habitat suitability	
Maximum Entropy	MAXENT	Probability	
Rule set from genetic algorithm	GARP	Incremental range	

Table 4.3 (Guisan and Zimmerman 2000; Elith et al. 2006; Redfern et al. 2006; Meynard and Quinn 2007; Guisan et al. 2007). These regression based models relax the strict linearity assumptions associated with other linear models allowing non-linear relationships between the response and explanatory variables to

be modelled (Wood 2006a). GAMs in particular, are useful for exploring these non-linear relationships (Austin 2007), and are often chosen to supplement GLMs for this reason.

Both GLMs and GAMs allow a variety of response variable distributions to be modelled including poisson and binomial, the latter of which is applicable to presence-absence data. The use of a link function ensures that predictions are bounded within a certain range. In the case of a binomial error distribution, for example, the use of a logit link ensures probability estimates of between 0 and 1.

Whereas GLMs are defined by linear predictors, GAMs use non-parametric smoothing functions to model the relationship between response and explanatory variables. Smoothers are applied independently to each explanatory variable with the response being calculated additively (Guisan and Zimmerman 2000). Due to this additive approach, the outputs of GLMs can be easier to understand (Redfern et al. 2006).

4.5.2 Maxent

Maximum entropy (Maxent; Phillips et al. (2006)) is a machine-learning niche based model designed for presence-only data, and is used in the final chapter. The strong performance of Maxent compared to other methods including BIOCLIM, ENFA and GARP (Phillips et al. 2006; Pearson et al. 2007; Elith and Graham 2009; Wisz et al. 2008; Tittensor et al. 2009) has led to its popularity among modellers over recent years and is the reason it is selected for use in this study. Combined with ease of use, Maxent is an attractive option for novice and experienced modellers alike.

The Maxent algorithm converges to the most uniform probability distribution across the study area given the constraints dictated by a sample of this target probability distribution; the presence records and their associated environmental variables. More specifically, the expected value of explanatory variables across the study area should be close to the average observed value for that covariate in the presence data (Phillips et al. 2006). Like GLMs and GAMs, Maxent is able to explore both continuous and categorical variables. Some theoretical similarities exist between Maxent and GLMs and GAMs, with regularization in a Maxent model with a threshold having a comparable effect to smoothing in a GAM with a logit link (Phillips et al. 2006). Maxent also uses an exponential distribution but, unlike GLMs and GAMs in which a link function can be used to constrain the predictions, Maxent's unbound probabilities can lead to high predictions for variables outside the study range (Phillips et al. 2006).

4.6 Model units

4.6.1 The intersect approach

Data for the individual environmental variables used in modelling studies commonly come from different sources and often have varying levels of resolution. Standardizing the data layers to ensure they have the same cell size, as is required by some modelling programs including Maxent, could result in the loss of resolution from one or more layers. To prevent this, an intersect approach was adopted which preserves data integrity and resolution as far as possible, where environmental data was collated from different sources and at different resolutions, and maintains ecologically relevant shapes and boundaries. The intersect approach allowed the relationships between the distribution data and environmental data to be investigated at the highest resolution available.

The units for the model were created by intersecting each of the environmental variable layers to give a single unique polygon layer. Raster layers had first to be converted into polygon layers. Layers can only be intersected if they overlap. During the intersect process, a new polygon is created wherever a polygon from one input layer is intersected by the boundary of a polygon from another layer. The resulting layer therefore matches the combined polygon boundaries of all input layers and contains data from all layers attached to each polygon (see Figure 4.4).

The intersect method resulted in unequally sized model units for both study sites which, whilst unsuitable for an effort-specific response variable such as abundance, is acceptable for a binomial response.

4.6.2 Gridded data for Maxent

As previously mentioned, Maxent requires that environmental variables are presented as gridded (raster) layers covering the same spatial extent and with identically sized and positioned cells. Polygon layers were gridded to an appropriate resolution, details of which are provided in Chapter 8.

4.6.3 Sample data

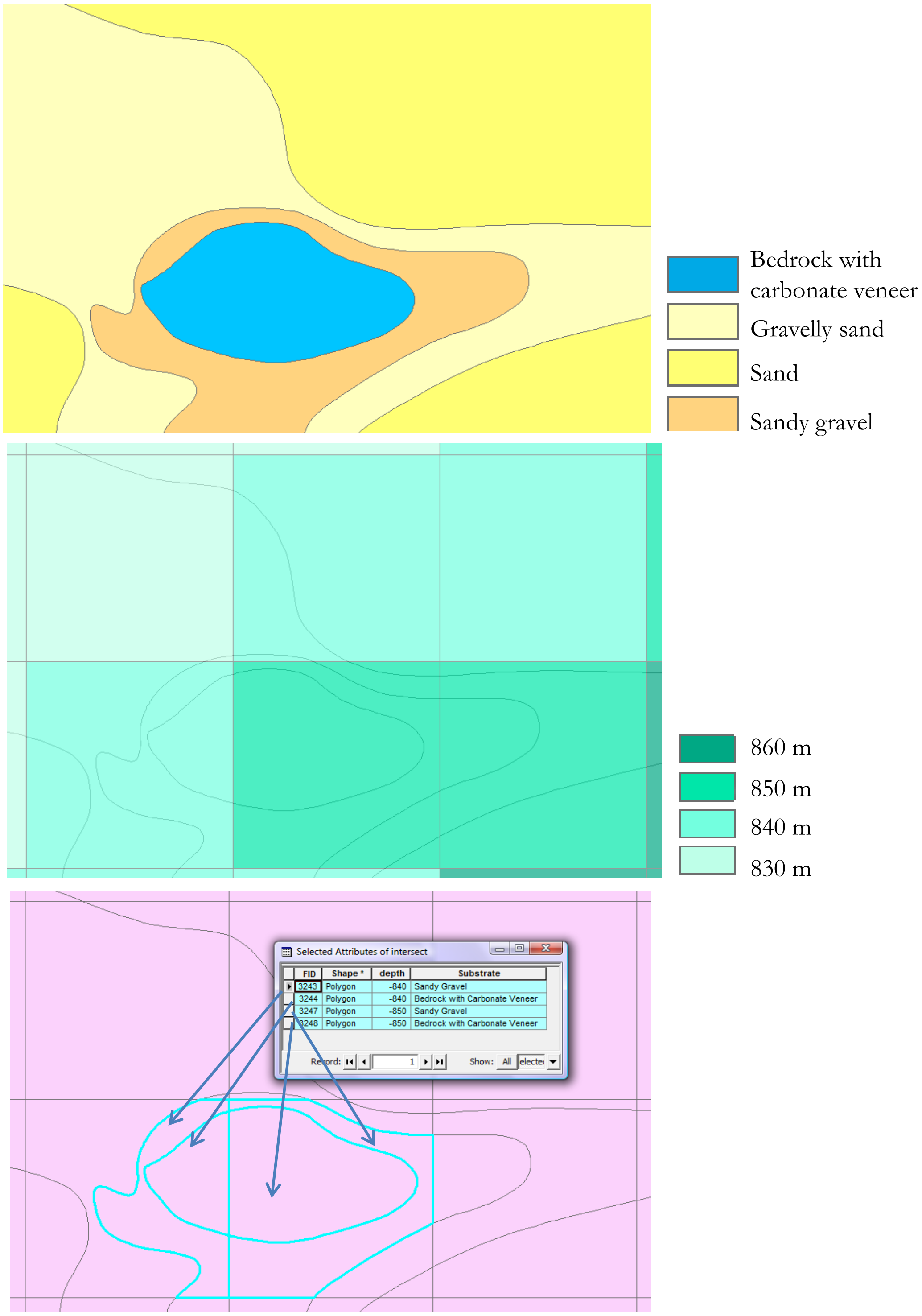
Distribution data were reduced to one record per intersected polygon, that is, a presence or absence record (Elith et al. 2006; Graf et al. 2006; Pearson et al. 2007). If a gorgonian was recorded at any place in that polygon, it was assigned a ‘presence’.

4.7 Practical modelling

4.7.1 Generalized Linear Models and Generalized Additive Models

All GLMs and GAMs were built in R 2.10.0 (R Development Core Team 2009), the latter using the mgcv package (version 1.5-6; Wood 2006b).

Prior to model fitting, pairwise comparisons of all of the predictors were made by building a matrix of scatter plots along with values of absolute correlations.



	FID	Shape *	depth	Substrate
▸	3243	Polygon	-840	Sandy Gravel
	3244	Polygon	-840	Bedrock with Carbonate Veneer
	3247	Polygon	-850	Sandy Gravel
	3248	Polygon	-850	Bedrock with Carbonate Veneer

Figure 4.4: ArcGIS screenshots demonstrating the intersect tool, using the Hatton Bank substratum polygon layer (top) and converted gridded bathymetry data (middle) to illustrate the process. The final frame is the resulting intersect polygon, containing the information from both intersected layers.

Where an environmental variable had a Pearson correlation coefficient of 0.7 or above with another variable (Muller et al. 2009) only the environmental variable with the lower UBRE score was included in the stepwise model building process.

The presence-absence of gorgonians were modelled as binomial GLMs and GAMs with a logit link function. Logistic GAMs were applied individually to each environmental variable. GAMs have the potential to overfit, especially with small data sets (Bradshaw et al. 2004; Gibson et al. 2007) and two steps were taken to combat this. Firstly, the default dimension (effectively the maximum number of degrees of freedom for a given smooth) was reduced from 10 to 4 as has been done in other spatial modelling studies using GAMs (Randin et al. 2006; Meynard and Quinn 2007; Embling et al. 2010). It is unlikely that any of the environmental variables investigated in this study would warrant a higher number of degrees of freedom. Secondly, in order to prevent potential overfitting to the data, the default value for the number of degrees of freedom estimated for each smoothing term in the GCV (generalized cross validation) score (default = 1) was rejected in favour of 1.4 (Kim and Gu 2004; Wood 2006a).

Variables with outliers were modelled with and without outliers to see if the outliers had any effect on the significance of the model terms.

A forward stepwise selection was carried out, using only the significant variables, ensuring that with each addition, model fit improved and the terms remained significant. The best (and therefore final) model was defined as the model with the lowest UBRE (Un-Biased Risk Estimator) score. The UBRE score provides an indication of model fit which also penalises for the number of variables (Wood 2006a). If the final model contained more than one variable, it was also compared to the simpler model using a chi-square test on model deviance and only retained if significantly better.

Variables which the GAM identified as significant but which were modelled as having a linear relationship with the response variable were subsequently modelled using a GLM. For univariate categorical models where only one level was found to be significantly different from zero, the model was compared to a null model using the chi-square test as above and only retained if the model containing the categorical variable was significantly better.

4.7.2 Maxent

Maxent was implemented using version 3.3.3 which is freely available from http://www.cs.princeton.edu/ schapire/maxent. Maxent's default settings for the regularization multiplier (1) and and convergence threshold (10^5) were accepted (Phillips et al. 2009). A logistic output was selected in order to facilitate comparison of Maxent and regression based model outputs.

4.8 Threshold definition

A threshold is required in order to transform the results of species distribution modelling from probability to presence or absence, that is, to dichotomise the predictions (Liu et al. 2005). Liu et al. (2005) recommended using an equal number of presence and absence records in the build data in order to counteract potential problems of using threshold sensitive performance indicators, or indeed the comparison of models with varying thresholds. The consequence of this is potential loss of valuable information, especially in small data sets where evening out the build data might result in the loss of a significant proportion of the overall data, as would be the case with the Lyme Bay data set. A prevalence approach proposed by Cramer (2003) was adopted:

$$Threshold = \frac{\text{number of presence records}}{\text{total number of distribution records}}$$

Sensitivity and specificity (two of the performance indicators used in the present study; see next section) were reported to be relatively insensitive to the proportion of prevalence data in the model-building data when Cramer's threshold was used (Liu et al. 2005). Note however that additional threshold definitions have been used in Chapters 7 and 8, details of which are provided in the relevant chapters.

4.9 Assessing model performance

The adoption of species distribution model outputs in conservation management lies in their ability to accurately predict the distribution of the species in question and managers will seek models that can demonstrate excellent performance in this respect. The three performance indicators outlined in Table 4.4 were selected because they offer a transparent and logical assessment of model performance.

The Correct Classification Rate (CCR; Fielding and Bell 1997) provides a measure of the overall predictive power of the model. Sensitivity was selected because it penalises for false absences which are 'costly' when trying to conserve a species (Fielding and Bell 1997). Equally, specificity is important because if a model performs poorly in terms of false positives, this can have negative financial and time implications for designing monitoring and survey programs (Fielding and Bell 1997).

Table 4.4: Calculation of threshold dependent performance indicators, from Fielding and Bell (1997). True positive (TP); true negative (TN); false negative (FN); false positive (FP); total number of samples (n). Scores range from 0 to 1, with 1 being the highest possible score.

Performance indicator	**Method of calculation**
Correct Classification Rate (CCR)	$\frac{TP+TN}{n}$
Sensitivity	$\frac{TP}{TP+FN}$
Specificity	$\frac{TN}{FP+TN}$

In addition to these three threshold-dependent performance indicators, area under the curve (AUC) scores were also calculated. Despite some criticism (Lobo et al. 2008), the AUC remains a popular metric for model performance because it assesses performance over all possible threshold values therefore removing the need to specify a threshold, which can be subjective. AUC scores are calculated from Receiver Operating Characteristic (ROC) plots where sensitivity is plotted against 1-specificity. The closer the curve to the top left corner (zero error), the higher the area under the curve. The AUC is measuring the model's ability to distinguish a presence record from an absence record. A score of 1 indicates that the model has perfect discrimination, whereas 0.5 indicates that the model is predicting no better than at random. A widely accepted system of scoring for the AUC (though with varying terminology) dictates that scores above 0.7, 0.8 and 0.9 are, respectively, acceptable, excellent and outstanding (Mingyanga et al. 2008). This terminology has been adopted for all the performance indicator scores in this study. Lobo et al (2008) recommend the additional use of the sensitivity and specificity as performance indicators which has been done in this study. One of the criticisms of Lobo et al. (2008) is that commission and omission errors (i.e. false positives and false negatives respectively) are weighted equally in the AUC metric. Whilst for some applications of spatial modelling this might be inappropriate, the potential contribution of SDMs to both future survey effort and conservation planning dictate that prediction errors associated with model outputs from this study should be weighted exactly so.

The performance of the models was assessed using a number of approaches. Firstly, the fitted values for the final model (using all the data) were compared to the observed values. Secondly, a threefold cross validation determined the robustness of the model. The full data set was randomly subdivided into thirds with the presence-absence ratio between the three groups of data equal, notwithstanding an odd number of distribution records. The entire model fitting process was repeated with each combination of two thirds of the data (hereafter referred to as 'training' data), culminating in the production of a new 'build' model. Predictions based on the final model derived from the training data were then tested on the remaining third (test data).

Repeated internal resampling was used to generate confidence intervals for the four performance indicators. Here, two thirds of the data were randomly selected without replacement and fitted to the final model. Predictions were made on the remaining data. This was repeated to a total of 1000 iterations for GLMs / GAMs and 100 times for Maxent, the difference in number being as a result of processing time and memory requirements. Where comparisons between the performance of different models were being made, Wilcoxon rank sum W tests (a non-parametric equivalent to independent samples t-tests; Dytham (1999)) were used to identify significance differences.

Lastly, the predictions of the final model were assessed using independent data where available (detailed in the relevant chapters).

4.10 Model predictions

Predicted habitat suitability layers were produced for each model. The Maxent package produces the predicted layers as standard as part of the output file. For the GLMs and GAMs, environmental layers were presented to the model as 'new data' on which predictions were made based on the final fitted model. Predicted layers were subsequently examined in ArcGIS with respect to, for example, test data, fishing effort and/or relevant spatial management measures.

Chapter 5

Using species distribution modelling and spatial fisheries data to inform monitoring of benthic recovery in a marine protected area

*Long term monitoring is a key element of the management of marine protected areas yet it can be costly, often requiring the optimisation of monitoring site selection. This chapter investigates the potential application of species distribution modelling to prioritise selection of areas for monitoring of benthic recovery in a marine protected area, using the statutory closed area in Lyme Bay as a case study. The closed area was established principally to protect rocky reefs and their associated epifauna from the effects of benthic trawling. The pink sea fan (*Eunicella verrucosa*) can be a dominant member of rocky reefs in this area and is highly sensitive to mobile benthic gear. Using* E. verrucosa *presence and absence records, in combination with data for environmental variables known to influence gorgonian distribution, a combined GLM and GAM approach was used to predict gorgonian distribution across Lyme Bay. The final model explained more than 50% deviance and performed well under different performance indicators in internal validation although had a mixed performance when applied to independent test data. Data on the spa-*

tial distribution of fishing effort prior to the closure were superimposed on the predictions. Areas with a high probability of sea fan presence that were associated with false positives in addition to past fishing activity were recommended for inclusion in future long-term monitoring programs of benthic recovery since it is possible that these areas were disturbed by fishing activity prior to the closure. This chapter presents a proof of concept for the application of species distribution modelling to monitoring efforts in marine protected areas.

5.1 Monitoring recovery within marine protected areas

Advocated from local initiatives through to international strategic recommendations, the use of marine protected areas (MPAs) as a tool for protecting areas of the marine environment is now recognised as having an integral role in the sustainable use of marine ecosystems, with legislative commitments to the same effect. While much attention has been focussed on the initial selection of appropriate sites for MPA designation, and on the configuration of networks of protected areas, there has also been considerable progress in the development of monitoring strategies for such areas, including the identification of appropriate indicators, and evaluation of the effectiveness of the management strategies (Pomeroy et al. 2005; Day 2008; Jackson et al. 2008).

Monitoring is commonly a legal requirement associated with the designation of protected areas (e.g. Special Areas of Conservation, designated under the EU Habitats Directive, require six yearly monitoring), and is critical in determining how well a marine protected area is fulfilling its conservation goals (Gerber et al. 2007). For example appropriate monitoring can facilitate the assessment of recovery from anthropogenic impacts on a site. Long-term monitoring also increases the understanding of the ecosystem in question (Stein and Cadien 2009), thereby influencing the protection and monitoring of similar ecosystems in other areas.

However, the knowledge gained from protected area monitoring programmes, with respect to the objectives of the protected area, depends critically on the correct selection of monitoring sites. Monitoring can also be prohibitively expensive and there is a trade off between the cost of monitoring and potential improvements in management resulting from the knowledge gained (Gerber et al. 2005; Baxter and Possingham 2011). Yet improved knowledge is an essential component of the adaptive management cycle and resources are always limited. Therefore the use of optimisation techniques in conservation planning is crucial (Moilanen et al. 2009) and, to this effect, a method of optimising appropriate monitoring site selection is required in order to achieve cost effective monitoring. Rodriguez et al. (2007) identified the potential for species distribution modelling to support the identification of areas for future sampling, including monitoring for changes in population numbers. The spatial nature of the outcomes of species distribution modelling aids its application in spatially driven management measures. Any protected area planning requires a habitat map as a starting point (Stevens 2005) and, in turn, any monitoring program requires a spatial framework within which the target species can be incorporated. To this effect it could be possible to use species distribution modelling to provide the spatial framework for a monitoring program by way of stratifying and optimising the design of survey programs to maximise cost-effectiveness. Simply put, species distribution modelling has potential as a decision support tool in the identification of appropriate monitoring sites.

The application of species distribution modelling to conservation in recent years has been varied. However, predictive modelling studies informing the current and future management of existing marine protected areas (e.g. Panigada et al. 2008; Bailey and Thompson 2009) are rare, especially for sessile species. More specifically, it is a method that has yet to be applied in the context of monitoring within a protected area although Carlson et al. (2007) applied a GLM to assess the recovery of a mobile species, the smalltooth sawfish, in the Everglades National Park. SDMs have not yet been applied to benthic recovery though it has obvious potential in this field.

5.1.1 Case study area: Lyme Bay

Following the 2008 Lyme Bay closure, the UK Government's Department for Environment, Food and Rural Affairs (Defra) funded a three year project investigating the ecological and economic implications of the closed area. Two elements of the three year project, were the identification of indicator species and the subsequent development of a long-term monitoring program designed to assess benthic recovery (Jackson et al. 2008; Stevens et al. 2008; Attrill et al. 2011). The benthic and socio-economic elements have both received an additional year of funding from Defra. Natural England has also agreed to extend the benthic monitoring for a further year.

The pink sea fan makes a suitable indicator species for long-term monitoring of the recovery of the Lyme Bay closed area by representing species with a low recoverability, low survivability and a low reproductive rate (Hiscock 2007b; Jackson et al. 2008; Attrill et al. 2011). Being an erect and slow-growing member of the reef epifauna, *Eunicella verrucosa* is also vulnerable to mobile benthic fishing gear. Benthic dredging for pectinids, up to the time of closure, had previously disturbed areas of seabed which might otherwise have been suitable for the pink sea fan. Scallop dredging has often been associated with negative impacts on epifauna and benthic habitats (e.g. Lart et al. 1993; Freese et al. 1999; Collie et al. 2000; Blyth et al. 2004) and has been cited as a limiting factor on the abundance of the *E. verrucosa*, ross coral (*Pentapora fascialis*) and dead man's fingers (*Alcyonium* *digitatum*) in Lyme Bay (Hiddink et al. 2007).

The aim of this chapter is to demonstrate the potential application of species distribution modelling to the development of a long-term monitoring programme. Using the Lyme Bay closed area as an example, the specific aim was to identify sites for inclusion in future programmes of long-term monitoring of benthic recovery following protection from mobile gear using predictive distribution modelling of *E. verrucosa* coupled with available data on historic fishing activity.

5.2 Methods

GLMs and GAMs were used to explore the influence of environmental variables on pink sea fan distribution in Lyme Bay, the methodology for which has been outlined in Chapter 4 and is summarised below.

5.2.1 Environmental variables

The environmental variables selected for inclusion in the model are detailed in Table 4.1. The units for the model were created by intersecting each of the twelve layers (i.e. substratum, depth, current and the annual minimum, mean and maximum values for SST, SPM and Chl. *a*) to give a single unique polygon layer.

5.2.2 *Eunicella verrucosa* distribution data

Only data collected during video surveys (Black 2007; Stevens et al. 2007) were used to construct the models. In total, 86 pink sea fan records were used in the model building process, of which 34 are presence records (Figure 4.1).

5.2.3 Logistic models

A forward stepwise selection was carried out, using only the significant variables, and the final model was defined as the model with the lowest UBRE score. Variables which the GAM identified as significant but which were modelled as having a linear relationship with the response variable were subsequently modelled using a GLM.

Maps of predicted pink sea fan distribution based on the model predictions were produced in ArcGIS.

5.2.4 Assessing model performance

The performance of the models was assessed using a number of approaches (detailed in section 4.9), including the calculation of threshold dependent and threshold independent performance indicators based on predictions made by the full data set, 'build' data sets (a randomly selected sample of two thirds of the full dataset) and repeated internal resampling. In addition, independent test data was available to test the predictive power of the Lyme Bay model, derived from video transects from the first year (2008) of the Lyme Bay monitoring program. The monitoring data set provided 70 test data points (28 presence, 42 absence).

5.2.5 Fishing activity

The fisheries data was provided by the Devon Sea Fisheries Committee (regional sea fisheries managers) and detailed the distribution of scallop dredging activity for the years 2005-2007 based on patrol boat records.

Scallop dredgers working close to reef margins may only fish for 275m or so before turning around and reworking an area (skipper John Walker, pers. comm.). In an attempt to display the potential footprint of scallop dredging activity (Eastwood et al. 2007; Stelzenmuller et al. 2008), 275m circular buffers were added to the point data for scallop dredging activity in order to avoid overestimating the potential footprint of the scalloping activity. However, the average vessel working in the area will fish for the twelve hours permitted by the byelaw and with up to twelve dredges (Devon Sea Fisheries Committee, pers. comm.) and so in reality it is likely that the spatial footprint of scallop dredging will be greater.

Data on the spatial distribution of scallop dredging activity was superimposed onto the binary presence-absence map of predicted *E. verrucosa* distribution in order to identify areas that had a high probability of sea fan presence, as determined by the model, but which were associated with absence records and past fishing activity.

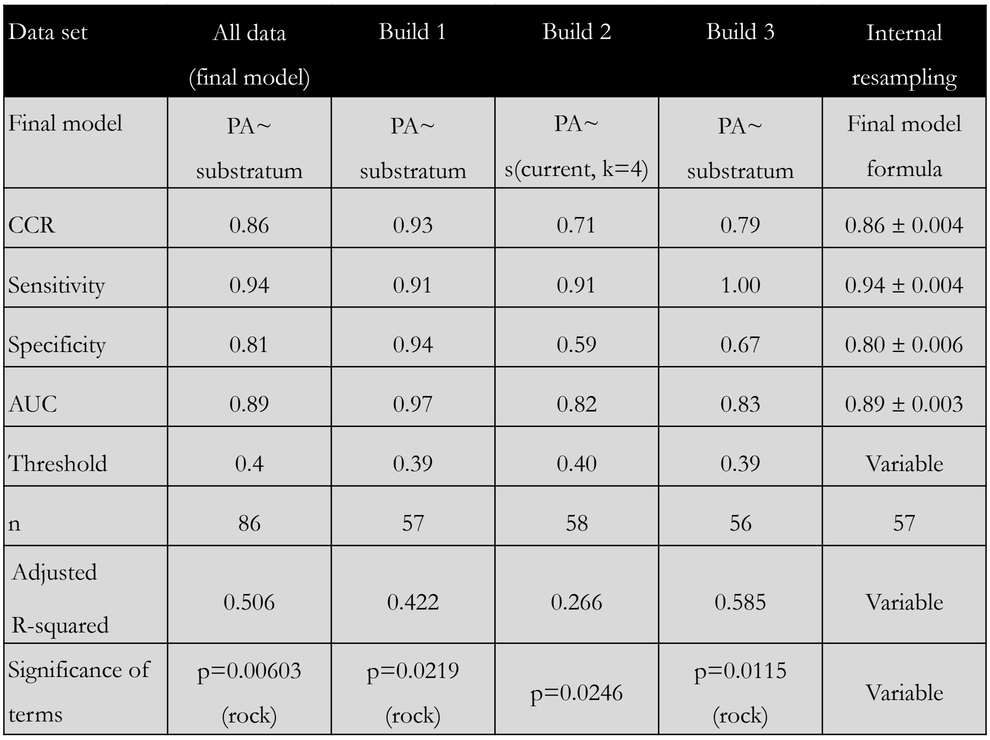
5.3 Results

5.3.1 Significant variables

Several environmental predictors were identified as having a significant relationship with the distribution of the pink sea fan in Lyme Bay and the structure of the final models for the full data set and build data sets is detailed in Table 5.1. Three of the final models were constructed as GLMs because they contained only categorical variables, therefore dismissing the need for smoothing terms.

Using the full data set, univariate models identified substratum, current, minimum SST, minimum SPM, mean Chl. *a* and the scour proxy (spring peak current velocity:maximum suspended particulate matter) as significant variables although substratum alone was selected by the GLM in the final model. Therefore the predicted map of distribution aligns exactly with the original map of substrata within the Bay (Figures 5.1 and 5.2), with 'rock and mixed substrata' areas associated with high probability of pink sea fan presence (0.76). No distribution records were available on the few 'rock' areas of the original substratum map although given that 'rock and mixed' areas are associated with a high probability of pink sea fan presence it is likely that the 'rock' areas will be at least as suitable and these areas are therefore hatched. The probability of presence on mixed and sedimentary ground fell below the threshold (at 0.22 and 3.18^{-09} respectively).

Table 5.1: Final models for the full data set and three ‘build’ data sets. Scores for the performance indicators are listed in addition to the adjusted R-squared which indicates the proportion of variance explained by the model terms. PA: presence-absence. For the internal resampling, the mean values and upper and lower 95% confidence limits are shown for each performance indicator.



Data set	All data (final model)	Build 1	Build 2	Build 3	Internal resampling
Final model	PA~ substratum	PA~ substratum	PA~ s(current, k=4)	PA~ substratum	Final model formula
CCR	0.86	0.93	0.71	0.79	0.86 ± 0.004
Sensitivity	0.94	0.91	0.91	1.00	0.94 ± 0.004
Specificity	0.81	0.94	0.59	0.67	0.80 ± 0.006
AUC	0.89	0.97	0.82	0.83	0.89 ± 0.003
Threshold	0.4	0.39	0.40	0.39	Variable
n	86	57	58	56	57
Adjusted R-squared	0.506	0.422	0.266	0.585	Variable
Significance of terms	p=0.00603 (rock)	p=0.0219 (rock)	p=0.0246	p=0.0115 (rock)	Variable

5.3.2 Model performance

Based on the selected performance indicators the final model performed well based on internal validation, as did the build models, illustrating mostly high levels of overall predictive accuracy, sensitivity and specificity (Table 5.1).

The final model for Build 2 included current, as a smooth, and did not perform as well as the other models. However, predictions were also made using a GLM constructed with the substratum data from Build 2 despite substratum not being a significant variable for this build. These predictions performed excellently

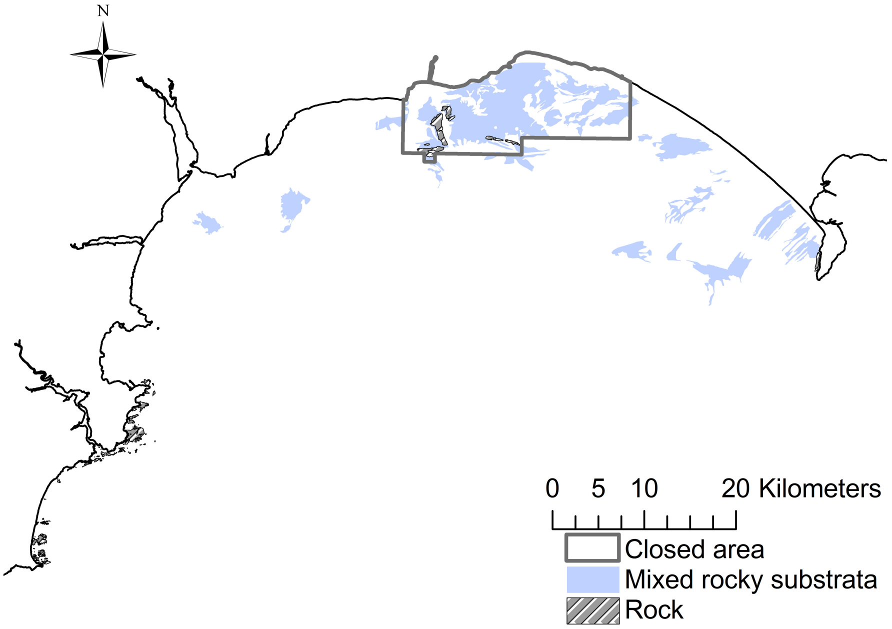


Figure 5.1: Map of Lyme Bay indicating areas (shaded) with a high probability of *Eunicella verrucosa* presence. These areas represent the 'rock and mixed' substrata areas in Lyme Bay according to the Devon Wildlife Trust biotope map. The hatched areas are 'rock' areas which, whilst not represented by any distribution data in the model building data, are likely to be as least as suitable as the 'rock and mixed' substrata.

(producing an AUC, CCR, sensitivity and specificity of 0.89, 0.86, 0.91 and 0.82 respectively).

The fact that similar significant terms were selected across the final and build models suggests that the final model is robust.

When presented with the independent data set, the final model was found to be highly sensitive, achieving a score of 0.86, but performed poorly in terms of specificity (0.38) which reduced its overall CCR to 0.57. The AUC score based on test data predictions was 0.61. Of the 70 independent test points, 27 were wrongly commissioned i.e. false positives. False positives are absence records located in areas predicted to be suitable for the species or community in question.

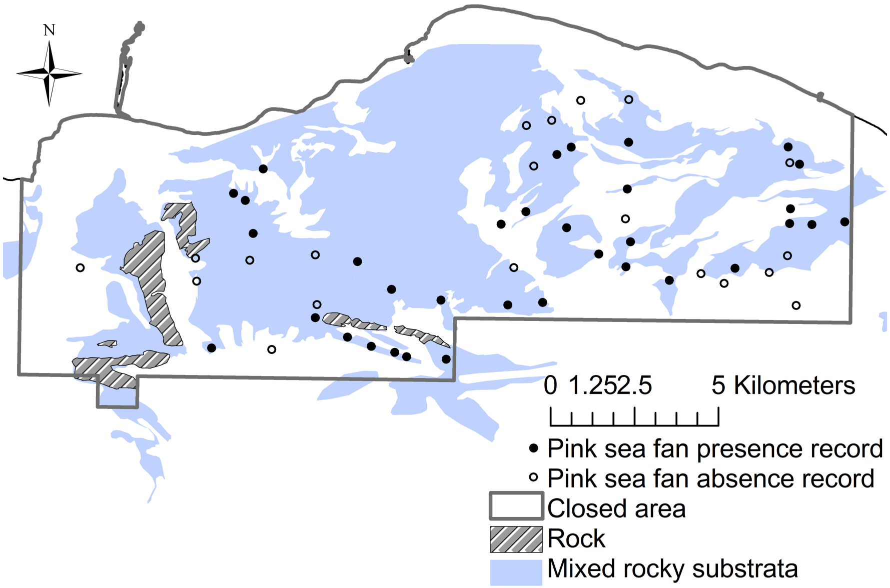


Figure 5.2: Close up of the Lyme Bay closed area. *Eunicella verrucosa* presence records and absence records used in the model building are mapped. The shaded areas are predicted to be suitable habitat for pink sea fans based on the univariate GLM with substratum. The hatched areas are also likely to be suitable.

5.3.3 Effect of fishing activity and prioritisation of future monitoring sites

Almost one third of the false positives in Lyme Bay were associated with past scallop dredging activity, nine of which are in the closed area (Figure 5.3).

Of those nine, seven are outside four small areas previously closed voluntarily to scallop dredging before the designation of the larger statutory closure and would not have been afforded this temporary protection. These four voluntary closures, established in 2006, included two earlier voluntary closures (Lane's Ground and Sawtooth Ledges, Figure 5.3) set up in 2001. These two elements (false positive and historical fishing activity) support the selection and prioritisation of those areas for inclusion in future monitoring of benthic recovery now that the area is closed.

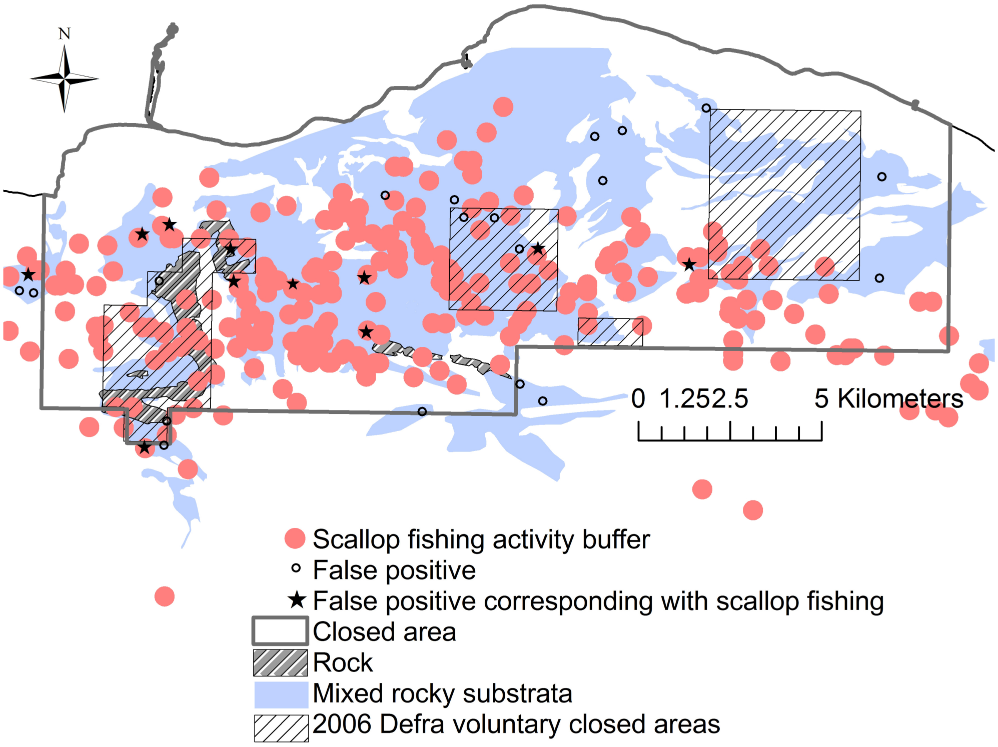


Figure 5.3: Distribution of fishing pressure (buffered point data) in 2005-2007 within the now closed area based on the potential 'footprint' of scallop dredging. The hatched boxed areas represent previous voluntary closed areas (from left to right; Beer Home Ground, Lane's Ground, East Tennants and Sawtooth Ledges). False positives are mapped. The stars represent false positives that coincide spatially with past scallop dredging activity.

5.4 Discussion

5.4.1 Significant variables

The fact that substratum alone was selected by the GLM in the final model for the full data set and that areas of rocky substrata are associated with a high probability of presence of *E. verrucosa* are, arguably, predictable outcomes given the importance of substratum to sessile species.

The individual logistic models constructed for *E. verrucosa* in Lyme Bay using the full data set identified substratum, current, minimum SST, minimum SPM, mean Chl. *a* and the scour proxy (spring peak current velocity:maximum suspended particulate matter) as significant predictors of its distribution. This is in agreement with those factors commonly reported to be primarily responsible for the distribution of gorgonians on a local scale which include water movement, sediment transport and substratum (Barham and Davies 1968; Kinzie 1973; Opresko 1973; Carpine and Grasshoff 1975; Hiddink et al. 2007; Hiscock 2007a), and Bryan and Metaxas (2007) found chlorophyll *a* concentration to have an influential role in the distribution of gorgonians on the continental margins of North America.

Water temperature is known to be important in gorgonian reproductive biology yet the significance of minimum SST in this study is less clear. Given that minimum SST is highly correlated with depth it is possible that this variable is simply reflecting the lack of pink sea fan observations at depth (with increasing depth generally associated with softer sediments in Lyme Bay).

5.4.2 Fishing activity and monitoring site prioritisation

The use of fishing effort data can enhance practical aspects of marine management, including monitoring survey design (Stelzenmuller et al. 2008), and is especially useful if linked to the recovery rates of benthic communities (Eastwood et al. 2007). Spatial data for bottom trawling has recently combined with spatial predictions of deep-sea stony coral distribution in order to identify areas of vulnerability to this activity (Clark and Tittensor 2010).

The results indicated that there were areas within the closure that were suitable for *E. verrucosa* but at which this species was not found, potentially as a result of pre-closure fishing activity. By mapping the model predictions and combining them with spatial fisheries data nine false positives (over one third of the false positives within the closed area) associated with past scallop dredging activity have been identified, five of which are part of the existing monitoring program, and are recommended for inclusion into future monitoring program design.

Species distribution models have recently been used to optimise survey strategies and site identification for monitoring the establishment of invasive species (Baxter and Possingham 2011; Gormley et al. 2011). Here, false positives have been used to optimise site identification for the long term monitoring of benthic recovery because it is possible that these areas were disturbed by fishing activity prior to the closure and may now be recolonised by the pink sea fan over time.

Pearson et al. (2007) argue that false positives are not necessarily failures of the model because absences at a site may arise from a variety of different reasons. In other words, absences arising from historical influences can compromise the predictive power of models (Hirzel et al. 2001).

The effects of scallop dredging and other forms of mobile benthic fishing on benthic communities is well documented and include: significantly reduced benthic biodiversity compared to static gear only areas (Blyth et al. 2004); significant loss of fragile epifauna (Freese et al. 1999); reduced structural diversity resulting from the loss of emergent epifauna (Collie et al. 2000), and the disruption of habitats and substrata (e.g. (Devon Wildlife Trust 1993; Hall-Spencer and Moore 2000). Devon Wildlife Trust (1993) also reported a marked reduction in fragile epifauna in an area fished by scallop dredgers compared to an unfished control site in Lyme Bay. Where the fishing activity also removes the substratum, as has been the case on mudstone reef areas in Lyme Bay, extended periods of recovery may be needed for ecological functioning (Bevilacqua et al. 2006).

However, the majority (roughly two thirds) of false positives within the closed area do not coincide spatially with the fisheries data presented here, so alternative explanations for non-occurrence must be sought. It is possible that these areas were worked by scallop dredgers in years outside those covered by the data, although such a dramatic spatial shift in focus of fishing effort is unlikely. Nevertheless, given the slow recovery of the pink sea fan, areas fished ten years ago could exert an influence on the present day distribution of the species. It is also possible that the estimate of the spatial footprint of scalloping is an underestimate that does not accurately reflect the true spatial pattern of fishing effort. Increasing the buffer to 500m, for example, means that two thirds of the false positives coincide with the buffered scalloping activity.

After comparing the environmental variables for the absence records in and outside the buffers, the average values are similar for all parameters. It is likely that factors outside the scope of the data available over the entire study area influence distribution here. Many of these absence records are all in the north east of the closed area with a long south west fetch. Anecdotal information from local fishers suggests that after conditions of sustained strong south westerly winds, and particularly when seasonal algal blooms occur, turbidity and sedimentation rates in this area are high, possibly making them less suitable for *E. verrucosa.*

It is also possible that the current Lyme Bay substratum map, which is itself interpreted from different data sources, does not adequately reflect the heterogeneity of the reef area. It is important to remember that predicted species distribution maps are not only subject to error within the predictive model but also underlying error in the maps of environmental variables used in the prediction.

Biological interactions such as competition and predation have not been considered and are frequently omitted from species distribution models (Guisan and Thuiller 2005; Austin 2007). However competition is not thought to have a significant influence on the distribution of gorgonians (Yoshioka and Yoshioka 1989; Mortensen and Buhl-Mortensen 2004; Watanabe et al. 2009).

5.4.3 Overall model performance

In the absence of any GLM/GAM studies concerning gorgonians or other corals that have used the same performance metrics as those presented in this chapter, the performance of models for other marine species has been selected for comparison. Willems et al. (2008) reported a CCR, specificity, sensitivity and AUC of 78%, 77%, 81.1% and 82.5% respectively using a GLM in their study of the tubicolous polychaete *Lanice conchilega*. An earlier study that developed a GLM for snow petrel nests in Antarctica reported scores of 76%, 73.8% and 77.2% for the same indicators respectively, excluding the AUC, and an overall accuracy of 69% based on test data (Olivier and Wotherspoon 2006). Based on a presence-only modelling approach (Maxent, see Chapter 8), Tittensor et al. (2009) obtained an average AUC score of 0.88 (based on 10-fold cross validation) for their global model of stony coral distribution on seamounts. More recently, Howell et al. (2011) obtained an average AUC score of 0.8 (also based on 10-fold cross validation) and sensitivity and specificity scores of 0.72 and 0.82 respectively for their model of *Lophelia pertusa* distribution on Hatton Bank and George Bligh Bank. An average sensitivity-specificity approaching 90% and an AUC of 0.89, as obtained in this study for the full model based on internal validation, compare favourably. However, the model performed poorly in terms of overall predictive accuracy based on independent test data, the main reason for which was the high number of false positives. Nevertheless, this needs to be taken into consideration when applying the model to conservation management within the Bay.

5.4.4 Monitoring implications

Long-term monitoring in the marine environment is costly, and there is strong pressure to demonstrate that limited resources are used in the most cost-effective manner. ‘Rationalising’ (i.e. reducing) the number of sites to the highest value locations, while keeping the survey design intact, is often required (Day 2008).

Effective monitoring programmes should link changes in ecosystem health to changes in environmental conditions (Cooper et al. 2009). In the current Lyme Bay monitoring programme, long lived species are included in a suite of indicators designed to assess the effects of the closure to mobile benthic gear on the benthic reef ecosystem. By focusing on 'potential distribution' of the pink sea fan, that is, unoccupied sites in (predicted) suitable habitat (Gormley et al. 2011), this chapter demonstrates a method that allows the optimisation of monitoring sites through the identification of false presences that takes into account the ecosystem health (using pink sea fan as an indicator) and environmental conditions (past fishing activity).

The development of Marine Conservation Zones (MCZs) around the UK coast, and indeed the designation of growing numbers of MPAs worldwide will increase the requirement for monitoring programmes and the concept developed in this paper can contribute to the growing evidence base upon which future monitoring programmes can be designed.

Of course, there are many other factors that need to be taken into account when designing monitoring programmes including the identification of appropriate indicators and reference areas where appropriate, and consideration of the spatial distribution of past and current activity which is relevant to the objectives of the closure, all of which have been taken into account in the current monitoring programme design (Stevens et al. 2008). Additional optimisation of long-term monitoring programs could be achieved by combining the results of similar modelling studies with other management tools such as the decision framework developed by Gerber et al. (2007) which would determine the number of years monitoring required to document marine reserve effects.

Reviewing the results of monitoring programs can inform future management and the fundamental importance of adaptive management in the marine environment is widely recognised (Salafski et al. 2001; Pomeroy et al. 2005; Day 2008; Stein and Cadien 2009). In the spirit of adaptive management, species distribution modelling offers great potential for inclusion in marine planning. It provides managers with a mechanism to maximise their available information and the ability to update their contribution simply as new and improved data becomes available.

As a greater number of spatial plans are formally adopted, and the number of protected areas in our seas increases, the available funding for subsequent monitoring programs may have to be scaled down accordingly. Bearing this in mind, this study provides a proof of concept for the use of species distribution models to assist in the prioritisation of monitoring sites and thus to add to a growing number of useful tools available to today's marine environmental manager.

Chapter 6

The influence of environmental data resolution on model performance

Species distribution models can provide a constructive antidote to the disparity in survey effort in marine systems. Concomitant to this inequality in survey effort comes high variability in the resolution of available environmental data and hence the availability of high resolution data for use in predictive spatial models. Many terrestrial studies have reported that data resolution can influence the accuracy of model predictions yet comparative studies in the marine environment are rare, especially in deep-sea areas. This chapter investigates the effect of using marine environmental data at different resolutions on the performance of predictive models. Using both study sites, different levels of environmental data resolution were used to construct three logistic models for Hatton Bank and two for Lyme Bay. The overall trend was toward model performance increasing with environmental data resolution, with significant differences in performance found between the different resolution models in both study sites. The reduction in predictive performance has implications for management and the wider implications of these results are discussed, together with recommendations for dealing with different levels of data resolution, calling upon terrestrial research on this topic.

6.1 Species distribution models and environmental data resolution

With deadlines upon governments worldwide for both regional and international legislative commitments to conservation mandates (including OSPAR, relevant to the Northeast Atlantic, and the World Summit on Sustainable Development), we are now in a position where we must reconcile "the need to know versus the need to act" (Ardron et al. 2008). To this effect, species distribution models have great potential to support marine conservation planning.

One aspect of habitat modelling that has not been adequately addressed in the marine environment is that of the spatial resolution of environmental data used to fit the models.

Data initiatives such as the Ocean Biogeographic Information System (OBIS) and the Marine Environmental Data and Information Network (MEDIN) have developed in response to the often fragmented nature of marine environmental data holdings and have worked to increase the availability of marine environmental data to end-users. However the resolution of data within such databases continues to be problematic, with data of various resolutions available. High resolution (10's of metres) data availability is sparse with only limited coverage.

Studies in the terrestrial environment have shown that model performance can vary as a result of a change in environmental data resolution, with both improvement, deterioration and little change in predictive accuracy and/or model gain reported in various studies as a result of decreasing resolution (Ferrier and Watson 1997; Tobalske 2002; Graf et al. 2006; Bryan and Metaxas 2007; Guisan et al. 2007) and that this, in turn, can influence management implications.

This chapter addresses the current knowledge and aims to determine the effect of marine environmental data resolution on habitat models from both inshore and offshore sites in terms of model accuracy and efficiency, that is, the total area of suitable habitat in relation to the percentage of the target species within it. Predictive accuracy and ecological insight are compared between the models and implications for conservation management discussed. Ultimately, the appropriate resolution for spatial analysis depends on the management objectives for which the model is being developed (Trani 2002). To this effect, this chapter also examines whether the resolution of environmental data available in the study areas is relevant to the spatial management of the area and if the model outputs can provide meaningful input to conservation management.

6.2 Methods

6.2.1 Environmental data

6.2.1.1 Hatton Bank

Data layers of depth, substratum and geomorphology were produced for use in modelling at the following cell sizes: high resolution (up to 50m), medium resolution (200m), and low resolution (mixed but a maximum of approximately 750m (0.0083° or 30 arc seconds)).

The high resolution depth layer was derived from multibeam bathymetry grids at 25m and 50m resolution. The high and medium resolution gridded data were not available for the whole Bank (Figure 6.1). For the medium resolution data this meant that only a small number of transects were available for inclusion in the models. Therefore the medium resolution depth layer was derived from multibeam bathymetry grids at 200m cell size located on the central summit of the bank, and the 50 and 25m grids used in the high resolution model regridded, or ‘downscaled’, to 200m so that medium resolution data was available for the whole Bank. The low resolution depth layer (30 second grid) was taken from the General Bathymetric Chart of the Oceans (GEBCO; IOC, IHO and BODC (2003)) and was available for the whole Bank.

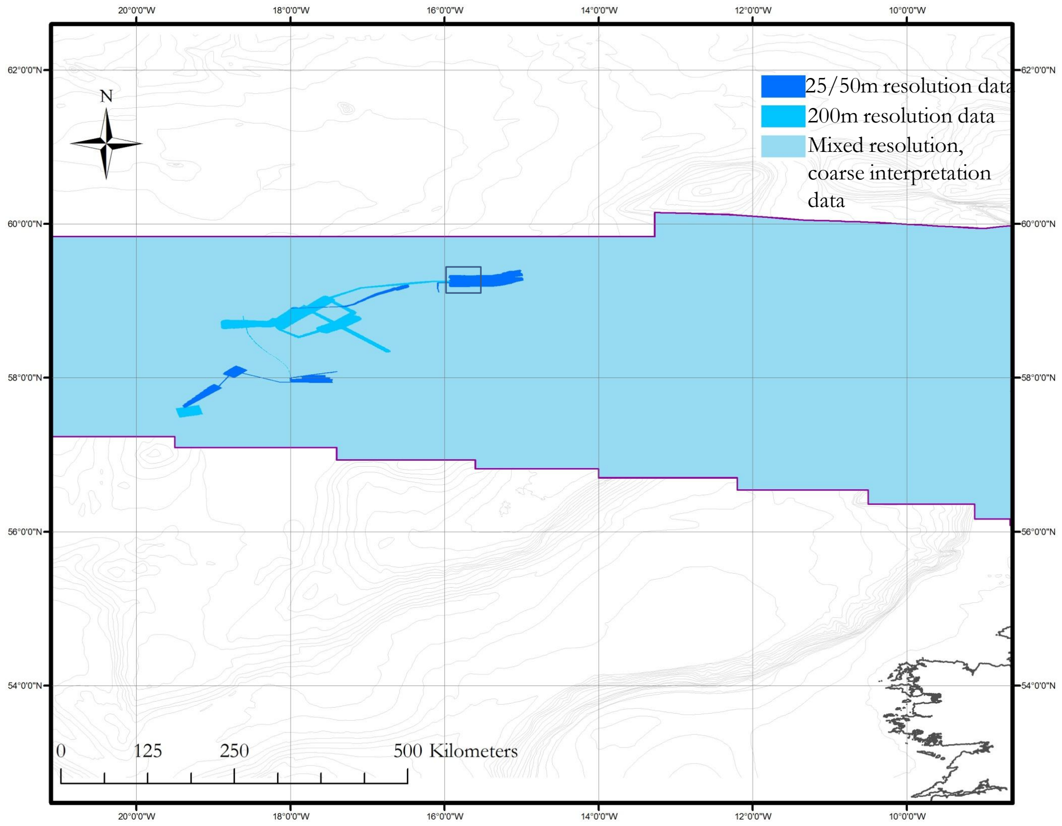


Figure 6.1: Availability of the high (HHRM), medium (HMRM) and low (HLRM) resolution environmental data on Hatton Bank. The boxed area represents the area covered by Figure 6.2 opposite.

Rescaling environmental data for use in spatial models, such as been done here, has been shown to have little impact on the performance of some species distribution models although this response was method dependent, that is, robustness to rescaling varied with different algorithms (Yesson and Tittensor, submitted). Davies and Guinotte (2011) have recently resampled low resolution environmental data at a finer resolution in order to improve a global model of habitat-forming cold-water coral habitat suitability.

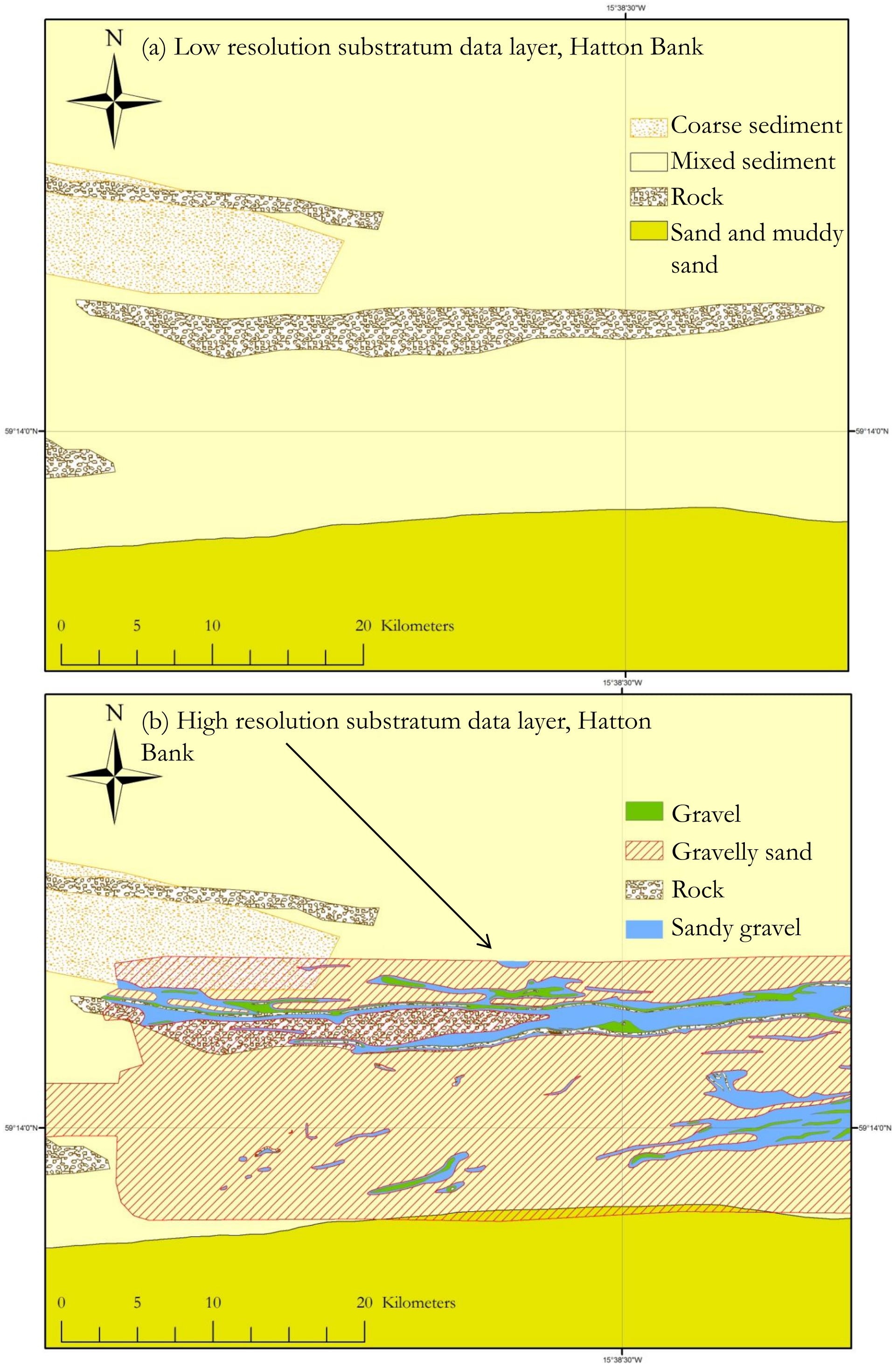


Figure 6.2: This close up of an area on Hatton Bank illustrates the difference in detail between the low resolution (a) and high resolution (b, superimposed on the low resolution) substratum layers. Much of the detail, both in terms of spatial extent and substratum type, is lost in the low resolution interpretation.

The substratum and geomorphology layers for both the high and medium resolution models were interpreted by colleagues at the British Geological Survey (BGS) using the aforementioned multibeam bathymetry and backscatter intensity grids (see Howell et al. (2011) for full details of multibeam echosounder acquisition and interpretation). Low resolution substratum and geomorphology layers were interpreted by colleagues at the National Oceanography Centre, Southampton (Jacobs and Porritt 2009), using data derived from the aforementioned multibeam echosounder surveys together with additional un-ground truthed multibeam echosounder data at 200m resolution from the north west flank of Hatton Bank, and the GLORIA long range, low resolution side scan sonar system, for which data were available over the whole bank. The GLORIA system's footprint varies between 175-675 metres and penetrates the top 5-10 metres of seabed. These low resolution data layers are therefore of mixed resolution which, whilst including both the high and medium resolution data, represent a coarse interpretation overall (Figure 6.2). All environmental data were prepared for use in the models using ArcGIS (ver. 9.2).

The respective models, will be referred to throughout as 'high' (HHRM i.e. Hatton high resolution model), 'medium' (HMRM) and 'low' (HLRM) resolution respectively.

Substratum and geomorphology were modelled as categorical variables. Depth was modelled as both a continuous and categorical variable, the latter using Jenks natural breaks (in ArcGIS) to define the categories (Day et al. 2008). As with the reclassification of the Lyme Bay DWT substrata (Table 4.2), the medium resolution geomorphology layer was also reclassified into fewer categories in order to increase the number of distribution records in each of the categories (Table 6.1).

Table 6.1: Hatton Bank medium resolution geomorphology and Lyme Bay low resolution substratum classifications

New geomorphology class	Original (Jacobs and Porritt 2009) Hatton Bank 200m resolution geomorphology classes included
Relatively flat seabed	Relatively flat seabed
Elongate feature	Escarpment; flank
Complex erosion feature	Furrow; iceberg plough mark; scour
Positive topographic feature	Pinnacle mound; ridge; ridge crest

New substratum class	Original Lyme Bay UKSeaMap seabed landscape classes included
Rock	Rock
Mixed	Mixed sediment
Sediment	Coarse sediment; mud and sandy mud; sand and muddy sand

6.2.1.2 Lyme Bay

Unlike Hatton Bank, where data for several predictors was available at different resolutions, the majority of variables were the same between the low and high resolution Lyme Bay models (LLRM and LHRM respectively) with the exception of substratum and depth. Here, the DWT biotope map represents the high resolution substratum data. This layer is also a mixed resolution layer interpreted from different sources (see Chapter 4 for details). The 'low' resolution layer is represented by the UKSeaMap 2010 substratum layer which includes seabed substrata (see Connor et al. (2006) for comprehensive methodology for the UKSeaMap project). Each grid cell was 0.02 decimal degrees (approximately 3.17 km^2). The UKSeaMap categories were modelled using their original categories and also as a reclassified version in order to increase the number of records in each category (Table 6.1). The low resolution depth layer was downloaded as a polygon, with a resolution of 1.8 km, from the Atlas of UK Marine Renewable Energy Resources.

6.2.2 Distribution data

Video transects, and the distribution data subsequently obtained from them, represent very high resolution data because they can offer continual observation of the seafloor over a certain distance. The use of video data to investigate the effects of environmental data resolution in species distribution models is especially interesting because the resolution of the video data can be severely limited by the resolution of the environmental data. For example, if reducing video transect derived species observations to one presence or absence record per grid cell then the number of species observations over 25m gridded acoustic data will be much higher than the number of observations for a 100m grid, as illustrated in Figure 6.3. Gorgonian distribution data was obtained from video footage in both study areas, the methodology for which has been outlined in Chapter 4.

Guisan et al. (2007) observed that at coarser environmental data resolution, potentially more distribution data are available because distribution data with a lower georeferencing accuracy might ‘fit in’ to the larger cell size. However, the methodology adopted for this study (i.e. reducing video data to one presence-absence record per intersect polygon) means that the exact opposite is true and that with larger cell size a smaller number of records are available for use in the model. In addition, the ratio of presence to absence points in the dataset (prevalence) changes at different cell sizes.

6.2.3 Modelling approach

The modelling approach adopted follows that outlined in Chapter 4. However, as differences in sample size and prevalence can influence model performance (Bryan and Metaxas 2007; Guisan et al. 2007; Pearson et al. 2007) internal resampling was repeated, standardising for the size and prevalence of the calibration dataset.

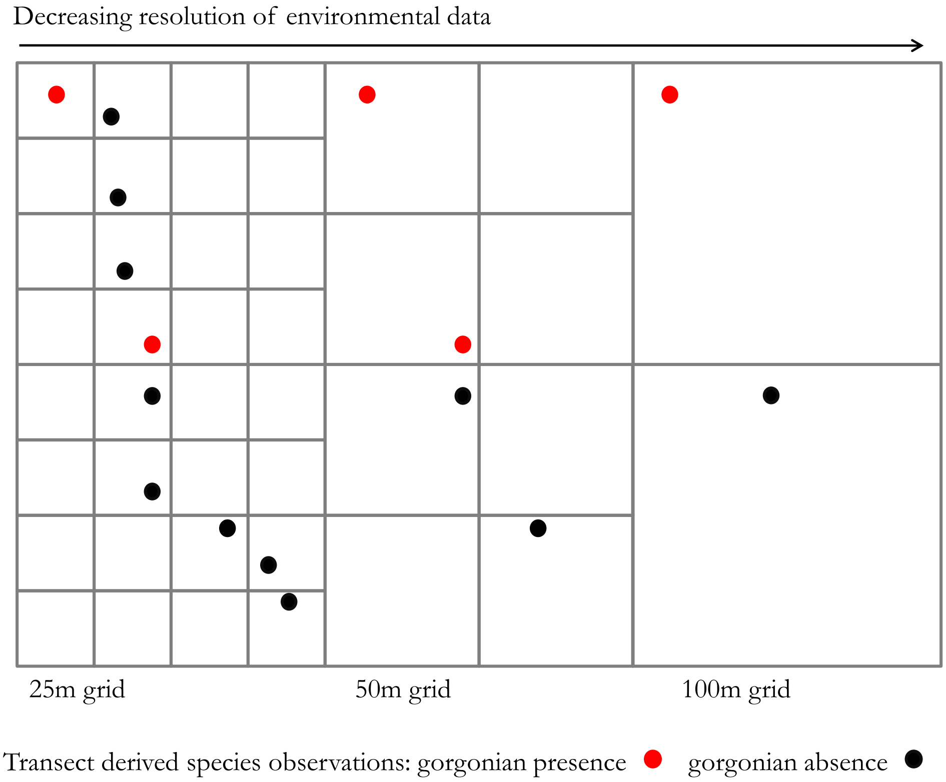


Figure 6.3: Diagram demonstrating the influence of gridded environmental data on the number of species observations (red dots representing presence records; black dots representing absence records) derived from video transect data. As resolution decreases (and cell size increases), the greater the reduction of observations across that cell.

The large difference in sample size between the different Hatton Bank models (n=120, 204 and 936 for the HLRM, HMRM and HHRM respectively) has the potential to influence the relative performance of the models and mask any true influence of data resolution. Given that the lower resolution dataset had the smallest number of presence records (Table 6.2), the size of the calibration dataset was set accordingly. Based on these criteria, resampling was performed with 34 presence (two thirds of the number of presence records in the low resolution dataset) and 34 absence records, repeatedly and randomly selected from each of the three data sets.

The same standardisation was carried out for the Lyme Bay data (using 22 presence and 22 absence records) although there was only a small difference in the number of records between the two models.

The final models were, however, built and mapped using the full data set because this is the reality of constructing models at different resolutions, where coarser resolution models will always have comparatively fewer data points.

Only three presence-absence records were represented in the HLRM *mud and sandy mud* substratum category. This caused problems for the automated random resampling because often, none of the three records were selected in the build data, meaning that no predictions could be made on those records in the test data. To prevent this problem, the resampling code was adjusted so that two of these three records were always in the build data. Whilst this removes the random element of the selection process, it was considered preferable to removing the three records from the resampling entirely.

As with Chapter 5, independent test data were available as an additional assessment of model performance for the Lyme Bay models.

6.3 Results

6.3.1 Significant variables

The structure of the final models for both study sites is outlined in Table 6.2 along with performance indicator scores obtained from the repeated internal resampling.

6.3.1.1 Hatton Bank models

Substratum was found to be the most influential variable in all three models. In each case, the probability of gorgonian presence increased with the hardening of substrata as illustrated by the high resolution model (Figure 6.4).

Geomorphology was found to have a significant influence on gorgonian distribution in both the HHRM and HMRM with positive and elongate topographic features respectively associated with the highest probabilities of occurrence. Figure 6.5 illustrates the increasing proportion of presence records with increasing relief for the HMRM. Erosion features (features that have negative relief with respect to the surrounding seafloor) had the most negative influence on gorgonian distribution in both models, followed by relatively flat areas of seabed. The HMRM using the reclassified geomorphology, although not significantly different from the original classification geomorphology univariate model, was found to be the best model when combined with substratum.

Depth was also found to be significant in all models. Following stepwise selection the categorical depth variable was included with substratum in the final HLRM and HHRM, explaining a significantly higher proportion of deviance than substratum alone (Anova, p=0.009 and p=<0.001 respectively). Depth categories 2 (592-675m; HLRM) and 4 (777.93-874.40m; HHRM) had the highest proportion of presence records. In all Hatton models, probability of occurrence decreased below ~700-800m depth and for the HHRM and HMRM this decline was steep.

The build models for each of the Hatton Bank models all contained variables included in the final model built using all the data suggesting that these models are robust.

Table 6.2: Comparative performance of Lyme Bay and Hatton Bank final models. Significant variables are also listed. Shaded rows relate to the final model; all others are from repeated internal resampling. Scores and standard deviation to three decimal places. All but the low resolution Lyme Bay final model were GLMs. Significance codes: 0 *** 0.001 ** 0.01 * 0.05. (c) categorical version of the variable; (r) reclassified version of the variable; (s) smoothing term used for continuous variable; geo. = geomorphology; subs=substratum.

Model attributes		Hatton (low)	Hatton (medium)	Hatton (high)	Lyme Bay (low)	Lyme Bay (high)
Final model*		subs + depth (c)	subs + geo. (r)	subs + depth (c)	s(current)	subs
Adjusted R-squared		0.225	0.159	0.367	0.29	0.506
n (n presence, n absence)		120 (51,69)	204 (59, 145)	936 (117,819)	84 (33,51)	86 (34,52)
Threshold		0.425	0.289	0.125	0.39	0.40
Significant terms identified by univariate models, starting with the best model (adjusted r-squared in parentheses).		Subs (0.167)*** Depth (c)(0.083) * Depth (s) (0.049)**	Subs (0.139)** Geo (r) (0.086)*** Geo (0.077)** Depth (s) (0.035)*	Subs (0.339)*** Geo (r) (0.161)*** Depth (c) (0.109)*** Depth (s) (0.035)***	Current(s) (0.290)** SSTmin (s) (0.210)* CHLmean (s) (0.117)* Interaction (0.091)**	Subs (0.506)** Current (s) (0.292)** SSTmin (s) (0.206)* CHLmean (s) (0.127)* SPMmin (s) (0.109) * Interaction (0.078)**
CCR	From repeated internal resampling	0.763 ± 0.055	0.697 ± 0.052	0.796 ± 0.031	0.723 ± 0.073	0.856 ± 0.056
Sensitivity		0.761 ± 0.093	0.731 ± 0.109	0.835 ± 0.069	0.868 ± 0.121	0.944 ± 0.060
Specificity		0.766 ± 0.083	0.684 ± 0.079	0.791 ± 0.040	0.629 ± 0.113	0.799 ± 0.089
AUC		0.773 ± 0.065	0.754 ± 0.055	0.891 ± 0.021	0.794 ± 0.072	0.889 ± 0.048

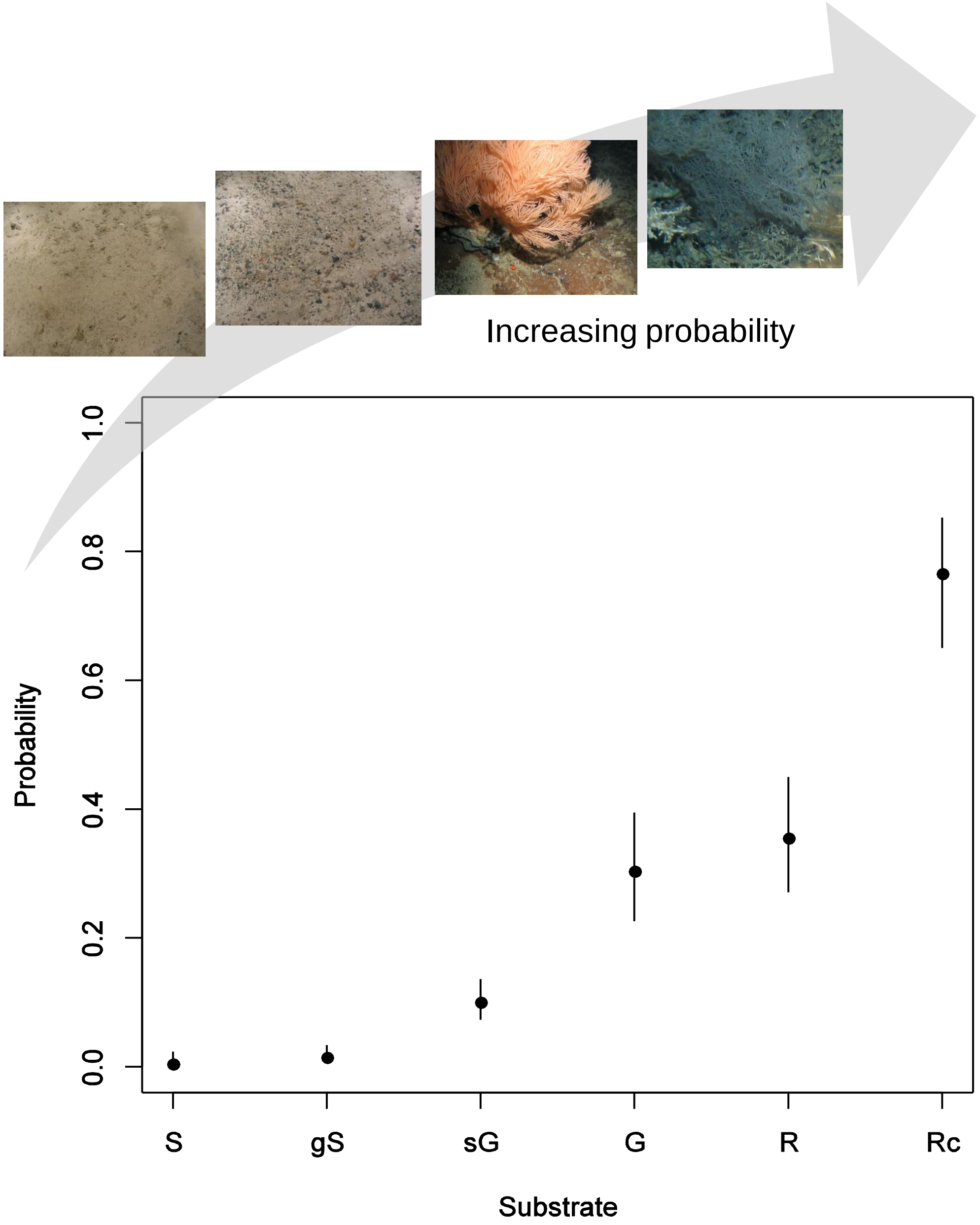


Figure 6.4: Probability of gorgonian occurrence with error bars, on a logistic scale, at each level of the categorical substratum variable for the HHRM. Sand (S), gravelly sand (gS), sandy gravel (sG), gravel (G), rock (R) and rock with a carbonate veneer (Rc). Photographs illustrate changes in substratum.

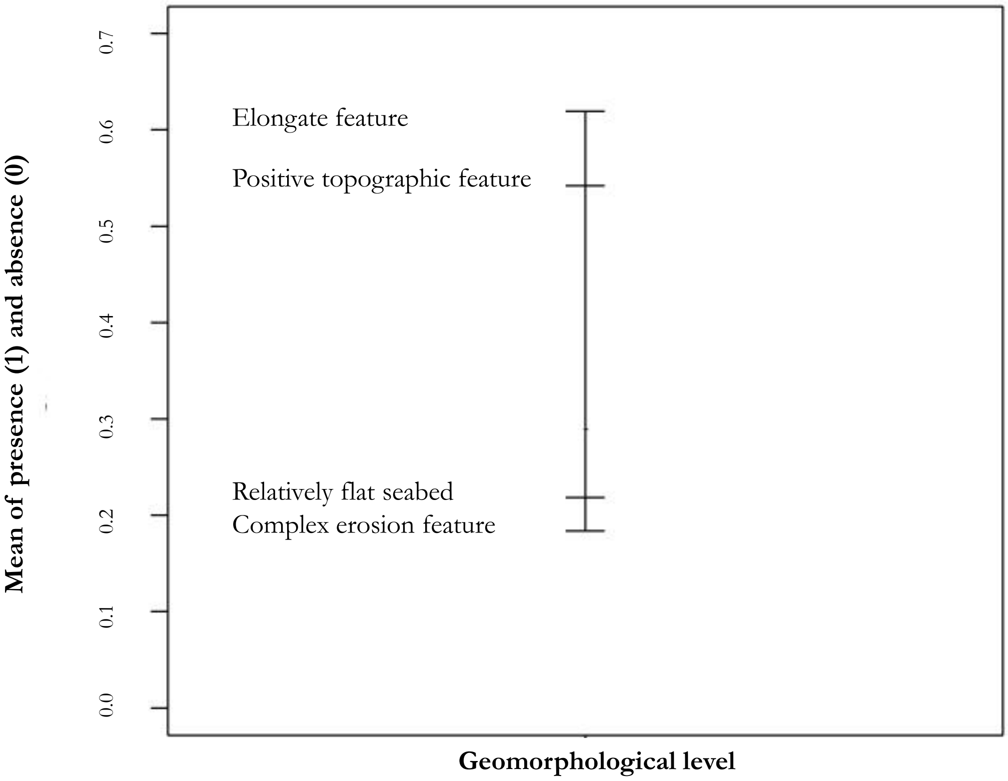


Figure 6.5: Design plot for the HMRM geomorphology model. The vertical axis shows the mean value per level of the categorical variable. The higher the value, the greater the proportion of presence records in that level.

6.3.1.2 Lyme Bay models

Unlike the LHRM, where substratum explained 51.8% and was highly significant, the UK SeaMap substratum layer was not found to be significant in explaining the presence of pink sea fans in Lyme Bay.

Current explained ∼29% deviance in the Lyme Bay models with probability of occurrence unlikely when spring peak current velocity exceeds approximately 0.4 m s $^{-1}$ (Figure 6.7). Current was the sole variable in the final LLRM.

Probability of occurrence had an inverse relationship with minimum SST (LLRM and LHRM) and minimum SPM (LHRM). A humped relationship was observed

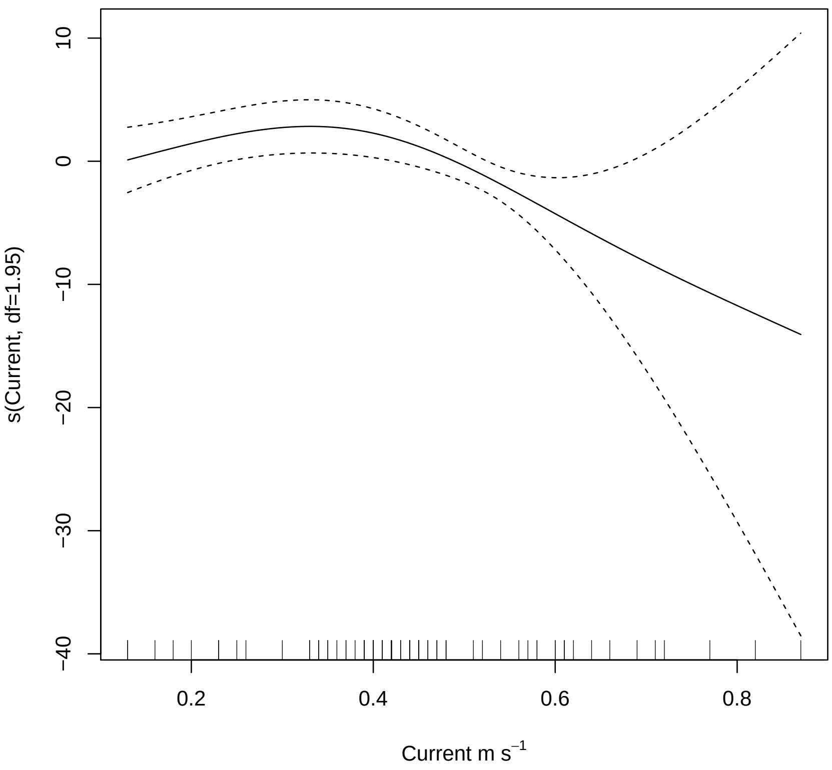


Figure 6.6: Generalized additive model illustrating the relationship between current speed and pink sea fan distribution based on the low resolution Lyme Bay model. Degrees of freedom for the smooth included in y axis label. X axis rug denotes observations.

between mean Chl. *a* (LHRM) with probability of occurrence highest at ∼2 mg m^{-3}.

For Lyme Bay, two of the three build models for the LLRM and LHRM had the same structure as the final models with all the data.

6.3.2 Model performance

6.3.2.1 Hatton Bank model

Significant differences were found for all four performance indicators after running Wilcoxon rank sum W tests (Appendix C). The HHRM consistently outperformed the other models for each indicator, with mean values near or exceeding 0.8 (Figure 6.7, Table 6.2).

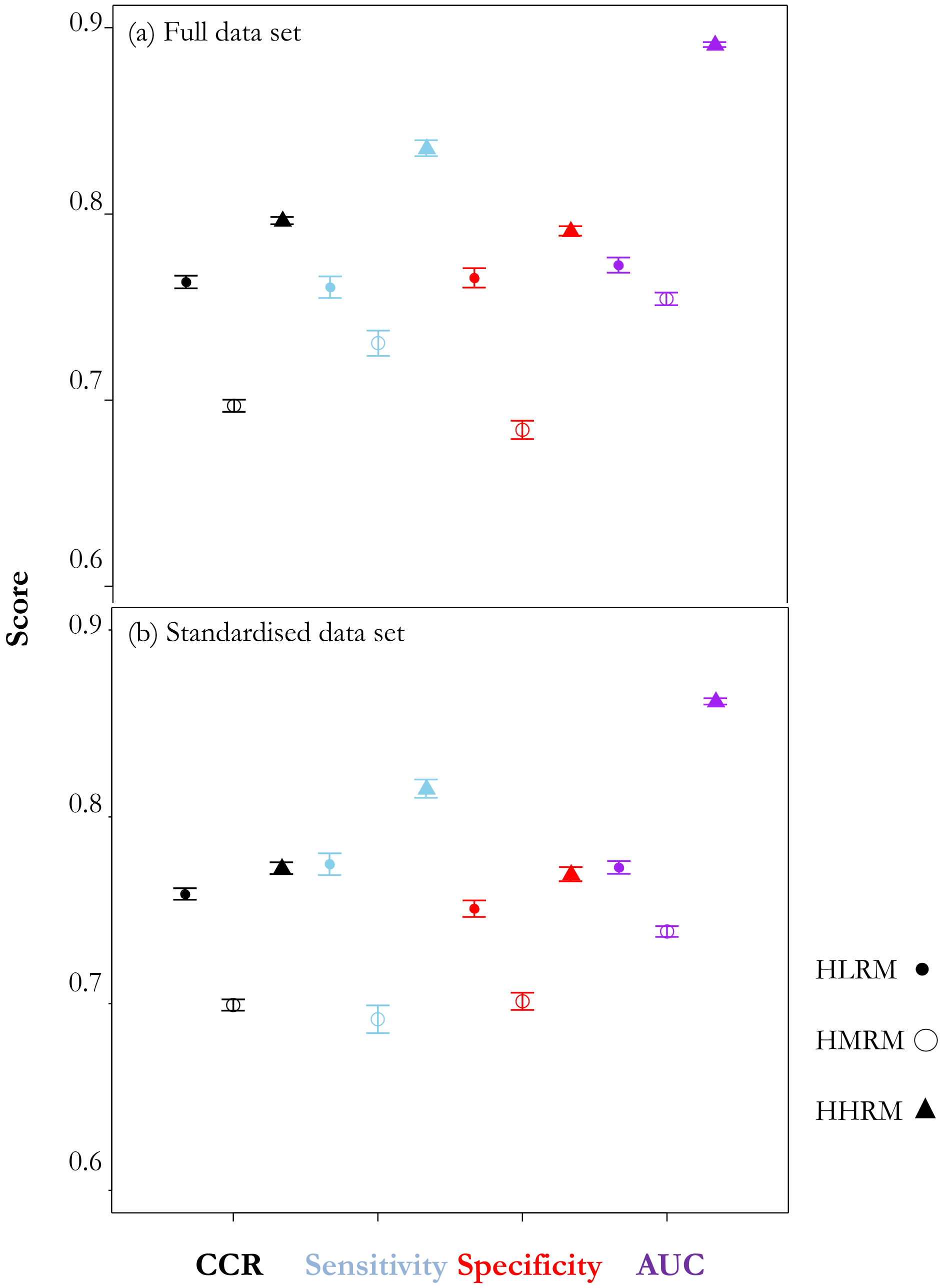


Figure 6.7: Mean scores ± 95% confidence limits for (a) the full data set and (b) the standardised data set Hatton Bank models. Correct Classification Rate (CCR); Area under the curve (AUC).

The HMRM has the poorest performance of the three models for each indicator. The relative performance of the models remained the same after the resampling had been standardised, providing confidence that sample size and threshold are having no significant effect on the relative performance of the models.

In addition to differences in mean performance indicator score, standard deviation consistently decreased with increasing resolution for each of the four performance indicators with only one exception (standard deviation for sensitivity was lower for the HLRM than for the HMRM).

6.3.2.2 Lyme Bay model

The Lyme Bay model constructed with the DWT substratum layer significantly outperformed the lower resolution model for all four performance indicators based on Wilcoxon rank sum W tests (Appendix D, Figure 6.8). As with the Hatton Bank models, these highly significant differences remained when the data was standardised.

6.3.3 Spatial outputs

Due to the difficulties of presenting meaningful maps at such large scales, a binary map has been produced for four of the five final models (the LHRM map was presented in the previous chapter) in accordance with the respective prediction thresholds (Figures 6.9 - 6.12). Similar maps colour coded to a range of values on the logistic probability scale were visually inadequate given the size permitted by this format and fine scale detail was lost from the higher resolution Hatton Bank maps. Instead, Figure 6.12 illustrates how predictions differ across the three different resolution models on an area of the central Hatton Bank.

Using all gorgonian records available in the distribution data, binary maps of habitat suitability for the HLRM, HMRM and HHRM respectively contained 91.4%, 90.8% and 91.4% of gorgonians in above-threshold areas, which can be considered highly successful. For Lyme Bay, the percentage of gorgonian records located within predicted suitable areas (including the independent test data), was 83% in the low resolution model and 92% in the high resolution model.

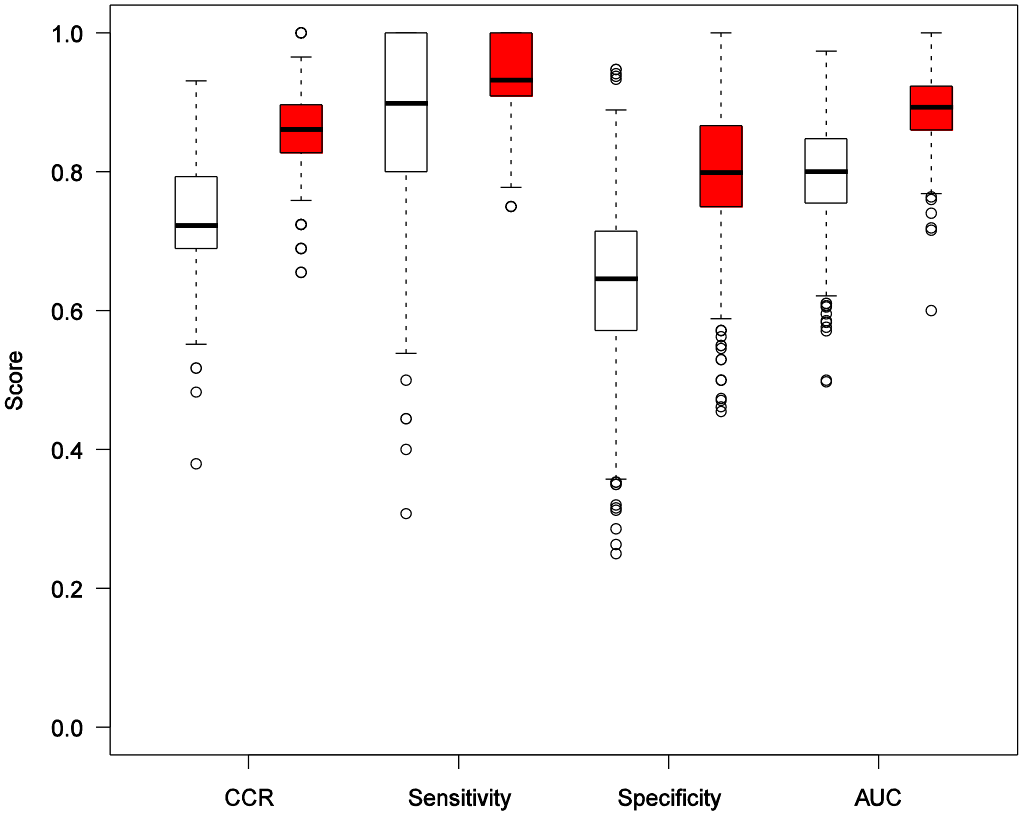


Figure 6.8: Boxplots illustrating the distribution of performance indicator scores between Lyme Bay models. The whiskers indicate the lowest and highest data still within 1.5 interquartile range of the lower and upper quartiles. LHRM data shown in red.

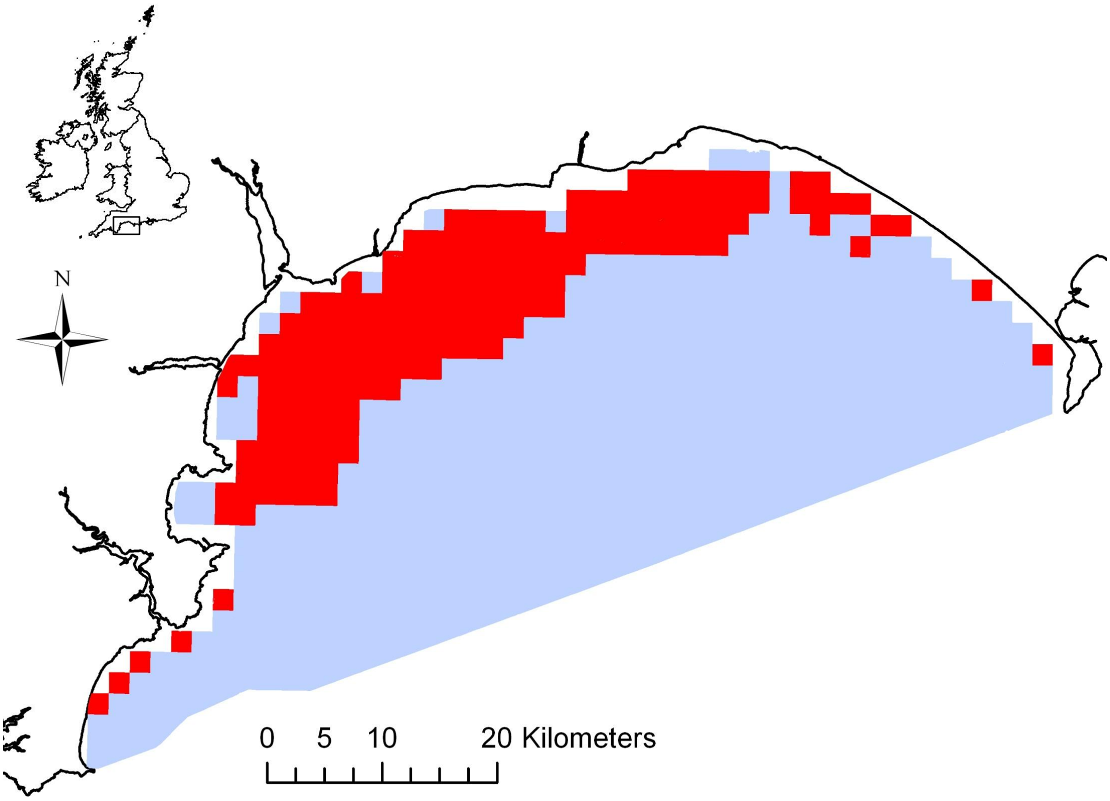


Figure 6.9: Binary map of pink sea fan distribution in Lyme Bay, according to a GAM fitted with the smoothed term current (LLRM). Areas predicted to be suitable for the pink sea fan are shaded in red. Light blue areas considered unsuitable, or at least, below the probability threshold of 0.39.

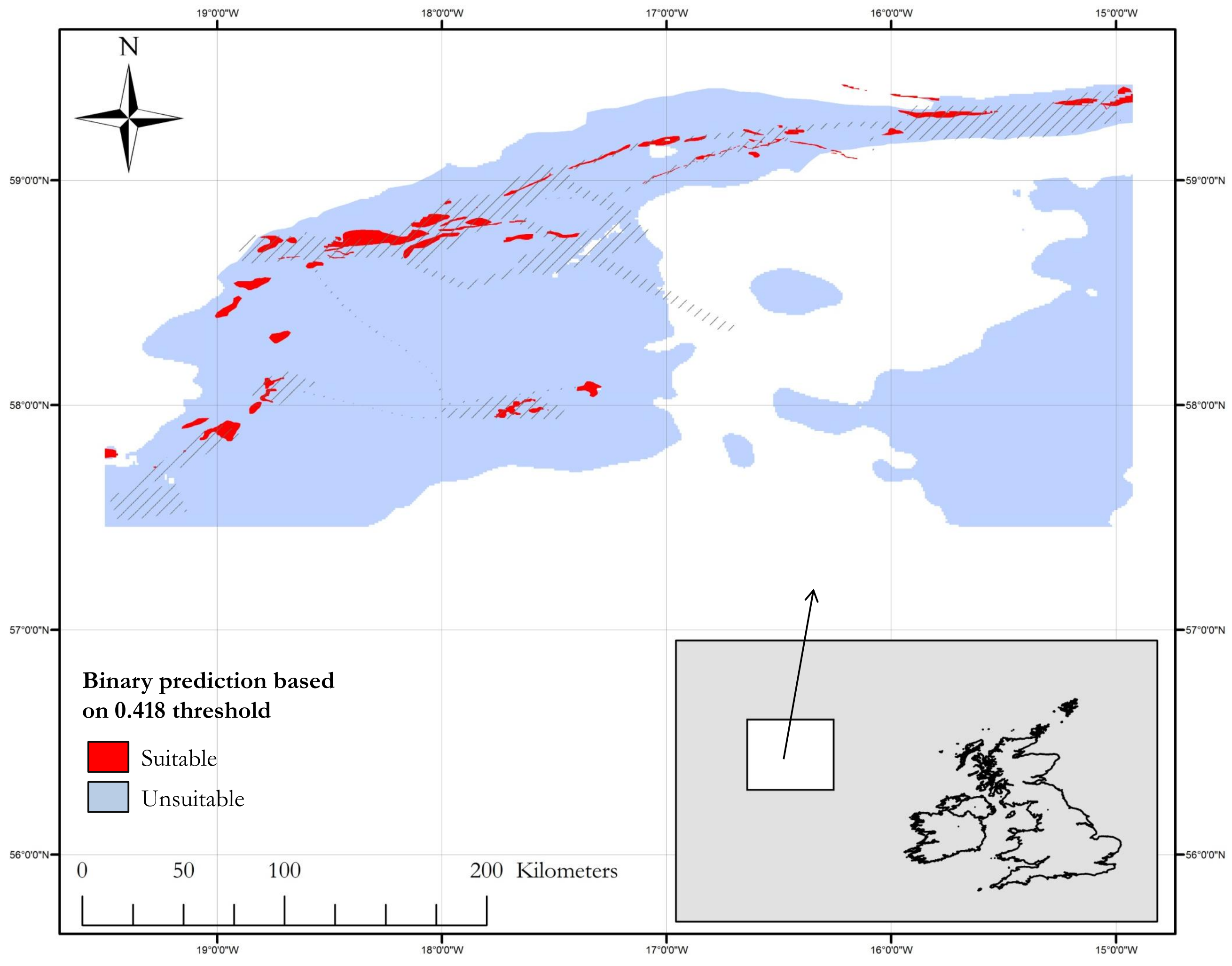


Figure 6.10: Binary map of gorgonian distribution on the Hatton Bank, based on a GLM fitted with the factor variables substratum and depth (HLRM). Areas predicted to be suitable for gorgonians are shaded in red. Light blue areas considered unsuitable, or at least, below the probability threshold of 0.418. The hatched area shows the area covered by the medium resolution data, for reference.

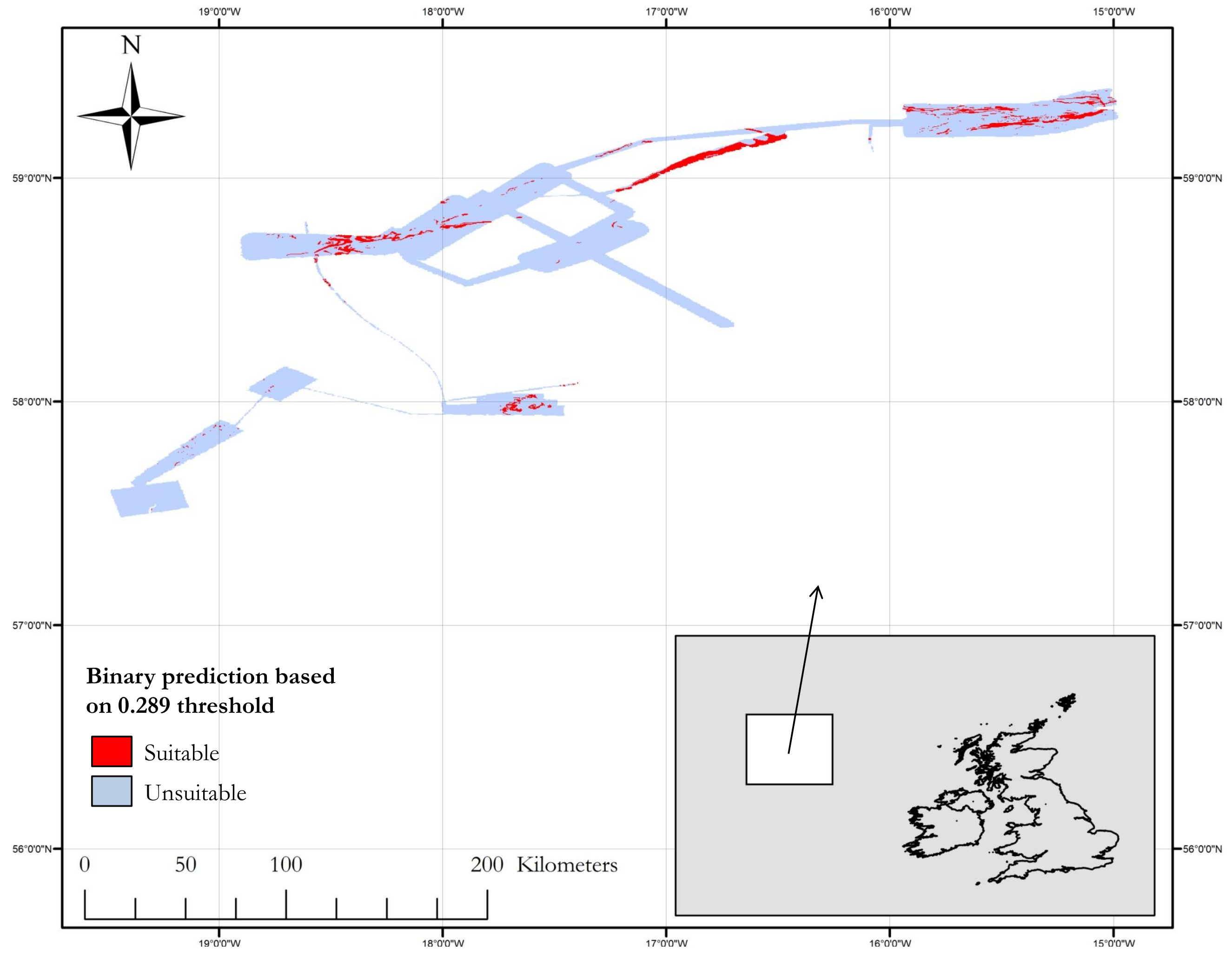


Figure 6.11: Binary map of gorgonian distribution on the Hatton Bank, based on a GLM fitted with the factor variables substratum and geomorphology (HMRM). Areas predicted to be suitable for gorgonians are shaded in red. Light blue areas considered unsuitable, or at least, below the probability threshold of 0.289.

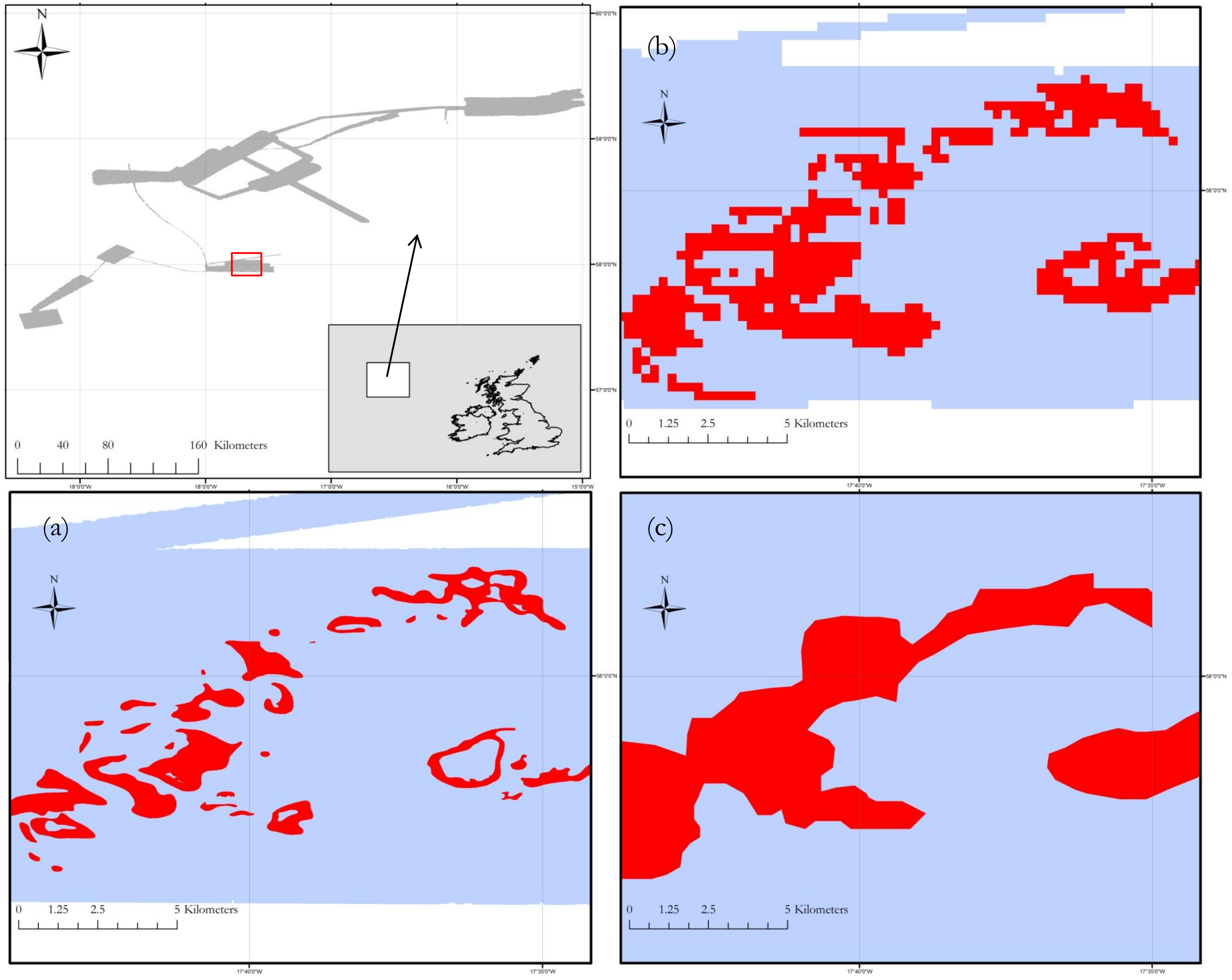


Figure 6.12: Binary maps of gorgonian distribution for the (a) high resolution, (b) medium resolution and (c) low resolution models for an area on the central Hatton Bank (boxed in red). Areas predicted to be suitable for gorgonians are shaded in red. Light blue areas considered unsuitable. The HHRM threshold is 0.125.

6.4 Discussion

6.4.1 Significant environmental variables

The importance of the various environmental predictors selected by the Lyme Bay models has been discussed previously (see section 5.4.1 for further explanation).

The role of substratum as a dominant influence on gorgonian (Mortensen and Buhl-Mortensen 2004; Watanabe et al. 2009; Edinger et al. 2011) and other deep-sea coral distribution, is well documented (Rogers 1999; Bett 2001; Dolan et al. 2008; Durán Muñoz et al. 2009) and the importance of hard substrata availability to gorgonian distribution is evident in each of the Hatton Bank models. Based on the logistic model outputs, probability of occurrence centres solely on rocky areas in the HLRM. In the HMRM and HHRM, occurrence is predicted to occur not only on rocky areas but also some gravel areas and, in the case of the HMRM, some sandy gravel areas. The highest predicted probabilities are reserved for rocky areas alone. Yet the availability of rocky substrata, including cobbles and boulders, does not on its own predetermine gorgonian occurrence, as demonstrated by Mortensen and Buhl-Mortensen (2004) and Watanabe et al. (2009) who found many unoccupied boulders and cobbles. Significant negative associations between sand and gorgonians have been reported for deep-sea gorgonians off Nova Scotia (Watanabe et al. 2009) which also support the results presented here.

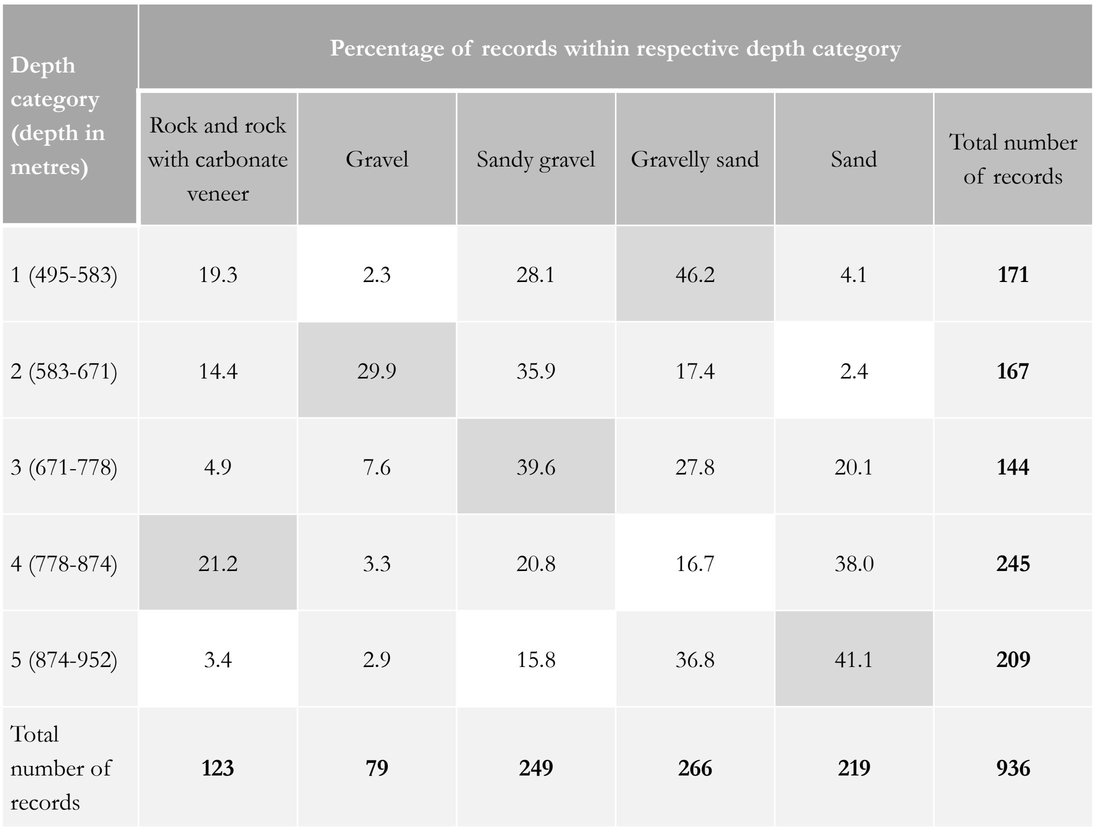
Geomorphological features have been linked to differences in faunal composition, including the distribution of deep-sea gorgonians (Mortensen and Buhl-Mortensen 2004; Edinger et al. 2011), and the preference of corals for topographic highs is often reported (Genin et al. 1986; Rogers 1999; Duineveld et al. 2007; Dolan et al. 2008; Guinan et al. 2009b; Durán Muñoz et al. 2009) in addition to reduced abundance or occurrence in bathymetric depressions (Guinan et al. 2009a). Therefore it is not surprising that positive features were associated with the highest probabilities for the HMRM and HHRM. The two geomorphological layers in the HLRM were not found to be significant although this may be explained by the distribution of records among different levels of the two categorical variables representing geomorphology.

Assessing the contribution of depth is more problematic. Closer inspection of the depth category in the HHRM reveals that the levels associated with increased probability of occurrence (levels 2 and 4) have respectively the third and first highest percentage of rocky records (taking rock and rock with carbonate veneer together) out of the five levels (Table 6.3). A similar pattern was found for the HLRM. This could reflect sample effort. In the HMRM probability of occurrence showed a marked decrease below ∼800m depth although again this pattern could be related to substratum because 18% of records shallower than 800m were rock whereas rock represented only 8% of records deeper than 800m. However, depth and substratum had a very low correlation across all three models.

Although Mortensen and Buhl-Mortensen (2004) and Watanabe et al. (2009) found depth to have an influence on deep-sea gorgonian distribution in the Northeast Channel (Atlantic Canada), this was thought to be as a result of factors that co-vary with depth (temperature for example) rather than depth *per se*. Depth was included in two thirds of the final models for a presence-only (Ecological Niche Factor Analysis; ENFA) modelling study of deep-water gorgonians (Bryan and Metaxas 2007).

The three Hatton Bank models explained, at most, just over a third of the variance within the data and it is possible that factors operating at smaller scales than captured by even the highest resolution are exerting an influence on gorgonian distribution. A single cobble is sufficient to support a gorgonian colony (Mortensen

Table 6.3: Representation of different substrata within each depth class for the Hatton high resolution model. The highest (dark shading) and lowest (no shading) percentages for each substratum level are highlighted. The categories 'rock' and 'rock with a carbonate veneer' are considered together. Depth categories are arranged in descending order of probability. The table illustrates a shift from the highest proportion of rocky substrata in the depth categories with the highest probability of occurrence through to highest proportion of soft substrata in depth categories considered unsuitable for gorgonians.



Depth category (depth in metres)	**Percentage of records within respective depth category**					
	Rock and rock with carbonate veneer	Gravel	Sandy gravel	Gravelly sand	Sand	Total number of records
1 (495-583)	19.3	2.3	28.1	46.2	4.1	**171**
2 (583-671)	14.4	29.9	35.9	17.4	2.4	**167**
3 (671-778)	4.9	7.6	39.6	27.8	20.1	**144**
4 (778-874)	21.2	3.3	20.8	16.7	38.0	**245**
5 (874-952)	3.4	2.9	15.8	36.8	41.1	**209**
Total number of records	**123**	**79**	**249**	**266**	**219**	**936**

and Buhl-Mortensen 2004) and gorgonians ostensibly on sandy substrata might in fact be on small cobbles within the sand habitat. As previously mentioned in Chapter 5, biological interactions including predation and inter-specific competition are not captured by these static models although they may exert considerable influence on the patterns of gorgonian distribution observed. In addition, human activities including bottom fishing can profoundly impact benthic communities and this is especially true of fragile epifauna. The effects of bottom trawling on deep-sea fauna are well documented and because of the slow growing nature and unknown recoverability of many deep sea corals it may be that areas previously suitable for supporting gorgonian colonies may never recover from previous fishing effort (Rogers 1999; Mortensen et al. 2005; Wheeler et al. 2005a,b; Davies et al. 2007; Rogers et al. 2007). [See also section 5.4.2].

6.4.2 The influence of environmental data resolution of model performance

Studies concerning the effects of data resolution on the performance of species distribution models commonly select arbitrary resolutions at which to test the model (e.g. Trani 2002; Bryan and Metaxas 2007; Guisan et al. 2007; Guinan et al. 2009b) or, at least, do not make explicit the link between the selected resolution and relevance to management. In this chapter, environmental data resolutions have been chosen based on the fact that these data are directly applicable to management and spatial planning because they are the data that are currently available to support management in each area.

In Lyme Bay, the model built with the Devon Wildlife Trust substratum data consistently outperformed the model built using UKSeamap substratum data, supporting the notion that higher resolution data leads to improved model performance (Ferrier and Watson 1997; Guisan et al. 2007). The HHRM model also consistently outperformed the HLRM and HMRM across the four performance metrics based on internal validation and achieved excellent average performance indicator scores.

The poor performance of HMRM with respect to HLRM is harder to explain, especially because the HLRM outperformed it on all four performance indicators. However, another deep-water gorgonian predictive modelling study reported that the mean value of seascape factors in the ENFA analysis varied less between the results of models built with medium (5km grid) and low resolution (9km grid) data than between models built with medium and high resolution data (1km grid) (Bryan and Metaxas 2007).

With respect to data quality, the HHRM data came from a system that had been calibrated to work to a maximum of 1000m and is therefore potentially better quality than the HMRM data which came from a system calibrated to work over a large depth range. The HLRM data has multiple sources and so is of variable quality.

Figure 6.13 reveals that the interquartile range for the HMRM often extends to lower scores for the lower and upper quartiles, when compared to the HLRM. Looking at the 100 lowest scoring models for each of the four performance indicators reveals that almost half of these (n=49) were common to three or more of the performance indicators in the HLRM. The same inspection of the HMRM data revealed that less than one third (n=32) were similar across three or more of the indicators. So differences in model performance can neither be attributed to differences in the random selection of the data or a particular combination of variables contributing to the lowest scores.

The relative performance of the HLRM and HMRM contradicts the results obtained in some studies. Bryan and Metaxas (2007) reported little change in model performance after changing the resolution of different layers. However this may be a result of the authors simply interpolating one data set at different resolutions, as opposed to comparing different data layers entirely. One possibility for the improved performance of the HLRM with respect to the HMRM is the generalisation of the input layers. Guisan et al. (2007) have suggested that coarsening data causes the merging of conditions that might not actually occur together, simply nearby, and that the unique detail of those individual locations might be lost as

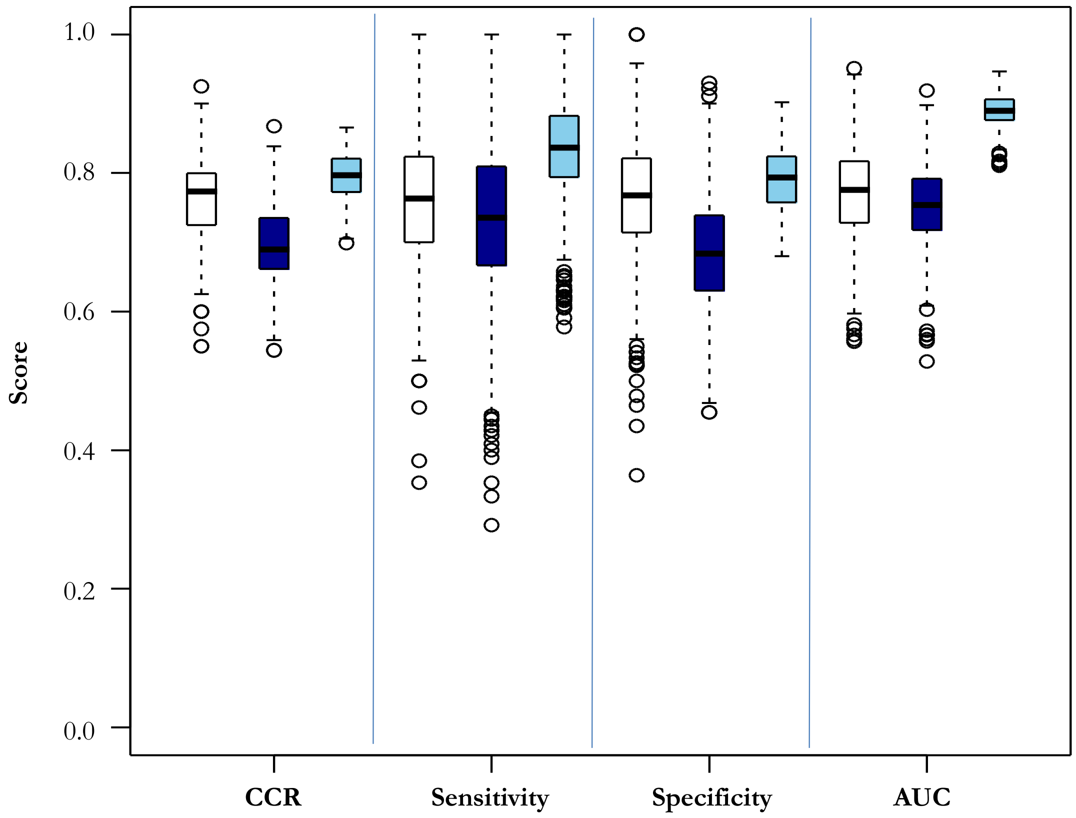


Figure 6.13: Boxplots illustrating the distribution of performance indicator scores between models. The whiskers indicate the lowest and highest data still within 1.5 interquartile range of the lower and upper quartiles. HLRM, no shading; HMRM, dark shading; HHRM, light shading. Correct Classification Rate (CCR); Area under the curve (AUC).

a result. However, for sessile species this might actually serve to improve model performance on face value. The merging of data into coarser units might lead to the right combination of suitable conditions within a cell despite these conditions not actually strictly overlapping spatially (Guisan and Thuiller 2005, see Figure 6.14 for explanation). This could ultimately result in an overestimation of model performance and potential problems if the model outputs were being used to target future survey effort.

Crucially, it is the highest resolution data in both the Hatton Bank and Lyme Bay

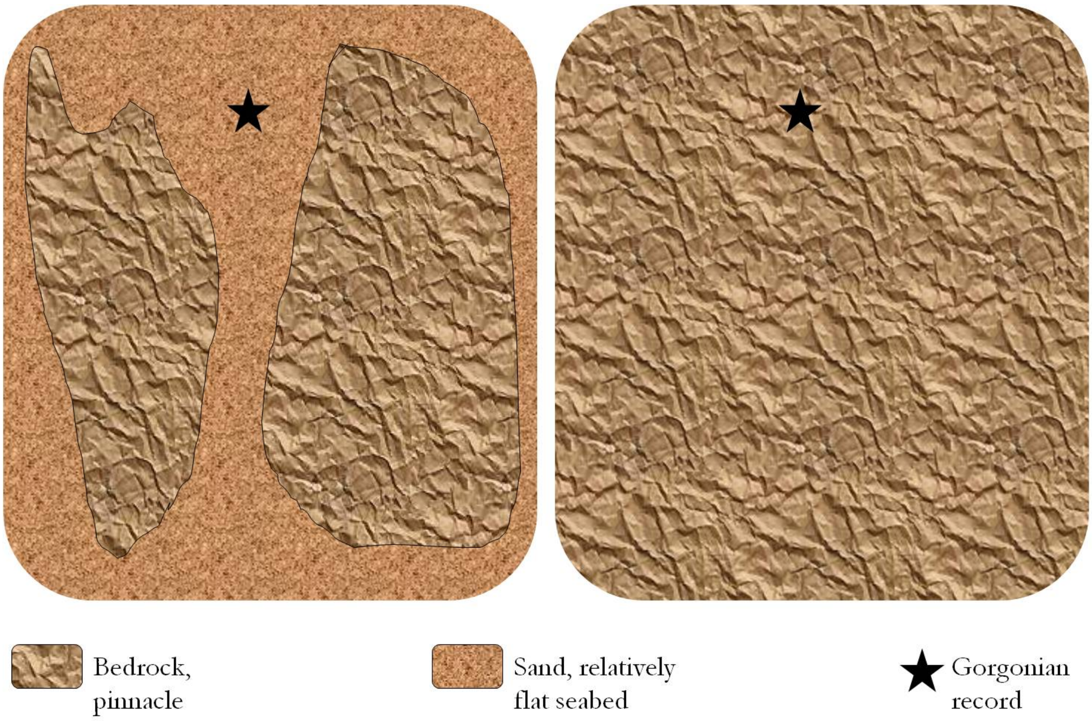


Figure 6.14: Illustration of potential consequence of merging / averaging spatial data with respect to species distribution modelling. On the left, the illustration shows a gorgonian record located within an area of sandy, relatively flat seabed between two bedrock outcrops. On the right, the data has been rescaled according to the maximum area of features in the cell, the result being that the data presented to the model is now a gorgonian record on a rocky pinnacle, as opposed to on sandy flat seabed.

study sites that performed significantly better than the other(s) and it is important to discuss the implications of this for conservation planning and management in each area.

6.4.3 Management implications

Although the influence of environmental data resolution on predictive power has been the focus of a number of studies, as previously discussed, little attention has been given to the subsequent connotations for management. Specifically, critical appraisal of any spatial differences in model output from the different resolution models (total area of predicted suitable habitat for example) appears to be entirely lacking.

Using the binary mapped output for all three Hatton models, more than 90% of known gorgonian records were included in 'suitable' (above-threshold) areas. The total above-threshold area for the HLRM and HMRM (223.8 and 271.7 km ^{2} respectively) is a much larger area than that of the HHRM (113.8 km ^{2}).

Efficiency, defined as the total area required for maximum protection of gorgonians (cf. conservation effort; Schlacher et al. 2010), is illustrated for the Lyme Bay and Hatton Bank models in Figure 6.15. Mirroring the relative performance of the models, it is the HHRM that is the most efficient, followed by the HLRM and HMRM on Hatton Bank and the high resolution model that is more efficient than the low resolution model in Lyme Bay. The Lyme Bay high resolution model is almost three times as efficient as the low resolution model with a total above-threshold area of 177 km^2. In addition 92% pink sea fans records were included in this above threshold area whereas only 83% were included in the above threshold area of the low resolution model, and at a spatial cost of 552.8 km^2. In other words, the highest resolution model includes a higher percentage of gorgonians at lower spatial cost. Cost efficiency in a conservation context is an important concept because it is more likely to be defensible in areas with high competition for space (Wilson et al. 2009), where managers may have to exclude or restrict the spatial extent of certain activities and will therefore be looking for the most efficient solutions. Furthermore, where percentage targets are included as a conservation objective or management target, for example aiming to protect 25% of suitable gorgonian habitat, then these figures will be significant.

The detailed maps in Figure 6.16 also illustrate the concept of efficiency. The maps illustrate the differences in total area of predicted suitable habitat between

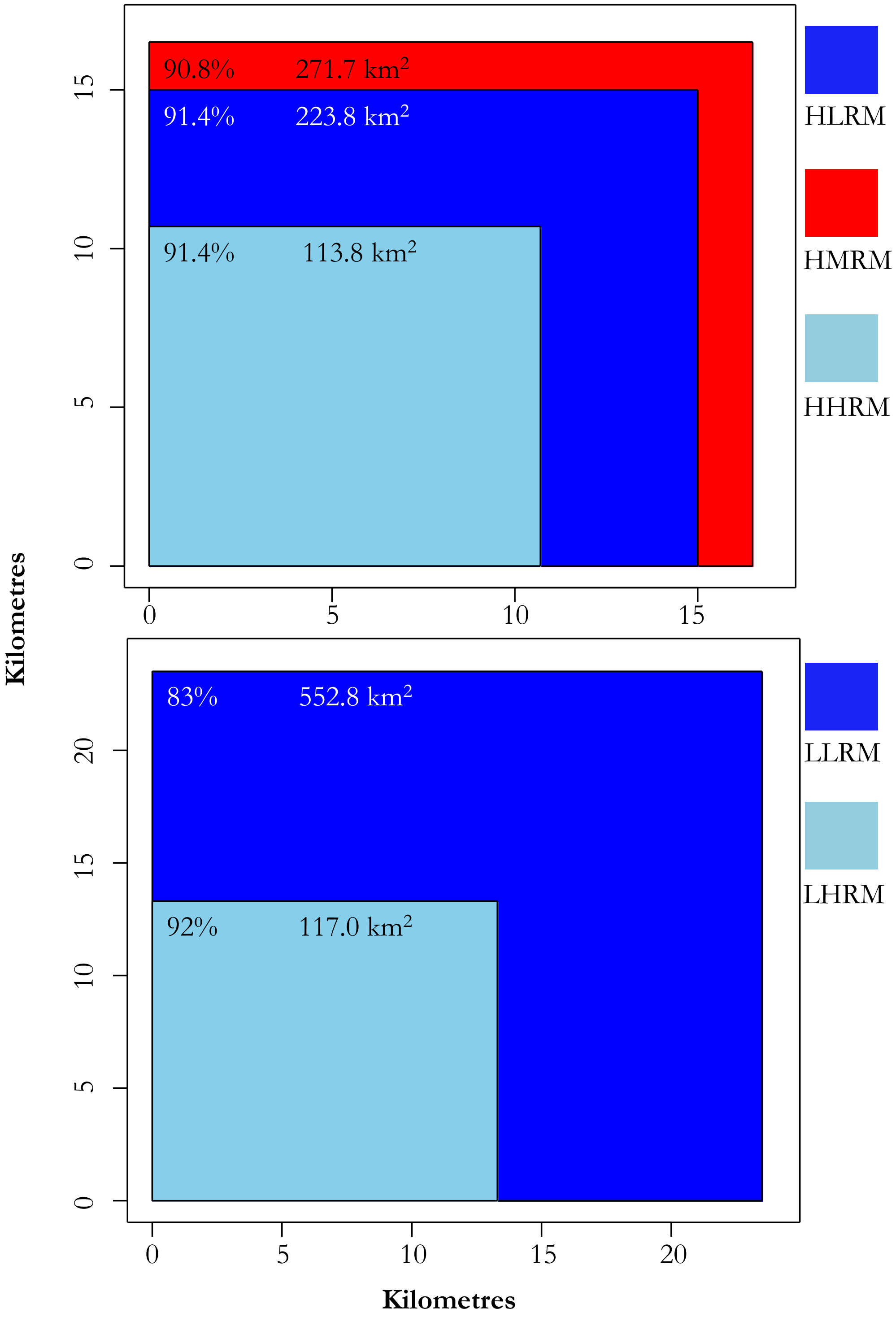


Figure 6.15: Efficiency of Hatton Bank (top) and Lyme Bay (bottom) spatial model outputs. The squares represent the total area of predicted habitat. The percentage listed in each square correspond to the gorgonian records included in the above-threshold area.

the HLRM and HHRM on a small area at the southern end of Hatton Bank where each model protected 100% of gorgonians.

The cost of survey work also warrants consideration and links back to differences in model performance as a result of resolution. The use of coarse resolution data was a criticism of an early deep-sea modelling study because of its inability to accurately resolve the true nature of the habitat (Etnoyer and Morgan 2007) so it is important that the means justify the end, especially when conflicting results have been reported with respect to resolution of data. Does the gain in model efficiency and performance justify the additional expense of collecting new higher resolution data? Muller et al. (2009), in their study on the Hazel Grouse *Bonasa bonasia*, found that although collecting high resolution field survey data took significantly longer, data derived from aerial photographs only slightly underperformed the model built with the finer data, therefore calling into question the justification for the additional expense associated with field survey data.

Given the high cost of collecting additional data offshore, and the fact that the deep sea is generally managed at a coarse scale (ICES statistical rectangle; Figure 6.17), consideration should be given to the resolution of acoustic data needed to produce predictive maps. In Lyme Bay, where spatial competition is arguably much higher and the costs of collecting data comparatively cheaper, that justification is simpler. Indeed in Lyme Bay, a new high resolution acoustic survey has recently been completed and it will be interesting to see how this influences the performance of subsequent models once the data are available.

The overall predictive power of the models in this chapter and their ability to discriminate between presence and absence records was at worst acceptable and, in some circumstances, excellent suggesting that use of any of the data resolutions would be appropriate for conservation management in data limited situations.

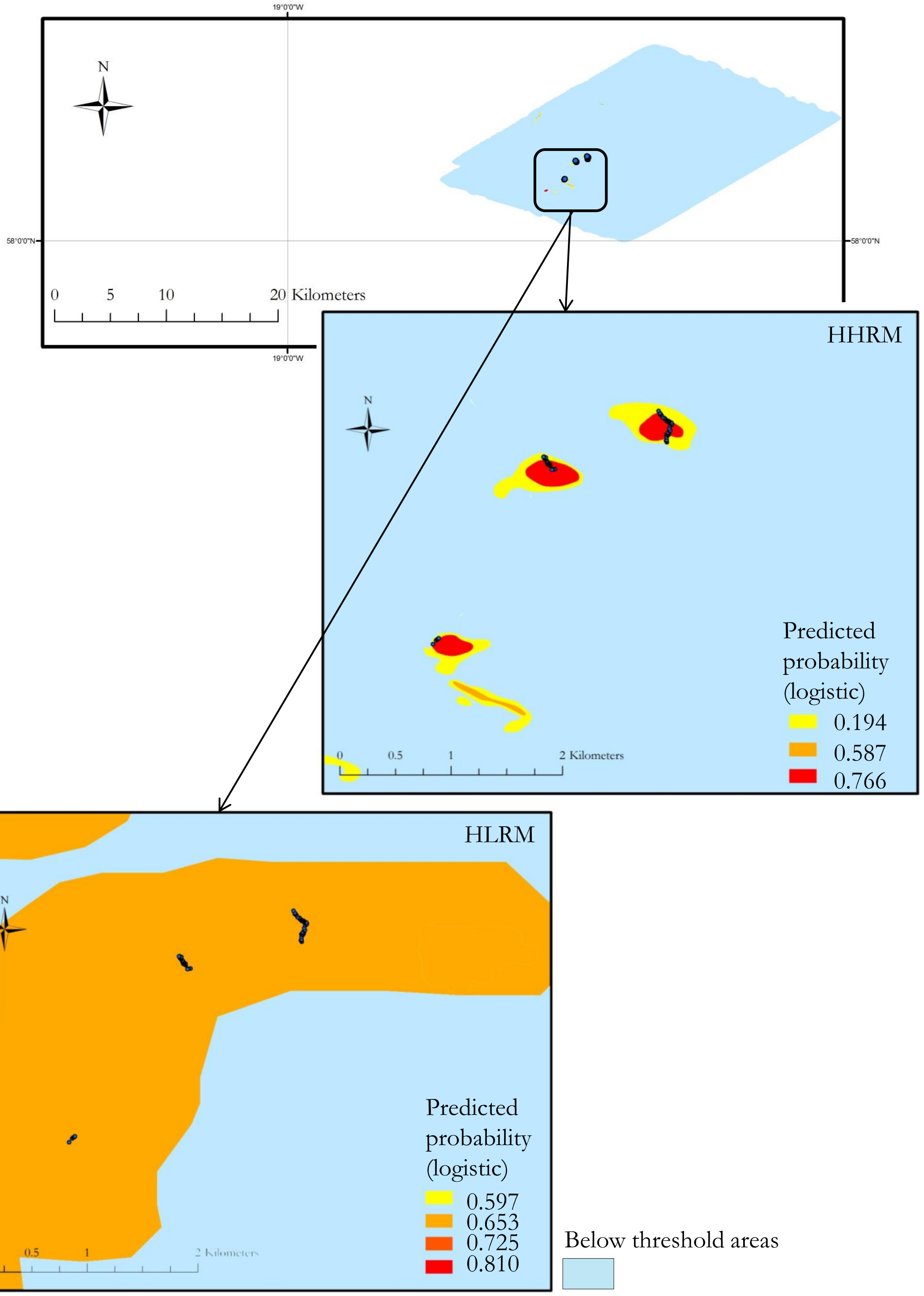


Figure 6.16: Spatial comparison of the efficiency of the HLRM and HHRM outputs for south Hatton Bank. Gorgonian records are marked by the dots. Blue areas indicate areas below the predicted probability threshold. Predicted probability values above the threshold, denoted by the warm colours, are detailed in the legend.

The lower resolution models often achieved excellent scores yet with spatially inefficient predictions. Therefore, based on the comparative performance of the models within both study areas, and when spatial efficiency was also considered, it was the high resolution models that consistently performed best. In addition some habitats of conservation concern, such as coral covered carbonate mounds, are small scale features that could only be detected and therefore mapped, with high resolution acoustic survey data.

It is prudent to be aware of the differences in model performance, and hence management and conservation gain, that can result from using data at different resolutions so that there is an impetus to adopt adaptive management principles. Adaptive management recommends a cyclical approach to management whereby experience learned along the way can feed back into the management system so that management can improve as it evolves (Salafski et al. 2001; Day 2008). Taking this principle into consideration, managers who are using predictive model outputs such as predictive maps should update the models and predicted layers if new and improved data becomes available. This is especially true for those variables found to have a significant influence on the distribution of the target species because it may lead to increased predictive accuracy and, ultimately, gain for management through e.g. more accurately targeted survey effort and/or increased conservation gain through more accurate spatial protection measures. In other words, existing data layers allow us to move forward with species distribution modelling but it is imperative to revisit and improve the models when possible.

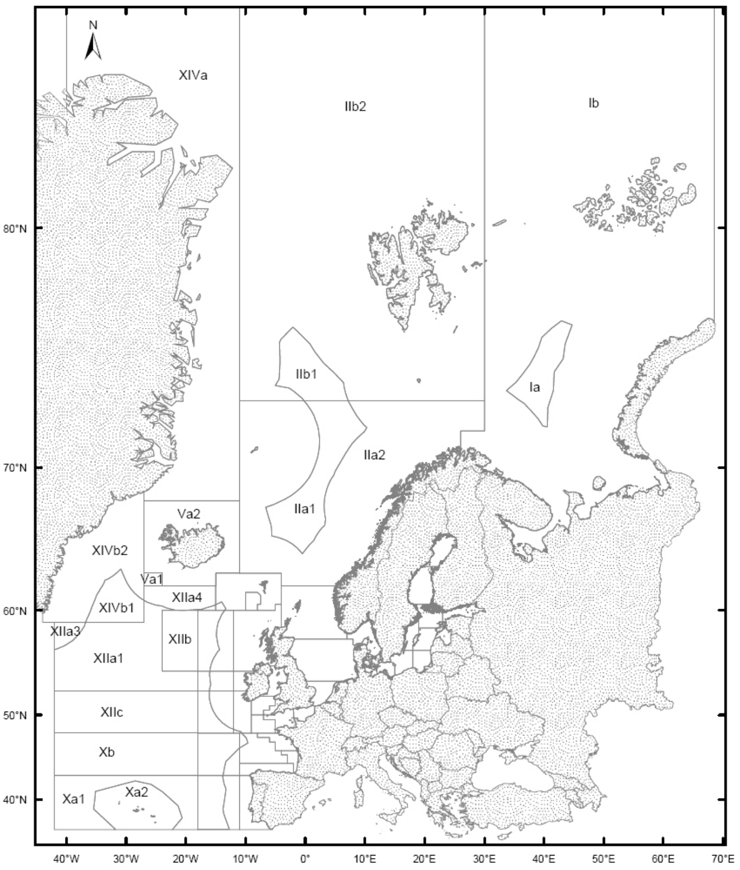


Figure 6.17: Map of ICES rectangles. Map courtesy of the Technical University of Denmark, National Institute of Aquatic Resources (DTU Aqua) from www.ices.dk

Chapter 7

Predicting outside the box; the use of proxy areas in species distribution modelling

Impending deadlines for biodiversity conservation targets and emerging policy on marine spatial planning dictate that information on the distribution of marine species and habitats is of utmost priority. The expense of survey work in the marine environment, and the vastness of open ocean areas, has meant that biological data is unavailable for many deep-sea areas. It is possible to 'transfer' the predictions made by models calibrated using data from one area onto another, providing that data for the relevant environmental predictors are available. However, the transferability of such models has received relatively little attention in the marine environment and it is not known if this provides useful results. This chapter investigates how well models built using data from one area predict the distribution of species in other areas with similar environmental characteristics, and builds upon the issue of data resolution, as discussed in the previous chapter, to determine if the resolution of environmental data used to build the model influences the model's transferability. Binomial Generalized Linear Models calibrated with Hatton Bank data for each of the three levels of environmental data resolution were transferred to George Bligh Bank. Rosemary Bank was an additional test site for the low resolution model. Based *on a suite of performance indicators, none of the models transferred well and, in the majority of cases, achieved a much lower score for each of the performance indicators than in the area the model was calibrated. The medium resolution model transferred best overall (with respect to performance indicators), in direct contrast to its performance in the previous chapter. However, the transferred models still provided useful information about the test sites and their potential contribution to management is discussed.*

7.1 Model transferability

Most species distribution modelling studies predict the location of suitable habitat within and around the distribution records used to build the models (Randin et al. 2006; Zanini et al. 2009). Put simply, the spatial habitat models fill in spatial knowledge gaps in a particular area. Less common is the application of models to new areas outside that of model calibration (Graf et al. 2006; Strauss and Biedermann 2007; Olivier and Wotherspoon 2008; Sundblad et al. 2009). The potential for models to be used in this way has positive implications for several facets of marine environmental management including guiding future survey effort, identifying areas that are potentially vulnerable to the establishment of invasive species and investigating how populations might respond to climate change.

The transferability or ‘transposition’ (synonymously referred to as ‘generalisability’ or ‘generality’ in the literature) of models refers to their ability to be calibrated in one context and successfully applied in another (Phillips 2008). Or in other words, a transfer from the area on which the model was based to a new but related environment. Despite the obvious potential benefit of models with high levels of generality in the marine environment, this subject has received little attention, especially in deep-sea areas where survey work is, comparatively, much more expensive. Yet because the deep ocean is less variable than shallower water areas over larger spatial scales the ability to transfer models would be particularly useful and seems likely to be applicable. Recent searches for generality studies of species distribution models in the marine environment revealed only a handful of examples (e.g. Jensen et al. (2005); Pittman et al. (2007)), none of which were in deep-water areas. The research in this chapter is therefore not only novel but crucial in determining the potential for the wider applicability of deep-sea models.

Transferability studies can broadly be split into those studies assessing *temporal* transferability (Jensen et al. 2005), that is, using a model calibrated with data from one time period to predict the presence or abundance of the species in another, and those assessing *geographical* or *spatial* transferability (Graf et al. 2006; Randin et al. 2006; Pittman et al. 2007; Olivier and Wotherspoon 2008; Bamford et al. 2009). Studies addressing both temporal and spatial transferability (Strauss and Biedermann 2007; Sundblad et al. 2009) appear to be less common.

One of the challenges in transferring models from one time or space is that response curves generated from the calibration data are frequently “incomplete descriptions of the responses of species to environmental predictors” (Thuiller et al. 2004). Hence, this realised niche is a truncated picture of the potential species range and this restriction will be passed onto the new data which may well extend beyond this range. Using data from different regions to calibrate the model is one way to improve transferability and combat the fact that dominant landscape features from certain areas can stunt the potential transferability of models between areas (Graf et al. 2006; Bamford et al. 2009).

Scale has also been implicated in differences in predictive performance with respect to generality. A study on snow petrel (*Pagodroma nivea*) nests in East Antarctica reported that the predictive performance of models calibrated with habitat scale data generalized better than those fitted with nest-scale characteristics (Olivier and Wotherspoon 2008). After demonstrating the significant influence of environmental data resolution on model performance in the previous chapter a logical progression is to investigate its influence on model generality.

This chapter therefore aims to answer two questions:
(1) How well do models calibrated in a discrete area of the deep Northeast Atlantic (Hatton Bank) transpose into other geographically independent areas?
(2) Is model transferability influenced by the resolution of environmental data used in model calibration? In other words, are models based on fine resolution data better able to predict species distribution in other areas or is coarser resolution data a better approximation to other environments?

The final Hatton Bank models for the three different resolution data sets from the previous chapter have been used to investigate the influence of scale on transferability.

7.2 Methods

7.2.1 Calibration site

Hatton Bank was selected as the calibration site (the site from which data is used to fit the models) due to the high number of transects and associated distribution records available on the Bank and also due to the availability of three different resolutions of environmental data, as discussed in the previous chapter. The Hatton Bank low, medium and high resolution habitat models are respectively referred to as the HLRM, HMRM and HHRM.

7.2.2 Test sites

Notwithstanding data availability, the main requirement for a suitable test site was that the environmental data should be within a similar range to that of the calibration site. Predicting outside the range of environmental data that the model was calibrated in (known as ‘extrapolation’) has not been investigated in this study, one of the main reasons for which is the significance of categorical variables in the final models, which are not suitable for extrapolation in the same way that continuous variables are.

Rosemary Bank and George Bligh Bank (Figures 7.1 and 7.2), the *test sites*, were selected based on the above criteria. Both sites are east of Hatton Bank. Based on the shortest distance between distribution records at each of the sites, the Hatton Bank site was 38 km and 253 km from the George Bligh and Rosemary Bank test sites respectively. George Bligh and Rosemary Banks are 162 km apart.

The following summary information about the test sites is taken entirely from Jacobs (2006). Survey work undertaken during Strategic Environmental Assessment 7 (offshore areas to the west of Scotland) revealed that both test sites have interesting geomorphological features including iceberg plough marks, ridge and trough couplets and channels (George Bligh), and ridges and parasitic cones (Rosemary Bank). Both Rosemary and George Bligh are moated, the base of the deeper parts of Rosemary Bank’s moat lying at over 2300 m depth. The summit of Hatton, George Bligh and Rosemary Banks lie at around 500 m water depth but some of the parasitic cones on Rosemary rise up to exceed the average summit depth by more than 150 m. See Jacobs (2006) for a comprehensive description of geomorphological features at the test sites and at several other areas in and around the Rockall Trough.

As a result of the incomplete coverage of high and medium resolution data (Table 7.1) in the Northeast Atlantic, only the George Bligh Bank was suitable to test the transferability of all three resolution models whereas Rosemary Bank was only a test site for the HLRM.

Although some transferability studies have calibrated models at two or more sites and then tested the successful application of the models on each of the other sites, this was not possible in this study due to lack of available data. For example, only a small number of records were available at the test sites, especially in comparison with the Hatton site, meaning that building a new model was not appropriate. Indeed, exploratory modelling with the low resolution data at one test site (based on a sample size of 24) revealed no significant predictors based on GAMs fitted to each of the environmental predictors.

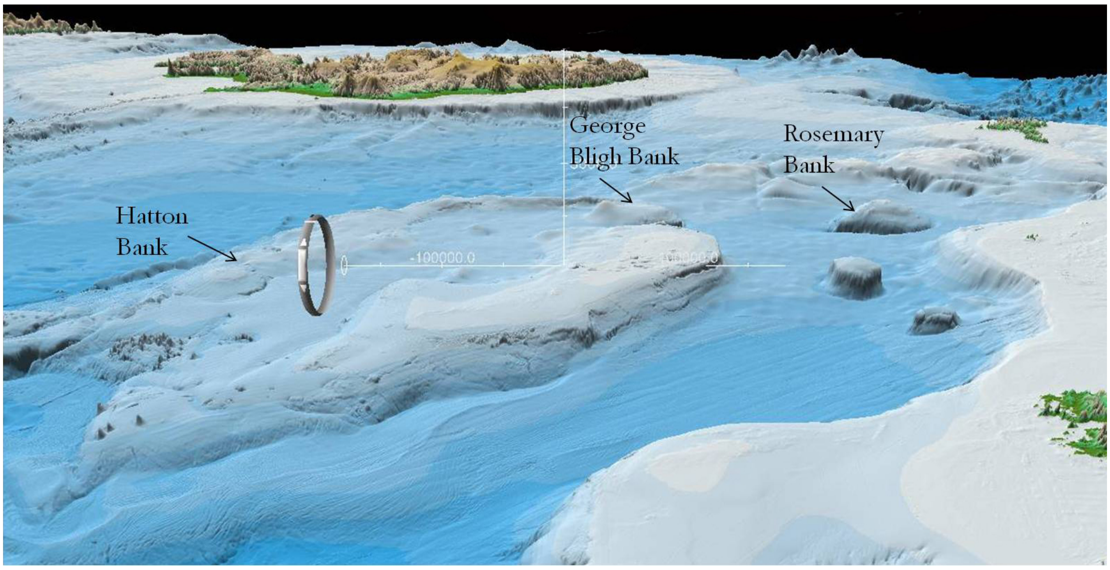


Figure 7.1: Three dimensional view of Hatton Bank, George Bligh Bank and Rosemary Bank and their location in relation to the UK continental shelf.

Having two test sites (George Bligh Bank and Rosemary Bank) for the low resolution data meant that it was possible to build new models with the Hatton data plus one of the test sites (referred to as ‘combination’ models from hereafter) and test the transferability on the remaining test site in order to investigate whether fitting models with data from more than one region improved the predictive performance in others, as suggested by Bamford et al. (2009) and Graf et al. (2006).

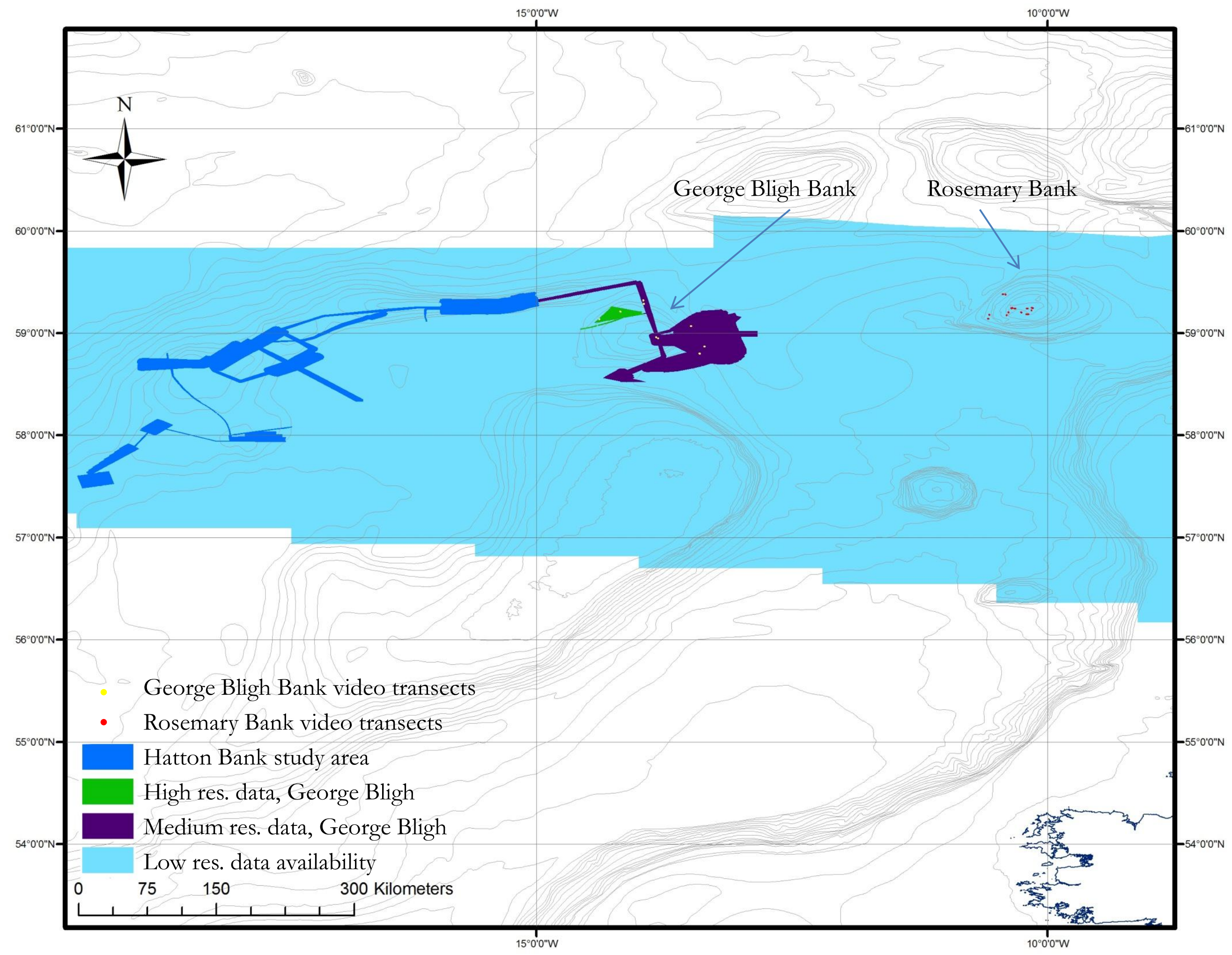


Figure 7.2: Spatial availability of various resolution environmental data across Hatton Bank, George Bligh Bank and Rosemary Bank. The location of video transects on the test sites are also illustrated.

To achieve this, models were constructed following the methodology outlined in Chapter 4.

The two combination models were as follows:

(1) a combined Hatton / George Bligh model, tested on Rosemary Bank, and

(2) a combined Hatton / Rosemary model, tested on George Bligh Bank.

No variables were found to be significant in the Hatton Bank / George Bligh Bank combination model and this model has not been developed any further.

Table 7.1: Availability of various resolution environmental data across Hatton, George Bligh and Rosemary Banks.

Data resolution	**Availability of specified resolution environmental data in study area**		
	Hatton Bank	George Bligh Bank	Rosemary Bank
25-50m (high resolution) acoustic data	✓	✓	
200m (medium resolution) acoustic data	✓	✓	
Mixed (low resolution) composite layer	✓	✓	✓

7.2.3 Data preparation

Environmental layers for the test sites were intersected as previously done for Hatton Bank (Chapter 4). To reduce variability in performance assessment, the video transect data from the test sites were also reduced to one presence or absence record per intersect polygon. The intersect polygon's attribute table was exported from ArcGIS and added as 'new data' into R. Predictions onto the new data were made from each of the three different resolution models. Model predictions were mapped in ArcGIS and compared to transect derived presence-absence data in the test areas.

Unpredictable effects may arise as a result of extrapolation (Thuiller et al 2004) and several new ‘levels’ (categories within a categorical variable) were found in the low resolution model test sites including muddy sand and sandy mud from the substratum variable. For that reason, predictions have only been made in areas within the range of calibration data, setting other probabilities to zero (Thuiller et al. 2004; Guisan and Thuiller 2005; Gray et al. 2008). As a result, some of the available transect data at the test sites were not used.

7.2.4 Appraisal of transferability

Randin et al. (2006) stipulated three conditions that had to be met for a model to be considered transferable. Firstly, internal validation in each region has to be comparable. Secondly, a model fitted with data from one region must have a comparable performance when projected into a new region and lastly, spatial predictions on the training data and test data have to match within both regions. Due to the small number of records in each of the test sites (<56), new models have not been built for the test sites and as such it was only possible to assess the second of these criteria; comparable performance. In other words, predictions in the test sites must achieve similar scores for each of the performance indicators.

The same performance indicators have been used as for previous data chapters, namely a combination of threshold-dependent (sensitivity, specificity and CCR) and threshold-independent (AUC) metrics. Threshold independent metrics are commonly recommended with some studies using these exclusively (Thuiller et al. 2004; Jensen et al. 2005; Strauss and Biedermann 2007; Bamford et al. 2009). However on face value AUC scores can appear to be comparable, even in cases where the type of prediction error can vary considerably so it is important to look at the shape of the Receiver Operating Characteristic (ROC) curves in addition to the area underneath them (Pearce and Ferrier 2000).

For example, comparable AUC scores were produced for two different algorithms in an assessment of transferability of North American bird models, yet Maxent was highly specific and the Genetic Algorithm for Rule-set Prediction model (GARP) was highly sensitive (Peterson et al. 2007). In other words, the 'success' of the transferred models was arguably different, depending on the purpose of the transfer, yet the comparable AUC scores gave the impression that the models performed equally well. See Figure 7.3 as an example.

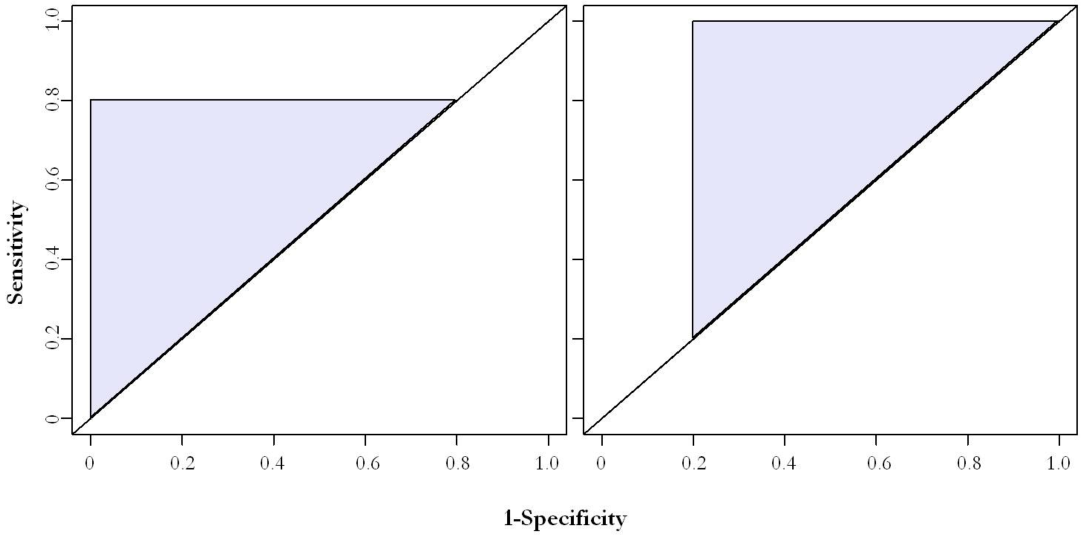


Figure 7.3: Receiver Operating Characteristic (ROC) plots illustrating how two plots with different shaped curves and, hence, different prediction errors, can have identical scores for the area under the curve (AUC, shaded).

The use of a training data derived (TDD, Table 7.2) threshold, as used in previous chapters, may be unsuitable when assessing model transferability to a new area because nothing is known (as far as the model is concerned) about the species' prevalence (Fielding and Bell 1997; Strauss and Biedermann 2007).

Strauss and Biedermann (2007) proposed a different method of threshold definition for assessing model transfer which uses the prevalence at the test site (%) to define the percentage of top predicted probabilities as presence. For example, a species found in one quarter of surveyed plots at the test site would result in 25% of surveyed plots with the top predicted probabilities defined as presence. However, the application of their method appears to be slightly counterintuitive because if knowledge already exists about the presence or absence of a species at the test site, as is required by this method, then there is less need to transfer model predictions into this area when simply building a new model might provide a more accurate output.

Table 7.2: Overview of George Bligh Bank and Rosemary Bank test site parameters. Number of transects refers to the total number of video transects undertaken at the test site. The number in brackets refers to the number of transects for which predictions are possible and from which the performance indicators scores were calculated.

Test site details	**Calibration data**				
	HLRM	HLRM	HMRM	HHRM	HLRM + Rosemary Bank
Test site	Rosemary Bank	George Bligh Bank			George Bligh Bank
No. Transects	14 (3)	8 (5)	6	2	8 (5)
No. occupied sites	7	14	24	15	14
No. unoccupied sites	22	10	32	40	10
Test site prevalence	24%	58%	43%	15%	58%
TDD threshold	0.425	0.425	0.289	0.125	0.389
sens=spec threshold	0.625	0.155	0.535	0.115	0.355

Instead, a threshold that aims to equalise sensitivity and specificity scores (referred to as sens=spec from hereafter) was adopted using the PresenceAbsence R library (Freeman and Moisen 2008). This is an appropriate choice because the transferred model results could just as easily be used to target future survey effort as for conservation effort and therefore commission and omission errors should be equally weighted. The sens=spec method has been adopted as a secondary method of threshold definition in this chapter in the interest of comparison with the TDD threshold.

7.3 Results

7.3.1 Performance of transferred models

Table 7.3 lists the scores for each of the performance indicators for the calibration sites and test sites. Transferred models did not perform as well as the calibration site model in 28 out of 35 cases (five transfers, seven comparisons). It is to be expected that the model does better at predicting data with which it was calibrated than on independent test data, but the scores were on average 31% lower for the test data.

With regard to the Hatton Bank / Rosemary Bank combination model, the three-fold cross validation proved to be quite variable, suggesting that the model may not be robust. However, predictions were made in order to compare the performance with models built using just one calibration site.

7.3.2 Performance metrics

The threshold-dependent metrics demonstrated variability between model and threshold definition method. Correct Classification Rate (CCR) and specificity were poor for all transferred models regardless of threshold, with the exception of the HLRM George Bligh transfer which demonstrated perfect specificity using the TDD threshold.

Based on sensitivity, the TDD method resulted in better scores than the sens=spec threshold in two out of five cases (with two tied scores). Specificity, in contrast, was better using sens=spec (again with two tied scores). However, where the sens=spec score was higher than the TDD score, the sens=spec score was still unacceptable. Where the TDD score was higher, the score was outstanding (>0.9).

Regardless of threshold definition method, the transferred models achieved a higher sensitivity score than specificity score in all but two cases. Average sensitivity scores based on the TDD method were 0.654, compared to 0.501 for sens=spec. The average specificity score for TDD was also higher than sens=spec, at 0.451 and 0.426 respectively.

The combination model transferred better to George Bligh than the HLRM in six out of seven scores, despite the generally low scores the combination model obtained based on its own observed data.

Scores for the sole threshold independent metric (AUC) were all lower than the calibration site scores, with the exception of the combined Hatton/Rosemary model. This model and the medium resolution transfer achieved AUC scores of >0.7.

The ROC curves in Figure 7.4 illustrate the varying performance among the different gorgonian distribution models. Plots *a*, *b* and *c* have a greater area under the curve than any of the remaining plots, as is confirmed by the AUC scores in Table 7.3. The shapes of these three curves is also similar, suggesting that neither one of the three different resolution models is performing especially differently with regard to sensitivity versus specificity at different thresholds.

Table 7.3: Comparative performance of calibration site and test site (transferred model) performance based on threshold-dependent and independent performance indicators. The results based on the TDD and sens=spec methods are presented for comparison. ↑ ↓ arrows indicate improvement / deterioration of score following transfer.

Model	**AUC**	**TDD threshold**			**sens=spec threshold**		
		CCR	SENS	SPEC	CCR	SENS	SPEC
Hatton (high res.)	0.901	0.826	0.829	0.825	0.826	0.829	0.825
	↓	↓	↓	↓	↓	↓	↓
Hatton (high res.)→ George Bligh Bank	0.453	0.291	0.533	0.200	0.291	0.533	0.200
Hatton (medium res.)	0.785	0.735	0.780	0.717	0.730	0.746	0.724
	↓	↓	↑	↓	↓	↑	↓
Hatton (medium res.)→ George Bligh Bank	0.729	0.643	0.958	0.406	0.696	0.750	0.656
Hatton (low res.)	0.820	0.775	0.765	0.783	0.775	0.765	0.783
	↓	↓	↓	↑	↓	↓	↓
Hatton (low res.)→ George Bligh Bank	0.500	0.385	0.111	1.000	0.462	0.556	0.250
Hatton (low res.)	0.820	0.775	0.765	0.783	0.775	0.765	0.783
	↓	↓	↑	↓	↓	↓	↓
Hatton (low res.)→ Rosemary Bank	0.400	0.500	1.000	0.400	0.333	0.000	0.400
Hatton / Rosemary combined model	0.647	0.584	0.793	0.451	0.611	0.569	0.637
	↑	↓	↓	↓	↑	↑	↓
Hatton / Rosemary combined model→ George Bligh Bank	0.771	0.538	0.667	0.250	0.647	0.667	0.625

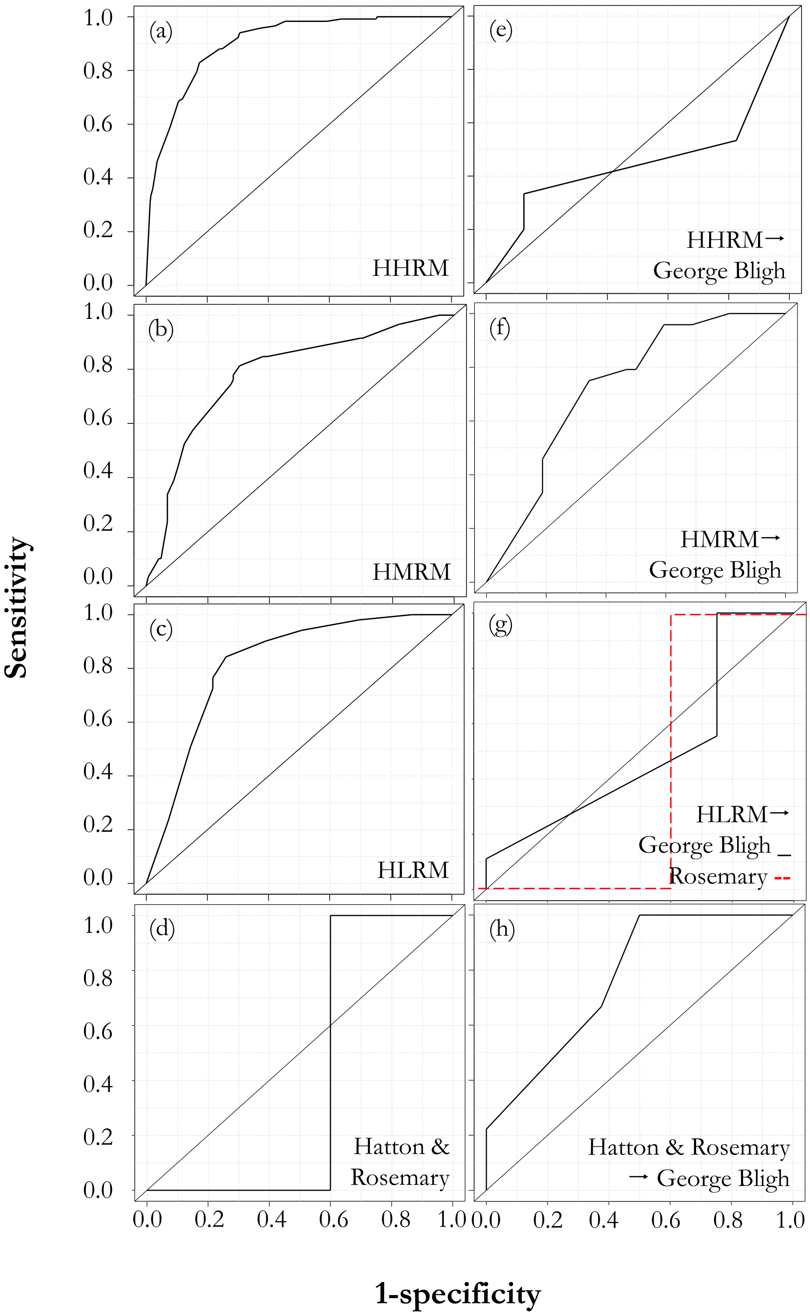


Figure 7.4: Receiver Operating Characteristic (ROC) plots for the Hatton Bank gorgonian distribution models and Rosemary and George Bligh Bank test site models. The 45° line starting at the origin represents chance performance and an area under the curve (AUC) score of 0.5. Plots *a*, *b* and *c* are ROC plots based on the high, medium and low resolution model calibration data respectively. Plot *d* illustrates the performance of the combined Hatton Bank and Rosemary Bank model. Plots *e* - *h* illustrate how performance changes when predictions are transposed onto another area.

Of the test site ROC plots, the medium resolution transfer (*f*) shows the greatest similarity to its parent plot. The medium resolution transfer also had the highest range of prediction values at the test site (n=12) which was at least three times higher than any of the other test sites based on both single and combined calibration site models.

Three of the plots in Figure 7.4 show deviation below the line of chance performance (0.5) suggesting very low predictive ability. Looking at the HHRM → George Bligh Bank ROC plot (*e*), for example, it is evident that above thresholds of 0.4, with the exception of a threshold of 1 which would assign all plots presence and therefore risk maximum false negativity, hardly any gain in sensitivity is observed whilst the number of false positives increases. The HLRM → Rosemary Bank ROC plot (*g*, dashed line) illustrates a highly dichotomised performance, with no true positives observed until a threshold of almost 0.6 is set.

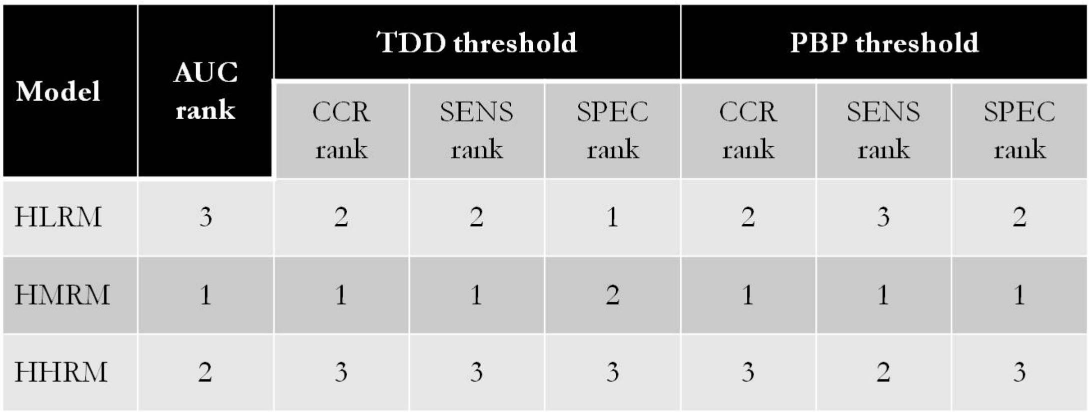
7.3.3 Influence of data resolution

A ranking system was used as a simple way of illustrating how data resolution influenced the performance of the transferred gorgonian distribution models (Table 7.4). Based purely on the single calibration site models, and where the scores for the two low resolution test sites were averaged, the medium resolution model achieved the highest score in six out of seven cases. The low resolution model ranked second overall and the high resolution model ranked the lowest, displaying the lowest scores in five out of seven cases.

7.3.4 Spatial outputs

The following series of maps represent the spatial outputs from this transferability study (Figures 7.5, 7.7 and 7.9). Substrata maps for the George Bligh and Rosemary study sites are also included (Figures 7.6, 7.8 and 7.9) to illustrate

Table 7.4: Ranking of threshold dependent and threshold independent performance indicators based on the three different data resolution models. The ranked performance for the HLRM is based on its average performance at the Rosemary and George Bligh Bank test sites. Rank 1 indicates the best performance. There were no ties in the ranking.



Model	**AUC rank**	**TDD threshold**			**PBP threshold**		
		CCR rank	SENS rank	SPEC rank	CCR rank	SENS rank	SPEC rank
HLRM	3	2	2	1	2	3	2
HMRM	1	1	1	2	1	1	1
HHRM	2	3	3	3	3	2	3

how the predictions of gorgonian distribution are linked to substratum; the most influential variable for all three calibration models.

A visual comparison between Figures 7.5 and 7.6, 7.7 and 7.8, and the two maps in 7.9 highlights several 'blank' areas in which predictions were not made as a result of the environmental variables lying outside the range of the training data.

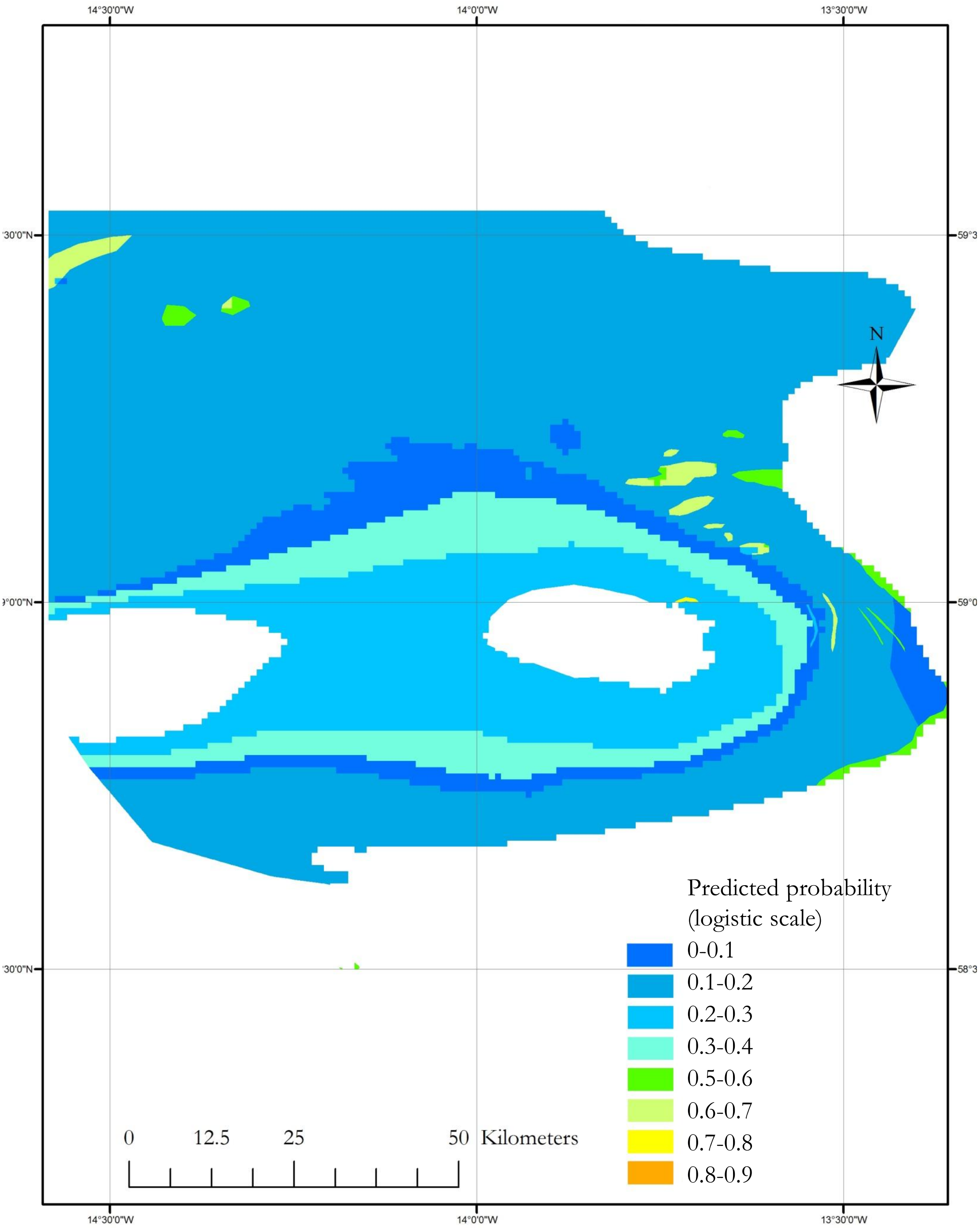


Figure 7.5: Spatial predictions of gorgonian distribution for the George Bligh Bank test site based on the transferred low resolution Hatton Bank model, containing categorical depth and substratum predictors. 'Blank' areas indicate areas in which the depth and/or substratum data were outside the range of the training data and in which predictions have not been made.

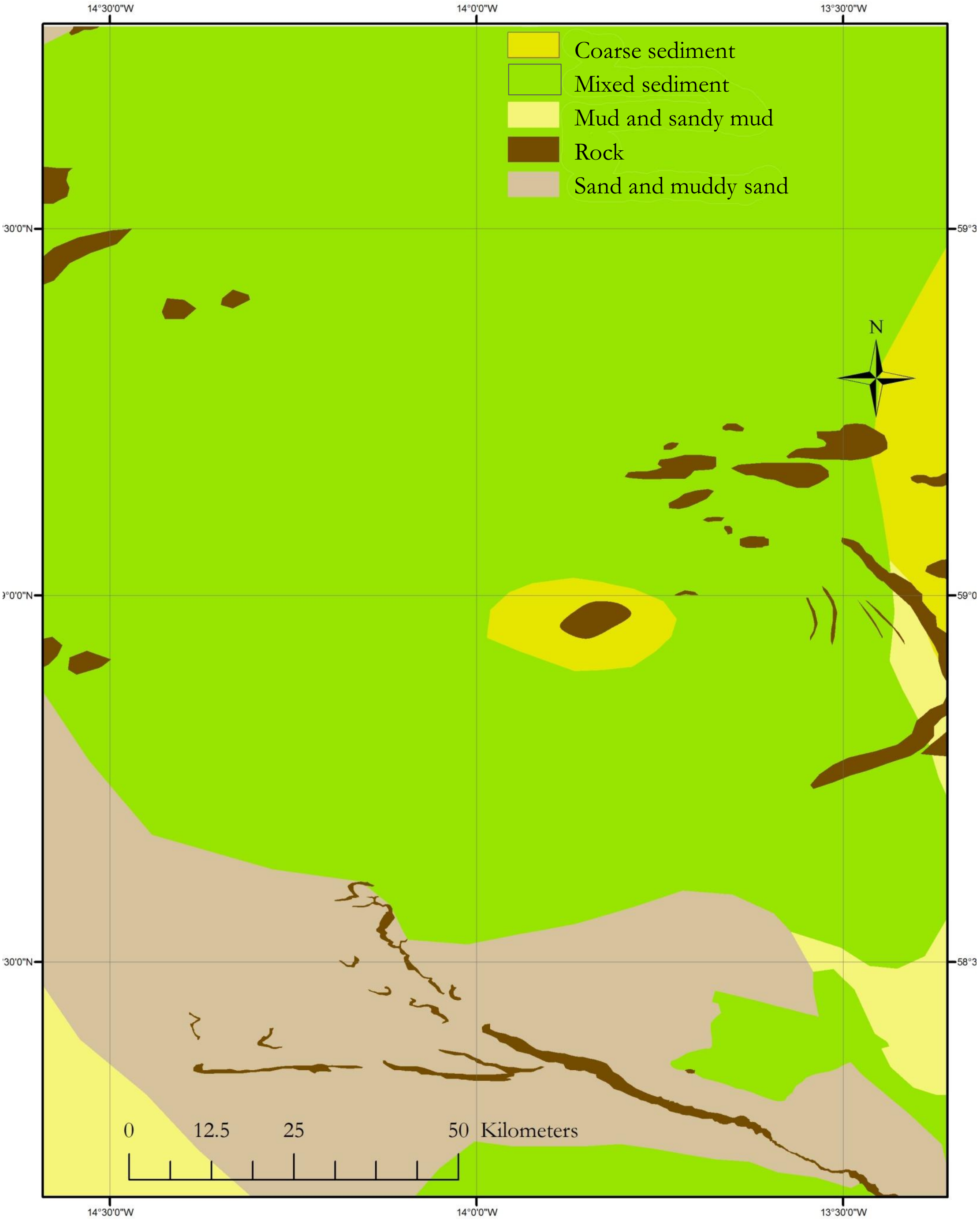


Figure 7.6: Low resolution substratum layer for George Bligh Bank test site.

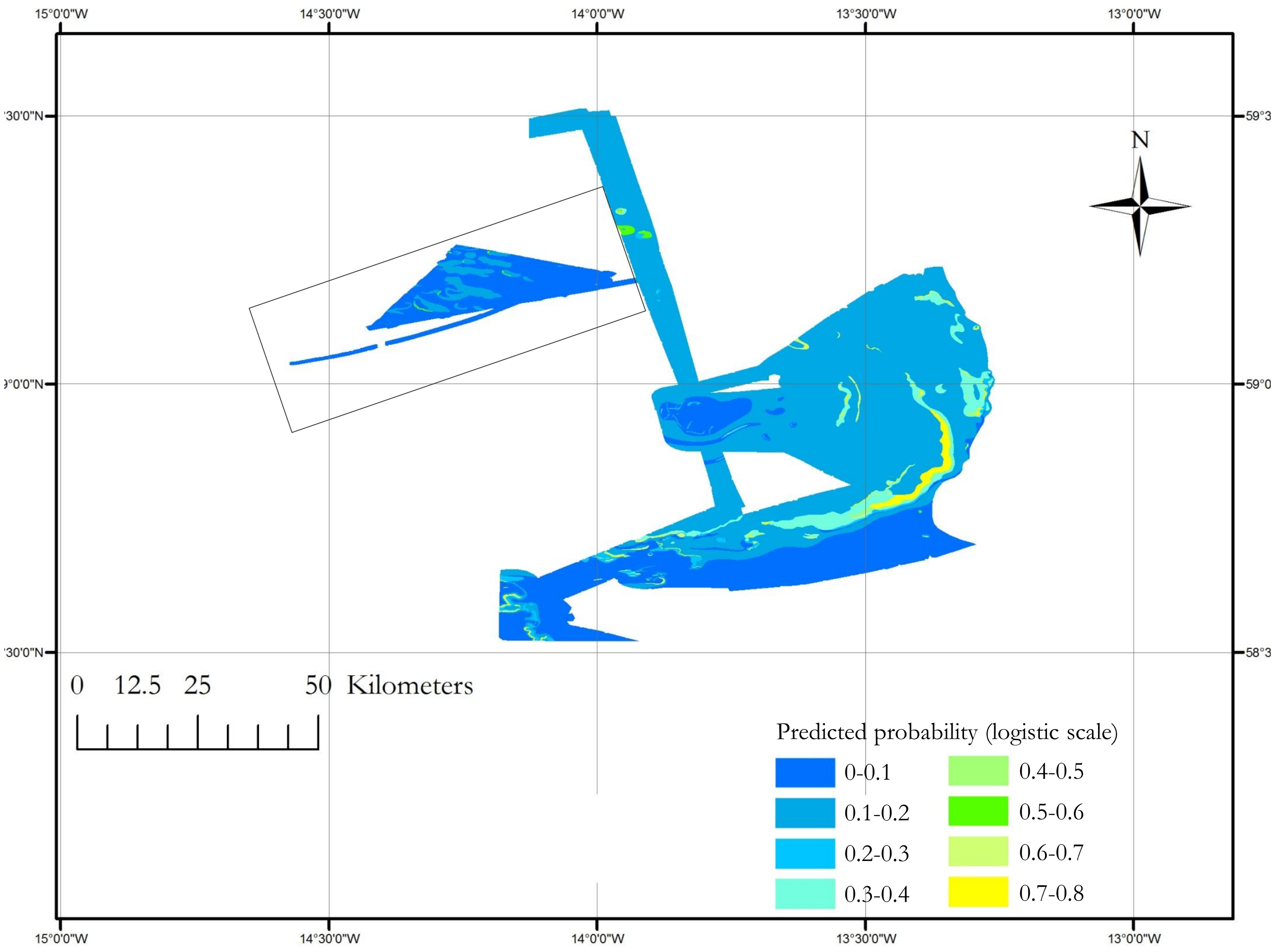


Figure 7.7: Spatial predictions of gorgonian distribution for the George Bligh Bank test site based on the transferred medium and high (boxed) resolution Hatton Bank models, containing categorical substratum and geomorphology, and substratum and depth predictors respectively.

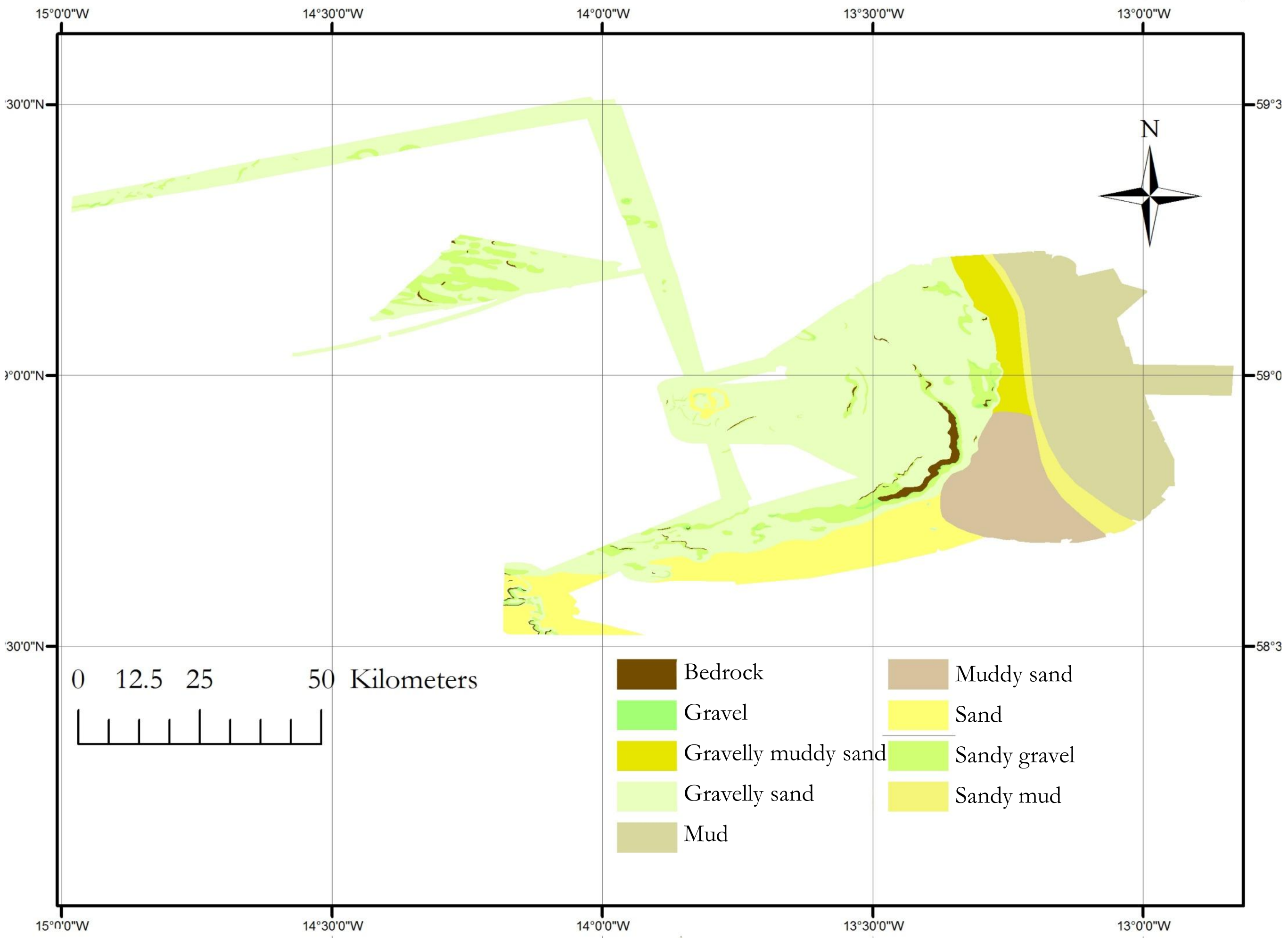


Figure 7.8: Combined medium and high resolution substratum layer for George Bligh Bank test site.

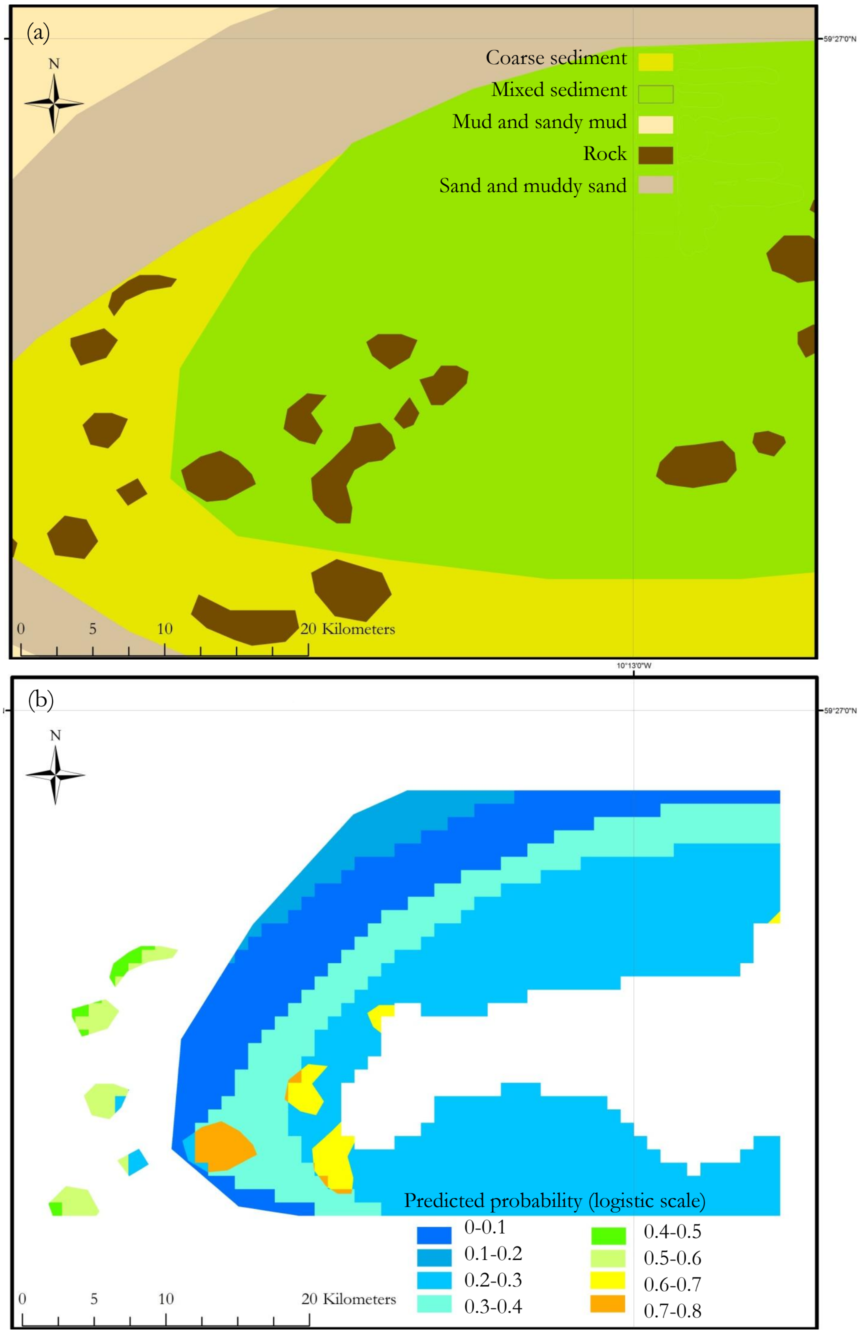


Figure 7.9: (a) Low resolution substratum layer for the Rosemary Bank test site and (b) spatial predictions of gorgonian distribution based on the transferred low resolution Hatton Bank model, containing substratum and depth predictors. 'Blank' areas indicate areas in which the depth and/or substratum data were outside the range of the training data and in which predictions have not been made.

7.4 Discussion

7.4.1 Performance of transferred models

Many reasons exist for differences in model performance with regard to the transferability of models in space and time, and a wide variation in observed performance has been reported including success, failure, asymmetric performance between sites and test site results outperforming calibration site predictions (Randin et al. 2006; Strauss and Biedermann 2007; Olivier and Wotherspoon 2008). Transferring models for eurytopic species, that is, those species that are able to withstand a wide range of environmental conditions, may be less successful than those species exhibiting a strong relationship with their habitat (Brotons et al. 2004; Strauss and Biedermann 2007). The influence of environmental variables on species distribution can vary across and between regions thus influencing a model's potential transferability to a different area (Randin et al. 2006; Zanini et al. 2009). In addition, the use of direct versus indirect variables (Guisan and Zimmerman 2000) may affect the predictive performance of a model in a different area. Models based on direct predictors should have a higher transferabilty since the influence of a direct predictor is expected to remain relatively constant over space and time (Graf et al. 2006; Randin et al. 2006; Strauss and Biedermann 2007; Gray et al. 2008; Sundblad et al. 2009). The choice of algorithm has also been cited as a reason underlying differences in transferability (Jensen et al. 2005; Randin et al. 2006).

Despite some high scores in the performance indicators for the transferred models they did not transfer well overall and only the medium resolution model transfer achieved more than one acceptable score for the performance metrics. Based on the criteria set out in the methodology, that models should have comparable scores based on observed calibration site and test site data, it is apparent that model transfer was unsuccessful in all cases when the full suite of performance indicators is considered. Other studies have reported similar poor levels of transferability. Based on the criteria Randin et al. (2006) proposed for transferability, more than half of the transferred models in their study failed. Variable transferability performance was reported by Bamford et al. (2009) who added that 'models of species distribution are not transferable between regions'.

However, the results in this chapter compare poorly with several transferability studies, such as Jensen et al. (2005) whose temporal model transfers had an overall average AUC score of at least 0.7. Graf et al. (2006) reported AUC scores of 0.9 or above for transferred models in their study and Strauss and Biedermann (2007) found that the majority of models successfully transfered in time and space, achieving performances significantly better than those one would expect by chance. A study on Caribbean reef fish reported overall accuracies of between 67.6-70.5% for predictions into new areas with AUC values exceeding 0.9 at one of the test sites (Pittman et al. 2007). In assessing performance of transposed models of snow petrel nests in the Antarctic, overall performance based on sensitivity and specificity scores from several different models ranged from 0.59 to 0.91 (Olivier and Wotherspoon 2008). Sundblad et al. (2009) reported good to outstanding AUC scores (0.75-0.93) in their transposed models for fish larvae in the Baltic Sea. With considerable success in transferred models in other studies, explanation must be sought for the lack of successful transfer in this study.

One potential reason for the poor transferability is the small number of test records and transects which will have represented only a small range of the training data (Table 7.2).

A problem that may be relevant to this study in particular is that due to the fact

that the final training data models contained only categorical variables, it had the potential to limit the spatial extent of predictions. When predicting into a new area a model is faced with three possible outcomes;
(1) a category level in the training data is found in the test data, making prediction possible;
(2) a new category level is encountered in the test data that is not found in the training data making predictions impossible, and
(3) a category level contained in the training data is not located in the test site.

It is the third outcome that has the potential to influence the performance of transfered models, especially in cases where that particular level is having a highly significant influence on the species in question. In the high resolution model, for example, half of the substratum categories, including the category that had the most significant positive effect on the occurrence of gorgonians on Hatton Bank (rock with a carbonate veneer) and the category that had the most negative influence on gorgonian occurrence (sand), were not observed in the test points. This no doubt has implications for the predictive power of the model because only those categories that have a (relatively) weaker relationship with the gorgonians according to the Hatton Bank model are transferred. Test sites should ideally have the same full range of values as the training data (Strauss and Biedermann 2007) and the fact that in some cases the test sites in this study did not has undoubtedly influenced model performance.

Spatial differences in environmental parameters not included in these models may also go some way toward explaining the poor transferability. Both test sites show evidence of strong current influence (Jacobs 2006) and it may be that Hatton Bank experiences a different current regime, which could influence the provision of food and the settlement of larvae, for example, and ultimately influence habitat suitability. Slope orientation (aspect), which may serve as a very general proxy for hydrodynamic processes e.g. local currents (Dolan et al. 2008) and which has also been shown to influence the distribution of deep-sea corals (Guinan et al. 2009a,b), may also be an influential factor in gorgonian distribution. If aspect was strongly correlated to one of the important modelled variables in the Hatton Bank model, for example, then the relationship of that variable to gorgonian distribution might not transfer as well to the test site if aspect had a different influence at the test site. Equally, evidence of trawling activity on Hatton and George Bligh Banks (Jacobs 2006) might have influenced their suitability and it is possible that gorgonians might once have existed at sites which may now be physically and biologically altered.

Of course, one thing that is not included in the models are biotic interactions. As has been mentioned previously, biological interactions, and factors other than abiotic influence on the species distributions, are not captured by the model and this will influence the ability of the model to predict into new areas (Thuiller et al. 2004; Randin et al. 2006; Sundblad et al. 2009).

Some studies have suggested that models calibrated with data from more than one region tend to perform better than those models calibrated using just one calibration site (Graf et al. 2006; Bamford et al. 2009), and this is generally supported by the results in this chapter; the combined Hatton Bank and Rosemary Bank model obtained better scores for the AUC, CCR and sensitivity following transfer to George Bligh than the single site (Hatton Bank) low resolution transfer, regardless of threshold. However, given the variability in the cross-validation for the combination model, this result should be treated with caution.

Differences in model parameters are also relevant to the observed transfer failure. In all apart from the high resolution model transfer, the prevalence at the test site was considerably different to that at the fit site (Table 7.1) and both under- and overestimation in test areas have been reported as a result of changes in prevalence with respect to the training data (Pearce and Ferrier 2000; Strauss and Biedermann 2007).

With regards to threshold, there did not appear to be an overall ‘winner’ between the two different methods selected because although the sens=spec threshold resulted in better scores than the TDD threshold in the majority of cases (where scores were not tied), the TDD threshold led to, on average, higher average scores for sensitivity and specificity. In terms of conservation, it would be tempting to select the most sensitive method and in this respect the TDD threshold definition method achieved the best results.

Based on the mixed results obtained here it would therefore seem prudent to advocate the use of threshold independent metrics exclusively when assessing model transfer. Nevertheless, the fact that AUC scores were generally much lower for transferred models compared to the calibration model (with the exception of the medium resolution transfer and combined model transfer) suggests that it is not merely the choice of threshold that is influencing transferability success.

Yet aside from the fact the the performance indicator scores suggest unsuccessful transfer of the models, it is important to examine the spatial outputs of the transfer. As previously explained, there are few areas of very high predicted probability of gorgonian presence due to the fact that not all categorical levels were found in the test sites. Yet by examining the areas with the highest probabilities, relative to other areas in the test site, those areas are exactly the areas one might expect to be suitable gorgonian habitat; rocky slopes and escarpments, for example. So the transferred models may provide useful information with regard to the relative suitability of sites in a test area if nothing else is known about it.

7.4.2 Influence of data resolution

Tables 7.3 and 7.4 suggest that on face value the medium resolution data Hatton Bank model performed better than the other resolution model transfers but it is important to take into account the fact the medium resolution model not only had the highest number of test records available (just) but also that every geomorphology and substratum category in the training data was found in the test data whereas both the low and high resolution models were incomplete in this respect.

This is an interesting result when the results of the previous chapter are considered yet this agrees with the study by Olivier and Wotherspoon (2008) who reported that habitat-scale models transferred better than nest-scale models. Olivier and Wotherspoon (2008) cited high variability at the small (nest) scale between different areas as a reason behind the more successful transfer of coarse scale models.

In this study it is more likely that the high resolution substratum layer fails to capture the occurrence of cobbles and boulders at the fringes of bedrocks areas but upon which gorgonians are found. As with other deep-water corals such as *Lophelia pertusa* (Guinan et al. 2009a), gorgonians can often be found on solitary boulders and drop stones in soft sediment areas (Mortensen and Buhl-Mortensen 2004; Wheeler et al. 2005b). One quarter of all deep-sea gorgonians observed off Nova Scotia were found on solitary stones (Watanabe et al. 2009) highlighting the difficulty of capturing this kind of spatial distribution even with high resolution data. Randin et al. (2006) question the ability of 25m resolution data to capture processes which may have influenced the transferability of the plant models in their study. The problem of using coarse resolution substratum data to identify patterns in deep-sea gorgonian distribution has been acknowledged (Bryan and Metaxas 2006) and Figure 7.9 illustrates the inability of even high resolution substratum data to capture some substratum driven gorgonian distribution by focusing on a transect illustrating a number of ‘false negative’ gorgonian records which are outside the boundary of the rock polygon. While the medium resolution model may also be subject to this error, the coarser resolution of acoustic data will result in larger buffer zones around areas of bedrock habitat leading to the inclusion of ‘fringe’ records. Similarly the low resolution model results in greater buffers around rock areas but clearly here they are too great and lead to increased error.

Without a greater number of test sites, or at least a higher number of records within a test site, it is difficult to define the extent to which data resolution is influencing the transferability of the models in this study but it certainly appears to do so to some extent. Alternatively, substratum and geomorphology (the environmental predictors included in the Hatton medium resolution model) are a more transferable combination than substratum and depth.

7.4.3 Implications for conservation planning

Ferrier and Watson (1997) urged caution when transferring models to other areas due to potential differences in data quality and this again links back to the availability of high resolution environmental data, especially for predictors such as substratum which appear to be indispensable for deep-sea gorgonian models. As it happens, the high resolution data model in this chapter was outperformed by both the medium (200m) and low (mixed) resolution data. The implication of this in terms of conservation management is that it may be inappropriate to transfer models built with high resolution data in deep-sea areas, for conservation planning, future survey targeting, or other purpose. Whilst the medium and combination low resolution model transfers demonstrated encouraging performance (based on the AUC and, for the medium resolution model, sensitivity), until it

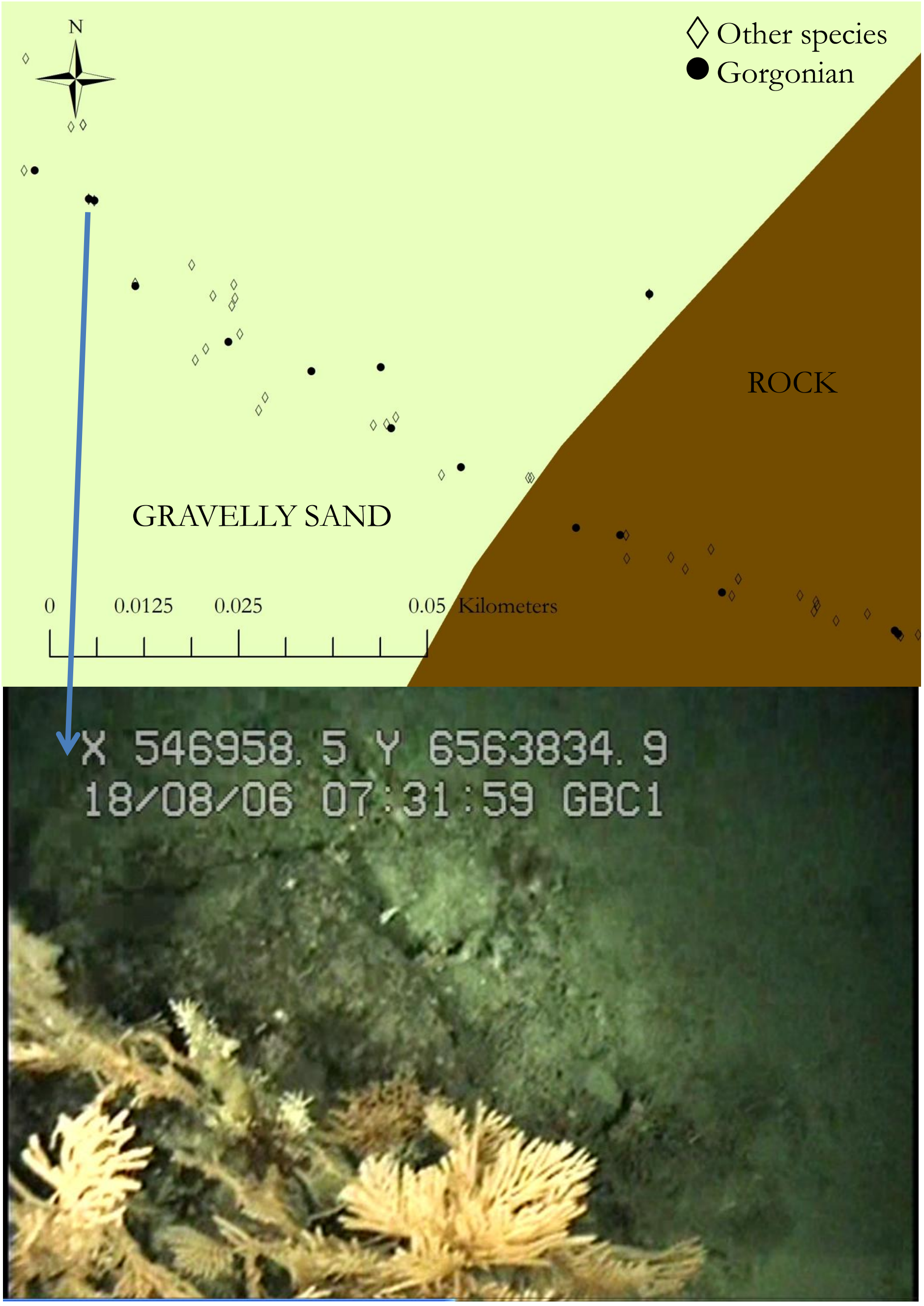


Figure 7.10: Video still from a George Bligh transect and the corresponding substratum layer and transect map highlighting the presence of gorgonians and other species. The screen shot from the video transect shows that one such gorgonian is in fact on a large drop stone (surrounded by a bed of gravelly sand). Small scale detail such as this is almost impossible to incorporate into even fine scale acoustic data such as this and explains some of the model error for transferred models.

is possible to build a wider collection of calibration and test sites to facilitate multi-directional model testing and with much higher sample sizes, model transfers should only be performed with extreme caution and only in an exploratory capacity. For example, they may be used to highlight areas of relative habitat suitability to inform future survey. Once again, the principle of adaptive management should be applied, and new data added to the models as and when it becomes available to try and improve transferability.

However these results are only based on the application of one modelling method in one or two other areas and using one group of species. As more distribution data becomes available for other areas in the Northeast Atlantic it will be possible to test the transferability on larger sample sizes and with a wider range of different species of conservation concern. This may serve to increase the confidence in the use of these models not only in deep-sea environments but to support conservation planning elsewhere.

Chapter 8

A comparison of performance between modelling approaches

The development of presence-only modelling techniques over recent years, including the Ecological Niche Factor Analysis (ENFA) and Maximum Entropy (Maxent), has led to numerous comparisons between presence only modelling methods and models requiring absence data, through the use of pseudo-absences. Maxent is proving extremely popular, both as a result of its excellent performance compared to other algorithms and ease of use. This chapter takes a novel approach and builds Maxent models using presence and *absence data and compares its performance to that of a Generalized Linear Model, using Hatton Bank as the study site. Two Maxent models were built; one in which all of the environmental variables were used, and one using only those environmental variables included in the final GLM (substratum and geomorphology). Though differences in the relative importance of the explanatory variables exist, the spatial predictions of the three models are very similar. Despite being applied as a pseudo presence-absence model, the Maxent model built with all the variables significantly outperforms the GLM based on the AUC. However, the relative performance of the models based on threshold-specific indicators is dependent on threshold choice, although the GLM generally outperforms the Maxent models. The superior performance of the full Maxent model compared to the reduced Maxent model suggests that Maxent may* *overfit to the data. Being a novel method, caveats and recommendations for future research are discussed.*

8.1 Presence-only and presence-absence models

A comparison of the performance of two or more modelling methods is a common focus of species distribution modelling studies and numerous examples exist of comparisons between presence-only (PO) models, those comparing PO methods with models that incorporate pseudo-absences (PsA) and comparisons between presence-absence (PA) methodologies. Where no absence data is available, PsA are sometimes generated in order to be able to use traditional PA algorithms, including regression based techniques, and to compare their performance with PO models.

Maxent (Phillips et al. 2006), an extremely popular PO model, has been cited in excess of 1500 times since its development in 2006. Maxent has performed very well in several model comparison studies (e.g. (Pearson et al. 2007; Wisz et al. 2008)) and has recently been used in the deep-sea (Tittensor et al. 2009; Clark and Tittensor 2010; Davies and Guinotte 2011; Howell et al. 2011). Deep-sea species distribution modelling studies have traditionally been presence-only (e.g. Clark et al. 2006; Bryan and Metaxas 2007; Tittensor et al. 2009) and with the exception of Woodby et al. (2009)), because absence data for the deep-sea is much less widely available. However this problem is not limited to deep-sea environments and, in fact, the majority of available distribution data is presence-only (Zaniewski et al. 2002).

Maxent has been compared with and indeed outperformed (based on AUC scores) GLMs and GAMs in studies using PsA data (Elith et al. 2006; Gibson et al. 2007; Williams et al. 2009) yet the relative performance of Maxent and a GLM/GAM using true presence-absence data does not appear to have been investigated. PA methods are advocated where PA data is available (Elith et al. 2011), yet evidence suggests that some modellers have used PO models regardless of whether or not they have absence data, reasons for which might include the apparent simplicity of certain PO methods. With this in mind, this chapter aims to compare the outputs of Maxent and a GLM/GAM, using true absence data, both in terms of model accuracy and the spatial distribution of predictions. The high resolution environmental data for Hatton Bank has been used for this study, following its superior performance in Chapter 6.

8.2 Methods

8.2.1 Model units

In order to ensure a fairer comparison of the two models, the intersect method outlined in Chapter 4 was not used to create the models units for the GLM/GAMs. Maxent requires that the data layers are presented in ASCII format with each environmental data layer having equally sized cells that are exactly aligned between layers and covering the same spatial extent. As previously mentioned, the intersect approach would have resulted in different sized and shaped units being used for the GLM/GAM, yet it was important to ensure that the same number of presence records were being used in Maxent and the GLM/GAM (Hirzel et al. 2001) and, crucially, that these records were sampling the same combination of variables at each point.

8.2.2 Gorgonian distribution records

For the GLM/GAMs the gorgonian distribution point data was used to sample the raster layers, whilst once again reducing the transects to one record per cell (n=459; 70 presence records, 389 absence records). Using the same presence data in the models ensures that absence is the only varying factor (Zaniewski et al. 2002). The presence-only data set has been created simply by extracting the presence records from the overall transect derived presence-absence data.

8.2.3 Environmental variables

The majority of available high resolution acoustic data for Hatton Bank is gridded at 25m but a section toward the north of the Bank is gridded at 50m. It is generally considered better practice to work to the coarsest resolution when preparing data for inclusion in SDMs and so the entire high resolution bathymetry coverage for Hatton Bank was regridded to 50m. This was also necessary because some of the derived layers, e.g. BPI, are calculated with reference to neighbouring cells and using coarse data at a finer scale would have been inappropriate.

The models were presented with the same (high resolution) environmental data layers as Chapter 6 with the addition of Bathymetric Position Index (BPI), rugosity, slope and aspect. These layers, derived from the multibeam bathymetry, were created in ArcGIS using spatial analysis and the Benthic Terrain Model (BTM). These terrain features provide added value to the bathymetry layer and a more holistic representation of the benthic environment influencing the distribution of benthos, and have been shown to be relevant to deep-sea coral distribution (Wilson et al. 2007; Dolan et al. 2008; Woodby et al. 2009; Howell et al. 2011).

Combined with slope, the orientation (including aspect), curvature and relative position (including BPI), and terrain variability (including rugosity) of the sea floor represent the four classes of bathymetric terrain analysis that can contribute valuable information to predictive modelling (Wilson et al. 2007).

Slope, as has been discussed in earlier chapters, is sometimes used as a proxy for increased current and differences in substratum and, subsequently, in the characterisation of different communities (Mohn and Beckmann 2002; Mortensen and Buhl-Mortensen 2005; Bryan and Metaxas 2007; Wilson et al. 2007; Guinan et al. 2009a,b). *Aspect* simply refers to the orientation of the dominant slope across the cell surface, which is relevant to the exposure of a face if, for example, the prevailing current or wave exposure is from a particular direction. The *BPI* provides an indication of the relative position of a cell, with respect to surrounding cells, which may be positive or negative. Both fine and broad scale BPI were calculated (accepting default settings in the BTM), the latter referencing a wider neighbouring area. Lastly, *rugosity* is a surface's crinkliness and is measured by the ratio of the surface area to the planar area in the areas surrounding the central cell. The more wrinkly the surface, the higher the rugosity. Flat surfaces will have a rugosity nearing 1. See Wilson et al. (2007) for details of algorithms used in terrain analysis and for further details about these features.

8.2.4 Maxent, adapted

As stated in the introduction, the published Maxent method (Phillips et al. 2006, 2009; Elith et al. 2011) has been 'tweaked' in order that absence data can contribute to the model (method, with permission, from Anna-Leenie Downie, PhD student, Finnish Environment Institute (SYKE), pers. comm. Method paper in prep.). In terms of data preparation and its presentation to Maxent, the differences between this novel approach and the 'standard' Maxent approach are small. Presence data are presented as a csv file as normal, but environmental variable values for each record are included, much like the samples with data (SWD) format outlined in the Maxent tutorial. The background samples, instead of being drawn at random from the study area (default n=10,000), are provided by the full presence-absence dataset, again with corresponding explanatory environmental variables, as a csv file. Maxent uses background data to inform the model about the relative likelihood of variables over the study area in order that they can be compared with those sites occupied by the species (Elith et al. 2011). Substituting background samples with absence records therefore enables the model to make this assessment based on observation, as opposed to randomly selected sites.

The model is then 'projected' onto the study area data layers. Given the problems outlined in the Chapter 7 regarding extrapolation and missing data, and the fact that Maxent's adoption of an unconstrained exponential probability distribution can lead to large predictions outside the calibration data range (Phillips et al. 2006), it was important to check the Multivariate Environmental Similarity Surface (MESS) plot as part of the model development (Elith et al. 2011). Simply put, the MESS plot highlights areas within the study region that fall outside the calibration data range and which could therefore result in highly irregular predictions.

Two separate Maxent models were built. The first used all the environmental variables without taking correlated variables into account, and generally reflects the approach adopted by most Maxent studies. The second used just the variables included in the final GLM.

8.2.5 Model evaluation

Model performance was evaluated based on internal resampling which has previously been described for the GLM/GAM. For Maxent, both models were rebuilt 100 times, each time using a randomly selected subset comprising two thirds of the full set of presence records. The resulting predicted values (n=100) at each of the presence (test) and absence sample points (n=412) was then used to calculate scores for the four performance indicators (AUC, CCR, sensitivity and specificity) as usual. Note that the AUC scores for the Maxent models presented here were not the ones generated automatically as part of the standard Maxent model output package. This is due to the fact that the automated Maxent AUC scores use background samples in place of absence data, and therefore the maximum obtainable AUC score in unknown, in comparison to when using true absence data when the maximum score is 1 (Phillips et al. 2006). To ensure a fairer comparison with the GLM AUC scores, the Maxent predictions were exported and the AUC scores calculated in R using true absence data.

Performance indicator scores based on Cramer's prevalence threshold definition and the threshold where specificity equals sensitivity were calculated. The addition of the specificity=sensitivity threshold to the model evaluation in this chapter is because Maxent is being used as a pseudo PA model so that, even though it is using absence data as the background, the probability distribution is still based on presence data only and therefore the ratio of presence to absence records is potentially less relevant to model assessment.

8.3 Results

8.3.1 Significant variables

Based on the Hatton Bank GAMs, significant variables (in order of increasing UBRE score) were substratum, geomorphology, BPI (fine scale), BPI (broad scale), aspect, rugosity, slope and depth. Fine and broad scale BPI were, unsurprisingly, highly correlated, as were slope and rugosity. The best and therefore final model (a GLM) contained substratum and geomorphology. The relative importance of significant variables according to the GAMs is not entirely in agreement with the full Maxent model in which depth and rugosity were more important than BPI. Based on the jackknife plot (Figure 8.1), the order of importance of variables according to Maxent was, starting at the top, substratum, geomorphology, depth, rugosity, BPI (fine and broad scale BPI made a similar contribution), aspect and slope.

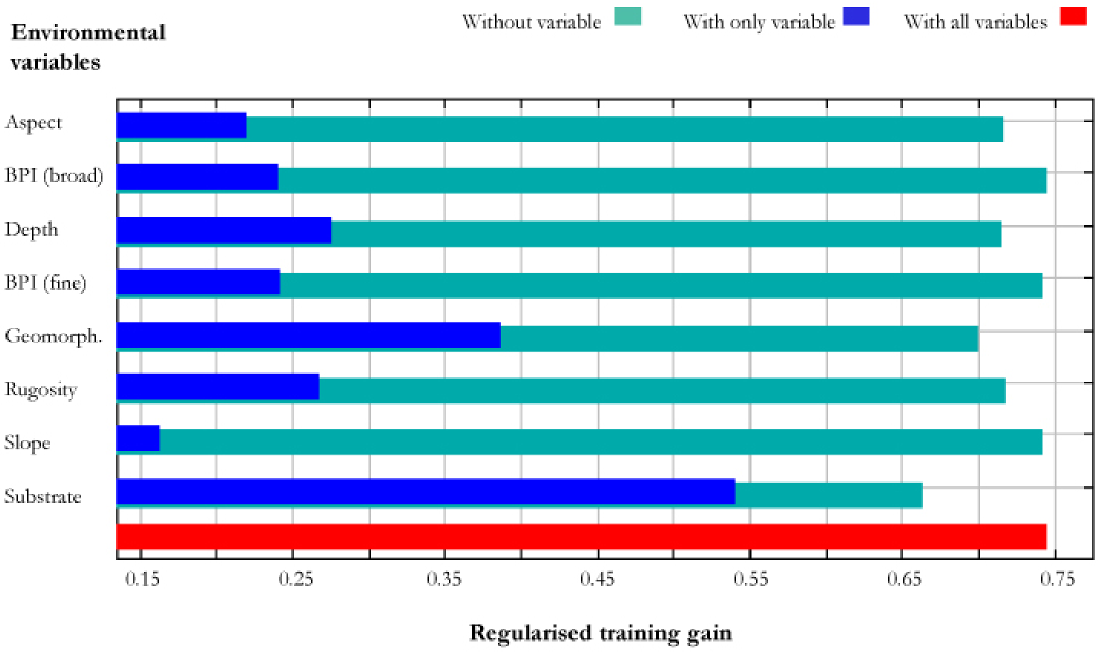


Figure 8.1: Jackknife of regularised training gain illustrating the relative importance of the different environmental predictors and the effect on model gain of the removal of each variable from the Maxent model for gorgonians on Hatton Bank.

With respect to the new variables used for the Hatton Bank models in this chapter, probability of gorgonian occurrence appeared to increase with BPI, rugosity and slope to a certain extent.

There were notable differences between the GAMs and Maxent with respect to the shape of the response curves for some variables. For example, the Maxent plot in Figure 8.2 suggests that probability of gorgonian occurrence increases both in bathymetric depressions and on topographic highs, with the latter being a more suitable habitat. The GAM agrees with this to a certain extent. Based on the area of the curve with the narrowest 95% confidence limits in the GAM plot, Figure

8.2 indicates that probability of occurrence increases almost linearly with fine scale BPI. However, there were few observation below BPI values of -5 and above +10, indicated by the 'rug' along the x axis, hence the wide confidence limits. Although it looks as though probability increases below BPI values of -4, only three out of the 22 observations below -4 were presence records. Gorgonians are therefore unlikely to be found in bathymetric depressions, a result also supported by the results of the geomorphology GLM where erosion features were associated with the lowest probabilities of gorgonian occurrence.

The GAM with aspect illustrated that north and north-easterly facing slopes were associated with the highest probability of occurrence. The Maxent plot for aspect (not shown) also supports this.

The GAM plot for rugosity (Figure 8.3) suggests a humped relationship with gorgonian occurrence, with probability of occurrence decreasing at rugosity value of 1.03 and potentially increasing again at values of $\sim$ 1.08. Once again however, there were few observations above rugosity values of $\sim$ 1.02 which meant that the confidence limits were very wide. Eight of the 22 records above 1.03 were presence records so an asymptotic relationship might be a more appropriate description, as illustrated by the Maxent plot.

An asymptotic relationship was found with regard to slope and gorgonian occurrence based on the GAM, with probability of occurrence increasing with slope up to approximately 10° above which probability hardly increased at all (although again there were much fewer observations after this point). In the Maxent model, probability of occurrence continued increasing until $\sim$27° where it finally levelled off (although there were no observations at slope above 30°).

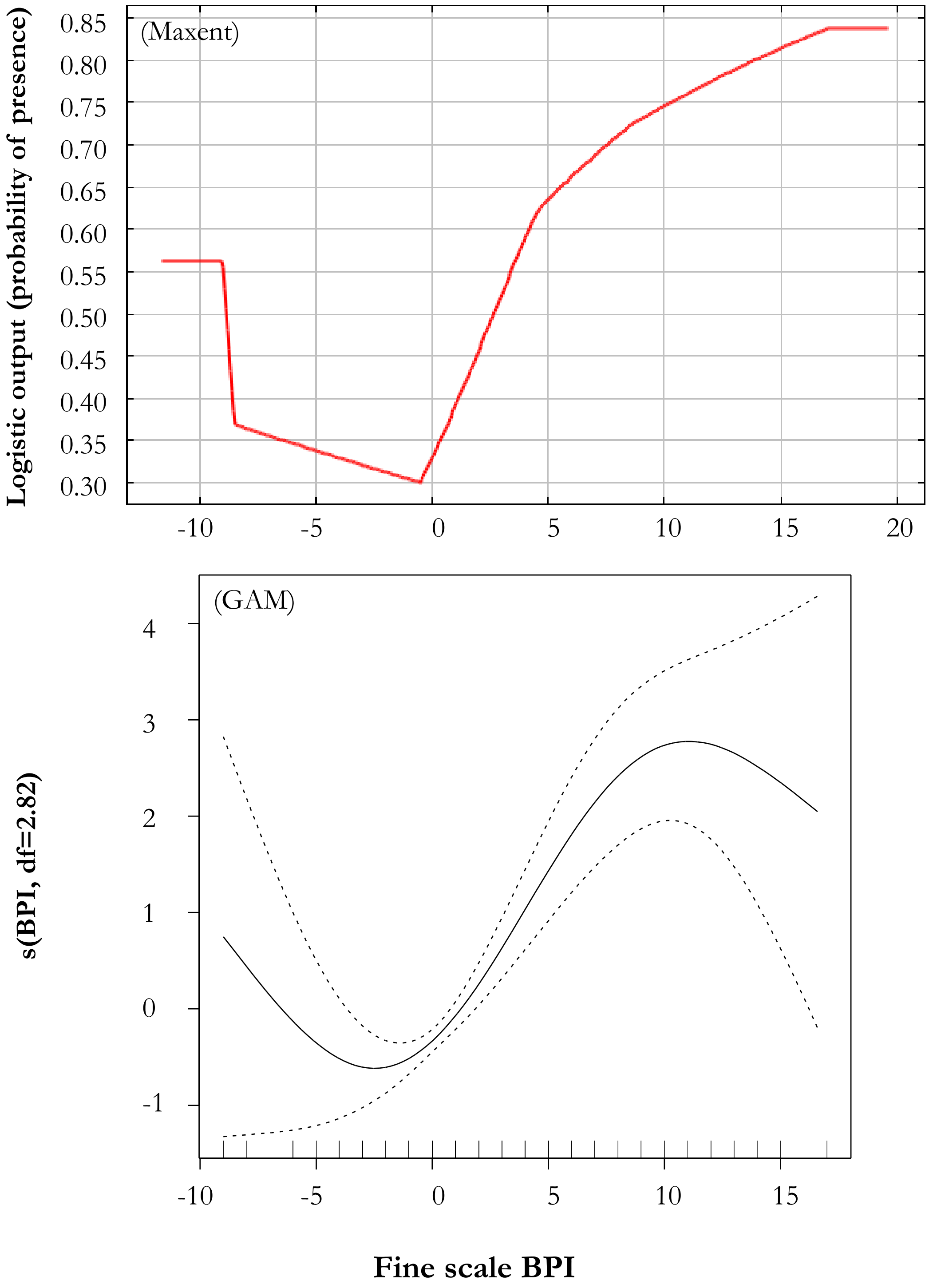


Figure 8.2: Maxent (top) and Generalized additive model (bottom) plots illustrating the positive relationship between fine scale BPI and gorgonian occurrence on the Hatton Bank. These plots are based on models containing only this variable.

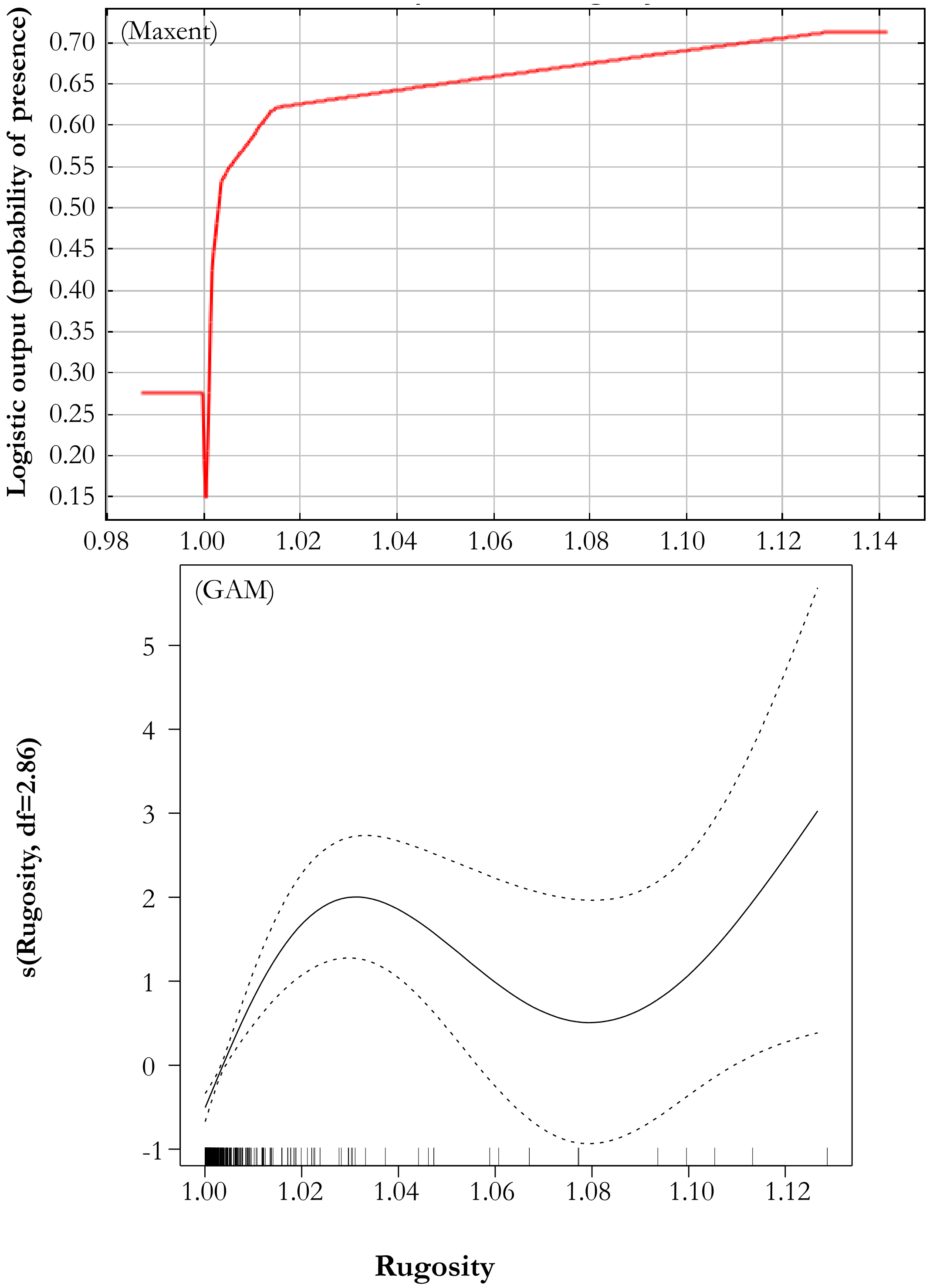


Figure 8.3: Maxent (top) and Generalized additive model (bottom) plots illustrating relationship between rugosity and gorgonian occurrence on the Hatton Bank. These plots are based on models containing only this variable.

8.3.2 Model predictions: a spatial comparison

Mapping the spatial predictions from both modelling approaches highlighted that there were smaller differences between the GLM and full Maxent predictions across a greater area than between the GLM and reduced Maxent model predictions (see Figure 8.4 as an example and Appendix E for large fold out maps of habitat suitability for gorgonians based on the three modelling approaches, and of differences between them). However, the full Maxent model had the largest maximum differences in prediction value with respect to the GLM.

The majority of differences in logistic probability predictions across Hatton Bank were small (difference in value <0.1) for both methods. These areas tended to be in areas of relatively flat seabed with a sand or gravelly sand substratum. In other words, all models were in agreement that the probability of gorgonian occurrence in these areas was very low.

For the vast majority (73% and >99%) of Hatton Bank, the GLM predicted lower probabilities than the full and reduced Maxent models respectively. This is illustrated non-spatially in Figure 8.5 which shows how the differences in predicted probability for each cell change as the full Maxent model predictions increase. It shows that there is higher agreement between the two models at lower probability values but that the difference increases slightly with Maxent predicted probability. This was not the case with the reduced Maxent model where the greatest difference between its predictions and those of the GLM, despite being <0.23, were characterised by sandy gravel which Maxent predicted as being of relatively low suitability overall but of higher suitability with respect to the GLM.

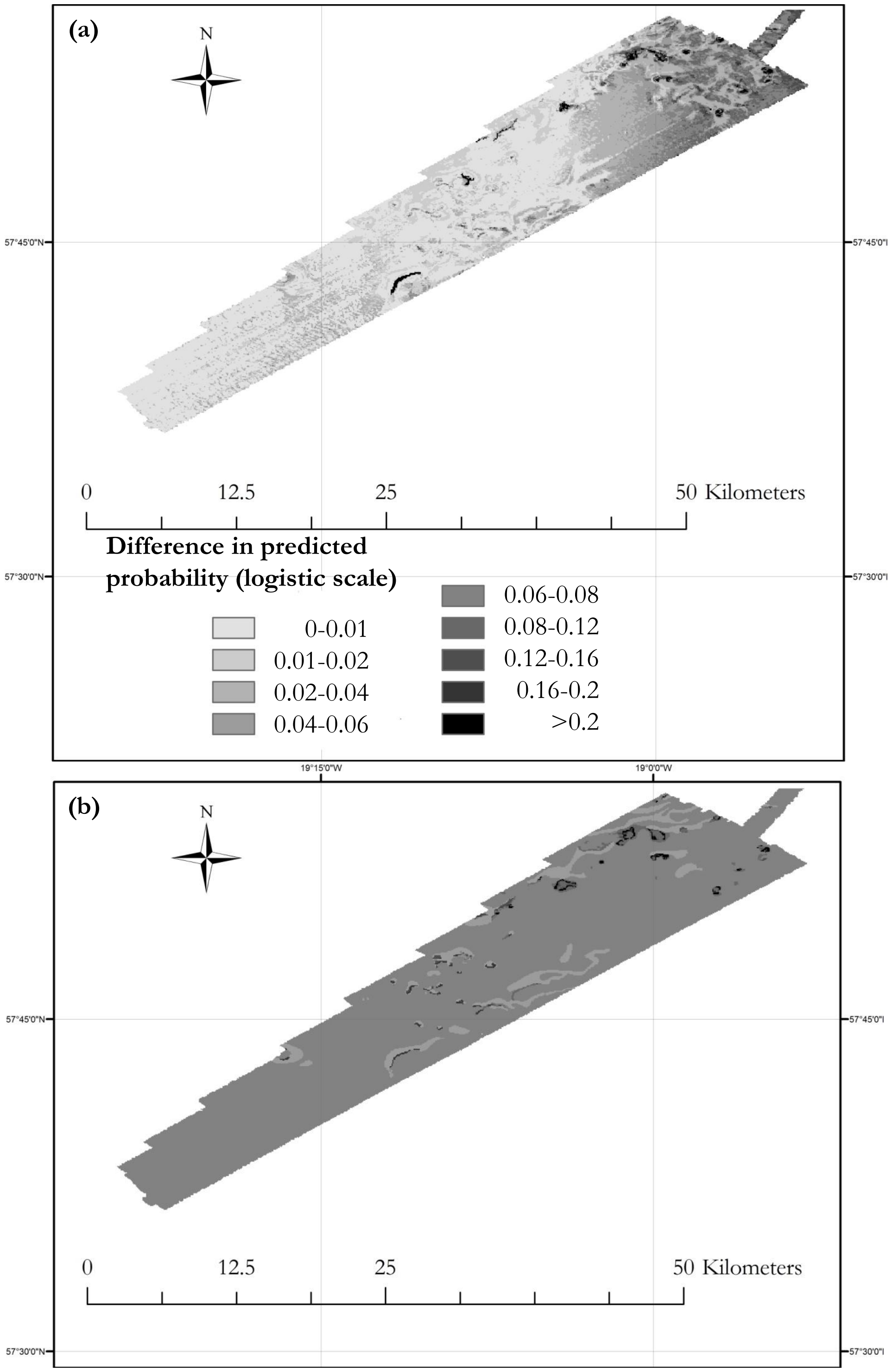


Figure 8.4: Spatial overview of differences between full Maxent and GLM predictions (a) and reduced Maxent and GLM predictions (b) on southern Hatton Bank. The key is relevant to both maps.

By studying the mapped predictions of the GLM and full Maxent model it is apparent that the small number of areas with large differences in spatial prediction are in fact areas where the GLM predicts a higher value than Maxent (Figures 8.6 and 8.7 provide an example).

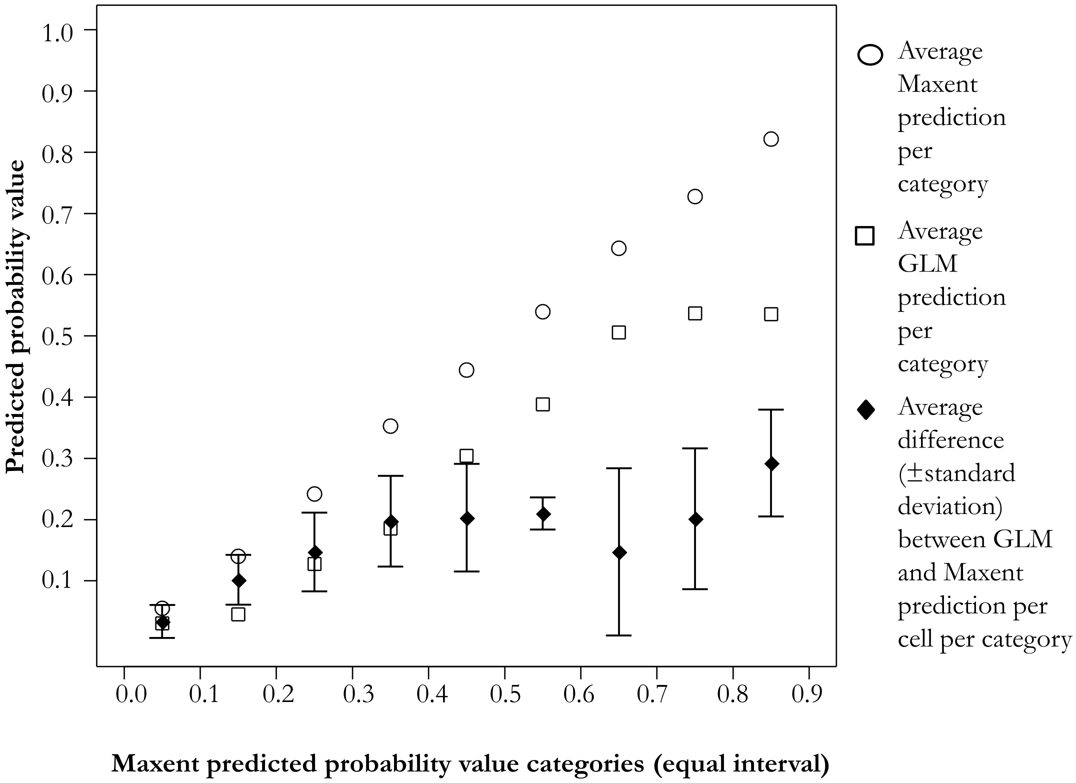


Figure 8.5: Graph illustrating the differences in model predictions per model unit (cell) on the Hatton Bank. The full Maxent model logistic probabilities have been divided into equal interval categories (x axis). For each of these categories, the average Maxent and GLM predictions have been plotted, along with the average difference (± standard deviation) between each pair of cells. The difference values do not take into account the direction of the difference, that is, which of the GLM or Maxent prediction is higher, although the overall trend is apparent from the other two points plotted in each category.

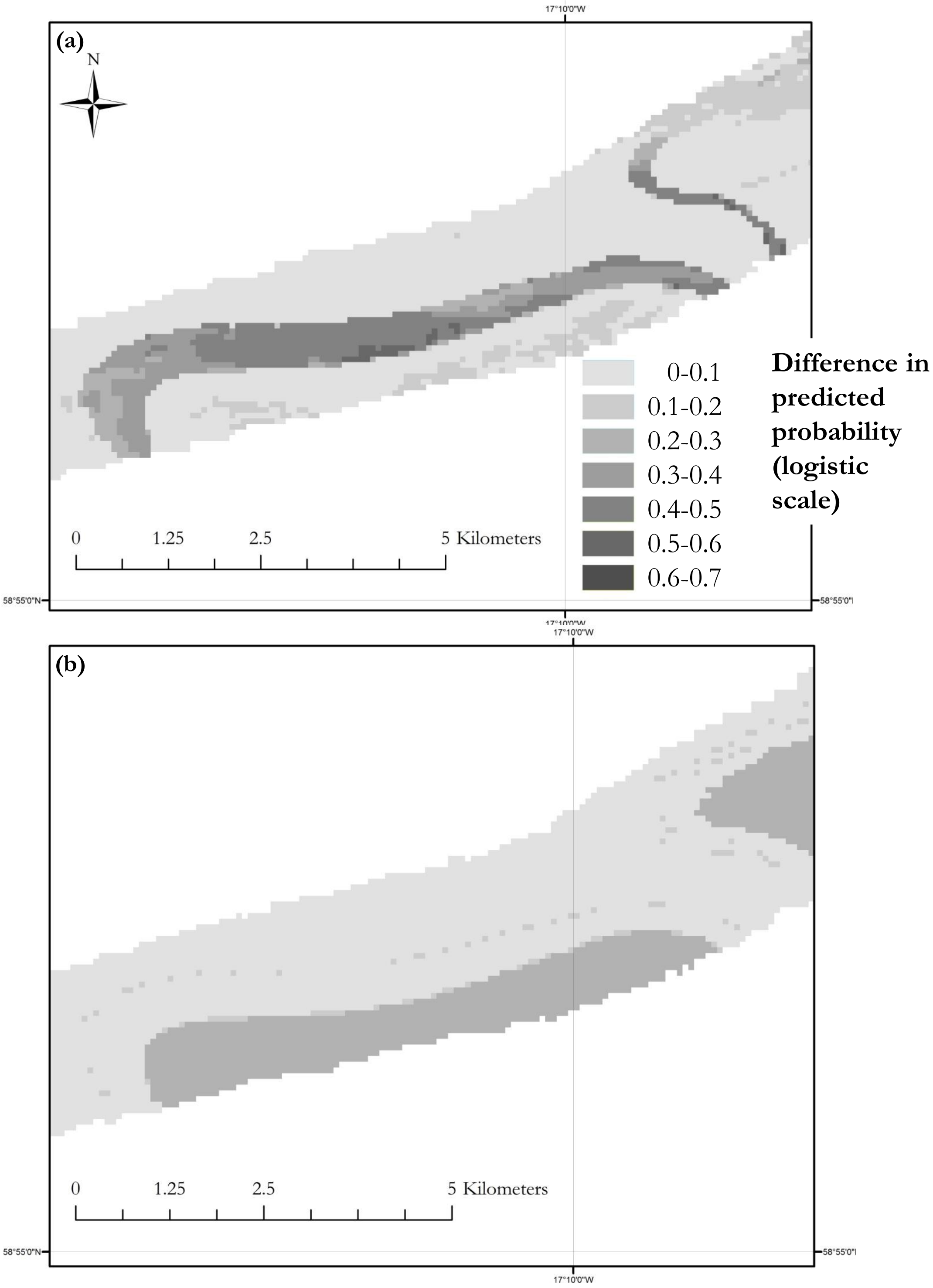


Figure 8.6: Differences between full Maxent and GLM predictions (a) and reduced Maxent and GLM predictions (b) on a small area of Hatton Bank. The key is relevant to both maps.

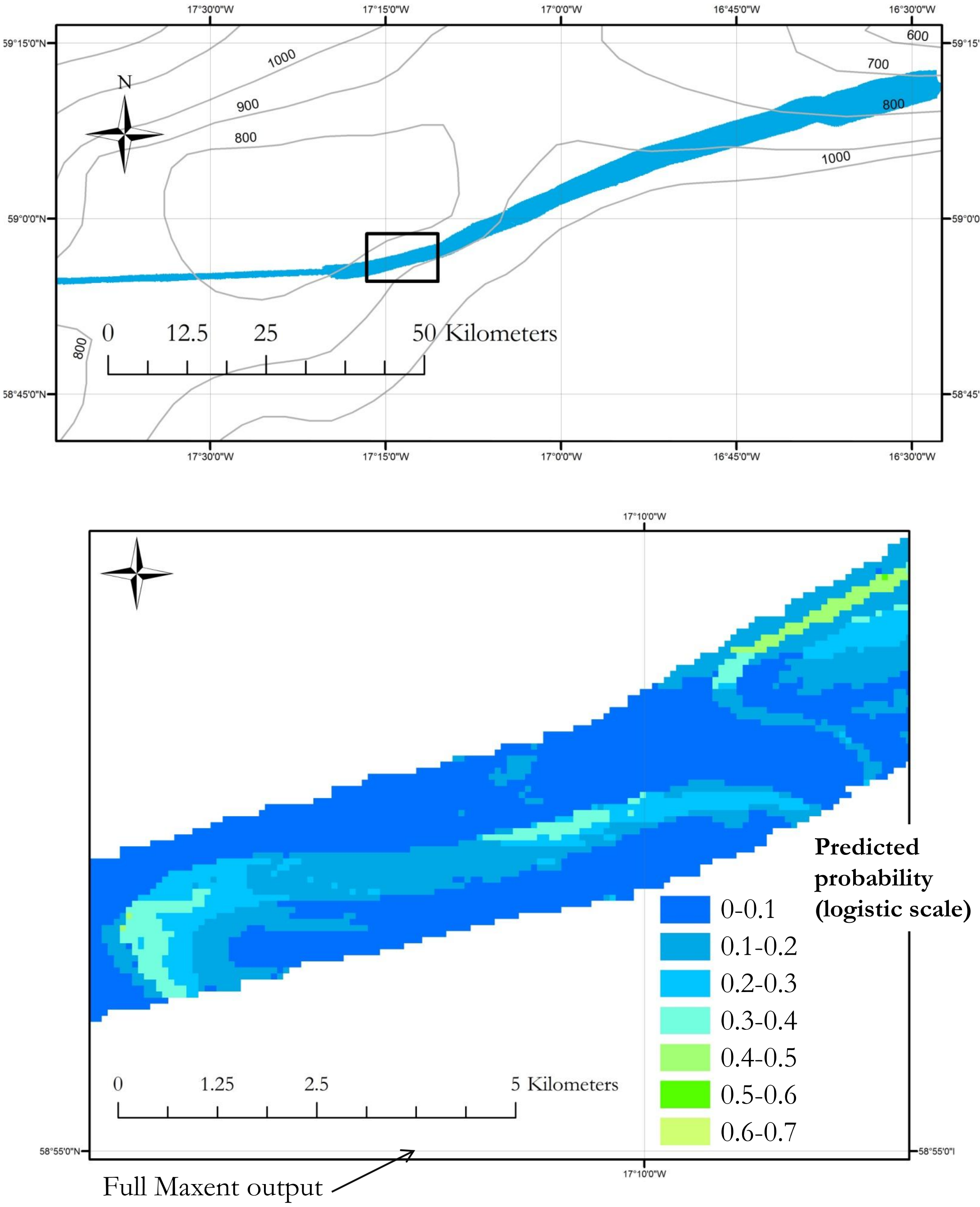
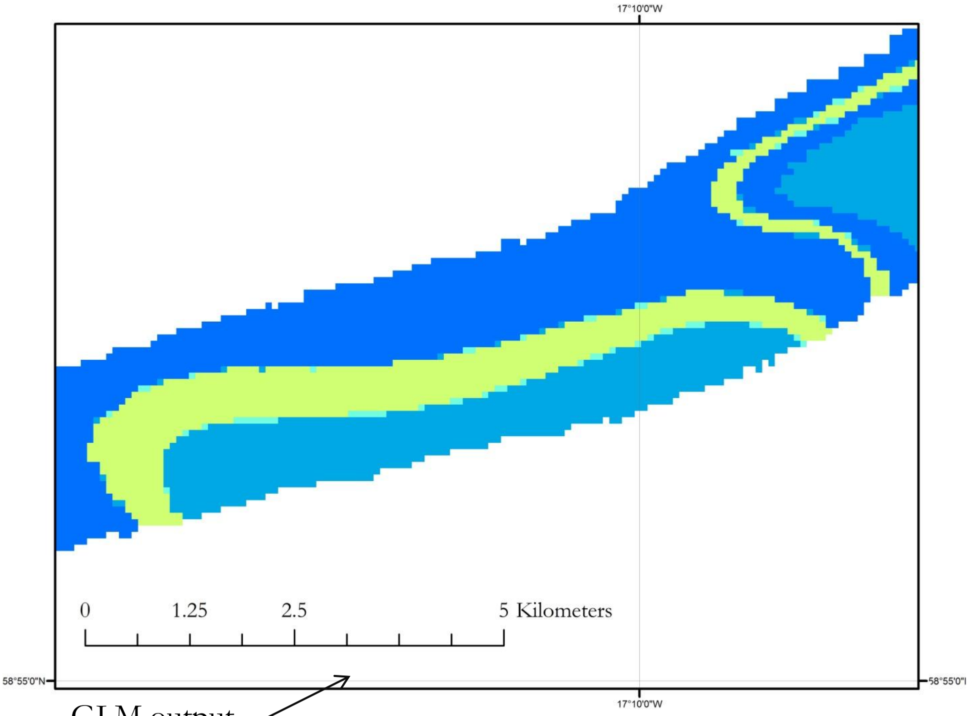
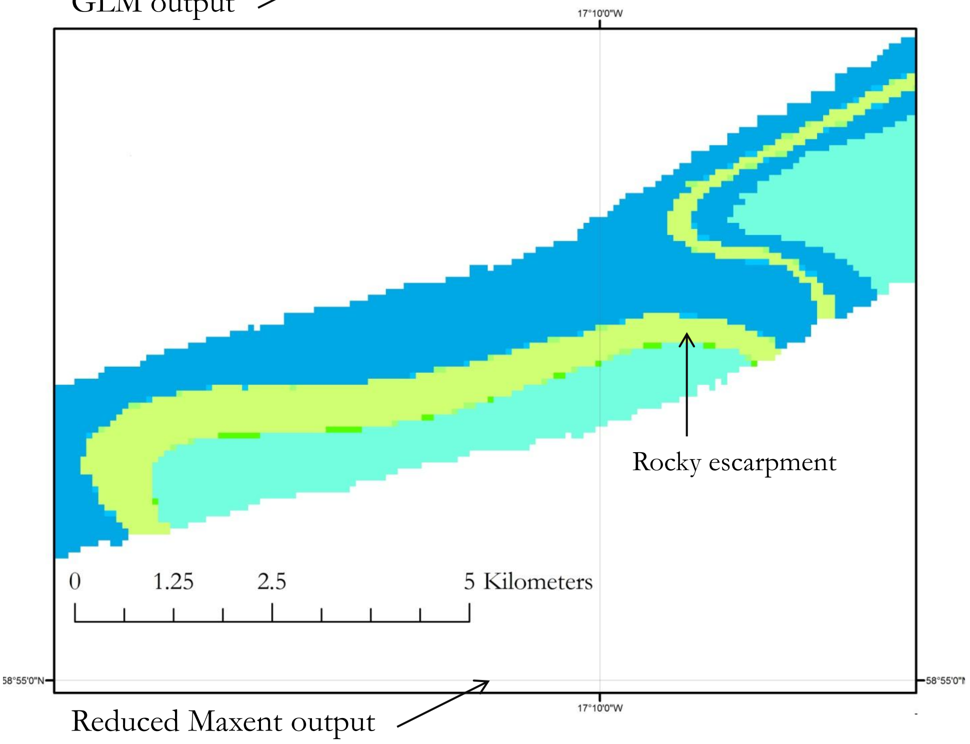


Figure 8.7: Close up of an area of Hatton Bank (boxed, top panel) illustrating the full Maxent (bottom, this page), reduced Maxent (bottom, opposite) and GLM (top, opposite) predictions. The curved feature illustrated is a rocky escarpment. The probability key is relevant to all three maps.



GLM output



Reduced Maxent output

8.3.3 Comparison of model performance

Table 8.1 and Figure 8.8 summarise the relative performance of the three modelling approaches. Based on internal resampling, the full Maxent model is significantly better than the GLM and reduced Maxent model in terms of AUC scores, although all three models obtain excellent average AUC scores. Comparison of the ROC plots (Figure 8.9), as recommended in the previous chapter, shows similarly shaped curves.

Table 8.1: Performance indicator scores for the Hatton Bank Maxent models and GLM based on internal resampling and using Cramer's prevalence threshold (A), the sens=spec threshold (B) and a threshold independent metric. = indicates no significance difference between model *a* and model *b* based on Wilcoxon rank sum tests. ** indicates an outright best score across the three models. The sens=spec threshold varied with each iteration, as did the Cramer threshold for GLM. The Cramer threshold for the Maxent models was 0.108.

Performance indicator	**Model *a***	**Model *a* score**	**Relative performance**	**Model *b***	**Wilcoxon rank sum test statistic (W)**	**Significance**
(A) Cramer's prevalence threshold						
CCR	GLM	0.793 ± 0.011**	>	Full Maxent	10000.0	$p = < 2.2^{-16}$
	Reduced Maxent	0.358 ± 0.030	<	GLM	10000.0	$p = < 2.2^{-16}$
	Full Maxent	0.518 ± 0.013	>	Reduced Maxent	7874.5	$p = 1.038^{-12}$
Sensitivity	GLM	0.756 ± 0.019	<	Full Maxent	9527.5	$p = < 2.2^{-16}$
	Reduced Maxent	0.920 ± 0.013	>	GLM	782.0	$p = < 2.2^{-16}$
	Full Maxent	0.937 ± 0.011**	>	Reduced Maxent	5667.5	p = 0.0457
Specificity	GLM	0.799 ± 0.015**	>	Full Maxent	10000.0	$p = < 2.2^{-16}$
	Reduced Maxent	0.324 ± 0.032	<	GLM	9998.0	$p = < 2.2^{-16}$
	Full Maxent	0.493 ± 0.014	>	Reduced Maxent	2151.5	$p =1.490^{-12}$

Performance indicator	**Model *a***	**Model *a* score**	**Relative performance**	**Model *b***	**Wilcoxon rank sum test statistic (W)**	**Significance**
(B) Equal sensitivity / specificity threshold						
CCR	GLM	0.781 ± 0.011	=	Full Maxent	4985.0	p = 0.5146
	Reduced Maxent	0.772 ± 0.013	=	GLM	5633.0	p = 0.0609
	Full Maxent	0.778 ± 0.008	>	Reduced Maxent	6056.0	p = 0.0049
Sensitivity	GLM	0.782 ± 0.011	=	Full Maxent	5285.5	p = 0.2406
	Reduced Maxent	0.787 ± 0.010	=	GLM	5228.5	p = 0.2871
	Full Maxent	0.780 ± 0.009	=	Reduced Maxent	5441.5	p = 0.1299
Specificity	GLM	0.781 ± 0.014	=	Full Maxent	4887.0	p = 0.6088
	Reduced Maxent	0.771 ± 0.014	=	GLM	5361.0	p = 0.1880
	Full Maxent	0.777 ± 0.008	>	Reduced Maxent	6163.5	p = 0.0022

Performance indicator	**Model *a***	**Model *a* score**	**Relative performance**	**Model *b***	**Wilcoxon rank sum test statistic (W)**	**Significance**
(C) Threshold independent						
AUC	GLM	0.850 ± 0.007	<	Full Maxent	4267.0	p = 0.0367
	Reduced Maxent	0.840 ± 0.009	=	GLM	5669.0	p = 0.0511
	Full Maxent	0.859 ± 0.005**	>	Reduced Maxent	6438.0	p = 0.0002

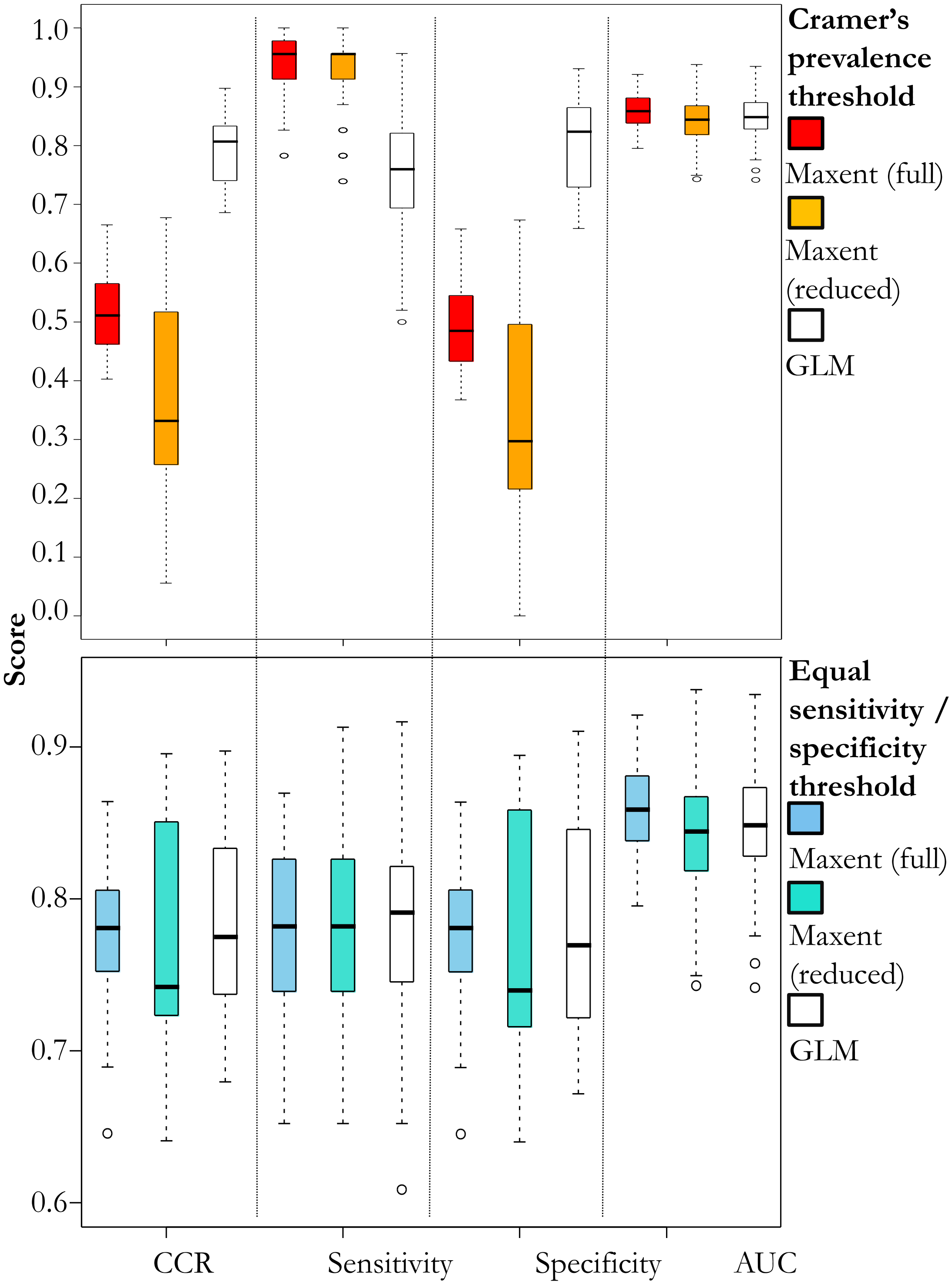


Figure 8.8: Comparison of Maxent and GLM/GAM performance indicator scores for the Hatton Bank models.

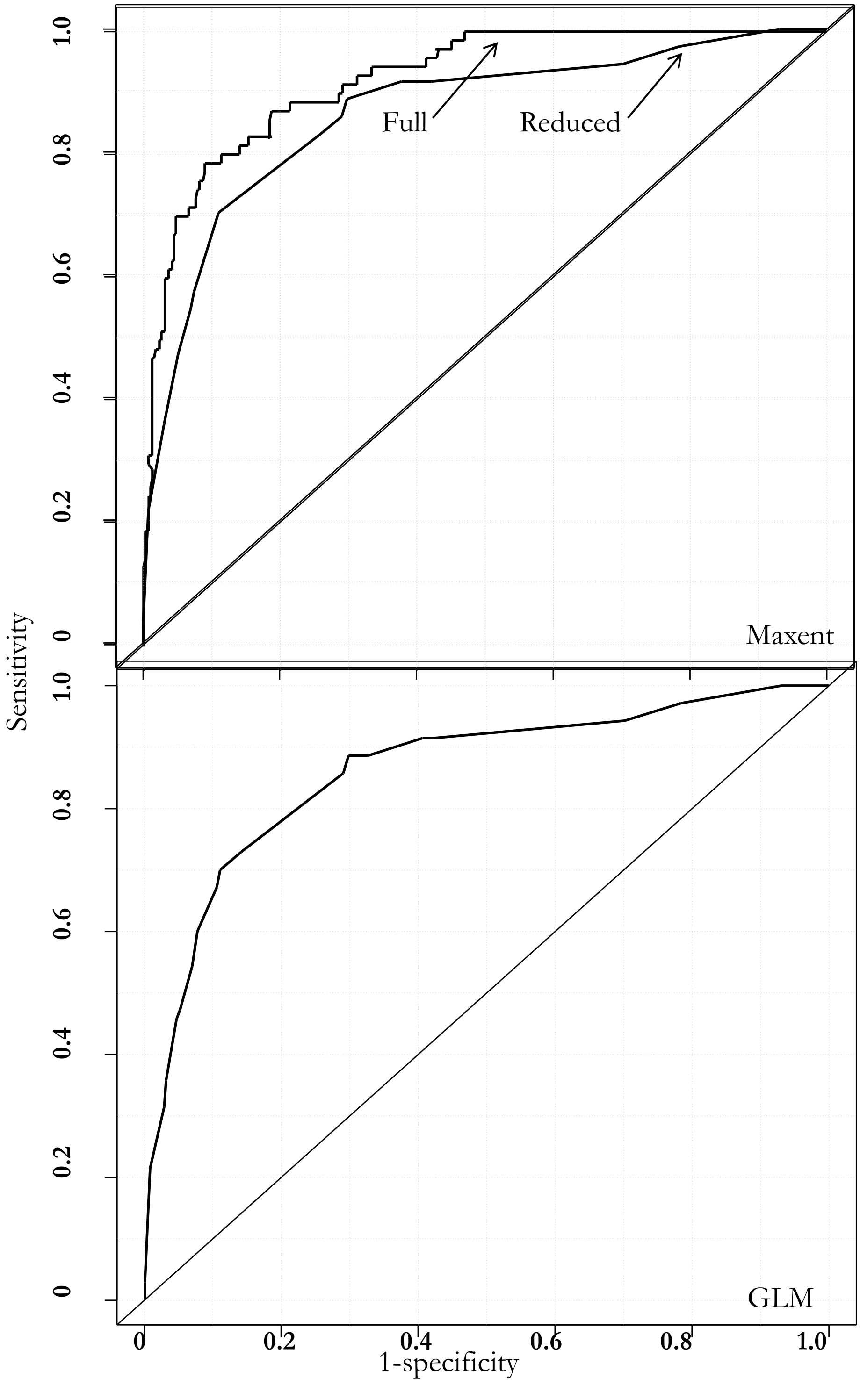


Figure 8.9: ROC plots for the Hatton Bank GLM and Maxent models.

Figure 8.8 shows clearly the effect of threshold selection on the relative performance of the models. Using the sensitivity = specificity threshold means that all three models produce acceptable average scores close to 0.8. With the exception of CCR and specificity, for which the full Maxent obtained significantly better scores than the reduced Maxent model, there were no significant differences in relative performance of the three models for the three threshold-specific performance indicators.

Use of the prevalence based threshold results in the performance of both Maxent models displaying a classic trade off between sensitivity and specificity. The GLM outperforms the Maxent models for both CCR and specificity and, while not displaying outstanding sensitivity like the Maxent models, achieves scores >0.75 across all three indicators. The Maxent models, in contrast, achieve very poor scores for two of the indicators.

8.4 Discussion

8.4.1 The relative importance of environmental variables

The focus of this chapter is on the relative performance of the different modelling approaches and because the importance of the different environmental variables has been discussed in previous chapters it will not be discussed at length again here, with the exception of the 'new' variables used in this chapter (namely aspect, BPI, slope and rugosity) because the use of bathymetric terrain analysis has been adopted in several studies mapping deep sea benthos, including gorgonians (Wilson et al. 2007; Woodby et al. 2009). But it is of interest that Howell et al. (2011), again using Maxent, also identified substratum and geomorphology as the two most important variables influencing the distribution of *Lophelia pertusa* reefs on Hatton Bank and George Bligh Bank.

Two studies in the North Atlantic cited a preference of corals for south facing slopes (Dolan et al. 2008; Guinan et al. 2009a) which is in direct contrast to the results obtained here where north and northeasterly slopes were favoured. However, the Dolan et al. (2008) and Guinan et al. (2009a) studies were focused on reefs in and around the Porcupine Seabight where prevailing currents come from the south west following the continental slope (New and Smythe-Wright 2001), whereas this study focuses on Hatton and George Bligh Banks where prevailing currents come from the north east. This suggests that corals have a preference for the direction of the prevailing current. Based on the aspect GAM and Maxent model, and in agreement with Howell et al. (2011), probability of gorgonian occurrence was lowest at a bearing of $\sim$300°.

In support of the results presented here, Dolan et al. (2008) reported that higher BPI values were associated with the distribution of the scleractinians *Lophelia pertusa* and *Madrepora oculata* on a carbonate mound in the Porcupine Seabight, southwest of Ireland. BPI was also found to have a significant influence on the distribution of the same two species in the Rockall Trough, with corals generally associated with areas with higher BPI values (positive elevations) (Howell et al. 2011) with the exception of a few cases where corals were found in topographically complex depressions (Guinan et al. 2009a) as predicted by Maxent.

Rugosity was found to be a significant factor in 80% of the models in Woodby et al.'s (2009) study of deep water benthos, including gorgonians and other corals, in the Central Aleutian Islands, southwest of Alaska. As with the results presented in this chapter, probability of coral occurrence increased with both rugosity and slope. Although Guinan et al. (2009a) reported fractal dimension a more important predictor than rugosity, it is a measure of surface complexity nonetheless and again, corals were associated with more complex surfaces. In contrast, Mortensen and Buhl-Mortensen (2004) did not identify a significant relationship between surface roughness and deep water gorgonians (*Paragorgia arborea*, *Primnoa resedaeformis*, and *Acanthogorgia armata*) in the Northwest Atlantic. However, surface roughness was calculated on the scale of the entire video transect and using a different method to the terrain analysis adopted by this and the other studies listed in this section.

Slope can be used as a proxy for increased current which is important for bringing food to deep-water corals (Mohn and Beckmann 2002; Mortensen and Buhl-Mortensen 2005; Bryan and Metaxas 2007; Wilson et al. 2007; Guinan et al. 2009a,b). However, slope is often used as a proxy for substratum in lieu of this information (Bryan and Metaxas 2007; Dolan et al. 2008) suggesting that substratum is a better predictor of gorgonian distribution as indeed the results presented in this chapter demonstrate. Although slope only explained a small amount of deviance in the GAM and was the least important variable in the Maxent model, its significant contribution to explaining gorgonian distribution is in agreement with other authors who have reported the probability of gorgonian and other coral occurrence increasing with slope (Mortensen and Buhl-Mortensen 2004; Leverette and Metaxas 2005; Bryan and Metaxas 2006; Guinan et al. 2009a,b). As noted in this analysis, Howell et al. (2011) reported an asymptotic relationship between slope and rugosity and the occurrence of the coral (*Lophelia pertusa*) on Hatton Bank.

Although the GAMs and full Maxent model are in agreement about the two variables with the greatest influence on gorgonian distribution (substratum and geomorphology), they differ in the relative importance of other variables. This may be due to a combination of factors including the distribution of presence data within the wider PA dataset, and the possibility that Maxent may overfit. Using rugosity as an example, half of the presence records are located within the top quarter of rugosity values (based on the full PA dataset), yet only a seventh of presence records were included in the first half of the data values. Consequently, Maxent may overestimate the importance of rugosity on gorgonian distribution based on the distribution of the presence records.

8.4.2 Spatial differences in model prediction

The majority of the study area is characterised by very small differences in predicted habitat suitability, suggesting that there is general consensus between the GLM and Maxent approaches regarding the relative suitability of different habitats within the study area. This is encouraging and suggests that Maxent does not appear to be adversely influenced by the lack of absence data in model calibration with respect to presence-absence (PA) models, as suggested by Elith and Graham (2009).

PA methods can assign lower probabilities to areas in which the species are present, but in which there may be a higher proportion of absences, which the presence-only model may otherwise identify as important habitat (Brotons et al. 2004). The fact that the GLM has predicted relatively higher probability than Maxent in some areas is probably because the GLM is quite conservative, only adding variables if they are significant and penalising quite heavily for their addition. The GLM probability value in Figure 8.6 is based solely on the fact that it is a rocky escarpment whereas Maxent has used a range of variables in its prediction. This suggests that Maxent may overfit to the data, although the regularization multiplier in Maxent aims to address this by forcing the model to focus on those variables that explain the most about the data (Phillips et al. 2006).

8.4.3 Model performance

Some authors have advocated the use of threshold-independent methods above all else, including recommendations specific to deep-sea modelling studies (Tittensor et al. 2009), while other authors recommend the use of a suite of performance indicators (Lobo et al. 2008) and so it is important that the performance across the range of metrics is presented.

The GLM had the most consistent performance based on the threshold-dependent metrics and while the full Maxent model AUC scores were significantly better than the GLM, the average scores based on resampling were very close and both excellent. Taking significant differences in performance into account, that is, the number of times the model had the outright best score, the full Maxent model and GLM had comparable performance.

However, due to the possibility that the full Maxent model might have overfitted to the data, it is a fairer to compare the GLM with the reduced Maxent model that used the same variables. In which case, taking significant differences in performance into account, the GLM only performed slightly better than the reduced Maxent model, although again the reduced Maxent model did have some very poor scores.

Maxent has performed well against PA models in other studies, despite using PsA data as opposed to the true absence data used in this study (Elith et al. 2006; Gibson et al. 2007; Williams et al. 2009). Gibson et al. (2007) found that Maxent only performed slightly better than a GLM (using PsA data) for a rare parrot species. Yet an early study by Ferrier and Watson 1997 found that GLMs and GAMs built with PsA data performed significantly better than and BIOCLIM (PO data). However, BIOCLIM is an older method than Maxent and Maxent has outperformed it in several studies (Elith et al. 2006; Hermanlimianto and van Ofwegen 2006).

Elith et al. (2011) have very recently applied Maxent as outlined in this study, and compared Maxent's performance built using presence and absence data as background data with Maxent models built using randomly sampled background data. The 'presence-absence' Maxent model produced predictions most consistent with ecological knowledge available for the species. Furthermore, the 'presence-absence' model achieved the highest overall AUC score based on five-fold cross validation with new data.

The results presented in this chapter demonstrate that Maxent has shown promising performance as a presence-absence model and, by virtue of its ease of use and excellent performance, might make a valuable contribution to marine conservation planning. However, Maxent was designed for presence-only modelling and whilst it shows some excellent performance in this study, further research is needed by its developers in collaboration with ecologists and other modellers to confirm whether indeed Maxent is an appropriate model for presence-absence data and, if so, whether the model could be further improved. If this is confirmed then there is no question that the position of Maxent as the model *du jour* will only increase.

Chapter 9

Discussion

This thesis comprises a collection of studies that set out to critically appraise the application of species distribution modelling in marine conservation planning by investigating fundamental challenges to their use and exploring solutions, and has demonstrated unequivocally their potential value to marine conservation management, thereby meeting the project aim and all of its objectives.

Two key problems that influence the employment of SDMs but have received little critical investigation in the marine environment were identified; environmental data resolution and model transferability. This study has evaluated the consequences of using environmental data at different resolutions (Objective 3), with specific reference to available data sets in the nearshore and offshore study sites, and of transferring deep-sea models (Objective 4), in order to allow managers to make informed decisions with respect to the best and most appropriate use of existing data.

This study has also used novel approaches and investigated their suitability for marine conservation planning, namely the use of model classification error in the spatial prioritisation of monitoring sites (Objective 2), leading to the development of a proof of concept for the application of SDMs to MPA monitoring, and the adaptation of an existing presence-only modelling method to include absence data (Objective 5). The latter will contribute to a much needed debate about the adoption of Maxent as a presence-absence model given its ease of use, excellent performance, and clear outputs.

Together, these studies contribute practical recommendations and novel applications within the wider species distribution modelling discipline, to ensure the ongoing improvement and development of models to support conservation planning.

Finally, the thesis has contributed to the bank of knowledge on gorgonian ecology and the environmental variables influencing their distribution on both local and landscape scales (Objective 1). It is the first study to model shallow and deep water gorgonian distribution in UK waters.

9.1 Species Distribution Models and management

In the absence of complete survey coverage it is necessary to turn to surrogates in order to inform conservation management (Ferrier and Watson 1997) and species distribution modelling in the marine environment has developed significantly over the past few years, especially within deep-water environments (Davies et al. 2008)).

A review of twenty recent marine conservation related species distribution modelling studies written over recent years (Cañadas et al. 2005; Clark et al. 2006; Carlson et al. 2007; Davies et al. 2008; Degnbol and Wilson 2008; Panigada et al. 2008; Bailey and Thompson 2009; Guinan et al. 2009b; Maxwell et al. 2009; Tittensor et al. 2009; Woodby et al. 2009; Clark and Tittensor 2010; Embling et al. 2010; Magris and Déstro 2010; Tittensor et al. 2010; Dambach and Rodder 2011; Davies and Guinotte 2011; Howell et al. 2011; Pittman and Brown 2011; Tracey et al. 2011) reveals that, whilst being valid studies that contribute to broadening the knowledge base of the target species or modelling methodology, their application in the majority of cases is ‘passive’. That is to say, they do not explicitly state the desired application of the results more specifically than being available to support marine conservation management. In only two of the papers have the outputs of the modelling been linked specifically to management decisions (in both cases, using marine mammal model outputs to identify boundaries for proposed SACs: Cañadas et al. (2005); Embling et al. (2010)).

A crucial stage has been reached in the application of marine species distribution models where it is necessary to start considering the end point application of these models: How can model outputs be more than maps? How can they best be used to inform conservation planning? Should metadata standards be developed for model outputs? How can predictive layers best be used with other conservation planning tools such as Marxan? If these models are to be applied in a management context then these questions need to be addressed. Two important areas of discussion and further research are therefore adding value to model outputs (creating more than maps of habitat suitability) and model endpoint specification.

9.2 Adding value to model outputs

As demonstrated in Chapter five and by several recent studies (e.g. Clark and Tittensor (2010); Tittensor et al. (2010); Dambach and Rodder (2011)), the combination of model outputs with additional activity layers or global climate change scenarios adds another dimension to the model and contextualises model outputs with respect to current management issues. The spatial footprint of human activities in coastal and offshore environments (Stelzenmuller et al. 2008; Benn et al. 2010) could be combined with species distribution model outputs and economic analyses, for example, to better understand how the vulnerability of different habitats might shift in a changing economic climate. Equally, species distribution model outputs might assist in the identification of potential synergistic cumulative impacts (see Rogers and Laffoley (2011)) before they necessarily occur, thereby adopting the precautionary principle. For example, global predictions of habitat suitability for cold water corals with respect to climate change scenarios (Tittensor et al. 2010) could be combined with maps of global trawling effort to identify areas in which are likely to be threatened by both activities and hence areas where we might expect to see some permanent loss of deep-water coral habitat. This would address both spatial and temporal vulnerability.

With particular relevance to deep-sea species distribution modelling, where video survey techniques are an important source of biological survey data, the need for research into indicator species that can be used as a proxy for the distribution of other species is central. The identification of a group of species that are highly conspicuous on video, and therefore suitable for generating presence-absence data, and whose presence is commonly associated with the presence (or absence) of other species of conservation importance or species richness (determined from the analysis of photographic stills, for example), would allow for proxy distribution modelling of other species or areas of high biodiversity.

Lastly, it would be of tremendous value to combine SDM outputs with biological traits in order to map ecosystem structure and function, and to identify areas characterised by particular biological traits. The outputs of this study, for example, when combined with the biological traits of the species used in the study (growth rates, fragility, longevity etc.) would help to identify areas of functional or ecological significance, as defined by the CBD criteria for identifying ecologically or biologically significant areas (2008 Decision IX/20 Annex 1) and FAO criteria for identifying vulnerable marine ecosystems.

9.3 Model endpoint specification

Model endpoint specification simply refers to the provision of and appropriate preparation of model outputs for external use, that is, use by a different person or organisation for conservation planning. To quote Sundblad et al. (2009), ‘maps of potential distribution will be of little use, or may even do more damage than good, e.g. by spatial misallocation of conservation, if the predictive capability is not communicated to end-users’. To this effect there are several facets of SDM outputs that warrant greater consideration than they are currently given.

The first concerns metadata and the apparent lack of metadata standards for SDM outputs. These standards should be developed so that anyone inheriting SDM outputs, such as GIS layers, is provided with enough information about the model that they can make an informed choice about the application of the outputs. At the very least, the metadata should include the modelling approach, details of the variables included in the final model and details of any thresholding methodology if a binary prediction is presented.

Furthermore conservation prioritisation should account for uncertainty, including with respect to SDM outputs (Elith and Leathwick 2009), yet model error, for example, is rarely mapped in the published literature. Managers will be faced with spatial choice when planning and the additional information provided by a map of model error, such as the standard error of model predictions, or confidence layers, may influence their decisions. Providing this information might also foster confidence in model outputs so it is important that all of this information is accessible.

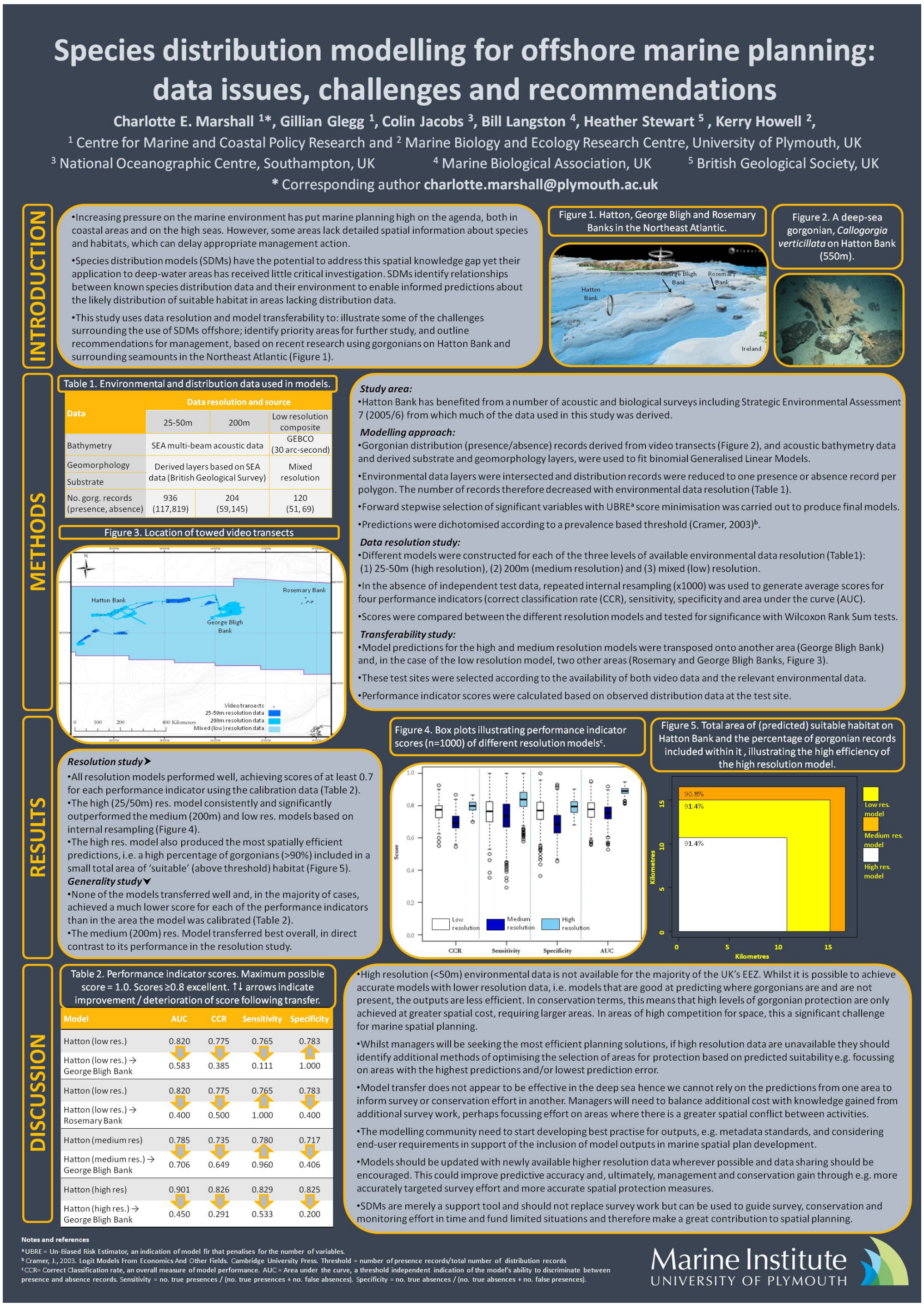
Further research is needed to determine the best approach for incorporating SDM outcomes into spatial prioritisation programmes such as Marxan (Loisells et al.

2003; Wilson et al. 2005; Leathwick et al. 2008). Wilson et al. (2005) studied the influence of using binary outputs versus probabilities of species occurrence in Marxan and encountered various problems including Marxan solutions that were inefficient and that missed targets. However, of the three different methods of threshold definition used and the two different methods of using predicted probabilities, no method appeared to consistently perform better than the other. If the outputs from a high resolution species distribution model are to be used in much coarser resolution planning units for example, should the precautionary principle be adopted and assign the value of the model unit with the highest predicted probability to the planning unit? Or should an average of the model unit probabilities be taken which, although easily justified, might result in the loss of valuable information about highly suitable habitat? It would be of great interest to further investigate the use of SDM outputs in Marxan, and other marine planning tools, using some sensitivity analyses.

The recent extension to 2020 of the Convention on Biological Diversity target deadline (protection of 10% of all marine and coastal ecoregions), progress in the identification and designation of Marine Protected Areas beyond areas of national jurisdiction, and ongoing development in marine planning, mean that species distribution models have both an urgent and long term contribution to make to marine conservation planning globally, and it is hoped that the outcomes of this thesis will contribute to this and inform best practice.

Appendix A

Conference posters



Species distribution modelling for offshore marine planning: data issues, challenges and recommendations

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INTRODUCTION

•Increasing pressure on the marine environment has put marine planning high on the agenda, both in coastal areas and on the high seas. However, some areas lack detailed spatial information about species and habitats, which can delay appropriate management action.

•Species distribution models (SDMs) have the potential to address this spatial knowledge gap yet their application to deep-water areas has received little critical investigation. SDMs identify relationships between known species distribution data and their environment to enable informed predictions about the likely distribution of suitable habitat in areas lacking distribution data.

•This study uses data resolution and model transferability to: illustrate some of the challenges surrounding the use of SDMs offshore; identify priority areas for further study, and outline recommendations for management, based on recent research using gorgonians on Hatton Bank and surrounding seamounts in the Northeast Atlantic (Figure 1).

Figure 1. Hatton, George Bligh and Rosemary Banks in the Northeast Atlantic.

Figure 2. A deep-sea gorgonian, *Callogorgia verticillata* on Hatton Bank (550m).

METHODS

Table 1. Environmental and distribution data used in models.

Data	Data resolution and source		
	25-50m	200m	Low resolution composite
Bathymetry	SEA multi-beam acoustic data		GEBCO (30 arc-second)
Geomorphology	Derived layers based on SEA data (British Geological Survey)		Mixed resolution
Substrate			
No. gorg. records (presence, absence)	936 (117,819)	204 (59,145)	120 (51, 69)

Figure 3. Location of towed video transects

Study area:

•Hatton Bank has benefited from a number of acoustic and biological surveys including Strategic Environmental Assessment 7 (2005/6) from which much of the data used in this study was derived.

Modelling approach:

•Gorgonian distribution (presence/absence) records derived from video transects (Figure 2), and acoustic bathymetry data and derived substrate and geomorphology layers, were used to fit binomial Generalised Linear Models.

•Environmental data layers were intersected and distribution records were reduced to one presence or absence record per polygon. The number of records therefore decreased with environmental data resolution (Table 1).

•Forward stepwise selection of significant variables with UBRE[a] score minimisation was carried out to produce final models.

•Predictions were dichotomised according to a prevalence based threshold (Cramer, 2003)[b].

Data resolution study:

•Different models were constructed for each of the three levels of available environmental data resolution (Table1): (1) 25-50m (high resolution), (2) 200m (medium resolution) and (3) mixed (low) resolution.

•In the absence of independent test data, repeated internal resampling (x1000) was used to generate average scores for four performance indicators (correct classification rate (CCR), sensitivity, specificity and area under the curve (AUC).

•Scores were compared between the different resolution models and tested for significance with Wilcoxon Rank Sum tests.

Transferability study:

•Model predictions for the high and medium resolution models were transposed onto another area (George Bligh Bank) and, in the case of the low resolution model, two other areas (Rosemary and George Bligh Banks, Figure 3).

•These test sites were selected according to the availability of both video data and the relevant environmental data.

•Performance indicator scores were calculated based on observed distribution data at the test site.

RESULTS

Resolution study➤

•All resolution models performed well, achieving scores of at least 0.7 for each performance indicator using the calibration data (Table 2).
•The high (25/50m) res. model consistently and significantly outperformed the medium (200m) and low res. models based on internal resampling (Figure 4).
•The high res. model also produced the most spatially efficient predictions, i.e. a high percentage of gorgonians (>90%) included in a small total area of 'suitable' (above threshold) habitat (Figure 5).

Generality study⮟

•None of the models transferred well and, in the majority of cases, achieved a much lower score for each of the performance indicators than in the area the model was calibrated (Table 2).
•The medium (200m) res. Model transferred best overall, in direct contrast to its performance in the resolution study.

Figure 4. Box plots illustrating performance indicator scores (n=1000) of different resolution models[c].

Figure 5. Total area of (predicted) suitable habitat on Hatton Bank and the percentage of gorgonian records included within it , illustrating the high efficiency of the high resolution model.

DISCUSSION

Table 2. Performance indicator scores. Maximum possible score = 1.0. Scores ≥0.8 excellent. ↑↓ arrows indicate improvement / deterioration of score following transfer.

Model	AUC	CCR	Sensitivity	Specificity
Hatton (low res.)	0.820	0.775	0.765	0.783
Hatton (low res.) → George Bligh Bank	↓ 0.583	↓ 0.385	↓ 0.111	↑ 1.000
Hatton (low res.)	0.820	0.775	0.765	0.783
Hatton (low res.) → Rosemary Bank	↓ 0.400	↓ 0.500	↑ 1.000	↓ 0.400
Hatton (medium res)	0.785	0.735	0.780	0.717
Hatton (medium res.) → George Bligh Bank	↓ 0.706	↓ 0.649	↑ 0.960	↓ 0.406
Hatton (high res)	0.901	0.826	0.829	0.825
Hatton (high res.) → George Bligh Bank	↓ 0.450	↓ 0.291	↓ 0.533	↓ 0.200

•High resolution (<50m) environmental data is not available for the majority of the UK's EEZ. Whilst it is possible to achieve accurate models with lower resolution data, i.e. models that are good at predicting where gorgonians are and are not present, the outputs are less efficient. In conservation terms, this means that high levels of gorgonian protection are only achieved at greater spatial cost, requiring larger areas. In areas of high competition for space, this a significant challenge for marine spatial planning.

•Whilst managers will be seeking the most efficient planning solutions, if high resolution data are unavailable they should identify additional methods of optimising the selection of areas for protection based on predicted suitability e.g. focussing on areas with the highest predictions and/or lowest prediction error.

•Model transfer does not appear to be effective in the deep sea hence we cannot rely on the predictions from one area to inform survey or conservation effort in another. Managers will need to balance additional cost with knowledge gained from additional survey work, perhaps focussing effort on areas where there is a greater spatial conflict between activities.

•The modelling community need to start developing best practise for outputs, e.g. metadata standards, and considering end-user requirements in support of the inclusion of model outputs in marine spatial plan development.

•Models should be updated with newly available higher resolution data wherever possible and data sharing should be encouraged. This could improve predictive accuracy and, ultimately, management and conservation gain through e.g. more accurately targeted survey effort and more accurate spatial protection measures.

•SDMs are merely a support tool and should not replace survey work but can be used to guide survey, conservation and monitoring effort in time and fund limited situations and therefore make a great contribution to spatial planning.

Notes and references

[a] UBRE = Un-Biased Risk Estimator, an indication of model fir that penalises for the number of variables.
[b] Cramer, J., 2003. Logit Models From Economics And Other Fields. Cambridge University Press. Threshold = number of presence records/total number of distribution records
[c] CCR= Correct Classification rate, an overall measure of model performance. AUC = Area under the curve, a threshold independent indication of the model's ability to discriminate between presence and absence records. Sensitivity = no. true presences / (no. true presences + no. false absences). Specificity = no. true absences / (no. true absences + no. false presences).

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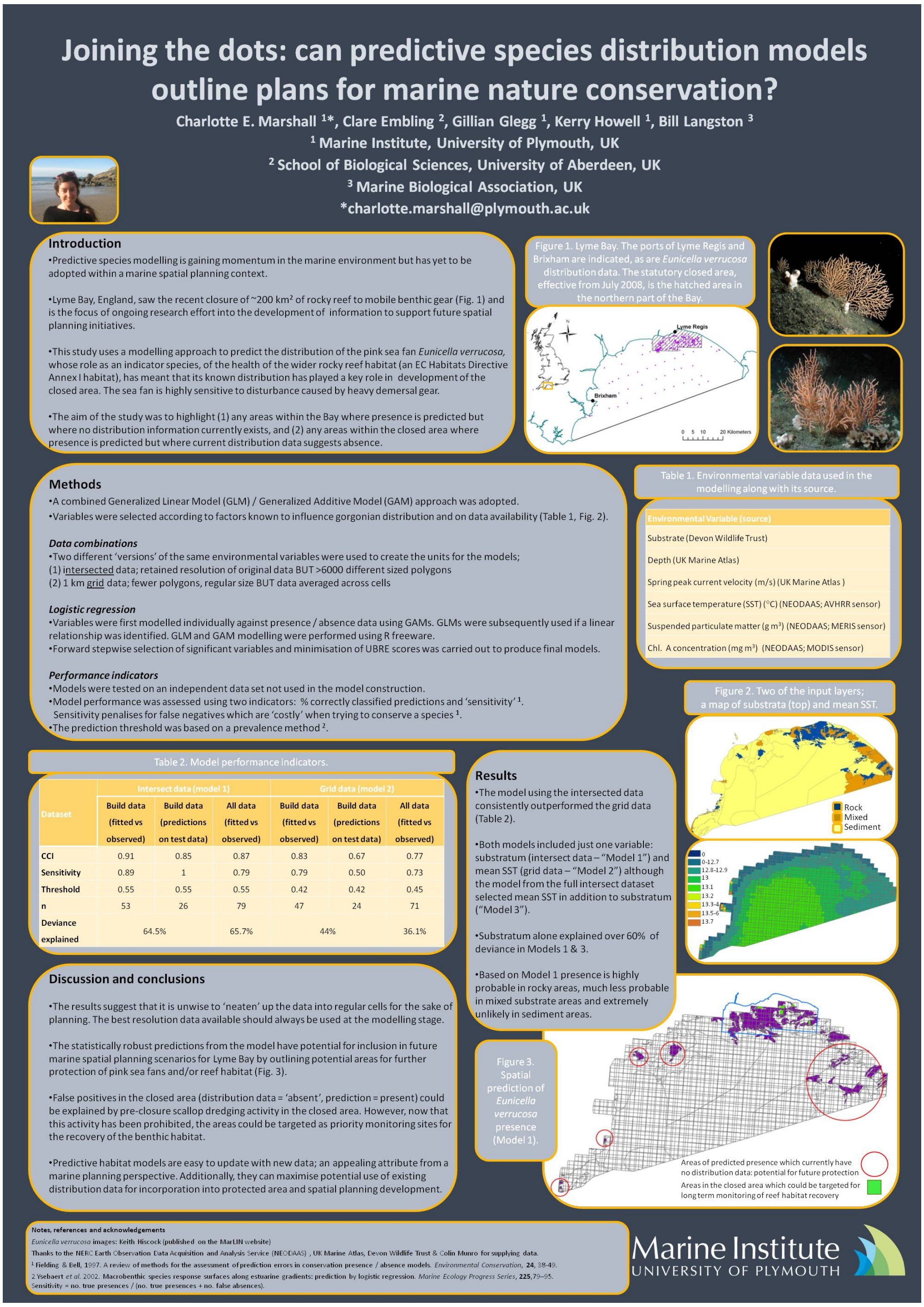

Joining the dots: can predictive species distribution models outline plans for marine nature conservation?

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Introduction

- Predictive species modelling is gaining momentum in the marine environment but has yet to be adopted within a marine spatial planning context.

- Lyme Bay, England, saw the recent closure of ~200 km² of rocky reef to mobile benthic gear (Fig. 1) and is the focus of ongoing research effort into the development of information to support future spatial planning initiatives.

- This study uses a modelling approach to predict the distribution of the pink sea fan *Eunicella verrucosa,* whose role as an indicator species, of the health of the wider rocky reef habitat (an EC Habitats Directive Annex I habitat), has meant that its known distribution has played a key role in development of the closed area. The sea fan is highly sensitive to disturbance caused by heavy demersal gear.

- The aim of the study was to highlight (1) any areas within the Bay where presence is predicted but where no distribution information currently exists, and (2) any areas within the closed area where presence is predicted but where current distribution data suggests absence.

Figure 1. Lyme Bay. The ports of Lyme Regis and Brixham are indicated, as are *Eunicella verrucosa* distribution data. The statutory closed area, effective from July 2008, is the hatched area in the northern part of the Bay.

Methods

- A combined Generalized Linear Model (GLM) / Generalized Additive Model (GAM) approach was adopted.
- Variables were selected according to factors known to influence gorgonian distribution and on data availability (Table 1, Fig. 2).

Data combinations

- Two different 'versions' of the same environmental variables were used to create the units for the models;

(1) intersected data; retained resolution of original data BUT >6000 different sized polygons
(2) 1 km grid data; fewer polygons, regular size BUT data averaged across cells

Logistic regression

- Variables were first modelled individually against presence / absence data using GAMs. GLMs were subsequently used if a linear relationship was identified. GLM and GAM modelling were performed using R freeware.
- Forward stepwise selection of significant variables and minimisation of UBRE scores was carried out to produce final models.

Performance indicators

- Models were tested on an independent data set not used in the model construction.
- Model performance was assessed using two indicators: % correctly classified predictions and 'sensitivity' [1]. Sensitivity penalises for false negatives which are 'costly' when trying to conserve a species [1].
- The prediction threshold was based on a prevalence method [2].

Table 1. Environmental variable data used in the modelling along with its source.

Environmental Variable (source)
Substrate (Devon Wildlife Trust)
Depth (UK Marine Atlas)
Spring peak current velocity (m/s) (UK Marine Atlas)
Sea surface temperature (SST) (°C) (NEODAAS; AVHRR sensor)
Suspended particulate matter (g m^3) (NEODAAS; MERIS sensor)
Chl. A concentration (mg m^3) (NEODAAS; MODIS sensor)

Figure 2. Two of the input layers; a map of substrata (top) and mean SST.

Table 2. Model performance indicators.

Dataset	Intersect data (model 1)			Grid data (model 2)		
	Build data (fitted vs observed)	Build data (predictions on test data)	All data (fitted vs observed)	Build data (fitted vs observed)	Build data (predictions on test data)	All data (fitted vs observed)
CCI	0.91	0.85	0.87	0.83	0.67	0.77
Sensitivity	0.89	1	0.79	0.79	0.50	0.73
Threshold	0.55	0.55	0.55	0.42	0.42	0.45
n	53	26	79	47	24	71
Deviance explained	64.5%		65.7%	44%		36.1%

Results

- The model using the intersected data consistently outperformed the grid data (Table 2).

- Both models included just one variable: substratum (intersect data – "Model 1") and mean SST (grid data – "Model 2") although the model from the full intersect dataset selected mean SST in addition to substratum ("Model 3").

- Substratum alone explained over 60% of deviance in Models 1 & 3.

- Based on Model 1 presence is highly probable in rocky areas, much less probable in mixed substrate areas and extremely unlikely in sediment areas.

Discussion and conclusions

- The results suggest that it is unwise to 'neaten' up the data into regular cells for the sake of planning. The best resolution data available should always be used at the modelling stage.

- The statistically robust predictions from the model have potential for inclusion in future marine spatial planning scenarios for Lyme Bay by outlining potential areas for further protection of pink sea fans and/or reef habitat (Fig. 3).

- False positives in the closed area (distribution data = 'absent', prediction = present) could be explained by pre-closure scallop dredging activity in the closed area. However, now that this activity has been prohibited, the areas could be targeted as priority monitoring sites for the recovery of the benthic habitat.

- Predictive habitat models are easy to update with new data; an appealing attribute from a marine planning perspective. Additionally, they can maximise potential use of existing distribution data for incorporation into protected area and spatial planning development.

Figure 3. Spatial prediction of *Eunicella verrucosa* presence (Model 1).

Notes, references and acknowledgements

Eunicella verrucosa images: Keith Hiscock (published on the MarLIN website)
Thanks to the NERC Earth Observation Data Acquisition and Analysis Service (NEODAAS) , UK Marine Atlas, Devon Wildlife Trust & Colin Munro for supplying data.

[1] Fielding & Bell, 1997. A review of methods for the assessment of prediction errors in conservation presence / absence models. *Environmental Conservation*, **24**, 38-49.
2 Ysebaert *et al.* 2002. Macrobenthic species response surfaces along estuarine gradients: prediction by logistic regression. *Marine Ecology Progress Series*, **225**,79–95.

Sensitivity = no. true presences / (no. true presences + no. false absences).

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Appendix B

Lyme Bay substratum description cross referencing

Table B.1: The supporting habitat descriptions for the Devon Wildlife Trust pink sea fan data (from the towed video reef survey) were cross-referenced with the Devon Wildlife Trust biotope layer. Only those data where the description matched were included in the model building. The table below lists the permitted matches.

Devon Wildlife Trust biotope layer substratum description	The following categories from the substratum description from Black (2007) were considered a `match' with the biotope layer.
Rock	Boulders Bedrock Bedrock and boulders
Rock and mixed substrata	Any of the above plus: Mosaic of mixed substrata and bedrock Bedrock with sediment veneer Mixed (if Black (2007) indicated that the habitat was suitable for supporting pink sea fans, because this meant that boulders were present or if the description mentioned large boulders)
Mixed substrata	Mixed (excluding the exceptions outlined above)
Gravel	Mixed (if Black (2007) indicated that the habitat was unsuitable for supporting pink sea fans because this meant that boulders were not present)
Sand, Mud, Mud and sand	Soft
Mud, sand and mixed	Soft Mixed (if Black (2007) indicated that the habitat was unsuitable for supporting pink sea fans because this meant that boulders were not present)

Appendix C

Wilcoxon test statistics for performance indicator analysis; Hatton Bank models (Chapter 6)

Table C.1: Comparative performance of the different resolution Hatton Bank models built with two thirds of the data, based on four performance indicators. Relative performance is indicated by < and >.

Performance indicator	**Model *a***	**Relative performance**	**Model *b***	**Wilcoxon rank sum test statistic (W)**	**Significance**
CCR	HHRM	>	HLRM	701135.0	$p = < 2.2^{-16}$
	HHRM	>	HMRM	950284.0	$p = < 2.2^{-16}$
	HMRM	<	HLRM	187822.0	$p = < 2.2^{-16}$
Sensitivity	HHRM	>	HLRM	745118.5	$p = < 2.2^{-16}$
	HHRM	>	HMRM	793292.0	$p = < 2.2^{-16}$
	HMRM	<	HLRM	428450.5	$p = 1.489^{-08}$
Specificity	HHRM	>	HLRM	598216.5	$p = 1.410^{-14}$
	HHRM	>	HMRM	885057.5	$p = < 2.2^{-16}$
	HMRM	<	HLRM	230234.5	$p = < 2.2^{-16}$
AUC	HHRM	>	HLRM	964426.5	$p = < 2.2^{-16}$
	HHRM	>	HMRM	991660.0	$p = < 2.2^{-16}$
	HMRM	<	HLRM	410411.0	$p = 1.991^{-16}$

Table C.2: Comparative performance of the different resolution Hatton Bank models standardised for sample size (with respect to the low resolution model) and prevalence, based on four performance indicators. Relative performance is indicated by < and >.

Performance indicator	**Model *a***	**Relative performance**	**Model *b***	**Wilcoxon rank sum test statistic (W)**	**Significance**
CCR	HHRM	>	HLRM	581711	p=1.195 $^{-10}$
	HHRM	>	HMRM	848488	p = < 2.2 $^{-16}$
	HMRM	<	HLRM	196978	p = < 2.2 $^{-16}$
Sensitivity	HHRM	>	HLRM	632625	p = < 2.2 $^{-16}$
	HHRM	>	HMRM	806096	p = < 2.2 $^{-16}$
	HMRM	<	HLRM	290432	p = < 2.2 $^{-16}$
Specificity	HHRM	>	HLRM	571122.5	p=1.744 $^{-08}$
	HHRM	>	HMRM	757746	p = < 2.2 $^{-16}$
	HMRM	<	HLRM	299874	p = < 2.2 $^{-16}$
AUC	HHRM	>	HLRM	930251	p = < 2.2 $^{-16}$
	HHRM	>	HMRM	989661	p = < 2.2 $^{-16}$
	HMRM	<	HLRM	312839	p = < 2.2 $^{-16}$

Appendix D

Wilcoxon test statistics for performance indicator analysis; Lyme Bay models (Chapter 6)

Table D.1: Comparative performance of the different resolution Lyme Bay models built with (a) two thirds of the data and (b) standardised for sample size (with respect to the low resolution model) and prevalence, based on four performance indicators. Relative performance is indicated by < and >.

(a)

Performance indicator	**Model *a***	**Relative performance**	**Model *b***	**Wilcoxon rank sum test statistic (W)**	**Significance**
CCR	LHRM	>	LLRM	940839.0	$p = < 2.2^{-16}$
Sensitivity	LHRM	>	LLRM	689288.5	$p = < 2.2^{-16}$
Specificity	LHRM	>	LLRM	883673.0	$p = < 2.2^{-16}$
AUC	LHRM	>	LLRM	867730.5	$p = < 2.2^{-16}$

(b)

Performance indicator	**Model *a***	**Relative performance**	**Model *b***	**Wilcoxon rank sum test statistic (W)**	**Significance**
CCR	LHRM	>	LLRM	941091.0	$p = < 2.2^{-16}$
Sensitivity	LHRM	>	LLRM	768659.5	$p = < 2.2^{-16}$
Specificity	LHRM	>	LLRM	950939.0	$p = < 2.2^{-16}$
AUC	LHRM	>	LLRM	924078.0	$p = < 2.2^{-16}$

Appendix E

Maps of predicted gorgonian habitat suitability for Hatton Bank based on Maxent and Generalized Linear Model outputs, and differences between the two sets of predictions (Chapter 8)

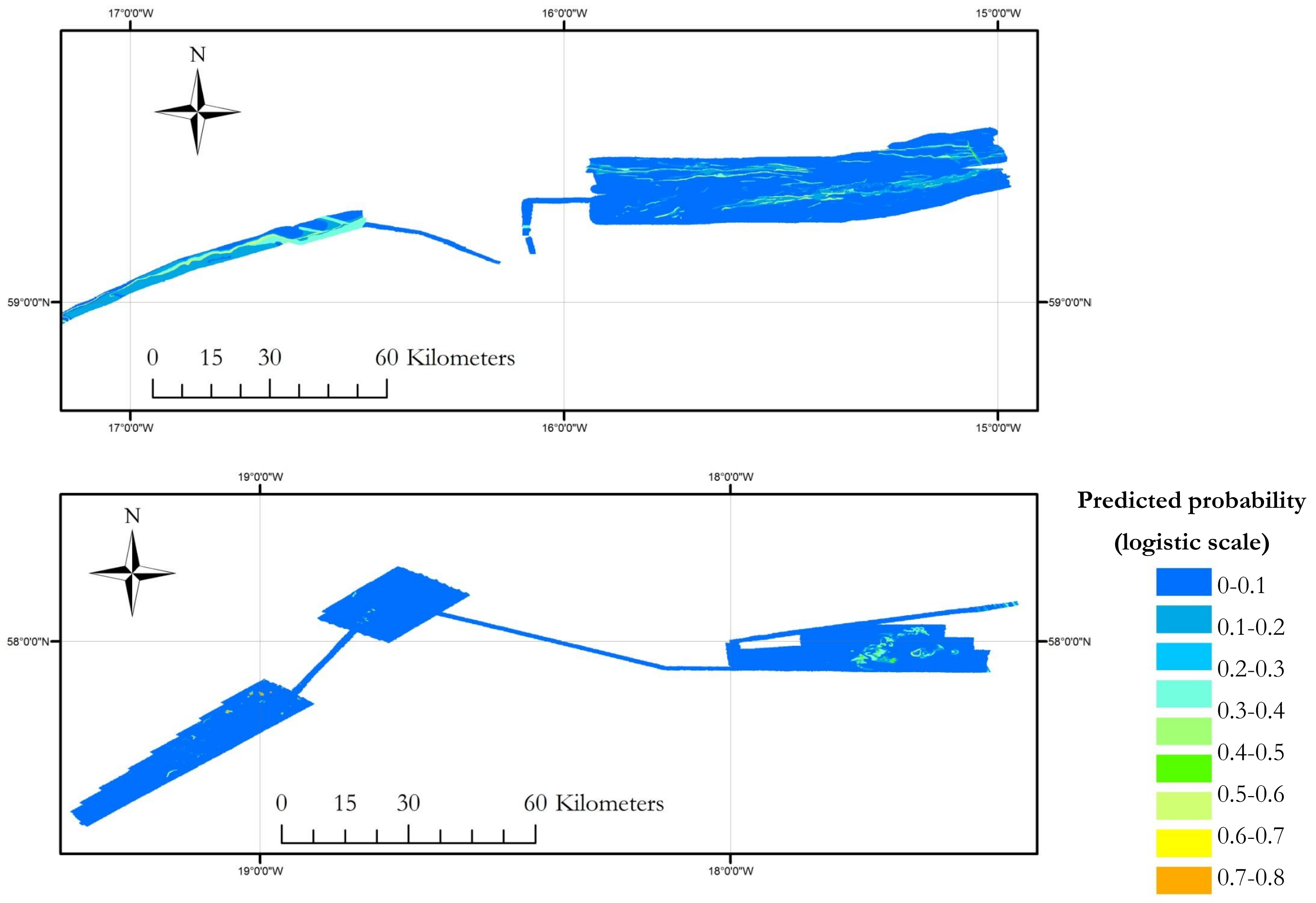

Figure E.1: Predicted probability of gorgonian occurrence on central (top) and southern Hatton Bank based on a GLM with the categorical variables substratum and geomorphology. The warmer the colours, the more suitable the habitat is predicted to be.

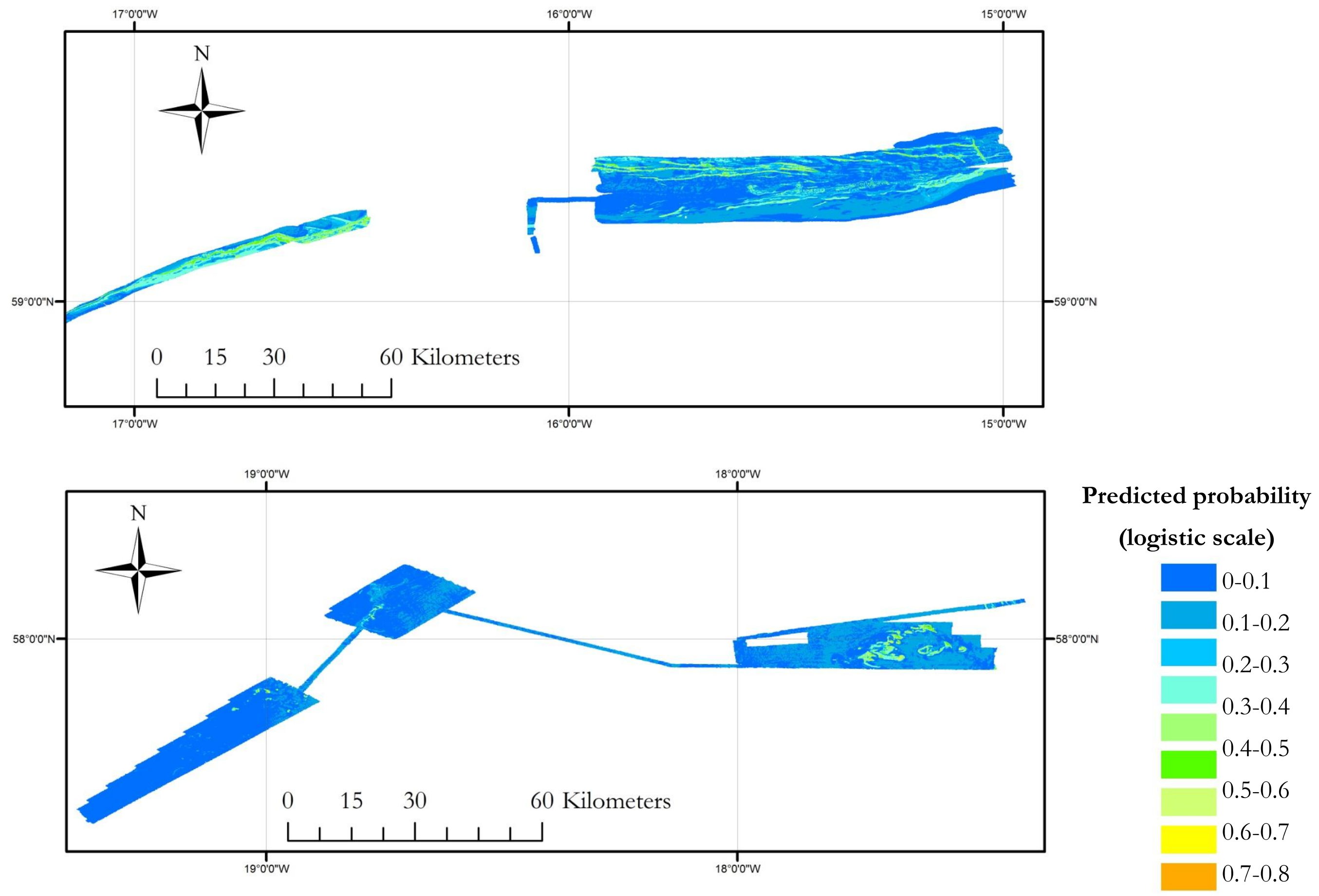

Figure E.2: Predicted probability of gorgonian occurrence on central (top) and southern Hatton Bank based on the full Maxent model. The warmer the colours, the more suitable the habitat is predicted to be.

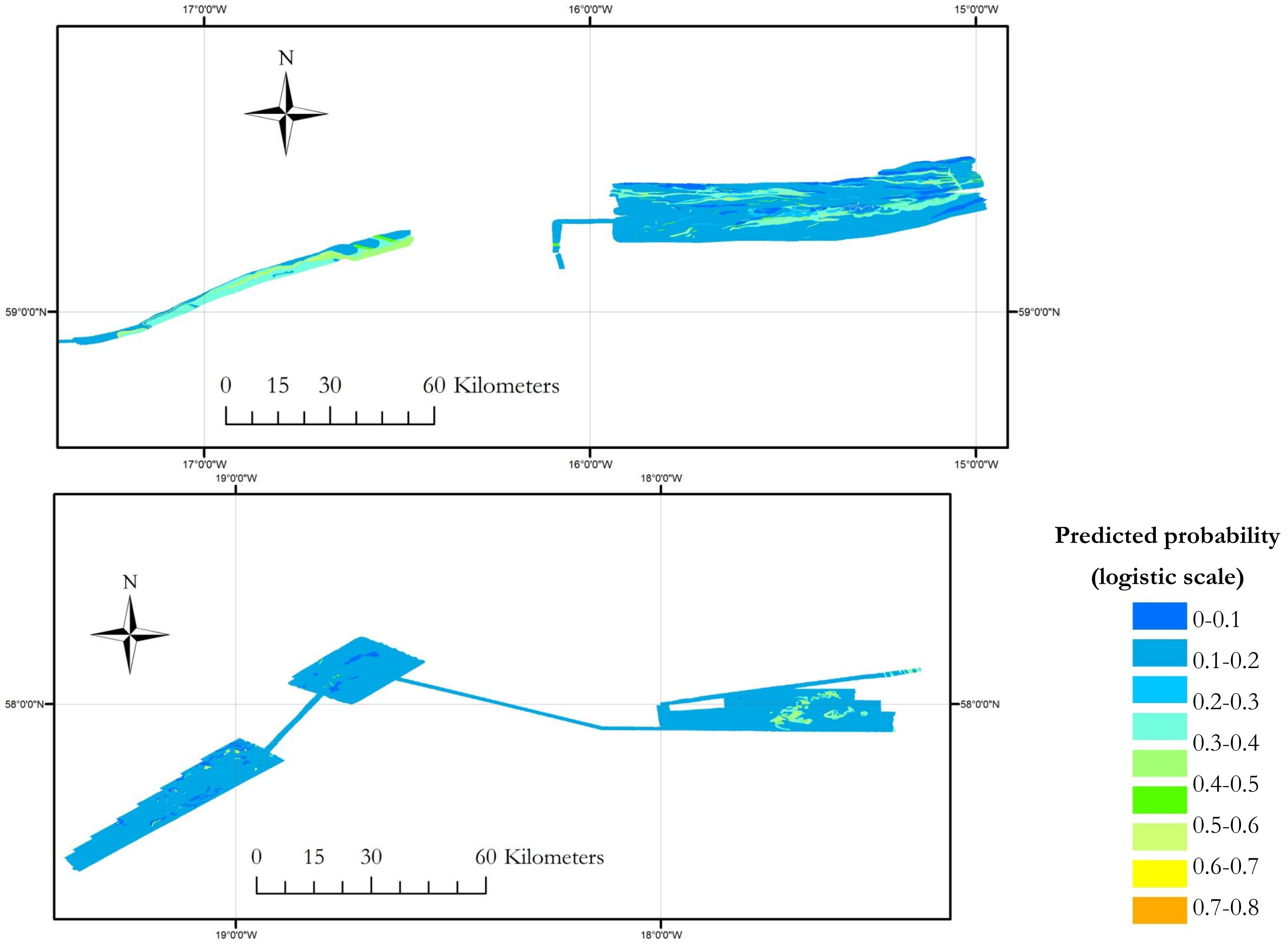

Figure E.3: Predicted probability of gorgonian occurrence on central (top) and southern Hatton Bank based on the reduced Maxent model with the categorical variables substratum and geomorphology. The warmer the colours, the more suitable the habitat is predicted to be.

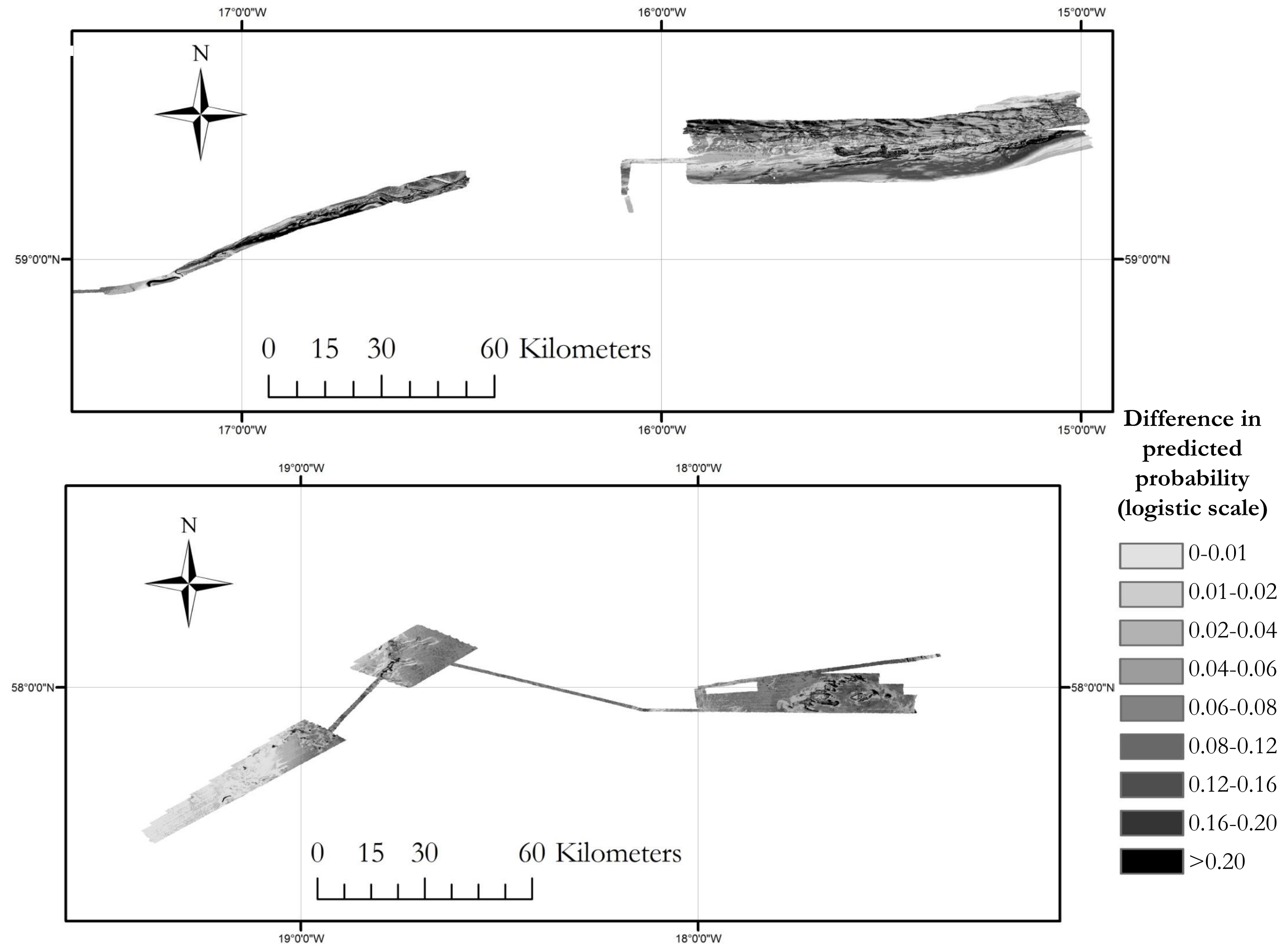

Figure E.4: Spatial distribution of differences in predicted probability of gorgonian occurrence between the full Maxent model and GLM outputs on central (top) and southern Hatton Bank. The darker the shading, the greater the difference in model predictions.

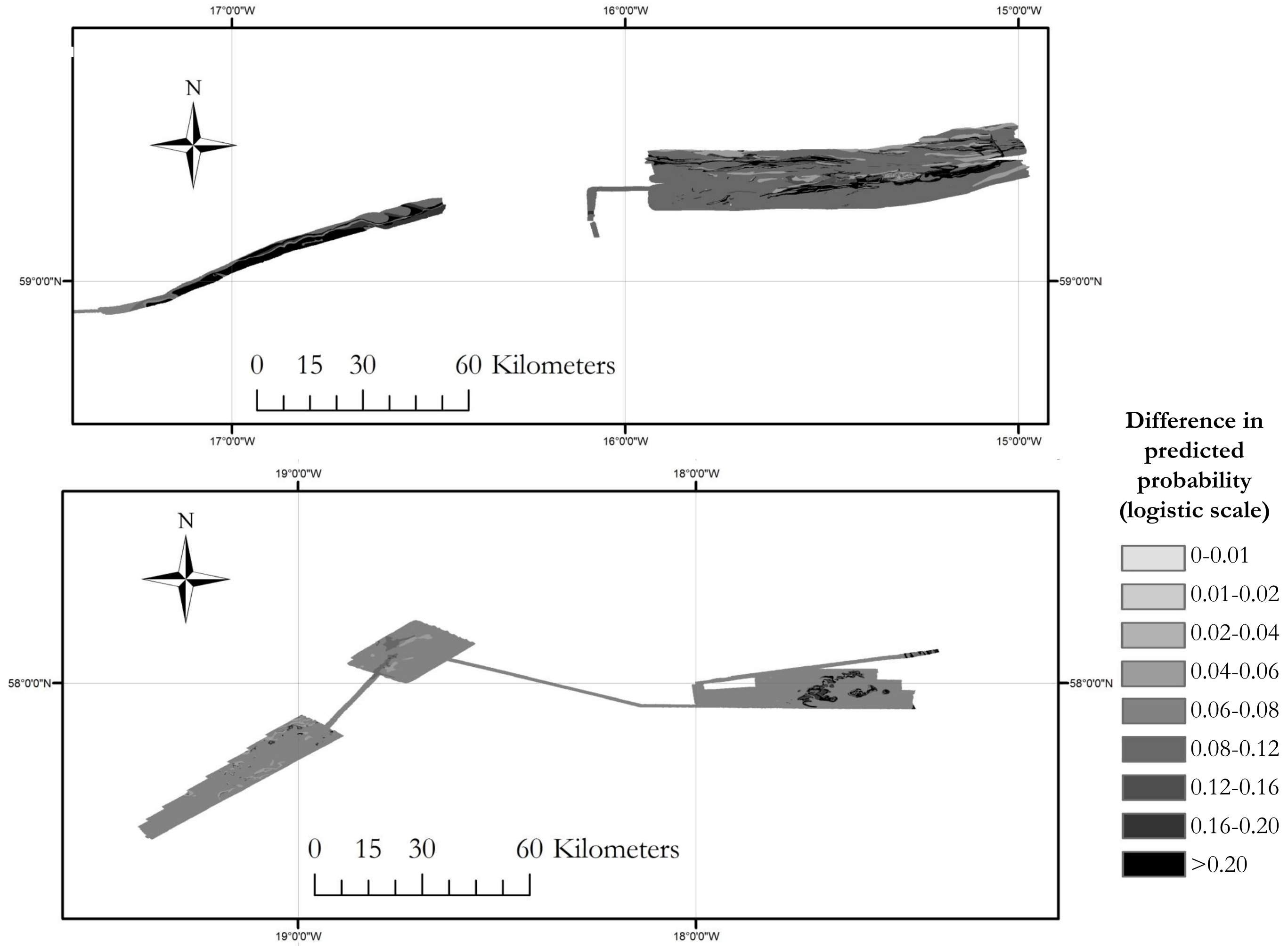

Figure E.5: Spatial distribution of differences in predicted probability of gorgonian occurrence between the reduced Maxent model and GLM outputs on central (top) and southern Hatton Bank. The darker the shading, the greater the difference in model predictions.

List of abbreviations

AUC	Area Under the Curve
BAP	Biodiversity Action Plan
BPI	Bathymetric Position Index
BTM	Benthic Terrain Model
CCR	Correct Classification Rate
Chl. *a*	Chlorophyll *a*
DWT	Devon Wildlife Trust
ENFA	Ecological Niche Factor Analysis
GAM	Generalized Additive Model
GLM	Generalized Linear Model
MCZ	Marine Conservation Zone
MPA	Marine Protected Area
OSPAR	Oslo/Paris convention (for the Protection of the Marine Environment) of the North-East Atlantic)
PA	Presence-absence
PO	Presence-only
PsA	Pseudo-absence

ROC	Receiver Operating Characteristic
SAC	Special Area of Conservation
SDM	Species Distribution Model
SENS	Sensitivity
SPEC	Specificity
SPM	Suspended Particulate Matter
SST	Sea Surface Temperature
TDD	Training Data Derived
UBRE	Un-Biased Risk Estimator
VME	Vulnerable Marine Ecosystem

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