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The utility of benthic infaunal production for selecting marine protected areas in the Irish Sea

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Award date:
2013

Awarding institution:
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The utility of benthic infaunal production for selecting marine protected areas in the Irish Sea

A THESIS PRESENTED TO BANGOR UNIVERSITY

FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

BY

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September 2013

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Summary

Many important marine ecosystem functions, goods and services rely on healthy, productive benthic communities, yet these communities are at risk from anthropogenic activity such as bottom fishing and aggregate dredging. Marine spatial management measures such as marine protected areas could help protect benthic communities from these activities and ensure the continued provision of the ecosystem goods and services that they support. The establishment of MPAs to protect benthic communities could be prioritised based on benthic invertebrate production, an indicator of benthic ecosystem quality that is comparable across different habitats. This thesis has considered the development and utility of modelled benthic infaunal production as a practical selection criterion for MPA design in the Irish Sea. The ability to model production over large scales and the spatial association between production and biodiversity have been investigated to determine whether or not benthic production can be and needs to be explicitly included as a selection criterion in MPA design to ensure protection from anthropogenic activities such as fishing.

Results indicate that an empirical, size-based model that incorporates strong environment-production relationships can successfully predict relative benthic infaunal production over large scales in the Irish Sea. The model can also investigate bottom fishing impacts and the subsequent recovery of benthic production and biomass, all of which have utility for informing MPA design. A lack of spatial association between benthic production and biodiversity suggests that sites where the protection of biodiversity and production could be achieved simultaneously are limited in number, and therefore marine ecosystem function needs to be explicitly included as a selection criterion in MPA network design to ensure protection from anthropogenic activities. The implications of results for the spatial management of benthic communities are discussed, and general recommendations for MPA network design are made.

Acknowledgements

First and foremost I would like to say many thanks to Dr Jan Hiddink, who has supported and guided me through this PhD, and provided many valuable comments. Thank you also to my supervisory committee, Prof Mike Kaiser and Prof Chris Richardson who have given sound advice and plenty of ideas.

Thank you to Dr Kirsten Ramsey at Countryside Council for Wales (CCW) (now Natural Resources Wales) for helpful discussions and providing empirically observed benthic community data, as well as access to other datasets held by CCW and Defra. Many thanks also to Dr Stefan Bolam at CEFAS for providing access to the empirically observed benthic infaunal production data described in Bolam et al. (2010).

Thank you to the masters and undergraduate students who volunteered for the Prince Madog cruise in 2011, and a big thanks to Matt and Daniel in particular who supported the data collection for Chapters 3 and 4.

Many thanks to all my family and friends for all the support and encouragement. In particular, thank you to Mum and Dad for having so much faith in my abilities.

Finally, thank you so much to Rob, for all your patience, understanding and support throughout, especially this last year. I would have struggled to make it through the last few weeks without you!

Dedication

I would like to dedicate this PhD thesis to 'Granden' and 'Reg'. I will miss you both.

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CHAPTER 1 – Introduction

1.1 SUMMARY

Benthic invertebrate communities provide and support the provision of many ecosystem goods and services, including food production. These communities and their functioning are under threat from anthropogenic pressures, particularly fishing and aggregate dredging. Marine protected areas (MPAs) are a form of marine spatial management that are fast becoming mainstream tools for managing anthropogenic activity and tackling declines in marine biodiversity and function. Since not all areas can be protected, MPA establishment needs to be prioritised based on informative selection criteria that match conservation objectives. Biodiversity or structural components of ecosystems have traditionally driven conservation effort. However, direct protection of ecosystem function by the use of functional selection criteria may better help maintain the flow of ecosystem goods and services, and achieve an ecosystem approach to management.

Of the suite of ecosystem processes operating in marine benthic communities, benthic invertebrate production is a possible functional candidate criterion for MPA designation. It plays a key role in marine ecosystems by mediating the flow of energy from primary producers to higher trophic levels, thus supporting commercial stocks. Benthic production has the potential to be modelled and compared over large scales, and it could also act as a proxy for other features of conservation interest, such as benthic biodiversity and higher predators.

Here the importance of benthic invertebrate communities and the threats to them are introduced. The practicalities of using modelled benthic production for selecting marine protected areas and the likelihood of benthic production as a proxy for other features of conservation interest are discussed, and three key research questions identified. These research questions form the focus of this PhD thesis and will be addressed in four research chapters.

1.2 CONTEXT

1.2.1 Marine ecosystem goods and services

Marine environments provide us with a suite of direct and indirect goods and services, the most apparent and well understood being food production (Beaumont et al. 2008). The provision of aggregates, fuel and energy in the form of gas, oil and tidal power, medicines, cosmetics, and recreational use are all examples of other direct benefits gained from the marine ecosystems (Beaumont et al. 2007). Indirect or supporting services are equally important, although are more difficult to quantify. These include climate regulation through exchange of atmospheric gases, flood and storm protection, waste remediation and nutrient cycling. Various ecosystem processes and functioning underlie the provision of these important services (Hein et al. 2006). For example; the fixation of carbon by marine organisms underlies climate regulation (Beaumont et al. 2007), the degradation of pollutants by bacteria in estuarine sediments aids remediation (Niepceron et al. 2010), and the mixing of sediments through bioturbation by benthic organisms facilitates nutrient cycling (Lohrer et al. 2004; Rossi et al. 2008; Ferron et al. 2009).

1.2.2 The importance of benthic invertebrate communities

Benthic invertebrate communities are those invertebrate communities living on and in the surface of seabed sediments. These communities commonly include polychaetes, bivalve molluscs, gastropod molluscs, crustaceans, echinoderms and attached cnidarians (anemones, hydroids, corals) and porifera (sponges) (Levinton, 2001; Kaiser et al. 2005). These invertebrates are grouped into epifauna, which are emergent species that live on the sediment surface, and infauna, which refer to those species that live either partially or entirely within the sediment (Kaiser et al. 2005). This thesis will focus on those infaunal macro-invertebrate communities typically associated with shallow continental shelf seas in temperate Europe.

Benthic invertebrate communities are recognised to play a key role in the provision of many goods and services (Snelgrove et al. 1997; Levin et al. 2001, Danovaro et al. 2008).

The position of benthic communities within trophic webs means that benthic macro-invertebrates are a key food source for commercial fish species, particularly demersal stocks, and are therefore important for supporting fish production (Christensen et al. 1996; Heath, 2005). Some benthic shellfish stocks, such as king scallop *Pecten maximus*, brown crab *Cancer pagurus*, European lobster *Homarus gammarus* and common prawn *Palaemon serratus* are also important fisheries in their own right.

Benthic invertebrate communities facilitate services such as nutrient and carbon cycling (Steele et al. 2007; Ferron et al. 2009), through the consumption, production, transfer and bioturbation of organic matter (Lohrer et al. 2004; Danovaro et al. 2008; Hiddink et al. 2009; Sandwell et al. 2009). Benthic invertebrates also contribute to habitat heterogeneity, through the creation of biogenic structures and reefs (Lenihan, 1999), such as horse mussel *Modiolus modiolus* beds and *Sabellaria* reefs, or through the creation of burrows and depressions. These features provide niches and refuges for other species, including other benthic invertebrates and juvenile fish species (Thrush et al. 2002).

1.2.3 Threats to benthic invertebrate communities

Growing recognition of the world-wide degradation of marine ecosystems has drawn attention to their lack of protection from anthropogenic activities (Jackson et al. 2001; Rabalais et al. 2009). This recognition extends to benthic ecosystems (Danvaro et al. 2008; Salomidi et al. 2012). Benthic invertebrate communities are at risk from a number of activities that can have a negative impact on benthic ecosystem function and thus the ecosystem goods and services that they support and provide (Danvaro et al. 2008). One of the best studied direct threats to benthic communities is fishing. Demersal fishing, such as bottom trawling and dredging, has been found to have a negative impact on the abundance, biomass, species richness and productivity of benthic invertebrates (e.g. Jennings et al. 2001; Collie et al 2005; Hiddink et al. 2006b; Reiss et al. 2009). These negative impacts result from the mortality and removal of individuals and a subsequent reduction in abundance and total biomass (Jennings et al. 2001).

The impact of fishing disturbance is stronger for some benthic groups than others, primarily due the negative relationship between body size, life history and fishing mortality (Querios et al. 2006). Large epifauna is considered most vulnerable to fishing (Thrush et al. 1998; Hermsen et al. 2003; Hiddink et al. 2006; Tillin et al. 2006), whereas infaunal communities have been found to be more resilient (Hiddink et al. 2006b; Jennings et al. 2002; Reiss et al. 2009). Some findings have even suggested that certain intensities of fishing can increase the abundance and productivity of infaunal communities, perhaps due to the release of opportunistic species from competition with larger, long lived species (Jennings et al. 2001; Hermsen et al. 2003; Querios et al. 2006). However, many of these observed positive effects are not significant (Jennings et al. 2001; Reiss et al. 2009), and conflicting evidence exists. For example, Hinz et al. (2008) found that the abundance and total productivity of nematode communities was negatively affected by bottom trawling.

The severity of fishing impacts on benthic communities also appears to differ between habitat types, largely driven by the differences in vulnerability of the associated communities (Collie et al. 2005; Hiddink et al. 2006b; Querios et al. 2006). For example, benthic communities in gravelly habitats, associated with high abundance of large, sessile epifauna, are considered more vulnerable than that in sand and mud habitats, which are associated with an increasing dominance of infauna (Collie et al. 2005).

Another direct threat to benthic invertebrate communities is aggregate dredging. Both removal from and placement of aggregates on the seafloor has localised, negative impacts on benthic invertebrates (Barrio Frojan et al. 2008; Wilber et al. 2008). Reductions in benthic invertebrate abundance, biomass and species richness and changes in community composition, for example, have been observed following dredging events (Newell et al. 1998; Foden et al. 2009), and studies into the recovery of benthic communities following aggregate extraction have found that recovery from these impacts can take from <1 year to > 10 years, depending on the habitat type and extent and magnitude of impact (Boyd et al. 2005; Foden et al. 2009). The extent of aggregate dredging in the UK is very small, covering less than 1% of the seafloor that is exposed to bottom fishing (for the period 2001-2007) (Foden et al. 2009). Due to the

highly localised and generally short-term impact of aggregate activity, it is not considered as great a threat to benthic production as fishing.

The rapidly increasing construction of offshore wind farms has raised interest and concerns over their possible effects on the marine environment (Lindeboom et al. 2011; Krone et al. 2013). Possible impacts that could affect benthic communities include disturbance of the areas during installation, e.g. pile driving (Lindeboom et al. 2011), and altered sediment regimes and seafloor togography (Wilson et al. 2010; Krone et al. 2013). However, research to date indicates generally positive benefit for marine invertebrate communities, because the increase of available hard substrata provides habitat, particularly for sessile epifauna and associated fauna (Andersson & Ohman, 2010; Lindeboom et al. 2011; Krone et al. 2013).

Land-based activities can also have an impact on benthic invertebrate communities. For example, eutrophication resulting from nutrient-rich freshwater runoff can trigger high rates of microbial decomposition of algal blooms and the subsequent depletion of dissolved oxygen in bottom waters. This results in hypoxia, or in extreme cases anoxia (Powers et al. 2005). Many studies have recorded the impacts of both short-term and long-term hypoxia and anoxia on benthic communities, all observing reductions in abundance (Powers et al. 2005; Diaz & Rosenberg, 2008; Seitz et al. 2009). If hypoxia is severe or prolonged the mass mortality of benthic fauna can result, and ecosystem function and productivity can be severely impaired (Diaz & Rosenberg, 2008; Seitz et al. 2009). These impacts of eutrophication are restricted to shallow coastal areas, with estuarine environments being the most susceptible.

Finally, climate change is considered the most wide ranging anthropogenic threat to the marine environment (Halpern et al. 2008; Brown et al. 2010). The various impacts of climate change, including rising temperatures, ocean acidification and increased magnitude and frequency of severe storm events (Pachauri & Reisinger, 2007) are all expected to have an effect on benthic invertebrate communities (Behrenfeld et al. 2006; Richardson & Schoeman, 2004; Nixon et al. 2009; Hinz et al. 2011). For example, climate change induced changes in primary productivity could alter the amount of organic

matter available to the benthos in areas of strong pelagic-benthic coupling (Behrenfeld et al. 2006; Richardson & Schoeman, 2004; Nixon et al. 2009). As temperature rises, the northward movement of both southern species and northern species is expected to occur (Hiscock et al. 2004; Southward et al. 2004), although analyses of long-term data from the English Channel suggest this has not happended for benthic invertebrates (Hinz et al. 2011). Ocean acidification, resulting from increasing uptake of atmospheric CO_2 by the oceans is expected to affect the biomineralisation rates of calcifiers such as bivalves (Thomsen et al. 2013). Kroeker et al. (2011) found that benthic invertebrate diversity, biomass, and trophic structure decreased with increasing acidification, driven by a loss of acidification-sensitive taxa. These climate-change driven changes are expected to have knock-on effects on ecosystem function (Kroeker et al. 2011).

From a marine management perspective, the indirect threats to benthic communities, such as climate change-induced changes and freshwater runoff-induced eutrophication and hypoxia, are difficult to prevent or control directly, compared to activities such as fishing and aggregate dredging. Reducing the impacts of eutrophication, for example, would require terrestrial water quality management to reduce terrestrial inputs into the marine environment (Diaz & Rosenberg, 2008), and preventing climate change impacts will require action on a global scale to reduce emissions of greenhouse gases. Mitigation measures at a local level to lessen the impacts of climate change on marine communities are possible, however. For example, Ling et al. (2009) found that protection of kelp bed benthic communities from fishing within MPAs reduced the chance of climate-driven phase-shifts to less productive sea urchin barrens.

1.3 PROTECTION OF BENTHIC INVERTEBRATE COMMUNITIES

1.3.1 Marine spatial management

Here the protection of benthic invertebrate communities from direct impacts of anthropogenic activities such as bottom fishing is considered, because these activities can be controlled from a purely marine management perspective.

Marine spatial planning and management refers to the comprehensive planning of all marine activities and uses in time and space, in order to reduce conflict and ensure the sustainable use of marine resources (Douvere, 2008). This spatial planning approach is becoming a prominent approach to the management of marine activities and conservation of marine ecosystems, and is expected to be a key tool for the implementation of ecosystem-based marine management, including the delivery of EU Marine Strategy Framework Directive objectives for Good Environmental Status (GES) (Douvere, 2008; Stelzenmüller et al. 2013). Marine protected areas (MPAs) are one form or aspect of marine spatial planning and management that are particularly popular for protecting marine communities and habitats from degradation, and ensuring that conservation objectives are not compromised by human activities (Douvere, 2008; Rabuat et al. 2009; Giakomi et al 2012). The spatial planning and zoning of activities of the Great Barrier Reef Park is a key example of this marine spatial management in action (Douvere, 2008).

With respect to the role of MPAs in protecting benthic invertebrate communities, both modelling and field studies have indicated that the protection of benthic communities from fishing activity in no-take MPAs is beneficial (Hermsen, Collie & Valentine, 2003; Collie et al. 2005; Hiddink et al. 2006b). For example, a greater abundance, biomass and diversity of benthic organisms vulnerable to fishing were observed in the Sackville Spur closed area compared to fished areas in the Northwest Atlantic (Frojan et al. 2012), and Collie et al. (2005) found a fourfold increase in production within an area closed to fishing on Georges Bank over a five year period. MPAs are expected to have a similar beneficial effect on benthic communities if they exclude activities such as aggregate

dredging, because they would prevent the removal and disturbance of the sediment and associated communities.

1.3.2 Current approaches to selecting marine protected areas in Europe

Within the EU, member states have committed to the establishment of a network of MPAs, known as the Natura 2000 network. This commitment is driven by the EU Bird- and Habitats Directives (hereafter EU Nature Directives), which in turn are driven at the international level by the Convention on Biological Diversity (CBD) and the World Summit on Sustainable Development (Sorensen & Thomsen, 2009; Giakoumi et al. 2012). Most recently the EU Marine Strategy Framework Directive (MSFD) requires member states to establish spatial protection measures that contribute to the current Natura 2000 network, as part of a programme of measures to achieve and maintain 'Good Environmental Status' of their marine waters. Northern Europe has a further obligation to establish a coherent MPA network under the Oslo-Paris (OSPAR) Convention.

The EU has a relatively well-established, centrally-driven approach to the establishment of MPAs (Sorensen & Thomsen, 2009), with defined ecological selection criteria outlined in both the EU Nature Directives and OSPAR Convention. These ecological criteria largely focus on features such as the presence of rare, threatened or declining species and habitats (European Commission Council, 1992; OSPAR Commission, 2003). The use of these 'structural' ecosystem features is driven by the key, global conservation objective; the conservation of biodiversity. This conservation goal is a feature of most environmental initiatives and policies (Salomon et al. 2006; Pressey et al. 2007), and stems from the CBD (2002), which marked the first international recognition of biodiversity decline. OSPAR selection criteria also include the presence of key stone species and maximising the representation of a range of habitats and species across the maritime area (OSPAR Commission, 2003).

Examples of sub-tidal European MPAs include the Doggerbank Special Area of Conservation Interest (SAC) in the North Sea (Netherlands), established to protect grey

seal *Halichoerus grypus*, common seal *Phoca vitulina*, and harbour porpoise *Phocoena phocoena,* and the South-West Porcupine Bank SAC off the west coast of Ireland, which was established to protect *Lophelia pertusa* reef habitat. EU MPAs in the UK include; the Fal and Helford SAC (South West England) (Langston et al. 2006) and Strangford Lough SAC (Northern Ireland), established to protect listed habitats, and the Cardigan Bay SAC (Wales), which was designated due to the presence of bottlenose dolphin *Tursiops truncatus* and harbour porpoise *Phocoena phocoena* (Kirsten Ramsey, pers. Comms). With respect to OSPAR MPAs, very few countries have identified sites that are additional to the current Natura 2000 network. An example of additional designation is the Sedlo Seamount, north of the Azores (OSPAR Commission, 2009), which was nominated for protection because seamounts are recognised to be biodiversity hotspots, and also important for supporting wide-ranging pelagic species (Gubbay, 2003).

1.3.3 Systematic conservation planning

Not all areas of the ocean can be protected. Limited resources for conservation (Myers et al. 2000), and conflicting human needs mean that space and resources for the establishment of MPAs is restricted. Many existing MPAs for nature conservation have been allocated on an ad-hoc, opportunistic basis (Stewart et al. 2003), and are often sited in areas where they simply do not conflict with other marine uses such as fishing. This approach may not necessarily result in effective conservation result, because those areas that do end up in MPAs may not be particularly valuable to conservation (Stewart et al. 2003). Systematic conservation planning is becoming increasingly utilised in the allocation of both terrestrial and marine protected areas, in order to help prioritise and maximise the achievement of conservation goals, whilst minimising costs (Margules & Pressey, 2000). It allows a structured and objective approach to site selection, involving the evaluation of potential sites against certain selection criteria. These selection criteria generally indicate the ecological quality of an area, or its value to conservation, and the metric used ultimately depends on the conservation objectives that are driving the MPAs establishment. Any costs resulting from the possible establishment of protected areas, such as socio-economic losses, can also be incorporated into the systematic conservation planning process.

Despite the centrally-driven approach to MPA establishment in Europe, systematic conservation planning has not been widely used (Giakoumi et al. 2012). Placement of Natura 2000 sites, for example, has been largely based on expert judgement regarding the EU Nature Directive and OSPAR ecological criteria (Jongman, 1995), rather than the objective evaluation of sites against these criteria.

1.3.4 Biodiversity versus functional selection criteria

There is a strong focus on single species and habitats in the EUs approach to MPA selection, with both EU Directive and OSPAR criteria relying heavily on structural metrics such as species presence, species richness, or presence of vulnerable habitats to direct conservation effort. Despite the conservation objectives of the legislative drivers, little attention is given to ecosystem processes, functioning, goods or services, with the exception of the consideration of keystone species within the OSPAR criteria. There are currently no criteria that directly relate to ecosystem functioning, or the provision of goods or services.

The recent paradigm shift towards 'ecosystem-based' management calls for a more integrated approach that considers the management of ecosystems as a whole, and focuses on ensuring the maintenance of ecosystem functioning and continued provision of goods and services, rather than the protection and persistence of a particular species (Beaumont et al. 2007; Tillin et al. 2008; Douvere, 2008). The single-species approach in traditional fisheries management, for example, is gradually being replaced with an approach that considers the wider ecosystem impacts of fishing (Reiss et al. 2009). Furthermore, the upcoming EU Marine Strategy Framework Directive advocates the ecosystem-based approach, and requires member states to achieve 'Good Environmental Status' for 11 environmental descriptors, which include ecosystem attributes such as sea floor integrity and food webs, in addition to biodiversity.

Despite this shift in focus under the ecosystem approach, functional indicators for assessing ecological quality or ecosystem state remain underdeveloped (Feld et al.

2009), and structural metrics such as species presence, abundance or community composition are primarily used (Young et al. 2008). This is because structural elements of ecosystems tend to be much easier to measure, communicate and manage, and because it is often assumed that biodiversity or structural ecosystem elements directly relate to ecosystem functioning (Millennium Ecosystem Assessment, 2005; Sandin & Solimini, 2009). That is, in the context of conservation management, if ecosystem structure is maintained, it is assumed that normal ecosystem functioning is also maintained. Some recent literature, however, has suggested that functional metrics of ecological quality or ecosystem health are needed to complement structural indicators (Jorgensen, 2000; Tillin et al. 2008; Young et al. 2008), because structural metrics do not always capture an ecosystems complete response to stresses (Young et al. 2008), and because the understanding of structure-function relationships has not yet reached a consensus (Young et al. 2008; Austin et al. 2008; Sandin & Solimini, 2009).

The ability to scale-up structure-function relationships identified in small-scale manipulations to a scale relevant to management and conservation efforts, in particular, is uncertain (Srivastava & Vellend, 2005). Both modelling and experimental studies have found that the contribution of both individual species and whole communities to ecosystem functioning can be context dependent, i.e. contingent on environmental conditions or disturbance regime, and also depends on the function in question (Cardinale et al. 2000; Cardinale et al. 2005; Boyer et al. 2009; Griffin et al. 2009; Hiddink et al. 2009). Therefore, although structural elements of ecosystems are often used as surrogates for functional attributes, they may not capture all the information regarding the functioning or condition of an ecosystem (Sandin & Solimini, 2009), especially when compared over large spatial scales.

In addition to this, with respect to MPA selection, the prioritisation of conservation effort in areas of highest species richness (so-called 'silver bullet' strategy) overlooks low diversity ecosystems that may be functionally important, and the protection of only rare, endemic species will miss a whole suite of organisms that may be critical for ecosystem processes (Gaston, 2010). Furthermore, because species composition and habitat type changes over large scales, as the driving environmental and biogeographical

processes change, it is difficult to directly compare the value or quality of ecosystems over these large areas based only on species presence, abundance or habitat type.

Given the above discussion, functional metrics are considered more useful for inferring ecological quality under the ecosystem-based approach compared to metrics such as species presence or species richness (Tillin et al. 2008). Those functional metrics that have been developed, for example, tend to be measures of ecosystem-level attributes that reflect the ecosystem processes underlying function (Hiddink et al. 2006b; Sandin & Solimini, 2008). The consideration and management of these types of ecosystem-level attributes is expected to be more effective for ensuring the continued provision of ecosystem goods and services compared to structural metrics. Therefore, although ecosystem processes may be more difficult to measure and are a more difficult concept to communicate to policy makers and managers compared to the presence of species or habitats, they are more likely to give a direct indication of an ecosystems ability to deliver goods and services, and are also comparable across different habitats and ecosystems.

In the context of selecting MPAs in the Europe Union then, a functional selection criterion could be developed to complement current structural criteria, in order to move towards an ecosystem approach to the management and protection of benthic communities and habitats, and help fulfil the ecosystem function objectives of the upcoming EU MSFD. Here the utility of benthic invertebrate production as a functional selection criterion for selecting 'functional MPAs' is investigated.

1.4 THE UTILITY OF BENTHIC PRODUCTION FOR SELECTING MPAS

1.4.1 Benthic invertebrate production and ecosystem goods and services

Any functional selection criterion developed for MPA design needs to have ecological and management relevance (Tierney et al. 2009), so should ideally reflect an ecosystem process that underlies the provision of important marine ecosystem goods or services. Benthic invertebrate production refers to the heterotrophic production of organic matter by benthic organisms per unit time and area (Cusson & Bourget, 2005). Although production can be measured for individual species, production at the community level is likely to be a better measure of ecosystem-level functioning. Benthic invertebrate production mediates the transfer of material through the food web, from primary producers to higher trophic levels (Seitz et al. 2009), and therefore plays a key role in energy flow and ecosystem dynamics (Tumbiolo & Downing, 1994; Brey, 2001). This productivity reflects the amount of energy available to the next trophic level, and thus mediates the carrying capacity of ecosystems for higher predators, including commercial fish stocks (Christensen et al. 1996; Heath, 2005; Hiddink et al. 2011; Rice et al. 2012), for example, found that in areas of reduced benthic invertebrate production due to bottom trawling, commercial fish condition was also reduced. Benthic invertebrate productivity is therefore important for supporting food production.

Benthic invertebrate production also plays an important role in the provision of ecosystem services such as nutrient and carbon cycling, because it mediates the consumption and transfer of organic matter (Steele et al. 2007; Ferron et al. 2009; Danovaro et al. 2008). Bioturbation by benthic invertebrates also mediates nutrient cycling (Lohrer et al. 2004; Hiddink et al. 2009; Sandwell et al. 2009). Although bioturbation rates depend strongly on community composition (Lohrer et al. 2004), more productive benthic communities are expected to have a high biomass, and therefore may exhibit greater bioturbation rates.

1.4.2 Benthic invertebrate production and ecosystem quality

Community secondary production has been used as a functional measure of ecosystem health because it is a direct measure of energy flow at the ecosystem-level. Valentine-Rose et al. (2011), for example, used fish community production as an indicator of ecosystem health in response to habitat fragmentation in sub-tropical mangroves, and Dolbeth et al. (2007) used benthic invertebrate production to assess the impact of eutrophication on the ecological integrity of an important estuarine ecosystem. To better understand its ability to reflect ecological quality, an understanding of how benthic invertebrate production is measured and how the life history characteristics of a benthic invertebrate population influence productivity is required.

Production is an ecosystem process and is therefore measured as a rate. Here, production refers to the somatic production of biomass by benthic macro-invertebrate fauna (i.e. does not consider production of reproductive tissue), per unit area and time. It is usually estimated as annual production (i.e. total organic matter produced in one year), and can be measured in wet weight, ash free dry weight, organic carbon or Joules (energy), for any given area or volume. When considering a community of organisms, production is a function of both the growth and mortality of individuals within that community over time (Brey, 2001). That is, both the addition of biomass through growth, and the loss of biomass through mortality, is considered.

The total production of a community is often related to the amount biomass present by dividing production estimates by the average biomass to give a production-biomass ratio (P/B) (Brey, 2001). Benthic invertebrate production can therefore be considered in terms of two different metrics; total community production and community P/B ratio. These two variables are not always found to co-vary (e.g. Bolam et al. 2010), and a decision needs to be made with respect to which metric best reflects ecosystem quality and could be utilised to direct marine spatial management. Both growth and mortality rates in natural populations are highly correlated to life history traits, and a consideration of these life history characteristics of benthic invertebrates gives an

insight into the value of using total production and community P/B ratios to inform the conservation of benthic communities.

In general, small-bodied organisms have higher growth rates and higher mortality rates than large-bodied organisms. Low biomass and high production exhibited by small-bodied organisms result in high P/B ratios, whereas the high biomass and low production of large bodied organisms result in low P/B ratios (Schwinghamer et al. 1986; Cusson & Bourget, 2005). The life span and motility of organisms also has a strong influence on production (Roberston, 1979; Cusson & Bourget 2005). Cusson & Bourget (2005) found a negative correlation between life span and production and P:B ratios, and a significant difference between the P/B ratios of motile VS non-motile species, with motile species tending to have higher P/B ratios than non-motile species. These two relationships result from a combination of factors. Longer lived species tend to increase in body size with age, and also invest more energy into respiration and reproduction than somatic growth. More motile invertebrate species are likely to have higher metabolisms and smaller body sizes than non-motile species, and therefore have higher P/B ratios (Cusson & Bourget, 2005).

Based on these observations, benthic communities that exhibit high P/B ratios could be expected to be characterised by small, short-lived, fast growing and motile species, whereas low P/B ratios would be associated with large, long-lived, non-motile species. Communities that have suffered perturbation can be dominated by small, fast growing opportunistic species and thus can be considered highly productive from a P/B ratio perspective (Srivastava & Vellend, 2005). P/B ratios are therefore not considered suitable metric to direct conservation effort, because high P/B ratios do not necessarily represent good ecological quality or ecosystem health.

In contrast to communities characterised by small, short-lived, fast growing species, communities dominated by large, long-lived species are likely to exhibit greater total production and biomass. Total production of benthic invertebrate communities is therefore expected to be a better estimate of quality over P/B ratios. Large, long-lived species are expected to be more characteristic of ecosystems that have not been

damaged or disturbed by anthropogenic activities, such as fishing, and therefore considered to better reflect a natural, healthy ecosystem state. Large, long-lived species, such as large bivalve molluscs are also often considered to have high conservation value, compared to, for example, annelid worms, because they are less numerous and more vulnerable to anthropogenic activities. The native oyster *Ostrea edulis*, quahog clam *Arctica islandica*, and horse mussel *Modiolus modiolus*, for example, are all large, rare long-lived bivalves that are conservation priority species in the UK, utilised in the current species-based, biodiversity approach to selecting marine conservation zones in England (Natural England & JNCC, 2010).

Total benthic invertebrate production may therefore be an ideal candidate for development as a functional selection criterion for the establishment of MPAs, because it is considered to a useful metric of good marine ecosystem quality that plays a strong role in providing both direct and indirect ecosystem goods and services. In addition to this, because total benthic invertebrate production is negatively impacted by bottom fishing and aggregate dredging (Murawski, 2000; Boyd et al. 2005; Hiddink et al. 2006; Foden et al. 2009), through the removal of total biomass (Jennings et al. 2001; Reiss et al. 2009), it is a useful indicator of ecosystem health in response to these anthropogenic stresses, and protection within no-take MPAs will have a positive benefit on ecological quality. Finally, benthic invertebrate production is process common to all marine environments, making it an ideal metric for comparing the quality of different habitats and ecosystems over large areas (Hiddink et al. 2006a).

This thesis will focus in particular on the use benthic infaunal production; the production of organic matter by those organisms live in or partially in the sediment (macro-infauna), as a candidate selection criterion for MPA network design. Infaunal production is chosen as the focus of this thesis because more data required for calculating production is available for this benthic invertebrate community type compared to epifauna, and infaunal communities are also considered to contribute substantially to overall benthic invertebrate community productivity. Table 1.1 indicates the variation in infaunal and epifaunal production and/or biomass across different habitat types (mud, sand, gravel and biogenic). These data suggest that infaunal

communities contribute significantly to benthic community biomass and productivity across a range of habitat types. In sandy sediments in particular, infaunal communities seem to contribute significantly to benthic invertebrate biomass compared to epifaunal communities. In gravelly habitats, on the other hand, epifaunal biomass appears to be generally higher than that for infauna. This is expected to be driven by the potentially greater habitat heterogeneity provided by coarser sediment, and a higher number of attached, sessile epifaunal invertebrate species. The figures from Bolam et al. (2010), however, indicate that infaunal production in coarse sediments can still be reasonable high (up to 896.6 kJ m^{-2} yr^{-1}).

Overall, the estimates in Table 1.1 suggest that consideration of only benthic infaunal production as a candidate selection criterion for MPA network design is justified because it is likely to provide substantial information about the total productivity of benthic invertebrate communities, and is therefore expected to be a good indicator of ecosystem quality.

Table 1.1. Range and mean production and/or biomass estimates for infaunal and epifaunal invertebrate communities in different habitat types. Source publications are included.

Habitat/ sediment	Infaunal production/ biomass Range (mean) kJ m^{-2} yr^{-1} / g WW m^{-2}	Epifaunal production/ biomass Range (mean) kJ m^{-2} yr^{-1} / g WW m^{-2}	Source publication
Mud	5.6 - 177.4 (52.8) g WW m^{-2} 65.9 - 700.7 (270.9) g WW m^{-2} 12.3 - 485.4 (144.1) kJ m^{-2} yr^{-1}	9.6 - 779.7 (208.9) g WW m^{-2}	Hinz et al. (2009) Hiddink et al. (2008) Bolam et al. (2010)
Sand	0.7 - 64.0 (22.62) g WW m^{-2} 10.8 - 422.4 (106.8) kJ m^{-2} yr^{-1}	0.5 - 7.7 (1.9) g WW m^{-2}	Hiddink et al. (2006) Bolam et al. (2001)
Gravel/ coarse	15.6 - 896.6 (128.9) kJ m^{-2} yr^{-1}	50 - 3101 (513) g WW m^{-2}	Bolam et al. (2001) Hermsen et al. (2003)
Biogenic	Data not available	Data not available	

1.4.3 Measuring benthic infaunal production over large areas

In order to use benthic infaunal production to compare ecosystem quality over large areas, it must first be measured over these large areas. As ready discussed, total community production is a function of the addition and loss of biomass through the growth and mortality of individuals within that community (Brey, 2001). The addition and loss of biomass is quantified over a specified time period, usually one year. There are various methods for calculating production. Direct methods require repeat sampling of abundance and mean mass or size of individuals in the community throughout the period of investigation (Cusson & Bourget, 2005). These include cohort-based methods such as the Allen curve and Incremental summation method, and the size-based Size frequency method (Brey, 2001). These methods are very time and data intensive, required time-series samping (Tumbiolo & Downing, 1994), and it is not realistic to use these methods when studying production over large scales (Bolam et al. 2010). Fortunately, indirect methods utilising empirical models that relate production and P/B ratios to one or more easily measured parameters have been developed (Brey, 2001). If accurate enough for purpose, these predictive models remove the need for intensive, time-series sampling (Cusson & Bourget, 2005).

Initial empirical models of benthic inverbrate production included one or two population parameters, such life span, mean body mass and population biomass (Brey, 2001). Due to the strong influence of environmental conditions on production, later models incorporated environmental variables such as temperature and water depth (Tumbiolo & Downing, 1994; Cusson & Bourget, 2005). There are now many different models that estimate production based on both these biotic (population/life history characteristics) and abiotic (environmental) variables (Tagliapietra et al. 2007). Reviews of these models (e.g. Cusson & Bourget, 2005) have indicated that the most accurate is that developed by Brey (2001), which is available online and regularly updated and requires life history, environmental and taxonomic parameters (Bolam et al. 2010). The Brey (2001) model (hereafter Brey model), however, still requires extensive benthic community sampling to provide numerical abundance and mean body mass data in order to calculate benthic community productivity.

Hiddink et al. (2006b) developed a size-based model of benthic biomass, production and species richness for the North Sea, from a model originally developed by Duplisea et al. (2002) that predicted the size-distribution of benthic assemblages and investigated trawling impacts. The Hiddink (2006) model (hereafter Hiddink model) extended the Duplisea (2002) model in a variety of ways, including the addition of a habitat parameter. This enabled the extended model to predict benthic community characteristics over larger spatial scales, where habitat data were available (Hiddink et al. 2006b). The dynamic, size-based nature of this empirical model means that minimal biotic data is required once parameterised, and so it is the least demanding in terms of benthic sampling.

This type of empirical modelling would be useful for creating a map or data layer of benthic invertebrate production to inform marine spatial management in the form of marine protected areas. For example, model outputs could highlight area of high benthic invertebrate productivity that could be prioritised for protection. In order to incorporate benthic invertebrate production in systematic conservation planning a data layer of model outputs could be included in reserve selection software such as MARXAN (Stewart et al. 2003). MARXAN (version 2.1.1.) is one of the most well-known conservation planning software available, used to design protected area networks that meet specified conservation targets whilst minimizing costs, through a process of simulated annealing (see Ball & Possingham (2000) for technical details of how Marxan operates).

In addition to predicting benthic production, the Hiddink model can also estimate the impacts of bottom fishing, and the capacity of benthic communities to recover following fishing impact. Both these metrics could also be useful for inform spatial management options to preserve benthic communities (Hiddink et al. 2006b). For example, knowledge of the extent and intensity of fishing impact could inform restorative management, and an understanding of the recovery potential of benthic communities, i.e. the time is takes for the benthic community to recover to a unfished state following

fishing impact, can help managers direct fishing impacts away from vulnerable towards resilience communities through spatial planning and measures.

The Hiddink model could also support the evaluation of spatial management options for no-take marine protected areas or bottom fishing closures by running the model under various different management scenarios and analysing the outputs. This would require management objectives for benthic invertebrate production and fishing to be clearly defined in order to assess the achievement of those objectives under the different scenarios. Therefore, the Hiddink model could not only provide the ability to map benthic invertebrate production for informing spatial management such as marine protected area design, but can also analysis, develop and evaluate spatial management options (Stelzenmuller et al. 2013) regarding bottom fishing. The model cannot, however, examine or assess cumulative effects, i.e. the combined effect of multiple human activities. The model is limited to predicting the impact of activities that have a size-dependent impact on benthic invertebrates (Hiddink et al. 2006a).

Using the Hiddink model to inform marine spatial management would require confidence in the accuracy of model predictions over large scales. Tillin et al. (2009) investigated the performance of the Hiddink model in predicting benthic secondary production for the Southern North Sea, by comparing model outputs with those obtained from the more direct and established Brey model. It was found that model outputs were not correlated, and that confidence in the Hiddink model was not great enough to be utilised for predicting production over large spatial scales around the UK (Tillin et al. 2009).

Several assumptions and limited datasets were utilised in the development and parameterisation of the Hiddink model (Hiddink et al. 2006). Carrying capacity parameterisation, for example, was based on a small dataset of chlorophyll-a content of sediment data, and interpolated chlorophyll-a sediment data were used to estimate benthic carrying capacity in the model. The influence of spatial grain and spatial extent was also not considered when parameterising the Hiddink model. The nature of observed ecological relationships can vary with the spatial grain and extent of analysis

(O'Neill et al. 1986; Wiens, 1989; Levin, 1992), therefore the importance of drivers of productivity may change as the grain and extent of analysis changes. As a result, confidence that the empirical environment-production relationships identified by Hiddink et al. (2006) during model parameterisation can be scaled up to the 9 km^2 scale of predictions is limited, and the degree to which the identified relationships apply over large areas is unknown.

In order to apply the Hiddink predictive model for the purpose of MPA design, it will require refining and re-parameterising for the particular area of interest. To predict benthic production in the Irish Sea, for example, a quantitative understanding of the relationship between the environmental conditions and the productivity of benthic communities in this area would be required, and an understanding of the influence of spatial grain size and extent on these relationships would be helpful to identify the optimal scale at which to make predictions. Ideally spatial continuous and easy to obtain environmental data would be used to support predictions of benthic invertebrate production. This would ensure that spatial continuous predictions could be made over large scales in most areas.

1.5 BENTHIC PRODUCTION AS A PROXY FOR OTHER FEATURES OF CONSERVATION INTEREST

1.5.1 Win-win conservation scenarios

In addition to being a stand-alone indicator of benthic ecosystem value, benthic invertebrate production could also act as an indicator for other features of conservation interest. If there is spatial covariance between production and these features, the use of benthic production as an MPA selection criterion could result in 'win-win' situations for conservation (Anderson et al. 2009). That is the protection of benthic invertebrate production could result in the protection of other features of conservation interest if they occurred in the same place. A weak association between different features or ecosystem services of interest has been found in the literature (e.g. Eigenbrod et al. 2009). However, these studies often compare disparate services, such as carbon

sequestration and recreation. In the context of marine conservation and management, there may be a greater possibility of concurrence between benthic production and other features of conservation interest. These features include higher predators and benthic biodiversity.

1.5.2 Benthic invertebrate production and higher predators

Objectives to conserve higher predators are common, given their recognised role as top-down regulatory forces (Ritchie & Johnson, 2009), and often charismatic nature (Perry, 2010). Higher predators can include important Habitat Directive species such as seals and dolphins, as well as commercial fish stocks that feed on benthic fauna. Highly productive areas may be associated with the presence of higher predators due to a greater ecosystem carrying capacity. Although the reliance of commercial stocks on benthic production, for example, has been quantified through stomach content- and stable isotope analyses of trophic dynamics, there is little empirical work that compares the importance of different areas of benthic production to higher predators, and directly links their presence to highly productive benthic communities.

1.5.3 Benthic invertebrate production and benthic invertebrate diversity

Areas of high benthic invertebrate production could be associated with a high number of benthic invertebrate species. This hypothesis is driven by the observed positive correlations between diversity and productivity in natural systems (Waide et al. 1999; Mittelbach et al. 2001), such as over latitudinal gradients (Cardinale et al. 2009), and also the findings of Biodiversity-Ecosystem Function (BEF) research (Balvanera et al. 2006; Srivastava & Vellend, 2005). This research investigates the effects of biodiversity on ecosystem function, and has indicated that the loss of diversity from an assemblage can reduce the rates of ecosystem processes associated with that assemblage (Hillebrand & Matthiessen, 2009).

Observed positive correlations in nature could exist due to simple covariation of production and diversity. For example, a correlation between species richness and

production could occur because both species richness and the production of community biomass are constrained by the availability of limiting resources, such as food supply (Loreau et al. 2001; Schmid, 2002; Cardinale et al. 2009).

In BEF research, the relationship between community diversity and community productivity has received the most attention (Cardinale et al. 2009). BEF experiments have indicated a general positive correlation between these two variables, and identified three primary causal mechanisms that create this relationship (Srivastava & Vellend, 2005; Hillebrand & Matthiessen, 2009). These propose that an increasing number of species increases resource use efficiency within a community. Evidence for these has been found in experimental communities where either initial species diversity is manipulated or species are sequentially removed from a community (Balvanera et al. 2006). The mechanism of facilitation refers to the process whereby the presence of certain species within the community benefits the growth or function of others, due to strong positive interspecific interactions (Hillebrand & Matthiessen, 2009). If more species are present in a community the opportunities for facilitation are considered greater. Complementarity refers to differences between species in resource utilisation for biomass production, which reduces interspecific competition and increases resource use efficiency. Finally, sampling or selection effects (also known as the functional dominance effect) refers to the situation when certain species contribute disproportionally to ecosystem production, and results in their loss having a large impact on this function.

Although there is empirical evidence to support these hypotheses regarding biodiversity-production relationships, the majority of BEF research to date is primarily focused on terrestrial systems and is largely restricted to relating primary production to autotrophic species richness, although this focus has diversified recently (Balvanera et al. 2006; Hillebrand & Matthiessen, 2009). There also is a strong reliance on small-scale, and short-term, artificial manipulative studies. Very few studies have investigated diversity-function relationships over large scales. Those that have offer different conclusions. Danovaro et al. (2008), for example, found a consistent positive association between species richness and several different functions within deep-sea ecosystems

over global scales. Other studies from marine and freshwater systems have found that the association between diversity and function can be moderated over environmental gradients or disturbance (Hiddink et al. 2008; Cardinale et al. 2005). These later two studies observed this pattern at the scale more relevant to management and conservation (Srivastava & Vellend, 2005). With respect to marine subtidal communities, a single study by Bolam et al. (2008) found a positive relationship between high biomass (total production) and high species richness, but not with community P/B ratios. It appears then, that the observed association between diversity and the function of interest is dependent both on scale, environmental gradients and the function in question (Harmelin-Vivien et al. 2009; Hiddink et al. 2009).

Overall, there is currently no consensus regarding the nature, strength and predictability of diversity-production relationships in natural systems (Hillebrand & Matthieseen, 2009).

1.6 PROTECTION OF BENTHIC PRODUCTION IN MPAS

1.6.1 Is targeted protection of benthic production required?

As already outlined, marine protected area design has traditionally focused on protecting biodiversity and habitat (Armsworth et al 2007), and the protection of biodiversity and habitat is a legal requirement demanded by the EU Natures Directives. This legal requirement means that conservation efforts cannot be re-directed from the protection these structural features, instead efforts will need to expand to encompass the protection of benthic invertebrate production in addition to biodiversity.

Given the above discussion regarding the association between benthic invertebrate production and other features of conservation interest, and the fact that there are many EU MPAs established and planned for biodiversity, perhaps the targeted protection of benthic invertebrate is not necessary. 'Biodiversity' MPAs may adequately protect benthic invertebrate communities and productivity, therefore removing the need for an additional, functional selection criterion for MPA design. On the other hand, biodiversity

MPAs alone may not achieve adequate protection of benthic invertebrate production and functional MPAs that specifically aim to restore or protect this important ecosystem process may be required. Clearly management or conservation objectives for benthic invertebrate production would need to be established in order to assess whether or not protection in biodiversity MPAs is sufficient, or whether or not a functional, benthic invertebrate production selection criterion should be developed to direct MPA design.

1.7 AIMS AND OBJECTIVES OF THESIS

1.7.1 Summary of current knowledge and understanding

Here benthic infaunal production has been proposed as a functional indicator of marine ecological quality that could inform ecosystem-based, marine spatial management. In particular, benthic infaunal production could be utilised as a selection criterion for directing MPA design. Benthic infaunal production is a process that plays an important role in the functioning of marine ecosystems, and underlies the provision of a number of ecosystem goods and services. The most important of these is its role in mediating the transfer of energy from primary producers to predatory species, providing food to higher trophic levels. Estimates of benthic infaunal production are therefore useful indicators of energy transfer efficiency and ecosystem carrying capacity (Rice et al. 2012).

With respect to the practicalities of using benthic production as a MPA selection criterion, in contrast to the current selection criteria used within the EU and OPSAR frameworks, benthic production has a greater utility than metrics such as species or habitat presence for comparing ecosystem quality and function across different areas or habitats. Furthermore, although not all threats to benthic production can be mitigated by MPAs, no-take MPAs are considered highly effective for protecting production from the impacts of bottom fishing and aggregate dredging, the biggest immediate threats to production. MPAs are therefore considered useful tools for preserving this important marine ecosystem process and the goods and services it supports. High productivity

may not always a good representation of ecosystem quality, however. If benthic production is utilised as a criteria, it is suggested the total benthic infaunal production is used, rather than P/B ratios.

There is potential to predict total benthic production estimates over large scales using empirical models based on allometric relationships, population dynamics and key environmental parameters. Although such models have recently been developed, they are not yet accurate enough to predict production over the scales required to inform MPA design. The consideration of spatial scale during model parameterisation is recommended to ensure greater confidence in predictions at a particular spatial grain and over large spatial extents.

Benthic production could have even greater utility as a selection criterion if it acted as a proxy for other features of conservation interest, such as higher predators and biodiversity. The use of this functional selection criterion could result in win-win conservation scenarios if this were the case. Although theory and observation from other trophic levels and systems suggest a positive relationship exists between production and diversity, there is limited empirical evidence of this association in marine subtidal environments. Whether or not the association is consistent at the scales at which MPAs are implemented is another question that remains unanswered. There is also currently little evidence that directly relates higher predators to areas of high benthic productivity.

Finally, if MPAs designated to protect biodiversity also protect sufficient amounts of benthic invertebrate production, a functional, benthic invertebrate production selection criterion would not be required.

1.7.2 Key research questions

Given the above discussion, it is clear that there are significant research gaps with respect to the development and utility of benthic production for selecting MPAs. These require addressing to determine whether or not it is possible and necessary to develop

benthic infaunal production as an MPA selection criterion, and also whether the use of this functional MPA criterion could result in win-win conservation scenarios. The following key research questions have been identified; i) can benthic infaunal production be modelled over large scales using easily obtained environmental variables? ii) Is there a spatial association between benthic infaunal production and biodiversity? iii) Does benthic infaunal production need to be explicitly included as a selection criterion in MPA design in order for it to be protected from anthropogenic activities such as fishing?

These research questions will be applied to benthic invertebrate communities in the Irish Sea, because of the easy availability of benthic community, environmental and fishing activity data. Due to the logistical constraints of manipulative work at depth and the scales at which the above relationships will be investigated, research will be largely restricted to the investigation of patterns of association between observed benthic infaunal production and environmental parameters, and modelled benthic infaunal production and biodiversity features of conservation interest found within spatially-explicit datasets.

To determine whether or not benthic infaunal production can be modelled over large scale using easily obtained environmental variables, Chapter 2 will first establish an understanding of the key environmental drivers of benthic production in the Irish Sea. Potential environmental drivers investigated include sea surface chlorophyll-*a*, seabed sediment type, modelled hydrodynamic conditions and characteristics and bottom fishing intensity. In particular, this chapter will investigate how any identified environment-production relationships vary with spatial grain (resolution of observation) and extent (total area over which observations are made), in order to inform a suitable scale for making predictions. Chapter 3 will then refine and re-parameterise the Hiddink empirical model of benthic communities in order to incorporate these identified environment-production relationships for the prediction of benthic infaunal production in the Irish Sea. Chapter 3 will compare the refined model predictions to independent, observed benthic community data in order to validate the model outputs.

To gain a better understanding of the use of benthic production as a proxy for biodiversity features, Chapter 4 will investigate the spatial association between benthic infaunal production and biodiversity features of conservation interest in the Irish Sea, such as benthic invertebrate diversity, cetacean abundance and species of conservation concern. This chapter will provide empirical evidence to determine whether or not benthic production is consistently, positively associated with other features of interest at the spatial scale of the Irish Sea, and therefore its utility to inform MPA design that achieves several conservation objectives (win-win conservation scenarios). The possible of the influence of spatial grain and extent on the spatial association between benthic production and biodiversity is recognised, and it would be useful to investigate the degree to which any observed pattern of association is mediated by spatial grain or extent. Unfortunately this was not possible due to spatial scale of available data and time constraints, and therefore the consideration of spatial scale is not included in the chapter.

Finally, Chapter 5 will address the extent to which MPAs networks designed to protection biodiversity also protect benthic infaunal production, and the degree of similarity between biodiversity MPA networks and functional MPA networks. This will help to determine whether or not a benthic infaunal production MPA selection criterion is required in addition to biodiversity criteria to achieve the protection of ecosystem function.

The results of the above chapters will help determine the utility of benthic infaunal production as a practical indicator of benthic ecosystem quality for the purpose of informing ecosystem-based marine spatial management, particularly MPA design. Such a functional selection criterion could have the potential to support the delivery of an ecosystem-based approach and help halt the continuing observed declines in both marine ecosystem function and biodiversity.

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CHAPTER 2 - The drivers of benthic production in the Irish Sea: a multi-scale analysis

2.1 AIM: To identify the primary environmental drivers of benthic production in the Irish Sea. The influence of spatial grain and extent on the importance of these drivers will be investigated in order to determine the most suitable spatial scale for predictive modelling.

2.2 ABSTRACT

Benthic communities play a key role in marine ecosystem functioning and provide food for commercial fish species, yet they are under threat from various anthropogenic pressures. Bottom fishing in particular can reduce the abundance, biomass, species richness and productivity of these important communities. Benthic secondary production, the heterotrophic production of organic matter by benthic macro-invertebrates per unit area and time, is a useful indicator of benthic ecosystem quality that could help prioritise marine protected area design to manage the impact of bottom fishing on benthic communities. Here the primary drivers of benthic production in the Irish Sea will be investigated in order to inform predictive model development for the purpose of advising MPA design. The influence of spatial grain (resolution of observations) and extent (total area under consideration) on the importance of these drivers will be examined to give an insight into appropriate spatial scales for predictive modelling. Chlorophyll-*a* concentration at the sea surface, seabed sediment type and bottom fishing activity were found to be the most important drivers of benthic production in the Irish Sea, and spatial grains up to around 20 km^2 were identified to be the most suitable resolution for predictive modelling. The importance of these environment-production relationships, however, was not consistent as the extent of analyses increased. Only chlorophyll-*a* was found to be a useful predictor of productivity across the whole extent of the Irish Sea area. Although this has implications for the confidence with which benthic secondary production can be predicted, these findings are considered a useful first step for informing the development of a predictive model of benthic production to advise MPA design.

2.3 INTRODUCTION

Benthic communities are recognised to play a key role in marine ecosystem function and the provision of goods and services (Snelgrove et al. 1997; Levin et al. 2001, Danovaro et al. 2008). Benthic macro-invertebrates, for example, are a key food source for many commercial fish stocks (Christensen et al. 1996; Heath, 2005), and benthic shellfish stocks, such as King Scallop *Pecten maximus*, Common Prawn *Palaemon serratus* and European Lobster *Homarus gammarus* are lucrative fisheries in their own right. Benthic communities facilitate nutrient and carbon cycling through the consumption, production, and transfer of organic matter (Danovaro et al. 2008), and certain benthic species play an important role in the creation of habitat heterogeneity. For example, filter feeders such as Horse mussels *Modiolus modiolus* create biogenic structures (Lenihan, 1999), and other organisms create burrows and depressions, all of which provide habitats for other species (Thrush et al. 2002).

Anthropogenic activity can have a negative impact on these various benthic ecosystem functions, goods and services. Bottom fishing and aggregate dredging, for example have been documented to reduce the abundance, biomass, species richness and function of benthic invertebrate communities through the removal and mortality of individuals (Jennings et al. 2001; Collie et al. 2005; Hiddink et al. 2006a; Reiss et al. 2009; Frojan et al. 2008; Wilber et al. 2008). The extent of aggregate dredging in the UK is very small, covering less than 1% of the seafloor that is exposed to bottom fishing (for the period 2001-2007) (Foden et al. 2009), therefore bottom fishing is considered a greater anthropogenic threat to benthic communities and their functioning.

It is recognised that the impact of bottom fishing on benthic communities can be managed through spatial management measures such as marine protected areas (MPAs) (Halpern, 2003; Duineveld et al. 2007; Hiddink et al. 2006c). Limited resources for conservation (Myers et al. 2000), and conflicting human needs, however, mean that the establishment of MPAs needs to be prioritised in some way, i.e. protecting areas of highest quality or value to conservation. Systematic conservation planning is becoming increasingly utilised in protected area design because it allows an objective approach to

site prioritisation, by evaluating potential MPA sites against certain selection criteria (Margules & Pressey, 2000). The specific selection criteria used to prioritise MPA placement depend ultimately on the conservation objectives that drive their establishment.

In the context of benthic communities, a suitable MPA selection criterion may be benthic community productivity. That is, the secondary production of organic matter by benthic macro-invertebrates per unit area and time (Cusson & Bourget, 2005). Community secondary production has been identified as a suitable functional indicator of ecosystem quality because it plays an important role in energy flow and ecosystem dynamics (Tumbiolo & Downing, 1994; Brey, 2001; Valentine-Rose et al. 2011). The productivity of marine benthic macro-invertrebrates mediates the transfer of material from primary producers to higher trophic levels (Seitz *et al.* 2009), and their position within trophic webs means that their productivity is key for supporting demersal fish stocks (Christensen et al. 1996; Heath, 2005). Flatfish nursery grounds, for example, have been found to be associated with high macrobenthic productivity (Wouters & Cabral, 2009).

Secondary production in benthic communities is also a process common to all marine ecosystems, making it an ideal metric for comparing quality across large areas and different habitats (Hiddink et al. 2006a). Furthermore, no-take MPAs have been shown to be effective for protecting the productivity of benthic communities (Collie et al. 2005; Hiddink et al. 2006c). Benthic secondary production is therefore considered a suitable selection criterion for prioritising the placement of no-take MPAs, because it is a useful indicator of ecosystem function and quality, and its protection within MPAs is likely to be beneficial for the continued provision of the goods and services that it supports. To inform the spatial management of benthic productivity, knowledge of its spatial distribution is required. Direct measurements of benthic production are very time and data intensive (Tumbiolo & Downing, 1994), therefore the development of empirical modelling techniques to predict benthic production would help facilitate the use of this indicator of ecosystem quality in MPA design.

Hiddink et al. (2006a) developed a size-based model of benthic biomass, production and species richness for the North Sea, from a model originally developed by Duplisea et al. (2002). The Hiddink (2006) model includes habitat/environmental parameters to enable it to predict benthic community characteristics over large spatial scales (Hiddink et al. 2006a). Tillin et al. (2009), however, found that confidence in the Hiddink (2006) model was not great enough to be utilised for predicting production outside the original area for which it was parameterised. This may be because the importance of different environmental drivers may vary across different areas. Bolam et al. (2010), for example, was unable to to explain the spatial variation in benthic secondary production across the UK continental shelf using a single suite of environmental characteristics. In order to apply the Hiddink (2006) predictive model to another area, it will require re-parameterising for that particular area. To predict benthic production in the Irish Sea, for example, a quantitative understanding of the relationship between the environmental conditions and the productivity of benthic communities in this area is required.

The relationships and interactions driving any one ecological pattern operate on a range of different scales (Levin, 1992); therefore the importance of the observed relationship between two variables is likely to be influenced by the spatial scale at which they are measured (O'Neill, 1989; Wiens, 1989). There are two aspects of spatial scale; (i) spatial grain, which is the resolution or unit size of observations, e.g. the quadrat, or the sample unit area within which measurements are made, and (ii) spatial extent, which is the overall area under consideration by a study. The ability to detect ecological relationships is dependent on both the spatial grain and extent of an investigation (O'Neill et al. 1986; Wiens, 1989), therefore the importance of drivers of productivity are likely to change as the grain and extent of analysis changes. To date, multi-scale analyses on the drivers of productivity across large areas have not been conducted, and the lack of consideration of spatial grain and extent by Bolam et al. (2010), for example, might explain why significant environment-production relationships were not identified.

Here then, the primary environmental drivers of benthic secondary production in the Irish Sea will be investigated at a range of spatial grains and extent, in order to examine

how any observed environment-production relationships change with spatial scale. The spatial grain at which the explanatory power of environmental variables is considered highest (i.e. a close correlation between observed and fitted values) will be considered the most appropriate scale at which to make predictions of benthic production for the purpose of informing MPA design. As the spatial extent changes, the importance of drivers may also change. Studying more than one spatial extent will help determining the degree to which a relationship driving productivity at in one area can be generalised to other areas (Thrush et al. 1997), giving an insight into the expected confidence in predictions over the whole Irish Sea area.

The environmental variables investigated are; remotely-sensed sea surface chlorophyll-*a* concentration, water column characteristics, including annual frequency of pelagic fronts, modelled tidal-induced bed shear stress (hereafter tidal shear stress), wave-induced bed shear stress (hereafter wave shear stress), seabed sediment type and bottom fishing intensity (estimated from vessel monitoring system (VMS) data). These variables are chosen because previous research has indicated that they may be important in driving benthic productivity.

Food supply in particular is considered a major limiting factor on biomass and production (Beukema & Cadee, 1997; Bourget et al. 2003), and higher rates of primary production, as indicated by sea surface chlorophyll-*a* concentration (Agboola et al. 2013) are expected to be associated with higher rates of secondary production (Schrum et al. 2006; Darnis et al. 2012). The amount of this resource that reaches benthic communities is dictated by the hydrodynamic regime (Kaiser et al. 2006), and therefore the presence of pelagic fronts (Schrum et al. 2006; Darnis et al. 2012), stratification (Bolam et al. 2010) and degree of shear stress experienced by the seabed (Hiddink et al. 2006) could be useful proxies for the amount of food available to the benthos. Tidal and wave-induced seabed shear stresses, for example, control the degree of water movement at the water-sediment interface, which in turn influences the availability of food to the benthos and growth rate (Warwick & Uncles, 1980; Snelgrove & Butman, 1994). High tidal shear stress impairs the supply of food, by transporting it away too quickly, and so reduces growth rates (Hiddink et al. 2006a). Conversely, if water

movement is too slow, benthos may not receive not enough food to maintain metabolism (Patterson & Black, 1999). Very high tidal shear stress can also impair benthic production if the force of water movement results in significant erosion of sediment. Wind-induced wave shear stress is stronger than tidal shear stress and can result in the re-suspension of sediments, which releases organic matter and can enhance secondary production (Kaiser et al. 2006), but, similarly, if it becomes too strong, sediment can be moved across the seabed and have negative effect on secondary production through habitat disturbance-induced mortality (Emerson, 1989; Hiddink et al. 2006a).

Sediment characteristics have a strong influence on benthic community composition (Van Hoey et al. 2004; Reiss et al. 2009), and may also influence productivity. Grain size and organic content in particular have been found to be associated with both community composition and biomass (Warwick et al. 1991). Ricciardi & Bourget (1999), for example, found that decreasing grain size correlated with increasing total biomass, driven primarily by an increase in deposit-feeder biomass. This study was limited to intertidal areas, however, and in contrast Bolam et al. (2010) found that the communities associated with coarser sediment often had higher total production values than other habitats across the UK continental shelf. Gravelly habitats in particular tend to be associated with greater numbers of large epifauna compared to finer sediments (Collie et al. 2005). Sediment characteristics are largely determined by the hydrodynamic regime (Warwick & Uncles, 1980), and as a result changes in productivity with sediment type may simply reflect differences in hydrodynamic conditions.

It is expected that local factors, such as sediment type will influence those benthic communities (and therefore perhaps their productivity) that are directly associated to that area, therefore any relationship between productivity and sediment type is expected to be found only at small spatial grains. Fishing intensity is expected to have a negative impact on benthic production (Jennings et al. 2001; Collie et al 2005; Hiddink et al. 2006b; Reiss et al. 2009), and is expected to be observed at small to medium spatial grains due to the inaccuracy of fishing intensity estimates derived from VMS data at very small and very large spatial grains (Mills et al. 2007, Lambert et al. 2012). Chlorophyll-*a*

at the sea surface and water column characteristics (e.g. presence of fronts, stratified versus well-mixed areas) are other potential drivers of productivity, due to their influence on food supply (Kaiser et al. 2006; Schrum et al. 2006). A relationship between these factors and productivity are expected to be observed at larger spatial grain sizes because they are unlikely to directly influence those benthic directly beneath on the seafloor, due to water movement (tides, currents), and they may also be overridden by more local and biological factors (e.g. competition, predation) at smaller scales.

The following hypotheses will be tested; (i) local factors such as seabed sediment type, tidal shear stress and wave shear stress are expected to have a relationship with benthic production at small spatial grain sizes. (ii) Fishing intensity is expected to have a negative relationship with benthic production, but this will not be observed at the smallest or largest grain sizes. (iii) Chlorophyll-*a* at the sea surface and water column characteristics are expect to have a relationship with benthic community production, and these relationship are expected to be observed at large spatial grains.

2.4 MATERIALS AND METHODS

2.4.1 Method overview

Benthic community production data, environmental data and bottom fishing intensity data was collated from existing data sources for the Irish Sea and Northern Celtic Sea for the time period 2004 to 2008. To investigate the influence of spatial grain on environment-production relationships these data were partitioned into nine different spatial grains within a restricted, 20,000 km^2 area using a gridded approach. To investigate the influence of spatial extent, data at a spatial grain of 5 km^2 was extracted for five increasing spatial extents that reached a maximum coverage of 100,000 km^2. Generalised least squares regression was used to elucidate the importance of the different environmental and anthropogenic variables that drive benthic community production at these different spatial grains and extents.

The benthic data used in analyses was restricted to a limited time period (2004 to 2008) because it is expected that benthic communities and productivity in the Irish Sea may change over time, for example due to changes in primary productivity or temperature under climate change (Jennings et al. 2002; Hinz et al. 2011). Temporal variation in production may complicate the analysis or influence the interpretations of results if this is not accounted for in the analysis. A maximum time period of five years within which benthic data was collected was set as criteria for inclusion in analysis, in order to minimise the chances of significant change in productivity over time.

2.4.2 Data collection

Empirical benthic infaunal production estimates

Key criteria for calculating empirical benthic community production are species-specific abundance and biomass data. Although many surveys of benthic macro-infauna have been conducted in the Irish Sea, the majority of these datasets do not include species-specific biomass records which are necessary for the calculation of benthic production. Given these criteria, and the limit of a five year time period, available benthic community abundance and biomass data for this study was restricted to that collected during five independent benthic surveys conducted across the Irish Sea, between November 2004 and May 2008. These research surveys were undertaken by Environment Agency Wales, the Countryside Council for Wales and the School of Ocean Sciences, Bangor University, each for different original purposes. See Table 2.1, Appendix 2.7.1 for details of these research surveys.

The number of stations sampled within each survey ranged from one to twenty one, giving a total of 49 stations of benthic infauna abundance and biomass data available for analysis. At each station, two to five replicate samples were taken, depending on the survey, and the most common gear used was the 0.1 m^2 Day Grab. Only data for those organisms collected using a 1 mm sieve were used for estimating benthic community production. Replicate grabs at a station were pooled and all species data were standardised to number of individuals and total wet mass (grams) per m^2. Species

where total wet mass equalled <0.001 g m^{-2} were removed due to a lack of a tangible biomass value and because they were considered to be inconsequential to subsequent calculation of community production estimates.

Total annual benthic infaunal production estimates (kJ m^{-2} yr^{-1}) for each station were calculated from species abundance and biomass per m^2 using an empirical model freely available in spreadsheet form on the Internet http://www.thomas-brey.de/science/virtualhandbook/navlog/index.html (Brey, 2001). This multiple regression model calculates total annual production (kJ m^{-2} yr^{-1}) and production/biomass (P:B) ratio (yr^{-1}) for a given population based on a number of population-specific and habitat-specific inputs (see Brey 2001 for a detailed description of model). Here each population represents a different species, and so species-specific biomass (kJ m^{-2}), abundance (individuals m^{-2}), mean individual body mass (kJ), life history trait and taxonomic data were input into the model, along with station-specific depth and mean annual bottom water temperature (obtained from http://www.gebco.net/data_and_products/gridded_bathymetry_data and http://cobs.pol.ac.uk/modl/polcoms/irish/index.php?plot=t&type=002 respectively. See Annex A for maps and further details of these environmental data).

To generate the energy values (kJ) required by the Brey empirical model, species biomass data (g WM m^{-2}) were converted to kJ m^{-2} using published conversion factors (Brey et al. 2010). Conversion factors at the family level of taxonomic resolution were used because these values were based on a greater number of studies than those at higher taxonomic resolution, and are therefore assumed to be more representative and provide more accurate estimates than individual species or genus conversion factors. Where there was a paucity of data at the family level conversion factors from a lower taxonomic resolution were used, for example class or phyla. Biomass data for those taxa with shells were converted to shell-free weights using wet mass with shell (g WM+shell) to wet mass (g WM) conversion factors before further energy conversion factors were applied. The empirical Brey model outputs include estimated P:B ratio (yr^{-1}) and total annual production (kJ m^{-2} yr^{-1}) values with 95% confidence intervals for each species at each station. Although no confidence intervals for community level estimates can be

calculated, pooled estimates are considered more accurate than individual population estimates (Brey, 2001).

In addition to the above 49 production estimates calculated from survey data, additional benthic infaunal production estimates from 50 stations sampled and calculated by CEFAS were obtained from Stefan Bolam (Bolam et al. 2010). These estimates of benthic infaunal production were calculated using the same Brey (2001) method outlined above, therefore the data were considered comparable. In total, ninety nine stations for which benthic community production data were available for analyses. Although these 99 stations cover the whole of the study area their distribution is not even. For example the North-Eastern Irish Sea has the highest concentration of available data, whereas offshore areas in general are poorly represented (see Figure 2.1).
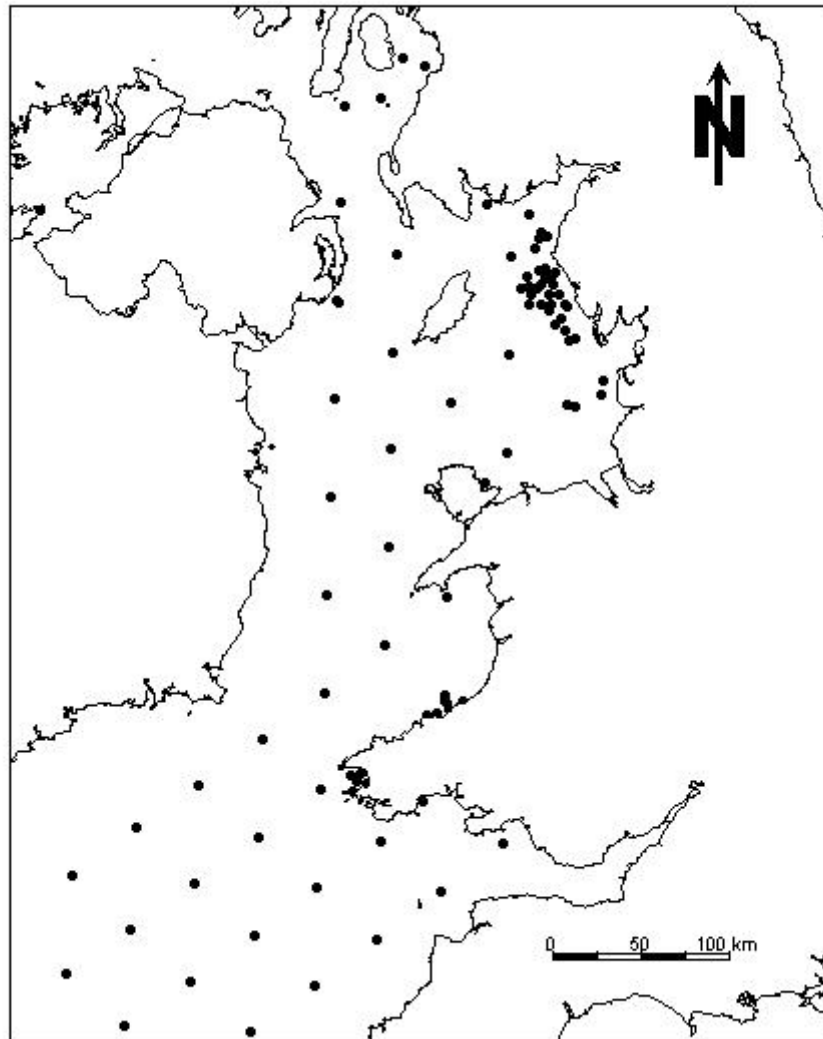
Figure 2.1. Distribution of benthic infaunal production estimates available for analysis.

Environmental data

The environmental variables investigated in this analysis include remotely-sensed sea surface chlorophyll-*a* concentration (mean values for 2004-2008), modelled tidal shear stress, wave shear stress, annual mean frequency of pelagic fronts, water column characteristics, and seabed sediment type. These variables were considered potentially important drivers of benthic community production because of their expected influence on food availability, and therefore growth rates, as well as mortality.

As already outlined in the introduction, chlorophyll-*a* concentration at the sea surface, the presence of pelagic fronts, and degree of mixed within the water column could be useful proxies for the amount of food available to the benthos (Schrum et al. 2006; Bolam et al. 2010; Darnis et al. 2012), and tidal and wave bed stress are also likely to effect the amount of food available to benthos (Emerson, 1989; Kaiser et al. 2005; Hiddink et al. 2006). Seabed sediment types are likely, in part, to reflect the degree of shear stress experienced in that particular area (Warwick & Uncles, 1980), and so could act as a proxy for hydrodynamic effects. There is also much work that has associated different benthic infauna communities to different sediment types (Snelgrove & Butman, 1994), and these differences in community composition could potentially drive differences in productivity. Depth was not included in this analysis because it was collinear with many of the other variables. Furthermore, because variation in depth and temperature are incorporated into the Brey model used to calculate benthic infauna production from abundance and biomass estimates they are excluded from further analyses as they have already been accounted for.

Remotely-sensed surface chlorophyll-*a* concentration data at a 1.1 km spatial resolution were provided by NEODAAS (NERC Earth Observation Data Acquisition and Analysis Serivces, http:/www.neodaas.ac.uk). These data were obtained from the MODIS sensor using the case 2 chl-*a* algorithm (OC5) for turbid shelf seas. An annual average for the years 2004 to 2008 was calculated from monthly composites for analysis (see Figure 2.7, Appendix 2.7.2 for a map of mean annual sea surface chlorophyll-*a* estimates). The annual frequency of pelagic fronts data were derived from oceanic thermal front metrics

obtained from remotely-sensed data sea surface temperature data (Miller et al. 2010). The annual frequency of pelagic fronts refers to the percentage of time that strong fronts occur in a particular area over a year. Annual mean front frequencies were extracted from 1.2 km resolution seasonal maps obtained from Defra via Dr Kirsten Ramsey (see Figure 2.8, Appendix 2.7.2 for a map of annual front frequency estimates used in the analyses here). Water column characteristic data was obtained from a classification produced by the UKSeaMap project (McBreen et al. 2011), which describes the ecological character of the water column based on various hydrographic parameters, including salinity, surface to seabed temperature difference and frontal probability, at a spatial resolution of 0.02 decimal degrees. This classification was structured according to four seasons (spring, summer, autumn and winter), and thirteen different water column types were defined in total. For the purpose of this analysis the water column characteristic classification for summer was used, because it is the time of year when the majority of sea surface primary productivity occurs. This time period is therefore considered more useful for understanding variation in benthic production across the study area (see Figure 2.9, Appendix 2.7.2 for a map of water column characteristic data used in the analyses here).

Tidal shear stress modelled for the European Shelf by Egbert et al. (2010) was downloaded from the OSU Tidal Data Inversion webpage, http://volkov.oce.orst.edu/tides/ES.html (for details see Egbert et al. 2010). The data have a spatial resolution of 0.03 decimal degrees, and represent total tidal-induced stress or force (N/m^2) experienced by the seabed (see Figure 2.10, Appendix 2.7.2 for a map of the tidal shear stress estimates used in the analyses here). In this analysis the fraction of the time that wave bed stress values exceeded 0.25 N/m^2 was used as a measure of wave shear stress. These values were obtained from a model developed by Dr Simon Neill for the Irish Sea (see Hiddink et al. 2009 for further details of model development). The spatial resolution of the raw data was 0.04 decimal degrees (see Figure 2.11, Appendix 2.7.2 for a map of the wave shear stress estimates used in the analyses here).

Seabed sediment data was obtained from the latest British Geological Survey (BGS) 1:250 000 scale digital Sea bed Sediment map, released 2011. These data indicated that there were twenty different seabed sediment types across the study area (see Figure 2.12, Appendix 2.7.2 for a map of the BGS seabed sediment data). The Folk triangle classification used by BGS was simplified by collapsing all sediments dominated by mud into 'Mud', all sediments dominated by sand into 'Sand', and all sediments dominants by gravel into 'Gravel'. No benthic community data were available for Rock and similar habitats, and so these and the remaining, undifferentiated seabed sediment types were grouped into 'Other' (for example, diamicton). This gave four major sediment types, Mud, Sand, Gravel, Rock and Other (see Table 2.2, Appendix 2.7.2 for sediment conversion table, and Figure 2.13 for the distribution of the re-classified sediment types). This simplification of the Folk triangle classification was done to improve replication within sediment types, and increase the statistical power of the analysis. In addition to this, it was considered more biologically appropriate to group very similar habitats together, as the subtle differences between different mud habitats, for example, were not considered likely to drive large differences in benthic communities. McBreen et al. (2008), for example, found that variation in benthic assemblage structure in the southern Irish Sea could not be explained using the full BGS Folk sediment classification.

Bottom fishing intensity data

Bottom fishing intensity estimates are derived from Vessel Monitoring System (VMS) data from the Marine Fisheries Agency (predecessor of the Marine Management Organisation). VMS data from bottom fishing vessels between the period 2004 to 2008 were cleaned and processed using the VMStools package and protocol developed by Hintzen et al. (2012). Fishing intensity in a particular area is likely to vary each year, and bottom trawling history, i.e. trawling impacts over several years, is expected to be a better indicator of benthic community composition than single year fishing intensity estimates (Hiddink et al. 2006a). Bottom fishing intensity data from several years is therefore used to better reflect cumulative fishing impact on the benthos (Lambert et al. in press).

Bottom fishing vessel types were grouped into three main classes; otter trawlers, beam trawlers and dredgers. A gear width of 60 metres and 24 metres was allocated to otter trawlers and beam trawlers, respectively. Different regulations regarding the maximum number of dredges are in force across the Irish Sea, depending on in which country and how many nautical miles from shore a vessel is fishing. Therefore gear width for dredgers was determined based on where in the Irish Sea a VMS position was identified. Table 2.3, Appendix 2.7.3 indicates these different administrative zones and the number of dredges and gear width allocated to dredgers found within them. To determine which VMS positions represented actual fishing activity fishing speeds for the three different vessel types were identified based on visual inspection of speed histograms, similar to the approach of Lee et al. (2010). Fishing speed for otter trawlers and dredgers was defined as one to four knots, whereas fishing speed for bean trawlers was defined as two to five knots. Interpolation between 2 hours VMS positions was not considered necessary given the spatial scales and time period over which data was being aggregated (Lee et al. 2010). The area swept by fishing gear represented by each 2 hour interval VMS record was determined from the fishing speed and fishing gear width associated with each record.

2.4.3 Partitioning data into different spatial scales

Analysis 1: how spatial grain size influences the identification of drivers of production

To investigate the effect of changing spatial grain size on the interpretation of relationships between environmental parameters and benthic production, a range of spatial grain sizes were selected within a restricted extent of 20,000 km^2 in the North-Eastern Irish Sea. This particular area was chosen because it is the area where the highest concentration of benthic community production data was available, and an extent of 20,000 km^2 was considered large enough to incorporate a large range of spatial grain sizes. Furthermore, this aspect of the analysis aimed only to investigate the influence of spatial grain. Different environmental variables may be more important than others in different areas of the Irish Sea, and this variation over a large extent may

reduce the ability of the analysis to identify the drivers of production. Conducting the analysis in a restricted area reduced the possibility of any potential regional effects.

The smallest grain size utilised here was the individual sites from which the benthic infaunal production data was obtained, representing total benthic infaunal production at 1 m^2. Following this a gridded approach was used to produce spatial grains that doubled in area with each increase in scale, beginning with 2.5 km^2, increasing to 5 km^2, 10 km^2 and so on until a maximum grain size of 320 km^2 (See Figure 2.15, Appendix 2.7.4 for an example of sampling designs used). A maximum grain size limit of 320 km^2 was chosen because larger grids cells (for example 640 km^2) would not fit within the restricted 20,000 km^2 extent chosen for this analysis.

Benthic infaunal production estimates from sites falling within the grid cells for each grain size were extracted and averages calculated. Averaged values of all continuous environmental variables were similarly calculated, whereas for categorical sediment type and water column characteristic data, the factor level with the largest area within a cell was extracted. Average annual fishing intensity estimates for the period 2004 - 2008 were calculated for each grid cell. For each spatial grain a standardised sample size of 15 grid cells were randomly selected from the total number of cells available for analysis within the 20,000 km^2 area, and all associated values were extracted for input into GLS models. 15 grid cells were chosen as the standard sample size because this is the maximum number of data available at the largest spatial grain size, 320 km^2.

Analysis 2: how increasing spatial extent influences the identification of drivers of production

Analysis 1 determined that the strongest and greatest number of relationships between environmental variables, fishing intensity and benthic community production are found between a spatial grain size of 2.5 to 20 km^2. Analysis 2 selected a spatial grain size of 5 km^2 and aimed to determine whether or not these relationships identified in the first analysis at 20,000 km^2 were consistent and applicable for all areas of the Irish Sea. If the production-environment relationships observed changed as spatial extent increased,

this would suggest that the strength of different processes influencing benthic community production varies across the Irish Sea. If the strength of these different production-environment relationships do vary across the Irish Sea, predicting benthic community production across the whole area using the results from one analysis may be difficult, because any variation in relationships is not captured. On the other hand, if production-environment relationships were the same across the Irish Sea, it is assumed that predicting production across the whole area would be simpler.

To investigate the possible effects of increasing extent on the relationship between environmental variables and benthic community production identified in the first analysis, the whole study area was divided into five different extents ranging from the same 20,000 km^2 area utilised in analysis one, increasing by 20,000 km^2 to a total area of 100,000 km^2. All benthic community production, environmental and fishing intensity data across the whole study area were standardised to grid cell area of 5 km^2 using the methods outline above, and within each of the five extents a standardised sample size of 20 grid cells were randomly selected for analysis. All associated values extracted for input in GLS models.

To ensure an even spatial distribution of data within each extent, each of the extents were further divided into 10,000 km^2 sections and an equal number of 5 km^2 observations/grid cells were randomly sampled from each section. For example, for the smallest extent of 20,000 km^2, five observations/grid cells were randomly selected from two 10,000 km^2 areas, and for the largest extent of 100,000 km^2 two grids cells were randomly sampled from within ten 10,000 km^2 areas that made up the total extent. This removed any bias towards the areas of high data concentration, such as the North-Eastern Irish Sea.

2.4.4 Statistical analysis

Dealing with spatial autocorrelation and variance heterogeneity

Generalised least squares (GLS) regression models were utilised to investigate the potential role of environmental factors in driving variation in benthic community production at each of the spatial grain sizes and extents outlined above. GLS regression was applied to the data described above using the gls() function from the nlme package in R (Pinheiro et al. 2012; R Core Team, 2012). This resulted in a total of nine GLS models for analysis 1 (spatial grain) and five GLS models for analysis 2 (spatial extent). GLS regression was used because it is able to accommodate spatial autocorrelation in model residuals, which was expected in this study due to the spatially explicit nature of the data (Zuur et al. 2009). Residual spatial autocorrelation is a form of dependency and occurs when residuals for data that are closer together in space are more similar than those for data that are further apart, purely as a result of the distance between them (Fortin & Dale, 2005). This phenomenon can lead to type 1 errors due to the estimation of inappropriately small standard errors for coefficients (Zuur et al. 2010). The presence of this dependency between residuals is therefore detrimental to the correct identification of drivers of benthic community production. GLS regression can accommodate residual spatial autocorrelation by the addition of autocorrelation structures to the error component of the regression model (Zuur et al. 2009).

To check for residual spatial correlation visual tools such as semi-variograms could not be employed because the number of data points was too small (N=15 or 20). Usually a minimum of fifty data points is required (Fortin & Dale, 2005). Similarly a spatial map of model residuals to check for clusters of similar residuals was difficult to interpret due to small sample sizes. In the absence of robust visual diagnostics, AIC scores for GLS models fitted with different autocorrelation structures were compared against a reference GLS model without such a structure. This comparsion of AIC scores was used to determine whether or not a correlation error structure was necessary to improve model fit, as recommended by Zuur et al. (2009).

Generalised least squares regression can also deal with heterogeneity in the variance of model residuals, a major violation of most regression approaches and a common issue in ecological data (Zuur et al. 2009). Although data transformation can be applied to remove heterogeneity, an increasing approach in ecological modelling is to take heterogeneity into account when estimating regression parameters because it can be a source of ecological information (Zuur et al. 2009). In GLS regression this heterogeneity can be modelled in the error component by the inclusion of a variance structure. Variance heterogeneity was investigated through visual inspection of standardised residuals vs. fitted values, and residual patterns for individual explanatory variables. Where homogeneity of variance was violated different common variance structures were added to GLS model and the models compared using AIC and likelihood ratio tests to identify the most suitable error structure.

Dealing with multicollinearity

In addition to issues of spatial autocorrelation and variance heterogeneity, the inclusion of many environmental variables in regression models may increase the chance of multicollinearity. Collinearity between explanatory variables is an issue because it can result in inaccurate regression coefficient estimates for individual predictors (Faraway, 2006). Pairplots and boxplots of environmental variables, Spearman's Rank correlation coefficients of explanatory variables and variance inflation factors (VIF) calculated for initial, simple linear models including all variables were investigated for multicollinearity before GLS models were run (as recommended in Zuur et al. 2010). Correlation coefficients greater than 0.7 calculated for pairs of drivers were considered to indicate collinearity between the relevant variables, and those variables with VIF scores greater than 8 were also regarded as a potential issue (following the approach recommended in Zuur et al. 2009). Where either approach highlighted potentially problematic explanatory variables the simple linear regression model was rerun with one of the collinear variables removed until VIF scores for all variables were lower than 8. GLS models were then constructing with the remaining variables using the methods outlined above.

Identification of environmental and anthropogenic drivers of production

Once the above protocols for removing collinear variables and obtaining optimal error structures for GLS models had been followed, likelihood ratio tests comparing full models against those with a dropped explanatory variable were performed in a sequential manner to identify which environmental factors are significant drivers of benthic community production.

Once all variables identified using likelihood ratio tests as unimportant in a model were removed partial residual plots were produced for the remaining variables that were considered important drivers of benthic production, and therefore useful predictors. These plots described the relationship between individual environmental drivers and benthic community production, whilst taking into account the influence of other environmental variables in the model. Comparing plots of each model within each separate analysis gives an indication of patterns and trends over spatial scale in the ability to identify drivers, and therefore helps highlight those scales at which benthic community production could potentially be predicted.

Overall explanatory power of GLS models

To gain a further understanding of which spatial grain and which spatial extent benthic infaunal production could be best predicted in the Irish Sea, the overall explanatory power of the GLS models for each analysis was compared using observed versus fitted values plots. This visual check was used in absence of a meaningful R-squared statistic for GLS models (Zuur et al. 2009).

2.5 RESULTS

2.5.1 Collinearity

Investigation of multicollinearity indicated a positive association between chlorophyll-*a* concentration and wave bed stress. This is unlikely to reflect a direct relationship, and is

more likely due to both variables having a negative association with depth, that is, chlorophyll-*a* concentration and wave bed stress are both likely to be greater in shallow, coastal waters. In analysis 1, VIF values from initial linear models indicated that wave bed stress should be dropped to reduce the effects of collinearity at four spatial grains (2.5 km^2, 5 km^2 10 km^2 and 20 km^2), because this variable exhibited the highest VIF value. High VIF values in analysis 2 also indicated that wave bed stress should be dropped for one of five of the models.

In analysis 1, VIF values also indicated that summer water column characteristic should be dropped from seven out of nine models at different spatial grains. In the models where summer water column feature was retained it was not found to be an important driver of benthic production, and therefore this variable was dropped from subsequent analyses.

Visual checks for collinearity indicated a possible association between sediment type and fishing intensity in the majority of models across both analyses. Specifically, fishing intensity tended to be lower on sand and gravel sediment types compared to muddy sediments. This is likely to reflect the targeted activity of the east and west Irish Sea *Nephrops* fisheries on muddy grounds. Despite this observation, VIF values did not suggest that either of these variables should be dropped from models, and both were retained throughout the analysis.

2.5.2 Analysis 1: how spatial grain size influences the identification of drivers of production

Generalised least squares (GLS) model results from all nine of the spatial grain sizes in this analysis suggest that sea surface chlorophyll-*a* concentration is an important driver of benthic infaunal production at all grains. From the site scale to 320 km^2 chlorophyll-*a* concentration was found to have a strong, positive relationship with benthic community production (Figure 2.2). At grain sizes larger than 80 km^2 (160 km^2 and 320 km^2) chlorophyll-*a* was the only variable identified to be an important driver of benthic production (Figure 2.2).

Sediment type is also highlighted as an important explanatory variable alongside chlorophyll-*a* concentration at four out of nine of the spatial grains in this analysis., these include the site scale, 5km^2, 20 km^2 and 40 km^2 but not 2.5 km^2,10 km^2 or 80km^2 to 320 km^2 (Figure 2.2). At these spatial grains benthic infaunal production was found to be significantly higher in sandy sediments compared to muddy sediment types. Although this effect of sediment type was insignificant at 80 km^2, AIC indicated its importance for the performance of the GLS model and so it was retained along with chlorophyll-*a* concentration (Figure 2.2).

Fishing intensity and tidal bed stress are found to have an effect at small spatial grains. Where sediment type is not significant (2.5 km^2 and 10 km^2), fishing intensity is found to have a significant negative relationship with benthic infaunal production (Figure 2.2). At 5 km^2 tidal shear stress has a significant positive influence on benthic production and is retained in the GLS model in addition to sediment type and chlorophyll-*a* concentration (Figure 2.2). This relationship between tidal bed stress and benthic production is not found at any other spatial grain. Wave bed stress, summer water column characteristic and annual frequency of pelagic fronts were not identified to have a relationship with benthic infaunal production at any of the spatial grain sizes included in this analysis.
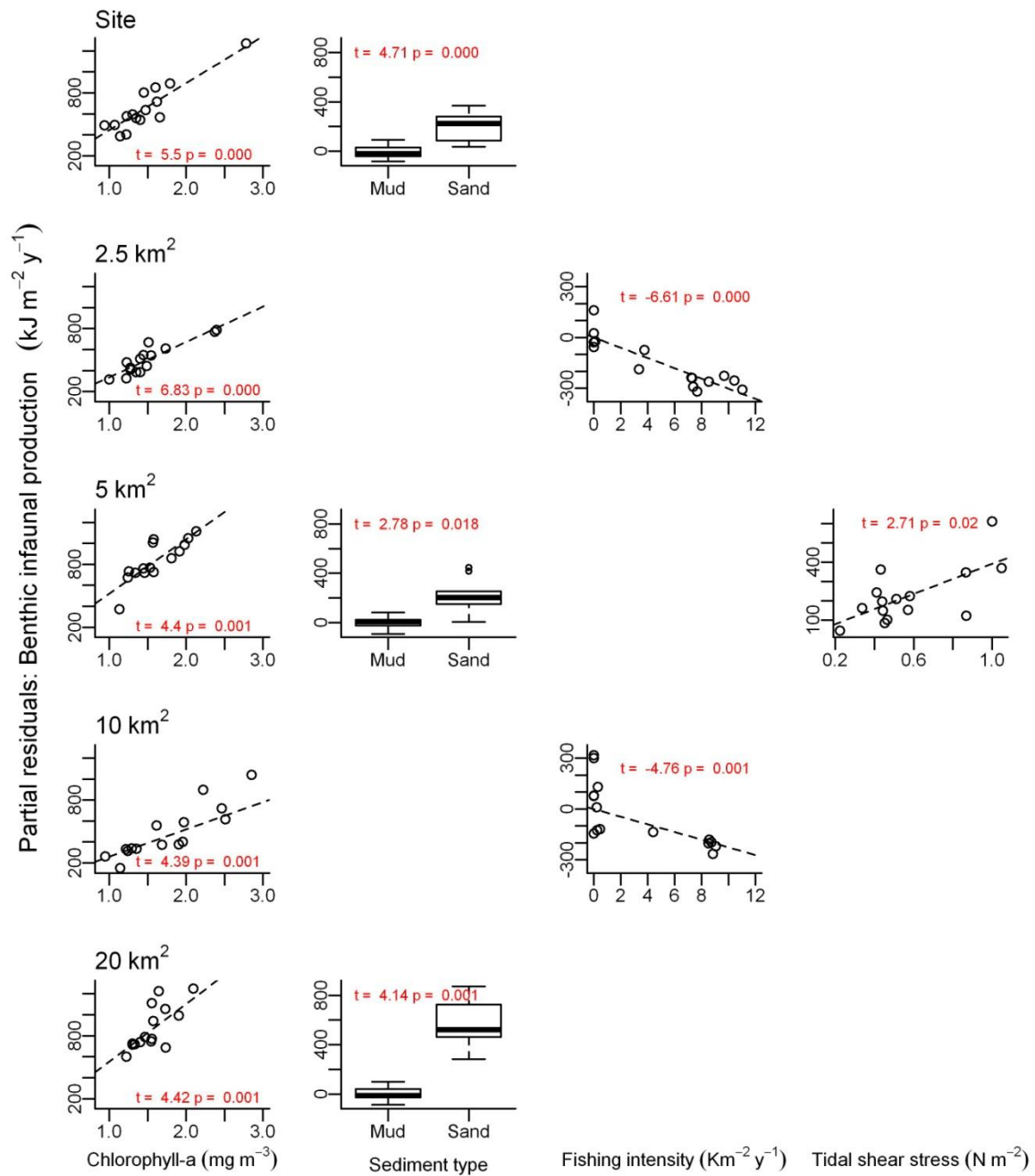
Figure 2.2. Partial residual plots indicating the environment-production relationships identified by optimal GLS models in analysis 1. Environment-production relationships are presented for all nine spatial grain sizes included in the analysis (site scale to 20 km²). Significant relationships are highlighted by the inclusion of statistics in red. Plots where no statistics are given indicate non-significant variables that have been retained in the model. For model fits see Figure 2.3. For further details of each model, see Table 2.4, Appendix 2.7.5.
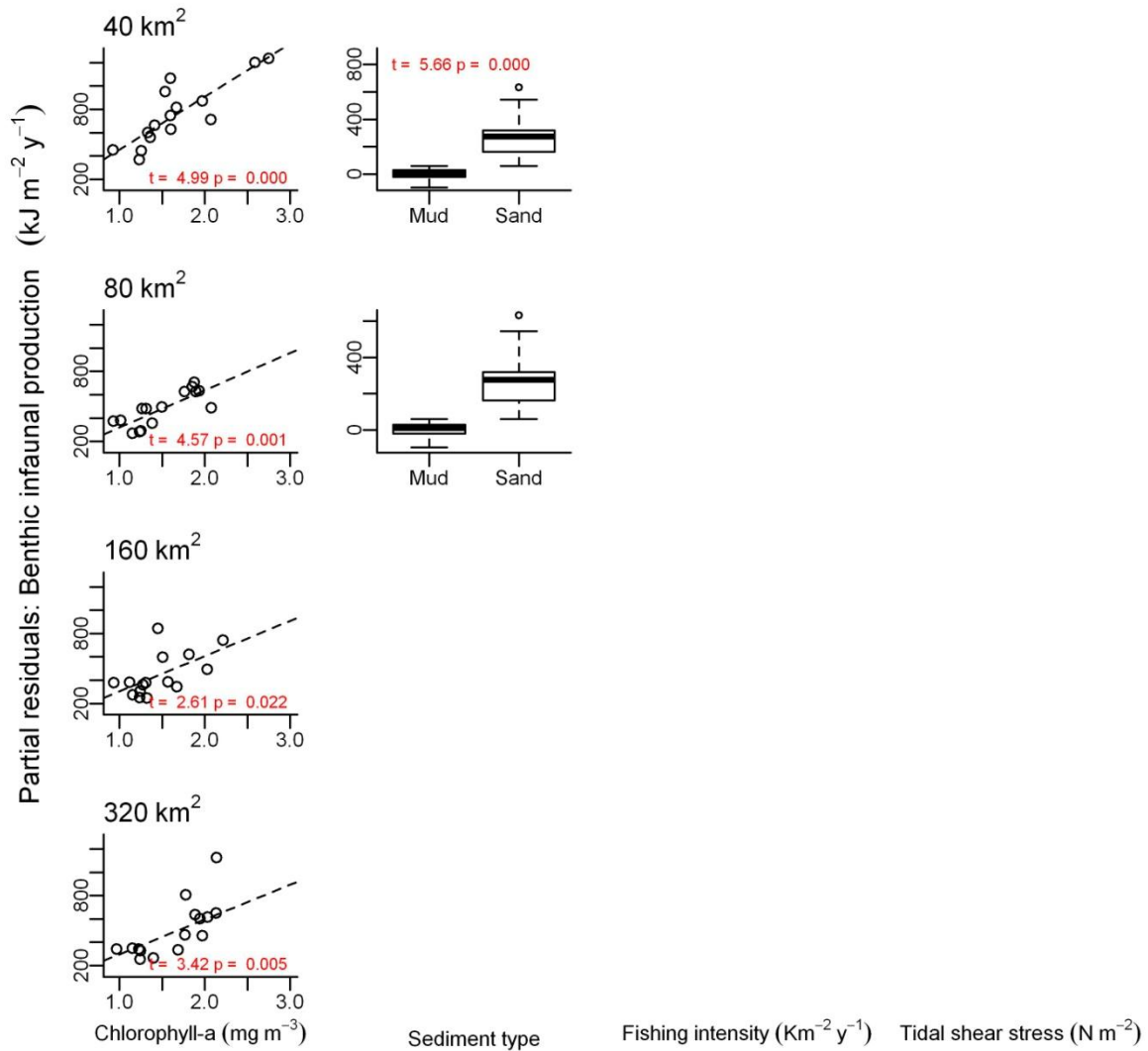
Figure 2.2. Partial residual plots indicating the environment-production relationships identified by optimal GLS models in analysis 1. Environment-production relationships are presented for all nine spatial grain sizes included in the analysis (40km^2 to 320 km^2). Significant relationships are highlighted by the inclusion of statistics in red. Plots where no statistics are given indicate non-significant variables that have been retained in the model. For model fits see Figure 2.3. For further details of each model, see Table 2.4, Appendix 2.7.5.

Plots of observed versus fitted values are given to indicate overall model fit for the optimal models identified at each spatial grain size. This is because GLS models do not produce a meaningful R-squared statistic (See Methods, section 2.4.4). These plots indicate that models for the smallest, site scale up to a spatial grain of 20 km² have a r-squared value greater than 0.9 (Figure 2.3). The close, positive association between observed and fitted values of these models suggest that they have the highest predictive ability. The lowest r² values are observed for optimal models at two largest spatial grains (160 km² and 320 km²). These models retained only one predictor variable, chlorophyll-*a* concentration.
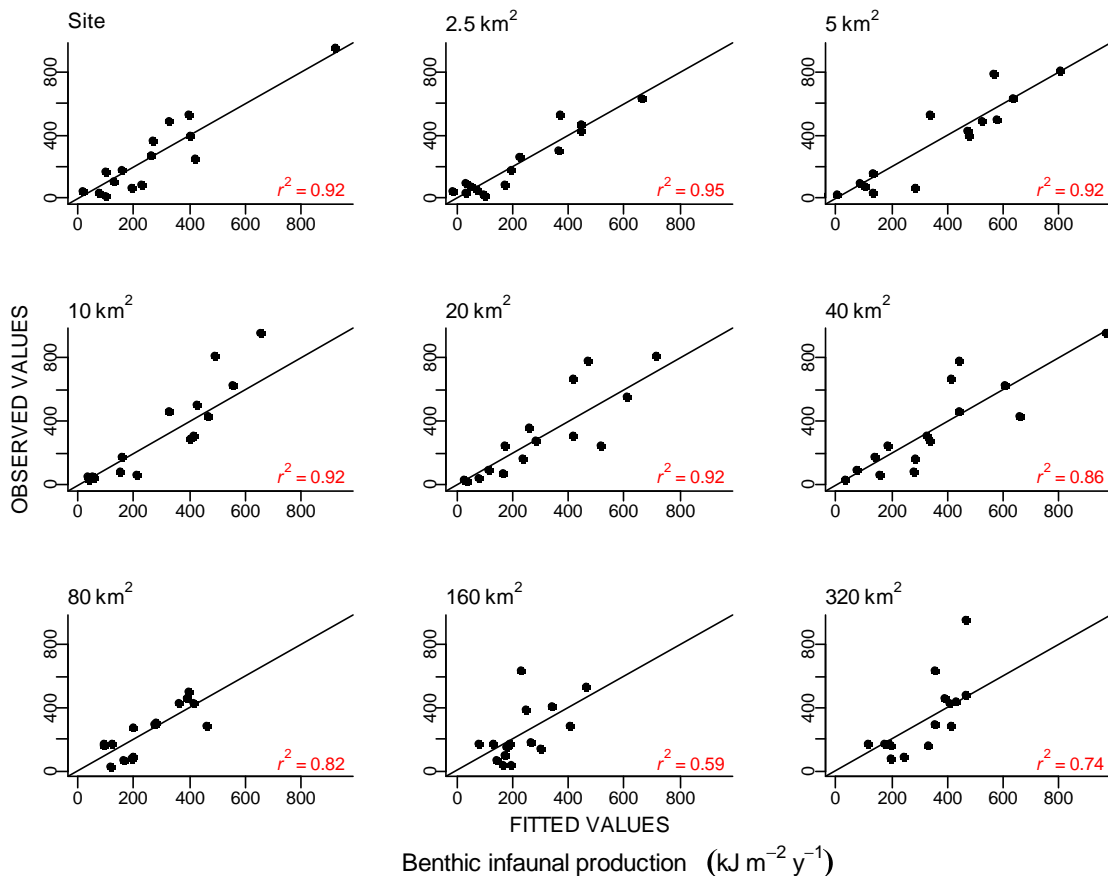
Figure 2.3. Observed versus fitted value plots indicating the explanatory power of optimal GLS models identified for each spatial grain size in the analysis (site scale – 320 km²). Pearson correlation coefficients are given to give a rough comparison of goodness of fit. The lines through the plots represent a 1:1 relationship.

2.5.3 Analysis 2: how increasing extent influences the identification of drivers of production

The results of analysis 2 suggest that the significant, positive relationship identified between chlorophyll-*a* concentration and benthic infaunal production at a spatial grain of 5 km^2 is consistent across the whole extent covered in this analysis, 100,000 km^2 of the study area (Figure 2.4). Sediment type and fishing intensity, on the other hand, are only found to be significant at the smallest extents (20,000 km^2 and 40,000 km^2). Benthic infaunal production is, again, higher in sandy sediment compared to mud at 20,000 km^2, and a negative relationship between production and fishing intensity is found at 40,000 km^2. Fishing intensity was also retained in the models at 60,000 km^2 and 80, 000 km^2 because removing this variable increased AIC values. Despite being highlighted in the previous analysis as a significant explanatory variable, tidal shear stress was not identified as a useful predictor at any extent.
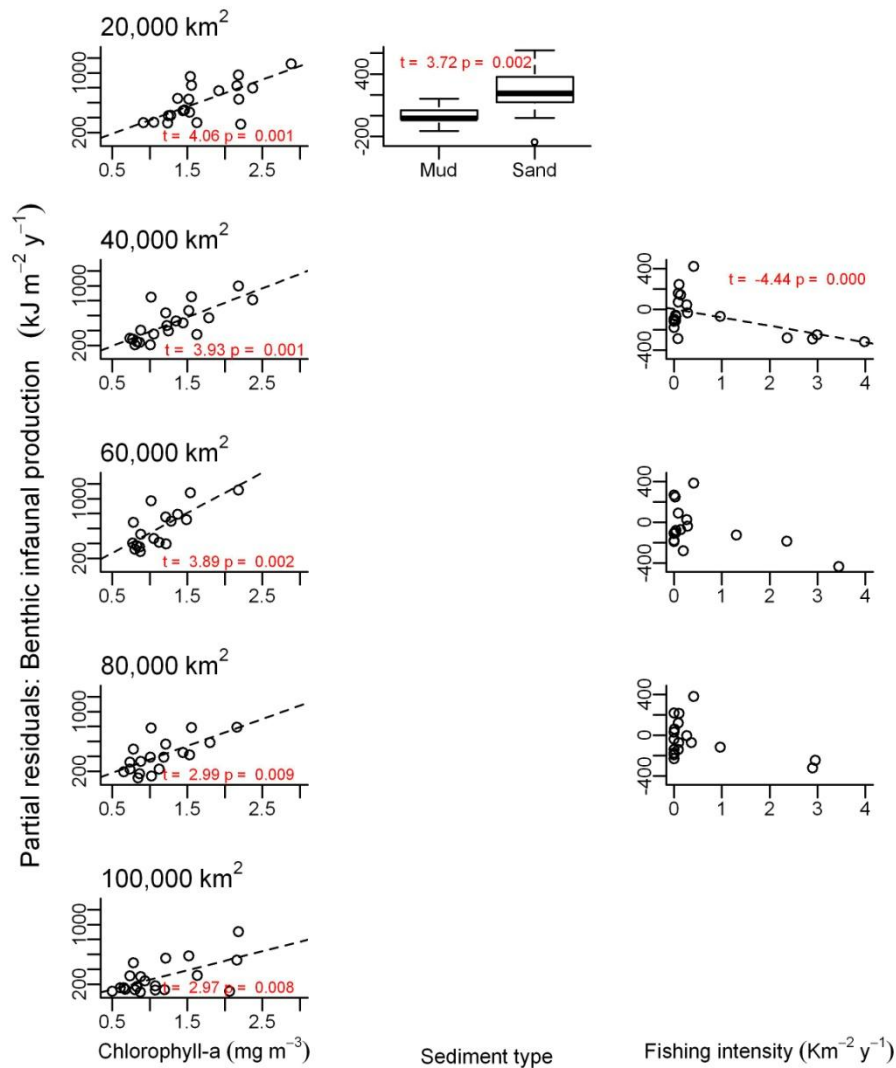
Figure 2.4. Partial residual plots indicating the environment-production relationships identified by optimal GLS models in analysis 2. Environment-production relationships are presented for all five spatial extents included in the analysis (20,000 to 100,000 km2). Significant relationships are highlighted by the inclusion of statistics in red. Plots where no statistics are given indicate non-significant variables that have been retained in the model.

Visual comparison of observed versus fitted production values for each GLS model at each extent suggest that predictive power of the optimal models is fairly good up to a spatial extent of 80,000 km² (Figure 2.5).
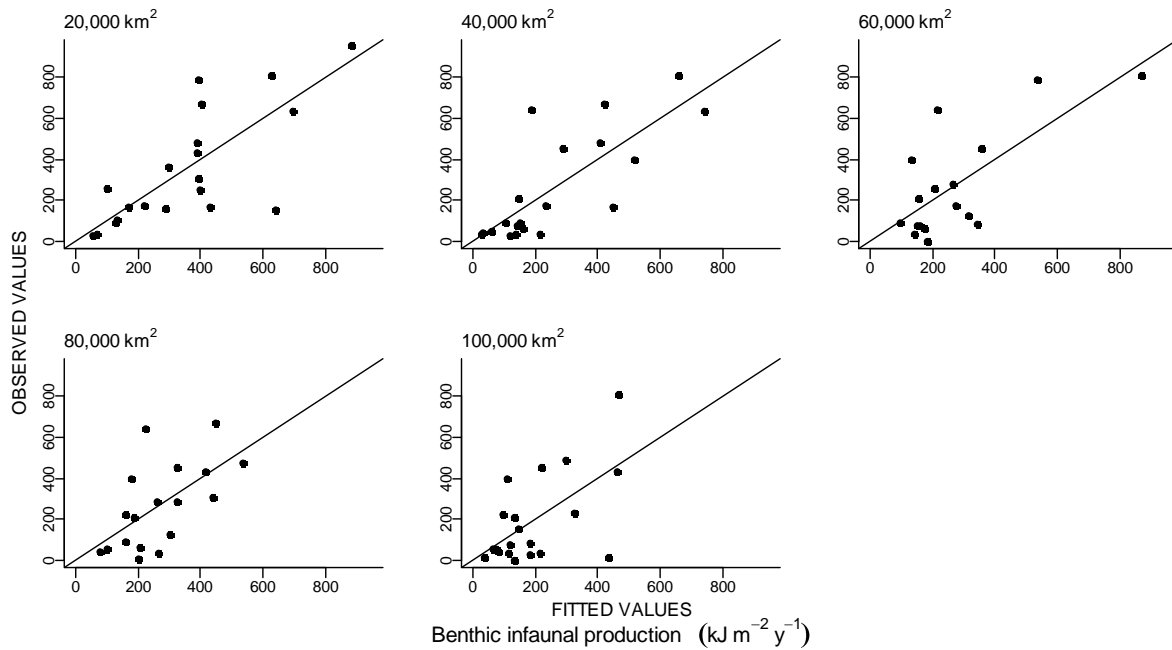
Figure 2.5. Observed versus fitted value plots indicating the explanatory power of optimal GLS models identified for each spatial extent in the analysis (20,000 km² – 100,000 km²). The lines through the plots represent a 1:1 relationship.

To give an initial indication of modelled benthic infaunal production for the Irish Sea, predicted benthic production estimates from the optimal model for 5 km² identified in analysis 1 were mapped in Figure 2.6. These predictions are only made for the sediment types sand and mud because these were the only factor levels included in the GLS model.
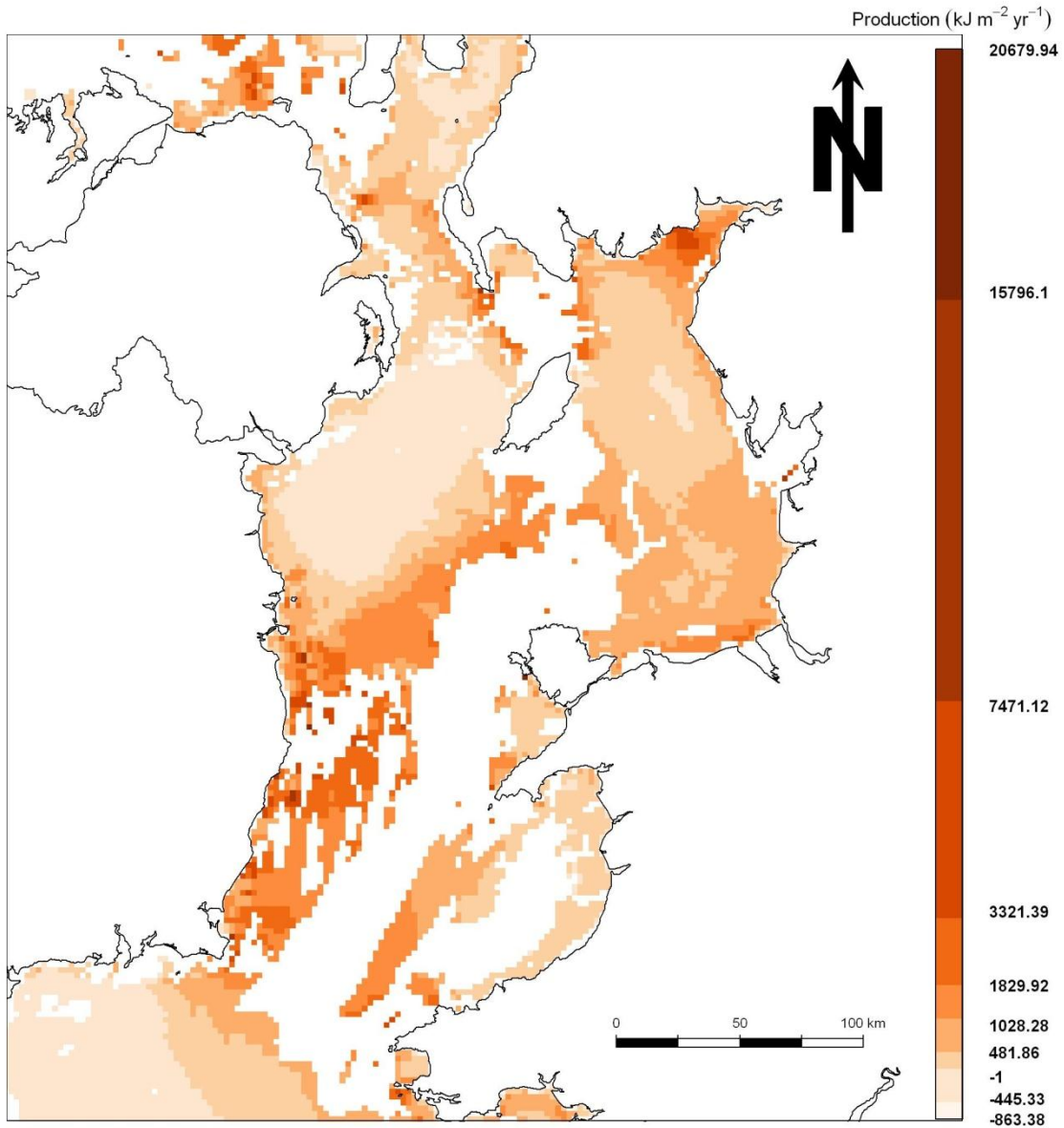
Figure 2.6. Modelled benthic infaunal production based on the outputs from the optimal model identified at a spatial grain size of 5km². This model includes chlorophyll-a at the sea surface, sediment type and tidal shear stress (see Figure 2a). Predictions are not made in the white areas because these are areas of gravel and other sediment types, which were not represented in the GLS model. See Figure 2.16, Appendix 2.7.6 for a map indicating the area where no predictions are made.

2.6 DISCUSSION

2.6.1 The drivers of benthic community production and the influences of spatial scale

Chlorophyll-*a* concentration at the sea surface, sea bed sediment type, fishing intensity and tidal shear stress are all found to have an important influence on benthic infaunal production. However, the spatial grain and extent at which these different relationships are examined has an effect on the interpretation of their importance. This has implications for the possible scales at which benthic infaunal production can be accurately predicted. Wave bed stress, water column feature and the frequency of pelagic fronts are not identified to be important drivers of benthic community production at any of the spatial scales included in this study.

Sea surface chlorophyll-a concentration

Out of the identified variables, sea surface chlorophyll-*a* concentration appears to be only driver that has a consistent relationship with benthic infaunal production across all spatial grains and extents in the analyses presented here. Primary production at the sea surface is a major source of food to the benthos (Ramsey & Snelgrove, 2003, Trimmer, Gowen & Stewart, 2003), and food supply is known to be a major limiting factor on benthic biomass and production (Beukema & Cadee, 1997; Bourget et al. 2003). Positive relationships between surface chlorophyll-*a* concentration and benthic biomass have been found in coastal areas in the Arctic and Atlantic Oceans, suggesting strong benthic-pelagic coupling in these areas (Grebmeiner at el. 1988; Piepenburg et al. 1997). The positive, linear relationship between chlorophyll-*a* concentration and benthic community production observed here suggest a similar benthic-pelagic coupling in the Irish Sea, and indicates that chlorophyll-*a* at the surface could be a useful proxy for the maximum carrying capacity of the benthic community, irrespective of the spatial grain at which it is measured.

Tidal shear stress

Food supply to the benthos is expected to be influenced by other factors other than the amount of primary production at the surface. These factors include hydrodynamic processes such and tidal and wave-induced shear stress, which control the degree of water movement at the water-sediment interface and the availability of food to the benthos (Wildish & Kristmanson, 1979; Warwick & Uncles, 1980, Patterson & Black, 1999). Here, wave stress was dropped from many models due to strong, positive collinearity with chlorophyll-*a* concentration. This is likely to be a result of their co-variance with proximity to the coast; both chlorophyll-*a* concentration and wave stress decreased with distance from the shore. Tidal shear stress, on the other hand, was found to have a positive relationship with production at 5 km^2, but only at a restricted spatial extent of 20,000 km^2. Lambert at al. (2011) similarly found an increase in benthic epifauna biomass with tidal velocity (closely related to tidal shear stress), and Hiddink et al. (2006a) found a positive influence of tidal shear stress on benthic infauna at low values of tidal stress, although this switched to a negative relationship as tidal stress increased. At higher levels of tidal shear stress a negative impact would be expected on growth due to a reduction in food supply source. Due to the distribution of the data here, not enough data was available at higher levels of tidal stress to determine the relationship between high tidal bed stress and benthic infaunal production in the Irish Sea. The fact that the positive relationship between tidal shear stress and production at 5 km^2 was only found at a restricted spatial extent of 20,000 km^2 suggests that the importance of tidal stress for driving benthic infauna may not be the same across the whole Irish Sea area.

Sediment type

The results indicate that sediment type is an important driving factor for benthic infaunal production, although unlike chlorophyll-*a* concentration, this is only found to be the case up to a spatial grain of 40 km^2 and a spatial extent of 20,000 km^2. Benthic infauna production is found to be significantly higher in gravel and sand sediments compared to muddy sediments. This result supports the findings of Bolam et al. (2010)

who found that benthic production tended to be greater in coarser sediments than fine grain sediments. Due to the strong correlation between sediment type and tidal shear stress (Warwick & Unlces, 1980), the relationship observed between production and sediment type at spatial grains up to 40 km^2 could potentially be an indirect association that reflects the direct influence of shear stress on the growth rates of benthic infauna. However, in the optimal model where tidal shear stress was retained, sediment type was also retained, suggesting that at this spatial grain they both have an independent influence on production. Alternatively, differences in community production between sediment types could reflect differences in community composition. For example, perhaps greater numbers of productive taxa are found in sandy sediments compared to muddy sediments. A review of animal-sediment relationships by Snelgrove & Butman (1994), however, indicated that benthic community composition is rarely explained by a single sedimentary characteristic.

Sediment type is considered a local factor, only having a direct influence on the benthic community residing within it. Therefore, a lack of a relationship between sediment type and productivity at a spatial grain larger than 40 km^2 is expected to be because the variation in sediment type is likely to be too high for a significant relationship to be identified between the sediment type and production. The fact that a relationship between sediment and benthic infauna production at the small spatial grain of 5 km^2 is only found within a restricted 20,000 km^2 extent in analysis 2 could reflect a specific regional effect that is not found elsewhere, perhaps because other drivers become more dominant and overwhelm the relationship between production and sediment type.

Alternatively, the reason that sediment type is not retained in optimal models for spatial extents greater than 20,000 km^2 could be because fishing intensity is retained in these models instead (at least up to 80,000 km^2). Initial observations during collinearity tests indicated that sediment and fishing intensity maybe associated, with muddy sediments being associated with higher fishing intensity. Despite this visual observation, both were retained in the analyses due to low VIF values. Interesting, for both analysis 1 and 2, sediment type and fishing intensity are not retained as predictors of benthic infaunal production within one model. For example, in analysis 1, at a grain size of 2.5 km^2 and

10 km^2 fishing intensity is retained as a predictor and sediment type is not. However, at the site scale and at 5 km^2 sediment type is retained as predictor whilst fishing intensity is not. The fact that sediment type is indicated to be an important driver of production at the site scale and at 5km^2 would suggest that it should also be important at the 2.5 km^2 scale. Similarly, the fact that fishing is indicated to be an important driver of production at 2.5 km^2 and 10 km^2 would suggest that it should also be important at 5 km^2. It appears likely, then, that low levels of benthic production are related to both muddy sediments and high levels of fishing intensity, and because of the relationship between them only one of these predictors is being retained in the optimal model. Partial least squares regression (PLSR) on transformed benthic infaunal production (to remove heterogeneity) may be a more suitable option for determining the individual effects of these variables on benthic infaunal production.

Given the above, that fact that both sediment type and tidal shear stress are retained in the optimal model at 5 km^2, when sediment type is expected to act as a proxy for shear stress, may be a result of sediment type actually acting as a proxy for fishing intensity in this particular model. Sediment type is still therefore considered a proxy for the influence of hydrodynamic regime, and therefore food supply on productivity, in other optimal models at different spatial grains, particularly at very small and very large spatial grains (e.g. at the site scale and at 40 km^2) where fishing intensity in not expected to have an effect due the inaccuracy of estimates derived from VMS data (Mills et al. 2007, Lambert et al. 2012).

Bottom fishing intensity

Bottom fishing intensity has a significant, negative impact on benthic community production at small spatial grain sizes (5 km^2 and 10 km^2) up to a spatial extent of $40,000 \text{ km}^2$. Many studies have identified a similar negative relationship between fishing and a number of different benthic community attributes, including abundance, biomass and production, for many different types of benthic community (e.g. Jennings et al. 2001; Collie et al. 2005; Queiros et al. 2006; Reiss et al. 2009; Lambert et al. 2011). The negative impact of bottom fishing on infaunal production is likely to result from the

removal of individuals, which reduces biomass and therefore overall community production (Jennings et al. 2001). There is expected to be a body size-specific impact on benthos, with those large, long-lived species being particularly vulnerable to bottom fishing (Queiros et al. 2006). The loss of these species would result in a disproportionate loss of total production from the community.

The fact that the negative relationship between bottom fishing intensity and benthic production is not observed at the larger spatial grains in this analysis is likely due to the fact that as grain size increases, the total area impacted by fishing tends to be overestimated, whereas the maximum fishing intensity tends to be underestimated (Mills et al. 2007, Piet & Quirijns, 2009, Dinmore et al. 2003). Increasing error in fishing activity estimates will reduce the possibility of accurately quantifying fishing impacts on the benthos (Lambert et al. 2012). Similarly, at very small spatial grain sizes, the 2 hour intervals between VMS positions can also result in inaccurate calculations of fishing activity because the exact area fished between positions cannot be determined (Lambert et al. 2012). This may explain the lack of a relationship identified between fishing intensity and benthic community production at the site scale in this analysis. Mills et al. (2007) recommended 3 km by 3 km grid cells as an appropriate compromise for accurately describing fishing effort, which equates to approximately 10 km², the maximum spatial grain at which fishing intensity was identified as a significant driver in this analysis.

The maximum extent of 40,000 km² at which a significant relationship with bottom fishing is observed includes the area of the west and east *Nephrops* fisheries, which are the most lucrative fisheries in the Irish Sea. This suggests that the significant effect of fishing intensity that is observed could result primarily from trawling activity for *Nephrops.* Beyond 40,000 km², although not significant, fishing intensity is still retained as a predictor, suggesting it has wider application across the Irish Sea.

2.6.2 Implications for predictive modelling of benthic communities in the Irish Sea

The results here can help inform the development of a predictive model of benthic infaunal production in the Irish Sea. This predictive model can identify areas of high benthic production that reflect good benthic ecosystem health and quality, and direct spatial management to protect them.

Chlorophyll-*a* at the sea surface, sediment type and bottom fishing intensity are found to be the most useful variables for predicting benthic infaunal production. These variables are particularly useful for predicting at the smallest, site scale, up to a spatial grain of 40 km^2. Tidal bed stress is also identified to be a useful predictor of benthic production at spatial grain of 5km^2. A visual comparison of the observed and fitted values for the optimal models at each spatial grain suggests that optimal model predictive ability greatest between a spatial grain of 2.5 km^2 and 20 km^2. The general minimum recommendation for MPA size is 5 km^2 (Roberts et al. 2003). Therefore, due to the good predictive ability of environmental variables at this scale and its relevance to marine spatial management, 5 km^2 is deemed the most suitable spatial grain at which to accurately predict benthic infaunal production for the purpose of marine protected area design.

The strong relationship between all four identified variables and benthic infaunal production at a spatial grain of 5km^2 cannot be assumed over the whole Irish Sea area, however. Only chlorophyll-*a* concentration is found to be a consistent predictor of benthic infaunal production across all the spatial extents included in the analyses here. Models where only chlorophyll-*a* is retained as a significant predictor do not perform as well for predicting benthic production, suggesting that other drivers not captured within this analysis are operating at this larger scale. These drivers may be those that were excluded from the initial analyses; temperature, depth and wave stress. Also, a simpler measure of stratification may have been more appropriate for identifying statistical relationships than the UKSeaMap water column characteristic used here, which had 13 different water column characteristic types in total for the whole Irish Sea area. A simple stratification index may have had greater statistical power.

The fact that sediment type, fishing intensity and tidal shear stress are only retained as predictors within the 20,000 to 40,000 km^2 areas included in the spatial extent analysis here suggest that there may be regional differences in the dominant drivers of benthic community production across the Irish Sea. Unfortunately, the uneven distribution of data available for this analysis means that the ability to conduct a detailed analysis within a different, restricted area of the Irish Sea other than the north-east area used in analysis 1 is limited, and thus the possible differences in the importance of drivers between different areas is difficult to determine. Despite the fact that not all predictors are retained at large spatial extents, the comparison of observed and fitted values from the optimal models identified in analysis 2 indicate that the ability to predict bentic production is fairly good up to a spatial extent of 80,000 km^2.

Initial prediction of benthic infaunal production in the Irish Sea, based on the optimal model identified in analysis 1, suggest that the most productive benthic communities occur in the Solway Firth, off the east coast of Ireland and north coast of Northern Ireland. Benthic production is also predicted to be relatively high along the north-west coast of England and in the centre of the Irish Sea (between the Isle of Man and Anglesey). Modelled benthic production estimates are lowest for area of mud in the west and east Irish Sea, and also along the Cardigan Bay coast and in the Northern part of the study area. These predictions are not biologically constrained, e.g. by maximum carrying capacity or competition dynamics, and are based on the linear environmental-production relationships identified here (explaining the negative predictions of production), therefore they are not expected to be an accurate representation of productivity in the Irish Sea. For example, in comparison to the benthic infaunal production estimates observed by Bolam et al. (2010), which ranged from 3.1 to 897.2 kJ m^{-2} yr^{-1} across the UK continental shelf, the modelled estimates here are much higher.

2.6.3 Conclusions

In summary, the findings here indicate that (i) chlorophyll-*a*, seabed sediment type, and bottom fishing intensity are important drivers of benthic infaunal production in the Irish Sea. (ii) The optimal spatial grain at which to predict benthic infaunal production from these drivers and inform MPA design is 2.5 – 20 km². (iii) Initial predictions indicate that the most productive benthic communities occur in the Solway Firth, off the east coast of Ireland and north coast of Northern Ireland, however, (iii) confidence in predictions of benthic infaunal production is low over a spatial extent of 80,000 km².

2.7 APPENDICES

2.7.1 Benthic community data used to calculate production estimates

Table 2. 1. Details of the five research surveys from which existing benthic infauna biomass and abundance data were obtained and used to calculate benthic infaunal production estimates. Where appropriate, the associated publication that originally used the data is also given.

Survey No.	Source	Location	Survey dates	No. of stations	No. of replicate samples at each station	Sample gear	Associated publication
1	Bangor University	North-East Irish Sea	18 - 26/11/04	21	4	0.1m^2 Day grab	Hinz et al. (2009) Trawl disturbance on benthic communities: chronic effects and experimental predictions. Ecological Applications 19(3): 761-773.
2	Bangor University	Irish Sea	23 - 30/06/07	14	2	0.1m^2 Day grab	Hiddink et al. (2008) Context dependency of relationships between biodiversity and ecosystem function is different for multiple ecosystem functions. Oikos 118(12): 1892-1900.
3	Countryside Council for Wales	Cardigan Bay , Wales	19 - 20/02/08	8	2-4	0.1m^2 Day grab	
4	Countryside Council for Wales	St Bridesbay, Wales	08 - 09/04/08	5	4	0.1m^2 Day grab	
5	Environment Agency Wales	Carmarthen Bay, Wales	14/05/08	1	5	0.1m2 Van Veen Grab	

2.7.2 Environmental data
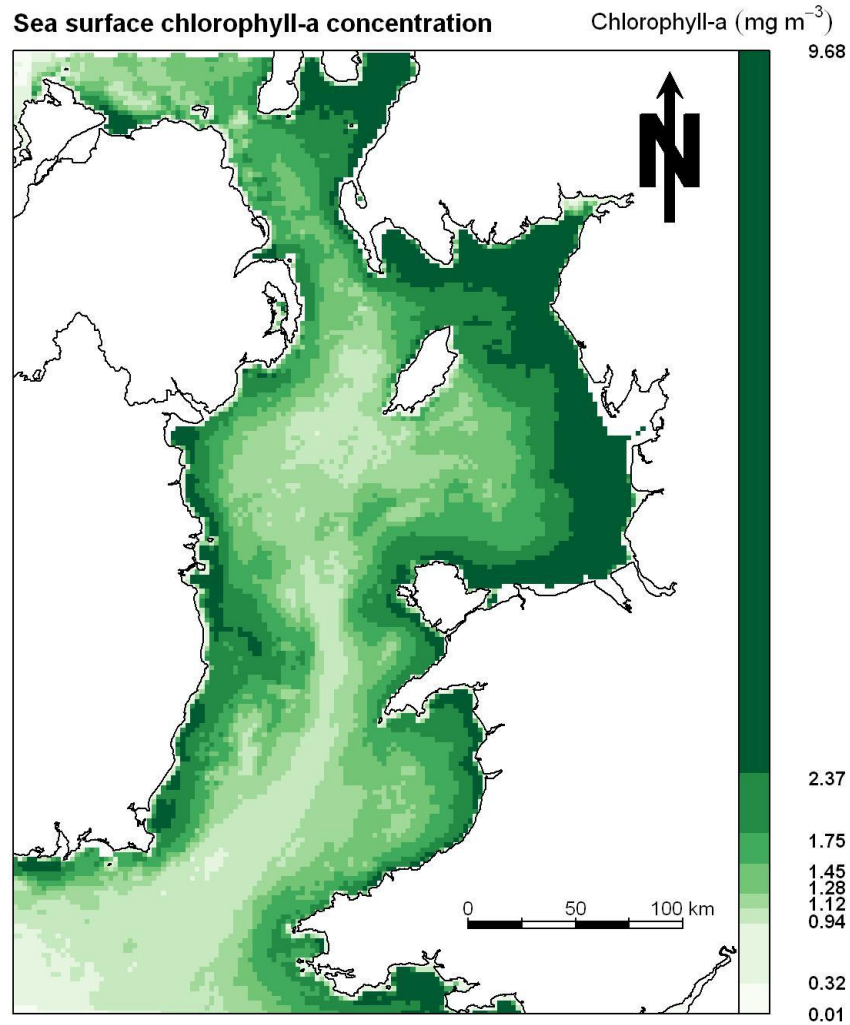
Figure 2.7. Mean annual sea-surface chlorophyll-a concentration for 2004-2008, calculated from remotely-sensed monthly composites obtained from NEODAAS (NERC Earth Observation Data Acquisition and Analysis Serivces, http:/www.neodaas.ac.uk). Data are presented at a spatial resolution of 5km².
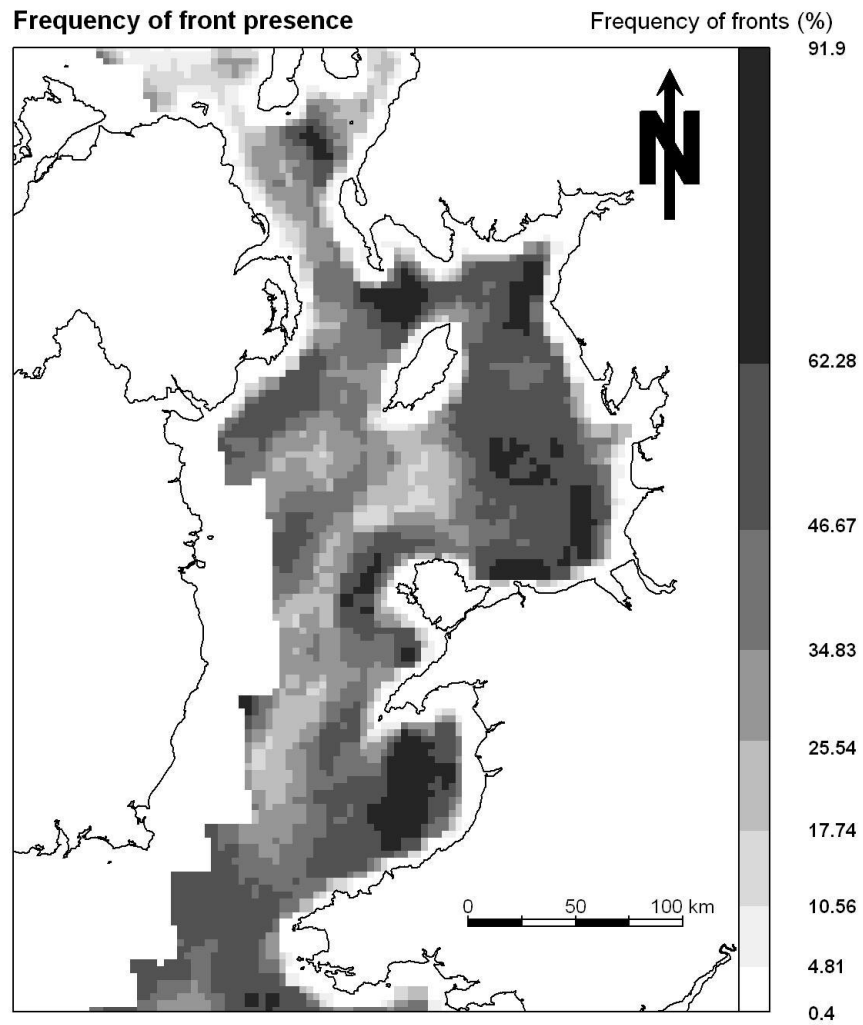
Figure 2.8. Annual front frequency data, extracted from 1.2 km resolution seasonal front frequency maps obtained from Defra via Dr Kirsten Ramsey. The annual frequency of pelagic fronts refers to the percentage of time that strong fronts occur in a particular area over a year. Front frequency was derived from oceanic thermal front metrics obtained from remotely-sensed data sea surface temperature data (see Miller et al. 2010 for technical details). Data are presented at a spatial resolution of 10 km^2.
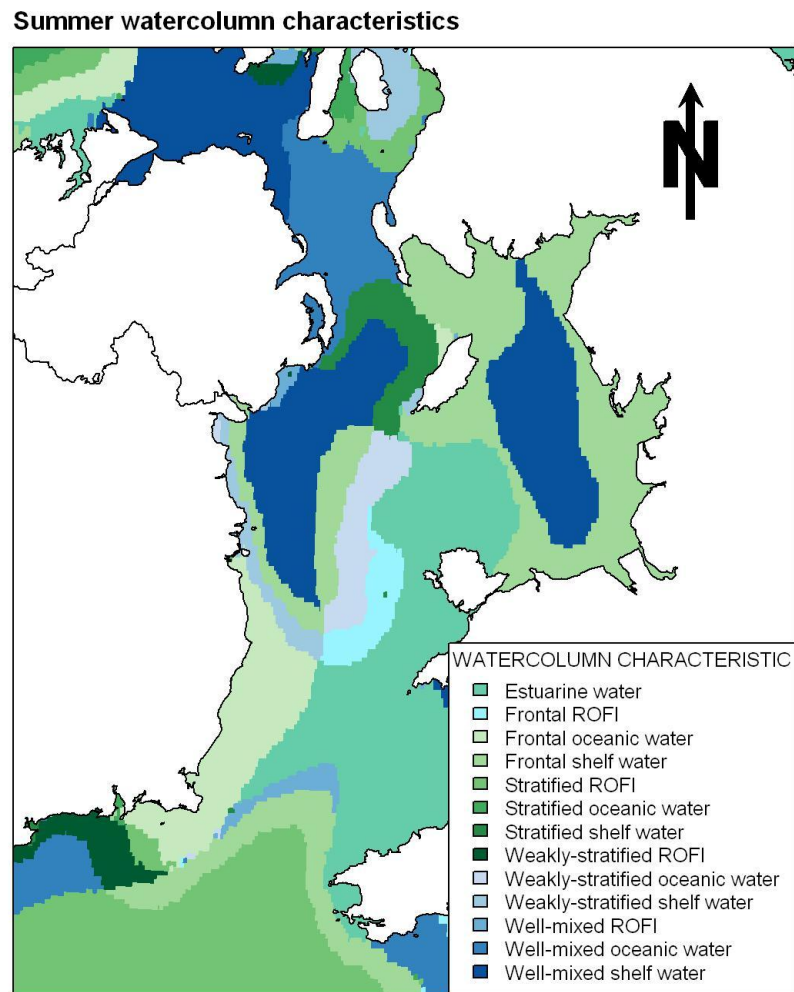
Figure 2.9. Summer watercolumn characteristic data obtained from the UKSeaMap project. Data are presented at a spatial resolution of 5 km².
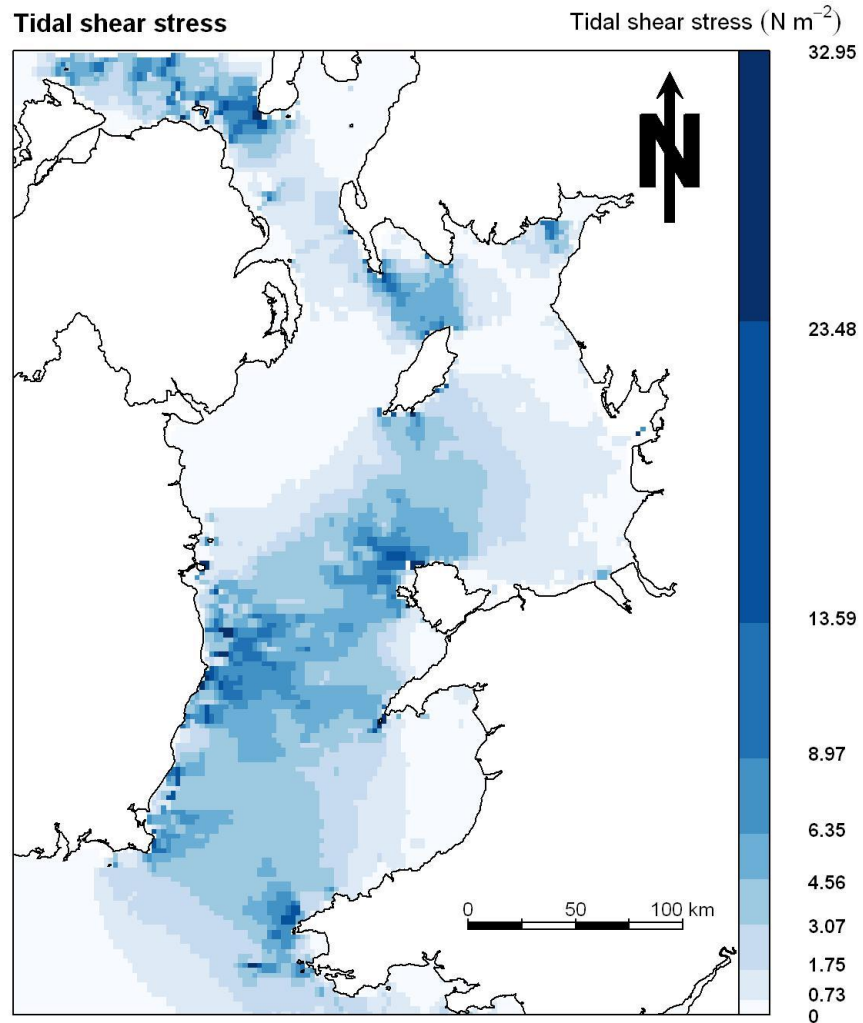
Figure 2.10. Total tidal-induced shear stress or force (N m^{-2}) experienced by the seabed, modelled for the European Shelf by Egbert et al. (2010). http://volkov.oce.orst.edu/tides/ES.html. Data are presented at a spatial resolution of 5km².
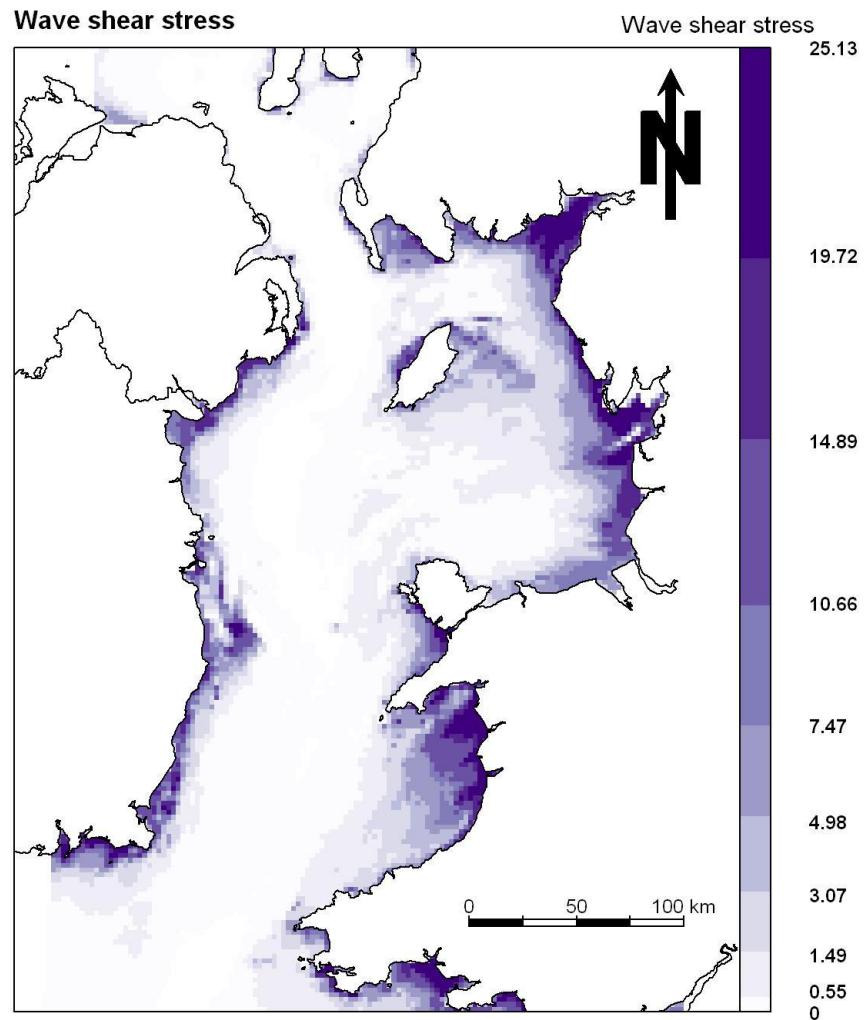
Figure 2.11. The fraction of the time that wave shear stress values exceeded 0.25 Nm^{-2} was used as a measure of wave shear stress experience by the benthic community. This metric was obtained from a model developed by Dr Simon Neill for the Irish Sea (see Hiddink et al. 2009 for further details of model developed). Data are presented at a spatial resolution of 5 km^2.

Brtish Geological Survey seabed sediment

BGS SEABED SEDIMENT
- GRAVELLY MUDDY SAND
- GRAVEL, SAND AND SILT
- GRAVEL
- GRAVELLY MUD
- GRAVELLY SAND
- MUDDY GRAVEL
- MUDDY SANDY GRAVEL
- MUD
- MUDDY SAND
- SANDY GRAVEL
- SANDY MUD
- SLIGHTLY GRAVELLY MUDDY SAND
- SLIGHTLY GRAVELLY MUD
- SLIGHTLY GRAVELLY SAND
- SLIGHTLY GRAVELLY SANDY MUD
- SAND
- DIAMICTON
- ROCK OR DIAMICTON
- ROCK AND SEDIMENT
- UNDIFFERENTIATED SOLID ROCK
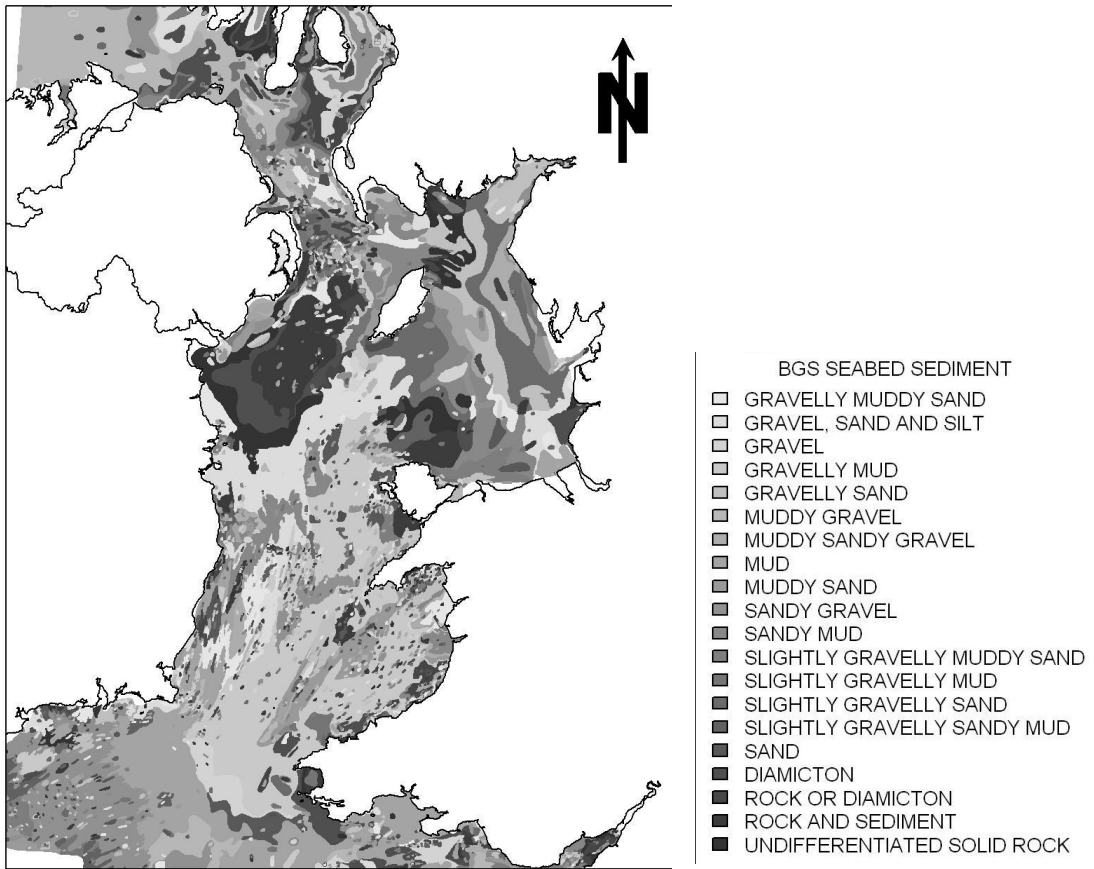
Figure 2.12. British Geological Survey Folk Triangle Classification for sea-bed sediment data.
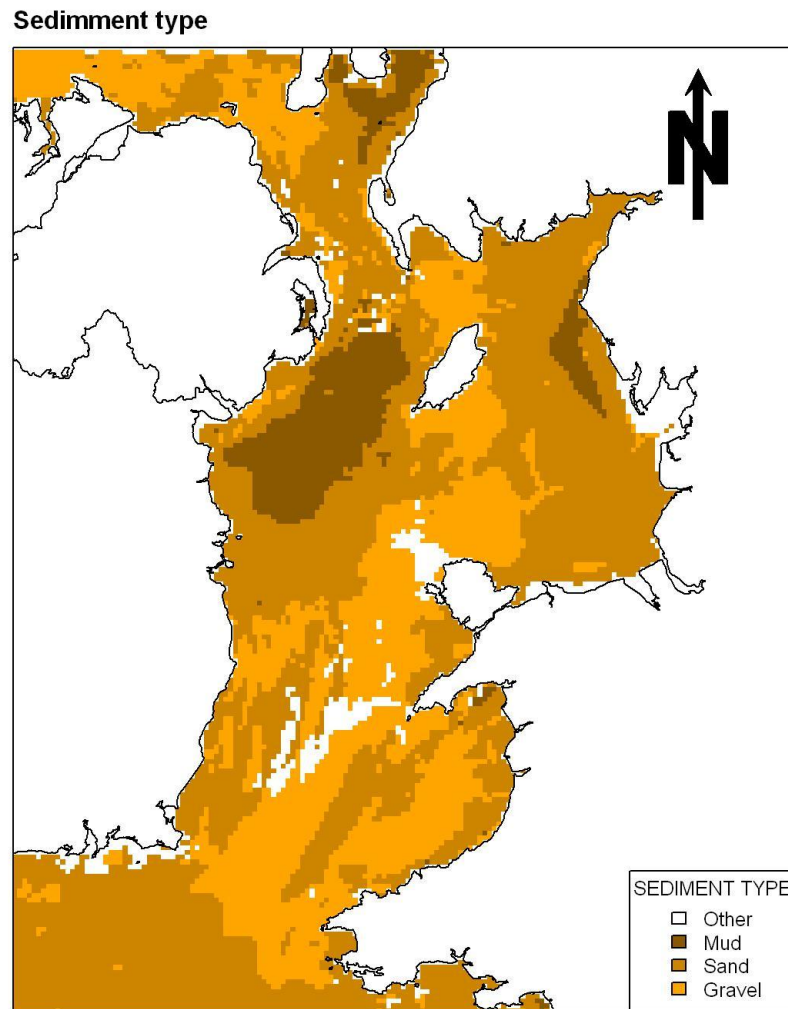
Sediment type

Figure 2.13. Sediment type converted from the British Geological Survey Folk Triangle classification using the conversions in Table 2.2. These simplified sediment types were used in all subsequent analyses. Data is presented at a spatial resolution of 5 km^2.

Table 2.2. Conversion table used to group British Geological Survey Folk Triangle sea bed sediment classifications into four sediment groups for statistical analysis.

BGS Folk Triangle classification	Sediment type
SANDY MUD	Mud
MUD	Mud
SLIGHTLY GRAVELLY SANDY MUD	Mud
SLIGHTLY GRAVELLY MUD	Mud
GRAVELLY MUD	Mud
SLIGHTLY GRAVELLY SAND	Sand
SAND	Sand
GRAVELLY SAND	Sand
MUDDY SAND	Sand
GRAVELLY MUDDY SAND	Sand
SLIGHTLY GRAVELLY MUDDY SAND	Sand
SANDY GRAVEL	Gravel
MUDDY GRAVEL	Gravel
GRAVEL	Gravel
MUDDY SANDY GRAVEL	Gravel
ROCK OR DIAMICTON	Other
UNDIFFERENTIATED SOLID ROCK	Other
DIAMICTON	Other
GRAVEL, SAND AND SILT	Other
ROCK AND SEDIMENT	Other

2.7.3 Fishing intensity data

Table 2.3. Scallop dredge gear width conversions used to calculate area swept for vessel monitoring system (VMS) records.

Administration	Distance from shore (nm)	Dredge limit (no. per side)	Dredge width (m)	Total gear width calculation	Total gear width (per vessel)
England	0 - 6	8	0.75	(8*2)*0.75	12
England	>6	18	0.75	(18*2)*0.75	27
Scotland	0 - 6	8	0.75	(8*2)*0.75	12
Scotland	6 - 12	10	0.75	(10*2)*0.75	15
Wales	0 - 3	4	0.75	(4*2)*0.75	6
Wales	3 - 12	8	0.75	(8*2)*0.75	12
Isle of Man	0 - 3	5	0.75	(5*2)*0.75	7.5
Isle of Man	3 - 12	8	0.75	(8*2)*0.75	12
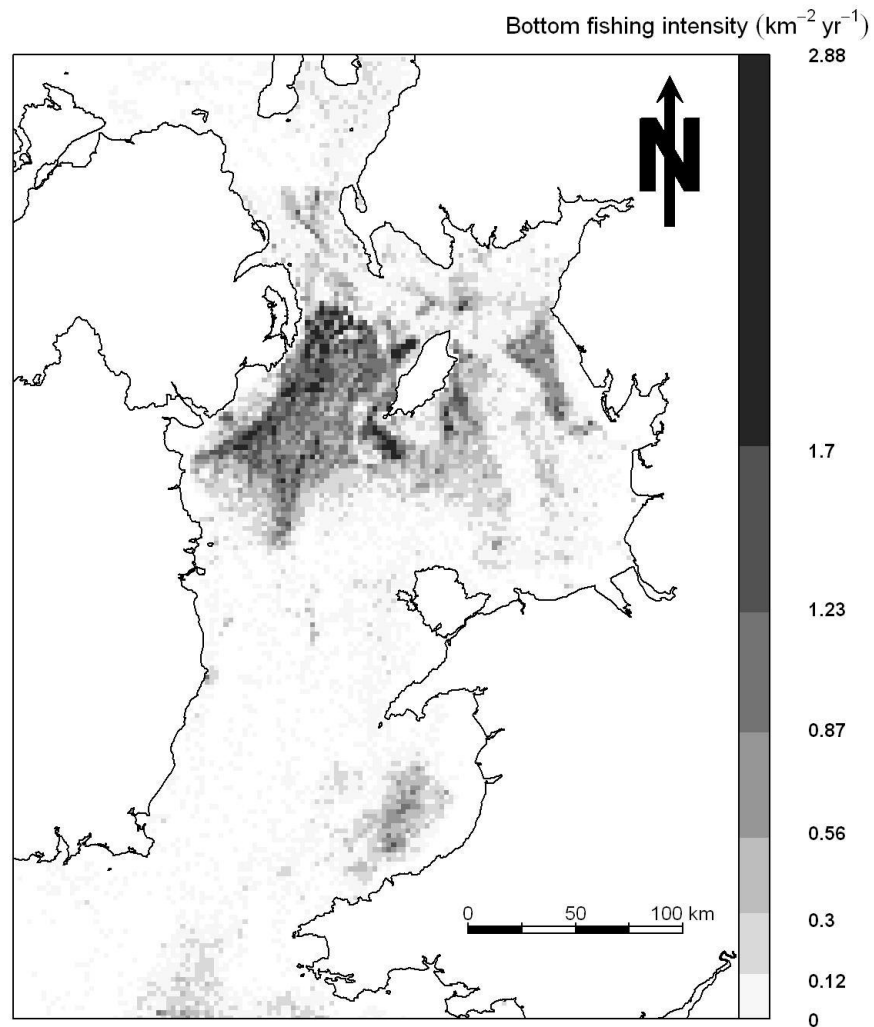
Figure 2.14. Fishing intensity estimates derived from vessel monitoring system (VMS) data (2008-2011) obtained the Marine Management Organisation. Data are presented at a spatial resolution of 5 km².

2.7.4 Sampling design

Figure 2.15. Examples of sampling design for analysis 1 (spatial grain size). Sampling design is illustrated for a grain size of (a) 2.5 km^2, (b) 20 km^2 and (c) 320 km^2. Greyscale is used to illustrate different sampling units, and is not respresentive of any measure or value.

2.7.5 Generalised Least Squares regression model details

Table 2.4. Regression model details and results for all optimal Generalized least squares (GLS) regression models identified in Analysis 1. Analysis 1 investigated production-environment relationships at nine different spatial grains in the Irish Sea.

Spatial grain	Correlation structure	N	Df	Variables retained	Coefficient	Std Error	F	P-value	Pearson's correlation coefficient (r)
Site scale	varPower	15	12	Chlorophyll-a	445.76	81.06	26.87	0.000	0.92
				Sediment type (sand)	209.53	44.50	22.17	0.000	
2.5 km²	NONE	15	12	Chlorophyll-a	336.27	49.25	51.02	0.000	0.95
				Fishing intensity	-30.19	4.57	34.93	0.000	
5 km²	NONE	15	11	Chlorophyll-a	519.49	118.01	38.40	0.001	0.92
				Sediment type (sand)	223.02	80.34	7.71	0.020	
				Tidal shear stress	390.87	144.23	17.62	0.018	
10 km²	varPower	15	12	Chlorophyll-a	260.22	59.34	23.90	0.001	0.92
				Fishing intensity	-22.64	4.76	22.65	0.001	
20 km²	varPower	15	12	Chlorophyll-a	552.05	124.91	31.26	0.001	0.85
				Sediment type (sand)	255.34	61.72	17.12	0.001	
40 km²	varPower	15	12	Chlorophyll-a	454.29	91.05	11.60	0.000	0.85
				Sediment type (sand)	287.15	50.74	32.03	0.000	
80 km²	NONE	15	12	Chlorophyll-a	319.84	70.05	20.04	0.001	0.82
				Sediment type (sand)	120.68	62.74	3.70	0.078	
160 km²	NONE	15	13	Chlorophyll-a	303.01	116.29	6.79	0.022	0.59
320 km²	varPower	15	13	Chlorophyll-a	297.99	87.18	11.68	0.005	0.74

2.7.6 Area of no model predictions
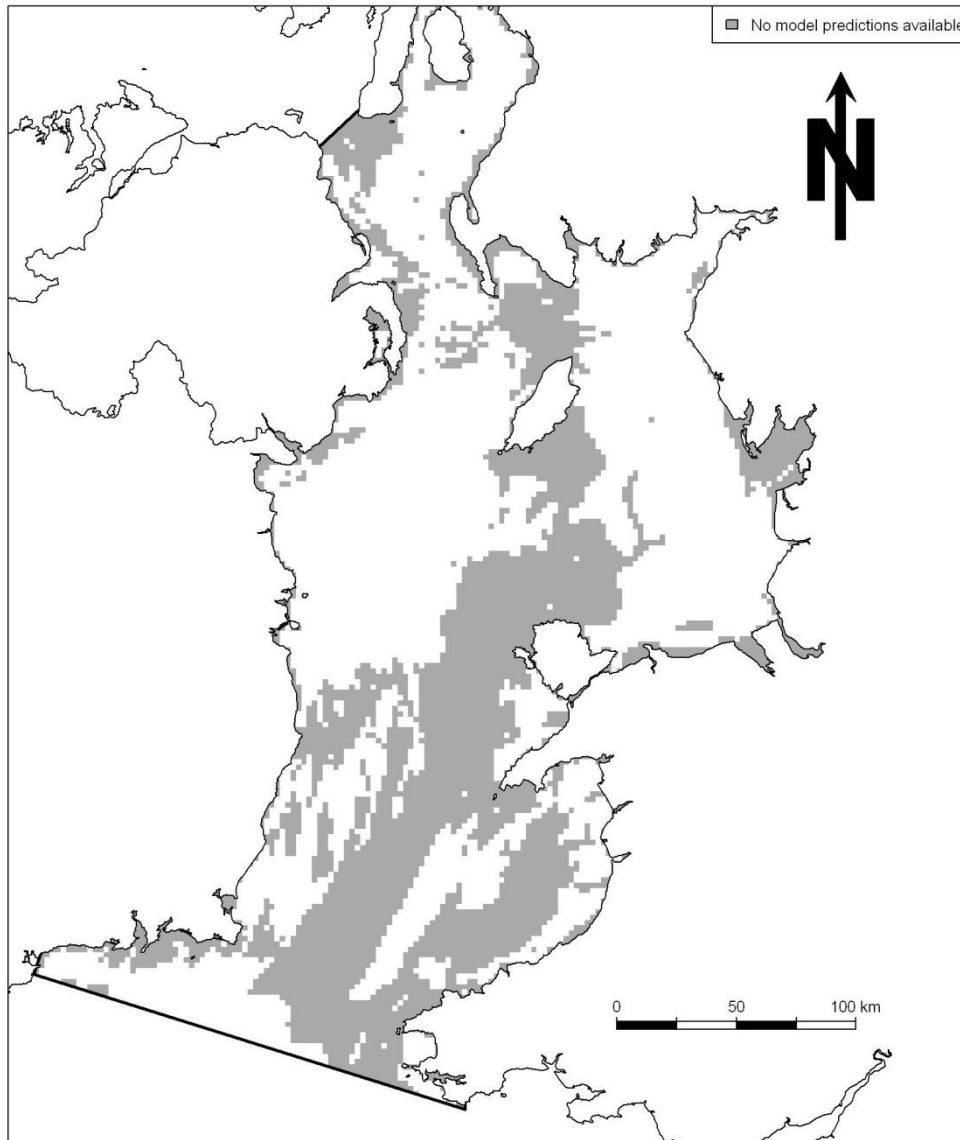
Figure 2.16. Areas of gravel and rock (identified by the grey colour) for which predictions from the optimal 5 km² Generalised least squares (GLS) regression model identified in Analysis 1 are not available. No predictions are made for these sediment types because they are not represented in the original model parameterisation data. See Figure 2.6 for further details.

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CHAPTER 3 - Modelling benthic infaunal production, biomass and recovery in the Irish Sea

3.1 AIM: To refine and re-parameterise an existing size-based model of benthic invertebrate communities for application in the Irish Sea. The model will predict benthic infaunal production and biomass, assess the impact of current bottom fishing activity on these attributes, and estimate the recovery time of benthic communities following fishing impact.

3.2 ABSTRACT

Knowledge of the spatial distribution of benthic infaunal production is required if this important ecosystem process is to be protected in marine protected areas (MPAs). Size-based models of benthic invertebrate communities are useful tools for predicting community productivity. If size-based models can be used to predict production over large spatial scales these models could help prioritise MPA site selection. Here the Hiddink et al. (2006a) size-based model of benthic production, biomass and bottom fishing impacts for the North Sea is re-parameterised and validated for the Irish Sea. In particular, the estimation of benthic community carrying capacity is improved and re-parameterised. The model predicts benthic infaunal production and biomass under fished and unfished scenarios at a spatial scale of 5 km². Estimates of fishing intensity incorporated into the fished scenario were obtained from vessel monitoring systems (VMS) data (2008-2011). The model outputs were validated with independent benthic infauna data from 19 stations in Irish Sea collected in 2011. 48% of the spatial variation in productivity can be explained. The model predicts that areas of high production and biomass are located along the North Wales coast, off the north-west coast of England, the Solway Firth. Predictions of bottom fishing impact indicate that fishing reduces Irish Sea production by 5.1% and biomass by 12.2% compared to the unfished scenario, and predictions of benthic community recovery from fishing suggest that the productivity of communities takes between 2.6 to 13.3 years to recover, whereas biomass takes 2.2 to 7.7 years. The spatial distribution of benthic production and biomass, areas of high

bottom fishing impact and long recovery time could all inform spatial management of benthic communities in the Irish Sea.

3.3 INTRODUCTION

Benthic infaunal production is an important marine ecosystem process that underlies energy and nutrient cycling, and supports demersal fish stocks (Tumbiolo & Downing, 1994; Danovaro et al. 2008; Heath, 2005; Wouters & Cabral, 2009). This indicator of benthic ecosystem health and quality could be used to direct spatial management measures such as marine protected areas (MPAs) (Collie et al. 2005; Hiddink et al. 2006b). To prioritise areas of high benthic infaunal production for protection in MPAs, knowledge of the spatial variation in productivity is required. Empirical models of benthic production could provide spatially consistent data to support MPA design.

Hiddink et al. (2006) developed an empirical, size-based model of benthic biomass, production and species richness for the North Sea, based on a model of trawling impacts originally developed by Duplisea et al. (2002). Size-based models are useful for modelling the productivity of marine communities because body size largely determines metabolic rate and subsequently rates of consumption and production (Sheldon et al 1977), and the body size distribution of a population is therefore a key parameter in the calculation of a population's productivity (Brey, 2001, Robinson et al 2010). Marine communities are size-structured, meaning that interactions between individuals are size-dependent. Size-based models can therefore capture marine population dynamics without the need to know the ecology for all species in a community (Blanchard et al. 2012). This generality allows size-based models to be applied to a range of different community and habitat types (Travers et al. 2007; Robinson et al. 2010). Finally, fishing impacts on benthic communities are size-specific, making size-based models useful for estimating the impact of bottom fishing on productivity (Queiros et al. 2006).

The Hiddink et al. (2006) model (hereafter Hiddink model) included habitat features to enable it to predict benthic community characteristics over large spatial scales and to

identify differences in vulnerability to trawling (Hiddink et al. 2006a; Hiddink et al. 2006b). Tillin et al. (2009), however, found that confidence in the Hiddink model was not great enough to be utilised for predicting production beyond the area for which it was parameterised. Many assumptions were made and limited datasets utilised in the development and parameterisation of the Hiddink model (Hiddink et al. 2006a). Carrying capacity parameterisation, for example, was based on a small dataset of chlorophyll-*a* content of sediment data, and interpolated chlorophyll-*a* sediment data were used to estimate benthic carrying capacity in the model. The influence of spatial grain and spatial extent was also not considered when parameterising the Hiddink model. As a result, confidence that the empirical environment-production relationships identified during parameterisation can be scaled up to the 9 km^2 scale of predictions is limited, and the degree to which the identified relationships apply over large areas is unknown.

In order to apply the Hiddink (2006) predictive model for the purpose of MPA design it will require refining and re-parameterising for the particular area of interest. To predict benthic production in the Irish Sea, for example, a quantitative understanding of the relationship between the environmental conditions and the productivity of benthic communities in this area is required, and an understanding of the influence of spatial grain size and extent on these relationships would be helpful to identify the optimal scale at which to make predictions. Here the Hiddink (2006) size-based model is improved and re-parameterised for application in the Irish Sea, based on production-environment relationships identified in the multi-scale generalised least square regression analyses outlined in Chapter 2. Chapter 2 examined how spatial grain size and extent influenced these environment-production relationships in order to identify the optimum spatial grain at which to make predictions and inform re-parameterisation of the model.

The model will predict benthic infauna production and biomass in the Irish Sea under current bottom fishing activity, estimated from vessel monitoring system (VMS) satellite data (obtained from the Marine Management Organisation). As outlined in Chapter 1, bottom fishing has been found to have a negative impact on benthic invertebrate

production and biomass, resulting from the removal and morality of individuals caused by fishing gear (Jennings et al. 2001; Reiss et al. 2009). The extent and magnitude of current bottom fishing impacts on benthic production and biomass at the scale of the Irish Sea can be estimated by comparing this model output to predictions made under an unfished scenario, and the nature of the dynamic, size-based model allows the estimation of the time it takes for the productivity and biomass of benthic communities to recovery following the cessation of bottom fishing. Time to recover estimates can be compared to current fishing intensity estimates to understand the current recovery status of the benthic communities in the Irish Sea. All these model output could inform the spatial management of benthic production in MPAs, by identifying areas of high benthic productivity, areas where trawling has a large negative effect, and areas that are slow to recover or in an un-recovered state for MPA prioritisation.

3.4 MATERIALS AND METHODS

3.4.1 Method overview

Here an existing size-based model of benthic invertebrate communities is re-parameterised and validated for the Irish Sea. This model of benthic biomass, production and species richness for the North Sea was originally developed by Duplisea et al. (2002) to predict the size-distribution of benthic assemblages and investigate bottom trawling impacts. The model was refined by Hiddink et al. (2006a) to include environmental parameters for application in the southern North Sea. The Hiddink et al. (2006) model (hereafter Hiddink model) made predictions of benthic community production and biomass at a spatial resolution of 9 km^2 in response to environmental conditions and bottom trawling. This model incorporated four environment-mediated relationships, including the effect of (i) tidal-induced shear stress on population growth (hereafter tidal shear stress), (ii) sediment erosion on mortality, (iii) sediment type on fishing mortality, and (iv) chlorophyll-a concentration of the sediment on benthic community carrying capacity.

As already outlined, the Hiddink model has some weaknesses, particularly the calculation of carrying capacity and lack of consideration of spatial scale. Furthermore, in order to apply to a different area of UK waters, it is likely that the model will need local parameterisation in order to reflect any differences in production-environment relationships. Environmental conditions in the North Sea and Irish Sea are very different; the North Sea is dominated by soft sediments and stratified waters (Heath, 2005), whilst the Irish Sea exhibits greater variation in hydrodynamic regime, seabed sediment type and depth (Bolam et al. 2010; Bowers et al. 2013).

Potential major improvements on the Hiddink model include refined parameterisation of benthic carrying capacity estimates and influence of tidal shear stress, and the identification of a suitable spatial scale for predictions, based on the observed multi-scale production-environment relationships identified in Chapter 2. Chapter 2 identified a spatial grain size between 2.5 km^2 and 20 km^2 to be suitable scale at which the explanatory power of production-environment relationships is greatest for making predictions. A spatial grain of 5 km^2 was chosen to make predictions here because of it is considered a relevant scale for informing MPA design. A review of 89 marine protected areas by Halpern (2003), for example, found that the median size of reserves was 4.0 km^2 (ranging from 0.002-846 km^2).

The relationships between benthic community production and environmental conditions in the Irish Sea identified in Chapter 2 included; (i) a positive relationship between production and remotely-sensed chlorophyll-a concentration in surface waters, (ii) variation in productivity with sediment type, (iii) a positive relationship between production and modelled tidal shear stress, and (iv) a negative relationship between production and bottom fishing intensity estimated from vessel monitoring system (VMS) records from the time period 2004 – 2008. See Chapter 2 for an outline of the data and methods used to identity these relationships. The Irish Sea specific production-environment relationships were incorporated by adding and adapting existing environment-mediated carrying capacity, growth and mortality functions in the size-based model. The sediment erosion-mortality function was removed because this relationship was not investigated for the Irish Sea.

To make predictions of benthic infaunal production at the 5 km^2 scale, remotely-sensed surface water chlorophyll-*a* concentration, sediment type, modelled tidal shear stress, and VMS derived fishing intensity data was collated a spatial resolution of 5 km^2 for input into the model (see Appendix 2.7.2 and 2.7.3 for distribution maps of these data).

3.4.2 Model development

The size-based model consists of 32 state variables. These 32 state variables are characterised by different body sizes and two different body types; 16 soft-bodied (SOFT, body size range: 1.9-500 mg AFDW) and 16 hard-bodied (HARD, body size range: 50-60 000 mg). The SOFT body size classes represent macrofauna such as polychaetes, whereas HARD body size classes represent macrofauna such as bivalves and crustaceans. Growth of population biomass within each of these 32 different body size and body type groups is modelled using modified Lotka-Volterra competition equations to give population biomass flux:

$$(1) \qquad \frac{\mathrm{d}B_t}{\mathrm{d}t} = B_i\, r_i \left(\frac{C_i - B_i - \alpha_{ij}B_j}{Ci} \right) - B_i \mathrm{Mort}_i$$

where *i* and *j* are two competing populations of animals, B_i is the biomass of animals in population *i* and B$_j$ the biomass of the competing animals in population *j*. C_i refers to the carrying capacity of the competitor *i*, r_i to the specific growth rate or rate of increase in biomass of *i*, and Mort$_i$ to the mortality rate of *I*. α_{ij} is the competitive influence of a unit of the competitor *j* biomass on the carrying capacity of population *i*. Here soft-bodied and hard-bodied animals are assumed to be in competition with each other (Wilson, 1990), so that in the model the biomass of HARD animals (those fauna with shells or exoskeletons, representing bivalves and crustaceans) has a negative effect on the carrying capacity of SOFT animals (representing soft-bodied fauna such as polychaetes) and vice versa. Specific growth rates for SOFT and HARD were derived by Duplisea et al. (2002) from Von Bertalanffy growth rate values (*k*) taken from Brey (1999). Specific mortality rates were subsequently derived from these specific growth rates. For details of all parameter values for all body size classes and body types see Table 2 in Duplisea et al. (2002).

The influence of environment on the productivity of benthic communities identified in Chapter 2 is incorporated into the model by adapting the estimation of benthic community carrying capacity, and the environment-mediated growth modifer and mortality functions that influence the Lotka-Volterra growth function. The key differences to the Hiddink model are the improvements made to the estimation of carrying capacity, and changes to a tidal shear stress-mediated growth modifier function. Both of these influence growth in the model, and are explained in details in the sections below.

Estimating the carrying capacity of the benthic community

Sea surface chlorophyll-*a* is expected to represent food potentially available to the benthos (Wolff, 1977; Bolam et al. 2010). Surface water chlorophyll-a concentration has been found to be an important driver of benthic community production at the 5km^2 scale across the whole of the Irish Sea area, indicating that it could be a useful proxy for the carrying capacity of benthic communities (see Chapter 2). Remotely-sensed surface water chlorophyll-*a* is therefore used to determine carrying capacity of the benthic community in the model, rather than chlorophyll-*a* content of the sediment data, which was used in the Hiddink model. This is considered an improvement on the Hiddink model because it allows benthic carrying capacity to be estimated from a remotely-sensed, spatially continuous environment variable that is easily obtained from NEODASS, rather than from interpolated chlorophyll-*a* content of the sediment from spaced observations which can be subject to interpolation error (Zhou, 1998). Furthermore, chlorophyll-*a* content of the sediment may limit estimates of carrying capacity because it only reflects food available to certain faunal groups, e.g. surface and subsurface deposit feeders (Burd et al. 2012). Suspension feeders are more likely to metabolise suspended organic material than that accumulated in sediment, and therefore chlorophyll-*a* at the sea surface may be a better estimate of total food availability and therefore maximum carrying capacity. It is recognised, however, that this will be modified by hydrodynamic regime, such as stratification, and the strength of bed shear stresses (Warwick & Uncles, 1980; Snelgrove & Butman, 1994; Kaiser et al. 2006; Bolam et al. 2010).

The relationship between chlorophyll-*a* and carrying capacity was determined by quantile regression describing how benthic community biomass (g WM m^{-2}) was limited by surface chlorophyll-*a* (mg m^{-3}) using 5 km^2 resolution data from across the Irish Sea (chlorophyll-*a* data obtained from NERC Earth Observation Data Acquisition and Analysis Serivces, http:/www.neodaas.ac.uk). These data represented an average from the period Jan 2004 to Dec 2008. Interestingly, an interaction between chlorophyll-*a* and sediment type was found in relation to total benthic infauna biomass, and quantile regressions describing the relationship between chlorophyll-*a* and biomass in different sediment types were used to parameterise benthic community carrying capacity in the model. Figure 3.1a and Figure 3.1b presents the results of 90th quantile regressions used for parameterising the carrying capacity estimates in sand and mud sediment types, respectively. For gravel there appeared to be no relationship between chlorophyll-a and benthic biomass, so carrying capacity was set at a fixed level of 1143.35 g MW m^{-2} based on 90th quantile regression without an intercept on the data available (Figure 3.1c).

Although such an interaction between chlorophyll-*a*, sediment type and benthic biomass is unexpected, the quantile regression results support the finding that sediment type is also an important driver of benthic infauna production at the 5km^2 scale (see Chapter 2). Higher rates of total benthic production in sandy sediments compared to muddy sediments are assumed to reflect the influence of hydrodynamics (Warwick & Uncles, 1980), which is known to influence food supply to the benthos and thus growth (Snelgrove & Butman, 1994; Kaiser et al. 2006). That is, sandy, coarser sediments are characteristic of areas that experience higher levels of tidal shear stress than areas of muddy sediment (Warwick & Uncles, 1980), and in these areas a greater current speed provides more food to the benthos (Hiddink et al. 2006; Lambert at al. 2011). Using sediment-specific relationships to calculate carrying capacity from chlorophyll-*a* allows the previously identified associations between both chlorophyll-*a* concentration and sediment type on production to be incorporated into the model.
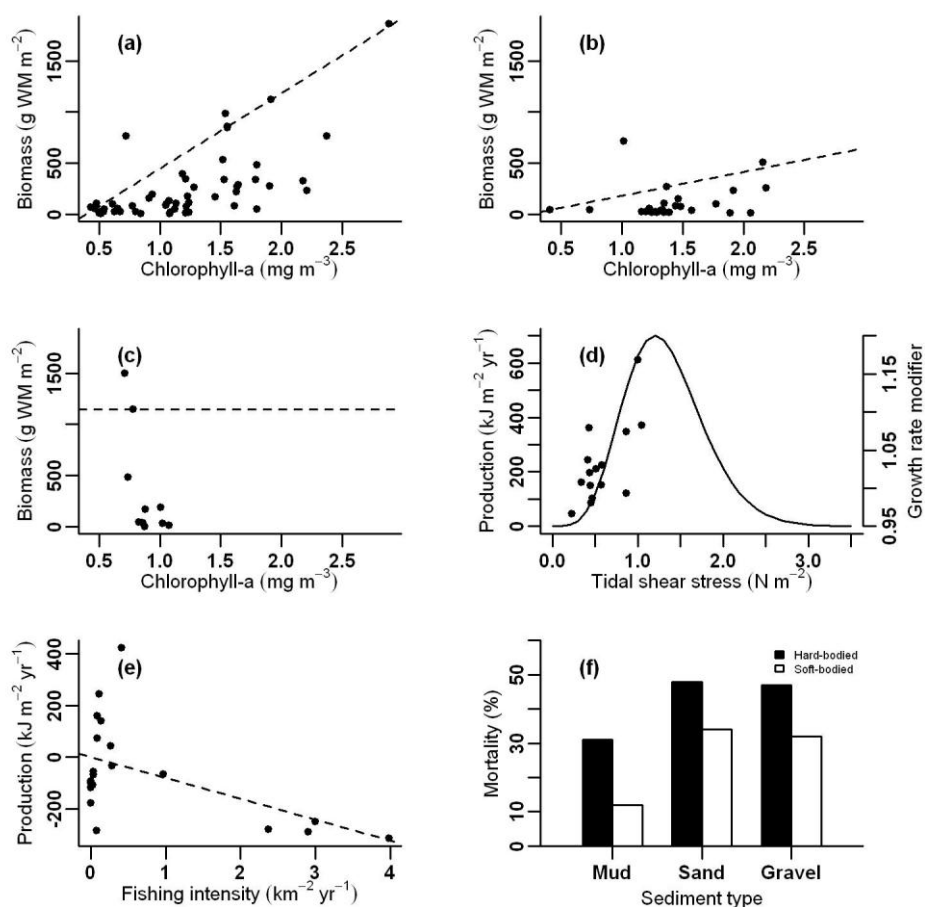
Figure 3.1. Parameterisation of the model. (a) 90th quantile regression describing the relationship between benthic infaunal biomass (g WM m[-2]) in sandy sediments and sea surface chlorophyll-a concentration (mg m^{-3}, annual mean 2004 to 2008). (b) 90th quantile regression describing the relationship between benthic infaunal biomass (g WM m[-2]) in muddy sediments and chlorophyll-a concentration (mg m^{-3}, 2004 to 2008). (c) 90th quantile regression without intercept between benthic infaunal biomass (g WM m[-2]) in gravelly sediments and chlorophyll-a concentration (mg m^{-3}, 2004-2008). The dashed lines on figures (a) to (c) represent the relationships used to parameterise carrying capacity in the model. (d) Gaussian relationship between benthic infaunal production (kJ m^{-2} yr^{-1}), infauna growth rate and tidal shear stress (N m^{-2}) parameterised in the model. The data points represent the observed relationship between benthic infaunal production (kJ m^{-2} yr^{-1}) and tidal shear stress (N m^{-2}) at a resolution of 5 km² in the Irish Sea (N = 15, $F_{[1,11]}$ = 7.34, p= 0.020). (e) Observed relationship between benthic infaunal production (kJ m^{-2} yr^{-1}) and fishing intensity (km^{-2} yr^{-1}) at a resolution of 5 km² in the Irish Sea (N = 20, $F_{[1,17]}$= 19.68, p = 0.000). (e) Percentage mortality per fishing event for hard- (solid bars) and soft-bodied (open bars) benthic invertebrates for the three sediment types included in the model, adapted from Hiddink et al. (2006a).

Effect of tidal shear stress on growth rate

Tidal shear stress is a measure of the degree of water movement at the water-sediment interface and is expected to have an important influence benthic productivity by mediating the availability of food to the benthos (Warwick & Uncles, 1980; Snelgrove & Butman, 1994). A positive linear relationship between benthic infaunal production and tidal shear stress over a range of 0.2 to 1 N m^{-2} has previously been identified in the Irish Sea at a spatial resolution of 5km^2 (see Chapter 2). Due to its influence on food supply this relationship between tidal shear stress and benthic production is included in the model by modifying the growth rate of benthic invertebrates in relation to different levels of tidal shear stress (Figure 3.1d).

The data used to identify the above, observed relationship between benthic production and tidal shear stress had a maximum shear stress of 1 N m^{-2}. However, tidal shear stress in the Irish Sea extends up to 1 N m^{-2} so additional information from previous studies and literature was used to inform the relationship between productivity and shear stress at values higher than 1 Nm^{-2}. An optimal bed stress range within which a sufficient amount of food is provided to the sea bed is expected (Kaiser et al. 2005; Hiddink et al. 2006a), because at high levels of tidal shear stress food is expected to be transported away too quickly, impairing uptake by benthic invertebrates (Hiddink et al. 2006a). Hiddink et al. (2006a) found an optimum relationship between benthic biomass and shear stress in soft sediments in the North Sea, therefore an optimum relationship was also included here.

An optimum relationship between tidal shear stress and benthic infaunal growth was built into the model by including a growth rate modifier function. This tidal shear stress-dependent growth rate modifier function identified a factor by which to multiply the normal, Lotka-Volterra estimated growth rate. The relationship between tidal shear stress and the growth rate modifier is described by the Gaussian curve shown in Figure 3.1d, modelled according to:

(2) $\qquad G = G_{\min} + (G_{\max} - G_{\min})e^{\frac{(S - S_m)^2}{-V}}$

Where G is the shear stress-dependent growth modifier factor, G_{min} is the minimal growth rate (0.95), G_{max} is the maximum growth rate (1.2), S is shear stress, S_m is shear stress at which the maximum growth rate is reached (1 N m^{-2}), and V is the variance of the Gaussian curve (0.085). This parameterisation reflected the assumed optimal relationship between tidal shear stress and growth, informed by the empirical findings of Chapter 2 and Hiddink et al. (2006a).

Impact of bottom fishing on mortality

Bottom fishing is expected to have a negative impact on benthic production (Jennings et al. 2001; Collie et al 2005; Hiddink et al. 2006b; Reiss et al. 2009), and a significant negative relationship between benthic infaunal production and bottom fishing has been found in the Irish Sea at a resolution of 5km^2 (Figure 3.1e). This negative impact of bottom fishing on benthic production was incorporated into the model by including habitat- and body type-dependent mortality functions. These were determined by Hiddink et al. (2006a) based on an extensive quantitative dataset of direct fishing impacts collated by Collie et al. (2000) (See Hiddink et al. 2006a for further details). Mortality rates are found to be highest in coarser sediments such as sand and gravel compared to finer sediments such as mud, and higher for hard-bodied benthic animals than for soft-bodied benthic animals (Figure 3.1f).

3.4.3 Making predictions

Environmental data for the Irish Sea

Remotely-sensed surface water chlorophyll-*a* concentration data at a 1.1 km spatial resolution were provided by NEODAAS (NERC Earth Observation Data Acquisition and Analysis Serivces, http:/www.neodaas.ac.uk). These data were obtained from the MODIS sensor using the case 2 chl-*a* algorithm (OC5) for turbid shelf seas, and an annual average for the years 2008 to 2011 was calculated from monthly composites (see Figure X, Annexe A). The tidal shear stress data used here was modelled by Egbert et al. (2010). This modelled data is available for the whole European Shelf, and was downloaded from

the OSU Tidal Data Inversion webpage, http://volkov.oce.orst.edu/tides/ES.html (for details see Egbert et al. 2010). The data have a spatial resolution of 0.03 decimal degrees, and represent total maximum tidal-induced stress or force (N m^{-2}) experienced by the seabed (see Figure 2.7, Appendix 2.7.2). Average chlorophyll-*a* concentration and tidal shear stress values were calculated at a spatial resolution of 5 km^2 across the Irish Sea.

Seabed sediment data was obtained from the latest British Geological Survey (BGS) 1:250 000 scale digital Sea bed Sediment map, released 2011 (see Figure 2.12, Appendix 2.7.2). The Folk triangle classification used by BGS was simplified by collapsing all sediments dominated by mud into Mud, all sediments dominated by sand into Sand, and so on, to give four major sediment types; Sand, Mud, Gravel and Other (see Table 2.1 Appendix 2.7.2 for a conversion table, and Figure 2.13, Appendix 2.7.2 for resulting map of the four different sediment types). This meant that sediment types were comparable to those used in Chapter 2. To scale sediment data up to a spatial resolution of 5 km^2, the sediment type that covered the greatest area within a 5 km^2 cell was assigned to that cell.

Bottom fishing intensity estimates were derived from Vessel Monitoring System (VMS) data provided by the UK Marine Management Organisation. Fishing intensity was measured as the number of times a 1 km^2 area is swept by fishing gear per year (km^{-2} yr^{-1}), calculated from bottom trawling and dredging VMS records within each 5 km^2 cell from the time period Jan 2008 to December 2011 (see Figure 2.13, Appendix 2.7.3). Fishing intensity in a particular area is likely to vary each year, and bottom trawling history, i.e. trawling impacts over several years, is expected to be a better indicator of benthic community composition than single year fishing intensity estimates (Hiddink et al. 2006a). Bottom fishing intensity data from several years was therefore used to better reflect cumulative fishing impact on the benthos (Lambert et al. submitted).

VMS data were cleaned and processed using the VMStools package in R and protocol developed by Hintzen et al (2012). Bottom fishing vessel types were grouped into three main gear classes; otter trawl, beam trawl and scallop dredge. A gear width of 60 metres

and 24 metres was allocated to otter trawlers and beam trawlers, respectively, following previous approaches by Hiddink et al. (2006a) and Hinz et al. (2009). Different regulations regarding the maximum number of dredges are in force across the Irish Sea, depending on in which country and how many nautical miles from shore a vessel is fishing (Beukers-Stewart & Beukers-Stewart, 2009). Gear width for dredgers was therefore determined based on where in the Irish Sea a VMS position was identified. The different administrative zones, associated number of dredges and total gear width can be found in Table 2.3, Appendix 2.7.3. Vessel speed was used to distinguish between steaming and fishing activity in order to determine which VMS positions to include in the calculation of fishing intensity. Fishing speed was defined using speed histograms, similar to the approach of Lee et al. 2010. Fishing speed for otter trawlers and dredgers was defined as one to four knots, whereas fishing speed for beam trawlers was defined as two to five knots.

The area swept by fishing gear represented by each 2 hour interval VMS record was determined from the fishing speed and fishing gear width associated with each record. Interpolation of fishing tracks between 2 hours VMS positions was not considered necessary here because data were being collated at $5km^2$ scale, and therefore fine scale detail of fishing tracks was not required (Lee et al. 2010). The total area swept by fishing gear in each $5km^2$ cell was calculated by summing the area represented by all the records occurring in the cell between 2008 and 2011. The number of times that each $5km^2$ cell was fished per year was then estimated to give fishing intensity ($km^{-2} yr^{-1}$). For example, one 2 hour interval VMS record for a 60m otter trawler travelling at 4 knots represents a fished area of 0.889 km^2, and if this was the only record found in a $5km^2$ cell over a four year period, the estimated fishing intensity would be 0.0445 $km^{-2} yr^{-1}$ for that cell.

3.4.4 Model application to MPA design

Predicting benthic infaunal production and assessing current bottom fishing impacts

Benthic infaunal production and biomass under current fishing activity for each 5 km^2 cell in the Irish Sea was predicted by running the model for 1500 time steps of 30 days, using the habitat and bottom intensity data described above. To assess the extent and magnitude of current bottom fishing impacts on benthic infaunal production and biomass these estimates were compared with predictions under an unfished scenario. Unfished production and biomass estimates were generated by running the same model for 1500 time steps of 30 days whilst setting bottom fishing intensity to zero. The difference between fished and unfished estimates were mapped to give an understanding of the spatial distribution of bottom fishing impacts, and to identify those areas that are most highly impacted. To understand the overall impact of bottom fishing at the scale of the Irish Sea, production and biomass estimates predicted under the fished and unfished scenarios were summed over all cells in the Irish Sea and compared.

Modelling benthic infaunal production under current fishing activity can identify areas of high productivity and inform the prioritisation of MPAs to protect benthic communities. Similarly, estimating the extent and magnitude of bottom fishing impacts on benthic infaunal communities could inform marine spatial management by highlighting areas of very high negative impact. These negative impacts could be mediated by spatial management measures such as permanent no-take MPAs, or effort restrictions that manage bottom fishing impact at some defined, acceptable level.

Estimating recovery potential and recovery status of benthic communities

In addition to predicting production, biomass and quantifying the impact of bottom fishing activity, the nature of the dynamic, size-based model used here allows the estimation of the recovery potential of benthic communities following cessation of bottom fishing. Recovery potential is measured by the time it takes for benthic

productivity and biomass to recover to a level expected in the absence of fishing (unfished), or near to an unfished state, chosen arbitrary to be 90% of the production and biomass estimates ($P_{0.9}$ and $B_{0.9}$) generated under the unfished scenario described above (Hiddink et al. 2006b).

Time to recovery estimates were generated by running the model for 1500 time steps of 30 days without bottom fishing, and then implementing a single fishing event and recording the time at which infauna production and biomass returned to the near unfished state, $P_{0.9}$ and $B_{0.9}$ respectively. These recovery potential estimates can be compared to current fishing intensity estimates to understand the current recovery status of the benthic communities in the Irish Sea. That is, whether or not the benthic community has recovered to the near unfished state, $P_{0.9}$ or $B_{0.9}$, since the last bottom trawling event (recovered to $P_{0.9}/B_{0.9}$ since last bottom fishing event = 1, not recovered to $P_{0.9}/B_{0.9}$ since last bottom fishing event = 0). Here, if bottom fishing intensity is lower than the inverse of the recovery potential of the benthic infaunal community, bottom fishing intensity is assumed to be high enough to prevent the community reaching a recovered state since the last fishing event.

Estimates of recovery potential and recovery status can inform marine spatial management by highlighting those areas that are vulnerable to bottom fishing, i.e. take a long time to recovery from fishing impacts, or are currently in an unrecovered state. These areas could be prioritised for benthic community protection in no-take MPAs. Alternatively, fisheries management measures such as effort limitation could be employed to reduce fishing intensity to a level that allowed the benthic community recovery.

3.4.5 Model validation

A research cruise on the RV Prince Madog was conducted in the Eastern Irish Sea during summer 2011 to collect independent benthic community data for model validation. Model predictions of benthic infauna production under current fishing activity were validated using observed benthic infauna production estimates calculated from this independent data.

Independent data collection

Benthic infaunal communities at 19 stations in the eastern Irish Sea were sampled using a Day grab. A limited area of the Irish Sea was sampled due to shiptime and funding constraints. Random sampling, stratified by sediment type was used to ensure a large range of habitats and environmental conditions (e.g. sediment type was assumed to act as a proxy for variation in tidal shear stress) were sampled within the limited time period and steaming distance available (see Figure 3.2 for sampling design). The largest range of environmental parameters possible within these restraints was covered in order to test the ability to the model to predict over different conditions.

Three grabs were taken at each station and samples were passed through a 1 mm sieve and all retained animals were preserved in 4% buffered formalin on board. Replicates were pooled and all species data were standardised to number of individuals and total wet mass in grams per m^2 (g WM m^{-2}). Species where total wet mass equalled <0.001 g m^{-2} were removed due to a lack of a tangible biomass value and because they were considered to be inconsequential to subsequent calculations of community production estimates.
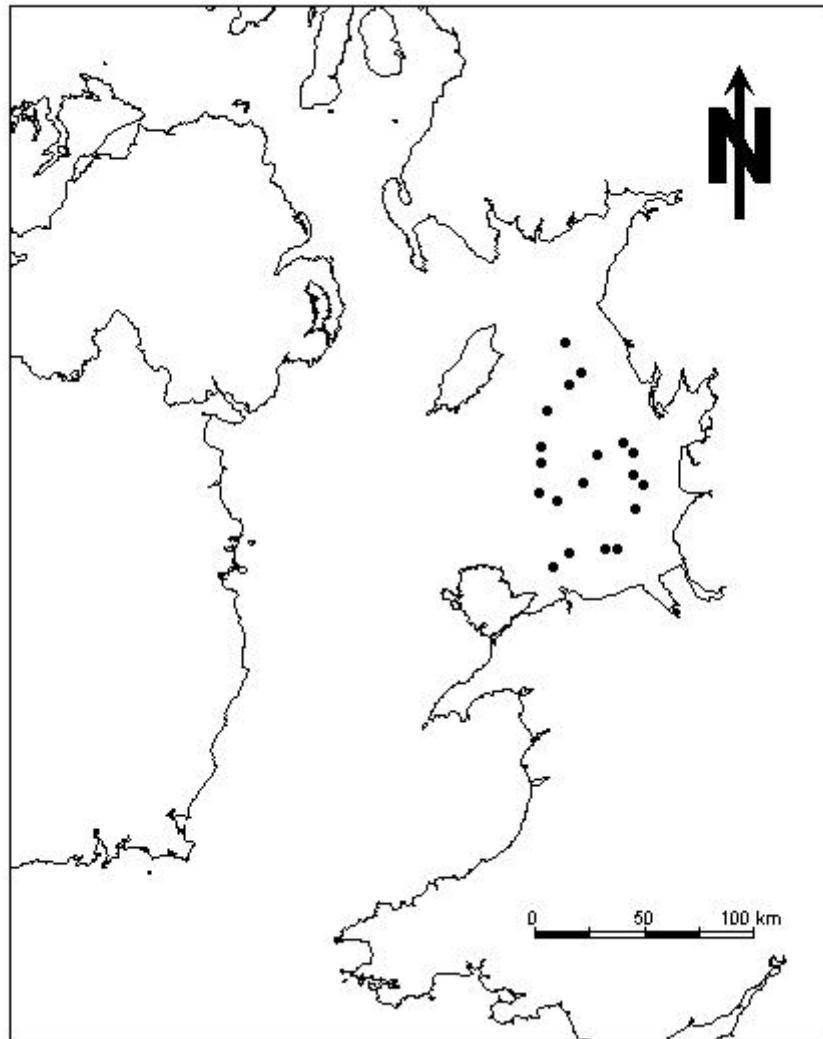
Figure 3.2. Research survey sampling design to collect independent benthic infaunal abundance and biomass data.

Benthic community production estimates

Total annual benthic community production estimates (kJ m^{-2} yr^{-1}) for each station were calculated from species abundance and biomass per m^2 using an empirical model freely available in spreadsheet form on the Internet http://www.thomas-brey.de/science/virtualhandbook/navlog/index.html (Brey, 2001). This multiple regression model calculates total annual production (kJ m^{-2} yr^{-1}) and production/biomass (P:B) ratio (yr^{-1}) for a given population based on a number of population-specific and habitat-specific inputs (see Brey 2001 for a detailed description of model). Here each population represents a different species, and so species-specific biomass (kJ m^{-2}), abundance (individuals m^{-2}), mean individual body mass (kJ), life history trait and taxonomic data were input into the model, along with station-specific depth and mean annual bottom water temperature.

Depth data for individual stations were extracted from GEBCO 30 arc-second gridded bathymetry data http://www.gebco.net/data_and_products/gridded_bathymetry_data, and modelled annual mean bottom temperature for the year 2004-2008 for each station was obtained from the National Oceanography Centre, Liverpool, http://cobs.pol.ac.uk/modl/polcoms/irish/index.php?plot=t&type=002.

To generate the energy values required by the Brey empirical model, species biomass data (g WM m^{-2}) were converted to kJ m^{-2} using published conversion factors (Brey et al. 2010). Conversion factors at the family level of taxonomic resolution were used because these values were based on a greater number of studies than those at higher taxonomic resolution, and are therefore assumed to be more representative and provide more accurate estimates than individual species or genus conversion factors. Where there was a paucity of data at the family level conversion factors from a lower taxonomic resolution were used, for example class or phyla. Biomass data for those taxa with shells were converted to shell-free weights using wet mass with shell (g WM+shell) to wet mass (g WM) conversion factors before further energy conversion factors were applied.

The Brey (2001) model outputs include estimated P:B ratio (yr^{-1}) and total annual production ($kJ \ m^{-2} \ yr^{-1}$) values with 95% confidence intervals for each species at each station. Although no confidence intervals for community level estimates can be calculated, pooled estimates are considered more accurate than individual population estimates (Brey, 2001).

Community size spectra comparison

Results of the model validation indicate that the absolute predicted values of benthic infauna production are approximately a factor 0.28 higher than the observed production estimates calculated from the independent data. This difference in absolute predicted and observed values may be a result of discrepancies in the absolute and relative abundance of different benthic infauna size classes between the independent data samples and those original data samples used parameterise the model (hereafter parameterisation data).

Any such discrepancies between the independent and parameterisation data would be highlighted by a comparison of the size distribution of the benthic infauna in samples from the respective datasets. Therefore, to search for discrepancies, and ensure that the independent data collected during the validation research cruise were comparable to the parameterisation data, normalised biomass size spectra for the communities were calculated on a base 2 logarithmic scale.

Biomass data were pooled across all 19 validation stations, and across 19 randomly selected stations from the parameterisation dataset. These 19 randomly selected stations were restricted to the eastern Irish Sea area to maximise comparability. Normalised size spectra for the independent and parameterisation data were determined by plotting the total biomass for each $\log_2$-based size class divided by the weight range of the size class interval, against the upper limited of the $\log_2$ size class. These two normalised size spectra were visually compared to identify any discrepancies in size distribution.

3.5 RESULTS

3.5.1 Model validation

The model was validated by comparing model predictions with empirically observed benthic infaunal production from 19 stations sampled in the eastern Irish Sea. A significant, positive correlation between relative observed and predicted production estimates indicates that 48% of variation in benthic infauna production can be explained by the model (Figure 3.3, Pearson's product-moment correlation; R^2 = 0.48, t = 2.26, df = 17, p = 0.037).
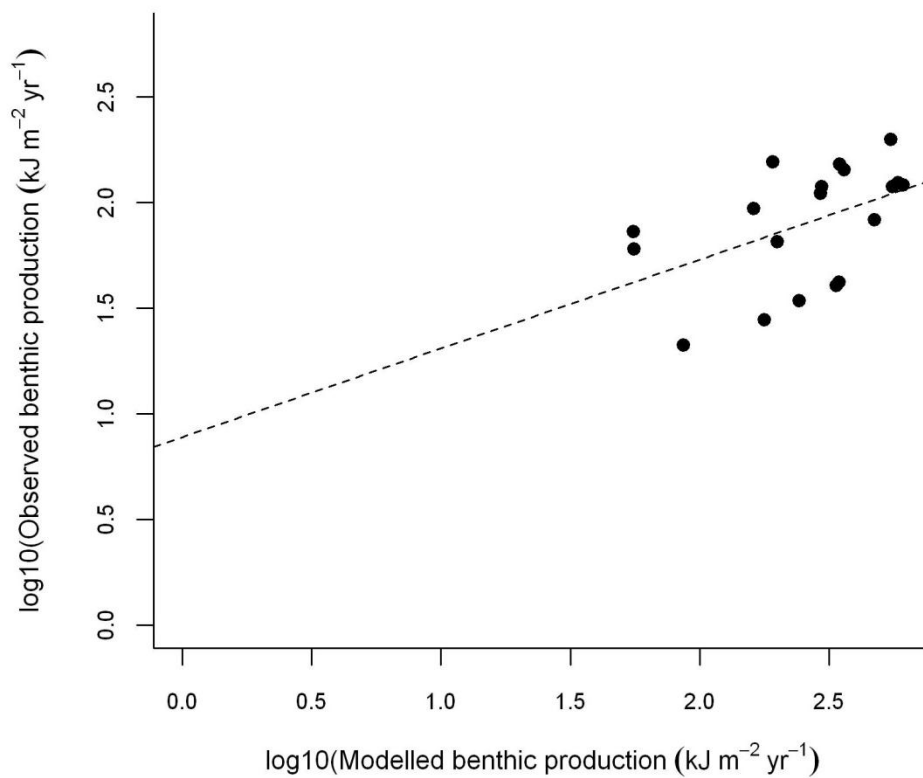
Figure 3.3. Model validation. A comparison of modelled benthic infaunal production under current fishing activity to 19 independent, empirically observed benthic infaunal production estimates, calculated from benthic community data collected in the eastern Irish Sea in 2011.

The predicted values of benthic infaunal production were a factor of 0.28 higher than the empirically observed values. Comparison of the normalised community biomass size spectra for the independent, empirically observed validation data and the original empirically observed data used to parameterise the model indicate that the validation data may be under-representing larger biomass size-classes in the benthic community in comparison to the data used to parameterise the model (Figure 3.4). These larger size classes contribute significantly to production estimates because larger bodied animals tend to be long-lived, slow growing animals with high total annual production. The potential under-representation of these larger-bodied animals in the validation data are likely to result in the disparity between the absolute values of predicted and empirically observed benthic production. A correction factor is applied to the model to account for this difference.
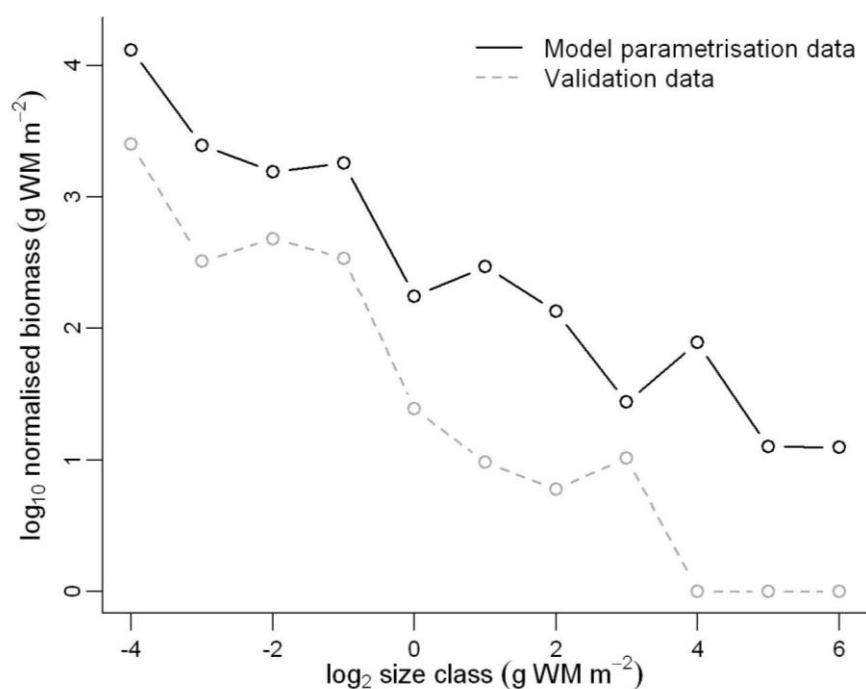
Figure 3.4. Comparison of normalised community biomass size spectra for the independent, empirically observed validation data and the empirically observed data originally used to parameterise the model.

3.5.2 Model predictions

Benthic infauna production

The spatial variation in predicted benthic infaunal production and benthic infaunal biomass under current fishing activity can be seen in Figure 3.5. Predicted benthic production estimates range from 0.8 to 1852.3 kJ m^{-2} yr^{-1}, and summed benthic infaunal production for the whole Irish Sea area under current fishing activity is 1.6*10^6 kJ m^{-2} yr^{-1}. Predicted benthic biomass estimates range from 0.7 to 1531.1 g WM m^{-2}, and summed biomass for the whole Irish Sea area under current fishing activity is 1.3*10^6 g WM m^{-2}. Benthic production and biomass estimates are highest along the north Wales coast and areas along the north-west coast of England, the Solway Firth and off the south-west coast of Scotland. There is also a small area of relatively high productivity and biomass just of the coast of Dublin, Ireland. Production and biomass are predicted to be lowest in the mud holes of the east and west Irish Sea, and in the centre of the Irish Sea. As expected, the general pattern of productivity and biomass in the Irish Sea follow the general pattern of sea surface chlorophyll-*a*, the primary driver of benthic carrying capacity in the model. This pattern was modified by sediment type, explaining the low estimates for the mud holes. However, it should be noted that high fishing intensity in these areas also contributes to the low estimates of production and biomass. As expected, higher estimates were also associated with optimum tidal shear stress levels for growth (1 N m^{-2}).
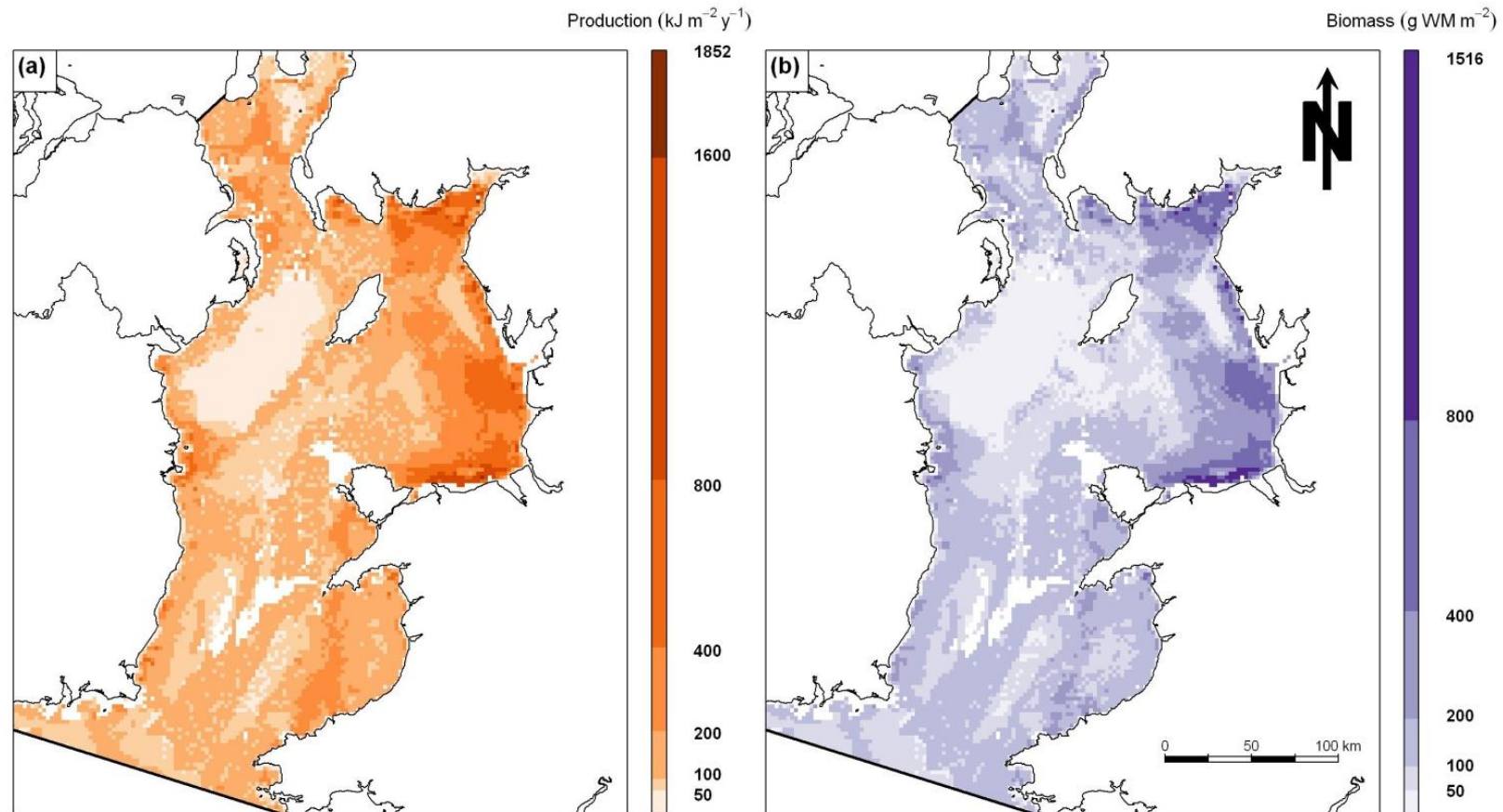
Figure 3.5. The spatial variation in modelled benthic infaunal (a) production and (b) biomass, predicted under current fishing activity in the Irish Sea. Figure 2.14, Appendix 2.7.2. gives the distribution of current fishing activity for comparison. Predictions are not made in the white areas because these are areas of hard substrate and the model was not parameterized to make predictions for this sediment type. See Figure 3.13, Appendix 3.7.1. for a map of the areas of hard substrate for which no predictions are made.

Bottom fishing impact

The predicted extent and magnitude of current bottom fishing impact on benthic infaunal production and biomass can be seen in Figure 3.6. Based on 2008-2011 VMS data, the model predicts that 51.4% of the Irish Sea area is impacted in some way by bottom fishing. Out of this 51.4%, only 37.8% of the Irish Sea experiences a decrease in benthic infaunal production in response to fishing. These negative impacts range from reductions of 435.7 to 0.01 kJ m^{-2} yr^{-1}. The remaining 13.6% of the Irish Sea is predicted to experience a slight increase in productivity in response to fishing impact, illustrated by the blue areas in Figure 3.6. In comparison, the impacts of bottom fishing on benthic biomass are more severe, with all areas impacted by bottom fishing predicted to experience a decrease in benthic biomass, ranging from reductions of 622.9 to 0.01 g WM m^{-2} (Figure 3.6).

Figure 3.7 presents the predicted changes in benthic production and biomass in response to bottom fishing for benthic infaunal communities in different sediment types. The greatest negative impacts in terms of reductions in both production and biomass were experienced by benthic infaunal communities in sandy and gravelly sediments, whereas benthic infaunal communities in muddy sediments were least impacted by bottom fishing. This is surprising, considering that muddy sediments in the Irish Sea experience the highest levels of fishing intensity (see a comparison of fishing intensity experienced by different sediment types in Figure 3.8). Figure 3.9 further indicates that the highest negative impacts experienced by benthic communities are not necessarily associated with the highest levels of fishing intensity. Benthic communities in gravel and sand that experience a loss of production or biomass greater than 200 kJ m^{-2} yr^{-1} or 200 g WM m^{-2}, for example, do not necessary experience the highest level of fishing intensity.

The negative impact of bottom fishing on benthic infaunal production and biomass results from a removal of larger bodied individuals, and a subsequent shift towards smaller individuals with lower total annual production. Only limited areas in the Irish Sea experience very high negative fishing impacts. Figure 3.7 and 3.9 indicates that the majority of negative impacts fall between a reduction of 100 to 0 kJ m^{-2} yr^{-2} for

production and 200 to 0 g WM m^{-2} for biomass. Those areas that lose more than 100 kJ m^{-2} yr^{-1} of production as a direct result of bottom fishing, for example, cover only 0.7% of the Irish Sea.

As mentioned above, bottom fishing also appears to have a positive impact on benthic production in 13.6% of the Irish Sea, indicated by Figure 3.6a. These areas experience a slight increase in production under bottom fishing. These positive impacts are not observed for biomass (Figure 3.6b, Figure 3.7b). Increases in production under fishing occur in all habitats across a range of fishing intensities (Figure 3.9a), but are limited to areas of relatively low to medium levels of production (8.9 to 429.1 kJ m^{-2} yr^{-1}). The range of positive impact varied from a 0.0002 to 70.8 kJ m^{-2} yr^{-1} increase in production. Overall productivity is only 5.1% lower than what would be expected under an unfished scenario. In comparison, benthic biomass is 12.2% lower than would be expected under an unfished scenario.
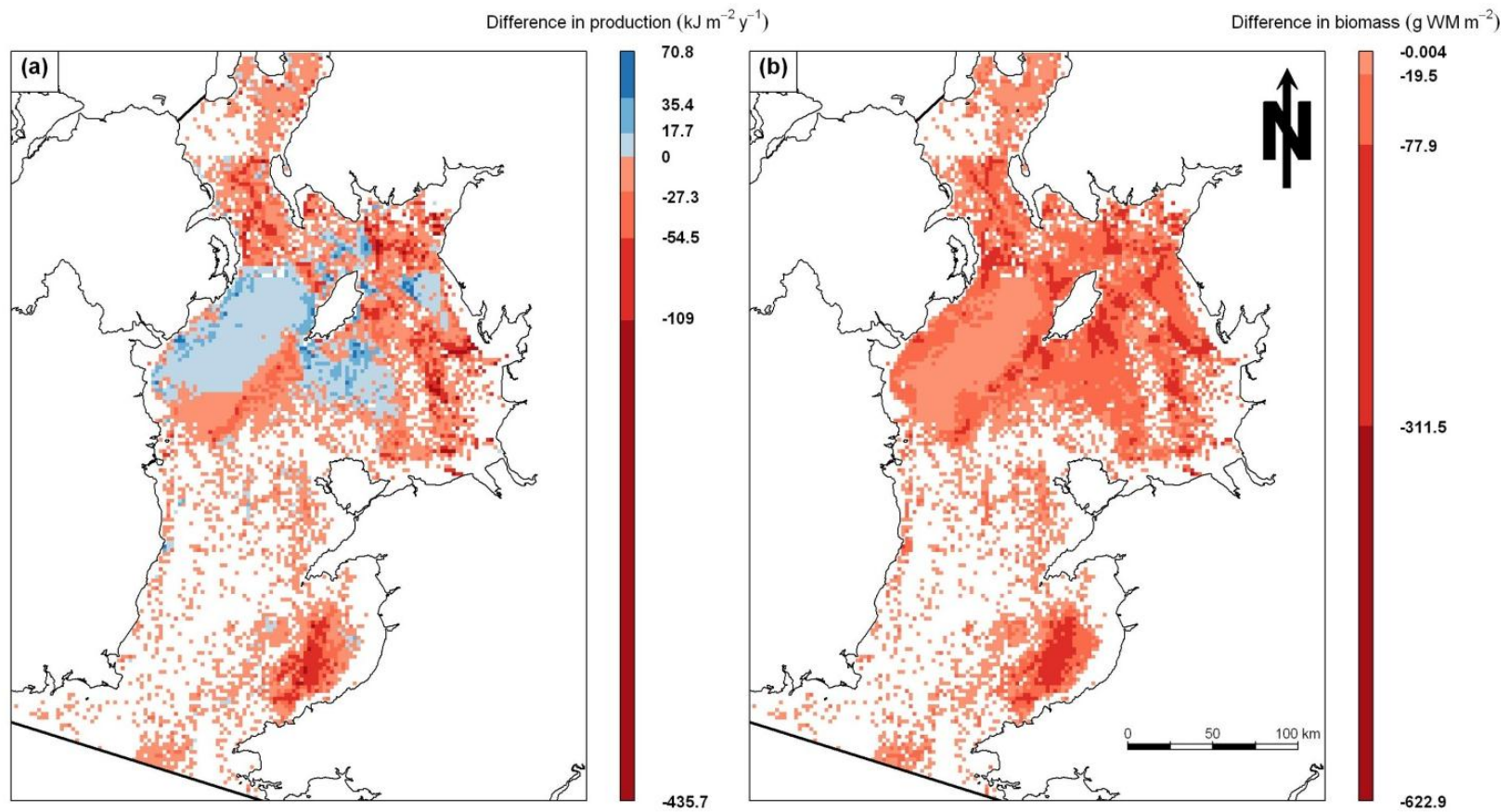
Figure 3.6. The predicted extent and magnitude of current bottom fishing impact on benthic infaunal (a) production and (b) biomass in the Irish Sea. Figure 2.14, Appendix 2.7.2 gives the distribution of current fishing activity for comparison.
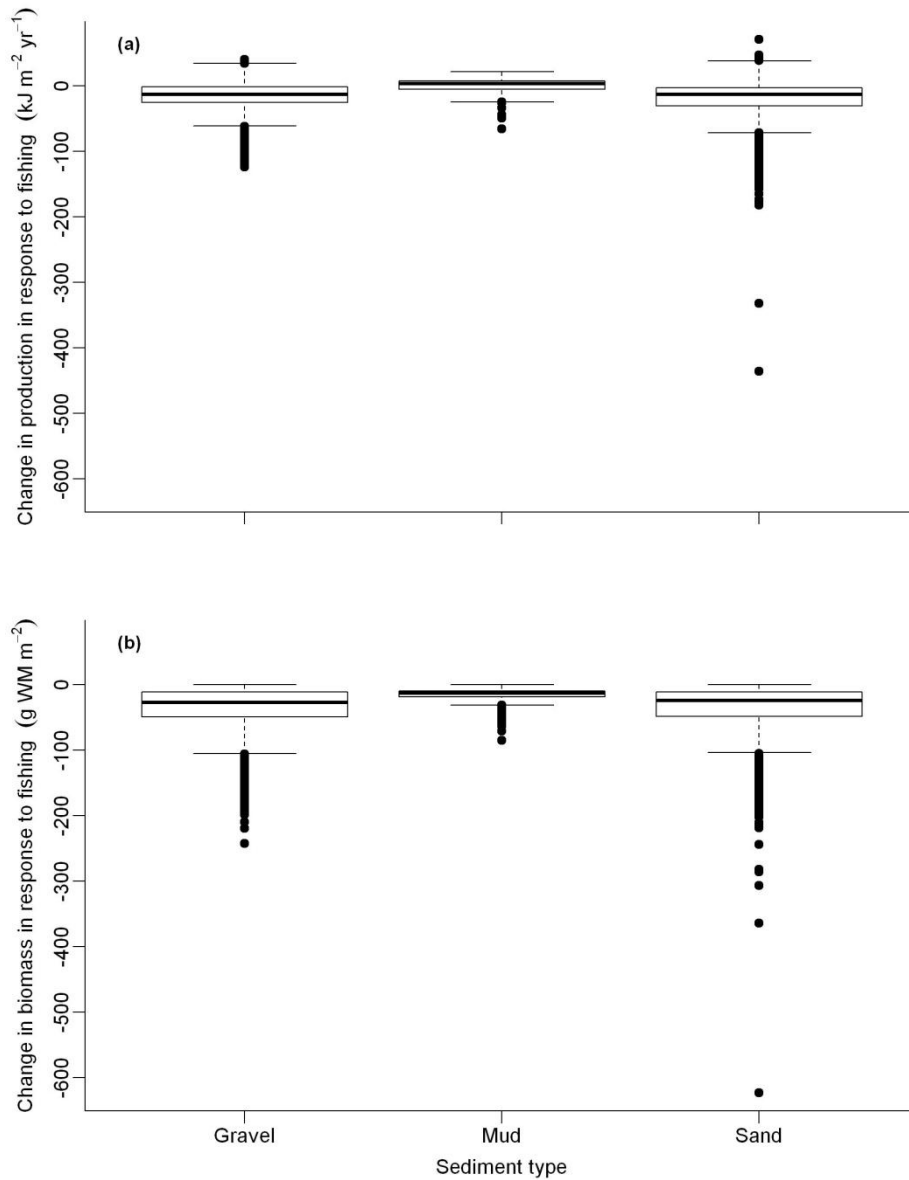
Figure 3.7. Predicted changes in benthic infaunal (a) production (kJ m^{-2} yr^{-1}) and (b) biomass (g WM m^{-2}) in response to bottom fishing, experienced by benthic infaunal communities in different sediment types; gravel, mud and sand.
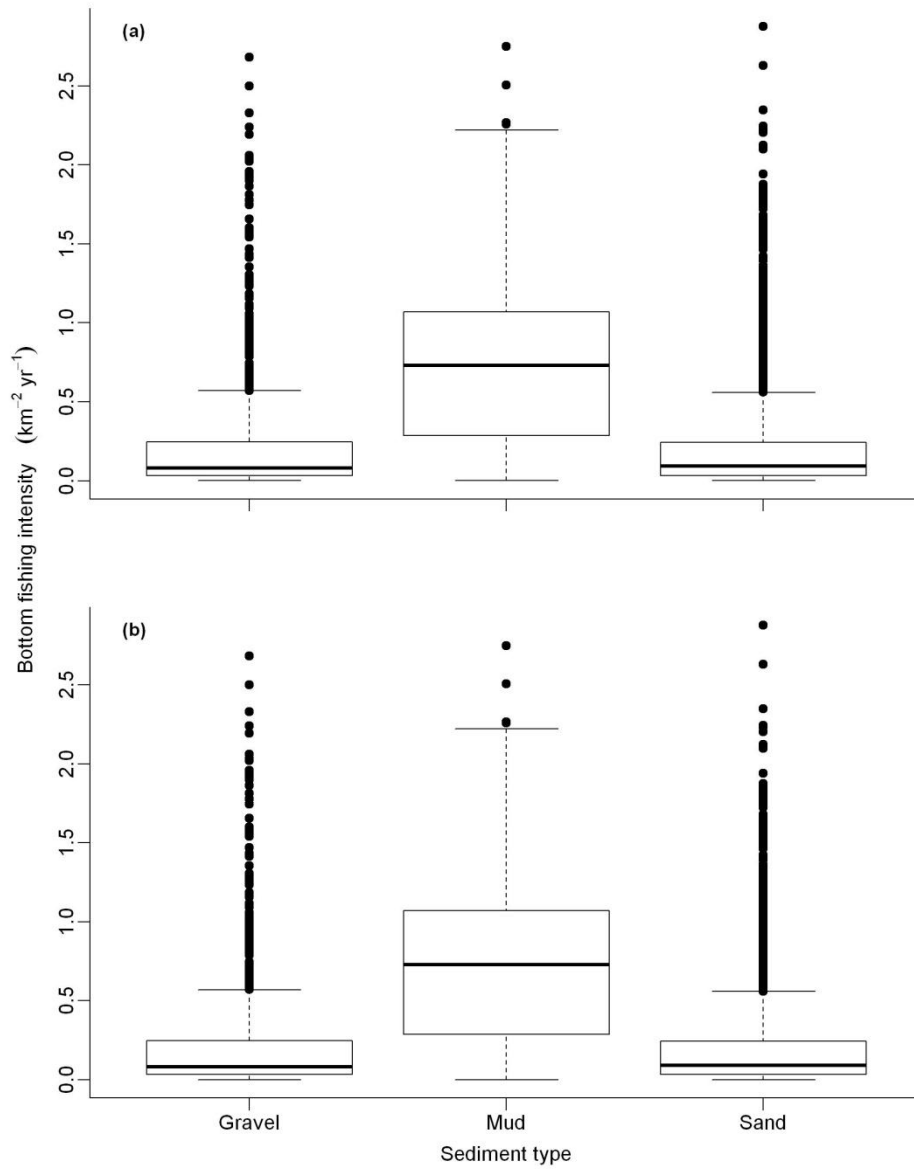
Figure 3.8. A comparison of bottom fishing intensity (km^{-2} yr^{-1}) experienced by benthic infauna communities in different sediment types; gravel, mud and sand.
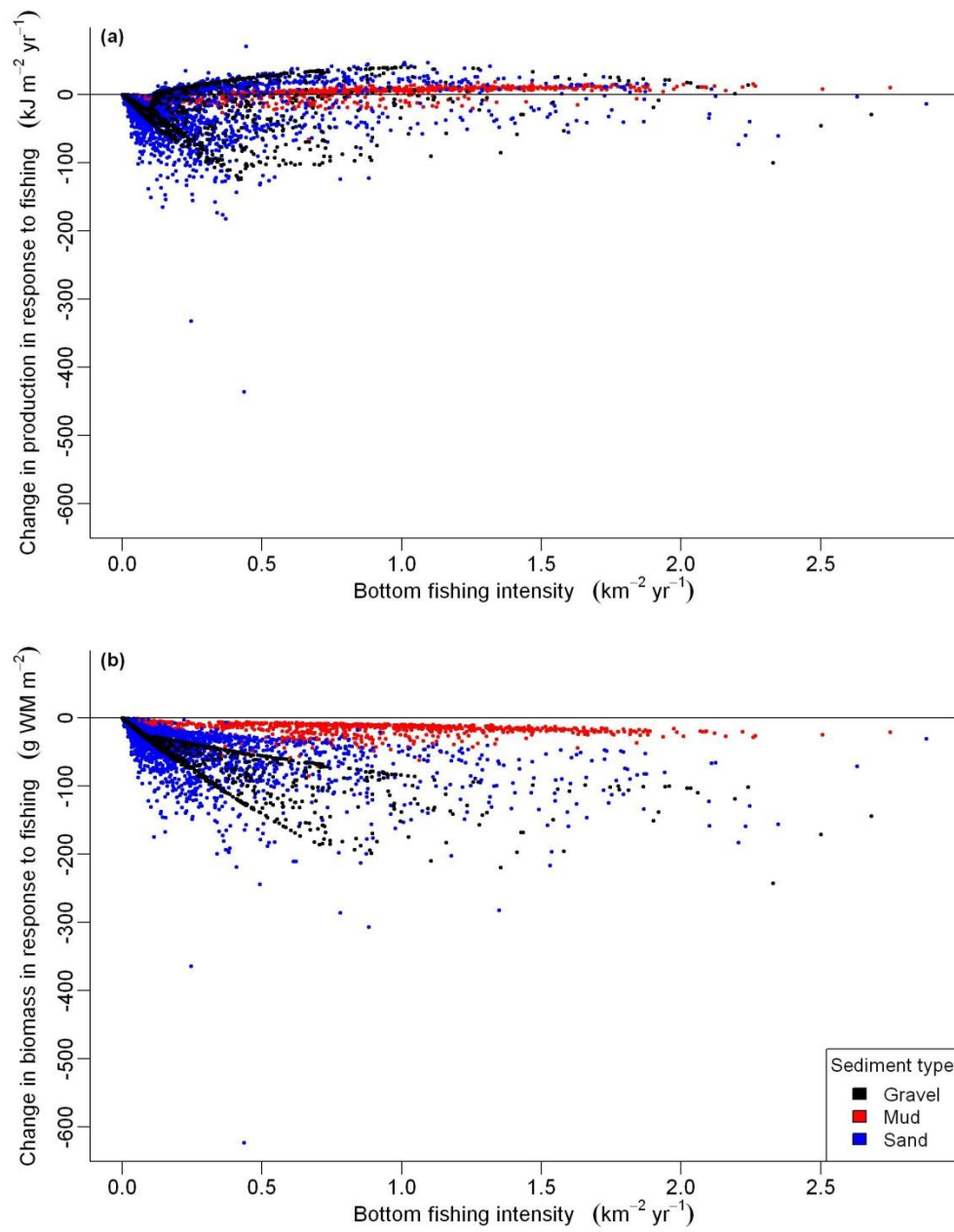
Figure 3.9. Predicted changes in benthic (a) production and (b) biomass in response to bottom fishing in relation to bottom fishing intensity (km⁻² yr⁻¹) and sediment type. The straight black line represents zero bottom fishing.

Recovery of benthic infauna communities

The time taken for the productivity of benthic infaunal communities to recover after fishing impact to a level expected in the absence of fishing ($P_{0.9}$) varied from 2.6 years to 13.3 years (Figure 3.10a). In comparison, time take for the biomass of benthic communities to recover to $B_{0.9}$ following the cessation of fishing ranged from 2.2 to 7.2 years (Figure 3.10b). Benthic infaunal communities in muddy sediments recover quicker from bottom fishing impacts compared to sandy and gravelly sediments (Figure 3.11). Estimates of recovery status from a comparison of recovery times and current fishing intensity ($km^2 yr^{-1}$) indicate that 27.2% of the Irish Sea experiences a bottom fishing intensity that prevents the predicted production of the benthic communities returning to $P_{0.9}$ after fishing impact (Figure 3.10c). In comparison, 20.6% of the Irish Sea experiences a bottom fishing intensity that prevents the predicted biomass of the benthic communities returning to $P_{0.9}$ after fishing impact (Figure 3.10d). As expected, benthic communities that are considered not recovered tend to be those that experience the highest levels of fishing intensity (Figure 3.11. Also see Figure 2.13, Appendix 2.7.2 for a distribution map of current bottom fishing intensity estimates for comparison). In these unrecovered areas fishing intensity is such that there is not enough time between fishing events to allow the productivity or biomass of the benthic infaunal community to recover to that expected under an unfished scenario ($P_{0.9}$ and $B_{0.9}$). Areas where the benthic infaunal community was estimated to be recovered (where production and biomass estimates were equal to or greater than $P_{0.9}$ and $B_{0.9}$) were characterised by relatively low fishing intensity (Figure 3.11).
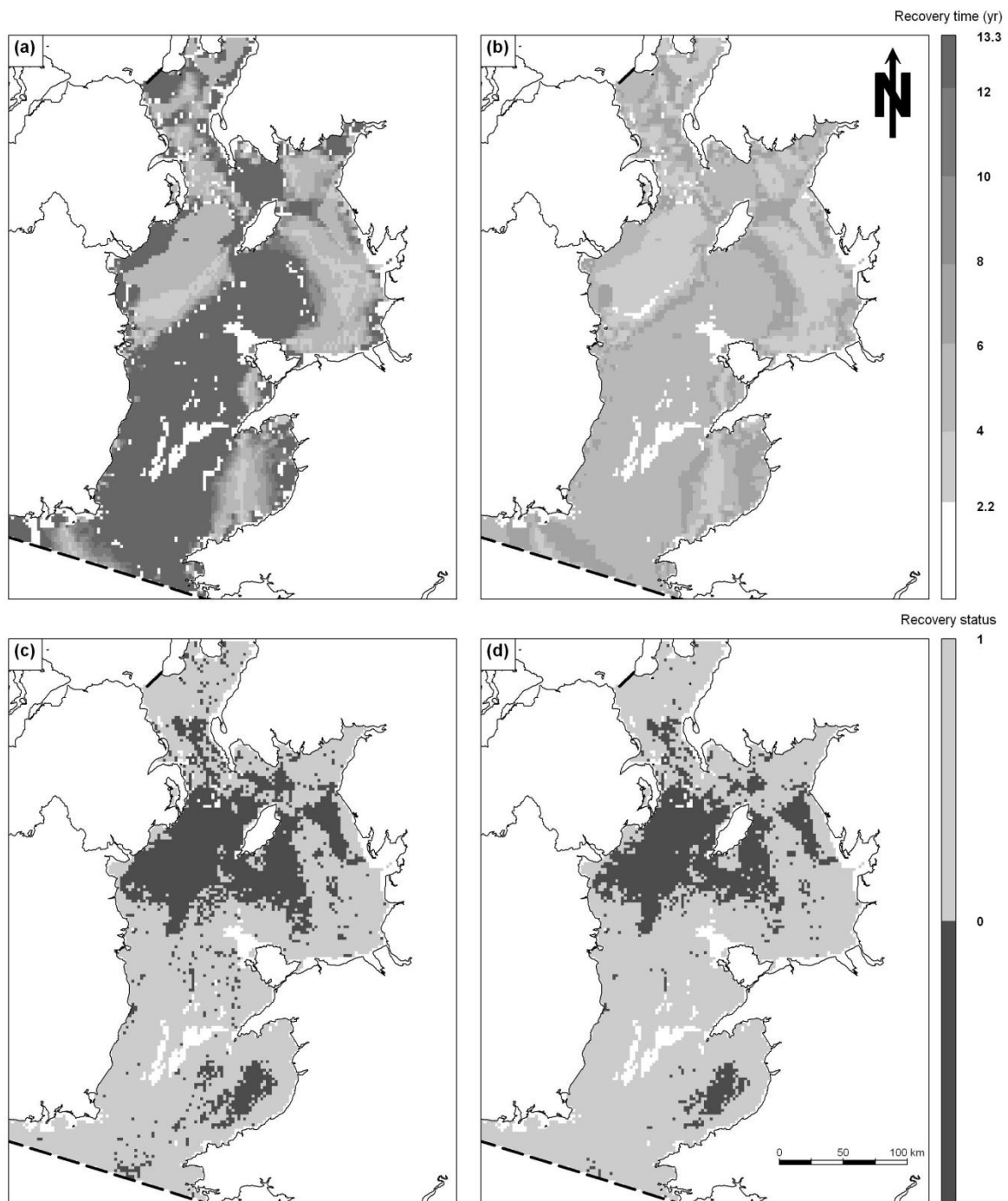
Figure 3.10. Estimated recovery time for the (a) biomass and (b) production of benthic infaunal communities in the Irish Sea (time taken to recover to $P_{0.9}$ and $B_{0.9}$ respectively), following the cessation of fishing, and subsequent estimated recovery status for benthic (c) biomass and (d) production. Recovery status 1: bottom fishing intensity is low enough to allow predicted (c) biomass and (d) production to recover to $B_{0.9}$ and $P_{0.9}$ (recovered). Recovery status 0: bottom fishing intensity is too high to allow the predicted (c) biomass and (d) production to recover to $B_{0.9}$ and $P_{0.9}$ (not recovered).
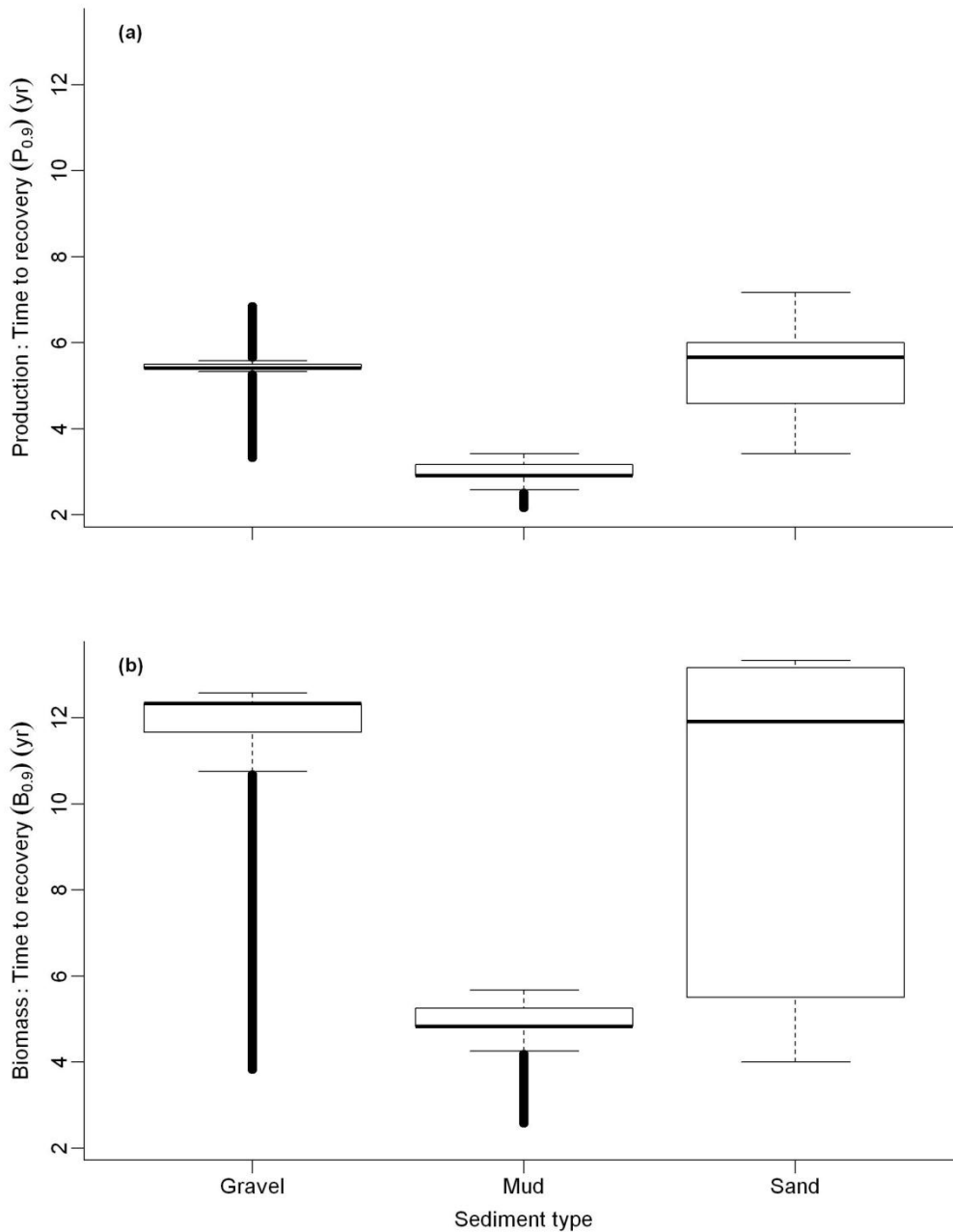
Figure 3.11. A comparison of estimated recovery times for the (a) production and (b) biomass of benthic infaunal communities in different sediment types; gravel, mud and sand. Recovery time refers to the time taken for the (a) production and (b) biomass of benthic communities to recovery to a level expected in the absence of fishing ($P_{0.9}$ and $B_{0.9}$, respectively), following the cessation of fishing.
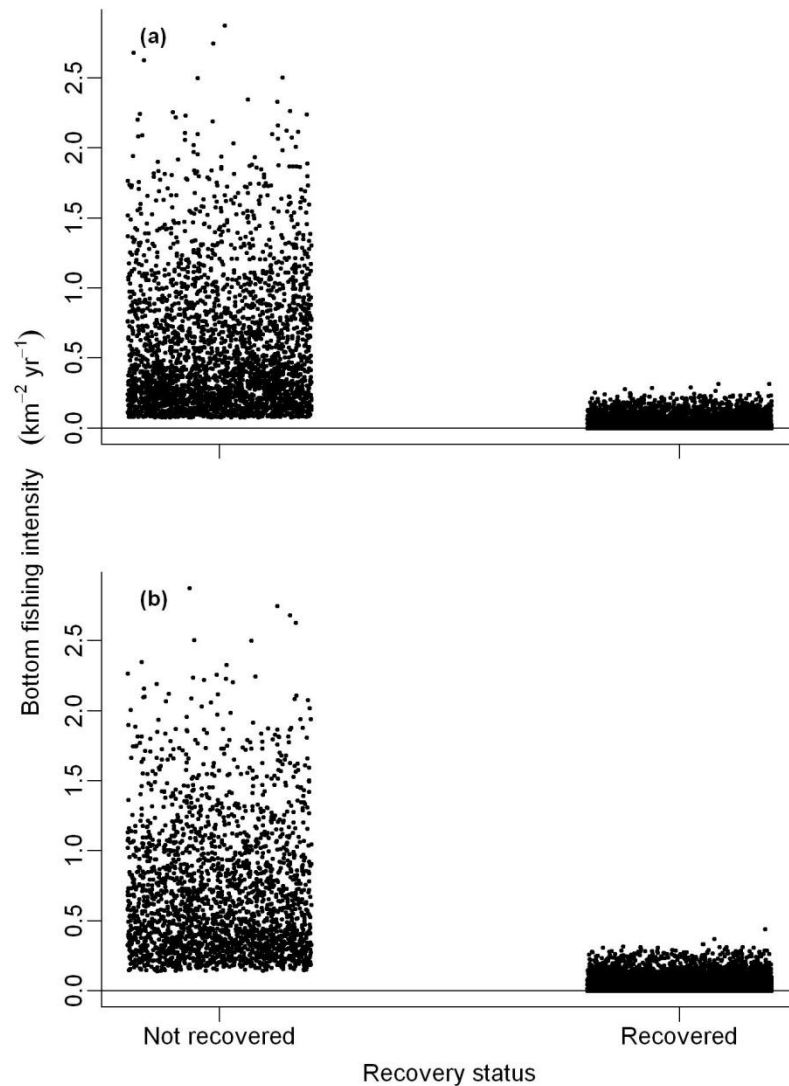
Figure 3.12. A comparison of bottom fishing intensity (km^{-2} yr^{-1}) experienced by benthic infaunal communities exhibiting different estimated recovery status for (a) production and (b) biomass. Not recovered: bottom fishing intensity is too high to allow predicted (a) production and (b) biomass to recover to $P_{0.9}$ and $B_{0.9,}$ respectively. Recovered: bottom fishing intensity is low enough to allow predicted (a) production and (b) biomass to recover to $P_{0.9}$ and $B_{0.9,}$ respectively. The straight black line represents zero bottom fishing.

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3.6 DISCUSSION

3.6.1 Overview

This is the first attempt to model benthic productivity over large spatial scales in the Irish Sea. The size-based model of benthic invertebrate communities refined and re-parameterised here explains 48% of spatial variation in benthic infaunal production in the Irish Sea. This model is based on allometric relationships, population dynamics and the influence of environmental conditions on growth and mortality. The fact that only 48% of variability is explained by this model indicates that there are other factors not accounted for that play a role in driving the productivity of benthic infaunal communities. These are expected to be processes such as recruitment, immigration, predation and facilitation (Hiddink et al. 2006a). However, the model does perform better at predicting variation in benthic invertebrate community attributes than the Hiddink (2006) model developed for the southern North Sea, which explained up to 39% of the variation of in epifaunal biomass. Therefore, despite the simplicity of the model, the validation results indicate that the relationships and dynamics capture by this size-based model are useful for helping predict large scale patterns in benthic productivity and the response of benthic communities to bottom fishing. These metrics could inform marine spatial management measures, including MPA design.

3.6.2 Model outputs

Benthic infauna production

Predicted benthic infaunal production under current fishing activity in the Irish Sea is highly variable, ranging from 0.8 to 1852.3 kJ m^{-2} yr^{-1}. Empirically observed estimates benthic infaunal production calculated by Bolam et al. (2010) across the UK continental shelf also indicated high variability in the Irish Sea, from 3 to 467 kJ m^{-2} yr^{-1}. The high estimates observed by Bolam et al. (2010) along the North-West coast of England

generally coincide with the high productivity predicted by the model, however predicted estimates tend to be higher than those observed by Bolam et al (2010).

In general, large scale spatial variation in production and biomass indicate that these attributes are higher closer to the coast, particularly where there is a high river input, driven primarily by the influence of sea surface chlorophyll-*a* concentration. Nutrient input from rivers can boost primary productivity in surface waters (Sarma et al. 2009; Kuzyk et al. 2010), and therefore benthic community carrying capacity in these areas is expected to be high. Spatial variation in estimates is also driven by seabed sediment type, with the highest estimates occurring in areas of high sea surface chlorophyll-*a* and sandy sediment. The improved predictive ability of the model developed here, compared to the Hiddink model, is expected to result from the refined calibration of benthic carrying capacity, which incorporates the identified relationships between production, sea surface chlorophyll-*a* and sediment type, and estimates carrying capacity from spatially continuous remotely-sensed chlorophyll-*a* data obtained from NEODASS. The re-parameterisation of carrying capacity here also the considered of the spatial grain at which environment-production relationships operate.

The results of the Irish Sea model validation and comparison between predicted and Bolam et al. (2010) estimates, however, suggest that the model maybe over-predicting in some of areas. This may be partly due to the fact that the relationship between chlorophyll-*a* and carrying capacity in muddy and sandy sediments is linear in the model, and growth is only limited by tidal shear stress and competition dynamics (estimated by Lotka-Volterra competition equations). It is expected that other limiting processes and factors such as recruitment, predation and habitat availability are likely to mediate total community biomass and total annual production (Hiddink et al. 2006; Rice et al. 2012).

The impact of bottom fishing

As expected, bottom fishing has a largely negative impact on the productivity and biomass of benthic infaunal communities, with communities in sand and gravel sediments experiencing the greatest impact. The parameterisation of bottom fishing impacts in the model reflects the previously observed sensitivity of benthic communities in these sediment types to bottom fishing (e.g. Collie et al. 2000; Collie et al. 2005; Hiddink et al. 2006a; Queiros et al. 2006), driven by the sensitivity of the different fauna associated with different sediment types (Collie et al. 2005; Queiros et al. 2006).

Although bottom fishing is predicted to effect benthic production and biomass in some way over large area of the Irish Sea (51.4 % in total), a comparison of overall productivity in the Irish Sea between fished and unfished scenarios indicates that current bottom fishing activity reduces total productivity by only 5.1% and overall biomass by 12.2%. This is in contrast to the southern North Sea, where it was predicted that bottom trawling in 2002-2003 reduced overall production by 21% and biomass by 56% (Hiddink et al. 2006b). The smaller overall impact of bottom fishing in the Irish Sea compared to the southern North Sea is likely to be because the fishing intensity experienced in the Irish Sea is generally lower than that experienced in the North Sea. For example, the maximum fishing intensity incorporated in the model is approximately 3 times a year (See Figure 2.14, Appendix 2.7.3 for a distribution map of fishing intensity in the Irish Sea), whereas in the southern North Sea fishing intensity can be much higher, and areas can be trawled more than 10 times a year (Hiddink et al. 2006b). In addition to this, most negative fishing impacts experienced by areas in the Irish are small. For example, 80% of the impacted area experienced a reduction in productivity of only 0.01 - 36 kJ m^{-2} yr^{-1}. There are some very small areas where bottom fishing can reduce production by up to 435.7 kJ m^{-2} yr^{-1} and biomass by up to 622.9 g WM m^{-2}, but these areas of highest negative impact are limited to a few 5km^2 cells only (figure 3.9).

Productivity is also seen to increase in certain areas, further contributing to the relatively small overall impact experienced by productivity in the Irish Sea in response to fishing. The observed increases in production are largely restricted to muddy areas,

particularly those associated with the important *Nephrops* fishing grounds in the east and west Irish Sea, but are also observed in some gravel and sand habitats. Increases in the production of certain size classes or faunal groups in response to fishing have been observed using both field experiment and modelling approaches. For example, Hiddink et al. (2008) predicted an increase in the production of small size classes at low levels of bottom trawling in the North Sea using the Hiddink model, and Jennings et al. (2001) observed small increases in polychaete production in some areas of the North Sea that were subject to moderate levels of fishing. An increase in productivity of small size classes in response to fishing is attributed to their competitive release following the removal of large-bodied individuals (Jennings et al. 2001; Hiddink et al. 2008). Although the total productivity of the benthic communities in Hiddink et al. 2008 was not predicted to increase under fishing, these estimates included epifauna as well as infauna. The fact that total production did not increase is therefore a due to loss of production by large-bodied organisms (Hiddink et al. 2008). Here only infauna are considered, and it appears that increases in the productivity of small infauna size-classes under fishing can outweigh the loss of large infauna size-classes, and result in an overall increase in total benthic infaunal productivity. These effects are only apparent in areas of low initial benthic infaunal production. In summary, the increase in total benthic infaunal production in chronically trawled areas (i.e. the *Nephrops* grounds) appears to be a result of the cumulative impact of reducing the number of large-bodied individuals and increasing the number and productivity of small-bodied individuals over time, to the point where the abundance and productivity of small-bodied individuals more than compensates for the loss of large individuals, and results in an increase in productivity above the level expected in the absence of fishing ($P_{0.9}$).

In contrast to the effects of bottom fishing on production, benthic communities in the Irish Sea only experience a reduction in biomass in response to fishing. This demonstrates that in areas where the fishing induced proliferation of small-bodied individuals increases the biomass and production of small size classes, these changes do not compensate for the loss of the biomass of large-bodied infauna. The difference in the overall reduction in production and biomass resulting from bottom fishing at the scale of the Irish Sea indicate that in general benthic biomass is more severely impacted than

benthic production. Similar patterns have been observed in the North Sea (e.g. Hiddink et al. 2006a, 2006b).

Recovery time of benthic communities

The recovery time of benthic infaunal communities following fishing impact in the Irish Sea varies spatially. Muddy sediments recover quickest from fishing impacts, whereas sandy and gravelly sediments take much longer, and are therefore considered more vulnerable to bottom fishing. These results are similar to the findings of Foden et al. (2010), who found that the recovery time of benthic communities increased with sediment hardness. In general, estimated recovery times broadly agree with the findings of other recovery studies; which estimate recovery times between < 3 and 12 years (Granfield et al. 2001; Hermsen et al. 2003; Blyth et al. 2004; Collie et al. 2005; Kaiser et al. 2006; Hiddink et al. 2006; Foden et al. 2010). These studies investigated the recovery of a range of community metrics, including abundance, community composition, biomass and production. It is expected that biomass and total production will take longer to recover to an un-impacted state that metrics such as abundance because recovery of these attributes requires time for both re-colonisation of individuals and growth, rather than just re-colonisation (Newell et al. 2004).

The recovery time of benthic communities in the Irish Sea may be overestimated by the size-based model used here because processes such as recruitment and immigration, and the environmental parameters that influence them, are not accounted for (Collie et al. 2000; Dinmore et al. 2003; Hiddink et al. 2006b). Lambert et al. (submitted) found that hydrodynamic regime and proximity to unfished areas influences the recovery time of epifaunal communities, and suggested that higher rates of recovery could occur in fished areas where individuals can recruit or immigrate from undisturbed and populated area nearby, and also in areas where currents facilitate recruitment via the delivery of propagule (Lambert et al. submitted).

Recovery time may also not be accurately predicted in some cases, because of the variation in recover potential between different species. It is expected that because

certain benthic species are more resilient or vulnerable to fishing impact, they are likely to vary in their ability to recover, regardless of size (Hiddink et al. 2006a). However, incorporating these various species-specific responses to fishing into predictive modelling is difficult because it would require substantial research to gain a detailed understanding of each species response. Species composition also varies with habitat and over large areas, so these species-specific responses would have to be known for each community type. Size-based estimates of community productivity, fishing impact and recovery rates are much easier to calculate and model over large areas, regardless of changes in habitat or ecosystem type (Hiddink et al. 2006; Travers et al. 2007; Robinson et al. 2010).

Recovery status of benthic communities

Even though infaunal communities in muddy sediments take the least time to recovery, the recovery status estimates here suggest that these areas are more likely to be in an unrecovered state (predicted production is less than $P_{0.9}$) than communities in sandy and gravelly sediment in the Irish Sea. This is because these muddy areas tend to experience the highest levels of bottom fishing intensity. This result contradicts the previous prediction that benthic infaunal productivity actually increases in these areas, such as the *Nephrops* grounds, in response to fishing (Figure 3.6a).

This discrepancy between estimated recovery status of production and predictions of productivity under current fishing activity in chronically fished areas highlight the difference in the implementation of fishing impact in the two different models (recovery model and production model). In the recovery model, a single fishing event is implemented on an unfished community, and recovery from this initial impact to a near-pristine level ($P_{0.9}$) is recorded to estimate recovery time and recovery status. In the production model, fishing events are implemented according to the frequency indicated by the fishing intensity data incorporated into the model, and the cumulative impacts of these repeated events are recorded through time

The cumulative impacts of chronic fishing on a benthic community may vary from a single impact on a previously unfished community, and result in the disparate outputs observed. In chronically fished areas, where the recovery of predicted production to $P_{0.9}$ does not occur between fishing events, each fishing event is estimated to have a smaller impact on total production, because the community consists of fewer large-bodied individuals (due to being removed by previous fishing events). The estimated fishing impacts for small-bodied individuals are less severe and they do not experience the same reductions in biomass and production (Hiddink et al. 2006a; Queiros et al. 2006). In addition to smaller impacts on production over time, the removal of large bodied individuals following each fishing event can cause the competitive release of smaller individuals, and result in an increase in the productivity of these size classes following fishing impact (Jennings et al. 2001; Queiros et al. 2006; Hiddink et al. 2008; Reiss et al. 2009). The fact that large-bodied individuals are lost is indicated by the fact that fishing-induced increases in production are always accompanied by a decrease in biomass (Figure 3.6b).

The above cumulative changes in community composition under chronic fishing have resulted in the total productivity of the benthic community increasing above $P_{0.9}$ in some cases, indicated by the 'positive' fishing impacts predicted by the production model. The discrepancy observed between these predictions and the outputs of the recovery model result then from the fact that the changes in benthic community size-structure over time under repeated fishing are not captured within the recovery model. Instead, only a single fishing event and subsequent recovery is implemented. As a result, it would appear that the recovery model used here has limited application for predicting recovery status in chronically fished areas, and therefore this metric is not considered useful for informing marine management.

In light of the above, although estimates of recovery status indicate that 25% of the Irish Sea is currently fished at an intensity that prevents the recovery of productivity to $P_{0.9}$, which is comparable to the southern North Sea (where 27.1% of the area had trawling intensity that was too high for production to exceed $P_{0.9}$) (Hiddink et al. 2006b), this is

expected to be an over-estimation of the extent to which communities in the Irish Sea are unrecovered.

3.6.3 Implications for management in the Irish Sea

Benthic infaunal production underpins the provision of important ecosystem goods and services, including fish production (Heath, 2005) and energy and nutrient cycling (Tumbiolo & Downing, 1994; Danovaro et al. 2008). Large scale reductions in benthic productivity will therefore affect energy flow through the marine food web (Hiddink et al. 2006). In the Irish Sea in particular the loss of macrobenthic production could potentially have a large impact on the commercial fisheries in the Irish Sea, because ecosystem modelling has identified that these stocks place a high demand on this productivity (Heath, 2005). The outputs of the size-based model developed here could inform spatial management of benthic infauna production to ensure that it remains available to higher trophic levels, and continues to support the provision of the ecosystem goods and services that are dependent on it.

Areas of high predicted benthic infauna production, such as off the North Wales coast, along the north-west coast of England, the Solway Firth and off the south west coast of Scotland, could be prioritised for protection within no take MPAs to ensure that this productivity remains available to the marine food web in these areas. Similarly, the modelled impact of bottom fishing on benthic infaunal communities and estimated recovery times could be used to identify sensitive or vulnerable communities and direct the use of no-take MPAs to protect these communities. For example, because sandy and gravelly sediments are more sensitive to fishing impacts and take longer to recover from impact than muddy sediments, these types of habitats should be prioritised for protection from bottom fishing, and fishing effort redirected to areas that are able to recover more quickly (Foden et al. 2010).

It should be noted, however, that re-directing bottom fishing to muddy areas may result in higher fishing intensity levels that no longer cause the slight increase in productivity currently predicted, and may therefore result in these communities exhibiting an

unrecovered state due to the high fishing intensity. Although infauna communities in muddy sediments in the Irish Sea are not considered as productive as sandy and gravelly sediments, indicated by the outputs of the size-based model here, they are clearly important to the fishing industry in the Irish Sea, reflected by the high fishing intensity that they experience. Hiddink et al. (2011) found that in area of high bottom trawling, commercial fish species condition was poorer compared to areas of lower fishing intensity. Therefore if increasing bottom fishing intensity in muddy areas (due to displacement from other areas) does result in reductions in productivity rather than the currently predicted increases, displacement into these areas may have a detrimental impact on the fisheries targeted. If predictions of fishing behaviour in response to MPA design are included in the size-based model here, the model can help resolve issues like this by initiating model runs under different MPA scenarios and evaluating their impacts on benthic production, biomass and recovery status. This model application is explored more in Chapter 5.

Maps of bottom fishing impacts could also inform restorative management, in that areas identified to be experiencing high levels of negative bottom fishing impacts or that have a negative recovery status could be protected in no-take MPAs to allow them to recover to unfished levels of productivity. The results here indicate that the few sandy and gravelly areas most highly negatively impacted by bottom trawling are not those areas that experience the highest levels of bottom trawling; therefore these areas could be prioritised for no-take protection without as much impact on fishing activity as would be if the areas did experience high levels of fishing activity.

No-take MPAs in any area where fishing occurs is likely to result in some conflict between conservation and fishing sectors, therefore rather than informing the design of no-take MPAs, scenarios of bottom fishing impacts could inform other forms of spatial management, such as rotational closures or effort restrictions (Collie et al. 2005; Lambert et al. submitted). Rather than permanently excluding fishing, these approaches could be used to manage fishing impact at a level that maintains a certain level of benthic productivity, or allows productivity to recover between fishing events. Although recommending a level of benthic production to maintain is beyond the scope of this

study, it could be based upon an amount of benthic production sufficient for supporting fish production (Hiddink et al. 2006b). This would ensure that in those areas important to fishing, benthic production would be available to support fish stocks and subsequently provide a benefit to the commercial fisheries that prosecute them (Hiddink et al. 2011).

Interestingly, overall productivity in the Irish Sea is reduced by only 5.1% under current bottom fishing activity in comparison to an unfished scenario. Benthic infaunal production in the Irish Sea therefore does not appear to be as heavily impacted by bottom fishing as may have been expected, given the fact that model estimates suggest that approximately 51.4% of the Irish Sea is affected by bottom fishing. This implies that substantial losses of benthic productivity in response to fishing, and thus reduced food availability for commercial fish stocks (Heath, 2005), may not be occurring in the Irish Sea, and suggests that substantial protection measures, such as no-take MPAs, for benthic communities may not be required. This is of course dependent on any ecosystem-level conservation or management objectives that are set. Futhermore, when the impacts on benthic biomass are considered, the extent and magnitude of impacts is perceived to be greater.

Finally, the model outputs regarding fishing impacts indicate that the effects of protection on benthic infauna production are context dependent. It appears that fishing in muddy sediments with benthic communities of low to medium productivity (9.8 to 457.2 kJ m^{-2} yr^{-1}) can actually increase benthic infauna production, and protection in no-take MPAs therefore results in a reduction in total benthic production, highlighting that the expected effects of protection from bottom fishing are not always realised. This increase in productivity under bottom fishing is not necessarily a positive ecosystem outcome if management objectives are to maintain benthic communities in a natural, undisturbed state. MPA network scenario simulation using size-based models like the one developed here can help in predicting the potential outcomes of protection (e.g. Hiddink et al. 2006c).

3.6.4 Conclusions

In summary; the findings here indicate that (i) the empirical, size-based model developed here can explain 48% of spatial variation in benthic infaunal production in the Irish Sea, suggesting that size-based models of community production and biomass are useful tools for informing marine spatial management. ii) Although size-based models can also provide additional metrics such as bottom fishing impact, and the recovery time and status of benthic production and biomass, estimates of recovery status are not considered useful for informing management because they do not reflect realistic fishing impacts in chronically fished areas. iii) Benthic infaunal communities in gravelly and sandy sediments are considered more sensitive and vulnerable to bottom fishing impacts than benthic communities in muddy sediments because they experience a greater predicted reduction in production and biomass as a result of fishing, and are estimated to take longer to recover from fishing impact. iv) Overall, the negative impacts of bottom fishing are predicted to be greater for benthic infaunal biomass than benthic infaunal production at the scale of the Irish Sea.

3.7 APPENDICES

3.7.1. Area of no model predictions
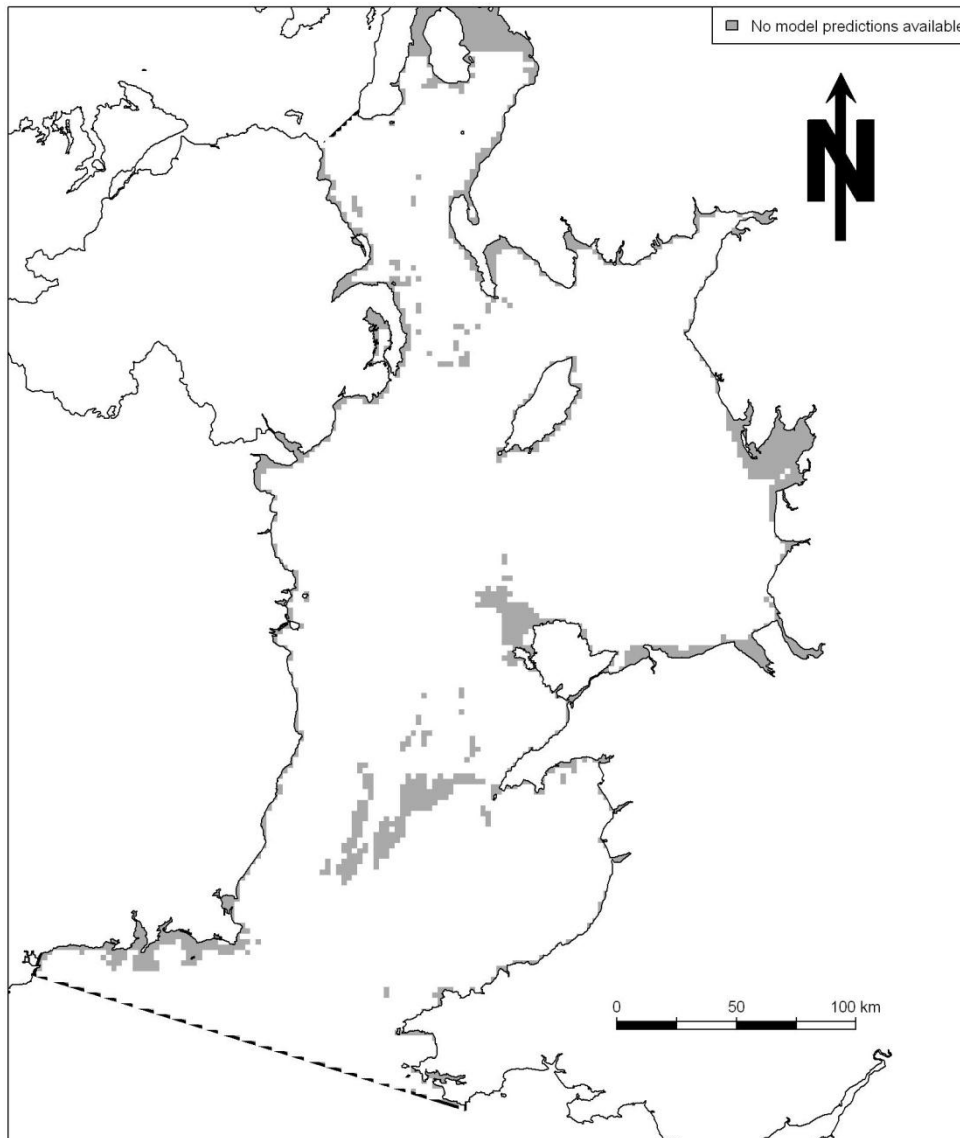
Figure 3.13. Areas of hard sediment where predictions from the benthic community model developed and parameterised in Chapter 3 are not available (see Figure 3.5 for model predictions of benthic infaunal production and biomass). No predictions are made for this sediment type because no parameterisation data were available.

CHAPTER 4 - The spatial association between benthic infaunal production and biodiversity features in the Irish Sea

4.1 AIM: To investigate the spatial association between benthic infauna production, an important marine ecosystem function, and three different biodiversity features in the Irish Sea; i) benthic infaunal diversity, ii) cetacean species abundance, and iii) the presence of conservation priority species; for the purpose of investigating potential overlaps and informing effective conservation planning.

4.2 ABSTRACT

Prioritisation of conservation effort in areas that protect both ecosystem function and biodiversity requires knowledge of the degree of spatial overlap between the two. Areas of overlap between function and biodiversity features would minimise the amount of space required for conservation purposes, particularly in the context of marine protected area designation. Here the spatial overlap between both modelled and empirically observed benthic production and three different biodiversity features of conservation interest that commonly direct marine protected area (MPA) designation is investigated. These three biodiversity features are; i) benthic community species diversity, ii) cetacean species abundance, and iii) the presence of conservation priority species. The modelled and empirically observed production data were obtained from a predictive size-based model of benthic infaunal production developed and validated for the Irish Sea and five independent benthic surveys conducted in the Irish Sea, respectively. Cetacean relative abundance estimates were from the Atlas of the Marine Mammals of Wales, and conservation priority species and habitats data were obtained from the NBN gateway (http://data.nbn.org.uk/) and Defra. Due to the spatial nature of the data, generalised regression models that can take account of spatial auto-correlation were employed for analysis. Results indicate that there is little spatial association between benthic production and biodiversity features in the Irish Sea. Significant positive associations were only found between empirical benthic production and benthic community species richness (F = 32.61, df = 47, p = 0.000), and between

modelled benthic production, and two diversity indexes, the Shannon-Wiener index of diversity (H') ($F = 14.14$, df = 44, $p = 0.001$) and Pielous's Evenness (J') ($F = 6.18$, df = 44, $p = 0.017$). No significant associations, positive or negative, were found for any other of the biodiversity features. It would appear that opportunities for MPAs that protect both benthic infauna production and biodiversity features simultaneously in the Irish Sea are limited. This implies that the protection of the biodiversity features included in the analyses may not automatically protect high levels of ecosystem function.

4.3 INTRODUCTION

Conservation has traditionally focused on protecting biodiversity and habitat (Armsworth et al. 2007). These features represent the structural elements of ecosystems. In recent years, however, there has been increasing recognition of the need to protect and manage ecosystem function in addition to ecosystem structure (Daily & Matson, 2008; Frid et al. 2008). Protection of biodiversity and habitat is a legal requirement demanded by the EU Birds and Habitats Directives, therefore conservation efforts cannot be re-directed from these structural features. Instead efforts will need to expand to encompass the protection of function in addition to biodiversity.

Conservation effort, particularly in the form of protected areas, is restricted due to limits on funding and competition for space with conflicting uses and activities (Myers et al. 2000; Parravicini et al. 2012). In the marine environment, for example, marine protected areas (MPAs) can compete with commercial fisheries, aquaculture, energy extraction and generation, aggregate dredging, shipping, and recreational uses (Douvere, 2008; Weslawki et al. 2010). MPA designation therefore needs to be prioritised and focused where maximum benefits can be achieved at minimum cost, both financially and in terms of impact on other users (Moore et al. 2004). Win-win conservation scenarios, where the protection of one function or conservation feature benefits other functions or features, are ideal solutions for minimising costs (Balmford et al. 2002, Crossman & Bryan 2009). In order to achieve win-win scenarios, however, spatial overlap between the ecosystem functions and conservation features in question is required (Anderson et al 2009).

Spatial overlap between marine ecosystem function and biodiversity

Benthic infaunal production is an important marine ecosystem function that has been modelled and mapped for the Irish Sea (see Chapter 3 or details of model development and parameterisation). Benthic infaunal production refers to the production of organic matter by benthic macro-invertebrates per unit time and area (Cusson & Bourget, 2005), and is important for mediating the flow of energy and material through the marine food web (Tumbiolo & Downing, 1994, Seitz *et al.* 2009). The production model uses easily obtained environmental data, including remotely sensed sea surface chlorophyll-*a*, modelled tidal bed stress, seabed sediment and fishing intensity, estimated from vessel monitoring system (VMS) data, to predict total annual production (kJ m^{-2} yr^{-1}) for benthic infaunal communities at a resolution of 5 km^2 across the whole Irish Sea. This provides an opportunity to investigate the degree of spatial association between a marine ecosystem function and biodiversity features at a regional scale.

Concurrence between benthic infaunal production and biodiversity features of conservation interest such as higher predators and benthic biodiversity may be expected. Higher predators include several important Habitats Directive cetacean species such as bottlenose dolphin, harbour porpoise and minke whale, and these species may be associated highly productive areas due to greater food availability (Kim & Oliver, 1989; Ballance et al. 2006). Areas of high benthic production could also be associated with a high number of benthic species. Correlations between diversity and productivity have been observed in natural systems (Mittelbach et al. 2001, Cardinale et al. 2009), and the findings of Biodiversity-Ecosystem Function (BEF) research indicate that the loss of diversity from an assemblage can reduce the rates of ecosystem processes associated with that assemblage, suggesting a positive association between diversity and productivity (Balvanera et al. 2006; Srivastava & Vellend, 2005). Although the majority of BEF research to date is primarily focused on terrestrial systems (Balvanera et al. 2006; Hillebrand & Matthiessen, 2009), Danovaro et al. (2008), found a consistent positive association between benthic diversity and several different functions within deep-sea ecosystems over global scale, and at a national scale, a study by Bolam

et al. (2010) found a positive relationship between biomass and species richness in UK subtidal waters.

Opportunities for win-win conservation scenarios have been investigated in the terrestrial environment, by quantifying the spatial overlap between ecosystem function and services such as pollination, carbon storage, and biodiversity (e.g. Chan et al. 2006; Naidoo et al. 2008; Anderson et al. 2009; Crossman & Bryan, 2009). In general, very weak associations have been found. For example, Naidoo et al (2008) found that at a global scale, ecoregions selected for their importance for biodiversity provided no more ecosystem provision than if ecoregions were selected randomly and Chan et al. (2006) found the average correlation (Pearson's r) between biodiversity and six different ecosystem services to be very low (0.04).

These terrestrial studies often compare functions and features that are not expected to be directly related or dependent on similar habitats or ecosystem components. For example, carbon storage and the number of terrestrial UK BAP priority species (e.g. Anderson et al. 2009). Furthermore, comparisons of the spatial distribution of these different functions and features were conducted at very large, global to national scales, which Anderson et al (2009) suggest may not always be appropriate for detecting patterns of association for informing management. Anderson et al. (2009) found that relationships between certain functions and biodiversity were significantly different in different areas of the UK, indicating that associations were location or region specific. Regional variation in the association between biodiversity and ecosystem function suggests that global or national approaches to identifying spatial concurrence are unlikely to be informative about the potential for win-win conservation scenarios at the scale at which spatial management is implemented. Regional approaches are therefore deemed more appropriate for identifying spatial concurrence between biodiversity and function to inform effective conservation planning.

In this chapter, the spatial association between benthic infaunal production, cetacean species relative abundance, benthic infaunal diversity, and the number of conservation priority species will be examined to investigate the potential for win-win conservation

scenarios in MPA designation at the regional scale of the Irish Sea. Conservation priority species included are marine UK Biodiversity Action Plan- (BAP) and OSPAR species (Olso and Paris convention for the protection of the marine environment of the North-East Altantic) (OSPAR Commission, 2008). Many of these species are features of conservation importance used as selection criteria for recommending Marine Conservation Zone (MCZ) designations in England, therefore spatial concurrence between benthic production and these species would offer great opportunities for win-win conservation scenario in MPA design. However, a positive spatial association with benthic production is not expected to be found, based on the results of previous, terrestrial studies.

Here both modelled and empirically observed benthic infauna production data are used to investigate spatial association between production and biodiversity features. The empirically observed (hereafter empirical) benthic production data has a limited spatial distribution, whereas the modelled benthic production data covers the whole of the Irish Sea area. Although the model for estimating empirical production is well established (Brey model, 2001), and the large scale, benthic infauna production model has been validated and confirmed representative of relative production (see Chapter 3 for model validation results), models are always simplifications of natural systems and so both estimates will be subject to a degree of error and uncertainty. If analyses with modelled and empirical benthic production generate similar results, greater confidence can be held in the conclusions made.

Three hypotheses will be tested; i) there is a positive association between benthic infauna production and benthic infauna diversity, ii) there is a positive association between benthic production and the relative abundance of cetacean species, and iii) there is no association between benthic production and the number of conservation priority species. Opportunities for win-win conservation scenarios for MPA designation will be determined by the extent to which there is significant overlap observed between benthic production and these biodiversity features, estimated by generalised regression models.

4.4 MATERIALS AND METHODS

4.4.1 Method overview

Spatial variation in modelled and empirically measured benthic infaunal production estimates were compared to the spatial distribution of three different groups of biodiversity features that currently inform conservation efforts in the UK seas. These include i) the species diversity of benthic communities, ii) the relative abundance of five cetacean species in the Irish Sea, which represent higher predators and as well as being and UK and EU conservation features, iii) the presence of benthic OSPAR and UK Biodiversity Action Plan (BAP) priority species.

4.4.2 Data collection and preparation

Observed benthic production estimates

Species-specific abundance and biomass data are needed for calculating empirical benthic infauna production. Although many surveys of benthic macro-infauna have been conducted in the Irish Sea, the majority of these data do not include the species-specific biomass records that are necessary for the calculation of production. Empirically observed benthic production estimates from a total of 74 stations in the Irish Sea were available for analysis. Infaunal production estimates were obtained directly for 25 stations (Bolam et al. 2010), and for the remaining 49 stations production estimates were calculated from available benthic infauna abundance and biomass data collected by six independent benthic surveys conducted between November 2004 and May 2008. The distribution of these 74 stations is not even across the Irish Sea (Figure 4.1). For example the North-Eastern Irish Sea has the highest concentration of available data, followed by areas of the Welsh coast. Further details of these stations and the data collection process can be found in Chapter 2. Total annual benthic infauna production estimates (kJ m^{-2} yr^{-1}) were calculated from species abundance and biomass per m^2 using an empirical model freely available in spreadsheet form on the Internet http://www.thomas-brey.de/science/virtualhandbook/navlog/index.html (Brey, 2001). This multiple regression model calculates total annual production (kJ m^{-2} yr^{-1}) and

production/biomass (P:B) ratio (yr^{-1}) for a given population based on a number of population-specific and habitat-specific inputs (see Brey (2001) for a detailed description of model). Here each population represents a different species, and so species-specific biomass (kJ m^{-2}), abundance (individuals m^{-2}), mean individual body mass (kJ), life history trait and taxonomic data were input into the model, along with station-specific depth and mean annual bottom water temperature. Further details of this model and its input requirements can be found in Brey (2001) and Chapter 2.
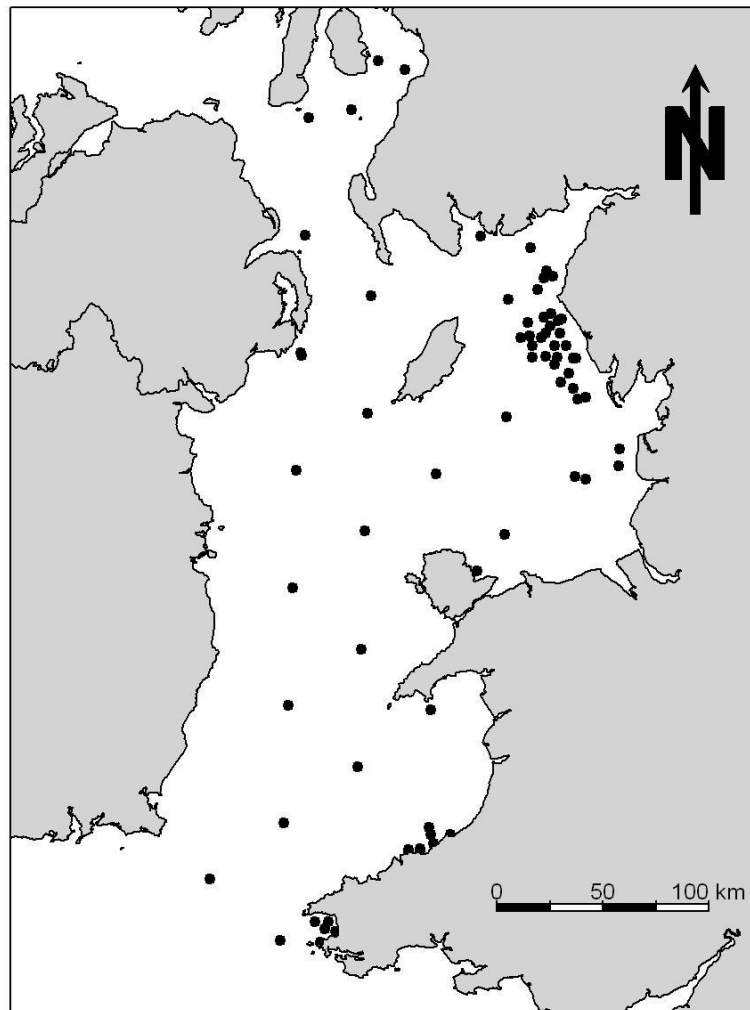
Figure 4.1. Distribution of benthic infaunal production estimates available for analysis.

Benthic diversity

Only the 49 stations for which raw species abundance data were available were included in the species diversity analysis. Three different indices of community or species diversity were calculated from the empirical species abundance data using the vegan package in R (R Core Team, 2012). These indices were community species richness, Shannon-Wiener diversity and Pielou's evenness. Species richness simply refers to the total number of species identified at each station. Shannon-Wiener diversity (*H'*) and Pielou's evenness (*J'*) are two different indices of diversity that are commonly calculated for communities from abundance data. These indices not only take into account the total

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number of species in a community, but also the relative abundance of those species, unlike species richness which is simply the number of species present. The Shannon-Wiener diversity values of H' can range from 0 to 1, with high values indicative a high number of species with an equal distribution, representing a diverse community. Lower values indicate fewer species with a less equal distribution, representing a less diverse community. The Shannon-Wiener diversity index is calculated by:

$$i)\ H' = -\sum_{i=1}^{S} P_i \log P_i$$

where S is the total number of species in the community, P_i is the proportion of individuals belonging to the ith species in the community. Values of H' can range from 0 to 1, with high values indicative a high number of species with an equal distribution, representing a diverse community. Lower values indicate fewer species with a less equal distribution, representing a less diverse community.

Pielou's evenness is different from the Shannon-Wiener diversity index because it focuses only on how equal a community is in terms of the numerical abundance of species, also known as species evenness. The evenness value J' ranges from 0 to 1, with higher numbers indicating a more even community. It is calculated from the Shannon-Wiener index by:

$$ii)\ J = \frac{H}{H_{max}}$$

where H_{max} is the maximum value of H if all species in the community were equally abundant.

For statistical analysis the three diversity estimates were directly compared to the benthic infaunal production estimates calculated from the empirical benthic community data collected at the forty nine stations outlined above. Modelled benthic production estimates were extracted for the same forty nine stations using ArcGIS 9.3.

Modelled benthic production

A predictive size-based model of benthic infauna production developed and validated for the Irish Sea was used to generate benthic infauna production estimates (kJ m^{-2} yr^{-1}) at a spatial resolution of 5 km^2 for the whole Irish Sea area (excluding areas of hard substrate because parameterisation data was not available for these areas). The original model was developed by Duplisea et al. (2002) for the prediction of trawling impacts on benthic communities, and was parameterised by Hiddink et al. (2006a) for application to the North Sea. This model was refined and re-parameterised for application in the Irish Sea, for the purpose of predicting the spatial distribution of benthic infauna productivity for large scale environmental parameters to inform marine protected area design. These environmental data include remotely sensed sea surface chlorophyll-a, modelled tidal bed stress, seabed sediment and fishing intensity estimated from vessel monitoring system (VMS) data. Both actual production and potential production without fishing impact can be predicted by the model, by altering the fishing intensity values input into the model. Here actual production is used for investigating spatial association with biodiversity features, because it was considered representative of the current status of benthic communities in the Irish Sea, and therefore most suitable for investigating spatial association with the current distribution of biodiversity features. For further details of model development and validation see Chapter 3.

Cetacean species sightings

Relative abundance data for the five most common cetacean species in the Irish Sea were obtained from the Atlas of the Marine Mammals of Wales (Baines & Evans, 2009). These five species are bottlenose dolphin (*Tursiops truncatus*), short-beaked common dolphin (*Delphinus delphis*), Risso's dolphin (*Grampus griseus*), harbour porpoise (*Phocoena phocoena*) and minke whale (*Balaenoptera acutorostrata*). All are listed as UK BAP priority species are protected under the EU Habitats Directive. The spatial resolution of this atlas is 10' latitude x 10' longitude and the data is collated from 1990 to 2009. A total of sixteen different survey projects contributed to the database and sightings rates were corrected for sea state and sampling method, which ranged from

land based sightings, to aerial and vessel surveys. Annual long-term standardised sighting rates and long-term standardised sightings for the months April to June were used in this analysis. Long-term standardised sightings rate refers to the mean sightings rate over the time period 1990 to 2009, in units of sightings per hour for the three dolphin species bottlenose, short-beaked common and Risso's dolphins, and individual counts per hour harbour porpoise and minke whale. The months April to June were analysed in addition to an annual average because this time period coincides with the marine spring bloom in the Irish Sea. High primary productivity during the spring bloom is expected to coincide with greater concentration of prey species, and therefore cetaceans may aggregate during this time of year (Dalla Rosa et al. 2012).

Conservation priority species

A list of relevant OSPAR (OSPAR Commission, 2008) and UK Biodiversity action plan (BAP) marine species (http://jncc.defra.gov.uk/page-5167) that occur in the Irish Sea as collated and the spatial distribution data for these species were obtained from Defra (via Dr Kirsten Ramsey, Countryside Council for Wales) and the NBN gateway (http://data.nbn.org.uk/). Many of these species were used as selection criteria in the English Marine Conservation Zone project. Only limited mobility species were included in the analysis because these species were expected to have a stronger association with benthic communities, due to their limited movement. For mobile species it would be difficult to discern whether from the records collated here whether or not they were actually associated with a particular area of the seabed, or if they just travelling over that area at the time of being recorded. Table 4.3, Appendix 4.7.1 lists all the limited mobility conservation priority species records in the Irish Sea included in this analysis. Only species data within 6 nautical miles of the coast were selected for analysis, due to that fact that most of the priority species data fell within this range. The lack of data beyond 6 nm is likely to be primarily a result of sampling bias in coastal areas, therefore excluding the area beyond 6 nm in order to reduce the effects of this sampling bias is considered justified. Inclusion of the whole Irish Sea area in analysis resulted in a very high number of priority species zero counts, resulting in heavily skewed data.

4.4.2 Statistical analysis

Regression analyses were used to determine whether or not there was a significant association between the spatial distribution of empirically measured and modelled benthic production and four groups of biodiversity features. Similarity between data that is in close proximity in space can lead to dependency or auto-correlation in regression model residuals. This auto-correlation needs to investigated and accounted because it can lead to Type 1 error, and can result in poor interpretations and conclusions (Zuur et al. 2009). This is very difficult to account for with simple Spearman rank and Pearson correlation analyses. Regression models can deal with spatial-autocorrelation through the inclusion of a spatial correlation structure.

To determine whether or not spatial auto-correlation was present and needed to be accounted for general regression models without auto-correlation structure were first fitted and Moran's I tests conducted on the fitted model residuals. Where auto-correlation in model residuals was detected a spatial correlation structure was incorporated into the regression model. Appropriate spatial correlation structures were chosen based on evaluation of alternative restricted maximum likelihood (REML) estimated models using Akaike Information Criterion (AIC) values (see Zuur et al. 2009 for further detail).

The type of regression model used for analysis was based on the distribution of the response variable. If the response variable was normally distributed (Gaussian distribution), or if data transformation was sufficient enough to normalise the distribution, a generalised least squares regression (GLS) approach was used. This regression approach can accommodate spatial auto-correlation by the inclusion of a spatial correlation structure to the error component of the regression model (Zuur et al. 2009). Where the response variable could not be normalised a generalised linear modelling (GLM) or generalised additive modelling (GAM) approach was utilised instead. For example, the priority species count data was heavily skewed to the left due to a high proportion of zeros and very few high number counts and could not be normalised by data transformation. These approaches extend the linear regression

model and allow the analysis of non-normally distributed data through the specification of a particular distribution family for the response variable and as well as the nature of the relationship (known as the link function) between the mean of the response and the explanatory variables (Faraway, 2006, Zuur et al. 2009). Here suitable distribution families and link functions were chosen for each individual analyses based on model comparison using the AIC. Those models with the lowest AIC score were considered optimal.

To enable the inclusion of spatial correlation structures in the GLM and GAM models, the glmmPQL() function from the MASS package (Venables & Ripley, 2002) and the gamm() function from the mgcv package (Wood, 2006) in R were used, respectively (R Core Team, 2012). The glmmPQL() function fits specified generalised linear mixed models using Penalized Quasi-Likelihood (see R-help files and Venables & Ripley (2002) for more details), and the gamm() function fits specified generalised additive mixed models (see R-help files and Wood (2006) for more details). Both functions can account for spatial autocorrelation in model residuals through the inclusion of a correlation structure. Unlike other regression models used in this study, the glmmPQL model does not enable selection of spatial autocorrelation structures using AIC comparisons or likelihood ratio tests. In absence of these tests visual comparison of semi-variograms of model residuals were used to choose the spatial correlation structure that removed the most apparent auto-correlation.

The decision to use a GLM or GAM was based on the nature of the relationship between benthic infaunal production and the biodiversity feature in question observed during data exploration. If a relationship was deemed to be non-linear, a GAM approach was used because it allows a non-linear relationship between the response and explanatory variables through the use of a smoothing function (Zuur et al. 2009). GLMs and GAMs that allowed the inclusion of a spatial correlation structure were used here, to ensure that any potential auto-correlation in model residuals could be accounted for. All statistical analyses were conducted in R software (R Core Team, 2012).

Computational difficulties were experienced when conducting initial analyses for some biodiversity features because the inclusion of a spatial auto correlation structure requires all pair-wise distances between data points to be considered, and this requires a large amount of computational power when a lot of data points are included in analysis. Therefore, in order to avoid computational problems data were either collated at a coarser spatial scale or sub-sampled to reduce sample sizes. For example, the analysis conservation priority species was conducted using data at a spatial resolution of 20km^2. This is because it was the smallest spatial scale at which computational difficulties were not encountered when running the analyses. i.e regression models did not converge using data with a spatial resolution of 5-15 km^2. Modelled and empirical benthic production estimates were averaged within 20 km^2 grid cells across the whole Irish Sea area, and the total number of conservation priority species present within each grid cell were calculated in ArcMap 9.3.

A description of the data, the type of regression model applied and details of data preparation and use of correlation structures for each of the biodiversity features is summarised in Table 4.1.

Table 4.1. Summary table of all data used in the analyses, included data distribution, the type of regression model applied and details of data preparation and correlation structures for analyses of each of the three groups of biodiversity features investigated.

Biodiversity feature	Production estimate type	Data distribution	Regression model type	Computational difficulties	Spatial resolution of production estimates	Sub-sampling	Transformation	Correlation structure
Benthic diversity	Modelled	Left-skewed	GLS	No	5 km^2	No	Log10	Various
	Empirical	Left-skewed	GLS	No	Point estimate	No	Log10	Various
Cetacean abundance	Modelled	Negative binomial (NB)	NB gamm	No	10' lat x 10' lon	No	None	Various
	Empirical	Negative binomial (NB)	NB gamm	No	10' lat x 10' lon	No	None	Various
Conservation priority species	Modelled	Negative binomial (NB)	NB glmmPQL	Yes	20 km^2	No	None	corRatio
	Empirical	Binary	NB glmmPQL	No	20 km^2	No	None	None

4.5 RESULTS

Benthic infaunal production and the three different groups of biodiversity feature examined here have very different spatial distributions. Regression analyses indicate that there is very little association between the spatial distribution of modelled and empirical benthic infaunal production these biodiversity features in the Irish Sea (Table 4.2).

Modelled production estimates indicate that benthic infauna production is highest in the north-east Irish Sea, particular in coastal areas off North Wales, north west England and the Solway coast. There are also relatively high in areas of production in Cardigan Bay, off the coast of Anglesey, the Llyn Peninsula, and Dublin. Production appears to be lowest in offshore areas, particularly in the Western and Central areas of Irish Sea, as well as close inshore in Cardigan Bay, Wales. Where available, empirical production estimates largely mirror this pattern (Figure 4.2).
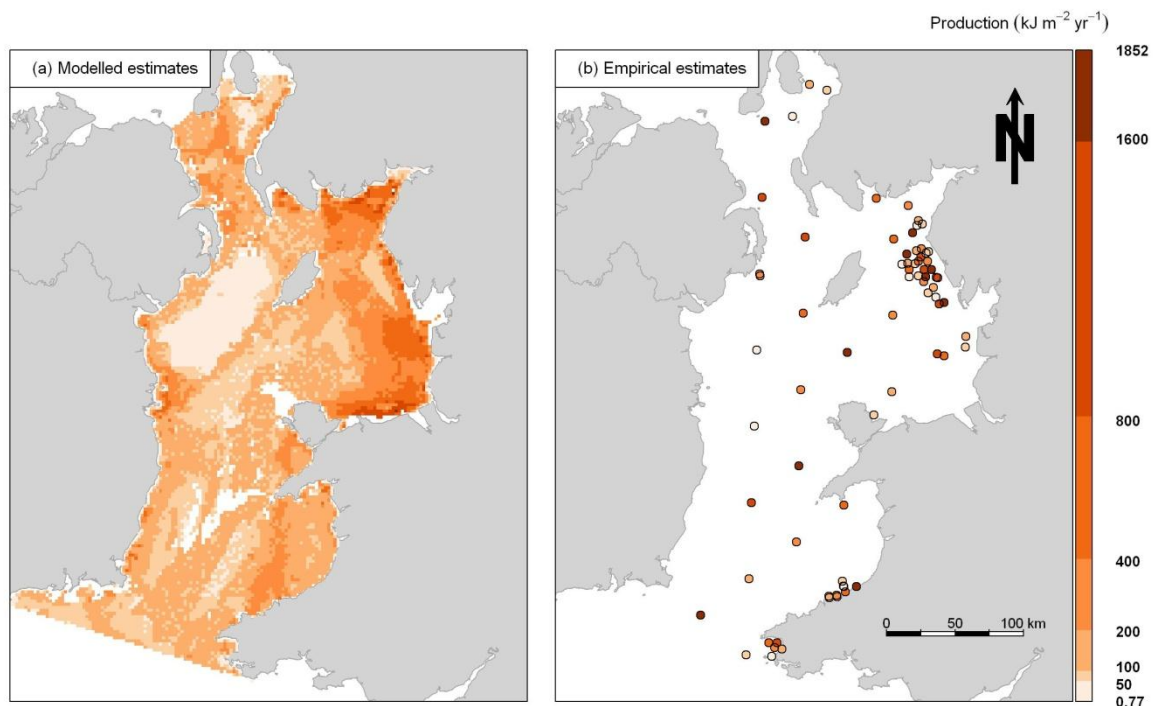
Figure 4.2. Modelled (a) and empirically observed (b) production estimates data used in analyses.

Table 4.2. Details for all statistical analyses and results regarding the spatial association between modelled and empirical infaunal production and biodiversity features of conservation interest in the Irish Sea.

	Biodiversity feature	Production data	Regression model	Correlation structure	N	Coefficient	Std Error	Df	*F*	*P*-value
Benthic diversity	Species Richness	Modelled	GLS	corGaus	46	0.08	0.09	44	0.81	0.374
		Empirical		corRatio	49	0.24	0.04	47	32.61	0.000 ***
	Shannon-Wiener diversity	Modelled	GLS	corGaus	46	0.73	0.19	44	14.14	0.001 ***
		Empirical		corExp	49	0.03	0.18	47	0.03	0.857
	Pielou's evenness	Modelled	GLS	corLin	46	0.13	0.05	44	6.18	0.017**
		Empirical		corExp	49	-0.07	0.04	47	3.61	0.064
Annual cetacean sightings	Bottlenose dolphin	Modelled	NB GAM	corRatio	264	1.56	1.38	262	1.31	0.254
		Empirical		corCompSymm	55	-3.65	4.37	53	0.33	0.407
	Harbour porpoise	Modelled	NB GAM	corCompSymm	264	-2.65	1.98	262	1.81	0.181
		Empirical		corCompSymm	55	-0.08	0.78	53	0.46	0.605
	Minke whale	Modelled	NB GAM	corRatio	264	0.24	1.32	262	0.03	0.856
		Empirical		corRatio	55	-0.21	1.51	53	0.02	0.887
	Risso's dolphin	Modelled	NB GAM	corGaus	264	-0.56	2.69	262	0.04	0.835
		Empirical		NONE	55	1	-	53	0.19	0.659
	SB Common dolphin	Modelled	NB GAM	corRatio	264	0.83	1.17	262	0.49	0.485
		Empirical		corRatio	55	0.53	0.36	53	2.14	0.149
Spring cetacean sightings	Bottlenose dolphin	Modelled	NB GAM	corRatio	264	1.45	2.10	262	0.48	0.489
		Empirical		corRatio	55	0.23	0.74	53	0.09	0.754
	Harbour porpoise	Modelled	NB GAM	corCompSymm	264	-0.62	1.14	262	0.30	0.582
		Empirical		corCompSymm	55	0.68	0.89	53	2.09	0.130
	Minke whale	Modelled	NB GAM	corRatio	264	1.80	1.77	262	0.98	0.310
		Empirical		corCompSymm	55	-4.93	7.05	53	0.81	0.372
	Risso's dolphin	Modelled	NB GAM	corRatio	264	-1.65	6.25	262	0.07	0.791
		Empirical		corCompSymm	55	-6.88	6.02	53	12.01	0.258
	SB Common dolphin	Modelled	NB GAM	corRatio	264	0.76	1.99	262	0.14	0.703
		Empirical		corRatio	55	0.59	0.37	53	2.66	0.108
Conservation priority species	Priority species	Modelled	NB GLM	corRatio	1185	-0.01	0.00	1183	-	0.240
		Empirical		NONE	35	-0.00	0.00	33	-0.14	0.889

Benthic production and benthic infauna diversity

On visual comparison of the distribution data, the spatial variation in both modelled and empirical production is most similar to the variation in species richness compared to the other measures of diversity (Figure 4.2, Figure 4.3). This is most apparent in the north-east Irish Sea where the majority of the data is clustered. The association between species richness and production is less apparent around the coast of west Wales, where species richness estimates are generally high and production estimates are low.

There was a significant, positive association between empirical production and benthic community species richness (Figure 4.4b, Table 4.2; $F = 32.61$, $df = 47$, $p = 0.000$), but no association between empirical production and the Shannon-Wiener diversity or Pielou's evenness indices (Figure 4.4). For modelled production, there was a positive, linear association between production and the Shannon-Wiener diversity index (Figure 4.4c, Table 4.2; $F = 14.14$, $df = 44$, $p = 0.001$) and Pielou's Evenness (Figure 4.4e, Table 4.2; $F = 6.18$, $df = 44$, $p = 0.017$), but no significant association between modelled production and species richness.

Figure 4.3. Three different benthic infaunal community diversity indices estimated for available data in the Irish Sea; a) Species richness, b) Shannon-Wiener diversity index, c) Pielou's evenness.
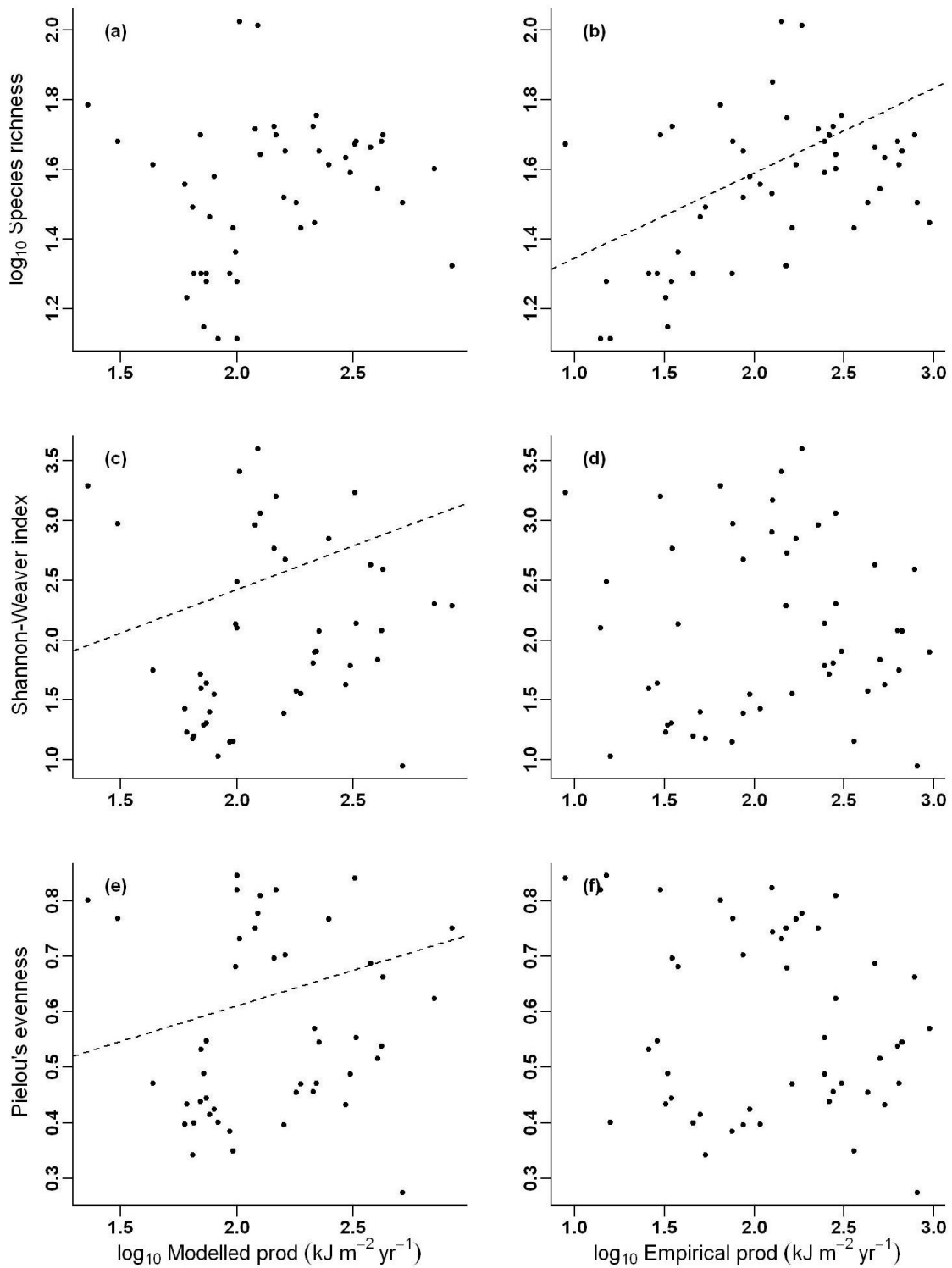
Figure 4.4. The relationship between modelled and empirical benthic production ($\log_{10}$ (kJ m^{-2} yr^{-1}) and three different indices of benthic community diversity, including a-b) Species richness ($\log_{10}$ (number of species), c-d) Shannon-Wiener index, and e-f) Pielou's evenness. N = 46 and 49 for modelled and empirical production, respectively.

Benthic production and long-term cetacean sightings

Visual examination of the long-term sightings rate distribution for the five cetacean species indicates a different spatial pattern for each species (see Figure 4.5 for bottlenose dolphin and harbour porpoise distribution, and Figure 4.10 & 4.11, Appendix 4.7.2 for the annual and spring distributions of minke whale, risso's dolphin and short-beaked common dolphin). The only cetacean species to have a strong, but not exclusive, presence in areas of high production are bottlenose dolphin and harbour porpoise (Figure 4.5). A difference between the annual and spring distributions for these two species is apparent. The spring distribution is less wide ranging for both species, particularly for harbour porpoise which has a very broad annual distribution across most of the Irish Sea. Both the annual and spring distribution for Bottlenose dolphin appears to be concentrated in Cardigan Bay.

The cetacean long-term sightings rate data were strongly skewed by a high number of zeros. As a result, negative binomial generalised additive models (GAM) were used to investigate the association between cetacean sightings and benthic production. Results for all cetacean species, for both annual long-term sighting rates and long-term sighting rates during the spring bloom (April to June) indicate no significant association with modelled or empirical benthic infauna production (Figure 4.6 & 4.7).
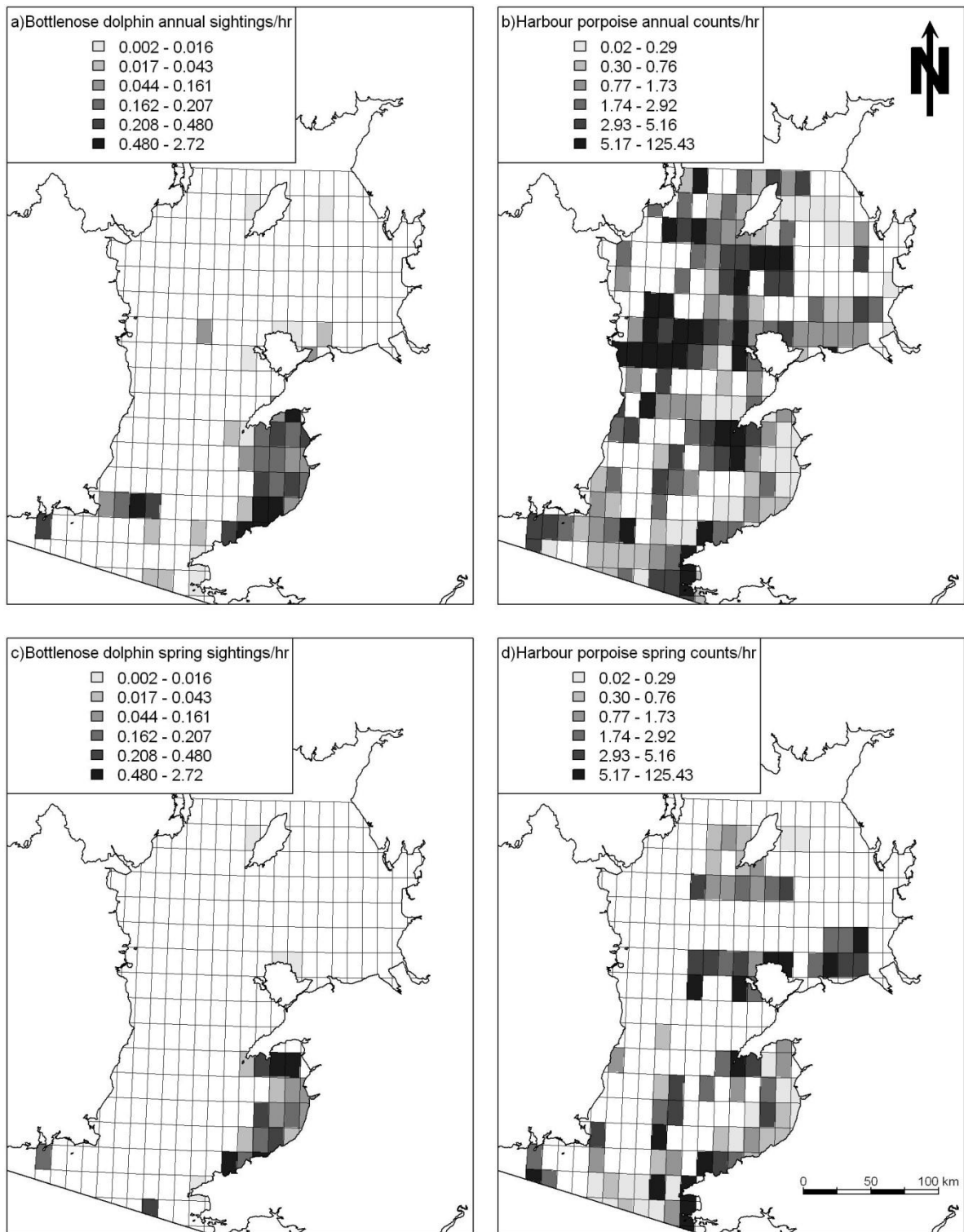
Figure 4. 5. Spatial distribution of annual long-term sightings rate for (a) bottlenose dolphin (*Tursiops truncatus*) and (b) harbour porpoise (*Phocoena phocoena*), and spring (April – June) long-term sightings rate for (c) bottlenose dolphin (*Tursiops truncatus*) and (d) harbour porpoise (*Phocoena phocoena*).

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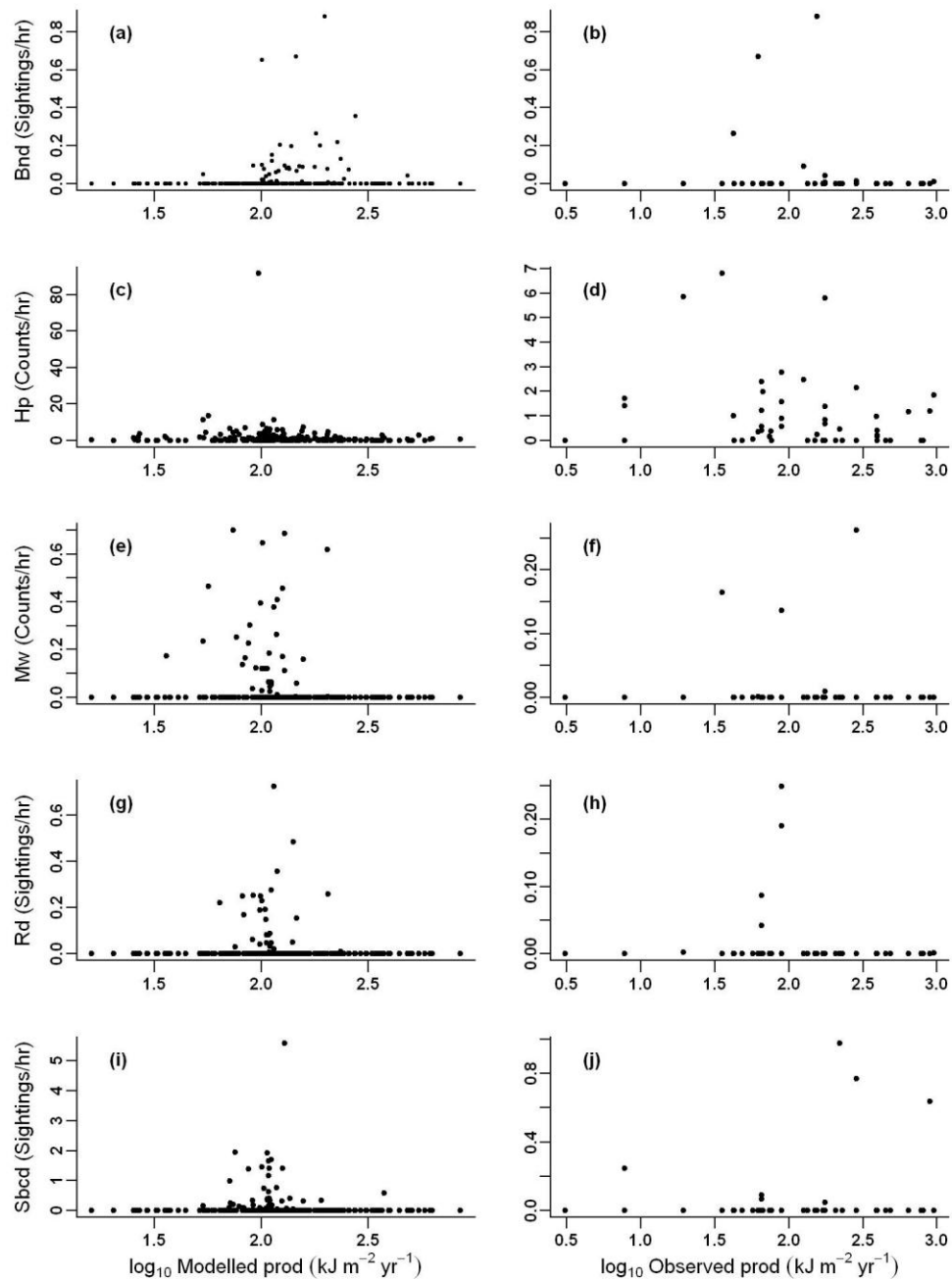
Figure 4.6. The relationship between empirical and modelled benthic production (kJ m^{-2} yr^{-1}) and the annual relative abundance of five different cetacean species, recorded at a spatial resolution of *10' latitude x 10' longitude*. The unit of relative abundance is annual long-term sightings rate (sightings/hr or counts/hr). The five cetacean species include; a-b) bottlenose dolphin (*Tursiops truncatus*), c-d) harbour porpoise (*Phocoena phocoena*), e-f) minke whale (*Balaenoptera acutorostrata*), g-h) Risso's dolphin (*Grampus griseus*), and i-j) short-beaked Common dolphin (*Delphinus delphis*). N = 55 and 264 for empirical and modelled production, respectively.
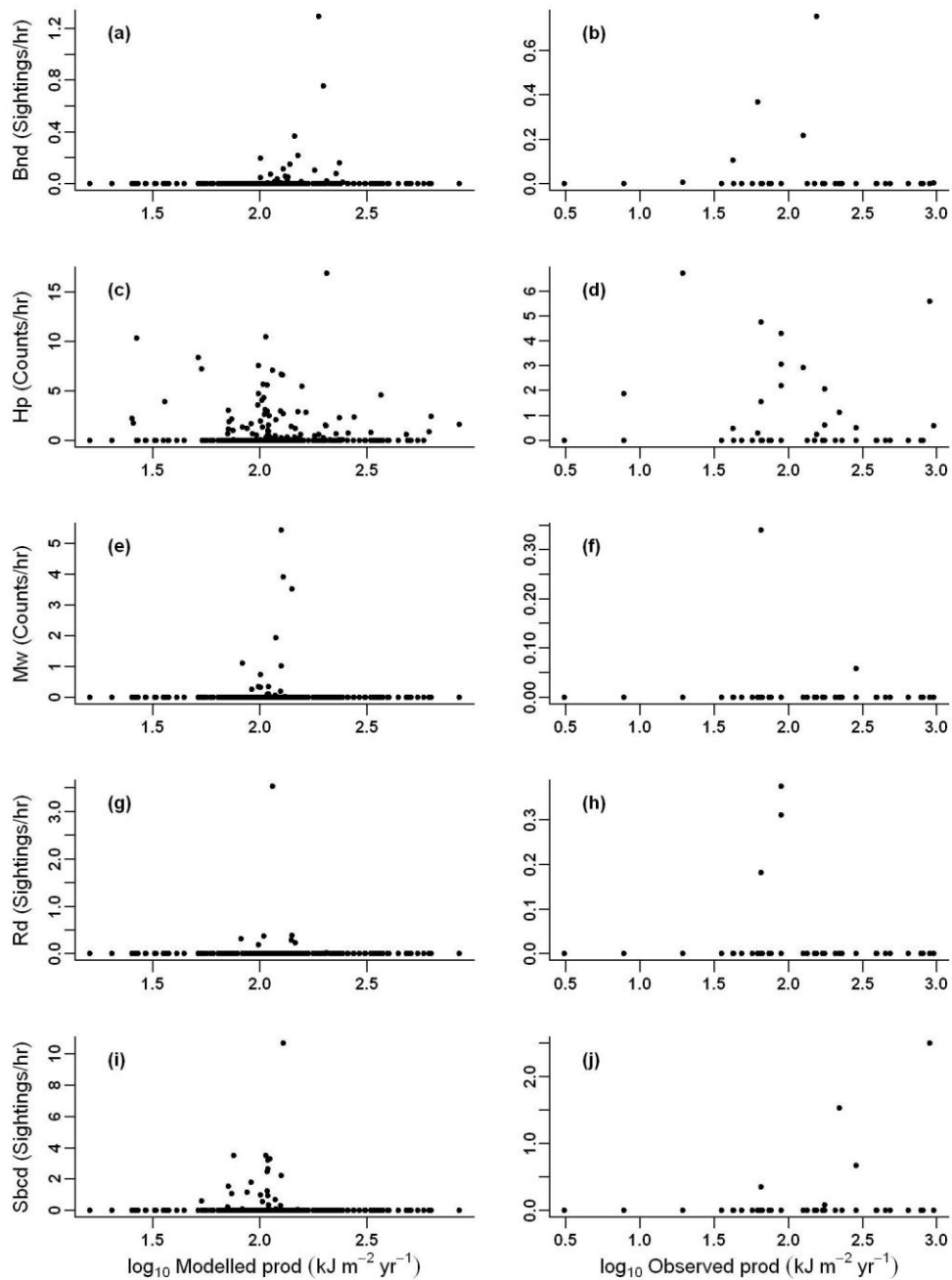
Figure 4.7. The relationship between empirical and modelled benthic production (kJ m⁻² yr⁻¹) and the relative abundance of five different cetacean species during spring (April-June), recorded at a spatial resolution of *10' latitude x 10' longitude*. The unit of relative abundance is spring long-term sightings rate (sightings/hr or counts/hr). The five cetacean species include; a-b) bottlenose dolphin (*Tursiops truncatus*), c-d) harbour porpoise (*Phocoena phocoena*)), e-f) minke whale (*Balaenoptera acutorostrata*), g-h) risso's dolphin (*Grampus griseus*), and i-j) short-beaked Common dolphin (*Delphinus delphis*). N = 55 and 264 for empirical and modelled production, respectively.

Benthic production and the number of conservation priority species

A visual comparison of the spatial distribution of the number of limited-mobility priority species and benthic infauna production in the Irish Sea suggests little consistent association between the two across the area studied. The number of priority species ranged from 0 to 2, and their distribution appears to be fairly scattered across the area included in the analysis, with most areas having 0 or 1 species present (Figure 4.8). The highest numbers of priority species (2 priority species) are found of the South Pembrokeshire coast and in and around Strangford Lough, Northern Ireland.

The benthic production and priority species data were heavily skewed by a high number of zero species counts, therefore a generalised linear model (GLM) with negative binomial distribution was used for both empirical and modelled benthic production. GLM results indicate no significant association between modelled or empirical benthic production and the number of priority species (Table 4.2). Figure 4.9 shows the raw data for empirical (N= 35) and modelled (N = 1185) production, respectively. Both are dominated by zero counts, followed by single species counts, particularly at lower values of benthic production.
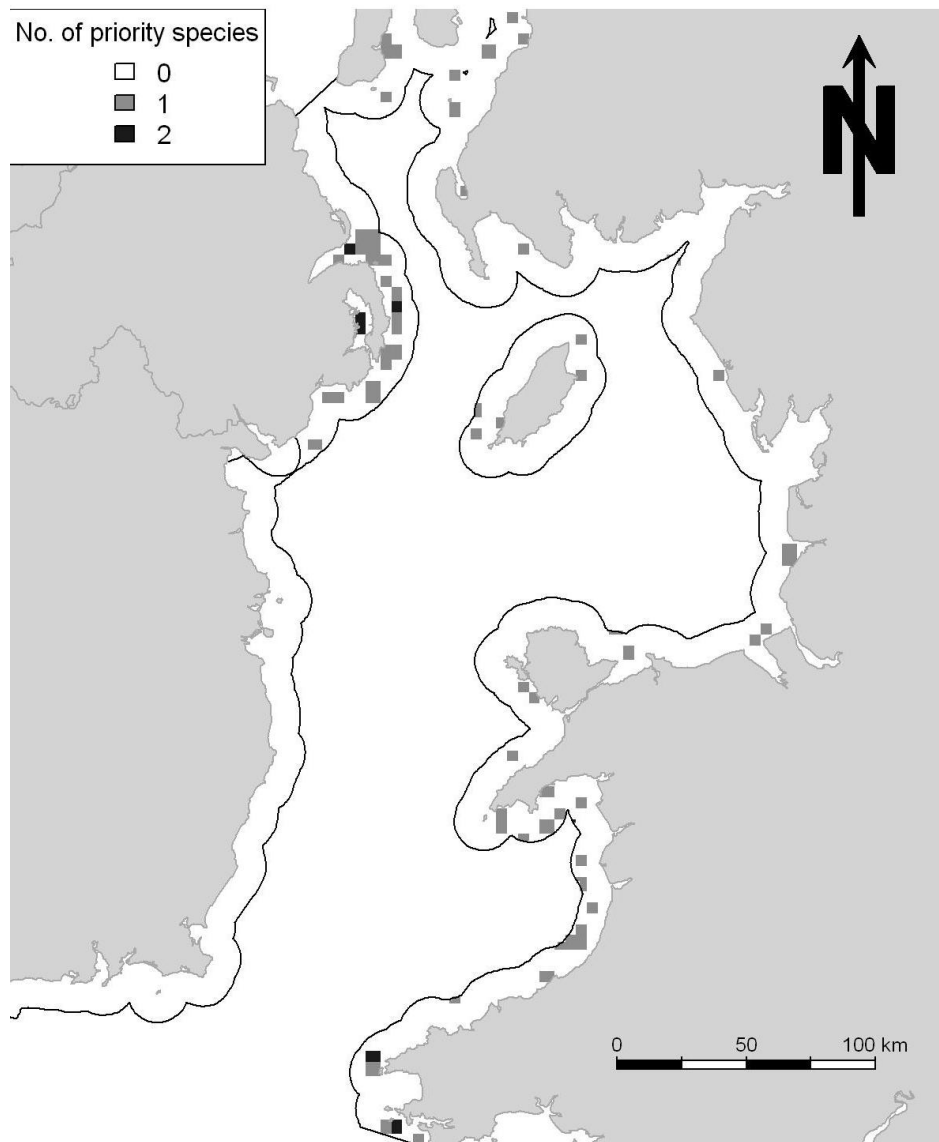
Figure 4.8. The distribution of limited-mobility conservation priority species records per 20 km², within 6 nm.
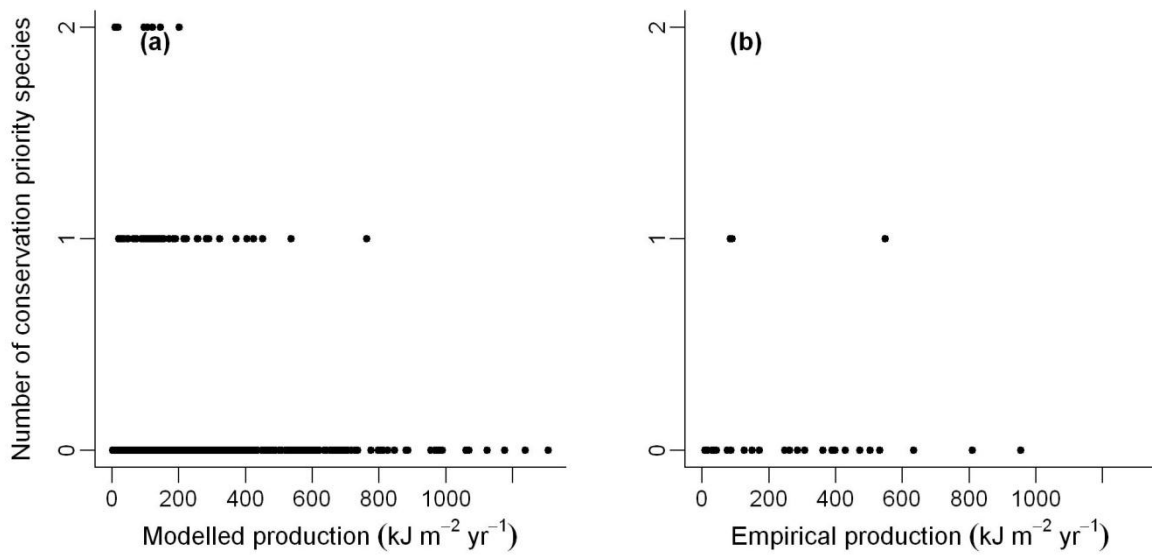
Figure 4.9. The relationship between (a) empirical and (b) modelled benthic production (kJ m^{-2} yr^{-1}) and the number of limited-mobility conservation priority species (UK BAP and OSPAR priority species), recorded at a spatial resolution of 20 km^2. N = 1257 and 41 for modelled and empirical production, respectively.

4.6 DISCUSSION

4.6.1 Overview

Out of the three groups of biodiversity features included in the analysis here, only benthic diversity was found to a have significant, positive spatial association with benthic production. No significant association was found between production and cetacean relative abundance, or the number of conservation priority species. This would suggest that designating MPAs to protect these later two biodiversity features will not result in substantial protection of the important ecosystem function benthic infaunal production. It would therefore appear that opportunities for establishing win-win conservation scenarios that protect both biodiversity and ecosystem function in the Irish Sea are limited. Of the three hypotheses tested, two were support by the results; i) a positive association between benthic production and benthic diversity, and iii) no association between benthic production and the number of conservation priority species. The hypothesis predicting a positive association between benthic production and cetacean relative abundance was not supported.

Both types of production estimates were included in the analyses here, in order to increase confidence in results, should both estimates exhibit positive associations. Empirical infaunal production (kJ m^{-2} yr^{-1}) is calculated by a multiple regression model that uses a number of population-specific and habitat-specific inputs (see Brey (2001) for a detailed description of model). Modelled infaunal production is predicted using a size-based model that includes several statistically-estimated environment-mediated growth and mortality functions. Both rely on statistically estimated relationships, and both have a limited number of inputs which are unlikely to represent all influences on benthic production. Therefore both models are unlikely to predict precise estimates. Despite this, agreement between results between empirical and modelled estimates is assumed to suggest greater confidence in the results. Here, where positive associations were found for the different measures of benthic infauna diversity, a significant relationship was only found for one production estimate, not both. Therefore,

confidence in the result is not as strong as if both production estimates had significant associations with diversity.

4.6.2 Benthic infaunal production and biodiversity features

Benthic production and benthic diversity

Here, the positive association between empirical production and species richness, and modelled benthic production and the Shannon-Wiener index and Pielou's Evenness suggests that both the number and relative abundance of different species could have an influence on the productivity of the benthic infauna community. The primary causal mechanisms for a positive relationship between species diversity and productivity put forward in biodiversity-ecosystem function research are facilitation and complementarity, which both propose that increasing species diversity increases resource use efficiency within a community (Srivastava & Vellend, 2005; Balvanera et al. 2006, Hillebrand & Matthiessen, 2009). Alternatively, observed positive correlations in nature could also exist due to simple covariance of production and diversity. A greater number of species may simply mean greater community abundance, resulting in high biomass and therefore productivity.

Causal mechanisms are not necessary for identifying potential win-win scenarios. As long as spatial concurrence exists consistently across the area of interest, there is potential to inform effective conservation planning. Available data for investigating the relationship between benthic production and benthic community is not expected to be representative of the whole Irish Sea area, therefore it is difficult to say that the result here can be generalised to this scale. However, the results do suggest that there is more likely to be an association between benthic production and benthic community diversity compared to the other biodiversity features included in the analyses here.

Benthic production and conservation priority species

The lack of a spatial association between benthic infaunal production and the number of conservation priority species is not unexpected because there is no particular biological justification for a high number of these species to be associated with highly productive benthic communities. In fact, in terrestrial ecosystems it has been observed that rare or endemic species are usually associated with low productivity habitats, such as savannahs (Bustamante et al. 2012) and serpentine soils (Jules et al. 2012). The list of species included in the analyses here is fairly diverse and the different species are not expected to be associated with each other because of different habitat requirements, so there is little likelihood of them occurring in the same area. Other studies have similarly found no or very little association between ecosystem services and conservation priority species (e.g. Chan et al. 2006; Naidoo et al. 2008). Conversely, Anderson et al. (2009) found an overall negative association between an ecosystem service, carbon storage, and number of terrestrial UK BAP priority species at a national scale (England).

Benthic production and cetacean relative abundance

Unexpectedly, no spatial association was found between benthic production and long-term sightings rate for the five priority cetacean species included in the analyses here. Marine mammal feeding activity has been shown to be associated with areas of high productivity, such as fronts and areas of upwelling (e.g. Scott et al. 2010; Thompson et al. 2012; Santora et al. 2012). However, the five species of cetacean included here have subtle differences in diet which may influence the possibility of them being associated specifically with areas of high benthic production. For example, Minke whale feeds on krill, plankton and small schooling fish in surface and near-surface waters. Short-beaked common dolphin and Risso's dolphin feed on epi-pelagic fish and cephalopods (NOAA fisheries, Office of Protected Resources; http://www.nmfs.noaa.gov/pr/species/mammals/cetaceans/).

Bottlenose dolphins and Harbour porpoise are most likely to target benthic or demersal fish, cephalopods and other invertebrates, therefore an association with benthic infauna

production could be expect for these two species in particular. Distribution maps do suggest that they do have a strong presence in areas of high production, however, they also a strong presence in areas of low predicted production and regression analysis confirm that there is no significant association when considering their distribution across the whole Irish Sea area.

The fact that cetaceans are highly mobile makes determining species-habitat associations difficult (Ballance et al. 2006). The greater the mobility of an animal, the more difficult it is to identify strong associations. The sightings rate data used in this analysis also only records surface activity of the cetaceans, therefore it is difficult to determine if the species are simply travelling through the area, or are in the area to feed. If the feeding ground of these species were known and mapped, the spatial pattern may be quite different to that determined from sightings data and may have yielded different results from those found here. Similarly, a stronger link may be found between cetaceans and their actual prey items, for example demersal fish, compared to between cetaceans and benthic productivity. Investigation of the association between benthic production and demersal fish, and demersal fish and cetaceans of conservation importance is recommended for future research.

4.6.3 Implications for conservation planning

The lack of positive spatial associations between benthic production and biodiversity features in the Irish Sea suggest limited scope for designating MPAs that protect both an important marine ecosystem function and biodiversity. Furthermore, the assumption that the protection of biodiversity, or ecosystem structure, will confer protection of ecosystem function or services is not supported by the findings. This reinforces recommendations that spatial concurrence between conservation priorities and ecosystem services should be empirically investigated in order to confirm the degree of overlap and inform effective conservation planning (e.g. Naidoo et al. 2008, Larsen et al. 2011). The results indicate that there is no general pattern of association between biodiversity and ecosystem function; a finding that is mirrored by other studies (Eigenbrod et al 2009). For example, findings range from no association between

ecosystem services and biodiversity priorities (Naidoo et al 2008), some positives associations, between freshwater services and biodiversity (Larsen et al. 2011), and the number of listed species and regulating services (Schneider et al. 2012), as well as negative associations, for example between carbon storage and conservation priority species (Anderson et al. 2009).

Understanding both potential win-win scenarios and trade-offs in conservation management of biodiversity and ecosystem function is essential for informing effective planning and prioritisation of effort (Power et al. 2010). Studies investigating spatial overlap between ecosystem services and conservation priorities like the one outlined here are an important step in this process. Although the results here indicate no great opportunity of win-win scenarios, the lack of a significant negative association suggests that strong management trade-offs between biodiversity features and benthic infaunal production do not occur. Conversely, Anderson et al. (2009) found a negative relationship between carbon storage and the number of conservation priority species in the UK, because the peat and moorland areas important for carbon storage in the UK had low numbers of these particular species. This indicates that conservation of carbon stores in the UK will have little benefit for conservation priority species, and if conservation efforts are limited, trade-offs will have to be made when considering their protection. Here, the lack of a distinct difference in the distribution of benthic productivity and biodiversity features suggests that optimizing protection for one of the biodiversity features will not retract sustainably from the protection of benthic production compared to if conservation was not focused on this one feature.

Although no obvious trade-offs between the protection of biodiversity and function are apparent here, the lack of significant spatial overlap suggests that a larger area will be required for conserving both ecosystem structure and function than if significant spatial congruence existed. This has cost implications not only for conservation, but also for other marine users, because the greater the area required for protection the greater the likelihood of conflict with these other users. Strong trade-offs are therefore likely to occur between conservation and conflicting uses such as fishing, as opposed to a trade-off between the protection of one conservation feature over another. Determining the

area of protection needed to conserve both biodiversity and ecosystem structure is beyond the scope of this study. This will, however, be partly addressed in Chapter 5. An approach similar to that of Chan et al. (2006) which compared the degree to which networks of protected areas for biodiversity met targets for different ecosystem services, and the amount of extra land networks would need to meet such targets, would be suitable for determining the area required for protection of all conservation features. The generation of networks to protect both biodiversity and ecosystem function would also be useful for further investigating the potential for win-win conservation scenarios and further informing efficient conservation planning.   Despite the weak correlations between biodiversity and individual ecosystem services found by Chan et al. (2006), the creation of networks to protect biodiversity identified that these networks did actually protect substantial amount of ecosystem services. This is because there were hotspots where biodiversity and areas important the functions in question did coincide. Naidoo et al. (2008) similarly found no consistent association between biodiversity and ecosystem services at a global scale, but were still able to identify areas important for both at local scales. Although no consistent association between biodiversity features and benthic production across the whole Irish Sea was found here, comparisons of the distribution maps do indicate some areas where high productivity coincide with the biodiversity features examined. For example a high relative abundance of bottlenose dolphin and harbour porpoise occur in areas of high productivity off the North Wales and in Cardigan Bay. The next step in determining the extent of win-win scenario in the Irish Sea would therefore be to generate protected area networks for biodiversity features and quantify the degree to which the networks also protect benthic production, and vice versa. In addition to this, the degree of similarity or overlap between alternative networks generated to protect biodiversity features and benthic production would indicate areas useful for protecting both, therefore highlighting potential areas for prioritising conservation effort.

The importance of spatial scale

The fact that a stronger association was detected between benthic infaunal production and benthic infaunal diversity compared to the other biodiversity features investigated

here is not unsurprising. This is because the benthic diversity and benthic diversiy data were extracted either at similar scales (modelled production), or directly from the same area (empirical production). In comparision the biodiversity feature data could only be investigated at a much larger spatial grain compared to the scale at which benthic production data was generated.

The general lack of association between biodiversity features and benthic infaunal production may also be a due to the large spatial extent at which data were analysed. Anderson et al. (2009) found distinct regional differences in the relationship between biodiversity and ecosystem services, when compared to the general pattern found for the whole of Britain. For example, although an overall negative association between biodiversity and carbon storage was found for the whole of the UK, when this analyses was broken down into 100x100km grid cells, a significant negative relationship remained for area of the north-west and uplands, but a significant positive relationship was found between biodiversity and carbon storage in south and east areas, where high biodiversity was associated with high-carbon habitats forest and wetland. This suggests that restricting analyses to one, large spatial extent may mean that opportunities for win-win conservation scenarios maybe missed. Here, the only analysis with a restricted extent is the comparison of benthic production and benthic diversity, limited primarily to the North East Irish Sea, and some stations around the coast of Pembrokeshire, Wales. This is the only analysis that yielded a significant association between biodiversiy and production. Analyses for cetacean relative abundance and conservation priority species were conducted at a much larger spatial scale, and no significant results were found. The results of Anderson et al (2009) would suggests that these analyses may have been conducted at too large a spatial extent for informing effective conservation planning, and a smaller scale, local approach may be more appropriate or identifying in-win conservation scenarios in the Irish Sea.

4.6.4 Conclusions

In summary, the findings here indicate that (i) the protection of biodiversity (ecosystem structure) will not automatically ensure the protection of ecosystem function,

suggesting that (ii) to protect biodiversity features and ecosystem function in the Irish Sea conservation planning will need to specifically consider and target both. (iii) Although no significant, consistent associations were found, visual comparisons of spatial patterns in the Irish Sea suggest that some areas of high benthic productivity do coincide with high biodiversity feature abundance or diversity; (iv) therefore a targeted, local approach is more likely to be successful for identifying win-win conservation scenarios than the Pan-Irish Sea approach described here.

4.7 APPENDICES

4.7.1 Conservation priority species

Table 4.3. The limited mobility OSPAR and UK Biodiversity Action plan species included in the analysis to investigate spatial association between benthic production and the number of conservation priority species. The table also indicates whether or not the species is also a criterion for the MZC selection process in England, and gives the data source.

Species of conservation importance	BAP/OPSAR species	MZC criteria (England)	Data source
Atrina pectinata (Fan mussel)	BAP	Yes	Defra
Edwardsia timida (Timid burrowing anemone)	BAP	Yes	Defra
Eunicella verrucosa (Pink-sea fan)	BAP	Yes	Defra
Funniculina quadrangularis (Tall sea pen)	BAP	No	Defra
Haliclystus auricula (Kaleidoscope jellyfish)	BAP	Yes	Defra
Hippocampus guttulatus (Long snouted seahorse)	BAP/OSPAR	Yes	Defra
Lithothamnion corallioides (Coral maerl)	BAP/OSPAR	Yes	Defra
Lucernariopsis campanulata (Stalked jellyfish)	BAP	Yes	Defra
Ostrea edulis (Native oyster)	BAP/OSPAR	Yes	Defra
Palinurus elephas (Spiny lobster)	BAP	Yes	Defra
Phymatolithon calcareum (Common maerl)	BAP/OSPAR	Yes	Defra
Tenellia adspersa (Lagoon sea slug)	BAP	Yes	Defra

4.7.2 Cetacean species
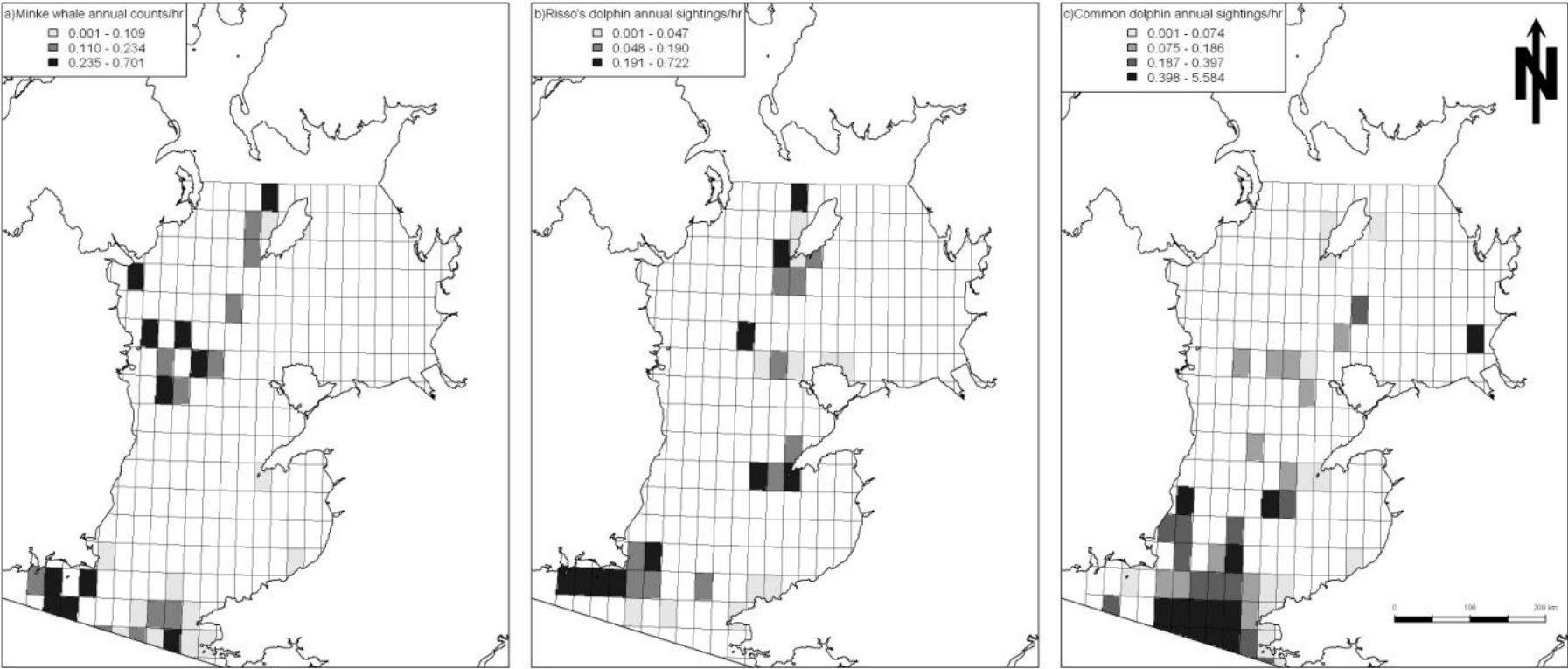
Figure 4.10. Distribution of annual long-term sightings for (a) minke whale (*Balaenoptera acutorostrata*), (b) risso's dolphin (*Grampus griseus*) and (c) short-beaked common dolphin *(Delphinus delphis).*
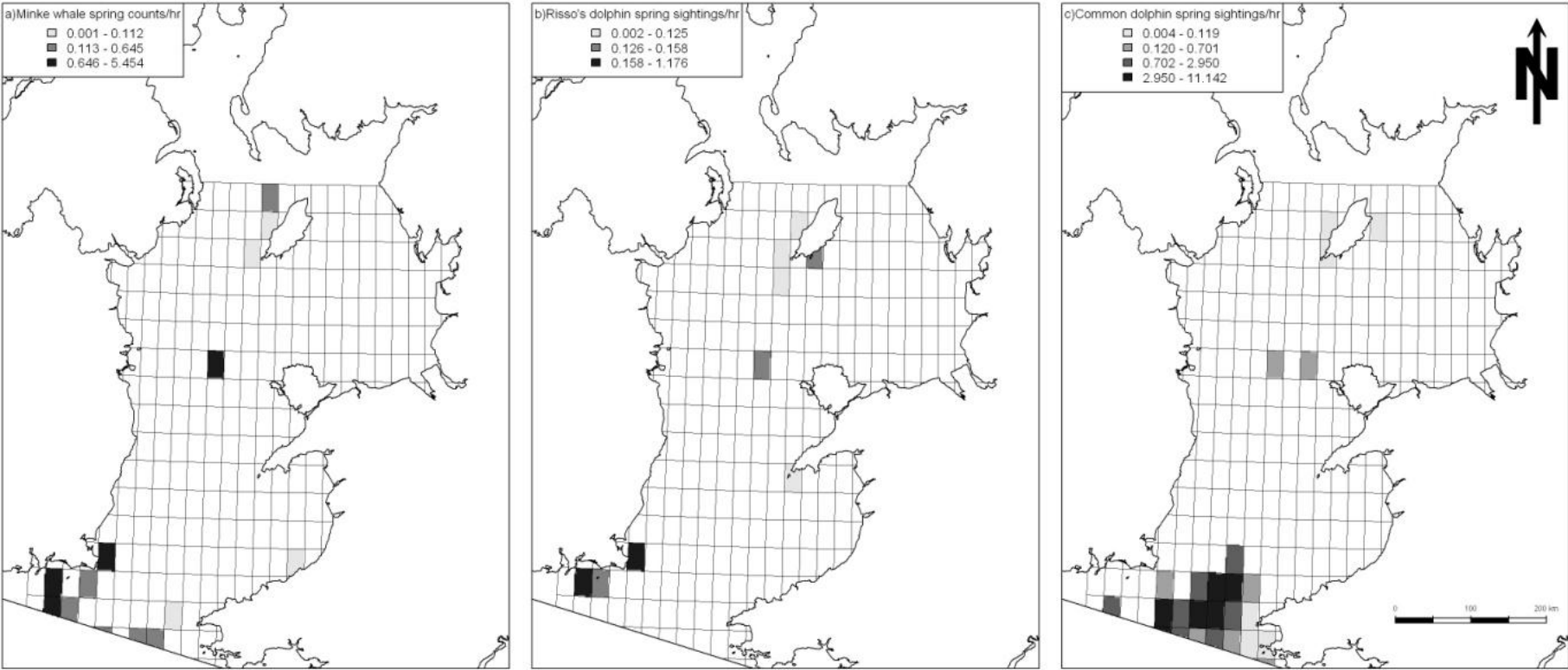
Figure 4.11. Distribution of spring long-term sightings (April – June) for (a) minke whale (*Balaenoptera acutorostrata*), (b) risso's dolphin (*Grampus griseus*) and (c) short-beaked common dolphin *(Delphinus delphis).*

CHAPTER 5 - Do marine protected area networks designed to protect biodiversity also protect ecosystem functioning?

5.1 AIM: To investigate the extent to which marine protected areas (MPAs) designed to protect biodiversity also protect an important ecosystem function, benthic infaunal production.

5.2 ABSTRACT

Safeguarding ecosystem functioning is gaining importance in conservation and environmental management. Benthic infaunal production is an important marine ecosystem process that mediates energy transfer through the marine food web. Benthic production could be protected in marine protected areas (MPAs), however, to date the majority of MPAs have been designated to protect biodiversity features such as species and habitats. Here the amount of benthic production that is protected by hypothetical biodiversity MPA networks in the Irish Sea will be compared to those designed to protect benthic infaunal production. In particular, a protection target of 30% of total benthic infaunal production in the Irish Sea is set (based on International recommendations for marine habitats), and the extent to which biodiversity MPAs met this target is investgiated, to determine whether or not targeted protection of ecosystem function using functional selection criteria is required. The biodiversity features included here are the species and habitats used to identify potential marine conservation zones in England. Different MPA networks are generated using the conservation planning software MARXAN. The influence of a fishing cost surface (that reflects the importance of an area to the fishing industry) on network outputs is investigated to determine if the consideration of socio-economic costs effects the amount of production protected or total network costs. Results indicate that biodiversity MPA networks do not protect 30% of benthic productivity in the Irish Sea, and a large total network area is required to protect both biodiversity and function. As a result these networks exhibit the highest costs to fishing. The inclusion of a fishing cost surface

reduces MPA benefits to production and total network costs. Overall, results suggest that ecosystem functioning should be explicitly included in MPA network design to ensure its protection.

5.3 INTRODUCTION

Marine protected area (MPA) designations tend to target the protection of biodiversity, specifically species or habitats of conservation importance (Frid et al. 2008). There is increasing interest in also managing and protecting ecosystem function, however, because it underpins ecosystem health and the provision of ecosystem goods and services (Beaumont et al. 2007; Beaumont et al. 2008; Tillin et al. 2008; Frid et al 2008; Curtin & Prellezo, 2010; Young et al. 2008). If there is a high spatial association or overlap between areas of high biodiversity and ecosystem functioning, the protection of biodiversity features in MPA networks, for example from fishing, could also protect those coinciding ecosystem functions that are damaged by fishing. These cases of spatial coincidence therefore offer opportunities for multiple benefits, or 'win-win' conservation scenarios (Balmford et al. 2002, Crossman & Bryan 2009). General links between biodiversity and ecosystem function have been made (Balvanera et al. 2006; Srivastava & Vellend, 2005), as well as between particular biodiversity features and function (e.g. Mumby et al. 2008; Smyth et al. 2013). Smyth et al. (2013), for example, found that in temperate estuaries, oyster reefs and seagrass beds remove significantly more nitrogen per unit area compared to intertidal and subtidal flats and salt marshes. This nitrogen removal is important because it reduces the chances of eutrophication events (Smyth et al 2013). If the high biodiversity oyster reefs and seagrass beds are protected, this function will also be maintained.

If biodiversity does not coincide with ecosystem functioning, targeted protection of important functions and processes will be required to ensure good ecosystem health and the continued provision of goods and services. To identify areas of good ecological quality and ecosystem functioning, some kind of indicator or metric of quality is required (Tillin et al 2008; Young et al. 2008). Benthic infaunal production is the heterotrophic production of organic matter by benthic infaunal macro-invertebrates per

unit time and area (Cusson & Bourget, 2005). This metric has been proposed as an ideal indicator of marine ecosystem quality because it directly reflects the flow of energy and material through the ecosystem (Valentine-Rose et al. 2011), and supports a number of ecosystem goods and services. In particular, this productivity is key for supporting higher trophic levels, including demersal fish species that eat benthic invertebrates (Christensen et al. 1996; Heath, 2005; Wouters & Cabral, 2009; Hiddink et al. 2011).

Chapter 4 found little spatial association between benthic infaunal production and biodiversity features, such as species of conservation importance, in the Irish Sea. This suggests that areas of high ecological quality are unlikely to be captured within MPAs designed to protect biodiversity. To ensure good marine ecosystem health and the continued provision of goods and services then, areas of high ecosystem quality indicated by high levels of benthic infaunal production may require targeted protection in MPAs. Other research has similarly found that areas of high biodiversity do not coincide with areas important for ecosystem goods and services (e.g. Chan et al. 2006; Naidoo et al. 2008; Anderson et al. 2009; Luck et al. 2009). Chan et al. (2006), however, found that despite a lack of spatial association between biodiversity and ecosystem functioning in the Central Coast eco-region of California, protected area networks designed to protect biodiversity did actually protect a significant amount of functioning.

In order to determine whether or not benthic infaunal production does require targeted protection in MPAs, an investigation into the amount of benthic production captured in MPA networks designed to protect biodiversity (hereafter biodiversity MPA networks) is required. Here, then, the amount of benthic infaunal production protected by hypothetical biodiversity MPA networks is investigated and compared to the amount of benthic production protected by networks designed using benthic infaunal production as a 'functional' MPA selection criterion (i.e. a selection criterion related to ecosystem functioning). These hypothetical MPA networks will be created in the systematic conservation planning software MARXAN (version 2.1.1.). In order to design networks, MARXAN requires numerical conservation targets for those features the network is being designed to protect. The biodiversity features included in the analysis are the broad-scale habitats and species and habitats of conservation importance used to

identify marine conservation zones in England, and the same conservation targets used for these features in England are applied here. Benthic infaunal production is broad-scale process that occurs across the Irish Sea, therefore a target of 30% is selected, based on general targets for broad-scale marine habitats proposed in international agreements. The World Summit on Sustainable Development (United Nations 2002) and the World Parks Congress (IUCN 2004), for example, outline targets of 20-30% of marine habitats to be protected within a governments jurisdiction (Lombard et al: 2007).

Given the lack of spatial association between biodiversity features and benthic infaunal production identified in Chapter 4, biodiversity MPA networks are not expected to protect 30% of production in the Irish Sea. If this is the case, benthic infaunal production will need to be explicitly included in MPA design in order to meet the 30% target, and a large total network area is expected to be required to meet conservation targets for both biodiversity and production.

The designation of MPA networks incurs costs and can result in conflict between different marine users, particularly when those networks exclude activities such as fishing (Naidoo et al. 2006). In addition to direct establishment and enforcement costs, the loss of revenue to the fishing industry through the loss of fishing grounds or displacement on to less favourable grounds is a major indirect cost of non-extractive MPAs (van der Geer et al. 2012; Hunt, 2013). These costs are known as opportunity costs (Chan et al. 2011), and can result in high levels of conflict (Di Minin et al. 2013). The greater the opportunity costs to the fishing industry, the higher the expected conflict between conservation and the fishing industry (van der Geer et al. 2012). MPA networks designated to protect benthic infaunal production may overlap with areas of high fishing activity, due to the potential importance of benthic infauna as food for demersal fish and therefore for demersal fisheries (Heath, 2005; Powers et al. 2005). If this is the case, networks to protect benthic infaunal production may incur higher opportunity costs and conflict with fishing compared to MPA networks designated to protect biodiversity. Costs and possibilities for conflict are important to consider in MPA network design because conflict can result in a lack of acceptance and therefore

compliance, which can reduce the effectiveness of the network for achieving conservation goals (van de Geer et al. 2012). If opportunity costs and conflict between activities is very high, management trade-offs between activities may be required to reduce conflict (Di Minin et al. 2013).

In order to designate effective MPA networks, the consideration of costs to other marine users can be incorporated into the conservation planning process (Naidoo et al. 2006; Richardson et al. 2006; De Minin et al. 2013). This can be done in MARXAN using cost surfaces, which allocate an opportunity cost reflecting the relative importance of different areas to other users. During the network design process MARXAN uses these cost surfaces to minimise the overall opportunity costs incurred by the network, by directing MPAs away from areas that are important to other users. The inclusion of a fishing cost surface in MARXAN would therefore reduce conflict with fishing activity, resulting in MPA networks that are more likely to be accepted, supported and therefore effective (van de Geer et al. 2012). If overlap between areas of high benthic production and fishing activity exists, the inclusion of such a cost surface may result in less benthic infaunal production being protected, or a larger total MPA network area to ensure that conservation targets for production are met whilst reducing conflict with fishing.

In summary, MPA networks designed to protect biodiversity and benthic infaunal production will be compared to address the following hypotheses; i) biodiversity MPA networks will not protect 30% of benthic infaunal production in the Irish Sea and, due to a lack of spatial overlap between biodiversity and high benthic productivity. ii) MPA networks designed to protect benthic infaunal production will incur higher opportunity costs than biodiversity MPA networks, due to an association between fishing activity and benthic productivity. If biodiversity MPA networks do not protect 30% of benthic infaunal production, benthic infauna production will need to be explicitly included in MPA design to ensure conservation targets for this important ecosystem process are met. If MPA networks designed to protect benthic infaunal production incur high opportunity costs greater conflict with the fishing industry is expected. This could mean that MPAs to protect benthic infaunal production may not be effective due to problems with compliance, or the need for management trade-offs will be required. The influence

of including a fishing cost surface that reflects fishing opportunity costs on network outputs will be considered to investigate how reducing conflict with the fishing industry may alter the amount of production protected and overall network size.

5.4 MATERIALS AND METHODS

5.4.1 Method overview

Three alternative selection criteria scenarios were implemented in MARXAN; i) biodiversity selection criteria only, ii) biodiversity and benthic infaunal production selection criteria, and iii) a benthic infaunal production selection criterion only. Each scenario was implemented with and without a fishing cost surface reflecting fishing opportunity costs, giving six network outputs in total. The extent to which these networks protect benthic infaunal production was compared, and the spatial similarity between networks, total network opportunity cost and area was also quantified and compared.

5.4.2 MPA network design

Marxan software

Marxan software has been widely used for designing marine protected area networks for both practical management and academic purposes (e.g. Smith et al. 2008; Ban et al. 2009; Edwards et al. 2009; Allnutt et al. 2012; Malcolm et al 2012). It is one of the most well-known conservation planning software available, and is considered appropriate for the purposes of this study. Marxan aims to design protected area networks that meet all specified conservation targets whilst minimizing costs, through a process of simulated annealing (see Ball & Possingham (2000) for technical details of how Marxan operates).

The area for which networks are to be designed is divided into planning units, and five types of input data inform the design process; i) the presence, number or percentage of each conservation feature in each planning unit, i.e. amount of benthic production or

number of species, ii) protection targets for each conservation feature (e.g. 30% of a species occurrence or area of habitat), iii) a specified cost for each individual planning unit, provided by a cost surface (i.e. the cost of incorporating that planning unit in the network, for example the cost of excluding fishing activity from that planning unit would be reflect by a fishing opportunity cost), iv) a user defined penalty for not achieving conservation feature targets and, v) a boundary length modifier value that constraints the total perimeter of the network and therefore influences the degree of patchiness or clumping of planning units in the network solutions.

There are a large number of possible network solutions that meet the conservation targets for the given MPA selection criteria, each made up of a different combination of planning units that achieve the targets set. MARXAN typically generates 100 of these possible networks through the process of simulated annealing. MARXAN then identifies the 'near-optimal' network that achieves as many conservation targets as possible whilst keeping network costs to a minimum. MARXAN does this by calculating an overall 'score' or ranking, from the total network cost (calculated from the cost surface) and penalty values (resulting from missed conservation targets) for each of the 100 networks generated. The lowest scoring network output as identified as the 'near-optimal' network solution for the conservation targets set.

In addition to the 100 different network solutions, including the identified 'optimal' solution, a selection frequency map that highlights the frequency at which each individual planning unit is incorporated into a network, summed over the total 100 runs is generated. This selection frequency map can be interpreted as a measure of planning unit importance for achieving the suite of conservation targets outlined for that particular 100 Marxan runs (Ardron et al. 2010). For example, if a planning unit has a selection frequency of 100, this indicates that the planning unit always has to be included in the network in order to meet a conservation target.

Study area and spatial scale

5 km^2 planning units across the whole Irish Sea area were used because this is the spatial scale at which benthic infaunal production is modelled for the Irish Sea (see Chapter 3). 5 km^2 is also considered an appropriate unit for comparing marine spatial management approaches across the area of study, a total of 57477 km^2, whilst still being relevant to scale of marine protected area network design. In a review of 89 marine protected areas by Halpern (2003), for example, the median size of reserves was 4.0 km^2 (ranging from 0.002-846 km^2). See Figure 5.1 for a map of the study area extent.
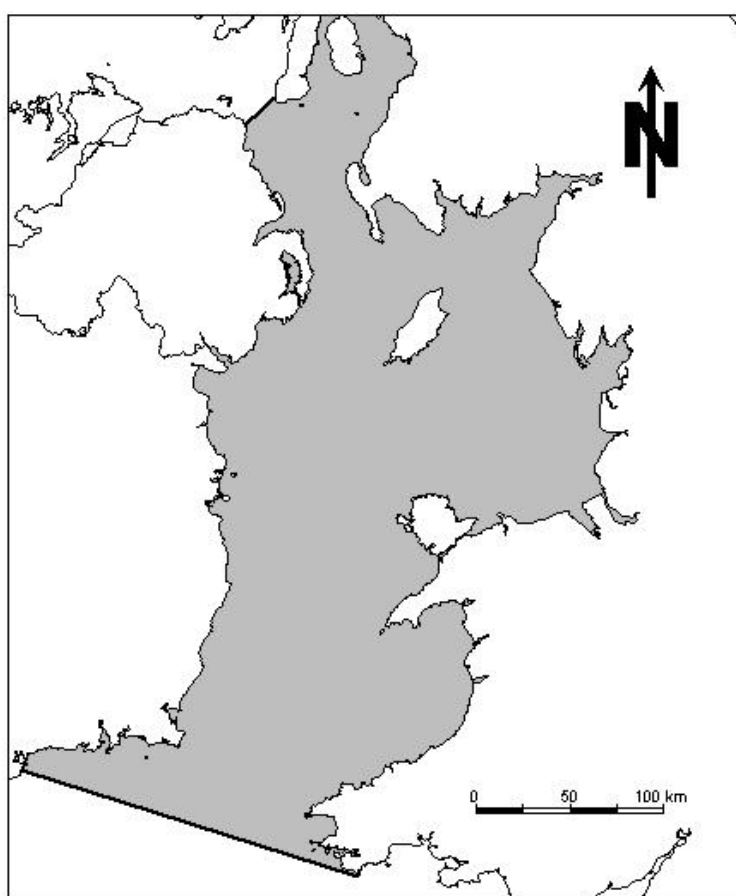
Figure 5.1. The Irish Sea. The extent of the area included in analyses is indicated by the blue area.

Biodiversity features and targets

Three different types of biodiversity features were included in the analyses here; i) broad-scale habitats, and ii) habitats and iii) species of conservation importance in the Irish Sea. The features chosen for network selection here are the same features included in the criteria for selecting Marine Conservation Zones (MCZs) in the Marine Conservation Zones project (Natural England & JNCC, 2010).

The broad-scale habitat data were modelled seabed habitat in the EUNIS Level 2 classification, obtained from the EUSeaMap Consortium. A complete list of broad-scale habitats included in the analyses here can be found in Table 5.1, and a map of the distribution of broad-scale habitats in the Irish Sea can be seen in Appendix 5.7.1 (Figure 5.10). Data layers of the spatial distribution of habitats and species of conservation importance, in the form of ESRI polygon and point shape files respectively, were obtained from the Countryside Council for Wales (CCW). These data layers were outputs from the DEFRA biophysical data layers project, which aimed to aid the designation of Marine Conservation Zones (MCZs) in England and Wales under the Marine and Coastal Access Act. Three species of conservation importance were removed from the analysis here, due to a lack of confidence in the data, as identified by JNCC & Natural England (JNCC & Natural England, 2012). These three species were ocean quahog *Arctica islandica*, horse mussel *Modiolus modiolus* and ross worm *Saballeria spinulosa*. These data were deemed to be of very low confidence, with many records considered incorrect or from unreliable sources (JNCC & Natural England, 2012), and therefore not suitable to indicate the species current distribution. The habitats and species of conservation importance included in this analysis are listed in Table 5.1, and their distribution can be seen in Appendix 5.7.1, Figures 5.11 and 5.12 respectively.

Conservations targets for broad-scale habitats are the same as those set out in the Marine Conservation Zone Project guidelines (Natural England & JNCC, 2010). A range of values was given in the Marine Conservation Zone Project guidelines for each habitat type, and here the middle value was chosen as a quantitative target in Marxan. For example, for low energy circalittoral rock, the recommended proportion of the total

habitat area to protect in the Irish Sea is 16-32%, giving a middle value of 24%. See Table 5.1 for the protection target allocated to each habitat type. These initial protection targets ranges set by the Marine Conservation Zone Project in England aim to ensure the protection of 70-80% of species associated with these broad-scale habitats, and the proportions given are based on a species-area curve approach developed by Rondinini (2011). It should be noted that despite the use of this best available ecological evidence, it is acknowledged that there are many assumptions made in the methods utilised to propose protection target, therefore the suitability of these targets is uncertain (Natural England & JNCC, 2010).

Numerical protection targets for habitats and species of conservation importance were not set by the Irish Sea Conservation Zone project, because not enough information was considered available to make an informed decision (Natural England & JNCC, 2010). Instead, other principles were used to determine that amount of these features to be protected by the Irish Sea MZC project, such as size and shape of MPAs, replication and connectivity between MPAs. Unfortunately it is difficult to include these principles for determining the protection of conservation features in Marxan software. Numerical protection targets are the best way for features of conservation importance to be included in the Marxan as MPA selection criteria, therefore numerical targets have been set for the purpose of the exercise here. These numerical targets were set higher than those for broad-scale habitats, because they are considered to be higher priority. A protection target level of 50% of the total area covered by each habitat and species was deemed appropriate (pers. comms Kirsten Ramsey, 2012). It should be noted that this 50% target is arbitrary, and is set to reflect their perceived higher importance compared to broad-scale habitats.

A total of 36 biodiversity features were included in this analysis. These consisted of 11 broad-scale habitats, 11 habitats of conservation importance, and 14 species of conservation importance. The total area of each broad-scale habitat and habitats of conservation importance was calculated for each planning unit, and the number of records for each species of conservation importance was calculated for each planning unit as input for Marxan.

Table 5.1. The 36 biodiversity conservation features and their associated conservation targets included in the network design process.

Structural conservation feature	Conservation target (%)
Broad-scale habitats	
High energy infralittoral rock	23.5
Moderate energy infralittoral rock	23.5
Low energy infralittoral rock	24
High energy circalittoral rock	19.5
Moderate energy circalittoral rock	22
Low energy circalittoral rock	24
Subtidal coarse sediment	23.5
Subtidal sand	22.5
Subtidal mud	22.5
Subtidal mixed sediments	24
Deep-sea bed	10
Habitats of conservation importance	
Blue mussel beds	50
Estuarine rocky habitats	50
Intertidal boulder communities	50
Maerl beds	50
Mud habitats in deep water	50
Sea-pen & burrowing megafauna communities	50
Sabellaria reefs	50
Seagrass beds	50
Sheltered muddy gravels	50
Subtidal sands & gravels	50
Tide swept channels	50
Species of conservation importance	
Alkmari romijni (Tentacled lagoon-worm)	50
Atrina pectinata (Fan mussel)	50
Cruoria cruoriaeformis (Burgundy maerl paint weed)	50
Dermocorynus montagnei (Little-lobed weed)	50
Edwardsia timida (Timid burrowing anemone)	50
Eunicella verrucosa (Pink-sea fan)	50
Haliclystus auricula (Kaleidoscope jellyfish)	50
Hippocampus guttulatus (Long snouted seahorse)	50
Lithothamnion corallioides (Coral maerl)	50
Lucernariopsis campanulata (Stalked jellyfish)	50
Ostrea edulis (Native oyster)	50
Palinurus elephas (Spiny lobster)	50
Phymatolithon calcareum (Common maerl)	50
Tenellia adspersa (Lagoon sea slug)	50

Benthic infaunal production and targets for protection

Benthic infaunal production was included as a conservation feature in MARXAN using a modelled data layer of benthic infaunal production. Benthic production was modelled at a spatial resolution of 5km^2 for the study area using an empirical, size-based model developed and parameterized for the Irish Sea (see Chapter 3 for details). Productivity under the current fishing regime in the Irish Sea was predicted so that the model output included in MARXAN was comparable to the current distribution of habitats and species used to select biodiversity MPAs. i.e. the species and habitat data used here represents the distribution of biodiversity features under current fishing pressure, therefore the distribution of benthic production under current fishing pressure was also used to select MPAs to protect ecosystem functioning. The model data layer used in MARXAN can be seen in Figure 3.5, Chapter 3.

The conservation target selected for production is 30% of all benthic infaunal production in the Irish Sea. The need for protection of benthic infaunal production is deemed more similar to broad-scale habitats than a feature of conservation importance, because it is broad-scale process that occurs across the Irish Sea, rather than having a small, restricted range. Due to a lack of specific ecological guidance for the protection of this ecosystem function, this 30% protection target is based on targets for marine habitats proposed in international agreements. For example, the World Summit on Sustainable Development (United Nations 2002) and the World Parks Congress (IUCN 2004) outline targets of 20-30% of marine habitats to be protected (Lombard et al: 2007), and the OSPAR Commission recommends that at least 10-20% of broad-scale habitats should be protected within the OSPAR MPA network (OSPAR Commision, 2003). A protection target of 30% for benthic infaunal production also makes it similar to those targets set for broad-scale habitats by the Irish Sea Conservation Zones project, which range from a minimum of 11% and maximum of 42% between habitats, with most broad-scale habitats having a protection target of 25-30%.

Selection criteria scenarios and cost surfaces

Three different selection criteria scenarios for MPA networks in MARXAN were investigated; i) 'Biodiversity only' selection criteria included conservation targets for broad scale habitats and species and habitats of conservation importance only, ii) 'Biodiversity + Production' selection criteria included conservation targets for both habitats, species and benthic infaunal production. Finally, iii) a 'Production only' selection criterion included conservation targets for benthic infaunal production. Each scenarios was run with two alternative cost surfaces, one standard (to act as a control) and one to represent fishing opportunity cost. These cost surfaces allocate a specified cost to each planning unit across the area of interest, and allows MARXAN to identify networks that minimize these costs.

The standard cost surface simply gave every planning unit a standard cost of 1, giving each planning unit an equal weight. This provided a standard against which to compare the effects of the other cost surfaces. The fishing cost surface incorporates socio-economic costs into the network design process by attributing a specific fishing opportunity cost to each 5 km^2 planning unit, based on the amount of bottom fishing that is expected to be lost should that planning unit be incorporated into a MPA network. Here it is assumed that excluding fishing from MPA networks results in a loss of fishing activity. Fishing activity can either be lost or displaced through the introduction of non-extractive MPAs. However, it is difficult to calculate the costs of displacement without modelling fishermen's displacement response, and this is beyond the scope of this study. Bottom fishing intensity (km^{-2} yr^{-1}) was calculated from 2010-2011 vessel monitoring system (VMS) data (obtained from the Marine Management Organisation) for each planning unit, using the same method outlined in Chapter 2. This bottom fishing intensity was used as a direct indication of the relative cost to the fishing industry if that planning unit were included in the network. A higher fishing intensity (km^{-2} yr^{-1}) therefore reflects a greater cost to the fishing industry should that planning unit be included in a network. This higher cost means that this planning unit is less likely to be included in the network. A comparison of the standard cost surface and fishing cost surface can be made in Figure 5.13, Appendix 5.7.2.

MARXAN conservation target penalty parameter

In addition to the conservation targets for each of the selection criteria and the cost surface included in the network design process, another important parameter is the user defined 'penalty' for not achieving conservation targets. The value of this parameter was calibrated for each selection criteria scenario to ensure that the conservation targets set for each selection criteria were met by the network solutions generated, by following the guidance given in the Marxan Good Practices Handbook (Ardron et al. 2010). Ensuring that conservation targets for selection criteria were met meant that any differences in total area or total lost fishing opportunity cost between scenarios were a result of differences in the selection criteria used, rather than because certain conservation targets were not met. See Table 5.4, Appendix 5.7.2 for a summary of the user defined conservation target penalties calibrated.

5.4.3 MPA network comparison

Comparing benefits to benthic production

The near-optimal network identified for each selection criteria scenario and cost surface combination outlined above were selected for comparison. Three selection criteria scenarios and two cost surfaces gave six different near-optimal networks in total. Both the immediate, short-term benefits of the MPA networks to benthic infauna production, and those benefits predicted to be accrued over the long-term were compared.

Immediate, short-term benefit was measured as the percentage of total benthic infaunal production in the Irish Sea protected within the different near-optimal networks. Excluding bottom fishing from these areas is expected to increase productivity over time as the benthic communities are allowed to recover from the negative impact of fishing (Collie et al. 2005; Hiddink et al. 2006b; Hiddink et al. 2006c). However, it should be noted that if bottom fishing is banned from an MPA, it is likely that the effort will be displaced elsewhere (Rijnsdorp et al. 2001; Dinmore et al. 2003). This behaviour can have a negative impact on benthic communities occupying the surrounding areas, and

could reduce or completely remove the benefit accrued from establish the MPA (Hiddink et al. 2006c; Abbott & Haynie, 2012). The long-term benefit of protection on benthic communities in the whole Irish Sea is modelled here to compare the potential long-term impacts of protection on productivity both within and beyond the boundaries of the different networks. This was done by simulating the impact of both excluding and removing, and excluding and displaced fishing from the proposed networks, using the same benthic infaunal production model used to generate the benthic infaunal production data layer.

To simulate the exclusion of bottom fishing from the MPA network, and the reduction of overall fishing effort in the Irish Sea the model was run as normal to equilibrium (1500 time steps of 30 days) with zero fishing activity in the areas designated for conservation. Total production values were then compared between networks. Displacement of the Irish Sea bottom fishing fleet in response to the designation of the MPA networks was simulated by running the production model as normal with zero fishing activity in the areas designated for conservation, but instead of completely removing the fishing effort from the model, fishing effort excluded from the network areas was re-distributed across the non-protected areas of the Irish Sea. Effort was re-distributed proportional to the current effort, so that fishing in those areas heavily fished will increase more than in those areas only lightly fished, following displacement from the protected area network. This same assumption was made by Hiddink et al. (2006c), when predicted impacts of displacement within ICES rectangles. This approach was taken because it was assumed that the current distribution of effort reflected the relative importance or value of grounds to the fishing industry, and that fishing vessels were more likely to move on to these more valuable grounds following displacement (Abbott & Haynie, 2012). In reality, a combination of removal and displacement to both heavily fishing and lightly fished grounds is likely to occur (Hiddink et al. 2006c; Suuronen et al. 2010). It is expected that the actual response would fall somewhere between the two outputs generated in this exercise.

Comparing total network cost

Total network cost was measured in two ways, i) total fishing opportunity cost, calculated by summing the fishing opportunity costs allocated to each planning unit included in the network (these fishing opportunity costs were obtained from the fishing cost surface), and ii) total network area (km^2), calculated by summing the area covered by all the planning units included in the network.

If total fishing opportunity costs are found to be very high for a particular network compared to others, this is assumed to reflect high conflict with the fishing industry, and could highlight the need for trade-offs in MPA network design (Di Minin et al. 2013). If total network area is very large, it is expected that total fishing opportunity costs will be greater, due to greater likelihood of overlap between conservation effort and fishing activity. Conflict with other users, not quantified here, and also general MPA costs, such as those associated with implementation and enforcement are expected to be higher for MPA networks that cover a greater area (van der Geer et al. 2012; Hunt, 2013).

Network similarity

The similarities between the different near-optimal networks designed using different selection criteria scenarios was assessed both visually and by quantifying the percentage of planning units that are shared between MPA networks designed using different selection criteria. A comparison of selection frequencies across the different networks was also made to compare the relative importance of different planning units between networks.

5.5 RESULTS

Six different 'near-optimal' networks were generated in total. Each network is made up of a different spatial configuration of planning units, and each varies in the total number of planning units included. A visual comparison can be made between the three selection criteria scenarios and the alternative cost surfaces in Figure 5.2.

Visual comparison of the networks indicate that biodiversity only and biodiversity + production networks cover a much greater area compared to production only networks. In addition to this, biodiversity only and biodiversity + production networks have some individual MPAs of much larger area compared to production only networks (Figure 5.2).

All biodiversity only networks include large MPAs in the south and west Irish Sea, including the area south of the Llŷn Peninsula in Wales. Biodiversity + production networks similarly have large MPAs in the south and west Irish Sea, and also north of the Isle of Man. Areas of Cardigan Bay are included in all three networks. These two networks tend to share smaller MPAs in the same areas, which reflect the distribution of the species of conservation importance included as conservation targets for those scenarios. For example, the same planning units in Strangford Lough, Northern Ireland and off the North-east tip of the Isle of Man are consistently included in all biodiversity and biodiversity & production networks. These areas cover the distribution of the species of conservation importance, *Lithothaminion coralloides* (coral maerl), and *Ostrea edulis* (Native oyster) and *Alkmaria romijni* (Tentacled lagoon-worm), respectively. Production only networks appear to be more variable, although areas along the North Wales coast across to Liverpool Bay are consistently included in the network outputs, as well as areas north and northeast of the Isle of Man, towards the Solway Firth. Benthic communities in these areas are predicted to be highly productive by the empirical, size-based benthic production model (Figure 3.5, Chapter 3).
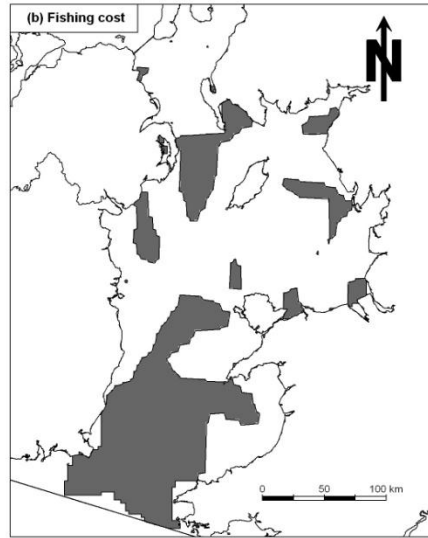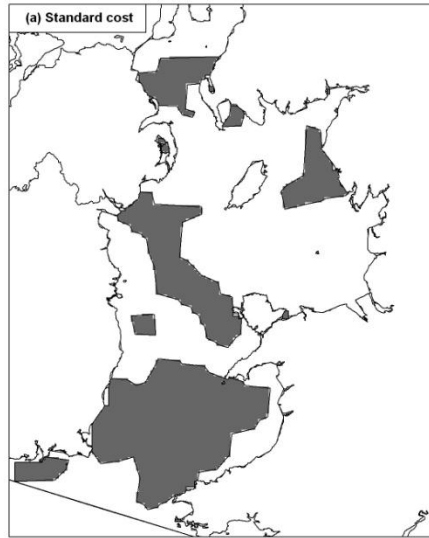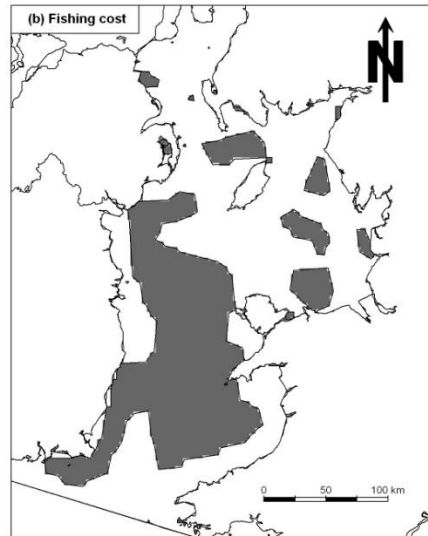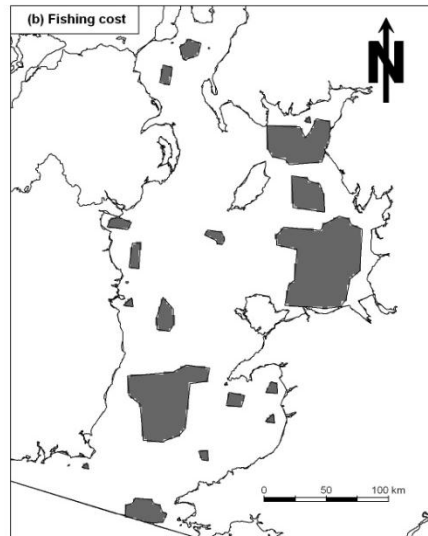
Figure 5.2. The six 'near-optimal' MPA networks identified by MARXAN for the different selection criteria (1 = Biodiversity criteria only, 2 = Biodiversity + Production criteria, 3 = Production criteria only) and cost surfaces (a = Standard cost surface, b = fishing cost surface. These 'near-optimal' MPA networks achieve the most conservation targets whilst keeping network costs to a minimum. See Methods section 5.4.2 for further detail about 'near-optimal' network selection.

5.5.1 MPA network benefits for benthic production

As expected, all biodiversity + production and production networks, where benthic infauna production is included explicitly as a conservation target, meet the 30% protect target for production. None of the biodiversity networks, designed only to meet conservation targets for biodiversity features, meet the 30% protection target for benthic production. However, a reasonably high percentage of benthic production is still protected by these networks, ranging from 26.5 to 28.6% (Table 5.2). In contrast, for production networks, between 5 and 6 out of 36 targets for all biodiversity features were met, depending on the cost surface used (Table 5.2).

With respect to the influence of a fishing cost surface on short-term benefits of the MPA networks on production, slightly less production was protected by the biodiversity and biodiversity + production MPA networks (Table 5.2). The inclusion of a fishing cost surface reduced the amount of production protected by 2.13 % for biodiversity networks and 5.58% for biodiversity + production networks. There was no difference for production networks, both protected 30% of production in the Irish Sea.

The long-term performance of the MPA networks for protecting benthic infaunal production and biomass in the Irish Sea was compared for two different fishing behaviour scenarios, reflecting two different potential responses of the Irish Sea bottom fishing fleet to the implementation of the networks. All networks, regardless of fishing behaviour scenario, resulted in an overall increase in benthic infaunal production in the Irish Sea (Figure 5.3). These increases in production varied between 0.98 and 2.4% of the pre-network implementation baseline value. Observed increases in total productivity under the displaced fishing behaviour scenario are smaller than those under the removed fishing behaviour scenario.

Table 5.2. The number of biodiversity conservation targets met and the total percentage of benthic community production protected by each MPA network.

Selection criteria scenario and cost surface	Number of biodiversity targets met	Percentage of production protected
BIODIVERSITY		
Standard cost	36	28.63
Fishing cost	36	26.50
BIODIVERSITY + PRODUCTION		
Standard cost	36	35.58
Fishing cost	36	30.00
PRODUCTION		
Standard cost	6	30.00
Fishing cost	5	30.00
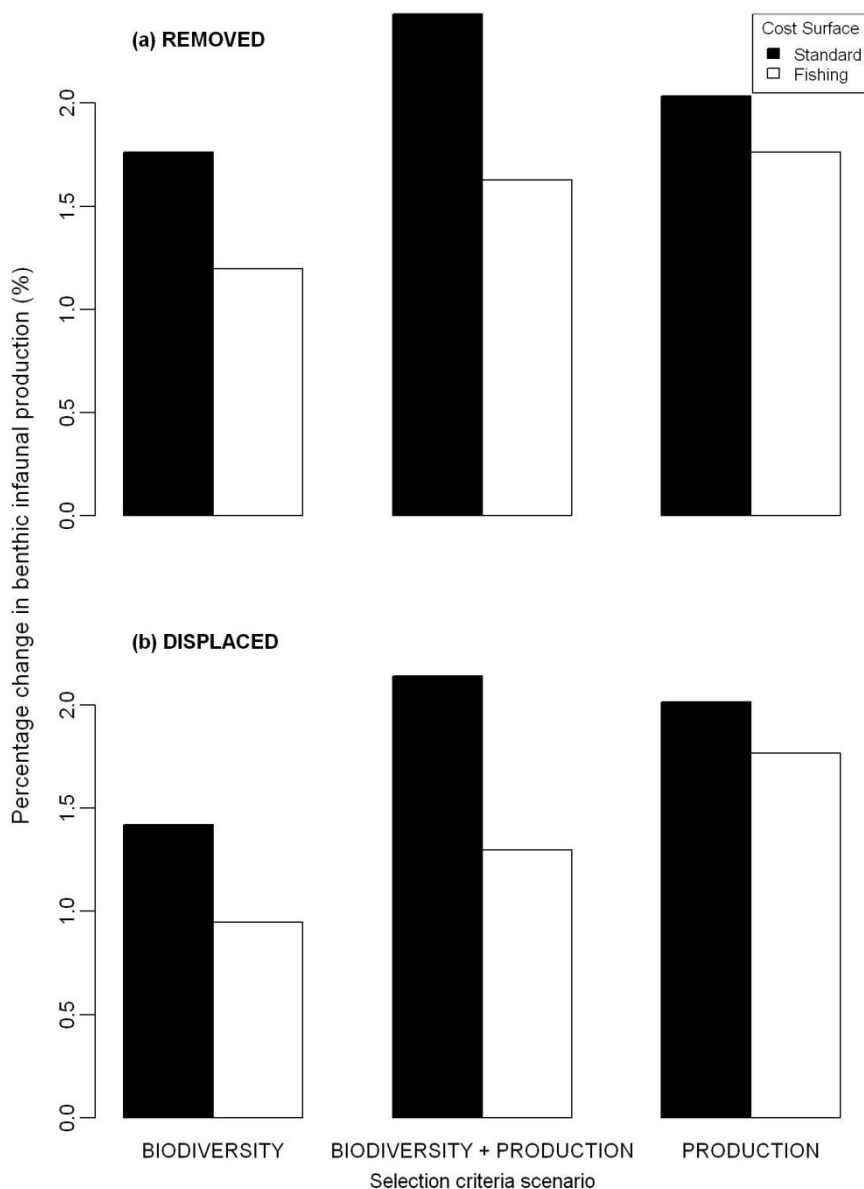
Figure 5.3. The overall percentage change in total benthic infaunal production in the Irish Sea resulting from the implementation of a bottom fishing ban in the 'near-optimal' MPA networks presented in Figure 5.2. Changes in benthic production in response to changes in fishing effort distribution are modelled using the predictive model developed in Chapter 3, and overall change is measured by the predicted percentage change in total benthic infaunal production relative to total production predicted in absence of the MPA networks. The change in production in response to two different fishing behaviour scenarios are compared; a) cessation of fishing in MPAs and not displaced elsewhere (no change is observed outside MPAs), and b) cessation of fishing in MPAs, and effort is displaced to the areas outside of the network, for each of the three MPA selection criteria scenarios (1) Biodiversity, 2) Biodiversity + Production, 3) Production).
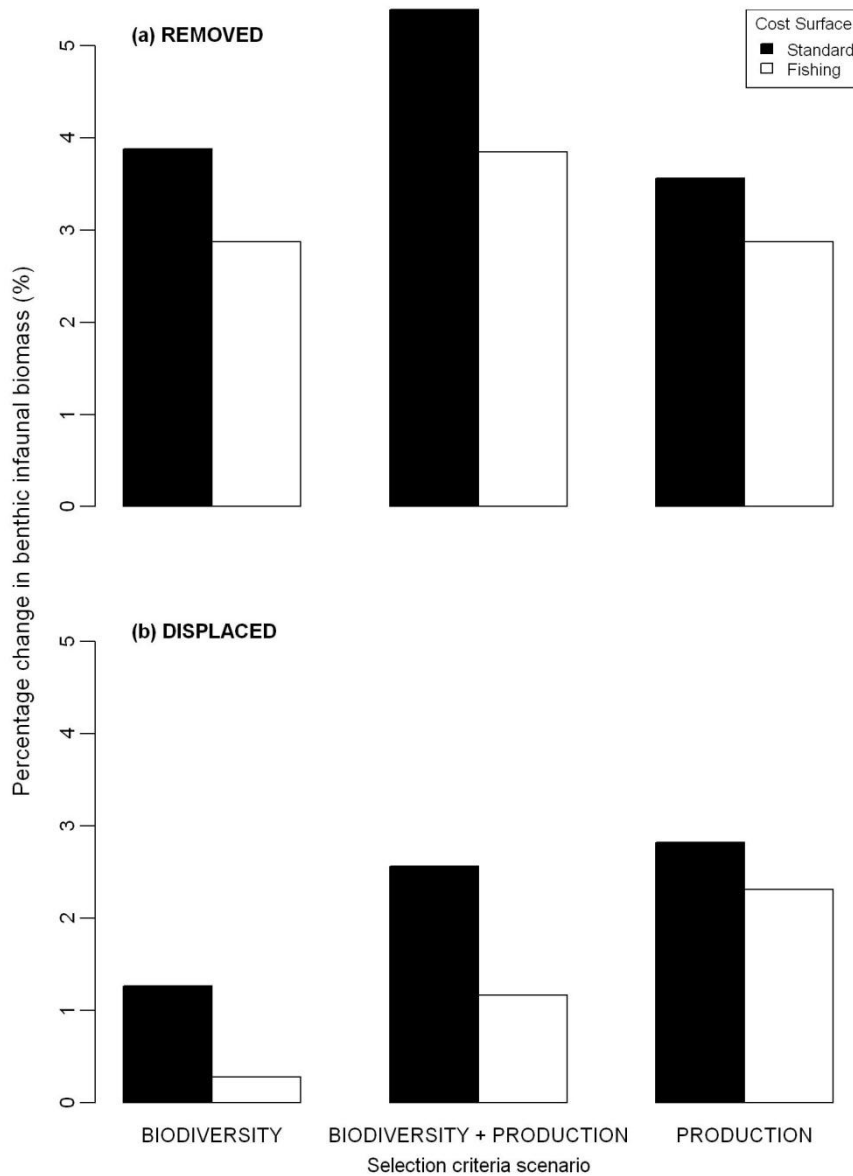
Figure 5.4. The overall percentage change in total benthic infaunal biomass in the Irish Sea resulting from the implementation of a bottom fishing ban in the 'near-optimal' MPA networks presented in Figure 5.2. Changes in benthic biomass in response to changes in fishing effort distribution are modelled using the predictive model developed in Chapter 3, and overall change is measured by the predicted percentage change in total benthic infaunal biomass relative to total biomass predicted in absence of the MPA networks. The change in biomass in response to two different fishing behaviour scenarios are compared; a) cessation of fishing in MPAs and not displaced elsewhere (no change is observed outside MPAs), and b) cessation of fishing in MPAs, and effort is displaced to the areas outside of the network, for each of the three MPA selection criteria scenarios (1) Biodiversity, 2) Biodiversity + Production, 3) Production).

The largest increase in total productivity across the Irish Sea of 2.4% (equivalent to 39011 kJ m^{-2} yr^{-1}) is observed for biodiversity + production networks (standard cost) under the removed fishing scenario. This drops to 2.2% (equivalent to 34350 kJ m^{-2} yr^{-1}) under the displaced fishing scenario. The lowest increase in productivity of 0.98% is observed for biodiversity networks (fishing cost) under the displaced fishing scenario (Figure 5.3). The production benefits accrued by production networks under the removed and displaced fishing scenarios are very similar (Figure 5.3). The inclusion of a fishing cost surface results in results in smaller benefits to production compared to the standard cost surface.

Under the removed fishing scenario, the impact of MPA implementation on benthic infaunal biomass exhibits the same general pattern; however the observed relative increase in total Irish Sea benthic biomass is higher than that observed for production, ranging from 2.9 to 5.2% of the pre-implementation total biomass (Figure 5.4).

Under the displaced fishing scenario, the benefits of MPA implementation are much lower compared to the removed fishing scenario, and the inclusion of the fishing cost surface results in greater benefits to biomass compared the standard cost surface, which is the opposite to the pattern observed for production.

The model outputs from the long-term benefit simulations were mapped so that the relative changes in benthic production and biomass can be visualized (Figure 5.5 and 5.6). In general, these figures indicate that even though the overall impact of protection on benthic infauna production is positive for all but one network under both fishing behaviour scenarios, there are always some areas that appear to be negatively impacted, both inside and outside the protected areas (Figure 5.5). In contrast, a different pattern is observed when investigating the impact of MPA network implementation on benthic infaunal biomass. Only increases in biomass, or positive benefits, are observed inside MPAs, and only reductions in biomass, or negative impacts, are observed outside MPAs. Figure 5.5 illustrates the changes in production, and Figure 5.6 the changes in biomass across the Irish Sea resulting from MPA network implementation. The three different selection criteria scenario networks generated with the standard cost surface are compared.

Negative impacts of MPA establishment on benthic infaunal production result from two different processes, i) displacement of fishing effort on to grounds outside the MPA network can have a negative impact on the benthic infaunal production in those areas due to the removal of biomass, and ii) the cessation of light fishing effort from areas where removing large-bodied benthic organisms results in the competitive release of fast-growing, small-bodied organisms can actually reduce overall productivity in these areas (Hiddink, Rijnsdorp & Piet, 2008). In displaced fishing scenarios, both processes can operate, whereas in the removed fishing scenarios, the slight negative impacts of MPA establishment observed inside MPAs result only from the changes in population dynamics brought about by the later process. The negative impacts on benthic infaunal production are always higher and more widely spread for the displaced fishing behaviour scenario, but are outweighed overall by the increases in production within protected areas.
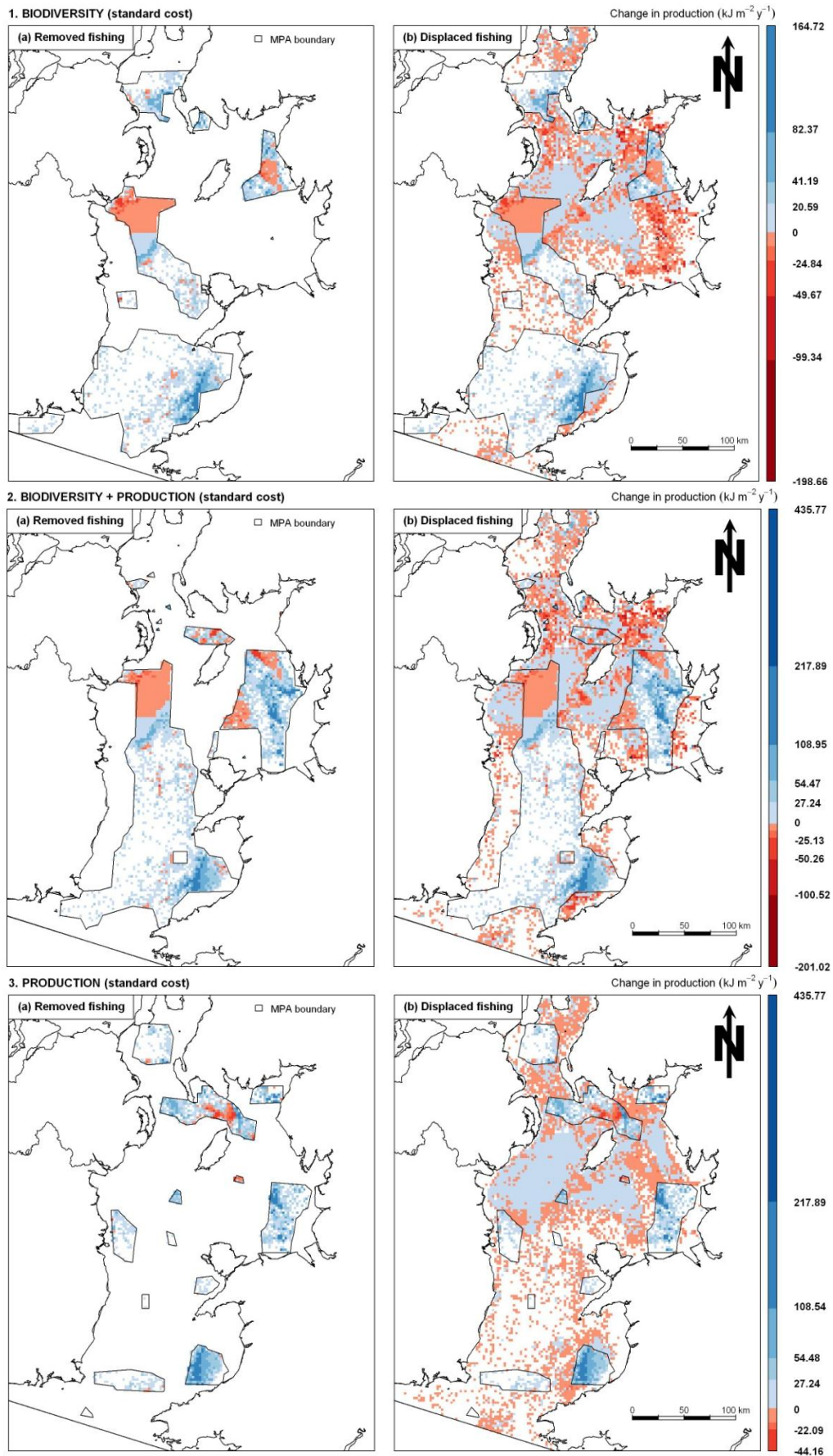
Figure 5.5. The mapped changes in benthic infaunal production resulting from the implementation of a bottom fishing ban in MPA networks (generated using the standard cost surface). Three different MPA selection criteria scenarios (1) Biodiversity, 2) Biodiversity + Production, 3) Production), and two different fishing behaviour scenarios are compared; a) cessation of fishing in MPAs and not displaced elsewhere (no change is observed outside MPAs), and b) cessation of fishing in MPAs, and effort is displaced to the areas outside of the network. See Figure 5.14, Appendix 5.7.3 for similar outputs for MPA networks designed using a fishing cost surface.
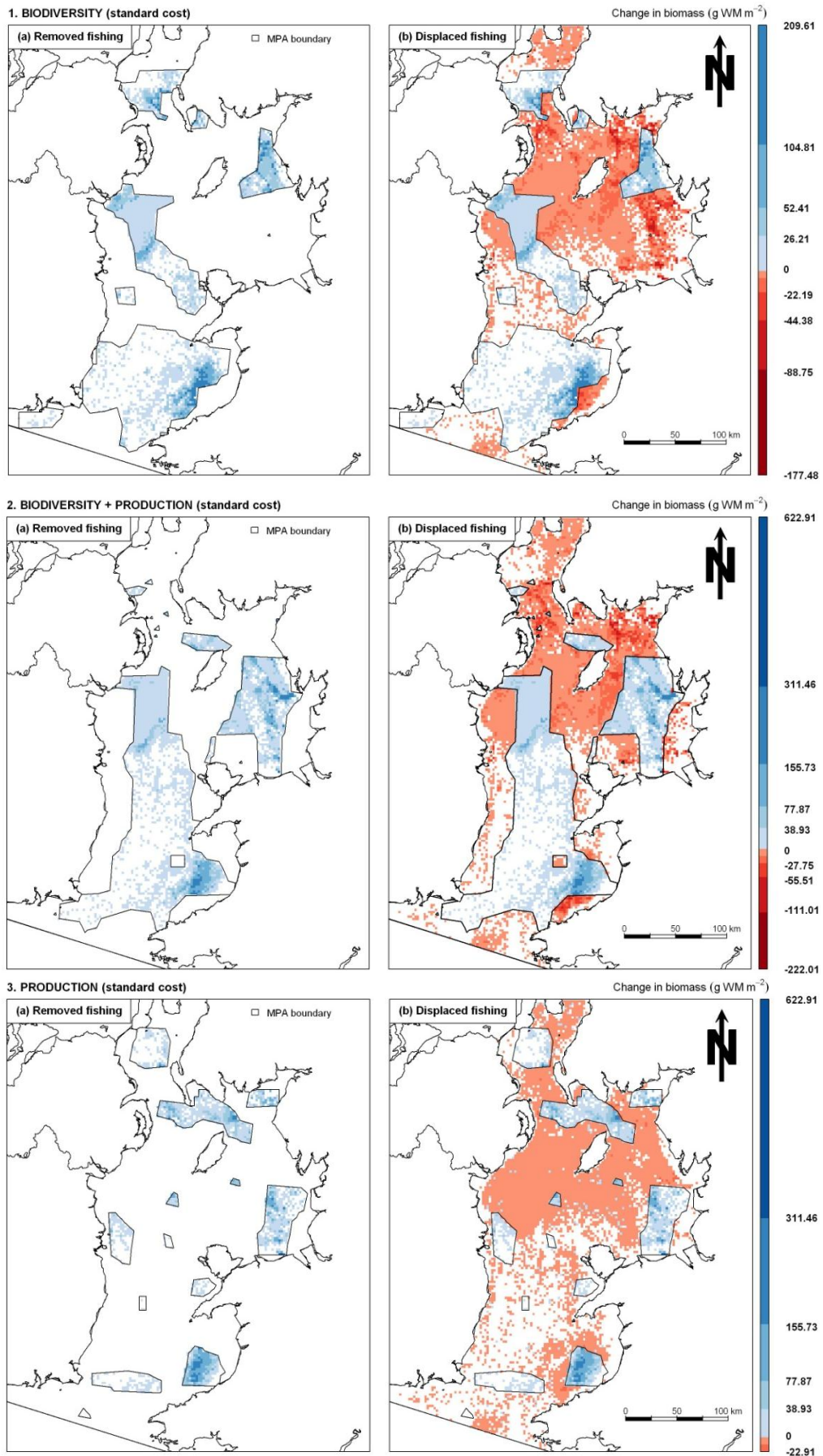
Figure 5.6. The mapped changes in benthic infaunal biomass resulting from the implementation of a bottom fishing ban in MPA networks (generated using the standard cost surface). Three different MPA selection criteria scenarios (1) Biodiversity, 2) Biodiversity + Production, 3) Production), and two different fishing behaviour scenarios are compared; a) cessation of fishing in MPAs and not displaced elsewhere (no change is observed outside MPAs), and b) cessation of fishing in MPAs, and effort is displaced to the areas outside of the network. See Figure 5.15, Appendix 5.7.3 for similar outputs for MPA networks designed using a fishing cost surface.

5.5.2 Total network size and cost

Total network cost is considered in terms of total network area and lost fishing opportunity, both total for the Irish Sea and per unit network area. A comparison of total network area between the different conservation scenarios can be seen in Figure 5.7. It is clear that production networks have a much smaller area than biodiversity and biodiversity + production networks. Unsurprisingly, biodiversity + production networks, with the greatest number of conservation targets, are the largest networks generated by MARXAN. The biodiversity + production MPA network with a standard cost surface is 2369 km² larger in areas than the biodiversity network and 12311 km² larger than the production network.
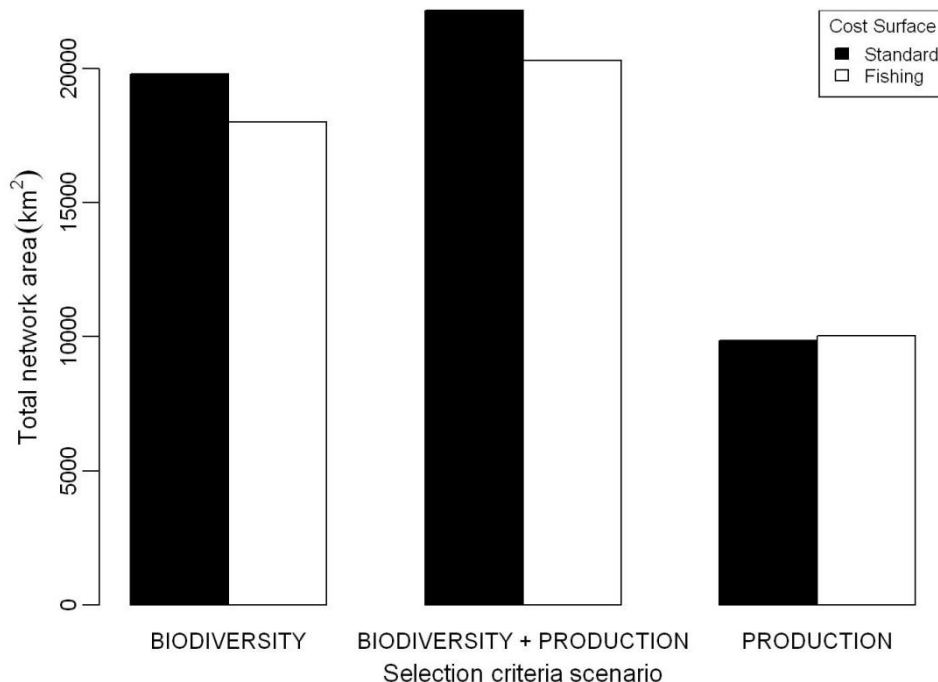
Figure 5.7. The total network area of the different MPA networks. Three different MPA selection criteria scenarios (i) Biodiversity, ii) Biodiversity + Production, iii) Production), and two different cost surfaces are compared; i) standard cost, ii) fishing cost.

Production networks also exhibit the lowest fishing opportunity costs compared to biodiversity and biodiversity + production networks. In contrast to production networks, biodiversity +production networks exhibit the highest opportunity cost (Figure 5.8). Total fishing opportunity cost is estimated to be 198.08, 578.68 and 701.75 km^{-2} yr^{-1} for production, biodiversity and biodiversity + production networks (standard cost surface), respectively (Figure 5.8a). Similarly, lost opportunity cost per unit area is estimated to be 0.020, 0.029 and 0.032 km^{-2} yr^{-1} for production, biodiversity and biodiversity + production networks (standard cost surface), respectively (Figure 5.8b).

With respect to the influence of different cost surfaces on total network costs, those networks generated using the fishing cost scenario exhibited the lowest lost fishing opportunity cost (Figure 5.8). These networks are therefore expected to exhibit the least conflict with fishing activity in the Irish Sea. With respect to total network area, the

inclusion of a fishing cost surface resulted in a smaller MPA network for the biodiversity and biodiversity + production selection criteria scenarios, whereas the inclusion of a fishing cost surface resulted in slightly larger total MPA network area for the production selection criteria scenario. The inclusion of a fishing cost surface therefore appears to concentrate conservation effort focused on biodiversity into a smaller area, yet spreads out conservation effort focused on productivity, in order to minimise costs to fishing.

The fact that the inclusion of fishing opportunity costs results in a larger area for production networks suggests that fishing activity may coincide with some areas that are important for benthic productivity. It is assumed that conservation effort to be shifted away from areas of high productivity over a larger area because these areas exhibit high fishing opportunity costs. The difference in area is very relatively small, however (186.60 km^2), compared to those difference observed for other selection criteria scenarios resulting from the inclusion of a fishing cost surface.
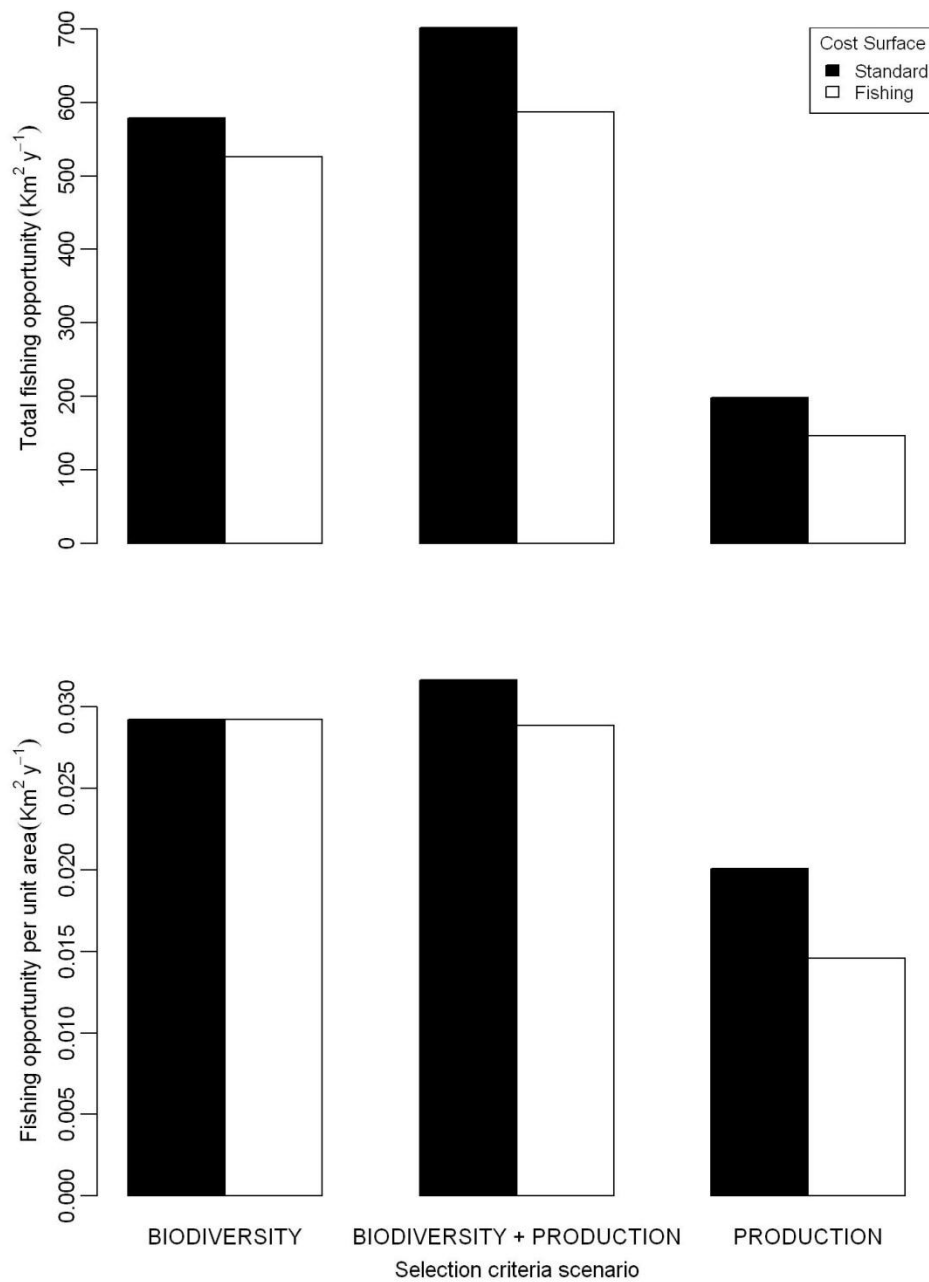
Figure 5.8. The total fishing opportunity costs and fishing opportunity costs per unit area incurred by the different MPA networks. Three different MPA selection criteria scenarios (i) Biodiversity, ii) Biodiversity + Production, iii) Production), and three different cost surfaces are compared; i) standard cost, ii) fishing cost.

5.5.3 Network similarity

A comparison of the number of planning units that are shared between networks designed using different selection criteria gives an indication of network overlap and therefore similarity. Table 5.3 presents the percentage of planning units, from those available over the entire Irish Sea area, that are shared between networks generated using the standard cost surface. The greatest network overlap occurs between biodiversity only and biodiversity + production networks, indicated by the fact that the two networks shared 19.4% of the same planning units available across the Irish Sea. This is in comparison to the overlap between conservation biodiversity and production networks, which share only 4.5% of planning units available in the Irish Sea. Approximately 2% more planning units are shared between biodiversity + production and production networks.

Table 5.3. The percentage of planning units, from those available over the entire Irish Sea area, that are shared between MPA networks generated under different selection criteria scenarios (standard cost only).

Network selection criteria scenario	Biodiversity	Biodiversity + production
Biodiversity	-	19.4
Production	4.5	6.6

Scatter plots and associated r^2 values comparing the relative importance of different planning units between networks generated using the standard cost surface (Figure 5.9) indicate that the correlation between the importance of certain planning units is the greatest for biodiversity and biodiversity +production networks, further supporting the results presented in Table 5.3 which indicate that biodiversity and biodiversity are more similar than biodiversity and production networks and production and biodiversity + production networks. Similar patterns in the similarity of networks was observed for those networks generated using the fishing cost surface (See Figure 5.16, Appendix 5.7.3 for scatter plots of selection frequency for networks generated using the fishing cost surface.)
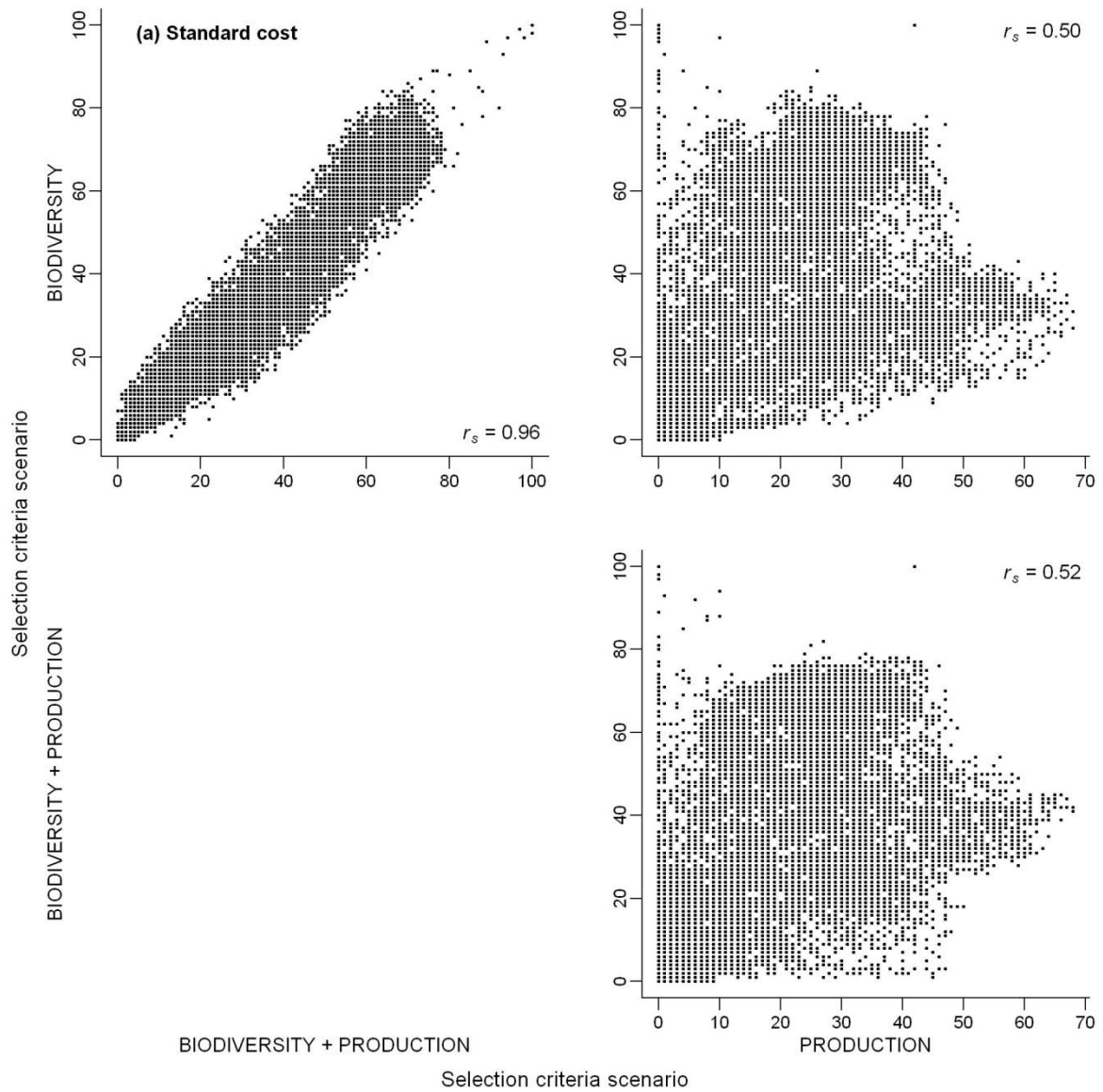
Figure 5.9. Scatter plots visualising the correlation between planning unit selection frequency for networks designed using different selection criteria (generated using the standard cost surface). Planning unit selection frequency reflects the relative importance of different planning units to the network, and a comparison of these frequencies between two networks gives an indication of the similarity between them. Associated r^2 values are also presented.

5.6 DISCUSSION

5.6.1 Overview

A limited number of studies have explicitly included ecosystem functioning in protected area design (e.g. Chan et al. 2006, Chan et al. 2011; Izquierdo & Clark, 2012), and only one has directly compared biodiversity networks with those designed to protect functioning (Chan et al. 2006). Although others studies have attempted to include ecosystem processes and services in network design, surrogates for these processes are often used, and only the short term, immediate effects of their inclusion investigated (e.g. Edwards et al. 2010). This study represents the first direct comparison of biodiversity selection criteria and a functional selection criterion, which directly reflects an ecosystem process, for the purpose of informing MPA design. This is also the first comparison of the long-term benefits of these different MPA selection criteria for the ecosystem process in question, benthic infaunal production.

The results indicate that MPA networks generated using biodiversity selection criteria do not meet the 30% protection target chosen for benthic infaunal production in the Irish Sea. There is little similarity between MPA networks designed to using biodiversity selection criteria and those designed using a functional selection criterion. This is because areas important for biodiversity do not coincide with areas of high benthic productivity. Those networks designed using both biodiversity and benthic infaunal production as MPA selection criteria have the largest total network area and offer the greatest benefits to productivity at the scale of the Irish Sea.

MPA networks designed to protect benthic infaunal production do not incur higher fishing opportunity costs than biodiversity MPA networks. In fact, production networks exhibit the smallest network area and the lowest fishing opportunity costs. As well as exhibiting the largest total network area, those networks designed to protect both biodiversity and benthic production also incur the highest costs to the Irish Sea fishing industry.

The inclusion of a fishing cost surface in network design, reflecting fishing opportunity costs, alters the amount of production protected by MPA networks, overall network size and, unexpectedly, the total fishing opportunity cost incurred. The inclusion of a fishing cost surface generally reduces the benefits of MPA networks for productivity, and can increase or decrease the total network area, depending on the MPA selection criteria used.

5.6.2 Comparison of MPA networks

Short-terms benefits of protection for benthic infaunal production

Although biodiversity networks do not meet the 30% conservation target for benthic infaunal production, they do met a high proportion of this target (between 0.79 and 0.85), equivalent to 26.5 and 28.6% of total benthic production in the Irish Sea. These figures are comparable to those targets set for broad-scale habitats (see Table 1). A similar result was found by Chan et al. (2006), who found that a terrestrial protected area network designed to conserve biodiversity also protected a considerable amount of ecosystem services, despite them not being explicitly included in the network design process. For example, over 60% of the total protection targets for services such as carbon storage, flood control and recreation were met by the biodiversity network. Protection targets for carbon storage, in particular, were fully met by the biodiversity network, because areas of high carbon storage are also very valuable for forest biodiversity conservation (Chan et al. 2006). In order for the biodiversity network to meet the 30% protection target for benthic infaunal production, a comparison of total network area between biodiversity and biodiversity + production networks suggest that approximately an additional area of 12-17% of the total biodiversity network area (2298 – 3329 km^2) would be required to meet the 30% conservation target for benthic production.

In comparison to the high proportion of benthic infaunal production protected by biodiversity networks, those networks designed to only protect benthic infaunal production protect between 5 and 6 out of 36 of the biodiversity features used in this

analysis. Chan et al. (2006) also investigated the performance of ecosystem networks for protecting biodiversity, and found that networks design to meet targets for ecosystem services only met approximately 50% of the protection targets for biodiversity, which is much higher than that met by the functional network generated here. The ecosystem service network generated by Chan et al. (2006), however, was designed to meet protection targets for six different ecosystem services compared to the one ecosystem function used here. Therefore the assumed greater relative area of this network generated by Chan et al. 2006 is expect to capture more biodiversity features than the small production networks generated here.

The fact that production networks protect so few biodiversity features suggest that high value areas for benthic infaunal production do not generally coincide with areas important for biodiversity features. This is supported by the finding that there is little similarity between those networks designated to protect biodiversity and those designated to protect benthic production, and also the findings of Chapter 4, which found no significant spatial association between benthic infaunal production and biodiversity features at the scale of the Irish Sea.

A similar lack of spatial concurrence between biodiversity and ecosystem services has also been found in many terrestrial studies (e.g. Naidoo et al. 2008; Anderson et al. 2009). At a global scale, Naidoo et al. (2008) found that areas important for biodiversity (terrestrial species richness) did not coincide with areas important for ecosystem services. For example, when prioritising ecoregions to conserve services such as carbon sequestration and water provision, only 22-35% of species that would be protected if conservation effort was focused on biodiversity were protected. This 22-35% was no more than would be protected if ecoregions were randomly allocated for conservation (Naidoo et al, 2008). Anderson et al. (2009) similarly found no positive spatial association between biodiversity (UK BAP species) and ecosystem services such as carbon storage and recreation at the UK scale.

A lack of consistent correlation between biodiversity and ecosystem services found in these studies is likely to partly result from the spatial extent of analysis. Both studies

found that at local scale, there were instances where areas important to both did coincide, suggesting that there are opportunities for protecting ecosystem services within networks design to protect biodiversity, but these need to be identified at smaller scale than at which the initial analysis was conducted. Here, the scale of the Irish Sea is considered relatively small scale compared to global and national scale at which Naidoo et al. (2008) and Anderson et al. (2009) conducted their analyses, yet the difference between biodiversity and production networks and the fact that the protection of highly productivity areas in the Irish Sea do not provide substantial benefits for biodiversity indicate that there are few areas where high biodiversity and high productivity coincide. This suggests that the 26.5 – 28.6% of production protected by biodiversity networks seems to be a result of the large network area, and the inclusion of some productive areas, such as off the north coast of Wales and areas of Cardigan Bay, rather than substantial overlap between high value areas for both biodiversity and production.

Long-term benefits of protection for benthic infaunal production

The success of MPA networks in protecting ecosystem function must be also measured by the impact they have beyond their boundaries. A number of studies have investigated the hypothetical displacement and redistribution of fishing activity following MPA implementation, and the subsequent impacts of this change in fishing effort distribution on benthic invertebrate communities (e.g. Dinmore et al. 2003; Hiddink et al. 2006b; Greenstreet et al. 2009). These investigations indicate that the benefits accrued within MPAs can either be greater or outweighed by the negative impacts experienced by benthic communities outside MPAs resulting from redistributed fishing impacts (Hiddink et al. 2006b; Greenstreet et al. 2009). Positive benefits refer to a reduction in fishing mortality (Greenstreet et al. 2009) and subsequent recovery of benthic biomass and productivity inside MPAs (Hermsen, Collie & Valentine, 2003; Hiddink et al. 2006c), and the negative impacts refer to higher fishing mortality of benthic invertebrates outside of the MPAs (Greenstreet et al. 2009), and a subsequent reduction in biomass and productivity in these areas (Dinmore et al. 2003; Hiddink et al. 2006c).

The trade-offs between the benefits and negative effects of MPAs depend on the MPA objectives, size, location and management (Dinmore et al. 2003; Hiddink et al. 2006c). For example, Dinmore et al. 2003 found that repeated temporary closure of an area in the North Sea to protect cod stocks would lead to a mean reduction in benthic productivity over time. Greenstreet et al. (2009) similarly found that MPAs to protect demersal fish species resulted in an overall increase in fishing impact on benthic communities at the scale of the North Sea due to displacement. In contrast, MPAs designed to reduce fishing impacts on benthic invertebrates, by protecting those areas most heavily impacted by fishing, did provide a small benefit to benthic communities at the North Sea scale, despite displacement effects (Greenstreet et al. 2009). Hiddink et al. (2006c) compared a number of different closed area configurations, again in the North Sea, and found that MPAs implemented in important fishing grounds tending to result in an overall negative impact on benthic communities, whereas those MPAs established in areas of less importance to fishing resulted in positive benefits. This is because closing areas important to fishing resulted in greater displacement of fishing effort into previously unfished areas, and the subsequent negative impacts outweighed those increases in biomass and production observed within the MPA as the benthic communities recovered (Hiddink et al. 2006c).

Here, modelled estimates of production and biomass under the different MPA network scenarios demonstrate both the positive and negative local effects of MPA implementation described above. Biomass and, in most cases, production increased within MPAs, whilst areas outside experienced a reduction in production and biomass due to the displacement of fishing activity (Hiddink et al. 2006c). Another effect of MPA implementation observed here is the fishing-induced competitive release of small, fast growing benthic species, which can occur in fished areas (Hiddink et al. 2008). This effect appears to lead to small negative impacts on production inside MPAs, where fishing is removed, or small positive impacts on production in area outside MPAs that experience displaced fishing. These effects are only observed for the productivity of benthic communities, not total community biomass. Only reductions in biomass are observed as a result of bottom fishing. These effects of displacement on production have not been previously documented in response to MPA implementation, but similar

positive responses of benthic productivity to fishing have been observed by other studies (e.g Jennings et al. 2001; Hiddink et al. 2008).

Despite the negative effects of hypothetical MPA network implementation described above, it is clear that the benefits of protection outweigh these negative effects, indicated by the overall positive impact of implementing MPA networks on benthic infaunal communities, measured at the Irish Sea scale. This overall positive impact is observed under both the removed fishing and displaced fishing scenarios, and for all network selection criteria scenarios. The overall positive benefits observed are greater for biomass than production, as also observed by Hiddink et al. (2006c).

Unsurprisingly, the removed fishing scenario results in the greatest benefit to benthic invertebrate communities. This was also found by Greenstreet et al. (2009). Benthic communities are expected to either benefit less from protection in MPAs under the displaced scenario, or in some cases suffer an overall negative effect, based on the impacts of displacement identified in previous studies (Dinmore et al. 2003; Hiddink et al. 2006c; Greenstreet et al. 2009). Here the benefits of protection still outweighed the negative impacts resulting from this displacement. In fact, despite the fact that biodiversity + production networks displaced the most fishing activity (indicated by highest fishing opportunity costs), these large networks deliver greater benefits to benthic productivity compared to those designed to protection only either biodiversity or production. This is interesting when compared to the results of Hiddink et al (2006c) and Greenstreet et al. (2009), which found that closing areas important for fishing, and therefore resulting in highest displacement, resulted in overall negative impact on benthic communities.

This apparent contradiction to previous findings may be a result of the fact that the MPA implemented here had different objectives to those previously investigated. Greenstreet et al (2009) and Hiddink et al. (2006c) implemented MPAs design to protect fish stocks, targeting areas of high fishing effort and mortality. Here biodiversity feature and areas of high productivity are targeted; therefore the displacement caused may not be as great as that observed in the North Sea. This would suggest that high fishing effort does not

occur in areas important for biodiversity and productivity in the Irish Sea. In addition to this, at a more general level, the impacts of fishing displacement may not be as severe in the Irish Sea compared to the North Sea because fishing effort and impacts are generally much lower the Irish Sea than in the North Sea. The findings of Chapter 3 support this notation, as they suggest that fishing activity in the Irish Sea only reduces total productivity by 5.1%, whereas in the southern North Sea fishing reduced production by 21% % (Hiddink et al 2006a). This difference is assumed to reflect a much greater fishing intensity experience by the benthic communities in the North Sea.

Biodiversity networks do not offer the same level of long-term benefit to productivity compared to production only networks. This is because they do not specifically target areas important for productivity, and their large areas results in high level of fishing displacement, resulting in greater negative impacts. Production networks are much smaller, and concentrated in areas of high productivity, therefore they protect more production whilst also minimising the displacement of fishing, offering greater overall benefit than biodiversity networks. This result agrees with those findings of Hiddink et al. (2006c) that indicate greater benefits are expected when less fishing effort is displaced.

When considering the influence of different cost surfaces on the amount of production and biomass protected, those networks generated using the fishing cost scenario exhibited the lowest fishing opportunity costs, therefore these networks are expected to exhibit the least conflict with fishing activity in the Irish Sea. It would therefore be expected that the negative impacts of displacement would be lower when a fishing cost surface were included, because less fishing effort would be displaced, and thus the overall benefit to production and biomass would be greater. Here, the inclusion of a fishing cost surface did result in a greater benefit to benthic biomass, for all network scenarios under the displaced fishing scenario. However, for biomass under the removed fishing scenario, and for all scenarios regarding the benefits of protection to production, the inclusion of a fishing cost surface resulted in a lower overall benefit to benthic infaunal production as a result of MPA implementation, which contradicts the Hiddink et al. (2006c) that greater benefits are expected when less fishing is displaced.

This reduced benefit for production in particular suggests that the fishing cost surface may be directing conservation effort away from areas of both high fishing effort and high productivity and biomass, suggesting that the two may coincide in space. Overall, results suggest that reducing displacement by incorporating socio-economic costs has greater benefit for benthic biomass than production. This is likely to reflect the fact that benthic biomass tends to be more strongly effected by fishing than production, as demonstrated by the results of Chapter 3.

Total network cost

Biodiversity + production networks exhibit the highest total network area, in order to meet conservation targets for both, and as a result exhibit the highest fishing opportunity costs. Production only networks, on the other hand, exhibit the lowest total network area and fishing opportunity costs. As expected, the cost to fishing is lower when fishing activity is taken into account in the network design process by including a fishing cost surface, as has been demonstrated by other studies (e.g. Richardson et al. 2006; Nadioo et al. 2006; Ban & Klein, 2009). With respect to a comparison of fishing opportunity per unit area the fact that networks to protect benthic infaunal production do not have the highest fishing opportunity cost per unit area would suggest that bottom fishing does not necessary concentrate more in area of high benthic productivity, compared to areas important for biodiversity features.

With respect to total network area, the inclusion of a fishing cost surface resulted in a smaller MPA network for the biodiversity and biodiversity + production selection criteria scenarios, whereas the inclusion of a fishing cost surface resulted in slightly larger total MPA network area for the production selection criteria scenario. The inclusion of a fishing cost surface therefore appears to concentrate conservation effort focused on biodiversity into a smaller area, yet spreads out conservation effort focused on productivity, in order to minimise costs to fishing.

The fact that the inclusion of fishing opportunity costs results in a larger area for production networks suggests that fishing activity does coincide with some areas that

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are important for benthic productivity. It is assumed that conservation effort is being shifted away from areas of high productivity over a larger area because these areas exhibit high fishing opportunity costs. The difference in area is very relatively small, however (186.60 km²), compared to those difference observed for other selection criteria scenarios resulting from the inclusion of a fishing cost surface.

5.6.3 Implications for management

The results here indicate that the protection of biodiversity in the Irish Sea will not automatically mean that 30% protection targets for the important ecosystem function benthic infaunal production are met. This functional, selection criterion needs to be explicitly included in the MPA network process in order to meet this 30% target, rather than relying on surrogates such as habitats (as in Edwards et al. 2010). Equally, MPA networks designed to protect benthic infaunal production will not meet conservation targets for biodiversity features. There is a risk then that a focus on ecosystem service provision in conservation may dilute the benefits for biodiversity (Chan et al. 2006). In light of this, both biodiversity features and ecosystem functioning must be explicitly considered if conservation effort aims to meet targets for both.

The success of biodiversity networks to meet conservation targets for ecosystem function depends on the conservation targets set. If the conservation target for benthic infaunal production was set to 25% here, for example, biodiversity networks would have been successful in protecting this ecosystem function. It should be noted that the establishment of numerical conservation targets can be fairly arbitrary, rather than based on solid ecological reasoning (Pfab et al. 2011). This should be kept in mind when considering the 'performance' of biodiversity only networks to protect benthic production.

The lack of spatial association between biodiversity and areas of high benthic productivity at the Irish Sea scale means that a larger total MPA network area is required to meet conservation targets for both. These networks will have high MPA implementation and management costs (Hunt, 2013), and implications for other marine

users (Richardson et al. 2006; van der Geer et al. 2012). For example, networks to protect both biodiversity and benthic infaunal production exhibited higher lost fishing opportunity costs, and would therefore expected to have a larger impact on the Irish Sea fishing fleet if implemented compared to the other networks.

The reduction of production protected, and slight increase in production MPA network size, when a fishing cost surface is included in MARXAN suggests that there may be conflict between the protection of benthic infaunal production and bottom fishing, and management trade-offs between conservation and fishing objectives may be required (van der Geer et al. 2012; Di Minin et al. 2013). These effects are very small, however, and contradict the findings of Chapter 2, which found a negative relationship between benthic infaunal production and fishing intensity. Further investigation into possible management trade offs with respect to benthic production and bottom fishing is recommended before any conclusions can be drawn.

5.6.4 Conclusions

In summary, the findings here indicate that (i) the protection of biodiversity (ecosystem structure) will not automatically ensure that 30% of benthic infaunal production in the Irish Sea is protected, and the protection of benthic infaunal production does not deliver great benefits to biodiversity conservation. Therefore, (ii) to meet conservation targets for both biodiversity features and ecosystem function in the Irish Sea conservation planning will need to specifically consider and target both. (iii) The consideration of lost fishing opportunity does reduce conflict between MPAs and bottom fishing, as observed in other studies, but also appears to reduce MPA benefits to benthic productivity.

5.7 APPENDICES

5.7.1 Biodiversity features

Broadscale habitats
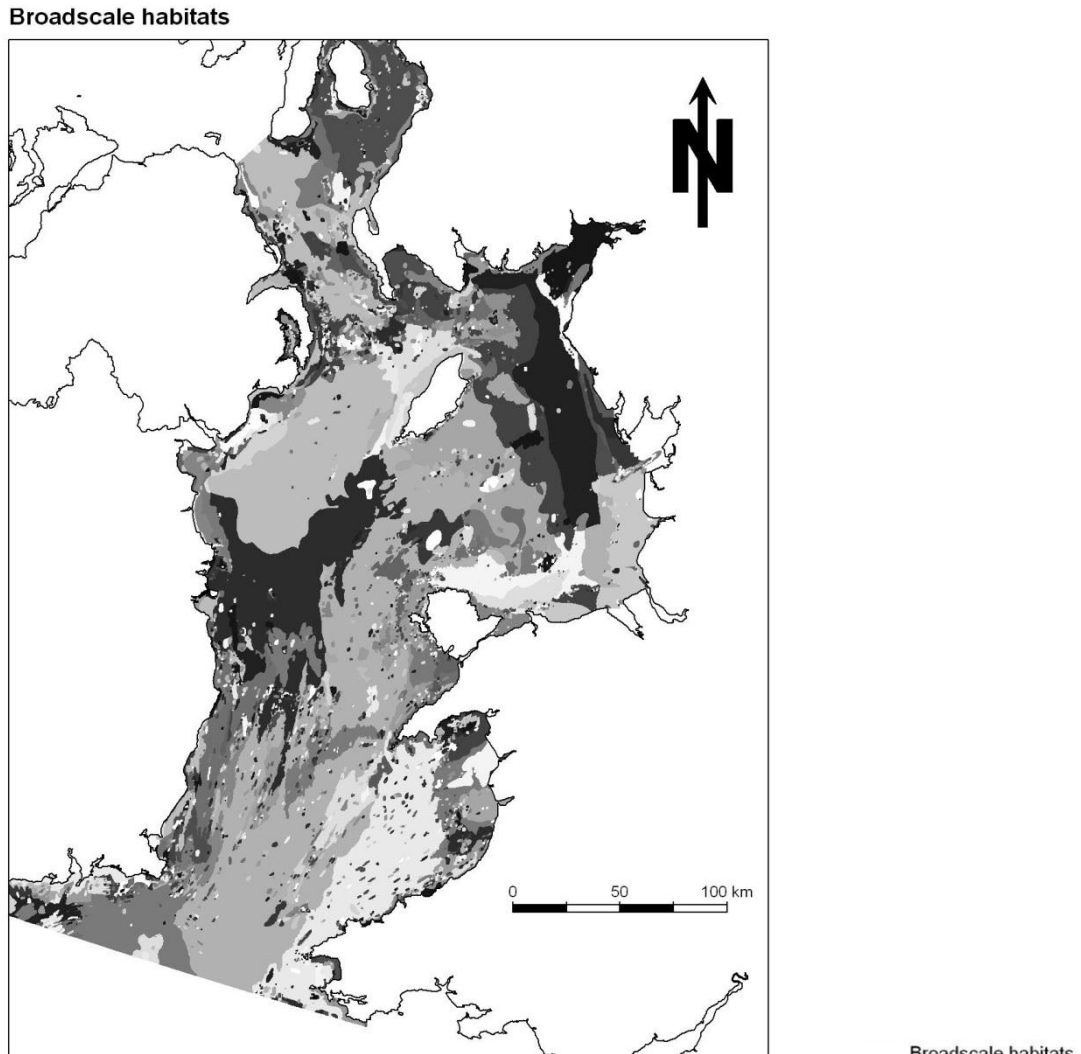
Figure 5.10. Broadscale scale habitats

Broadscale habitats

Deep-sea coarse sediment
High energy infralittoral rock
Moderate energy infralittoral rock
Low energy infralittoral rock
High energy circalittoral rock
Moderate energy circalittoral rock
Faunal communities on deep moderate energy circalittoral rock
Low energy circalittoral rock
Faunal communities on deep low energy circalittoral rock
Infralittoral coarse sediment
Circalittoral coarse sediment
Deep circalittoral coarse sediment
Infralittoral fine sand or infralittoral muddy sand
Circalittoral fine sand or circalittoral muddy sand
Deep circalittoral sand
Infralittoral sandy mud or infralittoral fine mud
Circalittoral sandy mud or circalittoral fine mud
Deep circalittoral mud
Infralittoral mixed sediments
Circalittoral mixed sediments
Deep circalittoral mixed sediments
Deep-sea mixed substrata
Deep-sea sand or deep-sea muddy sand
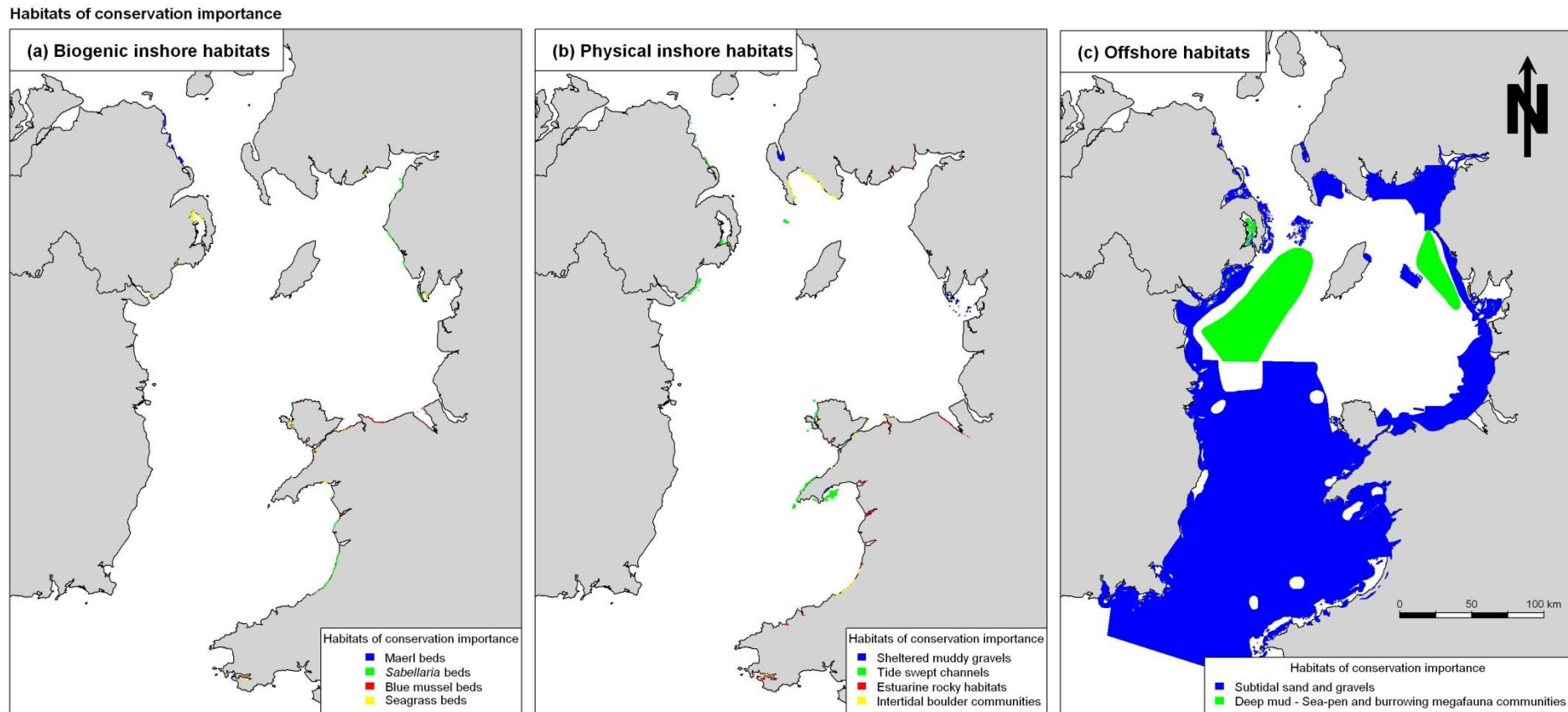
Figure 5.11. The spatial distribution of habitats of conservation importance used as biodiversity MPA selection criteria. For presentation the habitats of conservation importance are split between three maps. (a) biogenic inshore habitats (e.g. maerl beds, *Sabellaria* beds), (b) physical inshore habitats (e.g. sheltered muddy gravels, tide swept channels), and (c) offshore habitats (e.g. subtidal sand and gravels).
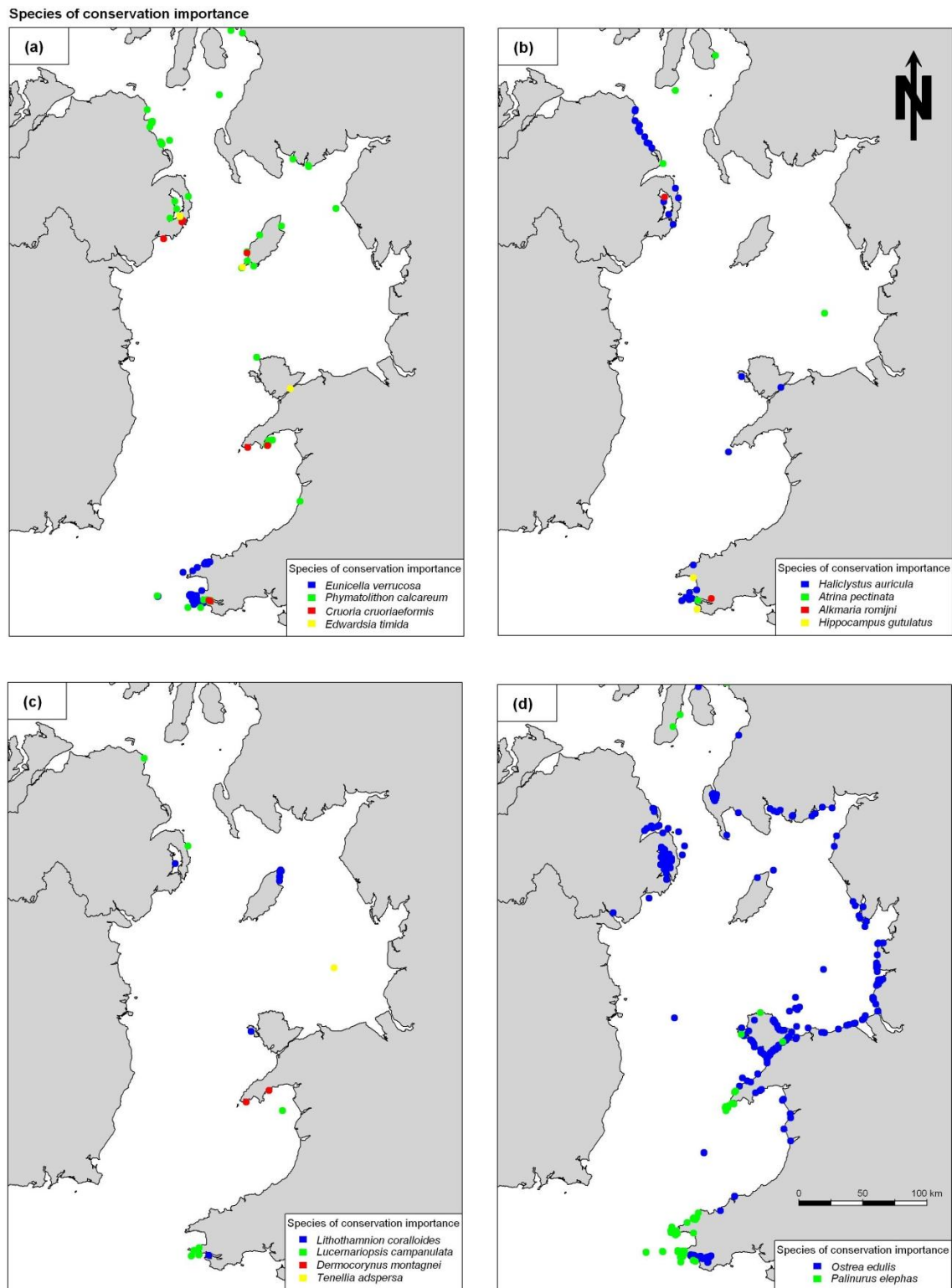
Figure 5.12. The spatial distribution of species of conservation importance used as biodiversity MPA selection criteria. To aid presentation the species of conservation importance are split between four maps (a-d).

5.7.2 MARXAN parameters
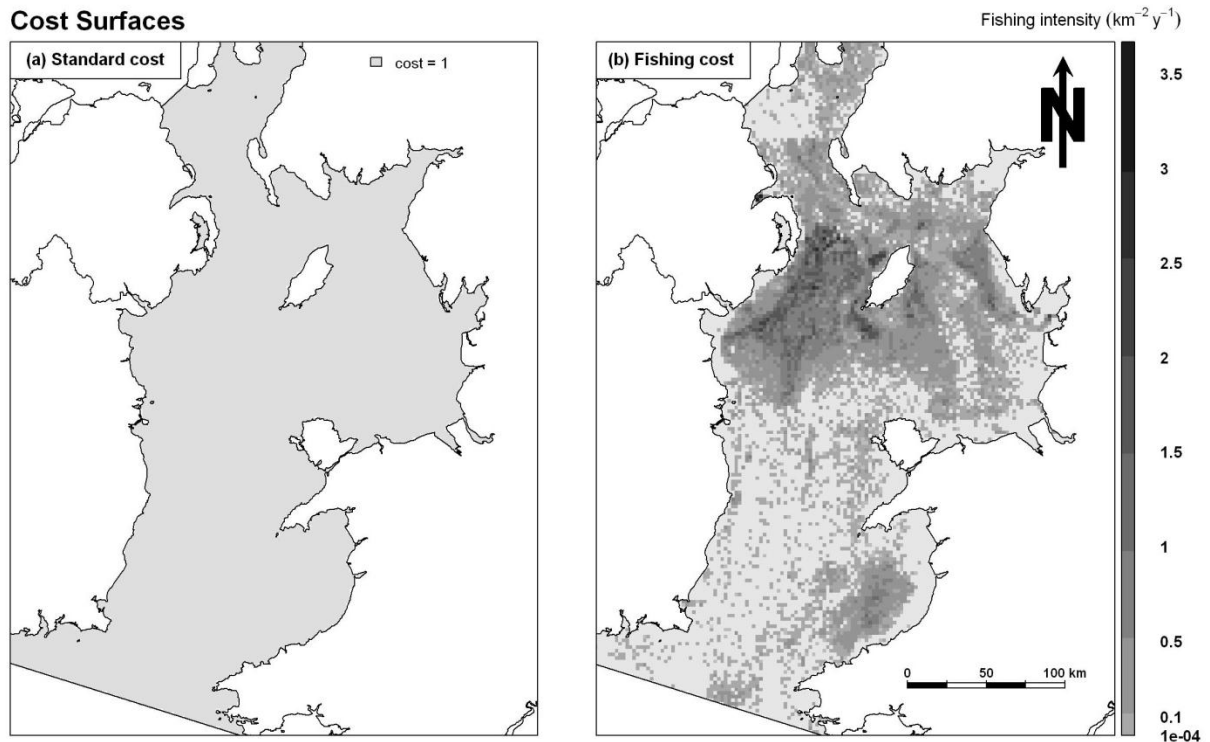
Figure 5.13. Standard cost and fishing cost surfaces for MARXAN, calculated at a spatial scale of 5 km².

Table 5.4. Table of user defined species penalty factors calibrated for the different network scenarios in MARXAN.

MARXAN parameter	Selection criteria scenario					
	BIODIVERSITY		BIODIVERSITY + PRODUCTION		PRODUCTION	
Cost surface	Standard	Fishing	Standard	Fishing	Standard	Fishing
Species penalty factor	6	12	12	14	2	2

5.7.3 Additional results
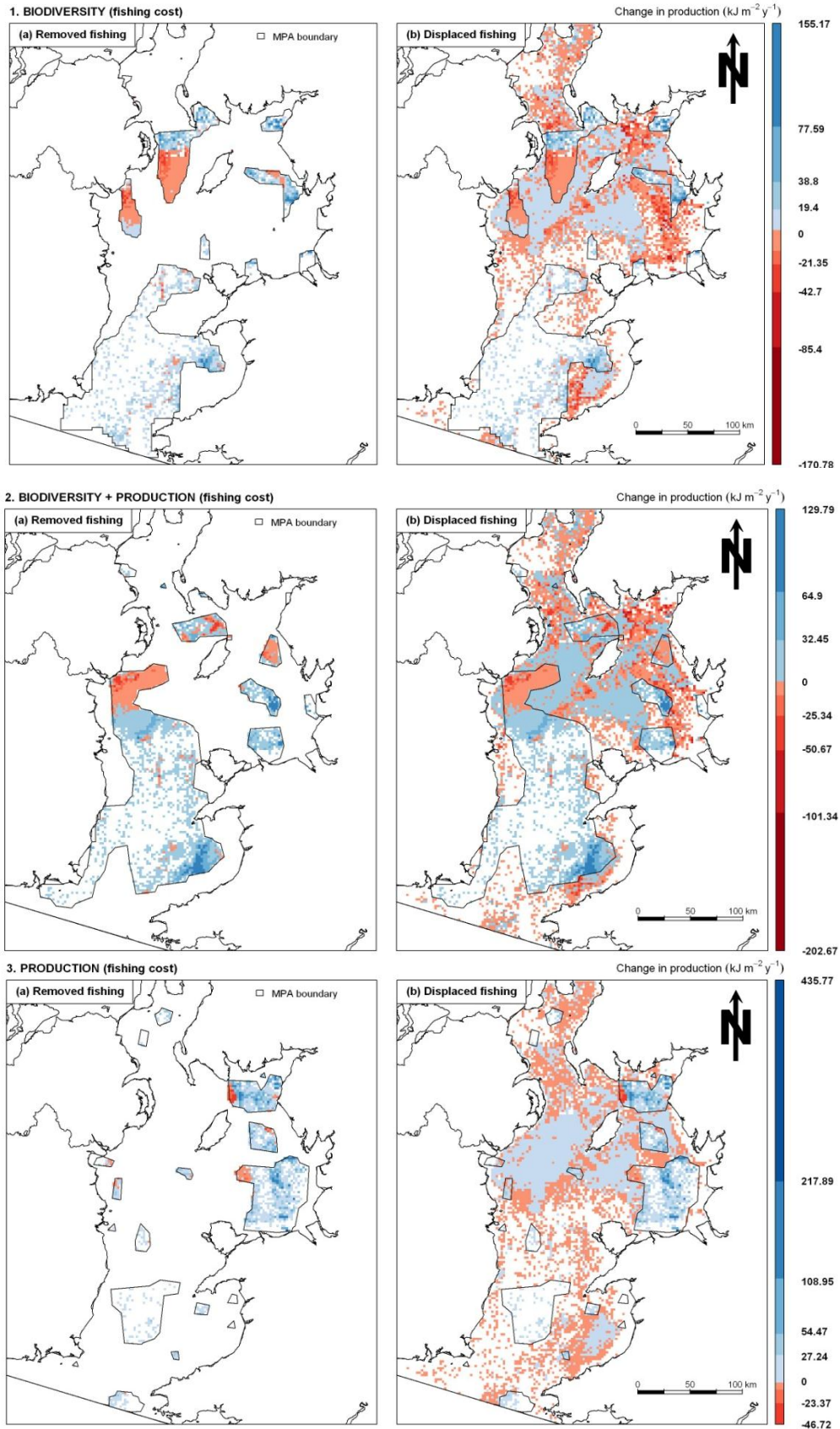
Figure 5.14. The mapped changes in benthic infaunal production resulting from the implementation of a bottom fishing ban in MPA networks (generated using the fishing cost surface). Three different MPA selection criteria scenarios (1) Biodiversity, 2) Biodiversity + Production, 3) Production), and two different fishing behaviour scenarios are compared; a) cessation of fishing in MPAs and not displaced elsewhere (no change is observed outside MPAs), and b) cessation of fishing in MPAs, and effort is displaced to the areas outside of the network.
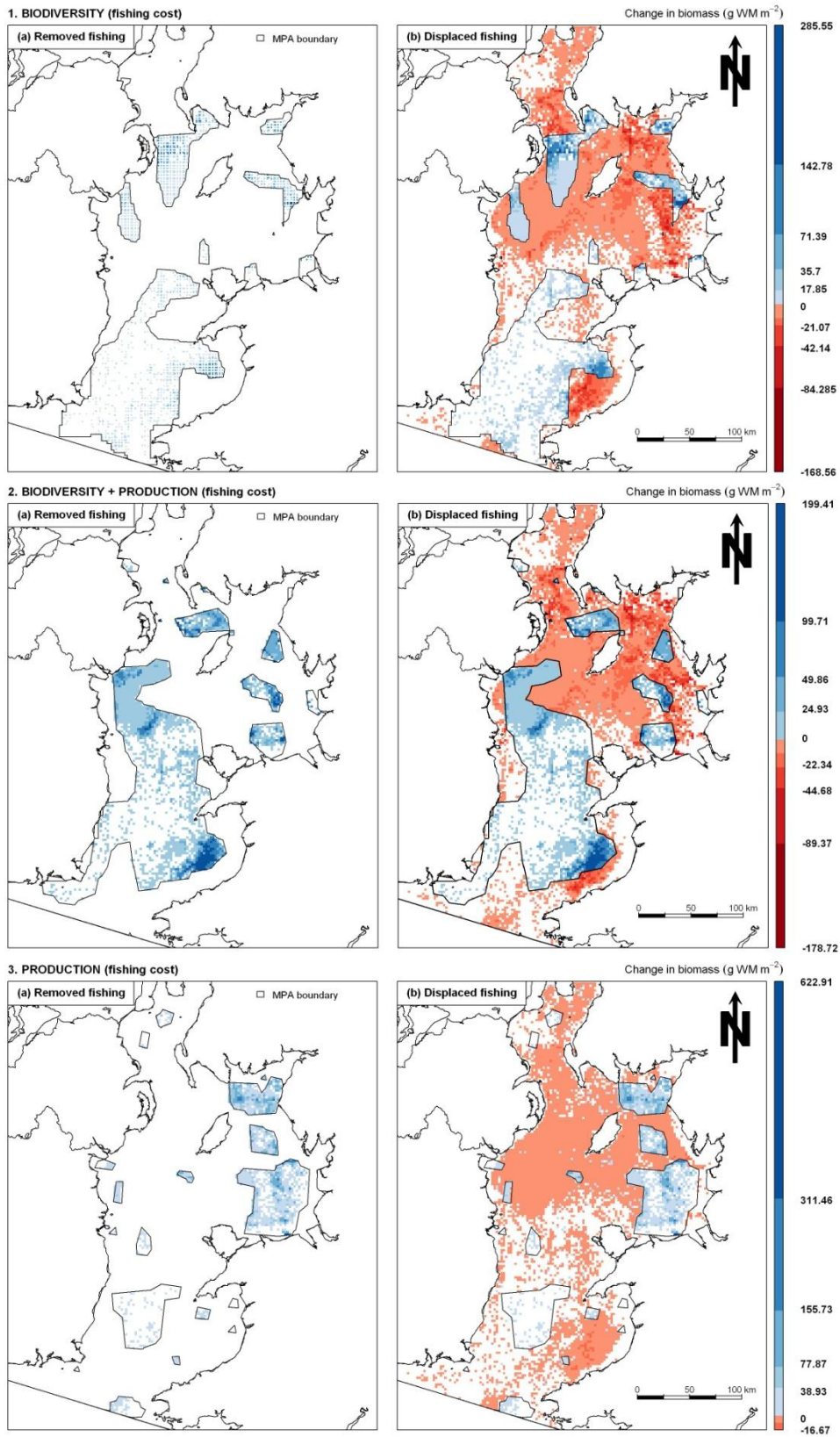
Figure 5.15. The mapped changes in benthic infaunal biomass resulting from the implementation of a bottom fishing ban in MPA networks (generated using the fishing cost surface). Three different MPA selection criteria scenarios (1) Biodiversity, 2) Biodiversity + Production, 3) Production), and two different fishing behaviour scenarios are compared; a) cessation of fishing in MPAs and not displaced elsewhere (no change is observed outside MPAs), and b) cessation of fishing in MPAs, and effort is displaced to the areas outside of the network.
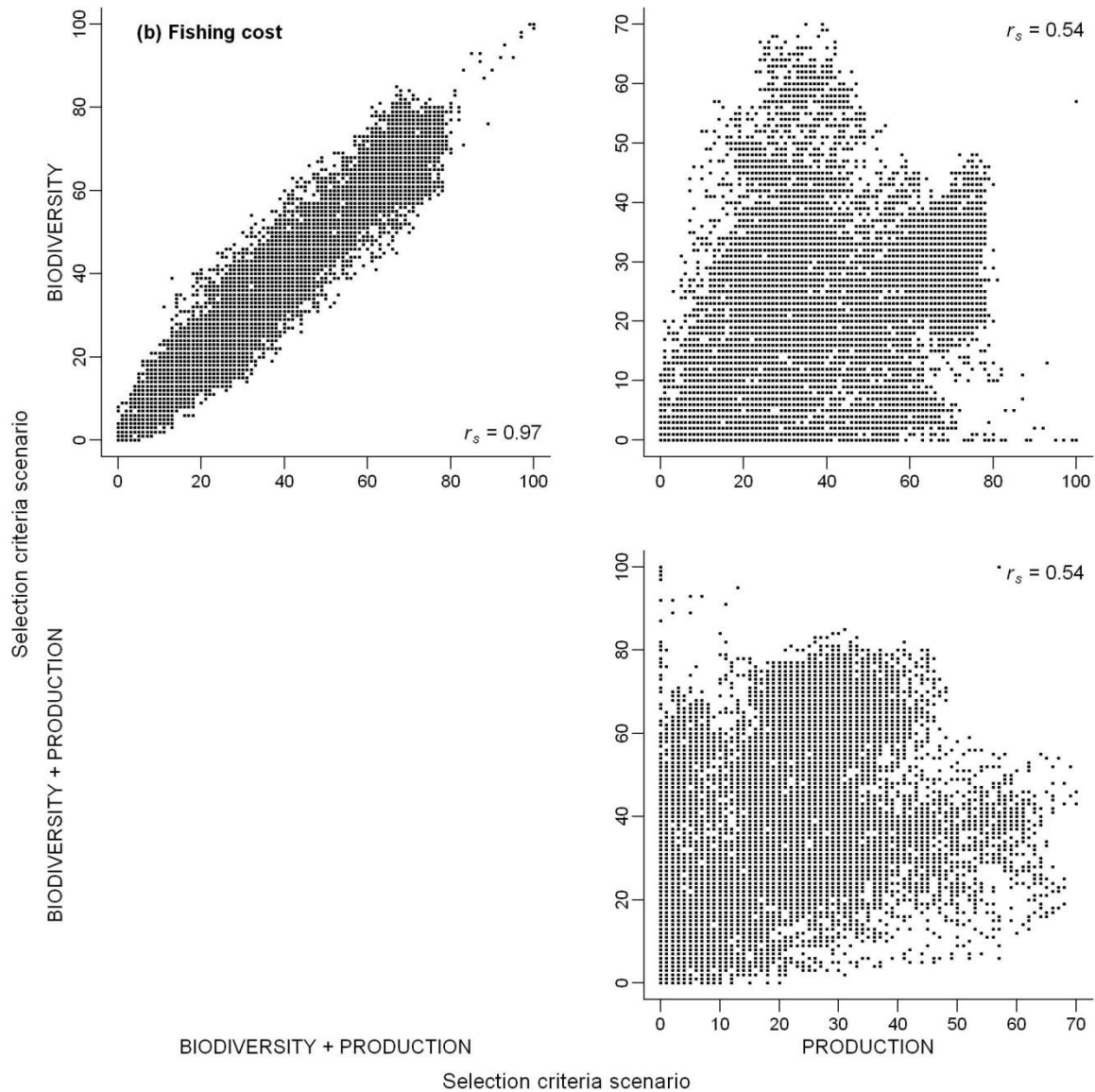
Figure 5.16. Scatter plots visualising the correlation between planning unit selection frequency for networks designed using different selection criteria (generated using the fishing cost surface). Planning unit selection frequency reflects the relative importance of different planning units to the network, and a comparison of these frequencies between two networks gives an indication of the similarity between them. Associated r^2 values are also presented.

CHAPTER 6 – General discussion

6.1 SUMMARY

This thesis has attempted to determine whether or not modelled benthic infaunal production could be a practical, functional indicator of benthic ecosystem quality for the purpose of selecting MPAs. The following research questions have been addressed in the context of the Irish Sea; i) can benthic infaunal production be modelled over large scales using easily obtained environmental data? ii) Is there a spatial association between benthic infaunal production and biodiversity? iii) Does benthic infaunal production need to be explicitly included as a selection criterion in MPA network design for it to be protected from anthropogenic activities such as fishing? The importance of considering spatial grain and extent in large scale modelling, and the wider application of size-based benthic community models to ecosystem-based marine spatial management has also been touched upon.

In this final chapter, the contribution of the four research chapter findings to addressing the key questions will be summarised and discussed, and general conclusions and recommendations regarding the utility of empirical predictions of benthic infaunal production for directing MPA network design will be presented. The wider application of size-based benthic community models to ecosystem-based marine spatial management and the limitations of the thesis will also be briefly discussed. Further work regarding the development of functional indicators of benthic ecosystem quality for informing marine spatial management will also be recommended.

6.2 SUMMARY OF RESEARCH CHAPTER FINDINGS AND IMPLICATIONS FOR MPA DESIGN

6.2.1 Modelling benthic production in the Irish Sea and application of predictions

Benthic infaunal production is a biological attribute of seabed communities that mediates energy transfer from primary producers to higher trophic levels (Tumbiolo & Downing, 1994; Brey, 2001; Seitz et al. 2009). This important ecosystem process is proposed as a functional metric of ecological quality because it is considered an indicator of the benthic ecosystems ability to deliver important ecosystem goods and services (Steele et al. 2007; Ferron et al. 2009; Danovaro et al. 2008; Hiddink et al. 2011; Valentine-Rose et al. 2011). Rice et al. (2012), for example, considered benthic secondary production as a potential indicator of good environmental status (GES) for the Sea-floor integrity descriptor under the European Union Marine Strategy Framework Directive (MSFD), because of its importance in energy flow and determining marine ecosystem carrying capacity. However, secondary production was not deemed a practical indicator because it is very difficult to measure and monitor directly, especially at the large scales relevant to the MSFD. Although an existing empirical, size-based model of benthic secondary production was available (Hiddink et al. 2006), its application was considered limited to the southern North Sea (Rice et al. 2012).

Chapters 2 and 3 of this thesis focus on the refinement and re-parameterisation of this existing size-based model to predict benthic infaunal production from easily obtained environmental data in the Irish Sea. This was to determine whether or not the model could be easily re-parameterised for application in other areas, and subsequently developed as a practical, functional indicator of benthic ecosystem quality for the purpose of informing marine spatial management, particularly MPA network design. These chapters present the first attempt to model benthic invertebrate production over large scales in the Irish Sea.

The size-based model that has been refined and re-parameterised here is the Hiddink et al. (2006) model of benthic invertebrate production, biomass and trawling impacts, which was originally developed for application in the southern North Sea (Hiddink et al.

2006a). This predictive model is based on allometric relationships, competition dynamics and the influence of environment variables on benthic infauna growth and mortality. Chapter 2 identified a suite of relationships between benthic production and spatially consistent, easily obtained environmental variables that operate in the Irish Sea, at range of different spatial scales. The results of this chapter were used to inform the re-parameterisation of growth and mortality functions in the model in Chapter 3.

The re-parameterised model can explain 48% of the variation in relative benthic infaunal production in the Irish Sea, at a spatial grain of 5 km². This is an improvement on the predicative ability of the Hiddink (2006) model, which could explain 29 - 39% of the variation in benthic biomass in the southern North Sea. The validation result indicates that the relationships and dynamics captured by the size-based model are useful for predicting relative benthic infaunal production. The spatial extent at which model predictions can consistently explain 48% of variation in production is uncertain, however, due to the restricted area from which independent benthic community data for the validation were obtained. The results of Chapter 2 indicate that the identified environment variables included in the model have good predictive power up to approximately 80,000 km², suggesting that the size-based model can accurately predict over equally large scales. Until an Irish Sea wide validation can be completed, the current validation and results of Chapter 2 regarding environment-production relationships at different spatial extents suggest that modelled benthic infaunal production could be a practical indicator of benthic ecosystem quality. This is because the ability to predict this important ecosystem process at this spatial extent negates the need for extensive, direct measurements of productivity, which are very resource intensive and not realistic for assessing ecological quality over large areas (Tumbiolo & Downing, 1994; Bolam et al. 2010; Rice et al. 2012).

Spatially consistent data layers of modelled benthic infaunal production enable ecosystem function to be easily incorporated into marine protected area design, as has been demonstrated in Chapter 5. In addition to productivity, the nature of the size-based model means that benthic infaunal biomass and the extent and magnitude of bottom fishing impact on benthic production and biomass can be predicted. The time taken for benthic communities to recover from fishing impacts, and thus recovery status of

communities can also be estimated. It should be noted, however, that the discrepancy between estimated recovery status of production and predictions of productivity in chronically fished areas, identified in Chapter 3, indicates that implementation of fishing impacts in the recovery model is not realistic for predicting benthic community recovery status in chronically fished areas. This is because the recovery model does not capture the effect of cumulative fishing impacts that can lead to an increase in predicted production above a level expected in the absence of fishing (see Chapter 3, Section 3.6 for further details). The recovery status metric is therefore not considered as useful for informing management compared to recovery time and estimated fishing impact. The functionality of size-based models to provide these two additional functional metrics increases their utility for informing marine spatial management. The possible applications of recovery time and fishing impact estimates have been outlined in the relevant chapter discussions.

Although the predicted increases in production under chronic fishing can exceed the level of productivity expected in the absence of fishing (i.e. a 'near-pristine' state), the benthic communities cannot be considered pristine or un-impacted by fishing because these changes reflect a shift in community composition and size spectra that is characteristic of perturbation, reflected by a simultaneous decline in biomass (Jennings et al. 2001; Srivastava & Vellend, 2005; Queiros et al. 2006). If management objectives are purely to maintain a certain level of productivity, then these increases could be viewed as positive. If management objectives aim to maintain benthic communities in their natural, undisturbed state, then these increases could be viewed as negative (Srivastava & Vellend, 2005). These possible increases in productivity in response to chronic fishing need to be born in mind if using modelled benthic infaunal production as an indicator of ecological quality. It should be noted, however, that despite these areas experiencing a slight increase in production under current fishing intensity in the Irish Sea, they are still estimated to have low productivity compared to other areas, therefore in the context of MPA network design to protect areas of high ecological quality, these areas are unlikely to be prioritised for protection.

Although these areas of increased productivity described above are unlikely to be prioritised for protection, due to low relative production, the above observations suggest that perhaps size-based predictions of benthic biomass should also be considered as an indicator of ecological quality and fishing impacts on benthic communities. Benthic infaunal biomass does not response positively to fishing, and can therefore be considered a more consistent indicator of fishing impact. Benthic infaunal biomass also tends to be more severely impacted by fishing in comparison to productivity. However, recover times for biomass tends to be much shorter than production, indicating a greater recovery potential and perhaps a lesser need for protection in areas where fishing intensity is low enough to allow biomass to recover.

Predicted benthic production and benthic biomass are closely associated and high pristine production and biomass estimates are both expected to reflect areas of high benthic ecosystem quality. In general, high benthic invertebrate biomass is not expected to reflect ecosystem perturbation in the same way that, for example, high P/B ratios might. However, high biomass could result from the dominance of a particular species, such as brittle-stars or slipper limpets, which would result in an uneven community (low Pielou's evenness, J'). Uneven communities dominated by one particular speices are often considered to be of low value to biodiversity. The decision regarding the best indicator of ecosystem function will ultimately depend of the definition of ecological quality used. If ecosystem function under a natural, unperturbed state is at the core of the definition, high biomass of the brittle-star *Ophiothrix fragilis*, for example may be considered high quality because of the key role *O.fragilis* feeding activity plays in pelage-benthic transfer (Lozach et al. 2011).

6.2.2 Benthic infaunal production in MPA design

At the scale of the Irish Sea, it would appear that there is limited spatial association between areas important for benthic infaunal production and biodiversity features, suggesting that benthic production is not a useful proxy for biodiversity over large scales, and opportunities for win-win conservation scenarios for biodiversity and ecosystem function at the scale of the Irish Sea is limited. Visually comparison of

distributions, however, suggests there may be possibilities for overlap between high productivity and certain features, especially cetaceans, at local scales. It seems likely that the lack of a spatial association between benthic infaunal production and biodiversity features of conservation interest here is partially a result of the spatial scale, particularly the spatial extent, at which the spatial association between them was investigated. The influence of spatial extent on the detection of relationships was clearly observed in Chapter 2 for environment-production relationships, and has been observed for ecosystem service-biodiversity feature relationships at a national scale in the UK (Anderson et al. 2009).

The lack of spatial associations also suggests that current biodiversity MPAs are likely to under-perform in terms of achieving an ecosystem-based approach to marine conservation and management. The establishment of MPA networks in Europe, for example, has been primarily driven by the EU Birds and Habitats Directive, with the aim to protect marine habitats and species of conservation importance (Frid et al. 2008; Giakoumi et al. 2012), many of which have been included in the analyses of Chapter 4 and 5. The fact that these biodiversity features do not appear to coincide with benthic infaunal production, an indicator of benthic ecosystem quality, suggests that these MPA networks are limited in their ability to protect the areas important for the delivery ecosystem services and goods that are supported by this important ecosystem process. This indicates that functional metrics such as benthic infaunal production and biomass are likely to be useful for complementing biodiversity features when identify areas of good ecological quality under an ecosystem-based approach.

With respect to suitable management measures, Chapter 5 confirms that overall, the establishment of no-take MPA networks are effective for protecting production from the impacts of bottom fishing in the Irish Sea, even when fishing effort is displaced from these protected areas. MPAs are therefore considered a useful spatial management tool for preserving this important marine ecosystem process and the goods and services it supports.

6.3 FINAL CONCLUSIONS AND RECOMMENDATIONS FOR MPA DESIGN

6.3.1. Final conclusions

The key research questions proposed at the beginning of this thesis have been answered; i) benthic infaunal production can be modelled over large scale using easily obtained environmental variables; ii) There is a lack of spatial association between benthic infaunal production and biodiversity features at the scale of the Irish Sea. Finally iii) benthic infaunal production does need to be explicitly included as a selection criterion in MPA design in order for it to be protected from anthropogenic activities such as fishing.

Although it is difficult to generalise the validation of the size-model model refined and re-parameterised here across the whole Irish Sea area, the Chapter 2 results regarding the spatial extent of environment-production relationships and positive validation result suggest that modelled benthic infaunal production could be a suitable candidate for filling the current gap in functional indicators of benthic ecosystem quality, and can be used to inform MPA network design over large areas. The approach to re-parameterisation using easily obtained environmental data here, particular by including remotely-sensed sea surface chlorophyll-*a*, has improved the predictive ability of the original Hiddink model, and suggests that it could be applied to different areas where remotely-sensed chlorophyll-*a*, sediment data and VMS data are available. However, it is recommended that the model is re-parameterised when applied to different areas to ensure confidence in predictions. Overall, modelled benthic infaunal production is considered a practical indicator of benthic ecosystem quality over large spatial scales.

The other metrics predicted by the size-based model here are also considered to have utility for informing marine protected area design. However the identified weakness regarding the estimates of recovery status in chronically fished areas (due to unrealistic implementation of chronic fishing impacts), suggests that this metric is not as useful as predictions of benthic infaunal production and biomass (both fished and unfished), negative fishing impact, or estimates of benthic community recovery time.

The consideration of a suite of functional metrics is considered more useful for informing spatial management, compared to reliance on a single metric, for several reasons. Firstly, the results of Chapter 3 regarding the 'positive' impacts of fishing on production alongside a decline in benthic biomass suggests that the use of both production and biomass rather just production aids the interpretation and understanding of patterns, and therefore is more useful for informing management. In this case, although the observed increase in production under fishing could be considered positive, the decrease in biomass confirms that the fishing impacts are a result of changes in benthic community size composition, which is not necessarily considered a positive ecosystem outcome. Secondly, different metrics could inform different management measures that meet similar ecosystem objectives, offering flexibility in management approaches. For example, recovery time of benthic communities could inform bottom fishing effort management that allows benthic productivity to recover in fished areas, as an alternative to using metrics to inform no-take MPA designation, which can result in large socio-economic costs. The use of several metrics can provide different options for spatial management and is expected to better help achieve the ecosystem-based approach from both an ecological and economical perspective, because it would allow a degree of flexibility with respect to these socio-economic considerations. Finally, the availability of several functional metrics means that multiple ecosystem objectives can be set and achieved, for example the protection of highly productive and highly vulnerability benthic communities (i.e. those that take a long time to recover from fishing impacts).

The results of Chapter 4 and 5 demonstrate that in order to protect those areas of high benthic ecosystem quality from damaging activities such as fishing, and thus achieve an ecosystem-based approach to marine spatial management, modelled benthic infaunal production is required to complement biodiversity criteria when selecting MPAs. This is because the use of biodiversity criteria alone is unlikely to identify those areas of high productivity that indicate high ecological quality and services provision. Due to a lack of spatial association between benthic production and habitats and species of conservation importance at the spatial scales investigated here, benthic infaunal production can only be considered a proxy for ecosystem goods and services, not biodiversity. It is expected,

however, that different patterns may be observed if similar analyses were conducted at different spatial grains and extents.

6.3.2 Recommendations for MPA design

The following general recommendations for MPA design are proposed based on the conclusions drawn by this thesis:

1. For MPAs to meet ecosystem-based management objectives, i.e. prevent degradation of ecosystem function and maintain the health and ability of marine ecosystems to provide goods and services (Douvere, 2008), it is recommended that a functional selection criterion that directly reflects ecological quality and is linked to ecosystem goods and services is utilised in the MPA design process. This is because common MPA selection criteria such as habitats and other biodiversity features, which have previously been considered proxies for ecosystem function (Balvanera et al. 2006; Srivastava & Vellend, 2005), are not expected to capture this type of ecosystem-level information. This recommendation is based on the results of Chapter 4 and 5.

2. Alternatively, the productivity of different habitats could be quantified to inform marine managers about the value of different habitats for production. i.e. which habitats would be best protected to ensure the protection of highly productive communities. This has been done here on a very broad, simplified scale; i.e. productivity in sandy, muddy and gravelly habitats, suggesting that the protection of gravelly and sandy habitats instead of mud would result in greater benefits for benthic production. However, to better match up with those biodiversity features commonly used to direct MPA design it would be useful to quantify and compare the benthic productivity at a higher resolution of habitat classification, for example, for *Modiolus modiolus* reefs, sea grass beds and sand banks. This has not been possible here, due to a lack of available benthic abundance and biomass data for these habitat types. Without dedicated sampling

effort, it is unlikely that the replication of data from different habitats types will be great enough to provide enough statistical power to allow such an analysis.

3. Using a suite of functional metrics for benthic ecosystem quality is expected to better achieve an ecosystem-based approach to marine spatial management compared to the use of one single metric on its own. This is because the use of several metrics would i) support better understanding of ecosystem quality and therefore better spatial management decision-making, ii) provide a range of possible ecosystem management objectives and iii) a greater range of management options for meeting these objectives. Flexibility in approaches to protection and management of benthic ecosystems is likely to reduce conflict with and costs to other marine users.

4. Due to the lack of spatial association observed between production and biodiversity features at the scale of the Irish Sea here, and the known influence of spatial grain and extent on the interpretation of relationships, as illustrated by Chapter 2, empirical investigations of spatial concurrence between ecosystem function and biodiversity for the purpose of prioritising MPA network design are recommended at local scales, and also at a spatial grain that is relevant to the scale at which spatial management measures are implemented to ensure that patterns of association are correctly identified.

6.4 WIDER APPLICATION OF SIZE-BASED MODELS TO MARINE SPATIAL MANAGEMENT

The empirical, size-based model of benthic invertebrate communities described here has wider application for marine spatial planning and management beyond its utility for informing MPA network design. For example, modelled benthic infaunal production could be a suitable indicator for the assessment and monitoring of good environmental status for sea-floor integrity under the MSFD (Rice et al. 2012). Although MSFD applies over all European waters, indicators will be developed and assessments made at appropriate regional scales. The process outlined in chapters 2 and 3 of this thesis could

provide guidance on how a size-based model could be re-parameterised for application in other regions, and provide metrics for assessment of GES. The ability to map production in the absence of fishing, the vulnerability of productivity to fishing impact (indicated by recovery time), and also the extent and magnitude of fishing impacts means that the size-based model outputs could have great utility for assessing GES. The difference between predicted production and production expected in the absence of fishing within a given area, for example, could be used as an indicator of state (Hiddink et al. 2006a; Rice et al. 2012), and the magnitude of predicted fishing impacts could be used as an indicator of response to pressure. The size-based model here can also predict benthic community size-spectra, another proposed indicator of sea-floor integrity under MSFD (Rice et al. 2012).

The size-based model outputs could also be used to inform an ecosystem-approach to fisheries management, by evaluating the impact of different bottom fishing management scenarios, including closed areas and effort restriction measures, on benthic communities, and evaluate trade-offs between food production and benthic community quality or health (e.g. Kaplan & Levin, 2009). Predictions of fishing impact and recovery time could help determine a level of fishing effort that sustains some proportion of benthic production or biomass in a relatively undisturbed state, or allows recovery of production and biomass between fishing events. This may be more beneficial than excluding fishing from particular areas, which can result in negative impacts due to displacement effects (Dinmore et al. 2003; Hiddink et al. 2006c; Greenstreet et al. 2009).

The model outputs could also inform marine environmental impact assessments. For example in areas proposed for new commercial fisheries, aggregate dredging or wind farm installation, the model outputs regarding current production and recovery time could be consulted to understand the current productivity of the area and, for bottom fishing, the potential vulnerability of the community to new activity. In highly productive areas, bottom fishing, aggregate dredging and wind farm installation may be discouraged in order to ensure that the productivity is preserved and made available to higher trophic levels in the marine ecosystem.

6.5 LIMITATIONS OF THESIS AND RECOMMENDATIONS FOR FURTHER WORK

Data availability

The limited availability of suitable benthic infaunal biomass and abundance data in the Irish Sea meant that only a limited dataset of empirically observed benthic infaunal production estimates were available for predictive model parameterisation, and for analyses in subsequent Chapters, such as the investigation of spatial association between empirically observed production and biodiversity. Furthermore, logistical constraints limited the number of independent benthic community data collected for model validation. Limited data for model parameterisation reduces confidence in the precision and accuracy of model predictions at the scale of the Irish Sea, and limited validation data means that this concern cannot be addressed. Clearly greater collection and availability of benthic invertebrate abundance and biomass data would help resolve these issues.

Limited application

Here only the productivity of benthic infaunal communities in soft sediments (mud, sand and gravel) are considered, therefore application of the model is restricted to soft bottom, offshore areas. The productivity of epifauna on soft sediments, of benthic communities on hard substratum, including inshore habitats, and the productivity of biogenic habitats such *Modiolus modiolus* and *Sabellaria* reefs is not considered. This is largely due to the lack of benthic production estimates for these fauna and habitat types. Sampling hard substrata, for example, using traditional techniques such as grabs is not advisable due to sampling inefficiency (Bowden, 2005), and the direct sampling of biogenic habitats is difficult because their sensitivity to sampling gear and conservation status deems sampling unethical or illegal (Cook et al. 2013). Unfortunately the equipment and methods for calculation of epifaunal biomass from non-invasive underwater photographic and video data were not available.

Epifaunal benthic communities are often considered very important for ecosystem functioning and the provision of ecosystem goods and services. *Modiolus modiolus* and *Mytilus edulis*, for example, are considered bioengineers because they create and modify habitat, providing complex habitat for a high diversity of epifaunal species (Ragnarsson and Raffaelli, 1999; Sanderson et al., 2008; Ragnarsson & Burgos, 2012). The formation of mussel beds can alter ecosystem functions such as nutrient flux, due to high bio-deposition rates (Hargrave et al. 2008; Ragnarsson & Burgos, 2012). In addition to this, the functional role of the brittle-star *Ophiothrix fragilis* in pelage-benthic transfer (Lozach et al. 2011), already been outlined in Section 6.2.1, provides another example of the importance of epifauna to ecosystem functioning. Many epifaunal species have also been identified as a major food source for fish (Braber & De Groot, 1973; Bowman et al. 2000), and therefore considered important for supporting fish production alongside infauna (Hiddink et al. 2011). Not considering the productivity of epifauna and biogenic habitats is therefore expected to miss a great deal of information regarding benthic ecosystems, including their ecological quality and ability to support ecosystem function.

The size-based model utilised here can be used to predict epifaunal production. The exclusion of this class of fauna here is purely a result of data deficiency. Therefore to incorporate epifaunal productivity targeted epifaunal abundance and biomass data collection is required. Unfortunately it is more difficult to quantify the biomass and thus productivity of epifauna per metre squared using traditional beam trawling methodology, because it's difficult to know exactly when the dredges or beam trawl become full with benthos whilst traveling along the sea bed, and therefore to relate the individuals caught back to a specified area and subsequently derive quantitative estimates. It is also difficult to accurately quantify epifaunal communities using grabs, because large species can be found at very low densities, and the efficiency to capture epifauna present at the seabed surface is limited. The movement of the gear through the water, for example, can cause shock waves that displace epifauna away from the sampling area (Lozach et al. 2011). If methods to calculate biomass estimates from photographic and video data can be developed (e.g. Lambert et al. 2011), epifaunal data collection for model parameterise may be possible using photographic or video survey techniques. Photographic or video seabed survey is especially expected to be the most

suitable method for quantifying epifaunal communities on hard substrate (Bowden, 2005).

Secondary production in biogenic habitats is expected to be more difficult to incorporate into the model. It is expected to be very difficult to calculate the biomass of all epifaunal species in biogenic habitats without direct sampling because of the complex 3D habitat structure that they can create. Aerial view photographic and video data are highly unlikely to be able unable to capture all species in these habitats, and even less likely to be able to accurately calculate their biomass. Furthermore, facilitation is expected to play a large role in community dynamics of biogenic habitat communities (Bozec et al. 2013), and this is not parameterised in the current model (Hiddink et al. 2006a).

Other models of ecosystem productivity

There are other models of ecosystem productivity that are utilised in European waters. The European Regional Seas Ecosystem Model (ERSEM), for example, is an ecosystem model that models biochemical and ecological processes in relation to large scale oceanographic drivers such as mixing (Allen et al. 2001). ERSEM incorporates primary producers as well as benthic consumers and decomposers, and can provide estimates of benthic community structure and function (including production), as well as recovery of these attributes in relation to fishing (e.g. Allen & Clarke, 2007).

Although ERSEM has includes and has wider application to different ecological processes than the size-based model developed here, benthic community dynamics are modelled at a lower resolution in ERSEM than in size-based models. This is because the benthic macro-invertebrate component of the ecosystem model is only divided into a few functional groups (Allen & Clarke, 2007), and benthic body size is not considered, despite it being very important to benthic community dynamics (Sheldon et al 1977; Brey, 2001; Blanchard et al. 2012). Furthermore, as models become more complex (i.e. incorporate more processes), they become more difficult to parameterise and uncertainty in the reliability of outputs increases (Raick et al. 2006). Therefore size-

based models like the one used here are considered more suitable for modelled benthic community attributes than complex ecosystem models such as ERSEM.

Other ecosystem functions and indicators to consider

This thesis has only considered the secondary production of benthic macro-infauna as an indicator of benthic ecosystem function. There are other benthic ecosystem processes and proxies that are commonly investigated in relation to ecosystem health, function and services. Oxygen concentration of sediment pore water, for example, is commonly used as a proxy for ecosystem health with respect to eutrophication (Ferreira et al. 2010; Rice et al. 2012). Nutrient cycling in particular is considered an important ecosystem service provided by benthic ecosystems (Hiddink et al .2009). Sediment nutrient fluxes are mediated by benthic invertebrate processes such as bioturbation (Lohrer et al. 2004; Rossi et al. 2008), bioirrigation (Murray et al. 2013) and habitat modification by bioengineers (Hargrave et al. 2008; Ragnarsson & Burgos, 2012; Rossi et al. 2013). Nutrient fluxes can be measured directly, or tracked using stable isotopes (Rombouts et al. 2013). Alternatively, the apparent redox discontinuity of the sediment (aRPD) (Hiddink et al. 2009) or estimates of community bioturbaiton potential from benthic community compositon (Queiros et al. 2013) can be used as proxies for bioturbation and thus nutrient fluxes (Hiddink et al. 2009; Queiros et al. 2013). There are no known attempts to model these benthic processes that mediate nutrient fluxes over large scales for the purpose of informing marine spatial management.

Determining the importance of benthic production to ecosystem goods and services provision

Quantitative links between benthic productivity and marine ecosystem goods and services could be made to strength the case for the use of benthic infaunal production as a functional indicator for MPA selection criteria. For example, the relationship between fish production and benthic production could be empirically investigated to better understand the importance of benthic productivity to fish production. As well as strengthen the ecosystem-based case for the protection of benthic community

production, this would also support the identification of necessary trade-offs between commercial fishing and benthic production to ensure healthy marine ecosystems and sustainable fisheries into the future.

6.6 FINAL SUMMARY

Overall, this thesis has indicated that size-based predictions of benthic infaunal production and associated metrics has great utility for informing an ecosystem-based approach to marine spatial management. Greater consideration of benthic ecosystem processes and functioning in marine spatial management is expected to support healthy and productive marine environments, and help ensure the continued provision of the ecosystem goods and services that we rely on in the long-term.

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