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Predicting the impact of towed fishing gears on emergent epifauna

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Predicting the impact of towed fishing gears on emergent epifauna

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by

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Abstract

In the context of an ecosystem-based approach to the management of marine resources, fisheries managers have to consider the effects of fishing impacts on seabed habitats to achieve sustainable use of marine resources. Bottom fishing, using mobile gears such as scallop dredges or otter trawls, impacts benthic habitats directly due to the need to maintain the gear in close contact with the seabed to maximize catches of target species. In this thesis, the loss of emergent epifaunal biomass due to fishing disturbance was quantified at the scale of an entire fishery. The results showed how fishing and the physical environment, i.e. substratum type and the overlying hydrodynamic regime, interact to determine the biomass and size composition of the resident emergent epifauna. A novel method was used to track the spatial movement of fishing vessels in the study and the implications of using alternate methods of fishing effort estimation to describe fishing impacts were analyzed. The results show that analytical methods (track reconstruction, density of position records) and the grid cell resolution used for the analysis can lead to the underestimation of fishing impact on epifaunal communities. This novel technique was then applied to enable the determination of the recovery of benthic communities of hard substrates. The recovery of species abundance, species composition and functional group structure was estimated to take from 1 to 4 years, and was significantly influenced by the prevailing hydrodynamic conditions. Finally, the application of a novel approach to monitoring habitat distribution and status was investigated. The technique utilized underwater imaging of a laser line applied to the seabed that allows the calculation of a habitat complexity index. Details of the implications of the various methods developed in this thesis and of the key findings to the implementation of an ecosystem approach to fisheries management were integrated in the general synthesis.

Chapters

Chapter 2 has been published in Marine Ecology Progress Series:

- Lambert G. I.[1], Jennings S.[2,3], Kaiser M. J. [1], Hinz H. [1], Hiddink J. G. [1], 2011. Quantification and prediction of the impact of fishing on epifaunal communities. MEPS Vol. 430: 71–86

Chapter 3 has recently been accepted for publication in the ICES Journal of Marine Sciences after minor revisions. The version presented here is an improved version of the first submission to the Journal, i.e. it includes the minor revisions suggested by the reviewers that were most relevant to this thesis:

- Lambert, G. I. [1], Hiddink, J. G.[1], Hintzen, N. T.[4], Hinz, H. [1], Kaiser, M. J. [1], Murray, L. G. [1], Jennings, S.[2,3] (in press). Implications of using alternate methods of Vessel Monitoring System (VMS) data analysis to describe fishing activities and impacts. ICES Journal of Marine Sciences

Chapter 4 is in preparation for submission:

- Lambert G. I. [1], Jennings S. [2,3], Kaiser M. J. [1], Davies T. W.[5], Hiddink J. G. [1] (in prep) Quantifying recovery rates and resilience of seabed habitats to bottom fishing.

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Introduction

1.1 Overview

Here I introduce the reasoning and main concepts behind the work carried out during this PhD with focus on the role of the benthos in marine ecosystem and the gaps in scientific knowledge that need to be addressed.

The first part of this introduction presents the empirical evidence for the impacts of towed fishing gears on the benthos. I then move on to describe some of the key functions of the benthos in the marine ecosystem that can be altered by human disturbance and which provide a rationale for the management of human impacts on benthic communities. To finish, I explain the development of ecosystem-based management and its role in mitigating the negative effects of fishing to meet management objectives for seabed habitats and processes. The literature on the impacts of fishing is extensively covered in the introductions and discussions of chapters 2 to 5 of the thesis and is therefore not reviewed in detail in the general introduction.

1.2 The impact of human activities on the benthos

1.2.1 Spatial extent of seabed disturbance from human activities

There are growing concerns over the sustainability of human impacts on seabed habitats due to the frequency and intensity of impacts from numerous human activities (e.g. Botsford et al. 1997, Daw & Gray 2005, Hilborn 2007). To support the diverse policy commitments to sustainable use of the sea it is necessary to understand both the extent and the effects of different human pressures.

Recent studies have assessed the variety and extent of human pressures on the seabed in the waters of England and Wales (Eastwood et al. 2007, Foden et al. 2011). The pressures result from oil and gas extraction, cables, wind farms, waste disposal, marine mineral dredging, fishing and wrecks. Eastwood et al. (2007)

organised the different pressures into 3 categories (excluding contaminants and non-physical disturbance such as noise): physical loss (obstruction and smothering), physical damage (abrasion, extraction and siltation) and biological disturbance (selective extraction). The authors did not attempt to measure the actual impacts that resulted from these pressures, but based on measurements of the areas impacted by the different activities they concluded that the most widespread pressure was selective extraction caused by bottom trawling. Foden et al. (2011) subsequently confirmed that towed bottom fishing gears accounted for almost 100% of the spatial footprint of human activities on the seabed in the UK (England and Wales) waters.

For this reason it is essential to identify and quantify the impacts of bottom fishing on the seabed. The resulting information can be used to assess the sustainability of impacts and, if they are not sustainable, to support the development of management methods to achieve sustainability.

1.2.2 Pressure on the seabed from different towed bottom fishing gears

The impact of bottom fishing on seabed communities depends primarily on gear design and sediment type (Hall 1999, Kaiser et al. 2006a). The most common towed gears used in Northern Europe are otter trawls, beam trawls and dredges. Bottom trawls differ in the way the horizontal opening is maintained, while dredges are always supported by a rigid frame. The way in which the opening is maintained is one of the factors that affect the extent of bottom contact by the gear.

The opening of beam trawls is maintained with a rigid beam between two ‘shoes’ and bottom contact is achieved by weighted chains or a chain mat between the shoes. As a result, the full width of the gear tends to impact the seabed (figure 1.1). The width of the gear is typically 4 to 12m and two beam trawls are usually fished simultaneously by a single vessel.

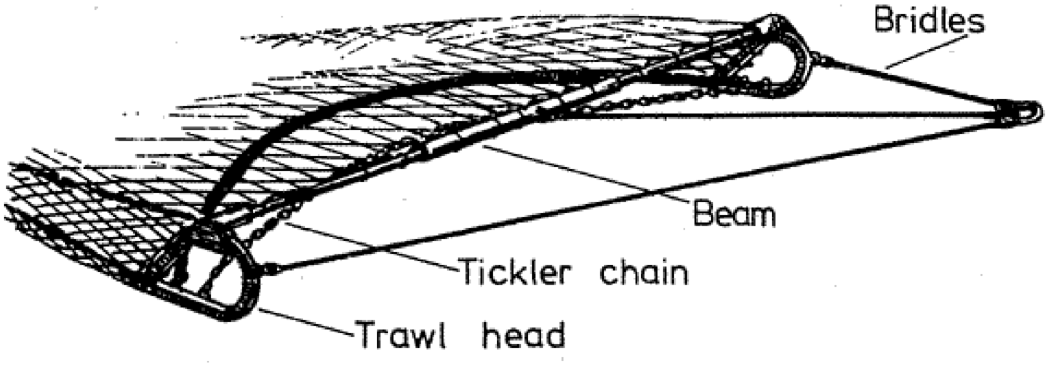

Figure 1. 1. Example of a beam trawl and features around the opening of the net (©FAO)

The impact of otter trawl is mostly restricted to the trawl boards that are used to keep the mouth of the trawl open and remain in contact with the seabed. When relatively heavy bobbins, rollers and tickler chains are rigged between the boards they can increase the total impact of the trawl that may otherwise have quite limited ground contact (figure 1.2).

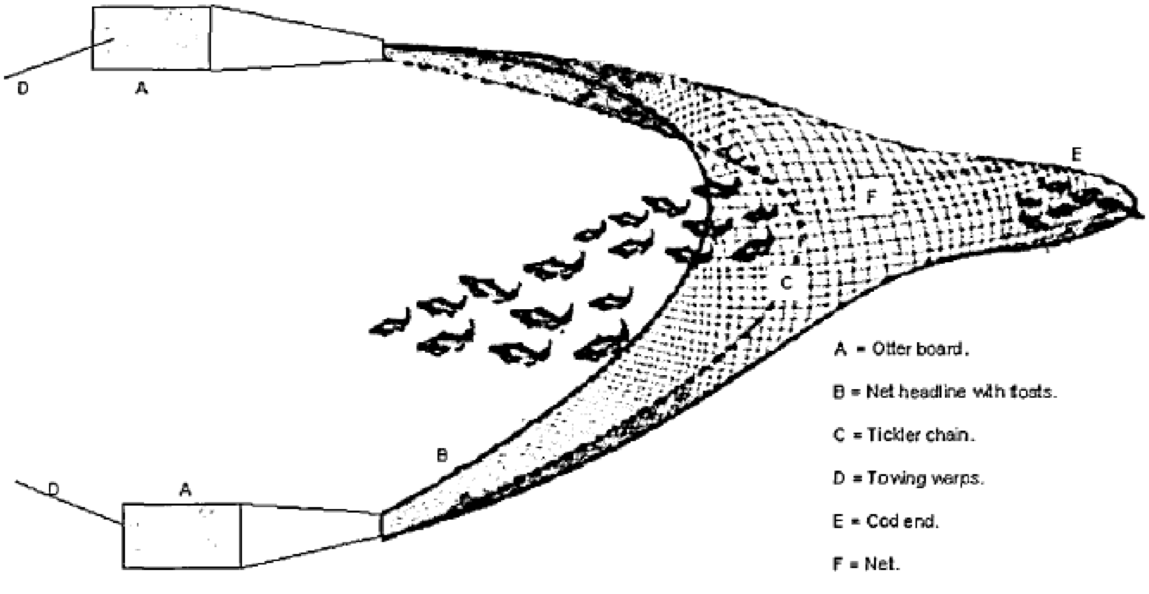

Figure 1. 2 Diagram of an otter trawl used in the North Sea fishery (from Percival 2004)

Dredges are much narrower than trawls, typically 0.75 to 2m wide, and consist of steel frames with teeth and fibre or metal chain-mesh bags that plough over and through the surface layers of the seabed (Watling & Norse 1998, Hall 1999) (figure 1.3). Scallop fishing vessels can tow anything between 2 dredges and 2 sets of 22 dredges depending on the vessel size and the requirements of regulations that govern the use of these gears.

Figure 1. 3 Picture of a standard Newhaven scallop dredge (from Kaiser et al. 2006a) (Photograph ©Michel Kaiser)

There also exist many variations to ‘standard’ towed fishing gears. These can be developed to improve catch rates and/or decrease environmental impacts. For example, scallop dredges can be mounted on skids and have a number of spring tines or a rubber lip instead of teeth (figure 1.4).

Figure 1. 4 Modified dredges. Left: New scallop dredge used around the Isle of Man (Andrews et al. 2011); right: N-Viro dredge (http://www.n-virodredge.com/)

Generally, the penetration depth of these gears is deeper in soft sediments than on compact or hard substratum types (Hall 1999), although penetration is further influenced by factors such as towing speed, warp length and weight of the gear. When bottom fishing gears are in direct contact with seabed habitat they impact the benthic organisms that are present by removing, crushing, burying and exposing them to predation (Watling & Norse 1998, Kaiser et al. 2006a).

1.2.3 Experimental vs. observational studies

Quantification of the effects of bottom trawling and dredging has usually been achieved by experimental or comparative studies (Hall 1999). Both approaches are of limited value when assessing impacts at the scale of a fishery because it is challenging to extrapolate from experimental or comparative impacts to the range of impacts that occur at the scale of a fishing ground.

Experimental approaches are often based on before/after control/impact (BACI) experiments. These approaches have numerous limitations that have been extensively reviewed by Underwood (Underwood 1991, 1992, 1993, 1994). Generally, the spatial and temporal scale at which BACI experiments are conducted are relatively small compared to the scales at which fishing occurs. Further, several control sites may be needed to minimise the possibility that a significant difference between sites is a chance event (Hall 1999, but see Pitcher et al. 2009).

Comparative approaches do not manipulate the environment but compare existing sites at various locations. These methods are impeded by the high natural variability that exists in subtidal environments; as it is very difficult to estimate whether two distant or even relatively close areas have the same environmental characteristics (e.g. productivity, wave or tide stress (Hall 1999)). Another limitation is the difficulty associated with defining whether an area has actually been fished (Hall 1999). To an extent, this limitation has been addressed by sampling multiple sites that are subject to different intensities of fishing in real fisheries (e.g. Deng et al.

2005, Hiddink et al. 2006c). This is increasingly achievable because fishing activity is now being measured on smaller spatial scales than was hitherto possible with the introduction of vessel monitoring systems (VMS) in many fisheries around the world. Prior to the introduction of VMS, pioneering research on high resolution large-scale descriptions of bottom fishing activity was based on experimental tracking of vessels (Rijnsdorp et al. 1998, Piet et al. 2000, Rijnsdorp et al. 2000, Rijnsdorp et al. 2001). In Europe, VMS was introduced for fishery control and enforcement purposes but are increasingly used to support the assessment of fishing activity and marine spatial planning (EC 1997, Dinmore et al. 2003, Murawski et al. 2005, Mills et al. 2007, Piet et al. 2007). All vessels >15m are monitored in Europe and they typically transmit position, speed and direction records at 2 hour intervals (EC 2009). Therewith these data, it is possible to map fishing intensity and great progress in quantifying fishing impact at high resolution and over large spatial scales has been made since VMS data were first made available to scientists.

One way of illustrating how the approach that is chosen to assess fishing impacts can influence the outcome of the analysis is to compare estimates of the rate of recovery of benthic communities post fishing-impact in different studies. Many of the studies that have been conducted at small temporal and spatial scales and using BACI experiments have led to estimates of recovery time that are less than one year (Van Dolah et al. 1987, Kaiser et al. 1998, Robinson et al. 2001, Pitcher et al. 2009). These results may not apply at the scale of the fishery because fishing grounds will have different recovery dynamics from small, seldom disturbed patches of the seabed where recovery is likely to occur through immigration rather than reproduction within the patch (Collie et al. 2000b, Jennings et al. 2001a). Thus meta-analyses and large-scale long-term studies of recovery following trawling impacts recovery time-scales, ranging from <3 years (Cranfield et al. 2001, Blyth et al. 2004) to 5-10 years in hard substratum habitats where sessile epifauna was initially present (Collie et al. 2000b, Collie et al. 2005, Kaiser et al. 2006a). Those findings have been corroborated by models of recovery through population growth rather than immigration that suggest recovery rates between 5 and 10 years (Dinmore et al. 2003, Hiddink et al. 2006b, Allen & Clarke 2007).

Overall, assessments of fishing impacts and recovery time are highly dependent on the survey and sampling design, even though the general effects of fishing on the seabed are generally qualitatively well understood.

1.2.4 Impact of mobile bottom fishing gears on benthic communities

In general, towed bottom fishing gears have been shown to change the composition of benthic communities. Recorded changes include reductions in the biomass, abundance, richness and productivity of vulnerable species such as sessile emergent fauna (Collie et al. 2000a, Jennings et al. 2001a, Hiddink et al. 2006c) while there have been some increases, or at least increases in dominance, of species such as scavengers and opportunistic r-strategists. While conflicting conclusions have been found regarding the response of scavengers to fishing, probably due to their mobility and variability in population size (Ramsay et al. 1998, Thrush et al. 1998), the benthic community in intensively fished areas tends to be dominated by r-strategists, i.e. opportunistic species which grow fast, have short life span and reproduce early (Pianka 1970). Lightly or non-fished areas are generally dominated by suspension feeders, large, fragile and long-living sessile organisms while higher relative abundances of small, short-lived epifauna, mobile or infaunal animals are found in heavily fished areas (e.g. Hall 1999, Kaiser et al. 2000a, Chícharo et al. 2002, Duplisea et al. 2002, Tillin et al. 2006).

Benthic communities are also indirectly affected by fishing through changes in predator–prey relationships, food availability, fluxes of chemicals, resuspension, and sedimentation (e.g. Percival & Frid 2000, Percival 2004, Petihakis et al. 2007). For example, large pulses of carbon are released to the water column and oxygen demand at the seafloor increases when accumulated organic material is exposed by trawling (Watling & Norse 1998). Duplisea et al. (2001) developed a model that showed how trawling in the benthos could enhance microbial carbon mineralisation pathways at the expense of faunal biomass. They suggested that intense trawling could create considerable instability in benthic function.

This list of changes in seabed communities and general properties of the benthic ecosystem in response to bottom fishing is not exhaustive. It only summarizes qualitatively some of the key findings that are relevant when taking account of benthic impacts in fisheries management.

1.3 The benthos in the marine ecosystem

1.3.1 Complexity of benthic processes: some insights into animal-mediated physics and biochemistry

The seabed is a highly complex environment where many ecological processes influence and are influenced by the processes occurring in the water column. At the sediment-water interface, substratum type and benthic communities play a major role in the deposition-resuspension of particles and in the recycling of nutrients such as carbon or nitrogen. These vertical exchanges between the sediment and the water column influence the timing and intensity of production cycles (e.g. Graf et al. 1982, Petersson & Floderus 2001).

The physical structure provided by the substratum can influence water flow and the flux of particles at very fine scales by creating turbulent mixing that influences the strength of benthic-pelagic coupling (Rosenberg 2001). Particle resuspension and deposition processes are also animal-mediated. In fact, Aller (1982) stated that the dominant agents of mass transport are often large bottom-dwelling animals that move particles and fluids during feeding, burrowing, tube construction, and irrigation. The bioprocesses involved have been summarized by Graf and Rosenberg (1997). Direct bioresuspension and biodeposition are affected by the biological activity of animals which selectively expel and capture particles of specific sizes. One of the most studied mechanisms is bioturbation; which refers to the biological reworking of soils and sediments (Meysman et al. 2006).

Bioturbation and irrigation by infauna lead to the transport of higher organic content surface sediments into the sediment and an increase in the depth of the oxic layer (Fauchald & Jumars 1979, Aller 1982). Indirect bioresuspension is enhanced by the roughness of the seabed which is affected by the presence and density of benthic organisms structuring the micro-topography of the sediment surface. Indirect biodeposition can be due to the presence of sticky or fluffy surfaces (e.g. mucus, bacterial mat) that may hold material, or to the settlement of particles between dense beds of animal tubes for instance (Graf & Rosenberg 1997).

Nutrient cycling relies on the deposition/ resuspension processes explained above but also on the quantity and quality of organic substrate that sinks to the seabed. This flux is influenced by many factors such as mixed layer and water column depth, zooplankton grazing and bacterial decomposition in the water column (Parsons et al. 1977, Percival 2004). The nutrients are then regenerated by benthic organisms and fuelled back into the pelagic system which in turn enhances primary production.

The nature of substratum type and associated communities therefore determines the inputs of nutrients back into the pelagic system, while secondary benthic production is also dependent on the inputs from the water column (Rosenberg 2001). Since the direct and indirect effects of fishing disturbance can modify the substratum and the communities that are found there they will also affect a range of ecosystem processes (Allen & Clarke 2007).

1.3.2 The multiple roles of habitat-forming species in the marine ecosystem

Through modifying the physics and biochemistry of the environment, benthic species can be considered as ecosystem engineers (*sensu* Jones et al. 1994). Ecosystem engineers are defined as “organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In doing so, they modify, maintain and create habitats”.

Emergent sessile species, such as hydroids and some bryozoans, can be considered as ecosystem engineers because they modify the physical environment and affect the distribution and development of other organisms in many ways. They modify the local hydrodynamics, the exchange of nutrients between the seabed and the water column (as explained in section 2.1) and the flow of larvae to the seabed (e.g. Wildish & Kristmanson 1997, Bruno & Bertness 2001, Bolam et al. 2002). They can further stabilize the sediment which will in turn influence the composition of the community (Meadows et al. 1998).

Emergent sessile species enhance structural complexity. Structural complexity is created by the variations in diversity, density and body shapes of organisms as well as their abundance. High variability in body morphologies exists between or within species groups reflecting different strategies to optimize encounter rates with particles (Abelson et al. 1993). Structurally complex environments created by sessile habitat-forming species may thereby increase habitat heterogeneity and the area available for settlement and which provide shelter for a variety of organisms such as fish recruits and small crustaceans (Connell & Jones 1991, Beck 1997, Bradshaw et al. 2003). Complexity is thus associated with increased abundance and richness of associated mobile species (e.g. Heck & Wetstone 1977, Bell & Westoby 1986, Beck 2000, Taniguchi & Tokeshi 2004, Gratwicke & Speight 2005).

Hence, sessile species play a prominent role in creating habitat complexity which can be modified by trawling disturbance. One of the main concerns in fisheries is how vulnerable those biogenic habitats are to fishing gears (Kaiser et al. 2006a). The presence and development of such habitats depends on a set of abiotic parameters such as the presence of hard surfaces to settle on and input of food from tidal currents. Large sessile species are generally expected to grow in relatively undisturbed locations. Undisturbed communities may have a low resistance to natural disturbance and might therefore be particularly sensitive to fishing disturbance (Collie et al. 2000b, Kaiser et al. 2006a).

Understanding the natural drivers of benthic community structure is therefore an important step towards being able to predict their resilience to fishing impacts. It is further essential to study the environmental requirements of benthic communities in order to be able to predict their distribution and thereby disentangle the effects of fishing from the effects of the environment and to manage the fishery accordingly.

1.3.3 Diversity of benthic habitats and communities in temperate continental shelves and environmental drivers

Subtidal habitats are influenced by many environmental parameters that vary in space and time and are therefore heterogeneous and patchy. To facilitate the development of management plans for habitat, some classifications schemes have been proposed. Two compatible schemes are in use in the UK, the JNCC Marine Habitat Classification for Britain & Ireland (Connor et al. 2004) and the European Nature Information System (EUNIS) classification. The EUNIS scheme describes habitats as 'plant and animal communities as the characterizing elements of the biotic environment, together with abiotic factors operating together at a particular scale'. The abiotic factors, or environmental variables, considered in the JNCC scheme are substratum type, depth, hydrodynamics and salinity.

One of the main drivers of benthic community structure is substratum type. Generally, substratum types can be organised into two major groups: soft sediment and hard substrata. The presence of a particular substratum type is related to the local hydrodynamic conditions. The presence and productivity of benthic communities accordingly display very different functional and taxonomical characteristics (e.g. Woodin & Jackson 1979, Ricciardi & Bourget 1999, Kuklinski et al. 2006). In low energy environments, soft sediment such as silt and clay predominate and deposit feeders are expected to be numerically dominant. As the energy of the environment increases, i.e. the water movement, the sediment gets eroded and the substratum becomes rocky. There, suspension feeders will dominate benthic communities (figure 1.5) (Wildish & Kristmanson 1997). However, it has been suggested that, in soft sediments, there is an upper limit of water movement beyond which the productivity of suspension feeders cannot further increase because of feeding inhibition and potential washout. If there is presence of hard substratum, some suspension feeders such as barnacles may be able to survive at higher flow velocities (figure 1.5).

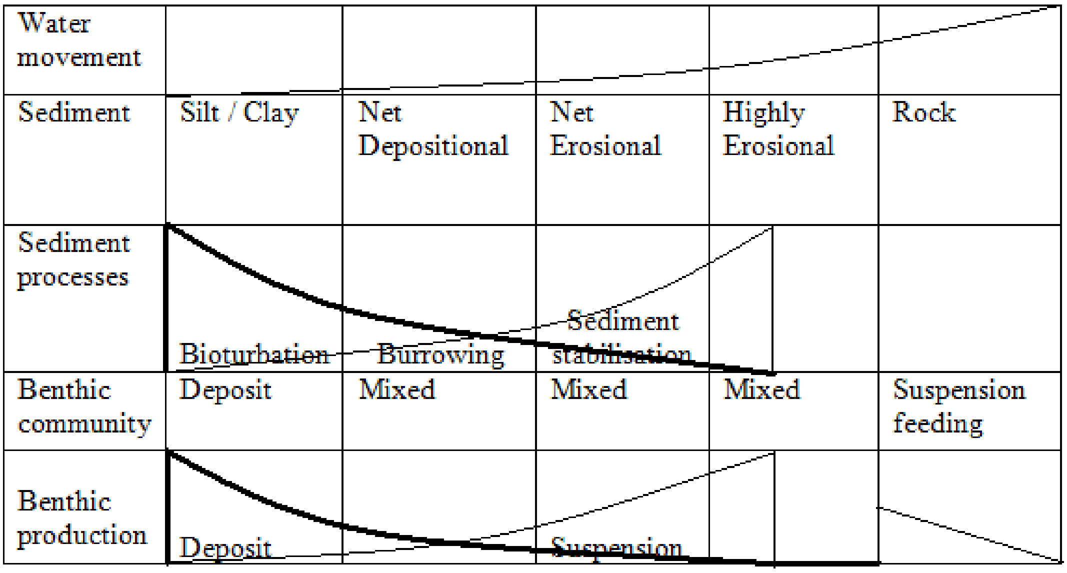

Figure 1. 5 Diagrammatic representation of benthic communities of the continental shelf along a gradient of increasing water movement energy (redrawn from Wildish & Kristmanson 1997). In "sediment processes", the bold line represents bioturbation and the fine line represents sediment stabilization. In "benthic production", the bold line represents deposit feeders and the fine line represents suspension feeders.

In addition, current velocity affects most functions of benthic organisms, especially those of sessile organisms. For example, the interception rate of passing particles by the organisms will increase with increasing current velocity (Graf & Rosenberg 1997). Currents speed generally impacts sessile distribution, settlement, growth and development (Warwick & Uncles 1980, Eckman & Duggins 1993, Abelson & Denny 1997, Hart & Finelli 1999) (figure 1.6).

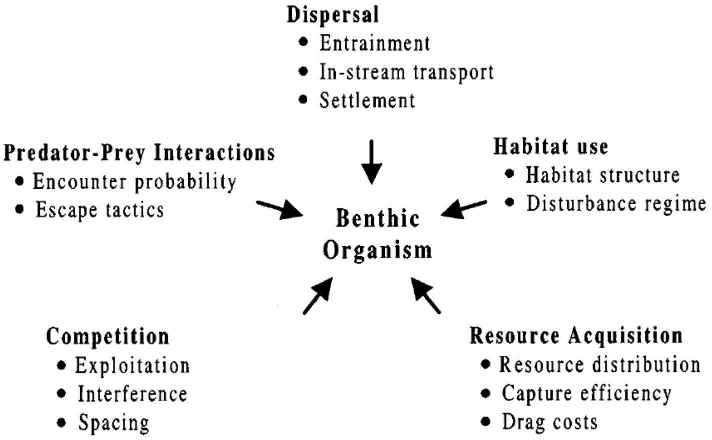

Figure 1. 6 Causal pathways by which flow can affect benthic organisms. Potential interactions not shown (from Hart & Finelli 1999).

Substratum type depends on water movement and water movement is generally correlated with depth. For example, mud flats are mostly found in deep areas with low shear bed stress while more exposed areas are characterized by coarser substrates. Other factors that affect benthic communities but are also related to depth are light, temperature, exposure time in the intertidal, chlorophyll a concentration, summer stratification, salinity and nutrient input from the rivers (e.g. Hiscock et al. 2004, Cusson & Bourget 2005). Therefore, depth as such does not influence benthic communities directly but can be used as a proxy for other environmental variables and has often been shown to be associated with community composition at local scales (Underwood et al. 1991, Witman & Dayton 2001, Rule & Smith 2007). However, general correlations between depth and benthic community structure have little predictive power since the correlations between depth and other factors can vary spatially and temporally. The impact of fishing on benthic communities will thus depend on the characteristics of the communities that, in turn, are a response to the environment.

1.4 Development of ecosystem approaches to fisheries management (EAFM)

1.4.1 Overview of the compartments and interactions in the marine ecosystem

Current fisheries policies emphasize the importance of ensuring the sustainability of fishing impacts on the marine environment as well as the sustainable provision of food, consistent with an ecosystem approach to fisheries (FAO 2003b, Sinclair & Valdimarsson 2003) and driven by processes such as the Rio Convention on Biological Diversity and the World Summit on Sustainable Development. The expectations of society, as reflected in these policies, are formalized at the scale of the fishery as management objectives. The objectives usually reflect the outcome of complex negotiations that take account of short and long-term economic, social and environmental interests and define acceptable levels of environmental impact. These are expressed as limits and/ or targets depending on jurisdiction.

Since bottom fishing impacts the marine environment, scientific advice is needed to determine the scale and magnitude of impacts and their acceptability in relation to policy and management objectives. In jurisdictions where management objectives are not formalized, scientific research helps to identify impacts and the extent to which they are sustainable. Given that some of the environmental effects of fishing can clearly be unsustainable, the need to manage the impacts of bottom fishing gears is recognized in a range of management plans.

The ecosystem approach to fisheries, or ecosystem-based fisheries management, has provided a framework within which it is possible to account for such impacts. There are many definitions of an ecosystem approach to fisheries, but an EAF is broadly used to ensure that the planning, development and management of fisheries will meet social and economic needs, but without jeopardizing the options for future generations to benefit from the full range of goods and services provided by marine ecosystems (FAO 2003b).

Thus, the EAF seeks to recognize all human-related interactions with the biotic-abiotic environment. This environment includes four main compartments: the biotic compartment (i.e. all living species), the abiotic compartment (i.e. the non-living, physical characteristics of the environment), the fishery compartment and the institutional compartment (i.e. the management strategies) (FAO 2003a). All are involved in a complex network of 2-way interactions (figure 1.7).

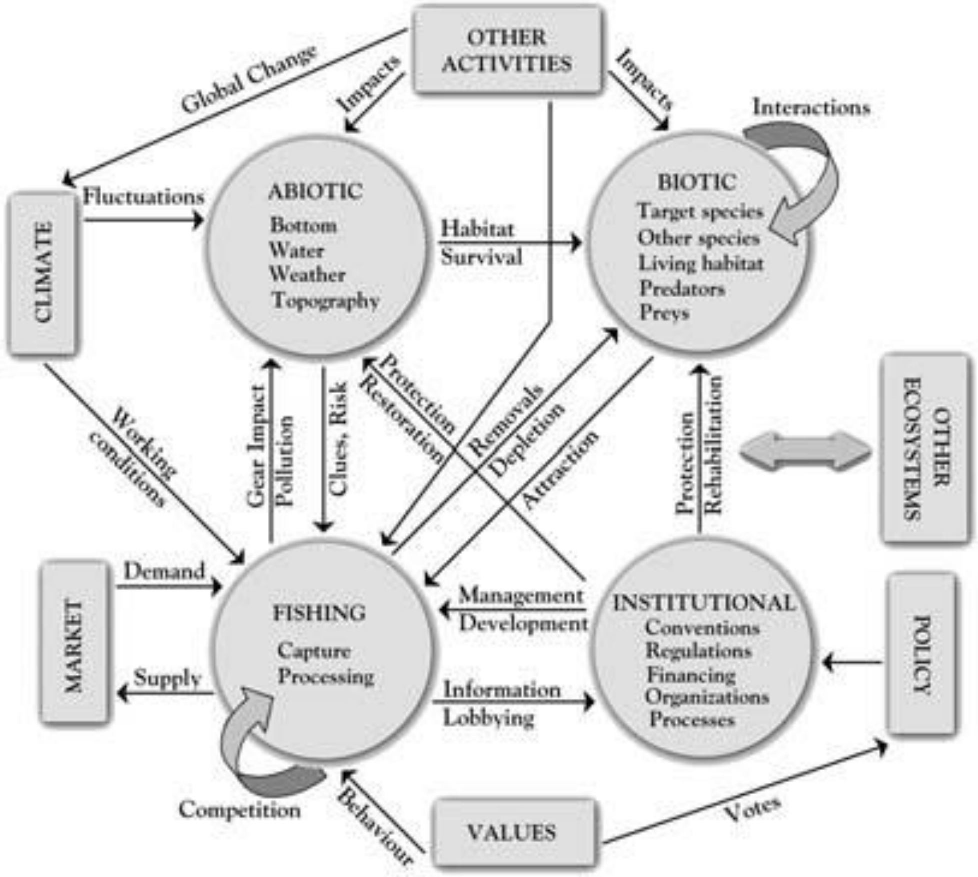

Figure 1. 7 Simplified diagram of a marine ecosystem and its components (from FAO 2003a)

1.4.2 The challenge faced by fisheries managers

Fisheries management has evolved alongside the expansion of fishing fleets as the economic, social and environmental consequences of unregulated fisheries have long been seen as undesirable. Trying to optimize the use of marine resources to address social, economic and environmental aspects of sustainability is challenging as social, economic and environmental objectives can be conflicting, at least in the short-term. As a minimum the EAF seeks to make all the trade-offs among objectives explicit in management decision making which is a significant step beyond conventional single species management that tended to focus on the trade-off between the state of stocks and economic or social benefits.

1.4.3 Conventions and agreements towards the implementation of an ecosystem approach to fisheries management

Alongside the increasing understanding of the wider effect of fishing activities and the failure of some management systems to meet their objectives, ecosystem protection measures have been integrated in some major international frameworks of fisheries and conservation since the 1980's. To cite only some of the most important ones, there is the 1982 United Nations Convention on the Law of the Sea, the 1992 Convention on Biological Diversity and the 1995 FAO Code of Conduct for Responsible Fisheries. In Europe, the Marine Strategy Framework Directive (MSFD) in 2008 aims to use an ecosystem approach to achieve Good Environmental Status (GES) in European seas by 2020. GES is defined by eleven descriptors including the maintenance of biological diversity of habitats and species and 'seabed integrity'. The arrival of the MSFD will be particularly influential because the MSFD defined a role for the Common Fisheries Policy in achieving GES. All in all, developing an ecosystem approach to fisheries (EAF) is now regarded, at least politically, a necessary step towards achieving the sustainable use of marine resources (FAO 2003b, Sinclair & Valdimarsson 2003).

Societal awareness of the specific needs to protect marine habitats and biodiversity from fishing impacts has increased since the early 1990's. Numerous regulations have been developed and implemented across the world under the guidelines of e.g. the Habitat Directive (EC 1992) and the MSFD (EC 2008c) in Europe, the Magnuson-Stevens Fishery Conservation and Management Act in the US (U.S.

Congress 1996) and the Convention on Biological Diversity (UNEP/CBD 2010) at the global scale. In transposing international commitments, in the UK, the Government has committed to putting in place an “ecologically coherent network” of Marine Protected Areas (MPAs) by 2012. The UK Biodiversity Action Plan has identified several priority species and habitats to protect. Amongst those habitats are horse mussel beds, maerl beds, subtidal sand and gravels and fragile sponge and anthozoan communities on subtidal rocky habitats, to cite only a few of the important vulnerable marine habitats that are potentially impacted by towed bottom fishing gears.

1.4.4 Impediments to the implementation of ecosystem approaches to fisheries management

Scientists and, more recently, fisheries economists, have been trying to quantify and integrate the interactions between ecosystem compartments into models that could be used to inform managers about the consequences of alternate management actions (e.g. development of Marine Strategy Evaluations (MSE) based on operational models such as Atlantis (Fulton et al. 2011)). Ecosystem models can be very useful to predict the impact of fishing a target species across the whole food web, or to predict the outcome of a specific management strategy such as the implementation of marine protected areas. In Europe, end-to end ecosystem models still under development and not directly used by fisheries managers yet but the development of the models has already benefited fisheries research through boosting cross-disciplinary collaborations and helping to identify gaps in knowledge.

Integrating all ecosystem compartments in a single model is very challenging. If a model manages to capture the complexity of the system to some extent, its implementation will often be impeded by the fact that it is too data intensive and that its parameterization can only be done in extensively studied ecosystems (Fulton et al. 2004a). Therefore, models have more often focused on one compartment, or even on one part of a compartment. Many models focus on the lower trophic levels (e.g. nutrient-phytoplankton-zooplankton-detritus (NPZD) models (e.g. Fennel et al. 2001)) or on the pelagic fish component of the biotic compartment (e.g. MSVPA (e.g. Livingston & Jurado-Molina 2000), OSMOSE (Shin & Cury 2004)) and fewer on the benthic compartment (e.g. Duplisea et al. 2002). However, in order to be able to predict changes from fishing or climate impacts, researchers are now collaborating to create end-to-end (E2E) models (Travers et al. 2007, Rose et al. 2010, Moloney et al. 2011).

E2E models take account of the whole abiotic-biotic marine system, sometimes even including the human pressure component (e.g. Atlantis). The creation of such models is still under-development as no existing model, or set of models, fully captures the whole picture without any flaw yet. An example is the Ecopath with Ecosim (EwE) model that has already been widely used around the world (Walters et al. 1997, Pauly et al. 2000, Christensen & Walters 2004). One of the issues associated with it is that it does not allow for the explicit modelling of environmental changes (Petihakis et al. 2007, Travers et al. 2007). It can however be modified to be used as a tool in more comprehensive E2E models including physical forcing, coupled benthic/pelagic food webs and nutrient recycling (Steele & Ruzicka 2011).

Other E2E models can be achieved by coupling several sub-models, i.e. NPZD, physical forcing, pelagic and benthic models, although linking model currencies (i.e. biomass or nutrients) and different spatial and temporal scales might be a non-negligible issue when sub-models have not been developed under the same framework (see reviews Travers et al. 2007, Rose et al. 2010). ERSEM is an example of such a piecemeal approach that has been developed under a single framework (Baretta et al. 1995). It is one of the most complex lower trophic level marine ecosystem models currently in use (Blackford et al. 2004). It is a biogeochemical model which couples a pelagic and a benthic sub-model and has been coupled to physical models such as GOTM (Allen et al. 2004) or to fish population models (Heath et al. 1997).

ERSEM represents the first attempt to integrate an explicit benthic compartment in an E2E model and it highlights the necessity to improve the current state of knowledge on seabed processes. The benthic-pelagic coupling is, in the model, described by the inputs of settling organic detritus into the benthos and diffusional nutrient fluxes into and out of the sediment (Allen et al. 1998) (figure 1.8).

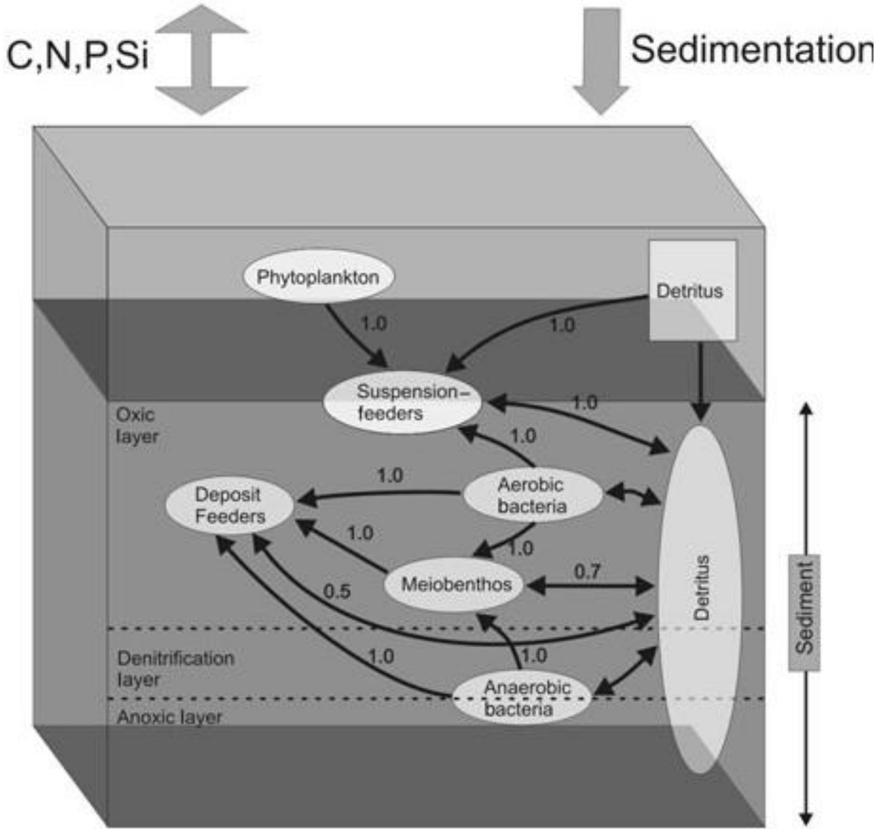

Figure 1. 8 Schematic representation of the benthic sub-model of the food web with energy flows and feeding preference factors as modelled in the ERSEM model (Petihakis et al. 2007)

There are several downfalls to this simplified benthic sub-model. One issue is that it does not integrate sediment resuspension/deposition or benthic primary production processes, while microphytobenthos has been shown to play a major role in photic seabed areas (Hochard et al. 2010). The model does not account for the effects of currents on sediment mixing and fluxes of carbon and other nutrients (Allen & Clarke 2007) (but see IGBEM model by Fulton et al. 2004b). Blackford (1997) has identified one of the key tasks in the future development of the model as being the coupling of physical sediment processes with the biology.

The rather gross definition of processes in the benthic compartment is a common feature to most ecosystem models. However, seabed topography and benthos must be considered integral parts of the physical dynamics, the biogeochemical cycling and food web processes leading to fish capture (Steele & Ruzicka 2011). As long as empirical information is lacking to strengthen the calibration and reliability of the models and as long as uncertainty cannot be assessed, the outcomes of any management recommendation will be ambiguous and will consequently be reluctantly taken onboard by stakeholders. Indeed, it is perhaps not surprising that most of the developers of ecosystem models see them as more valuable for scenario exploration than for tactical management. This message has not always been taken on board by the user community.

1.4.5 Identification of some gaps in empirical benthic knowledge

A range of scientific knowledge is needed to support management advice on the impacts of fishing and the development of management measures. While we have shown that there are many assessments of the effects of towed fishing gears on benthic habitats and the possible ramifications of these impacts, there is much less knowledge about the variations in sensitivity of habitats to fishing disturbance and the effects of fishing at the scale of management units (typically the fishery). One of the key issues is the absence of detailed information on the fine-scale distribution of habitats and fishing activity. Knowing with precision where and when a certain fishing activity occurred would help with quantifying the effect of fishing on benthic communities and, combined with having accurate recovery time estimates, would help identify the habitats to protect to meet different management objectives.

As mentioned earlier, progress on the quantification of fishing impact can be made through the use of VMS data that give information on fishing distribution and intensity. VMS is a form of satellite tracking using transmitters onboard fishing vessels. However, there are several caveats associated with the use of VMS data in fishing impact studies. These include incomplete coverage of vessels, long durations between position records and a lack of information on whether a vessel is actually fishing when the position is reported (Lee et al. 2010).

These caveats impede the reliable estimation of fishing extent and impact on the seabed. One of the major issues related to these caveats is that of the scale of aggregation at which fishing intensity is estimated (e.g. Piet & Quirijns 2009). Rijnsdorp et al. (1998) conducted pioneering work on the topic and showed how the apparent patchiness of fishing effort decreased with increasing scale of analysis. Thus the distribution of fishing effort only became random at the smallest cell size investigated, 1x1 mile squares. Therefore, it has been advocated that the size of the grid cells used to calculate fishing intensity should be the “smallest possible” (Rijnsdorp et al. 1998, Dinmore et al. 2003, Reiss et al. 2009). Failure to work at a resolution that adequately describes the heterogeneity of fishing pressure in time and space can lead to inaccurate estimates of the magnitude of fishing impacts (Mills et al. 2007, Piet & Quirijns 2009).

The number of studies looking at the recovery rates of marine benthos following fishing disturbance, either empirically or based on models, is very limited. The first obvious reason is logistics. Places where fishing has been banned for many years are very rare (Blyth-Skyrme et al. 2006). Moreover, monitoring such places over long periods of time would also require the availability of long-term funding. Subtidal sampling is generally complicated and costly which is probably one of the reasons why applications of ecosystem models to assess the wider effects of bottom fishing disturbance have been limited by the lack of empirical knowledge on the relationship between sediment biogeochemistry, water column inputs, environmental variables and benthic communities' responses.

Furthermore, recovery of benthic communities of disturbed patches is difficult to predict since it occurs through different processes. The recovery of chronically disturbed benthic communities on fishing grounds will be dependent on recruitment and population growth rather than on immigration from adjacent (or remote) untrawled areas, which is likely to be more important in smaller scale experimental trawling studies (Hiddink et al. 2006b). Recruitment on hard surfaces will depend on the pool of larvae or asexually produced fragments available in the water column shortly after the disturbance event. Those larvae and fragments may come from neighbouring areas but some larvae may also come from very remote areas, several tens of kilometers away (e.g. Pineda et al. 2007).

1.5 Objectives of the thesis and outline of the chapters

To summarize, the impact of towed fishing gears on the sessile epifaunal communities is of great concern to fisheries scientists and managers. There are, however, several gaps in our current understanding of the seafloor processes due the complex interactions between benthic communities and their environment. This impedes the modelling of the benthic compartment in ecosystem models that are currently being developed to advise fisheries managers. There is also a need to quantify and map the direct and indirect impacts of fishing activities and to predict the potential for recovery of structurally complex habitats to sustainably manage the marine ecosystem. The general objective of the present thesis was therefore to address some of these issues by determining the environmental drivers of sessile epifaunal community structure at large scales (tens of kms), by quantifying the impact of fishing and by assessing the potential for recovery of those communities and associated species. The thesis concludes by discussing the value of the methods and results for informing some management options that would limit the impact of fishing on benthic communities and habitats.

Chapter 2 deals with the issue of determining what the drivers of sessile epifaunal communities are. The effects of various environmental drivers are disentangled from the effect of fishing and the response of sessile habitat-forming species is analyzed. The vulnerability of those species to towed fishing gears and the associated loss in ecosystem function is determined. The implications for management are discussed.

Chapter 3 deals with the issue of the lack of accuracy in estimates fishing effort distribution. This issue is addressed by comparing different approaches for modelling fishing tracks based on VMS data. The chapter also focuses on understanding how spatial and temporal scales influence our estimates of fishing impact on benthic communities.

In Chapter 4 I develop a novel approach to analyze the potential for recovery of habitats in chronically fished grounds. The method relies on the estimation of the last disturbance event and on the analysis of the state of the benthic communities at given locations. Thereby, it combines multiple events at different stages of recovery to model the overall recovery trajectory of the habitat and associated species. The study tries to answer the question of the potential for communities to recover to a pre-fished state and to quantify the recovery rate in relation to environmental conditions.

Chapter 5 describes an indirect effect of fishing on benthic communities. The objective was to measure habitat complexity to analyze the relationship between mobile epifauna and complexity created by sessile epifauna and substrates. Two novel approaches were used to quantify habitat complexity, one based on the use of a laser line and one based on the heterogeneity in the pixel values of seafloor pictures.

Quantification and prediction of the impact of fishing on epifaunal communities

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Authors' contribution:

I analysed the pictures, conducted all the analyses and wrote the manuscript.

Simon Jennings, Michel Kaiser and Jan Hiddink supervised the work and helped at different stages: discussing the ideas, structuring the manuscript, writing it up.

Jan Hiddink further helped with the choice of the statistical methods.

Hilmar Hinz gave me access to the data, helped me with the identification of some species on the pictures and the interpretation of the results.

All authors proofread the manuscript before submission to the Journal.

2.1 Abstract

The loss of emergent epifaunal biomass due to fishing impacts has not been quantified at the scale of an entire fishery. Here, based on an analysis of the impacts of the scallop dredge fleet around the Isle of Man, Irish Sea, we show how fishing and the physical environment act to determine the biomass and size composition of emergent epifauna. The epifauna create habitat structure that is used by juvenile scallops and other species, thus providing an important ecosystem service. Epifauna were identified and quantified based on photographs taken during an extensive survey of the territorial waters of the Isle of Man. On hard substrata, the effect of tidal velocity on total biomass (g m^{-2}) and the maximum size (g) of the largest organism encountered in each taxon was positive while wave stress and fishing frequency had a negative impact. We used the results to predict the distribution of biomass and maximum size and to quantify the total effects of fishing. Fishing frequency was the most important factor that affected maximum size of the epifauna, resulting in a mean decrease in size of 17% (range 0 to 66%). Total biomass was predominantly affected by wave stress and tidal velocity while fishing caused a mean biomass decrease of 8% (range 0 to 34%), equivalent to 1.8 g wet weight m^{-2}. The results have implications for management because they provide an assessment of the overall impact of fishing at the scale of an entire fleet and inform the identification of areas where seabed habitats are most vulnerable to fishing.

2.2 Introduction

Developing an ecosystem approach to fisheries (EAF) is regarded as a necessary step towards achieving the sustainable use of marine resources (FAO 2003b, Sinclair & Valdimarsson 2003). In part, EAF requires that managers take account of fishing impacts, including those on seabed habitats. Bottom fishing, with towed gears such as beam trawls and scallop dredges, has direct (extraction of biomass, physical disturbance) and indirect effects (e.g. modification of trophic interactions) on benthic habitats (Kaiser et al. 2002a). The majority of fishing impact studies have focused on communities found in soft sediment and gravel habitats (Collie et al. 2000b, Kaiser et al. 2006a).

Emergent epifaunal species are here defined as all sessile or semi-sessile organisms that settle on hard surfaces or organisms with part of the body structure emerging from sediments. The growth forms, from encrusting to upright, create different levels of structural complexity and provide a source of food and/or shelter for other species. Epifauna are vulnerable to bottom fishing impacts and encrusting rather than upright emergent species dominate in fished areas (Collie et al. 1997, Bradshaw et al. 2001). Reductions in the abundance of emergent species are expected to lead to decreases in the range of ecological niches available for associated fauna (Gili & Hughes 1995, Collie et al. 1997, Bradshaw et al. 2003). Many emergent sessile species are associated with a micro-community of epifauna, e.g. caprellid amphipods on hydroids, or the fauna associated with pomatocerid tube worm heads (Kaiser et al. 1999). However, the response of emergent species to fishing has proved difficult to quantify in a systematic way owing to the difficulty of sampling fauna attached to hard substrata, variation in life-history traits (colonial versus single individuals, senescence of some hydroids in winter), variation in body-form with environmental conditions and the absence of precise estimates of the frequency and intensity of fishing impacts (Van Dolah et al. 1987, Kenchington et al. 2007).

Sessile epifaunal species and other habitat forming organisms are widely distributed on the continental shelf and display a range of life history traits and morphological characteristics that influence the environments where they are found and their vulnerability to fishing impacts. There is limited information on growth, reproduction, mortality and the ecological requirements of the sessile species that occur in northern European waters (see BIOTIC database, MarLIN website http://www.marlin.ac.uk/biotic/). The distribution of these biota is affected by substratum stability, turbidity, nutrient supply, light availability, temperature and hydrodynamic conditions that in turn affect the resilience of the habitat to fishing disturbance (Hall 1994, Jennings et al. 1999, Callaway et al. 2002). A better understanding of the relationships between fishing, structure and size of epifaunal species and their environment is a requirement for EAF, since it can inform debates about the extent to which impacts compromise management objectives, the consequences of alternate management options and the effects of interaction between fisheries and the environment (Hiddink et al. 2007).

Here, we assess the relationships between the biomass of sessile epifauna, fishing intensity and the environment to better understand the effects of fishing on benthic habitat forming epifauna. The main focus of this paper is to quantify the impact of fishing on sessile fauna that live on hard substrata. The present research was conducted in the territorial sea surrounding the Isle of Man, UK, where the scallop dredge fishery and the management restrictions applied to that fishery create gradients of fishing impacts on hard substrata. The seabed surrounding the Isle of Man has been fished by scallop dredgers for the last 60 years (Bradshaw et al. 2001). The availability of high resolution fishing effort data for these fisheries permitted a reliable quantification of fishing impacts on sessile species across an environmental gradient.

2.3 Material and methods

2.3.1 Data collection

Survey design

One hundred and twenty stations were sampled within the 12 nautical mile territorial limit of the Isle of Man in August 2008 (figure 2.1). The stations were located on a regular grid with 5km spacing to provide a comprehensive coverage of the seabed features around the island. Photographs of the seabed habitat were taken with a high resolution Canon 400D digital camera installed in an underwater housing and fitted to a sledge such that the objective lens pointed perpendicularly towards the seabed from a height of 60cm above the seabed. The sledge was towed for fifteen minutes at each station at a speed of 0.5 to 0.7 knots, covering an average distance of about 300m, as calculated from the starting and ending positions of each tow. Every nine seconds, a 10-mega-pixel photograph was taken (ca. 100 pictures per station), each photograph recorded an area of 0.14 m^2. At each station, prior to the sledge tow, a 0.1 m^2 Day grab was used to sample the sediment and a continuous CTD profile (depth, salinity and temperature) was recorded while the water column density was recorded every metre.

Still photographs analysis

Quantification of the habitat forming epifauna was based on a detailed analysis of the still photographs. Since such analyses are very time-consuming, ten still photographs from each selected station (ca. every 10th picture) were analysed using the grid and area measurement functions of Image J software 1.43 (National Institute of Mental Health, USA). All the benthic habitat-forming organisms on the photographs were identified to the lowest possible taxonomic level. Identified species were from the phyla Porifera, Cnidaria, Bryozoa and Chordata (class Ascidiacea) and Mollusca (class Bivalvia) and Arthropoda (family Balanidae).

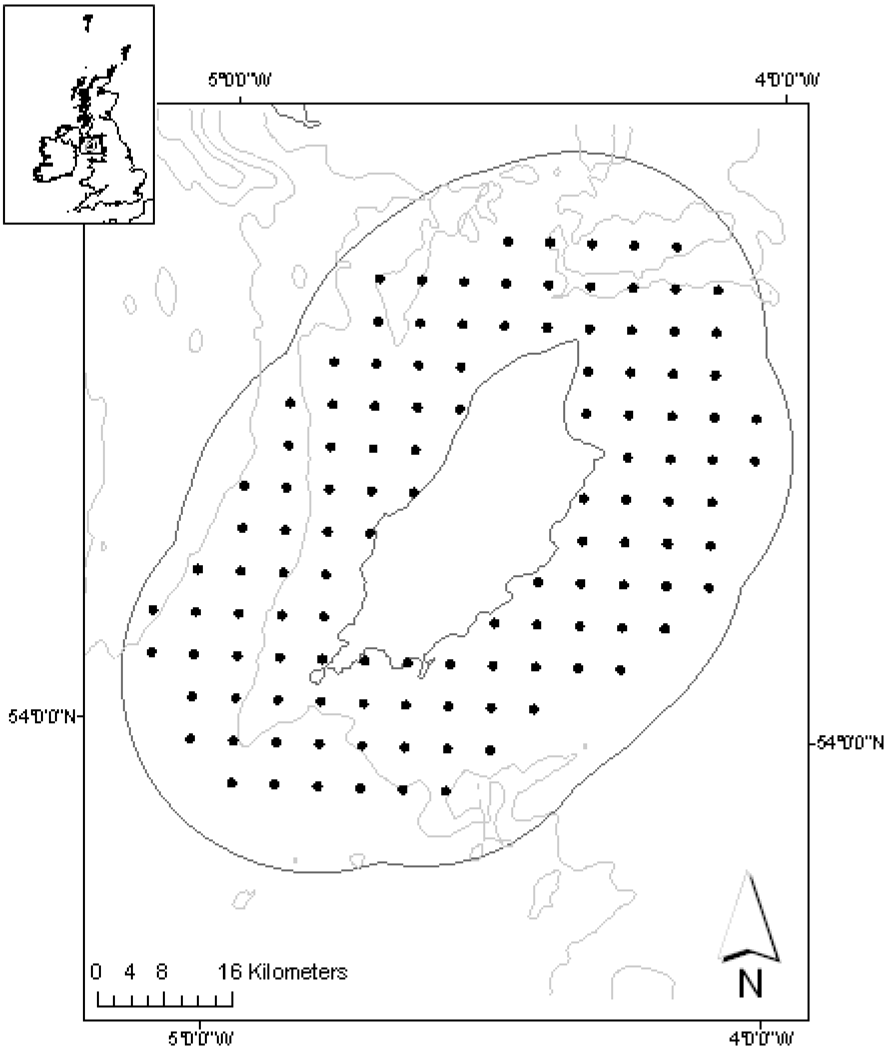

Figure 2. 1 Location of the 120 stations surveyed within 12 nautical miles of the Isle of Man. Light grey lines are 50 m bathymetric depth.

Hereafter, the different groups are referred to as sponges, cnidarians, bryozoans, tunicates, bivalves and barnacles respectively. Despite the high quality of the images, identification and quantification of the sessile epifauna presented some significant challenges. First, some encrusting species were identified that could not be reliably related to any taxonomical group. Second, epifaunal Annelida could not be quantified as it was impossible to distinguish between live and dead specimens as live tubeworms are usually retracted in their tubes. Third, the taxonomy of many organisms could not be resolved below the level of phylum, as most organisms necessitate microscopic study to identify distinguishing features. Species were, therefore, mostly grouped into phyla, although cnidarians were split into the classes: Hydrozoa (hydroids) and Anthozoa (dead man's fingers and anemones). In addition to the taxonomic groupings, analyses were based on two major functional traits: (i) body plan, colonial vs. solitary, and (ii) body shape, two dimensional encrusting vs. hard calcified species such as bivalves and barnacles vs. flexible organisms such as emergent cnidarians, bryozoans, tunicates and sponges (see Annex A for details on the dominant species).

To quantify the coverage of each taxon, a grid of 96 intersection points was superimposed onto each photograph and the number of intersection points covered by the each taxon recorded. Each point represented 1/96, i.e. 1.04% of the total coverage.

Biomass estimation of habitat forming species

Although coverage describes one aspect of community structure, biomass is also a relevant metric when assessing the effects of human impacts, because size distributions of individuals as well as their frequency of occurrence can be modified. Consequently, we analysed two dimensional encrusting species in terms of coverage but we estimated the biomass for emergent species. To enable us to estimate biomass from the images, upright sessile organisms, collected with a scallop dredge in the Isle of Man in October 2009, were used to determine relationships between the area of organisms (in the pictures) and mass. Each organism was weighed to ±0.001 g and then pinned to a flat wooden panel on the bottom of a deep tank filled with seawater, before being photographed with the same equipment and same camera position used during the photographic survey. The area covered by each organism was calculated with ImageJ. Organisms were classified into those that could be treated as two dimensional (hydroids, mound shape sponges and bryozoans such as *Flustra foliacea* and *Cellaria sinuos*a) and those to be treated as three dimensional (ascidians, anthozoans and erect sponges). The equations linking area of coverage to mass are given in Annex B.

On the survey photographs, the area covered by each taxon recorded under the intersection points was measured with ImageJ. Before applying the area-mass equations to estimate biomass from the survey photographs, it was necessary to correct for the orientation of the organism in relation to the seabed, which varied in response to current speed. A subsample of 18 organisms was used to link the area covered by an organism lying on the seabed to the area covered by this same organism tilted at 20, 45 or 80 degrees from the seabed. The correction factors obtained were respectively 1.09, 1.24 and 1.91. On the survey photographs, the angle of exposure was estimated visually, along with the number of layers when the species formed a multilayer clump. An estimation of the flat area covered by each recorded organism was then obtained by multiplying the covered area by its correction factor and by the number of layers. The corrected mass was then determined by applying the area-mass equations to the corrected area for each organism (Annex B). All biomass data were fourth-root-transformed prior to statistical analyses to reduce heteroscedasticity in the data. The maximum size reached by any organism within each group (in g) and total biomass of the whole community (in g.cm^{-2}) per station were reported. Total biomass was the sum of individual mass measurements.

Fishing effort data

Fishing effort data for king and queen scallop dredging vessels were obtained from the European Community Satellite Vessel Monitoring System (VMS). UK and Isle of Man VMS data within the 12nm off the Isle of Man coast were provided by the Isle of Man Ministry of Fisheries. Because the information for the Isle of Man fleet came from fishermen’s log-books and because all the UK vessels in these waters were above 15m and fitted with VMS transceivers, we achieved 100% coverage of fishing vessel activity for the period 2007-2008. In the absence of pre-2007 data, we assumed that the distribution of the effort was consistent among years because fishers were most likely to repeatedly return to locations that they knew from past experience (Kaiser 2005). The VMS data do not indicate whether a vessel is fishing when its position is recorded but its speed can be used as an indication of its activity. The data obtained by the Department of Agriculture, Fisheries & Food were filtered on the assumption that speeds between 1.2 and 3.2 knots indicated fishing activity as scallop fishing gear as used in waters around the Isle of Man is most effective when fished within this range of towing speeds (Jenkins et al. 2001). We defined fishing intensity as the number of times an area of 1km^2 was swept by fishing gears in one year (y). A fishing frequency of 1 y^{-1} means that the 1km^2 area has been swept once on average during a one year period. Each VMS record was assumed to represent 2 hours of fishing as this is the recording interval. The area dredged by each vessel per unit time was calculated as the product of fishing speed and gear width. Fishing speed was calculated as the average fishing speed per vessel based on all VMS records for that vessel. To calculate gear width, vessels fishing within 3nm were assumed to use 10 dredges (each with a width of 0.76 m), while vessels fishing between 3 and 12nm were assumed to carry 16 dredges, the maximum numbers of dredges allowed in each of these fishing zones respectively. The sum of the area dredged in each 1km^2 cell was calculated with ArcGIS 9.3, giving the actual fishing frequency. Fishing frequency ranged from 0 to 2.8y^{-1}, similar to the range of fishing intensities estimated for other areas in European shelf seas (Jennings et al. 2001a, Hiddink et al. 2006c).

Environmental data

The depth at the sampled stations ranged from 6 to 100m. Salinity and temperature measurements were excluded from further analyses because the measured ranges were narrow and not expected to have a differential effect on the species of interest within the survey area. This is because the species of interest were euryhaline (able to tolerate a wide range of salinities) whereas the recorded range of bottom salinity was narrow (32.9 to 34.2‰). Similarly, the average sea surface temperature range was narrow, 14.0-15.5°C. The bottom temperature range was slightly wider, 12.6-15.8°C, but still represented only a snapshot in time that was unlikely to influence epifaunal distributions. The extent of stratification did vary among stations and an index of stratification, the potential energy anomaly (PEA), was calculated from the density profiles. PEA is the difference between the actual PE of the water column and the PE of the same water column after being vertically mixed (eq. 1). The higher the PEA value, the more stratified the water column. PEA was calculated as:

(eq. 1) $$PEA\ (Joules.m^{-3}) = \frac{1}{h}\sum_z gz(\bar{\rho} - \rho)\Delta z$$

where h = total depth of the water column, g = 9.81m.s^{-2}, $\bar{\rho}$ = density of one block of water in the water column (1 block every metre), ρ = density of the vertically mixed water column, z = depth of the block of water (Simpson et al. 1982).

A sample of 50cm^3 of the surface sediment in the grab sample was removed for particle-size analysis. Samples were stored in the dark at 3°C. Laboratory analysis followed standard methods (Eleftheriou & Moore 2005). The percentage of mud in the sediment was considered as a factor that could affect epifaunal distributions as it is a surrogate for substratum stability. An unstable substratum might not be suitable for the development of sessile organisms. As the presence of coarse substratum precluded some grab collections, substratum type was qualitatively identified from the still images (i.e. mud (Mu), sand (S), sand-shell (SS), maerl (Ma), mixed gravel (MG) and hard (H) (including cobbles and rocks)). We also considered the percentage of living bivalves as an environmental parameter, since many other species appeared to settle on their shells regardless of the dominant substratum type at the station.

Estimates of wave-induced bed shear stress and tidal velocity at the study sites, were obtained from a model developed for the Irish Sea (see detailed description in Hiddink et al. 2009). The wave stress is a measure of the orbital velocity (m.s^{-2}) due to waves at the seabed and the tidal velocity is the peak speed (m.s^{-1}) of the depth-mean current at the time of mean tides (i.e. midway between spring and neap tides).

Long term data series of chlorophyll a (chl a) and turbidity were downloaded from NEODAAS (NERC Earth Observation Data Acquisition and Analysis Service, http://www.neodaas.ac.uk/). Surface chl a and turbidity averages (where K_{490} is the diffuse attenuation coefficient at 490nm) were obtained from the MODIS sensor (1km scale resolution). The data provided were monthly averages for the period 2002-2007. They were provided as GeoTIFF files, in digital numbers (DN). Mean summer chlorophyll a and turbidity per 1km^2 cell was calculated for the whole period, with ArcGIS 9.3. We adopted this approach because the overall productivity and biomass in the food web will depend on time-integrated production rather than instantaneous rates. Data were extracted for each station and, based on the recommendations given by the data provider, the following equations were applied:

(eq2) $MODIS\ Chlorophyll\ a\ (mg.m^{-3}) = 10^{\lfloor (DN \times 0.015) - 2 \rfloor}$

(eq3) $MODIS\ Turbidity\ K_{490}(m^{-1}) = 10^{\lfloor (DN \times 0.011176) - 2 \rfloor}$

The wave stress and percentage of living bivalve data was corrected by logarithmic transformation to achieve homogeneity.

2.3.2 Data analysis

Identification of the responses of habitat forming species to dredging activities and to environmental gradients

To identify the environmental factors that affect the coverage of encrusting species and the maximum size and total biomass of emergent ones, we used univariate quantile regressions (Koenker & Bassett 1978, Cade & Noon 2003). Quantile regressions are linear models that allow the response data to be split into quantile classes. The function fits a model by minimizing a weighted sum of absolute residuals (see Cade et al. 1999 for further details on the method). For instance, the 95th quantile describes the function in which 95% of the observations are under the fitted line. Such a quantile can be used to examine how the biomass of the fauna is limited by a factor, regardless of the presence of other limiting factors (Blackburn et al. 1992, Cade & Noon 2003). The 75th, 80th, 85th, 90th and 95th quantiles of epifaunal coverage and biomasses measurements of different functional and taxonomic groups were tested in relation to fishing frequency and to each environmental variable to determine which parameters were inducing a response of the epifauna and at which quantile levels they showed an effect. The choice of these five quantiles was adapted from an approach used to detect species responses (Vaz et al. 2008). The use of different quantiles did not impair the interpretation of the results as the regressions were only used to detect potential limiting factors rather than to compare responses among variables. Although looking at five different quantiles led to over-estimates of the number of significant responses, the use of the quantiles was necessary to identify all the potential limiting factors to include in the final multi-linear models.

Linear rather than non-linear quantile regression models were used because the fit of non-linear models often depends on the starting values given as inputs. A strong statistical test would then be required to test for the goodness-of-fit, as no such test exists for non linear quantile regressions so far as we are aware. First and second order polynomial linear quantile regressions of epifaunal biological data on fishing frequency and environmental parameters, both raw and log-transformed (except for the initially log-transformed wave stress and percentage of living bivalves data), were statistically tested to identify the shape of the responses. The standard errors, on which the goodness of the fit was estimated, were calculated using a standard bootstrapping method implemented in R (R Development Core Team, http://www.r-project.org/). The highest significant quantile was kept for each significant model within each species group. In each species group, the significant models were then compared by using the Akaike's Information Criterion (AIC) (Venables & Ripley 2002). The model with the lowest AIC was selected. We could consequently summarize, for each species groups, which external factors were likely to affect their maximum size and total biomass and the shape of the response.

Univariate quantile regressions could only be applied to numerical variables. Therefore, the effect of substratum type on epifauna was studied separately by analysis of variance. The individual effects of the different substratum types were analyzed with a multiple comparison *post hoc* Tukey test.

Spatial autocorrelations

The existence of spatial autocorrelations in the biomass data would affect the significance of the relationships between species distribution and external factors as identified from the analyses described above. The Moran's I and Geary's C weighted spatial autocorrelation indices are generally used to check for such autocorrelations (Jumars et al. 1977, Southward et al. 2005, Kraan et al. 2009). The

Moran's I test detects global autocorrelations within the whole study area while the Geary's C test is more sensitive to local autocorrelation in close neighbourhoods.

The weights are inversely proportional to the distance^2 between stations. However, because the sampling area surrounded the Isle of Man, the distance between eastern and western stations was interrupted by the land mass and hence was not informative about spatial autocorrelation. The near surface currents flow from the south to the north of the island on both the western and eastern coasts, which divided the sampling area in terms of ecological connectivity. The spatial autocorrelation analyses were thus conducted separately within the western stations and within the eastern stations. The tests were performed at the species group level, i.e. bivalves, barnacles, hydrozoans, anthozoans, bryozoans, sponges and tunicates.

Identification of the drivers and prediction of epifaunal development using a multivariate approach

The explanatory variables, or factors, showing a consistent and significant effect across all or most functional and taxonomical groups, as identified from the univariate quantile regression analysis, were retained for further analyses. The objective was to assess the relative contribution of these factors to the development of habitat forming communities in hard bottom areas. Most classical multivariate analyses techniques cannot be used because explanatory variables are noisy, partially redundant or co-linear (Cushman et al. 2008). We checked for co-linearity of potential explanatory variables by calculating the Spearman's rank correlation coefficient for each pair of parameters. We found that most factors were significantly correlated (table 2.1). Depth was directly excluded as a potential explanatory factor because it could only impact the epifauna indirectly through its correlation to the other environmental gradients. Stratification was highly correlated with depth (correlation coefficient = 0.86, $p < 0.001$) and other factors so this was also excluded. Since we could not make measurements of mud content at the hard bottom stations, the percentage of mud was also excluded from the multivariate analyses. We used Partial Least Squares (PLS) regressions for our multivariate analyses, with the PLS package in R (Mevik & Wehrens 2007). PLS has only recently been applied to terrestrial and fresh water ecology studies (Rossi et al. 2008, Zhang et al. 2009) while it has been widely used in other scientific fields, especially in chemometrics; the science of extracting information from chemical systems by data-driven means (Wold et al. 2001). PLS regressions have been developed to deal with cases where there are many explanatory variables in relation to the number of observations and/or with cases of severe multicollinearity (Carrascal et al. 2009). A PLS regression is a linear regression of one or more response variables onto a number of components called latent variables. The latent variables are linear combinations of the factors, also called predictor variables. They are constructed so that the original multi-collinearity is reduced to a lower number of orthogonal factors. PLS regression differs from principal component analysis (PCA) because PLS regression maximizes the covariance between the scores and the response (Mevik & Wehrens 2007, Rossi et al. 2008) while PCA maximizes variance of the scores. The variance explained and the root mean squared error of prediction (RMSEP) were used to determine the number of relevant components. The Variable Importance in the Projection (VIP) approach (Chong & Jun 2005) was used to order the pertinent original explanatory variables by rank importance. To determine the final model we selected the explanatory variables with VIP values greater than 1, the standard criterion for factor selection (Chong & Jun 2005). We calculated the coefficients of the linear regression between predicted response values and observations and we extracted the regression coefficients of the significant factors in the PLS regression to estimate the final model and test the goodness of the fit. The computations were done in R with the function VIP.R available online at http://mevik.net/work/software/VIP.R. All continuous factors were log-transformed to correct for heteroscedasticity.

Table 2. 1 Pearson correlation coefficients for all combinations of environmental variables and fishing frequency. PEA: potential energy anomaly. Significance levels: ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, · : $p < 0.1$ Depth in m, PEA in Joules.m^{-3}, Tidal velocity in m.s^{-1}, Turbidity in m^{-1}, Mud in %, Wave stress in m.s^{-2}, % Bivalve in % cover, Fishing frequency in y^{-1}

	Depth	PEA	Chlorophyll a	Tidal velocity	Turbidity	Mud	Wave stress	% Bivalve	Fishing frequency
Depth	1	0.86***	-0.43***	0.25*	-0.65***	0.48***	-0.66***	-0.11	-0.1
PEA		1	-0.34***	0.04	-0.69***	0.60***	-0.53***	0	0.01
Chlorophyll a			1	-0.12	0.72***	-0.18 ·	0.08 ·	0.16	-0.17 ·
Tidal velocity				1	0.12	-0.37***	-0.41**	-0.18 ·	-0.18 ·
Turbidity					1	-0.51***	0.26***	0.02	-0.17 ·
Mud						1	-0.25***	0.17	0.13
Wave stress							1	0.05	0.07
% Bivalve								1	-0.03
Fishing frequency									1

2.4 Results

Impact of scallop dredging on benthic epifauna

The maximum size and total biomass of the emergent habitat-forming organisms were significantly limited by fishing frequency (figure 2.2, table 2.2), but there was no relationship between fishing frequency and the coverage of encrusting species (table 2.2).

At the functional level, solitary, colonial and flexible groups were negatively affected (i.e. exhibited significantly decreasing responses), and hard body species appeared to be positively affected, (i.e. exhibiting significantly increasing responses). Analyses at the taxonomic level revealed some differences among taxa. The biomass and maximum sizes of Cnidaria were negatively related to fishing frequency, although for the maximum size of Anthozoa this was not a significant relationship (figure 2.2, table 2.2). The relationships between maximum size and total biomass of Balanidae, Bryozoa and Ascidiacea with fishing frequency were not significant (figure 2.2). Porifera and Bivalvia responded positively to increasing fishing frequency. There were few data for Bivalvia and Balanidae and consequently for the overall hard body functional group and these data were unlikely to represent the response of these groups to fishing disturbance. The survey design and the image analysis method were not well adapted to biomass estimation for small species such as barnacles or to motile, gregarious and/or semi-buried bivalves. Indeed, bivalves recorded in the images were primarily free-swimming queen scallops; only half of the images at one of the stations covered a *Modiolus* bed, while king scallops were only recorded in the images from two stations.

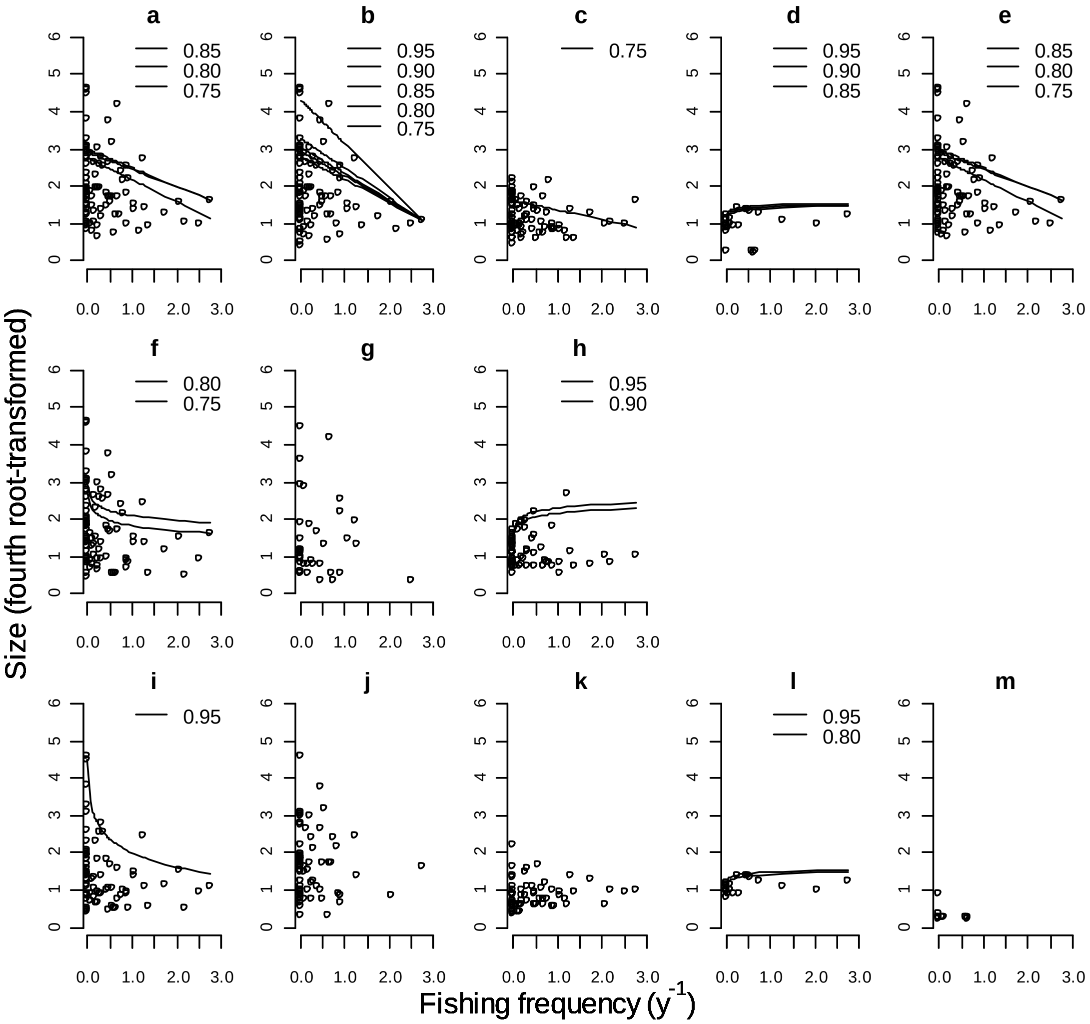

Figure 2. 2 Relationship between maximum size of the different species groups and fishing frequency.Size is the fourth-root transformed maximum biomass (g) observed at each station. Black lines are the significant quantile regressions. Significant quantiles are listed in each panel. Equations and statistics of the highest significant quantiles are given in table 2.2. Functional groups: (a) emergent epifauna, (b) colonial species, (c) solitary species, (d) hard body species, (e) flexible species. Phyla: (f) Cnidaria, (g) Bryozoa, (h) Porifera. Families: (i) Hydrozoa, (j) Anthozoa, (k) Ascidiacea, (l) Bivalvia, (m) Balanidae

Table 2. 2 Results of the quantile regressions of the species biological measurements on fishing frequency: sign of the impact (positive +, negative -), slope estimates and probabilities. $_{log}$ indicates whether the factor was log-transformed (see methods for model selection). No entry corresponds to no significant impact. See also figure 2.2.

Species group	Variable	Dredge impact	Slope	p-value	Quantile
Encrusting	Coverage				
Emergent	Maximum size	-	-0.492	0.010	85
	Total biomass	-	-0.805	0.013	80
Colonial	Maximum size	-	-1.172	0.047	95
	Total biomass	-	-0.768	0.021	80
Solitary	Maximum size	$-_{log}$	-0.098	0.030	80
	Total biomass	$-_{log}$	-0.117	<0.001	95
Hard body	Maximum size	$+_{log}$	0.059	0.017	95
	Total biomass	+	0.657	0.040	80
Bivalvia	Maximum size	$+_{log}$	0.060	0.032	95
	Total biomass	+	0.657	0.043	80
Balanidae	Maximum size				
	Total biomass				
Flexible	Maximum size	-	-0.492	0.011	85
	Total biomass	-	-0.482	0.017	85
Cnidaria	Maximum size	$-_{log}$	-0.191	0.034	80
	Total biomass	-	-0.597	0.036	90
Hydrozoa	Maximum size	$-_{log}$	-0.543	0.002	95
	Total biomass	$-_{log}$	-0.454	0.012	95
Anthozoa	Maximum size				
	Total biomass	-	-0.592	0.031	90
Bryozoa	Maximum size				
	Total biomass				
Porifera	Maximum size	$+_{log}$	0.146	0.025	95
	Total biomass	$+_{log}$	0.254	0.024	95
Ascidiacea	Maximum size				
	Total biomass				

Epifaunal responses to environmental variables

Analyses of variance revealed that the coverage of encrusting species, as well as the maximum size and total biomass of emergent biota, varied significantly with substratum type (table 2.3, figure 2.3), such that fauna with the greatest maximum size and total biomass occurred on stable substrata, i.e. mixed gravel and hard bottom. In contrast, for hard-bodied non-sessile species there was no relationship between biomass and/or size and substratum type.

Univariate quantile regressions revealed that all functional and taxonomical groups, except for encrusting species, hard bodied species and Porifera, followed similar significant patterns along the different environmental gradients. Maximum sizes and total biomass peaked or decreased with depth, increased with tidal velocity, peaked or decreased with stratification, increased with chlorophyll a, decreased with mud content of the sediment, increased with turbidity and decreased with wave stress (figure 2.3, table 2.4, see Annex C for equations and statistics). Although the functional and species groups did not all respond significantly to all the environmental factors (table 2.4), the similarity of the responses did not justify the grouping of the emergent sessile epifauna at different functional or taxonomical levels. Within the group of emergent flexible species, only Porifera had a divergent response as the maximum size and total biomass appeared to decrease in the highest range of the tidal velocity gradient. The Porifera were also positively influenced by the percentage cover of bivalves. However, the responses of the Porifera group to the different variables were likely to be biased because of spatial autocorrelations, see later. The bivalve biomass estimates followed a different pattern as they increased with the mud content of the sediment. Encrusting species and barnacles did not show any response with any of the environmental gradients.

In summary, these results show that the biomass of only the emergent epifauna is largely related to the external factors considered in this study. Substratum category, fishing frequency, depth, stratification, tidal velocity, chlorophyll a, turbidity, mud in the sediment and wave stress were all potential drivers of the emergent epifauna.

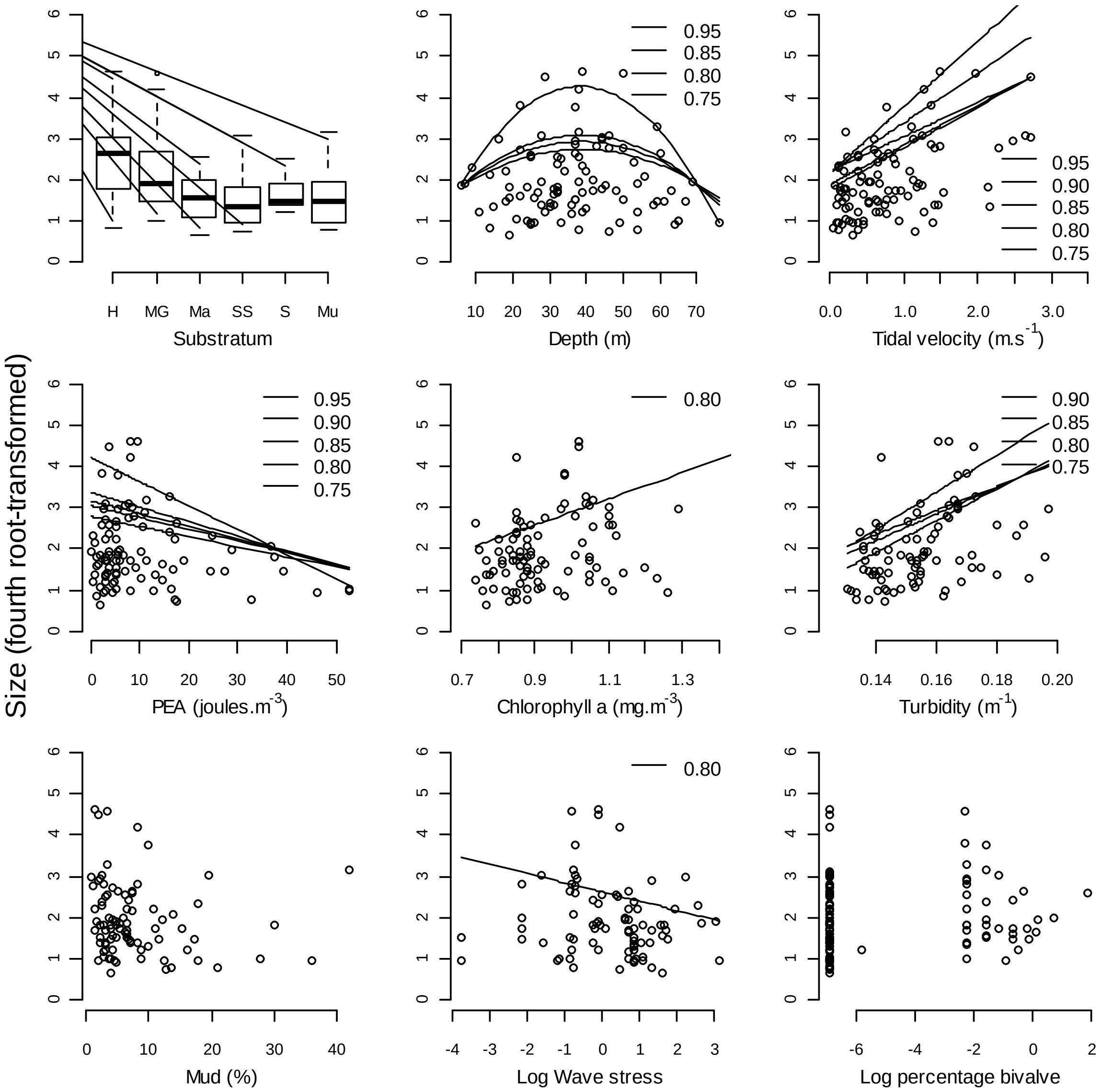

Figure 2. 3 Maximum size in the overall sessile community in relation to different environmental parameters. Substratum types are hard (H), mixed gravel (MG), maerl (Ma), sand-shell (SS), sand (S), mud (Mu). Size is the fourth-root transformed maximum biomass (g) observed at each station. Black lines are the significant quantile regressions (see Annex C for statistics, see also table 2.4). Significant quantiles are listed in each panel. PEA: potential energy anomaly.

Table 2. 3 ANOVA of the species biological measurements in relation to substratum type. MS = Maximum size; TB= Total biomass. Significance levels: ***p < 0.001, **p < 0.01, *p < 0.05. Significant comparisons between substratum types are revealed by Tukey's HSD test.

Species group	Variable	Anova			Tukey test		
		df	F	p-value	Significant comparison	Difference	p-value
Encrusting	Coverage	5	6.703	<0.001***	Sand-Hard	-0.136	0.003
					Mud-Hard	-0.145	<0.001
					Mud-Mixed gravel	-0.105	0.006
					Mud-Sand shell	-0.102	0.027
Emergent	MS	5	4.379	0.001**	Sand shell-Hard	-1.020	0.020
					Mud-Hard	-1.000	0.007
	TB	5	11.197	<0.001***	Sand shell-Hard	-1.509	0.009
					Sand-Hard	-1.769	0.001
					Mud-Hard	-2.204	<0.001
					Sand-Mixed gravel	-1.328	0.017
					Mud-Mixed gravel	-1.763	<0.001
Colonial	MS	5	2.406	0.043*			
	TB	5	10.179	<0.001***	Sand-Hard	-1.512	0.016
					Mud-Hard	-2.249	<0.001
					Mud-Mixed gravel	-1.891	<0.001
Solitary	MS	5	8.780	<0.001***	Sand shell-Hard	-0.688	0.001
					Sand-Hard	-0.678	0.002
					Mud-Hard	-0.722	<0.001
					Sand shell-Mixed	-0.531	0.016
					gravel	-0.521	0.027
					Sand-Mixed gravel	-0.565	0.002
					Mud-Mixed gravel		
	TB	5	10.595	<0.001***	Sand shell-Hard	-1.030	0.002
					Sand-Hard	-1.180	<0.001
					Mud-Hard	-1.306	<0.001
					Sand-Mixed gravel	-0.841	0.012
					Mud-Mixed gravel	-0.966	<0.001
Hard body	MS	4	0.434	0.550			
	TB	5	2.500	0.035*			
Bivalvia	MS	4	1.005	0.437			
	TB	5	2.359	0.045*			
Balanidae	MS	4	0.932	0.513			
	TB	5	0.825	0.535			
[a]Flexible	MS	5	4.383	0.001**	Sand shell-Hard	-1.041	0.017
					Mud-Hard	-1.000	0.007
	TB	5	10.915	<0.001***	Sand shell-Hard	-1.521	0.009
					Sand-Hard	-1.760	0.001
					Mud-Hard	-2.200	<0.001
					Sand-Mixed gravel	-1.301	0.023
					Mud-Mixed gravel	-1.742	<0.001

[a]All taxonomic groups were not given as they were all showing the same pattern as the overall flexible group

Table 2. 4 Environmental factors limiting the maximum size and total biomasses of the different species groups. Equations and statistics are given in Annex C. See also figure 2.3. MS = Maximum size; TB= Total biomass. + and – indicate the response shape of the significant quantile regressions (+- and -+ correspond to convex and concave response curves). $_{\log}$ indicates whether the environmental variable was log-transformed (see methods for model selection).

Depth in m, PEA in Joules.m^{-3}, Tidal velocity in m.s^{-1}, Turbidity in m^{-1}, Mud in %, Wave stress in m.s^{-2}, % Bivalve in % cover, Fishing frequency in y^{-1}

Species group	Variable	Depth	Tidal velocity	Stratification	Chl a	Mud	Turbidity	Wave	%Bivalve
Encrusting	Coverage								
Emergent	MS	+-	+	-	+		+	$-_{\log}$	
	TB	+-	$-+_{\log}$	$-_{\log}$	$+_{\log}$	$-_{\log}$	$+_{\log}$	$-_{\log}$	
Colonial	MS	+-	+		$+_{\log}$		$+_{\log}$		
	TB	+-	$+_{\log}$	$+-_{\log}$	$+_{\log}$	$-_{\log}$	$+-_{\log}$	$-_{\log}$	
Solitary	MS		$-+_{\log}$	-	$+_{\log}$	-	+-		
	TB		+	-	$+-_{\log}$	$-_{\log}$	+		
Hard body	MS		$+-_{\log}$			$+_{\log}$		$-_{\log}$	
	TB	+-	+-						
Bivalvia	MS		$+-_{\log}$			$+_{\log}$		$-_{\log}$	
	TB								
Balanidae	MS								
	TB								
Flexible	MS	+-	+	-	+		$+_{\log}$	$-_{\log}$	
	TB	+-	$-+_{\log}$	$-_{\log}$	$+_{\log}$	$-_{\log}$	$+_{\log}$	$-_{\log}$	
Cnidaria	MS		+	-	+		$+_{\log}$	$-_{\log}$	
	TB	+-	$+_{\log}$	-	$+_{\log}$	$-_{\log}$	$+_{\log}$	$-_{\log}$	
Hydrozoa	MS		$-+_{\log}$		$+_{\log}$		$+_{\log}$		
	TB	-	$-+_{\log}$	-	$+_{\log}$	$-_{\log}$	+-		
Anthozoa	MS	+-	$+_{\log}$	$+-_{\log}$			$+_{\log}$	$-_{\log}$	
	TB	+-	+	-	$+_{\log}$	-	+	$-_{\log}$	
Bryozoa	MS		+	-					
	TB	-	+	-	$-_{\log}$				
Porifera	MS		-						$-+_{\log}$
	TB		+-	-		-+			$-+_{\log}$
Ascidiacea	MS	-		-+		$-_{\log}$			
	TB	-		$-_{\log}$		$-_{\log}$			

Spatial autocorrelations

Sponge biomass was strongly spatially autocorrelated in both the western and eastern areas (table 2.5). There was no other strong spatial autocorrelation within the eastern stations. The cnidarian species, Hydrozoa and Anthozoa, were only spatially autocorrelated in the western area, with a low Moran's I value. All other species groups did not show any strong pattern which suggested that, although not all species were independently distributed, the responses of the sponge biomass to external factors should be interpreted with caution.

Table 2. 5 Results of the Moran's I and Geary's C spatial autocorrelation tests.

Area	Species Group	Moran's I	Moran's I p-value	Geary's C p-value
East	Bivalvia	0.007	0.212	0.704
East	Balanidae	0.005	0.096	0.156
East	Hydrozoa	0.034	0.01	0.169
East	Anthozoa	0.01	0.171	0.042
East	Bryozoa	0.035	0.005	0.031
East	Porifera	0.077	<0.001	<0.001
East	Ascidiacea	0.017	0.09	0.89
West	Bivalvia	0.027	0.018	0.416
West	Balanidae	-0.004	0.116	0.893
West	Hydrozoa	0.128	<0.001	<0.001
West	Anthozoa	0.068	<0.001	<0.001
West	Bryozoa	-0.013	0.825	0.903
West	Porifera	0.081	<0.001	<0.001
West	Ascidiacea	0.037	0.005	0.208

Identification of the factors driving epifaunal characteristics

Based on the above results, to assess the impact of the different factors driving maximum size and biomass in a multivariate analysis, we conducted the analyses on the combined biomass of the emergent sessile epifauna, including hard bodied species and Porifera. These data were combined because the biomass of the component groups was low.

The responses of epifaunal biomass to depth, stratification and mud content of the sediment were not accounted for in the multivariate analyses (see methods).Owing to the significant effect of substratum type, and because it was the only categorical variable, we modelled stable habitats separately from unstable habitats using the remaining five factors in the PLS regressions. For both maximum size and total biomass in stable habitats, five latent variables were identified, from which we kept the first two because the RMSEP decreased only slightly with an increasing number of components. The variability explained by these two components was 90% (52 + 38) for maximum size and 90% (45 + 45) for total biomass; and the responses were similar for both biological measurements. The VIP values indicated that fishing frequency was the most important factor, followed by tidal velocity and wave stress for maximum size. For total biomass, wave stress and tidal velocity preceded fishing frequency (table 2.6). The VIP values of chlorophyll a and turbidity were less than 1 on both components and so discarded. A similar model could not be fitted to data for unstable mud or sand substrata as the RMSEP values increased with the number of latent variables. This showed that no combination of the above factors could explain the variability of biomass.

Table 2. 6 Variable importance in projection for each original variable in latent variables 1 and 2 (LV1 and LV2) for both maximum size and total biomass of habitat-forming organisms in hard-bottom areas.

	Maximum size		Total biomass	
	Comp1	Comp2	Comp1	Comp2
Fishing frequency	1.40	1.45	0.95	1.16
Tidal velocity	1.28	1.30	1.39	1.34
Wave stress	1.17	1.07	1.46	1.34
Chlorophyll a	0.14	0.18	0.17	0.21
Turbidity	0.01	0.02	0.01	0.03

In stable substratum areas, the linear regressions relating predicted and measured biomass were significant (F = 11.7, p = 0.001 and r^2 = 0.18 for maximum size; F = 8.8, p = 0.005, r^2 = 0.14 for total biomass). The equations were the following:

(eq. 4) $\sqrt[4]{W} = 0.956\widehat{W} + 2.163$

(eq. 5) $\sqrt[4]{B} = 0.960\hat{B} + 2.201$

With W and B being the measured maximum size (g) and total biomass (g.m^{-2}), and $\widehat{W}$ and $\hat{B}$ being the corresponding predicted values calculated from the following equations:

(eq. 6) $\widehat{W} = 0.231V - 0.163S - 0.068F$

(eq. 7) $\hat{B} = 0.217V - 0.180S - 0.027F$

with tidal velocity (V) in m.s^{-1}, wave stress (S) in m.s^{-2} and fishing frequency (F) in y^{-1}. All were multiplied by 100 and increased by +1 before being log-transformed. Equations 6 and 7 were used to predict the distribution of the epifaunal biomass around the Isle of Man with and without fishing activities during the year preceding the sampling (figure 2.4). The loss of total biomass due to fishing was estimated between 0 and 34%, with an average of 8%, equivalent to 1.8g.m^{-2}, while the decrease in size due to fishing was estimated between 0 and 66%, with an average of 17%.

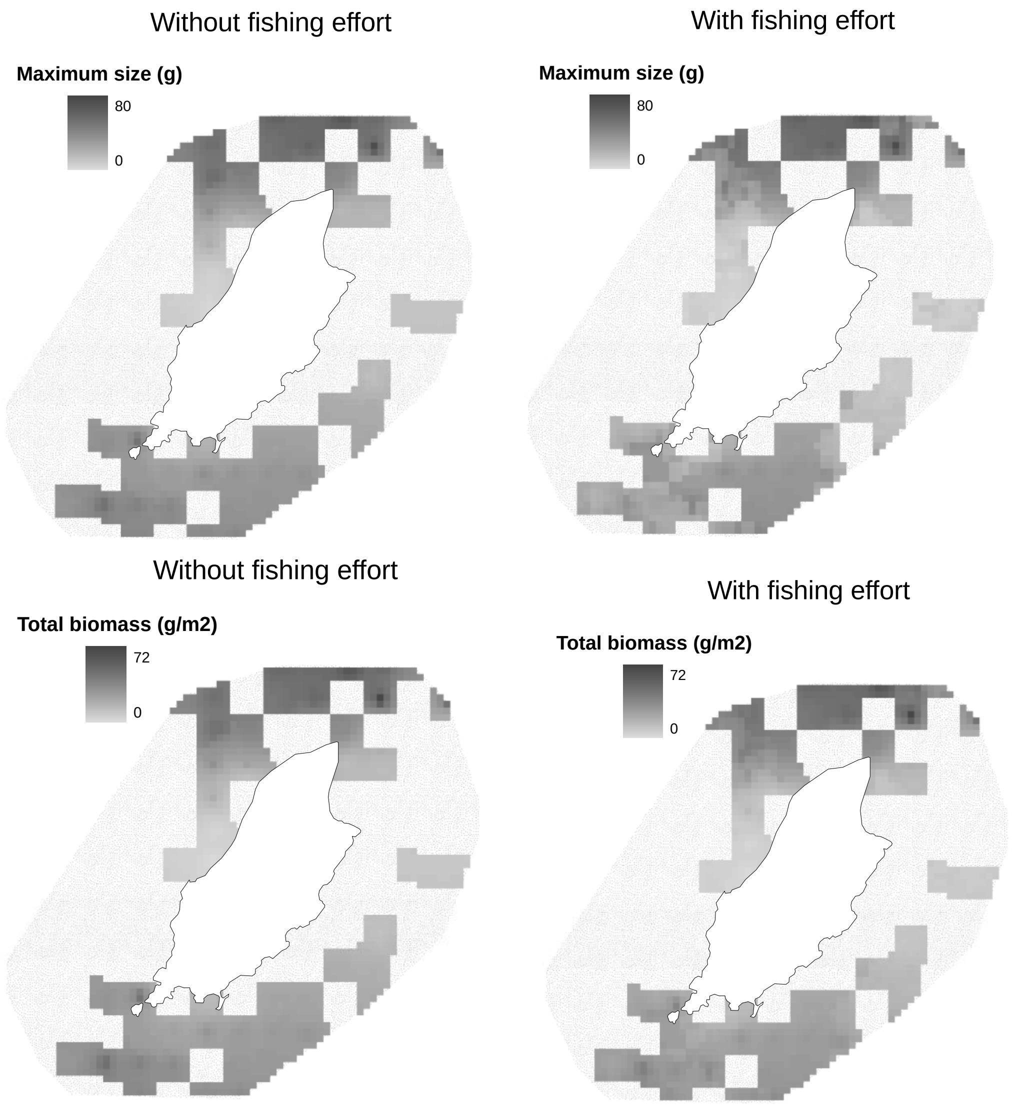

Figure 2. 4 Predictive maps of potential maximum size (top) and total biomass (bottom) of sessile epifauna based on the presence of hard substrata and the hydrodynamics conditions without (left) and with (right) fishing effort. The dotted area represents unstable substratum types.

2.5 Discussion

Scallop dredging changes the size distribution and biomass of sessile epifauna, although the effects were not significant at all taxonomic levels. The effects are demonstrated in the present study at an appropriate scale for the assessment and management of fisheries using an approach that has hitherto been limited to the study of soft-sediment communities that are technically simpler to sample (Hiddink et al. 2006c). The changes in emergent epifauna with fishing observed here are qualitatively consistent with patterns in other fished areas (Auster et al. 1996, Collie et al. 1997, Thrush et al. 1998, Collie et al. 2000a, Bradshaw et al. 2001, Kaiser et al. 2006a), however our results provide new insights into the magnitude of fishing effects at the scale of an entire fishing fleet and the interaction between the effects of fishing and the environment. The final estimate of biomass loss due to fishing has, however, to be interpreted with caution as most organisms had very flexible structures that impaired some estimates of coverage or biomass based on photographic methods.

Studies of fishing impacts are usually based on experimental manipulations of fishing intensity, comparisons of fished and unfished areas or trends in time series (Eleftheriou & Robertson 1992, Thrush et al. 1995, Auster et al. 1996, Hill et al. 1999, Kaiser et al. 2006a). These studies have sought to reduce variability due to the environment within the experimental design to focus on fishing effects. Conversely, we sought to assess fishing impacts at a large and fishery relevant scale while taking account of the environmental variation that was present.

Our results showed that the distribution of habitat forming species was not only dependent on the fishing frequency but also on the availability of hard substratum, tidal velocity and wave stress. At the scale of our study, chlorophyll *a* and turbidity did not explain the observed distribution of the epifauna. Hard substratum provides an opportunity for these fauna to settle and develop. The responses of the epifauna to wave stress and tidal velocity were mostly monotonic which may have been due to the range covered by the gradients and to the lack of data in the extreme values of the gradients. Stronger tidal currents were generally associated with a higher biomass of emergent epifauna, consistent with the dependence of production on water flow that influences feeding efficiency, colony morphology and patch size (Wildish & Kristmanson 1997, Coma et al. 1998, Rees et al. 1999). Increasing wave stress was associated with a decrease in the biomass and maximum size of the emergent epifauna, consistent with the recognition that it can be a source of mortality in benthic communities (Emerson 1989). Wave induced mortality is known to impact community structure to a water depth of approximately 50m on continental shelves (Oliver et al. 1980, Hall 1994, Hiddink et al. 2006c), but below 50m it is unlikely that wave erosion will dislocate or damage organisms that are anchored to the seabed or substratum (Wildish & Kristmanson 1997). Our study revealed peak biomass and body sizes at intermediate depth, which may correspond to an area of where there is an optimum trade-off between tidal currents and wave stress (see also Kaiser et al. 2006b).

The analysis of taxon specific responses to fishing and the environment was informative about more complex interactions in the epifaunal communities. Although spatial autocorrelations might have influenced the significance of the responses, sponges were the only taxon limited by the percentage cover of bivalves, which reflected the affinity of sponges for *Modiolus* beds and their colonisation of living queen scallop shells. The total biomass and maximum size of sponges and bivalves both decreased at the highest tidal velocities, which may reflect their larval settlement abilities or their feeding modes. The efficiency of passive suspension feeding tends to rely upon the flux of seston while active suspension feeding is most likely determined by seston concentration (Lesser et al. 1994). Bivalves, barnacles and most sponges are active suspension feeders while hydroids and anthozoans are mostly passive feeders (Labarbera 1984, Wildish & Kristmanson 1997, Coma et al. 1998, Bell & Okamura 2005). Colony morphology may also have an important influence on feeding success since it influences the relationship between flow and prey-capture success (Sebens & Johnson 1991, Coma et al. 1998). The complex upright structure of some passive emergent epifauna might induce a higher efficiency in particle capture at higher flow regimes than their smaller active suspension feeder counterparts, such as the sponges observed at the studied sites.

The community studied herein was similar to the cobble community described by Henry et al. (2006) on the Western Bank, northwest Atlantic, being dominated by hydroids such as *Hydrallmania falcata*, *Abietinaria abietina* and *Halecium halecinum*, as well as the anthozoan *Alcyonium digitatum,* bryozoan *Cellaria* *sinuosa* and tunicate *Ascidia spp*. However, Henry et al. (2006) reported that the biomass of these habitat-forming species was not affected by fishing. This apparent contradiction can be explained because Henry et al. (2006) studied the impact of a single pass of an otter trawl whereas repeated scallop dredging over longer time periods in a real fishery will have greater impacts on benthic habitats and fauna (e.g. Collie et al. 2000b).

Reductions in the biomass of epifauna reduce habitat complexity (Cranfield et al. 2004, Sanderson et al. 2008). The present study further suggests that, not only the overall biomass decreases, but also the size distribution moves towards small body-sized organisms, and although not the primary focus of the present study, this loss in complexity is expected to affect other species such as mobile epifauna or juvenile fish that rely on the shelter or food that habitat heterogeneity provides (Auster et al. 1996, Scharf et al. 1998, Bradshaw et al. 2003). Because of the loss in biomass of sessile organisms due to fishing, the fishery may also have a direct impact on the recruitment of scallops if it reduces habitat to an extent that habitat availability becomes limiting, as scallop spat have been observed to settle on emergent species such as the bryozoans *Cellaria sinuosa* (figure 2.5, Paul 1981, personal observation). Further research on the degree of specialisation of the associations between scallop spat and sessile organisms would be very relevant to fisheries management in light of the findings of the present study.

Encrusting species may benefit from the removal of erect species that compete for space and food (Collie et al. 2000a, Bradshaw et al. 2001). In our study, the group of encrusting species, consisting of unidentified two dimensional bryozoans and sponges, did not show any response to fishing disturbance. Identifiable sponges, however, showed a positive response to fishing intensity. Although these were categorised as emergent epifauna, most species are mound shaped and encrusting (e.g. *Myxilla incrustans* or *Hemimycale columella*), and, thus, the increase in biomass may be a response to the removal of other, more upright, epifauna. Additionally, sponges are known to be able to adapt their body-form in response to physical environmental conditions (Bell & Barnes 2000). If the sponge species observed in our study are able to adapt their body-form to a less vulnerable encrusting morphology, they may benefit from the impact of fishing on the competing epifauna.

Quantile regressions and partial least squares regressions are rarely adopted in studies of human and environmental impacts (see Vaz et al. 2008, Carrascal et al. 2009 for further details), but were valuable tools to reveal relationships in a dataset with multiple interacting environmental factors. Quantile regressions can handle zero-inflated datasets (Vaz et al. 2008), which was useful when studying variation in rare taxonomic groups. As with other linear regression methods these approaches can provide misleading results if the numbers of observations are not evenly distributed along fishing or environmental gradients, and they have been criticised for describing potential rather than realised patterns (Eastwood et al. 2003). The use of partial least square regressions (PLSR) was intended to eliminate these limitations while dealing with the problem of co-linearity among predictors. The outcome of the PLSR was significant for the hard bottom areas, and consistent with the responses identified by the quantile regressions. Additional tests of the predictive model will require further data collection in areas with comparable environmental conditions.

Figure 2. 5 Settlement of Aequipecten opercularis spat on the complex sessile turf of bryozoa Cellaria sinuosa and hydroid Sertularella gayi, illustrating the role of emergent epifauna as a settlement substrate for scallops. Sample collected by a scallop dredge during the October 2009 survey in the Isle of Man waters (Photograph © Hilmar Hinz)

We have shown that it is possible to quantify and model the biomass and size distribution of emergent habitat forming species. The main model predictors were hard substratum availability, fishing frequency and hydrodynamics knowledge. These habitats previously have been under-represented in studies designed to quantify the impact of fishing activities on seabed biota, as these communities are problematic and time-consuming to sample in a quantitative and repeatable way. The communities associated with hard substrata are of conservation importance because they tend to be dominated by epifaunal turfs that have high levels of associated diversity and provide as source of prey and shelter to species of commercial importance. Including only natural factors in the model, it was possible to predict the potential distribution of these habitats and thus to identify areas that were potentially sensitive to fishing impacts from areas where, despite the absence of fishing, sessile species were not likely to develop (figure 2.4). Based on our model, we limited the mapping to the distribution of sessile epifauna on hard substrata. Further research would be necessary to provide a complete map of habitat sensitivity as all soft substratum areas (dotted grey area on the maps, figure 2.4), were not modelled. In these areas, anemones, *Modiolus*, maerl beds and special bed forms have been observed. Our study provides an important step towards being able to quantify the loss in ecosystem services associated with sessile fauna in relation to fishing frequency, such that it will be possible to formulate management strategies to assess the sustainability and mitigation of such effects.

2.6 Annexes

2 0 Annex A1 – List of species, or species groups, representing the top 90% of the cumulative biomass by substratum type.

Indeterminate species were grouped as indet. A number was given to species that could be identified but not assigned to taxa. Total biomass represented the cumulative biomass calculated from the analysis of the photographs.

Substratum	Species	Total biomass (g)	Percentage	Cumulative percentage
Mud	*Alcyonium digitatum*	101.28	23	23
Mud	Anemones indet.	89.09	21	44
Mud	*Nemertesia spp.*	76.36	18	62
Mud	Sponges indet.	54.44	13	74
Mud	*Cellaria spp.*	36.94	9	83
Mud	*Sertularella spp.*	18.2	4	87
Mud	Hydroids indet.	16.04	4	91
Maerl	*Alcyonium digitatum*	131.37	42	42
Maerl	Hydroid 5	45	14	56
Maerl	*Myxilla incrustans*	23.59	8	64
Maerl	*Dysidea fragilis*	22.55	7	71
Maerl	Sponges indet.	13.54	4	75
Maerl	*Modiolus modiolus*	12.56	4	79
Maerl	Anemones indet.	12.12	4	83
Maerl	Sponge 8	6.43	2	85
Maerl	*Hemimycale columella*	5.76	2	87
Maerl	Hydroid 6	5.73	2	89
Maerl	*Aequipecten opercularis*	5.1	2	91
Sand	*Cellaria fistulosa*	77.01	40	40
Sand	Sponges indet.	28.72	15	55
Sand	Hydroids indet.	25.32	13	68
Sand	*Alcyonidium diaphanum*	17.45	9	77
Sand	Anemones indet.	12.1	6	83
Sand	*Cellaria spp.*	7.92	4	87
Sand	*Abietinaria abietina*	7.55	4	91
Sand shell	*Alcyonium digitatum*	182.8	34	34
Sand shell	*Abietinaria abietina*	89.46	16	50
Sand shell	*Clavelina lepadiformis*	77.35	14	64

Sand shell	*Halecium halecinum*	52.41	10	74
Sand shell	*Kirchenpaueria pinnata*	50.86	9	83
Sand shell	*Urticina felina*	36.92	7	90
Pebble	*Alcyonium digitatum*	2351.26	53	53
Pebble	*Alcyonidium diaphanum*	1008.25	23	76
Pebble	*Nemertesia antennina*	473.77	11	87
Pebble	Anemones indet.	187.72	4	91
Cobble	*Alcyonium digitatum*	2484.18	45	45
Cobble	*Cellaria sinuosa*	759.87	14	59
Cobble	*Nemertesia antennina*	632.11	12	71
Cobble	Hydroids indet.	419.09	8	79
Cobble	Sponges indet.	207.4	4	82
Cobble	Anemones indet.	133.87	2	85
Cobble	*Flustra foliacea*	111.42	2	87
Cobble	*Urticina spp.*	89.62	2	89
Cobble	*Nemertesia spp.*	58.54	1	90
Hard	*Hydrallmania falcata*	668.68	47	47
Hard	*Alcyonium digitatum*	181.82	13	59
Hard	*Alcyonidium diaphanum*	176.48	12	72
Hard	*Urticina spp.*	141.43	9	81
Hard	*Abietinaria abietina*	65.46	5	85
Hard	*Nemertesia antennina*	63.53	4	90
Hard	Hydroids indet.	20.72	1	91

2 0 Annex A2- Taxonomical and functional groups of species from Annex A1

Species	Phylum	Class	Body plan	Body shape
Abietinaria abietina	Cnidaria	Hydrozoa	Colonial	Flexible
Aequipecten opercularis	Mollusca	Bivalvia	Solitary	Hard body
Alcyonidium diaphanum	Bryozoa	Gymnolaemata	Colonial	Flexible
Alcyonium digitatum	Cnidaria	Anthozoa	Colonial	Flexible
Anemones indet.	Cnidaria	Anthozoa	Solitary/Colonial	Flexible
Cellaria fistulosa	Bryozoa	Gymnolaemata	Colonial	Flexible
Cellaria sinuosa	Bryozoa	Gymnolaemata	Colonial	Flexible
Cellaria spp.	Bryozoa	Gymnolaemata	Colonial	Flexible
Clavelina lepadiformis	Chordata	Ascidiacea	Colonial	Flexible
Dysidea fragilis	Porifera	Desmospongiae	Colonial	Flexible
Flustra foliacea	Bryozoa	Gymnolaemata	Colonial	Flexible
Halecium halecinum	Cnidaria	Hydrozoa	Colonial	Flexible
Hemimycale columella	Porifera	Desmospongiae	Colonial	Flexible
Hydrallmania falcata	Cnidaria	Hydrozoa	Colonial	Flexible
Hydroid 5	Cnidaria	Hydrozoa	Colonial	Flexible
Hydroid 6	Cnidaria	Hydrozoa	Colonial	Flexible
Hydroids indet.	Cnidaria	Hydrozoa	Colonial	Flexible
Kirchenpaueria pinnata	Cnidaria	Hydrozoa	Colonial	Flexible
Modiolus modiolus	Mollusca	Bivalvia	Solitary	Hard body
Myxilla incrustans	Porifera		Colonial	Flexible
Nemertesia antennina	Cnidaria	Hydrozoa	Colonial	Flexible
Nemertesia spp.	Cnidaria	Hydrozoa	Colonial	Flexible
Sertularella spp.	Cnidaria	Hydrozoa	Colonial	Flexible
Sponge 8	Porifera		Colonial	Flexible
Sponges indet.	Porifera		Colonial	Flexible
Urticina felina	Cnidaria	Anthozoa	Solitary	Flexible
Urticina spp.	Cnidaria	Anthozoa	Solitary	Flexible

2 0 Annex B- Equations used to calculate species biomasses based on photographs measurements

Organisms	Unit	Equation	x parameter	Details	Conversion factor (Brey 2001)
2D-organism	g WW	$0.001x^2+0.046x$	area covered in cm^2	$r^2=0.92$, this paper	
3D-organism	g WW	$0.014\ x^2+0.720x$	area covered in cm^2	$r^2=0.88$, this paper	
[a]*Balanus crenatus*	g AFDW	$\exp(x-2.03)/0.24$	basal diameter in cm	(adapted from Asmus 1987)	Total weight to wet tissue weight=0.010 AFDW/WW= 0.038
Pecten maximus	g WW	$\exp(-12.14)*x^{3.22}+\exp(-34.51)*x^{7.63}$	length in mm	(adapted from Allison 1994)	
Aequipecten opercularis	g WW	$\exp(-9.79)*x^{2.74}+\exp(-18.93)*x^{4.51}$	length in mm	(adapted from Allison 1994)	
Modiolus modiolus	gWW	$\exp(-10.88+3.00*\ln(x))$	length in mm	(adapted from Brown et al. 1976)	
Modiolus modiolus	gWW	$\exp(-9.96+3.32*\ln(x))$	height in mm	(adapted from Brown et al. 1976)	

[a]*Balanus crenatus* is the most abundant species in the UK subtidal waters, so this equation was applied to all barnacles.

2 0 Annex C - Results of the quantile regressions of the species biological measurements on environmental factors: slope estimates and probabilities, referring to table 2.4 in the paper.

Species	Variable	Factor	Slope	p-value	Quantile
Emergent	Maximum size	Depth	0.176	0.003	95
			-0.002	0.004	
		Tidal velocity	1.598	<0.001	95
		Stratification	-0.059	0.036	95
		Chlorophyll a	3.163	0.021	80
		Turbidity	45.362	0.008	90
		Wave	-0.222	0.022	80
	Total biomass	Depth	0.103	0.015	90
			-0.001	0.007	
		Tidal velocity	1.589	<0.001	80
			0.481	0.014	
		Stratification	-0.532	0.036	85
		Chlorophyll a	4.670	0.042	90
		Mud	-0.587	0.045	85
		Turbidity	11.923	0.014	95
		Wave	-0.890	0.039	95
Colonial	Maximum size	Depth	0.188	0.007	95
			-0.002	0.012	
		Tidal velocity	1.598	<0.001	95
		Chlorophyll a	2.994	0.019	80
		Turbidity	7.044	0.009	90
	Total biomass	Depth	0.077	0.044	85
			-0.001	0.017	
		Tidal velocity	1.134	<0.001	95
		Stratification	0.915	0.040	80
			-0.331	<0.001	
		Chlorophyll a	8.326	0.045	95
		Turbidity	-153.792	0.022	80
			-42.928	0.019	
		Mud	-0.728	0.025	85
		Wave	-0.948	0.031	95
Solitary	Maximum size	Tidal velocity	0.824	0.006	85
			0.301	0.026	
		Stratification	-0.024	<0.001	95
		Chlorophyll a	2.202	0.007	90
		Turbidity	281.096	0.003	95
			-808.712	0.008	
		Mud	-0.022	0.022	75

	Total biomass	Tidal velocity	0.549	0.004	80
		Stratification	-0.022	0.037	80
		Chlorophyll a	1.654 -5.692	0.005 0.024	95
		Turbidity	13.506	0.040	95
		Mud	-0.287	0.042	80
Hard body	Maximum size	Tidal velocity	-0.378 -0.195	0.007 0.012	95
		Mud	0.264	<0.001	95
		Wave	-0.101	0.010	95
	Total biomass	Depth	0.068 -0.001	0.024 0.025	90
		Tidal velocity	1.436 -0.514	0.031 0.041	80
Bivalvia	Maximum size	Tidal velocity	-0.371 -0.195	0.033 0.038	95
		Mud	0.264	<0.001	95
		Wave	-0.100	0.011	95
Flexible	Maximum size	Depth	0.176 -0.002	0.003 0.004	95
		Tidal velocity	1.598	<0.001	95
		Stratification	-0.059	0.025	95
		Chlorophyll a	3.163	0.020	80
		Turbidity	8.446	0.044	95
		Wave	-0.222	0.022	80
	Total biomass	Depth	0.098 -0.001	0.017 0.005	90
		Tidal velocity	1.590 0.481	<0.001 0.015	80
		Stratification	-0.533	0.036	85
		Chlorophyll a	8.276	0.036	95
		Turbidity	11.923	0.014	95
		Mud	-0.587	0.044	85
		Wave	-0.890	0.039	95
Cnidaria	Maximum size	Tidal velocity	1.171	0.006	95
		Stratification	-0.020	0.030	75
		Chlorophyll a	3.471	0.020	85
		Turbidity	4.790	0.044	90
		Wave	-0.249	0.028	85
	Total biomass	Depth	0.133 -0.001	0.035 0.030	95
		Tidal velocity	0.780	0.005	95
		Stratification	-0.045	<0.001	95
		Chlorophyll a	6.304	0.039	95
		Turbidity	11.249	0.004	95
		Mud	-0.471	0.047	80

		Wave	-0.303	0.040	80
Hydrozoa	Maximum size	Tidal velocity	1.707 0.612	0.022 0.048	90
		Chlorophyll a	5.304	0.030	90
		Turbidity	7.082	0.021	90
	Total biomass	Depth	-0.022	0.032	75
		Tidal velocity	2.203 0.714	0.001 0.010	95
		Stratification	-0.036	0.028	95
		Chlorophyll a	7.896	0.007	95
		Turbidity	908.752 -2692.902	0.022 0.035	95
		Mud	-0.898	0.009	95
Anthozoa	Maximum size	Depth	0.113 -0.002	0.028 0.020	95
		Tidal velocity	0.316	0.029	85
		Stratification	-0.044	0.047	90
		Turbidity	5.321	0.024	80
		Wave	-0.252	0.039	85
	Total biomass	Depth	0.066 -0.001	0.020 0.007	90
		Tidal velocity	0.653	0.031	80
		Stratification	-0.024	0.029	95
		Chlorophyll a	2.726	0.021	85
		Turbidity	24.539	0.030	80
		Mud	-0.035	0.012	90
		Wave	-0.262	0.029	75
Bryozoa	Maximum size	Tidal velocity	1.190	0.049	85
		Stratification	-0.104	0.041	95
	Total biomass	Depth	0.047	0.012	95
		Tidal velocity	1.741	0.031	95
		Stratification	-0.027	0.014	95
		Mud	-0.755	0.004	90
Porifera	Maximum size	Tidal velocity	-0.223	0.033	90
		%Bivalve	0.393 0.048	0.003 0.008	75
	Total biomass	Tidal velocity	1.796 -0.651	0.004 0.005	95
		Stratification	-0.024	0.017	95
		Mud	-0.049 0.001	<0.001 0.034	80
		%Bivalve	0.454 0.052	0.067 0.122	80
Ascidiacea	Maximum size	Depth	-0.008	0.038	85

	Stratification	-0.062 0.001	0.004 0.038	90
	Mud	-0.270	0.116	95
Total biomass	Depth	-0.010	0.023	90
	Stratification	-0.235	0.037	80
	Mud	-0.265	0.036	80

Implications of using alternate methods of Vessel Monitoring System (VMS) data analysis to describe fishing activities and impacts

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Authors' contribution:

I came up with the idea, conducted all the analyses and wrote the manuscript.

Simon Jennings, Michel Kaiser and Jan Hiddink supervised the work and helped at different stages: discussing the ideas, structuring the manuscript, writing it up.

Niels Hintzen gave me access to the VMS library for R that he was developing as part of a European project, taught me how to use it and verified some of my code and results.

Hilmar Hinz helped me with the interpretation of the results and suggested one of the analyses.

Lee Murray provided me with the VMS data and expert advice on the use of the datasets.

All authors proofread the manuscript before submission to the Journal.

3.1 Abstract

Understanding the spatial distribution and intensity of fishing activity is a prerequisite for estimating fishing impacts on seabed biota and habitats. Vessel Monitoring Systems (VMS) data provide information on fishing activity at large spatial scales. However, successive position records can be too infrequent to describe the complex movements of fishing vessels. We collected high frequency position data to assess how polling frequency and the method of analysis affected the estimates of fishing impact on the seabed and associated epifaunal communities. Comparisons of known positions with predictions from track interpolation showed that the performance of interpolation depended on fleet behavior. Descriptions and indicators of fishing intensity were significantly influenced by the analytical methods (track reconstruction, density of position records) and the grid cell resolution used for the analysis. We showed how these factors can lead to the underestimation of fishing impact on epifaunal communities. It is necessary to correct for such errors if we are to be able to quantify the effects of fishing on various ecosystem components and hence to inform ecosystem-based management. Thirty minute polling would provide a desirable compromise between achieving precise estimates of fishing impacts on the seabed and minimizing the cost of data collection and handling.

3.2 Introduction

Ecosystem approaches to fisheries management often take account of the sustainability of fishing activities on the ecosystem, including seabed habitats (FAO 2003b, Sinclair & Valdimarsson 2003). However, the capacity to assess ecosystem impacts will be influenced by the availability of detailed information on the location and intensity of bottom fishing activities. In Europe, vessel monitoring systems (VMS) were introduced for fishery control and enforcement purposes but are increasingly used to support the assessment of fishing activity and marine spatial planning (EC 1997, Dinmore et al. 2003, Murawski et al. 2005, Mills et al. 2007). Given the original purpose of VMS, the use of VMS data for research and impact assessment presents some limitations. These include incomplete coverage of vessels, long durations between position records and a lack of information on whether a vessel is actually fishing when the position is reported (Lee et al. 2010). At present, the latter is inferred from a range of vessel speeds that relate to typical towing behaviors in different métiers (Dinmore et al. 2003). Generally, only vessels >15m are monitored in Europe and they typically transmit position records at 2 hour intervals (EC 2009). Hence, researchers have to make assumptions and interpretations when VMS data are used as the main source of information on fishing activities in impact studies of towed gears on seabed habitats.

Even if methods can be developed to distinguish position records associated with fishing and non-fishing activities, it remains necessary to define methodologies and appropriate scales for reporting fishing activity and assessing its impact on the seabed. One option is to use the density of VMS position records as an index of fishing intensity. There are two ways in which this could be done, firstly by using the density directly as an index, and secondly by assigning an effort value to each VMS record and aggregating these values to a grid. These two approaches are probably most appropriate when describing activity in intensively fished areas and/or over large temporal and spatial scales, as they may underestimate intensity when applied to small areas and/ or short time periods due to the lack of replication. The latter scaling issues are particularly relevant if VMS were to be used for real-time spatial management of a fishery. For towed gears, a more complete assessment of the area fished can be made by interpolating between fishing position records. The simplest approach is to use straight line interpolation between successive records, although this might underestimate track length and area fished when position records are infrequent (e.g. every 2 hours), because most vessels fishing with towed bottom gears are not expected to maintain a straight course for such periods. An alternate method of track reconstruction is cubic Hermite spline interpolation (Hintzen et al. 2010). This technique integrates information regarding the vessel speed and heading at each polled position when computing the modelled vessel track. The latter method has been applied only to the Dutch flatfish beam trawl fishery to date, but may be applicable to other towed gear fleets. Once tracks have been ’reconstructed’, a grid of any given scale can be superimposed on the tracks and fishing activity can be reported per unit time per unit area and, when gear dimensions are known, as area swept per unit area per unit time. The grid scale of analysis that is used to accumulate fishing positions or to estimate fishing time or area has a significant effect on the interpretation of fishing distributions and the assumed impacts of fishing. For example, in any given region, the apparent extent of area without any fishing will decrease as the scale of the analysis is increased; with the result that total estimated fishing impact on the seabed will appear to be higher at larger scales of analysis (e.g. Dinmore et al. 2003, Piet & Quirijns 2009). For these reasons, it is desirable to conduct the analysis of fishing intensity at the finest resolution possible, or at a resolution below which the distribution of activity is assumed to be random (Dinmore et al. 2003). The resolutions used to compute fishing intensity vary considerably: 1 km^2 for the study of *Nephrops* trawling on benthic macrofauna or scallop fishing on habitat-forming species (Hinz et al. 2009, Lambert et al. 2011), 1 nm^2 (nautical miles), 6.25 km^2 for the study of trawling impacts on benthic infauna (Queirós et al. 2006, Reiss et al. 2009), 9 km^2 for study of beam trawling impacts on benthic communities (Hiddink et al. 2006b) and 5 nm^2 for study of dredging impact on benthic communities (Hill et al. 1999, see also review from Lee et al. 2010). However, these high resolution analyses are vulnerable to the deficiencies in VMS data, since track reconstructions that do not capture the true path of the fishing vessel will lead to greater under- or overestimates of the intensity of effort at high resolution.

The grid scale of analysis is also important when fishing activity is used as a pressure indicator of the state of the environment. For example, the EU directives on the Data Collection Framework (DCF) define standardized indicators of the integration of environmental protection requirements into the Common Fisheries Policy (COM 2008, EC 2008b, 2008a). The DCF indicators 5, 6 and 7 are pressure indicators that quantify the distribution of fishing activities, the aggregation of fishing activities and the non-impacted area of the seabed. Although the indicators are intended to describe trends in pressure rather than absolute pressure, the distribution of fishing is likely to be under-estimated, the aggregation of fishing activities overestimated and the non-impacted area of the seabed overestimated if the indicators are calculated from individual position records as opposed to known or reconstructed tracks.

Detailed assessment of the performance of methods for estimating fishing activity is challenging when the real tracks of vessels are not known. However, in some cases, positions are recorded more frequently that the 2 hour interval that is used as a standard in European fisheries. These high frequency data allow interpolated positions based on the 2 hour data to be compared with known positions. The Isle of Man scallop dredge fishery is one of these cases, where position records of some vessels in the fishery were recorded at 10 to 20 minute intervals during the years 2008-2010. Here, we use these data to compare estimates of fishing activity determined with point density and track reconstruction methods at a range of spatial and temporal scales. We then use the resultant estimates of fishing activity to determine and compare the values of fishing pressure indicators for the distribution of fishing activities, the aggregation of fishing activities and the non-impacted area of the seabed. Further, we assess the consequences of differences in estimated fishing activity distributions for the benthic community, based on an empirical analysis of the relationships between fishing pressure and the ecological status of the benthic community.

3.3 Material and methods

3.3.1 Interpolation of tracks

VMS position, time, speed and anonymous vessel identification data for king scallop dredgers (DR) and queen scallop otter trawlers (OT) in the territorial waters of the Isle of Man for the period 2008-2010 were provided by the Isle of Man Department of Environment, Food & Agriculture (DEFA). The data included Isle of Man and UK vessels ≥ 15m. All vessels ≤ 15m fishing in the 3nm zone were also reported. Details on the species targeted were obtained from combining VMS data to logbooks. A unique identifier was created for each row of data combining catch date and vessel identifier and was then used to merge VMS and logbooks (further details in Murray et al. 2011). The data included high poll rate data resulting from control programs led by DEFA and a specific request to provide additional high poll rate data for the present study. Prior to analysis, we removed duplicate VMS records and records close to port (within 1km of a port), erroneous position records allocated to land and selected records associated with fishing activity based on vessel speed (i.e. removal of 43383 records) (Lee et al. 2010). Initially, we identified position records associated with fishing by including all records with speeds of 0-6 kn to extract the tracks of individual vessels (Lee et al. 2010). However, based on direct observations of the fishing vessels operating in these fisheries and an analysis of the speed frequency distribution, subsequent calculation of fishing intensity was restricted to speeds ≤3.4kn. The 3.4kn cutoff was chosen based on the observation that data above this speed included several hundreds of VMS records that were situated in a known steaming corridor to the north of the Isle of Man. Any data points indicating a vessel speed between 0 and 3.4 in the fishing area, i.e. not close to port, were considered to indicate fishing activity as vessels may stop to empty dredges or perform maintenance tasks (Murray et al., 2011).

‘Real’ tracks, i.e. the exact paths followed by fishing vessels, were needed to parameterise and test the performance of different interpolation methods. ‘Real’ tracks were assumed to be described by the high poll rate data, and compared with interpolations based on increasing time intervals of up to 2h. A total of 86 and 12 vessel-days of ‘real’ tracks (position records at intervals <20min, 4134 fishing pings) could be extracted from the 2008-2010 VMS dataset for DR and OT respectively. The interpolation methods tested were the commonly used straight line (SL) and the cubic Hermit spline (cHs) as developed by Hintzen et al. (2010). In brief, the cHs method uses information on vessel position, heading and speed at time t and $t+1$ to define a trajectory. The combination of speed and heading are represented by vectors and vector length is multiplied by a parameter *fm* which influences the curvature of the interpolations. Hintzen et al. (2010) describes two parameter optimisation methods, one by minimising the distance between the high poll frequency track (assuming straight line interpolation between successive points) and the interpolated track or by optimising the length of the interpolated track to be as close as possible to the length of the real track. Here, the former was adopted as the aim was to evaluate the accuracy of prediction for fishing locations.

3.3.2 Indicators of fishing pressure

Once the best models for predicting OT and DR fishing positions had been defined, the models were applied to the 2008-2010 VMS dataset in order to build a dataset of interpolated positions. Any extraneous data points (speeds >3.4 kn) had been previously removed as explained above. Two datasets were thus used in the analyses: the latter ‘cleaned’ dataset, hereafter referred to as the raw VMS dataset, and the dataset of interpolated positions. Interpolated positions were obtained by describing each interpolated track as a series of 10 points at equal time intervals, the first and last were the known positions at 2 hour intervals and the intervening points were the predicted positions. To quantitatively compare the spatial extent of fishing activity as estimated from raw VMS data or interpolated tracks, we calculated Data Collection Framework (DCF) pressure indicators 5, 6 and 7 (COM 2008, EC 2008b, 2008a) and tested for the influence of spatial resolution on the derived estimates. Indicator 5 measures the area where fishing activity is reported for any defined bottom fishing fleet and area. Indicator 6 measures the aggregation of fishing activities and is defined as the area in km^2 in which 90% of the total activity for a defined bottom fishing fleet in a defined area occurs. Indicator 7 measures the proportion of a defined area where no fishing activity is reported for a defined bottom fishing fleet. The DCF and associated documentation recommends that the analysis should be based on position records in 3 km x 3 km grid cells and recommends that it would be preferable to move from 2 hour VMS position records to 30 minutes. The dataset of interpolated tracks was therefore also used to create a 30 min poll rate dataset. The DCF indicators were then calculated for each of the 3 VMS datasets, i.e. raw VMS, interpolated tracks and 30min poll rate datasets, along a grid cell size-gradient from 0.5 km x 0.5 km to 5 km x 5 km, with steps of 0.5km x 0.5km. Analyses were made on log-transformed scale as changes were expected to occur faster at the smallest scales. As grid size was defined with constant units in km, longitudinal and latitudinal VMS position records were projected into the Universal Transverse Mercator (UTM) geographic coordinates system.

3.3.3 Fishing impact on epifaunal biomass

The relationship between fishing intensity and the biomass of sessile epifauna around the Isle of Man has previously been described using point summation of raw VMS data to estimate fishing intensity on a grid of 1 km x 1 km cell size (Lambert et al. 2011) (point summation described below). However, other methods of fishing intensity estimation such as using interpolated tracks might be used for this purpose and we considered the effects both of using different methods and their application at a range of spatial scales. The objective of this analysis was to assess how any differences in estimated fishing activity distributions impacted on the relationship with the benthic community data and to assess the extent to which this affected the subsequent estimates of the impact of fishing on the benthic community. Fishing intensity was estimated at 120 stations within 12nm of the Isle of Man where the seabed community had been sampled during a 2008 survey of benthic habitats (see Lambert et al. 2011). Fishing intensity was estimated with four methods at each station: (i) raw VMS data and grid, (ii) interpolated positions and grid, (iii) raw VMS data and Euclidean distance and (iv) interpolated positions and Euclidean distance. The grid method, (i) and (ii), involved the placement of a grid over the whole sampled area and thereby associating each benthic sample station to a grid cell and thence to the corresponding fishing intensity calculated within the cell. The Euclidean distance method, (iii) and (iv), refers to cells that were defined by radial distance, i.e. based on the circular area surrounding each benthic sample station (Walter et al. 2007). The method places the 'station' at the centre of the area for which the fishing intensity is calculated. The methods were applied at a series of spatial scales. Fishing intensity was calculated for the 12 month period prior to sampling as past scallop fishing activities would have determined the state of the seabed communities in 2008. Only data for 2007-2008 were available. These data were not linked to information on vessel type, but analyses of data for 2008-2010 allowed us to identify the location of a *Nephrops* fishing ground to the west and south west of the island and the 15 stations in this area were therefore excluded from the analysis so that it focused solely on areas fished by king scallop dredgers during winter months and queen scallop otter trawlers during summer months. There are no other significant bottom fishing metiers that operate in the area.

For all four methods, fishing intensity was calculated by estimating the 'area swept' by point summation. Point summation consists of summing the 'area swept' attributed to each VMS point in a defined cell. The area swept was calculated by multiplying the time interval between positions, the fishing speed and the width of the gear. Otter trawls were assumed to be 18.3 m wide, based on logbooks data, and dredges from the UK were assumed to fish with the maximum number of dredges permitted by management regulations, giving gear widths of 7.6 m in the 0 to 3nm zone and 12.16 m within the 3 to 12nm zone (Lambert et al. 2011). These assumptions are likely to have lead to an over-estimation of fishing activity following a precautionary approach to estimating the impact of fishing as not all vessels can deploy the maximum width of gear allowed (Murray et al. 2011). Estimates of swept area associated with individual position records were then summed over a defined time period or area for analysis. Fishing intensity is defined as the summed swept area divided by the surface area of the cell (y^{-1}). Fishing intensity was calculated for cell sizes ranging from ca. 0.5 km x 0.5 km to 5 km x 5 km for cells defined by the grid method corresponding to areas of 0.25 km^2 to 25 km^2 for cells defined by radial distance, i.e. Euclidean method. The latter led to overlap between cells, and fishing activity that belonged to several cells was independently attributed to each cell in which it fell, i.e. one fishing point could be attributed to 2 or more stations following the Euclidean distance method.

It was expected that, independent of the method, fishing intensity would vary with cell size in relation to the intensity of fishing activity around each station. Stations where fishing intensity is very high at high resolution are likely to be attributed lower intensities when they are treated as part of larger areas and intensity is averaged for these areas. The opposite phenomenon can be expected for lightly or non-impacted stations. These scale effects were examined before we assessed how they affected the apparent relationship between fishing and epifaunal biomass. The relationship between fishing intensity and scale was modelled for a range of quantiles from 0.1 to 0.9. Regressions on the 10th quantile (0.1) modelled changes for the stations with the lowest fishing intensity estimates along the scale gradient while regressions on the 90th quantile (0.9) modelled changes for the stations with the highest fishing intensity estimates along the scale gradient. The slope and significance of the quantile regressions for each one of the four fishing intensity estimation methods described the changes in scale-dependent fishing intensity estimates from the least impacted stations (quantile 0.1) to the most impacted stations (quantile 0.9). The resolution gradient was log-transformed for reasons previously explained.

Since scale-dependent changes in fishing intensity estimates at the station level were expected to impact the apparent relationship between fishing and epifaunal biomass, we determined how the number of significant relationships between the biomass of sessile epifauna and fishing intensity varied with each fishing estimation method along the spatial resolution gradient. Relationships were tested with linear quantile regressions (Koenker & Bassett 1978, Cade & Noon 2003, Lambert et al. 2011). Quantile regressions split the response data into quantile classes. In the present study, they can be used to examine how the biomass of the benthic fauna is limited by a factor (fishing intensity), regardless of the presence of other limiting factors (Blackburn et al. 1992, Cade & Noon 2003). The 75th, 80th, 85th, 90th and 95th quantiles of epifaunal biomass measurements of a range of functional and taxonomic groups (Lambert et al. 2011) were tested in relation to fishing intensity. For the analyses of impact on biomass we included only stations where fishing intensity was $\leq 1\text{y}^{-1}$ as the fishing intensity was strongly right-skewed with only a very few stations (generally less than 5) fished more than once each year.

The impact of using a specific method and a specific scale for the quantitative assessment of fishing impact on sessile epifauna would further affect the predicted changes in epifaunal biomass at a regional scale; in this case the Isle of Man territorial sea. The mortality caused by dredging and otter trawling reduces epifaunal biomass. Concomitantly, some of this 'lost' biomass will be replaced by recruitment and growth. At any given station, the equilibrium relationship between biomass in the absence of fishing pressure ($\text{B}_{I=0}$) and fishing impacted biomass ($\text{B}_{I=F}$) can be expressed as

$$B_{I=F} = B_{I=0}e^{-F}$$

where e^{-F} is the proportion of $B_{I=0}$ remaining at a fishing intensity F.

We assessed how the predicted regional biomass of the sessile epifaunal community would vary when using different methods for calculating fishing intensity, with F based on raw VMS data on a grid, interpolated positions on a grid, raw VMS data and Euclidean distance and interpolated positions and Euclidean distance, at resolutions of 0.5 km x 0.5 km to 5 km x 5 km. The value of e^{-F} was estimated empirically from the slopes of the significant quantile regressions between sessile biomass and fishing intensity. It was expressed as the predicted proportion of $B_{I=0}$ that remained when F increased from 0 to 1 y^{-1}. The estimates of e^{-F} and thus $B_{\text{I=F}}/B_{I=0}$, the proportion of remaining biomass resulting from a fishing intensity of 1y^{-1}, obtained by the significant quantile regressions were averaged for each of four fishing intensity estimation methods at each resolution.

3.4 Results

Interpolation of tracks

With cubic Hermit spline (cHs) and straight line (SL) interpolations, the spatial accuracy of interpolated tracks decreased as the time interval between VMS position records increased (figure 3.1) and cHs better approximated the real tracks than SL at any given time interval. For position records at 120 min intervals, both interpolation methods tracked real dredging (DR) tracks with comparable precision; the distance between real tracks and interpolations improved by just 2% with cHs. The value of the optimized *fm* parameter declined rapidly towards 0 (reflecting a straight line track), when time intervals exceeded 90min (time interval=120min, *fm*= 0.0419) (figure 3.1). The real otter trawl (OT) tracks were better described by cHs interpolations than SL, such that the distance to the real track at 120min time intervals was 17% smaller. At 120 min intervals, the reduction in the error of estimation of real track length by cHs was only 8% (ca. 0.5km) for DR compared with 35% (ca. 2.6km) for OT (figure 3.1). Consequently, the results did not justify the use of a more complex model than SL for interpolating DR tracks, and hence the subsequent estimation of fishing effort based on modelled tracks used this approach. However, cHs interpolations were judged to be more appropriate for interpolating OT tracks (*fm*=0.1522).

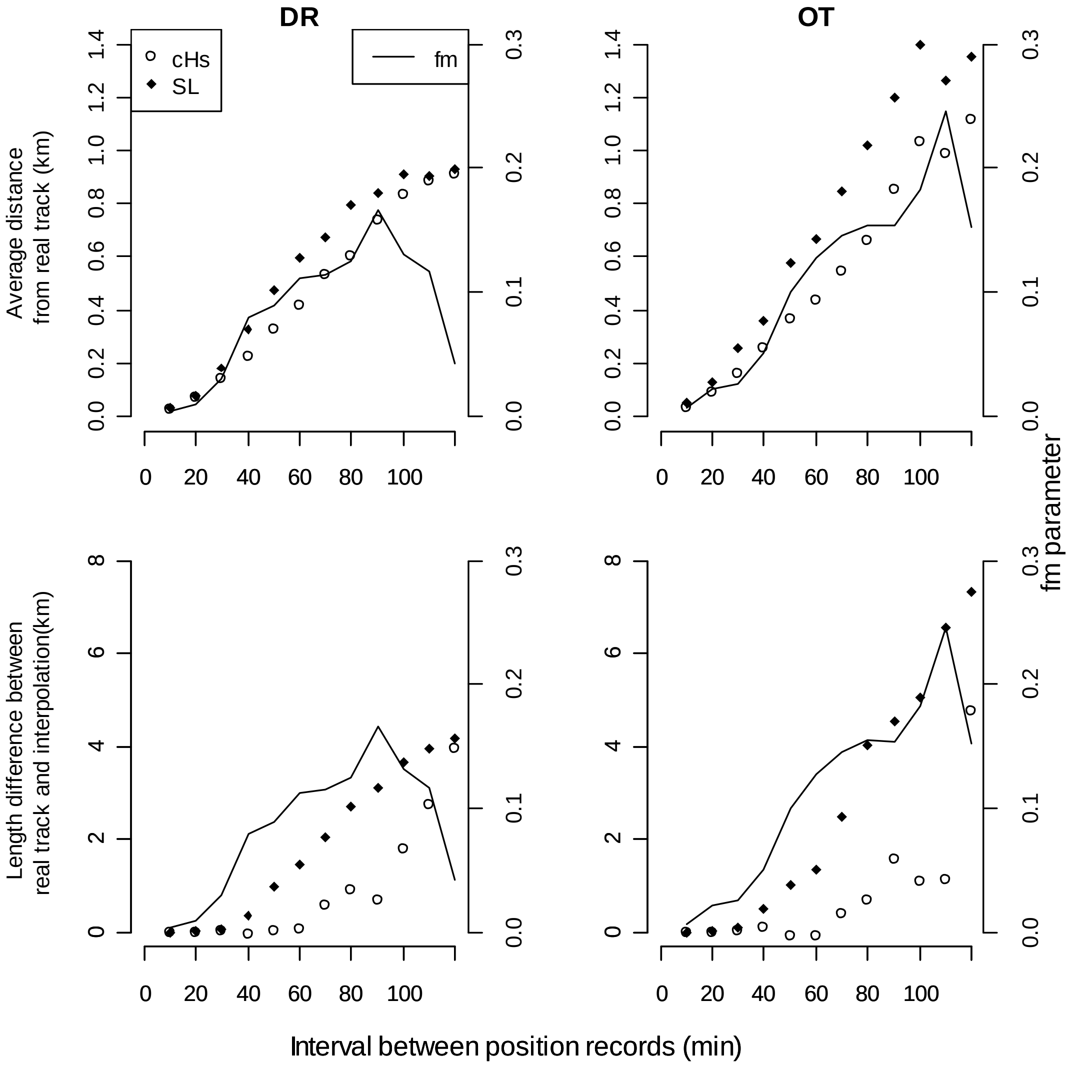

Figure 3. 1 Distances between interpolated and known positions of tracks for dredgers (DR) (left) and otter trawlers (OT) (right). The distances are presented as a function of the interval between successive VMS position records (min). The upper panels represent the average distance (km) between real and interpolated tracks. The lower panels represent the difference in length estimates (km) between real and interpolated tracks. The optimised *fm* parameter shows how the interval increase affects the perceived behaviour of the fleet.

Indicators of fishing pressure

DCF indicators 5 and 6 showed that the area fished increased with the scale at which they were calculated, while DCF 7 mirrored these trends with a resultant decrease in the extent of the non-fished area (figure 3.2). The use of interpolated VMS data, or 30min interval-interpolated VMS data, led to consistently higher estimates of DCF indicators 5 and 6 and lower estimates of DCF indicator 7 than when they were calculated with non-interpolated, raw VMS data (figure 3.2 and 3.3). At the recommended resolution of 3km x 3km and poll intervals of 30min, the area fished was estimated to be 9.5% smaller when DCF indicator 5 was calculated using raw VMS data than when it was calculated with interpolated VMS data. Aggregation of fishing activity, the focus of DCF indicator 6, was similarly 10.5% lower when computed using raw VMS data which implied the greater area covered by the interpolated data corresponded to areas that were fished recurrently. For DCF indicator 7, the area of the seabed that was not impacted by fishing decreased by ca. 18% when estimated from 30 min-interpolated rather than raw data (figure 3.3).

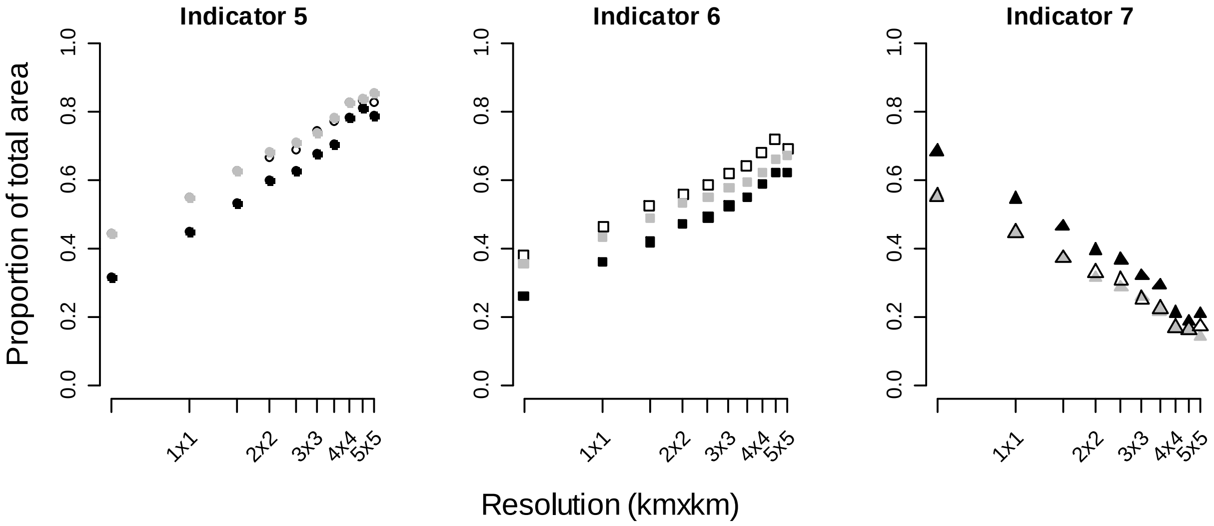

Figure 3. 2 Estimated values of DCF indicators when calculated at a range of grid resolutions from high (0.5kmx0.5km) to low resolution (5x5km). Black-filled symbols represent raw VMS data, grey-filled symbols represent data interpolated to 30 min intervals, open symbols represent interpolated data. DCF indicator 5 represents the distribution of fishing activity, DCF indicator 6 represents the aggregation of fishing activity and DCF indicator 7 represents the unfished area. All indicators are expressed as a proportion of the total area of the Isle of Man territorial sea.

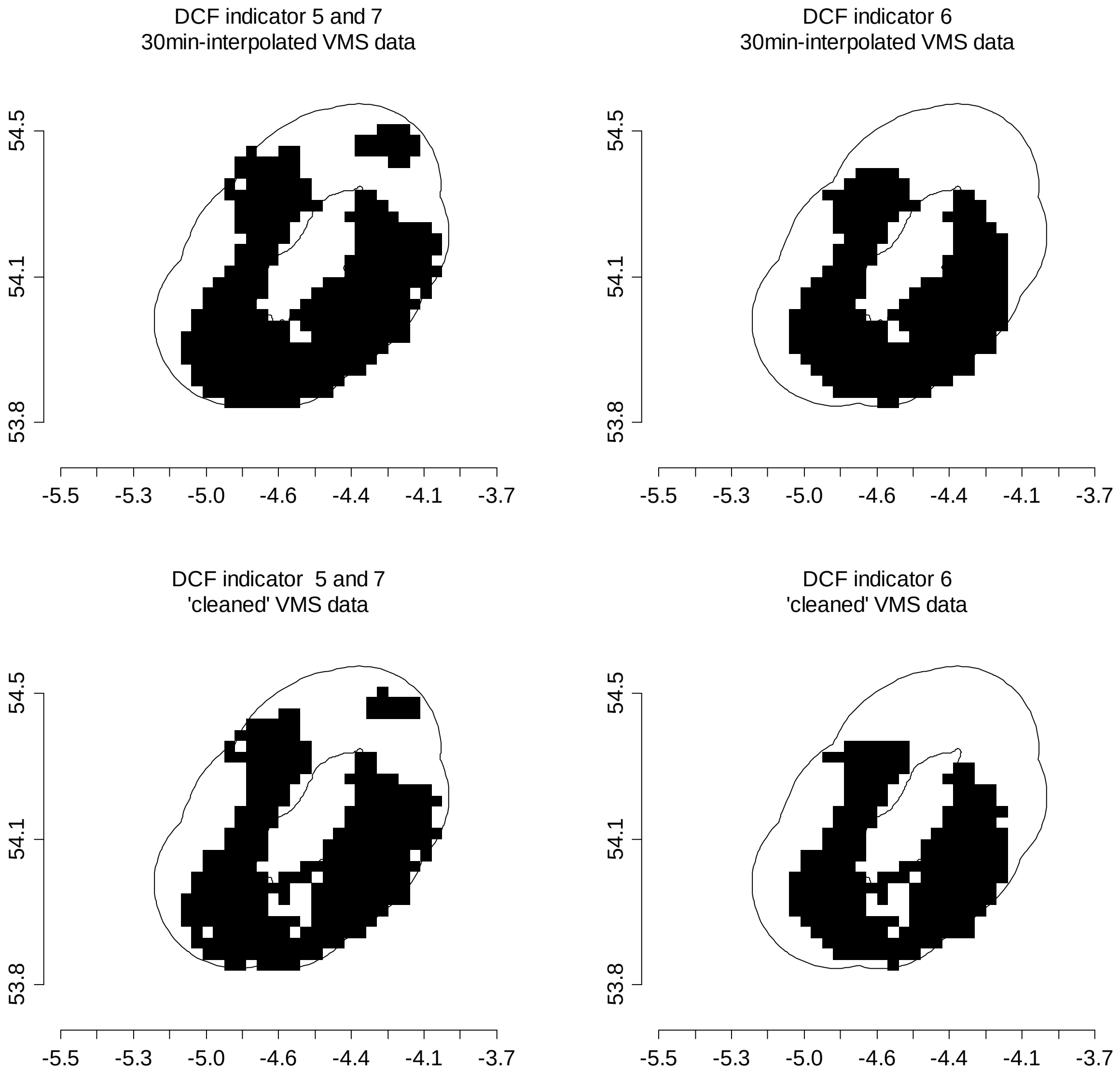

Figure 3. 3 Maps of the annual distribution of the fishing activity that was used to calculate DCF indicator 5, 6 and 7; shown with 3kmx3km grid cells. Upper panels: 30min- interpolated VMS data; lower panels = raw VMS data. Black cells= impacted by scallop fishing gears, white area within the 12nm limit (black line) = non-impacted area of the seabed.

Fishing intensity and the benthic community

The estimated fishing intensity at each station changed consistently with the resolution of analysis. The coefficients of the slope of the quantile regressions between fishing intensity and scale were positive in the lowest range of quantiles and negative in the highest range of quantiles. Thus, for the least impacted stations, estimated fishing intensity increased with increasing resolution, while for the most impacted stations, estimated fishing intensity decreased with increasing resolution, with the steepest changes in estimated intensity occurring at the highest resolutions (figure 3.4 & 3.5). All four methods for estimating fishing intensity (raw VMS data with grid, interpolated positions with grid, raw VMS data with Euclidean distance and interpolated positions with Euclidean distance) confirmed this trend, with the exception of the estimates based on interpolated positions that did not significantly decrease with increasing resolution in the highest range of quantiles.

Despite the changes in the fishing intensity estimates among the different methods and scales of resolution, there was broad qualitative evidence that, in general, increasing fishing intensity reduced sessile epifauna biomass (figure 3.6). However, the significance of the results differed according to the methods and scales by which fishing intensity was calculated. Across the gradient of grid cell resolution the number of significant quantile regressions peaked at a spatial scale between 2 km x 2 km and 4 km x 4 km. There was a significant second degree polynomial relationship between number of significant relationships and spatial scale ($df = 47$, $p<0.001$, $r^2=0.52$) (figure 3.7). In this range, i.e. 2km x 2 km and 4 km x 4 km, the relationships between fishing intensity, as estimated from interpolated tracks and Euclidean distance, and epifaunal community biomass were the most consistent. Grid based methods and raw VMS data gave the least consistent results across the different spatial resolutions used to estimate fishing intensity.

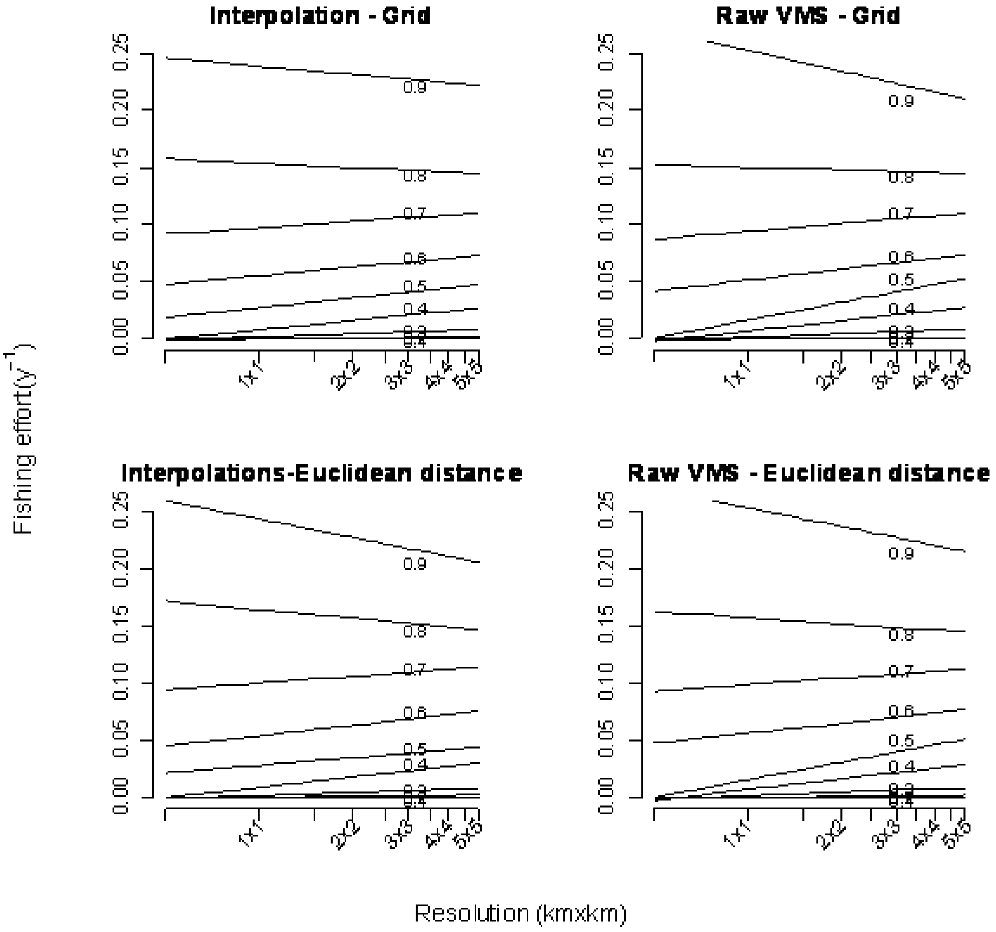

Figure 3. 4 Changes in fishing intensity estimates along the resolution gradient. Fishing intensity was estimated using the four methods shown on the panels. Changes are modelled separately at different quantile levels, from the 10th to the 90th quantile, i.e. 0.1 to 0.9, showing the changes in fishing intensity estimates from the least to the most impacted stations. Slopes and significance per quantile are shown in figure 3.5.

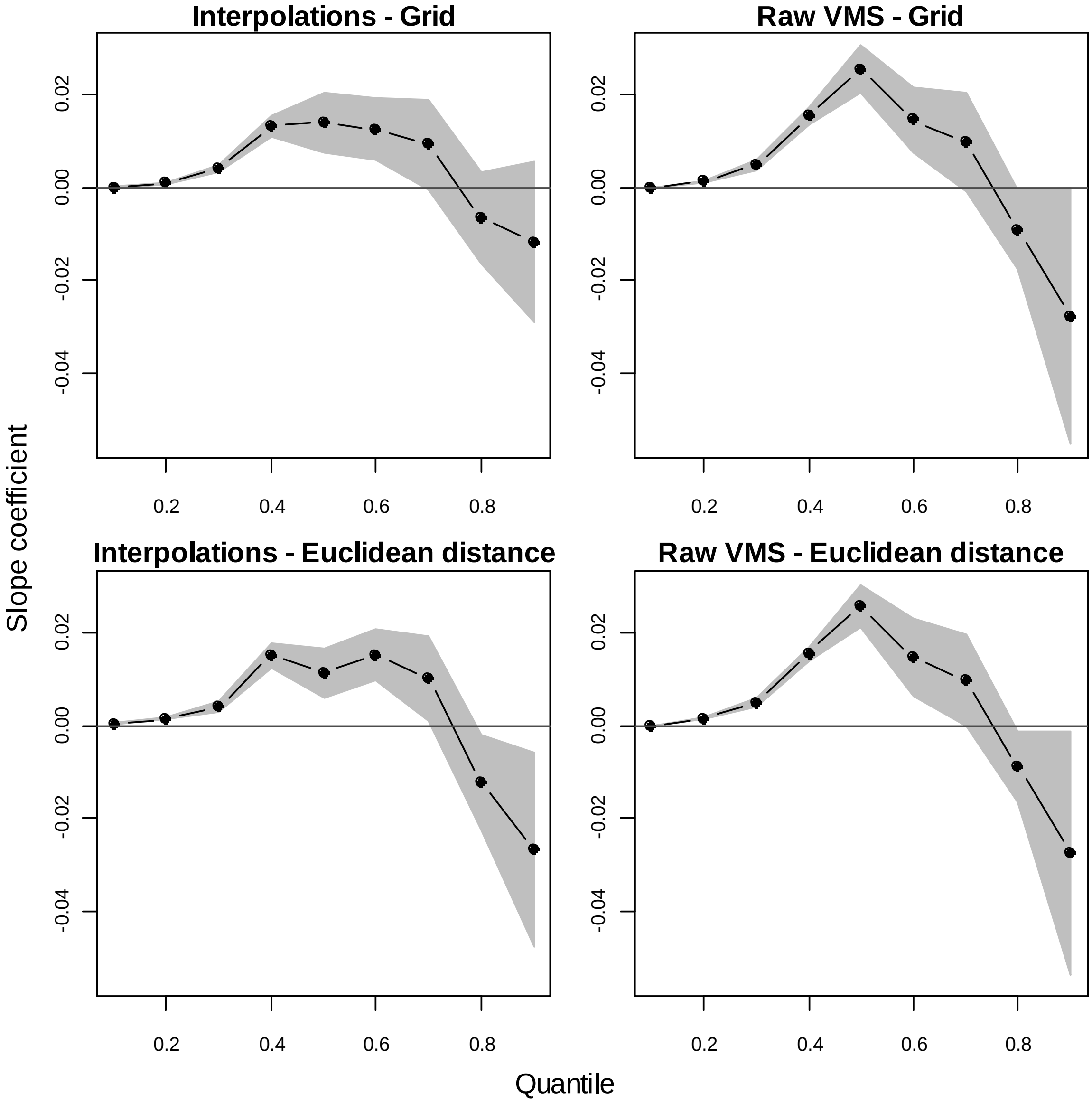

Figure 3. 5 Slope coefficients of the quantile regressions “fishing intensity ~ scale” as a function of the quantiles at which the regressions were tested. Fishing intensity was estimated using the four methods shown on the panels. The grey area represents the interpolated confidence interval of each effort coefficient estimate. The slope is significant when the confidence interval surrounding the estimate does not include 0. Quantile regressions “fishing intensity ~ scale” are shown in figure 3.4.

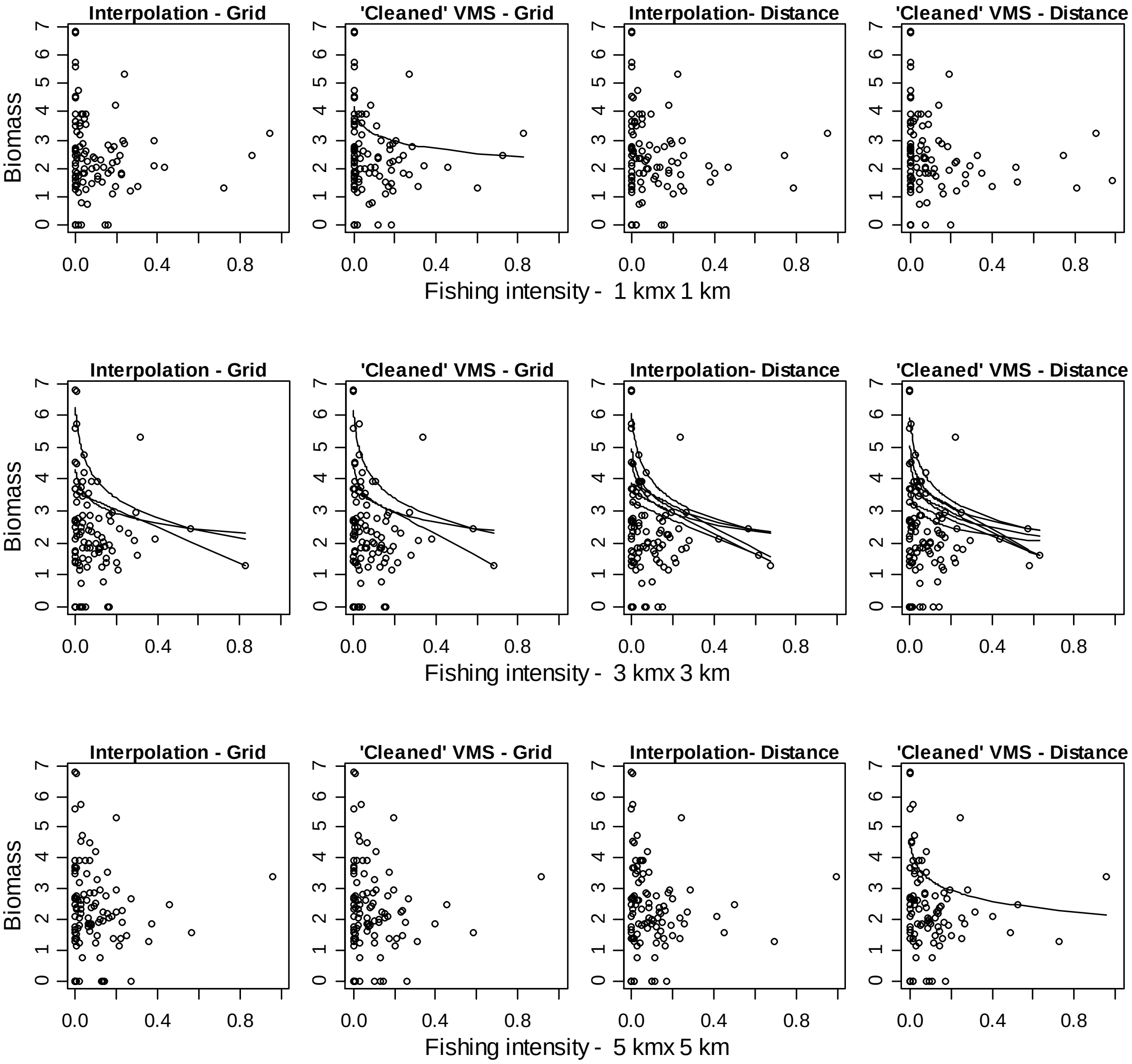

Figure 3. 6 Relationships between fourth root-transformed biomass of emergent epifauna and fishing intensity measurements. Biomass was fourth-root transformed consistently with the methods described in Lambert et al. 2011. The upper panels represent fishing intensity calculated at a 1kmx1km resolution, the middle panels are for 3kmx3km resolution and the lower panels are for 5kmx5km resolution. Each row represents 4 scenarios where fishing intensity at the sampled stations is calculated on a grid or based on Euclidean distance and where VMS data are used either raw or interpolated. Only significant quantile regressions are shown.

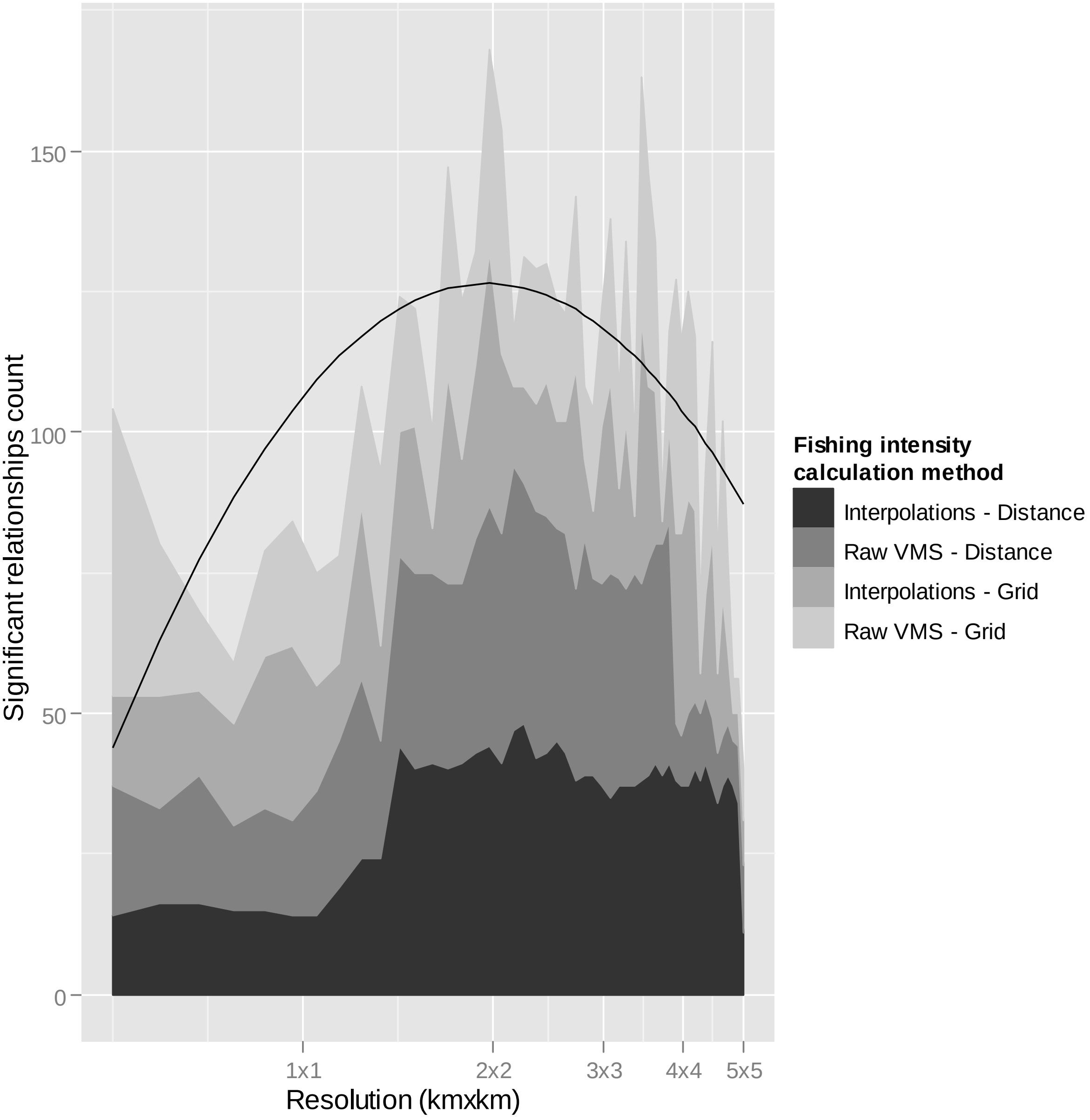

Figure 3. 7 Cumulative number of significant relationships between biomass and fishing intensity as a function of the resolution chosen to calculate fishing intensity. Fishing intensity was measured using four different methods (see legend). The number of significant relationships derives from univariate quantile regressions between biomass at different taxonomical and functional levels and fishing intensity gradients (see methods). The line represents the fitted model linking the total number of significant relationships to the resolution of analysis.

The estimated proportion of epifaunal biomass that remained after being impacted by fishing varied between 0 and 0.5 depending on the method and resolution used to estimate fishing intensity. A value of 1.0 for the remaining proportion of biomass occurred as a result of non-significant relationships between total biomass of epifauna and fishing intensity for certain combinations of method and resolution (figure 3.8). Grid-based outputs were those most affected by spatial resolution as highlighted by the variation in the remaining proportion of epifaunal biomass, while Euclidean-based outputs were more stable. Excluding the resolutions at which no significant quantile regression had been observed, the estimated proportion of the remaining epifaunal biomass after a fishing impact of 1 y^{-1} decreased as scale increased for both Euclidean distance-based methods, i.e. higher spatial resolutions significantly decreased the perceived effect of fishing activities. The fit of the linear model that showed the decrease in predicted remaining biomass with lower resolutions of estimation of fishing effort was better when fishing effort was calculated from interpolated tracks than from raw VMS data (respectively df=30, $p<0.001$, $r^2=0.49$ and df=30, $p=0.037$, $r^2=0.11$, figure 3.8)

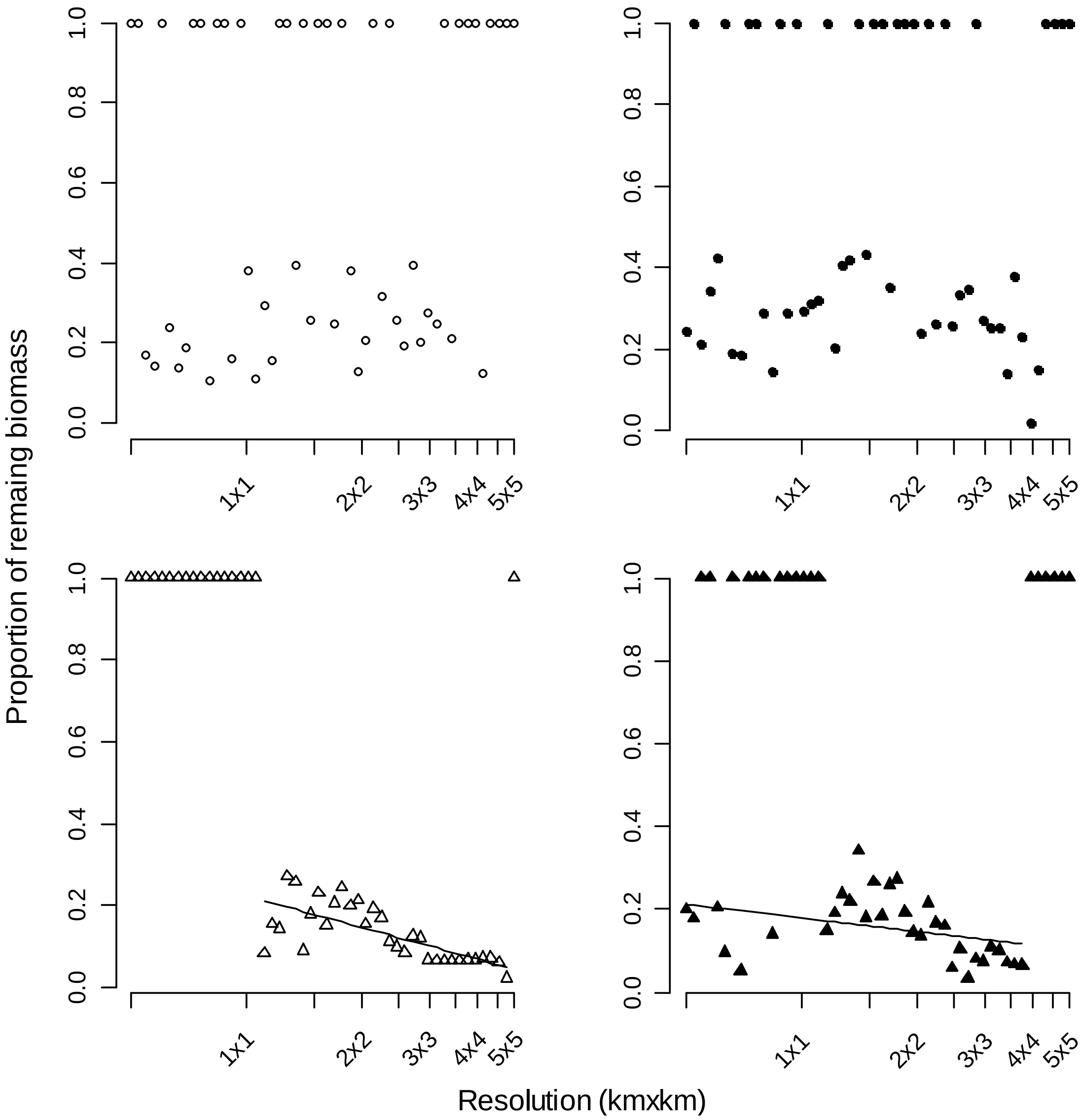

Figure 3. 8 Proportion of remaining biomass after a fishing impact of $1y^{-1}$ as a function of the spatial resolution at which fishing intensity is calculated. A proportion of 1 reflects non-significant quantile regressions. Fishing intensity was measured using four different methods. Circles are for fishing intensities calculated on a grid (top row), triangles for fishing intensities calculated from Euclidean distance (bottom row). Open symbols represent interpolated data (left column), black-filled symbols represent raw VMS data (right column). Significant linear regressions are also displayed (excluding proportion of remaining biomass equal to 1, see text for statistics).

3.5 Discussion

There are many potential approaches that can be used to analyse VMS data. Our results show that these different approaches have both strengths and weaknesses depending on the scale at which the analysis is undertaken and the scientific questions addressed using fishing intensity data. Our results also illustrate the general challenges of using relatively infrequent position records, which are considered sufficient to meet many fisheries enforcement needs, to describe the distribution and wider ecosystem impacts of fishing activities. Unusually, we were able to quantify the performance of methods for estimating fishing intensity from infrequent VMS records because we had access to more frequent position records.

Straight line and cHs interpolation led to different results for the different fleets, and both Isle of Man fleets behaved differently from the Dutch beam trawl fleet, for which the method was developed and applied by Hintzen et al. (2010). The Netherlands fishery consists of large vessels that trawl over relatively homogeneous substrata, with a minimum delay between hauling and redeploying the gear. The Isle of Man scallop fishery targets restricted grounds in daylight hours. The high polling frequency VMS data and information from the fishers (pers. comm.), demonstrated that Isle of Man vessels tend to go back and forth over the same ground leading to complex track patterns in fishing grounds that may only be 3 to 5 km in the longest dimension. Within the Isle of Man fleet the fishing tracks of scallop dredgers and queen otter trawlers have different characteristics. Dredgers can make sharp 180 degree turns to dredge directly alongside their previous tracks while otter trawlers usually require larger turning circles (pers. obs. LM, HH). These differences in behaviour explain why straight line interpolation fitted better the tracks of scallop dredgers while cHs was a better method for otter trawlers.

While our results show that more frequent position records are desirable to better describe fishing tracks, increased polling comes at increased cost. The European Commission recommended that 30 minutes would be a suitable compromise between providing better information for calculating fishing pressure indicators and minimising the cost of additional polling. However, our results show that there is always an error in the spatial location of the tracks for the Isle of Man scallop fishery even at the lowest poll frequencies. Although accurately interpolating fishing tracks from 1 or 2h VMS data is possible for fisheries such as the Dutch flatfish beam trawl fishery (Hintzen et al. 2010), the present study demonstrated that this rule cannot be applied across different fleets without first considering behavioural patterns specific to that fleet. Reducing the polling frequency from 2h- to 1h would reduce the error by a factor of approximately 2 for dredgers and by 3 for otter trawlers and improve estimates of track length and thereby wider ecosystem impacts. In practice, our results show that the different characteristics of different fisheries mean that no single polling rate will provide the best compromise between cost and the resolution of fishing activity. Regulators, ideally informed by research that takes account of the non-regulatory uses of VMS data, will need to consider whether it would be practical for different rates to be used by different fleets and how such fleets would be defined. Alternatively, a random high frequency polling would provide the necessary data to compute the degree of uncertainty in modelled estimates of fishing intensity and would allow fine tuning of the applied methods as appropriate.

More frequent information on fishing positions, as obtained by more frequent polling or track reconstruction, will yield point density estimates that better capture the true distribution of fishing activity. The difference in the values of the DCF indicators showed that the "true" distribution of fishing activities was underestimated by ca. 10% when tracks were not interpolated. This means that areas that would be considered unimpacted when using raw VMS data based on a 2h polling interval had actually been impacted to some extent by fishing gears. This is especially relevant given that the first pass of a trawl or dredge has proportionately greater impacts on the benthic community than subsequent passes over the same area (Hiddink et al. 2006c). The difference between the values of indicators based on interpolation and raw VMS data decreased as the scale of analysis increased. For the Isle of Man territorial waters, the difference between unfished areas estimated from raw VMS data or interpolated data decreased from ca. 500 km^2 to ca. 50 km^2 with increasing grid cell resolution. This difference occurs because the finer resolution analyses reflected better the heterogeneity in fishing effort distribution. Failure to work at a resolution that adequately described this heterogeneity can lead to overestimates of the magnitude of fishing impacts irrespective of the method used to calculate fishing intensity (Mills et al. 2007, Piet & Quirijns 2009).

Different grid cell resolutions and methods of fishing intensity estimation changed the significance of the relationships between fishing intensity and epifaunal biomass. The most significant relationships were associated with spatial resolutions of 2 km x 2 km to 4 km x 4 km. This may seem inconsistent with other studies of fishing impacts that attempted to use the "smallest possible" grid cell to quantify fishing pressure often on the basis that the distribution of fishing was assumed to be random at that scale (Rijnsdorp et al. 1998, Dinmore et al. 2003, Reiss et al. 2009). There are two potential reasons for this discrepancy. Firstly, observed changes in the benthic fauna of an impacted site may also depend on the effects of fishing impacts in the area surrounding that location. These impacts may, for example, define how fast animals can recolonise the station through direct immigration or larval recruitment. Such effects will be accounted for if fishing intensity is estimated at larger spatial scale. Secondly, the spatial resolutions of 2 km x 2 km to 4 km x 4 km that lead to the most significant relationships between biomass and fishing intensity were based on one year's VMS data. If there is year to year variation in fishing intensity, but recovery from fishing impacts takes place over longer periods, aggregated annual data over larger scales may provide a more reliable picture of the distribution of fishing activities and a better assessment of their cumulative impacts on the benthic community. To avoid increased patchiness within the cells, the selection of grid cell resolution is a trade-off between the need to aggregate sufficient records to obtain a reliable index of intensity over an appropriate time period and the need to ensure that the effect of patchiness is not overlooked.

The scale of analysis also affects the predicted remaining biomass after fishing. The estimated fishing intensity at stations subject to the greatest impacts at small scales will tend to be influenced by lower impacts in surrounding areas while the opposite phenomenon can arise at the least impacted stations. The decrease in the remaining biomass of sessile organisms predicted when the scale of analysis increases may thus reflect the decrease in the estimated fishing intensity at the stations that were highly impacted at the highest resolutions. This is because highly impacted stations at which very low biomass was observed will be attributed a lower fishing intensity estimate which would create a steeper decrease in biomass along the fishing gradient.

Preferred methods of fishing intensity estimation depend on the objectives of the study and the spatial and temporal resolution of VMS data that are available. The present results broadly support the conclusions of Lee et al. (2010) who suggested that point density methods on ‘cleaned VMS data’ were suitable for providing information on patterns of fishing activity on large space and time scales but that track based methods would be more appropriate when attempting to ascertain the spatial impact of vessels using mobile gears over shorter periods of time. Given the diversity of fisheries and fishing intensities the spatial and temporal trade-offs will vary among fisheries, so no singular solution will exist and a compromise has to be adopted if the same resolution is applied to multiple fisheries. For mapping fishing activity, 3 km x 3 km has been considered a reasonable compromise (Mills et al. 2007). However, resolutions higher than 3 km x 3 km would be needed to describe the effects of specific disturbance events on seabed habitats, especially given the typical resolution of biological sampling. For instance, the time since the last fishing disturbance event will affect community composition at a sampling station, and such a station will typically cover a much smaller area than 3 km x 3 km (Tillin et al. 2006).

In general the results show that more frequent position records and finer analytical resolutions would support more accurate and informed assessment of fishing activity and its subsequent impacts on benthic biota. While the current data collected in Europe have provided new insights into the distribution of fishing activity on smaller time and space scales than was hitherto feasible, the limitations of these data are apparent when such data are used to describe impacts at local scales over short time periods. Clearly, higher polling frequencies provide more information on real tracks and overcome the need for more complex and fleet specific interpolation methods, but our results do not suggest there would be a fleet specific optimum. Rather, we conclude that the existing 2h intervals are too long and that any achievable reduction in polling frequency would be desirable. A reduction to 30 minutes may be an appropriate intermediate target, and would provide significant benefits when VMS data are used for mapping activity and assessing fishing impacts, but the long-term target would be to increase polling frequency to a rate that is appropriate for the behaviour and fishing grounds of a specific fleet.

Quantifying recovery rates and resilience of seabed habitats to bottom fishing

Lambert G. I., Jennings S., Kaiser M. J., Davies T. W., Hiddink J. G. (in prep). Quantifying recovery rates and resilience of seabed habitats to bottom fishing.

Authors' contribution:

I came up with the idea, conducted all the analyses and wrote the manuscript.

Simon Jennings, Michel Kaiser and Jan Hiddink supervised the work and helped at different stages: discussing the ideas, structuring the manuscript, writing it up and proofreading it.

Simon Jennings had a strong input on the direction to take with the paper and suggested the model to use (i.e. the logistic regression)

Thomas Davies was involved at the early stages of the work in the discussions on the use of functional groups and gave me some statistical advice at the later stages.

Chapter 4 – Benthic recovery

4.1 Abstract

Measurements of recovery rates of marine habitats after fishing disturbance provide insight into habitat resilience and can thus be used to assess the sustainability of impacts and inform the development of management strategies. We measured the post-disturbance recovery rates of diverse marine benthic communities found on coarse and hard substrata across >4000 km^2 of seabed where the patchy distribution of bottom fishing in space and time creates a mosaic of habitat patches at different stages of recovery. Recovery rate was predicted using a novel analysis of the relationship between elapsed time since the last fishing event and community composition. By studying many locations in the fishing ground, this approach achieved uniquely high replication of recovery events. The history of fishing events at each location was described from satellite tracking of fishing vessels (vessel monitoring system (VMS) data). Recovery of species abundance, species composition and functional group structure was estimated to take from 1 to 4 years, and mostly depended upon the prevailing hydrodynamic conditions. For those species that had large adult body size, recovery rates were affected by the proximity of a high abundance of the same species and recovery could take longer than 4 years. We show that detailed site-specific recovery trajectories can be measured at sea-basin scales to estimate the overall recovery rate of benthic communities and to describe differential sensitivity to fishing. The results support assessment of impact and resilience, allowing managers to set sustainable targets for bottom fishing impacts. The results also show that the protection of a proportion of fauna that are sensitive to fishing disturbance can enhance recovery rates in adjacent areas.

4.2 Introduction

Mobile bottom fishing gears modify the biomass, diversity, productivity and composition of benthic communities (Collie et al. 1997, Kaiser & De Groot 2000, Jennings et al. 2001a, Hiddink et al. 2006c). These changes, in turn, affect a variety of ecosystem processes, such as nutrient cycling, sediment stabilization, enhancement of structural habitat complexity and provision of habitat and food for fish (Rhoads & Germano 1982, Bolam et al. 2002, Thrush & Dayton 2002, Solan et al. 2004).

The resilience of a habitat, community or process to fishing impacts can be reported as the inverse of recovery time from a defined disturbance event (Hiddink et al. 2007). Consequently, measurements of recovery time can be used to define sustainable rates of impact on benthic habitats and associated communities. This information is needed to inform fisheries and conservation target setting, for example, the allocation of fishing rights in fisheries that use towed bottom-fishing gears (e.g. Holland & Schnier 2006a). For example, greater fishing effort might be acceptable on, or redirected to, habitats that can recover quickly (i.e. < 1 year). Habitats that recover slowly could be protected for periods that are judged necessary to meet defined management targets such as maximizing benthic production or maintaining habitat complexity (Hiddink et al. 2006b). An understanding of recovery and sensitivity could also be used to support management based on Individual Habitat Quotas (IHQ) where fishers trade habitat impact quota units with a total quota set to maintain a target habitat “stock” (Holland & Schnier 2006b, Hiddink et al. 2007). Such approaches are at the forefront of current considerations regarding how we might implement ecosystem-based approaches to management in the marine environment

Recovery time is expected to depend on the magnitude of natural variation as well as the intensity of fishing disturbance (Kaiser 1998). Thus communities found in unconsolidated sediments are expected to be well adapted to a disturbed environmental regime while more stable communities, found in consolidated sediment and in hard bottom areas, will take longer to recover (Collie et al. 2000b, Kaiser et al. 2006a).

Consequently, even infrequent fishing events may maintain them in a modified state (Foden et al. 2010). Recovery rates for gravelly to hard-bottom areas often have been assessed at small temporal and spatial scales using Before After Control Impact experimental designs (Underwood 1994). Some results suggest recovery times of less than a year (Van Dolah et al. 1987, Kaiser et al. 1998, Robinson et al. 2001, Pitcher et al. 2009), but it is arguable whether these apply at larger scales. This is because entire fishing grounds will have different recovery dynamics; because reproduction and growth may make a greater contribution to observed recovery than immigration (Collie et al. 2000b, Jennings et al. 2001a). Meta-analyses and large-scale long-term studies suggest recovery times from <3 years (Cranfield et al. 2001, Blyth et al. 2004) to 5-10 years for hard-bottom habitats where sessile epifauna initially were present (Collie et al. 2000b, Collie et al. 2005, Kaiser et al. 2006a).

Existing empirical studies of recovery have been based on a single location or a small number of replicate locations. In reality, fishing pressure is patchily distributed in space and time such that on any fishing ground there will be a mosaic of habitat patches at different stages of recovery, depending on the history of fishing in these patches. With the advent of satellite Vessel Monitoring Systems (VMS) that describe the fine-scale distribution of fishing activity in space and time, it is possible to harness the patchiness of fishing activity potentially to look at multiple replicate recovery trajectories. This provides a novel and powerful means by which to measure recovery on real fishing grounds at fishery- and management- relevant scales.

The Isle of Man territorial sea (ca. 4000 km^2) provided an ideal opportunity to assess recovery of benthic communities on hard substrata in response to bottom fishing disturbance as the area is fished by a scallop dredging and bottom trawling fleet that is completely monitored with high polling frequency VMS. Here, we take advantage of this situation to link the status of epifaunal communities at multiple locations to the known history of fishing at those locations. The approach enabled us to describe the patterns of recovery for the habitats on this fishing ground and to estimate the proportion of habitat in different recovery states.

4.3 Methods

The study was conducted in the territorial waters of the Isle of Man, United Kingdom, which have been fished for over 60 years. The study was conducted in three stages. First, we collected information on the abundance and structure of benthic epifaunal communities (Methods 4.3.1) and fishing activity in the area (Methods 4.3.2 and 4.3.3). Second, we studied how fishing impacted the structure of the communities at the sampled stations to identify characteristics of the communities that were related to fishing disturbance (Methods 4.3.4). Third, we estimated the date when each sampled station was last fished and linked this to the state of the community and thereby estimated recovery time (Methods 4.3.5). The time of the last fishing disturbance event was estimated from VMS data that were used to interpolate fishing tracks (Methods 4.3.3).

4.3.1 Biological data collection

The seabed habitats across the territorial waters of the Isle of Man were surveyed systematically in August 2008. Photographs of the seabed were taken at 120 stations located on a regular grid with 5km spacing within the 12 nautical miles limit of the territorial sea. A sledge, on which a high resolution Canon 400D digital camera was fitted, was towed on the seabed for 15min at each station. Every 9 s, a 10 megapixel photograph was taken (ca. 100 pictures per station); each photograph recorded an area of 0.14 m^2.

The pictures were used to identify and quantify the benthic epifauna present at each station to the lowest possible taxonomic level. Between ca. 10 and 50 pictures per station were analyzed; the number of pictures depended on picture quality and time constraints. Soft substratum habitats (mud and sand) were removed from the analyses as the major component of the benthic communities in those habitats is composed of infaunal species that could not be observed on the photographs. Data on the identity and abundance of epifauna were used to describe species richness and species composition. In addition, to support an indirect assessment of the impacts of fishing on ecosystem function, functional composition was described from the taxonomical composition of the communities at each station. Functional composition was defined by 11 traits (Bremner et al. 2003, Bremner 2005). The traits were chosen to include information on morphology, life history and ecology of the benthic species (table 4.1). The primary source of information was the BIOTIC database located on the Marlin website (http://www.marlin.ac.uk/biotic/). Further information was collected from Bremner (2005) and from Tillin et al. (2006). Each trait was composed of several modalities, e.g. the life span trait was composed of 3 modalities: <2years, 2-5years, >5years. We used a fuzzy coding approach. For each modality of each trait and for each species, a score was given from 0 to 3 depending on the affinity of the species to the modality. One species could have a score in several modalities for the same trait. The score by modality was then translated as a percentage of the overall trait for each species. When no information was available, we assigned a value of 0 to each category of the trait or used the values of a taxonomically similar species if these were available. Each modality score per species was then expressed as a percentage of the trait to which it belonged. The percentage attributed to each modality was then multiplied by the abundance of the species at each station. Finally, the "modality abundances" were summed per station to obtain an index of function. Attributing a value of 0 to each modality of a trait for a particular meant that information was missing for that species-specific trait, and led to its elimination from the analyses pertaining to that trait.

Information on abundance, richness and taxonomical and functional composition was then used to identify the features that were sensitive to fishing disturbance and that had potential for recovery.

Table 4. 1 Traits and modalities investigated in the functional composition analyses (adapted from Bremner et al. (2003) and Bremner (2005)).

Trait	Modality
Size	Small (<2cm)
	Small-medium (3-10cm)
	Medium (11-20cm)
	Medium-large (21-50cm)
	Large(>50cm)
Life span	<2years
	2-5years
	>5years
Reproductive method	Asexual
	Broadcast spawning
	Sexual- planktonic larvae
	Sexual- mini-adults
Adult mobility	None
	Low
	Medium
	High
Attachment	None
	Temporary
	Permanent
Movement	Sessile
	Swim
	Crawl
	Burrow
Body flexibility	>45°
	10°- 45°
	<10°
Body form	Flat
	Mound
	Upright
Feeding habit	Deposit-detritus
	Filter-suspension
	Opportunist-scavenger
	Predator
	Grazer
Sexual differentiation	Gonochoristic
	Synchronous hermaphrodite
	Sequential hermaphrodite
Sociability	Solitary
	Gregarious
	Colonial

4.3.2 Fishing effort estimation

The main bottom fisheries using towed gears in the territorial waters of the Isle of Man are scallop dredging, otter trawling for queen scallops, and trawling for *Nephrops*. The latter does not overlap with the scallop fishery and occurs in the offshore mud substratum in the south-east of the territorial waters. The latter was not considered here since the study focused on hard bottom or mixed substrata. Vessel Monitoring System (VMS) position, time, speed and anonymous vessel identification data for king scallop dredgers and queen scallop otter trawlers for 2007-2008 were provided by the Isle of Man Department of Environment, Food & Agriculture (DEFA). The data included Isle of Man and UK vessels ≥ 15m. The positions of all vessels ≤ 15m fishing in the 3nm zone were also reported since they were also fitted with VMS. Vessels licensed to fish for queen scallop were assumed to use scallop otter trawls in summer and vessels licensed to fish for king scallops were assumed to use scallop dredges in winter, the king scallop fishery is closed during the summer months from 01 June to 01 November. Prior to analysis, the VMS dataset was screened to remove duplicate position records, records close to port, erroneous records allocated to land and records not associated with fishing (Lambert et al. in press). Interpolation methods were used to re-create the course followed by the vessels and to map of fishing activity. Scallop dredging tracks were interpolated by straight lines and otter trawling tracks cubic Hermit splines (Hintzen et al. 2010, Lambert et al. in press). Fishing effort was estimated from the VMS interpolated positions that fell into a 9km^2 circular area centred on each station. Area swept was calculated by multiplying fishing speed by fishing time and gear width. Gear width estimates were not available for June 2007-October 2008 so we assumed that gear widths were the same as those recorded in logbooks from November 2008-October 2010. Vessels from the Isle of Man that were fishing in 2007 and still fishing in 2008 could thus be attributed a swept gear width. Scallop dredging vessels for which no information was available, i.e. some vessels from the Isle of Man and all UK vessels, were attributed a gear width based on their "vessel capacity units" (VCU) as the gear width used by scallop dredgers is known to linearly increase with VCU (Murray et al. 2011). Otter trawlers for which no information was available were attributed a swept width value of 18.1m, as averaged from the logbooks for 2008-2010 (Lambert et al. 2011). The estimated area swept was then divided by 9 because the size of each cell was $9km^2$ and the resulting fishing effort corresponded to the number of times that the overall area was fished during the 2007-2008 period.

4.3.3 Last disturbance event estimation

VMS data were also used to estimate the timing of the last fishing event at each station. To determine this date, all fishing events within a 564m radius of each station ($1km^2$ circular area) were identified from the interpolated VMS data. Photographic observations at each station were based on a linear transect with a mean length of ca. 370m (minimum 110m to maximum 810m). The date of the last disturbance event was defined as the date when half of the cumulative effort within the $1km^2$ area had been reached, working back from the sampling date, such that a considerable portion of the photographic transect would be likely to fall within the fished area of seabed. Fishing effort was calculated as described above but within $1km^2$ cells. The area swept was then re-calculated in a chronological order from the most recent to the oldest interpolated VMS position, until half of the overall fishing effort was reached, date at which the last disturbance event was set.

4.3.4 Impact of fishing on epifaunal communities

The area of sampling needed to be the same at each station to compare abundance and richness among stations. In practice, the number of valid pictures varied from 10 to 50 per station Given that a large amount of information would be lost if only those stations where the maximum number of pictures could be analysed were included, or if a minimum number of pictures per station were included, we considered the effects of including 15, 25, 35 or 45 pictures in the analyses; which restricted the number of stations to 62, 57, 48 and 30 for each analysis respectively. To achieve this, pictures were sub-sampled at random within stations where available pictures exceeded the thresholds of 15, 25, 35 or 45. Fifty sub-sampling iterations were used in each run to assess quantitative and qualitative differences in the results.

We assessed the impact of fishing on taxonomical composition and functional composition to determine characteristics, other than abundance and richness, for which recovery might be assessed. This was predicated on the assumption that there must be a detectable impact for a detectable recovery to occur. The effect of fishing on the taxonomical and functional composition were tested by analysis of similarities (ANOSIM) (Clarke & Ainsworth 1993) and permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001), using the “vegan” package in R. ANOSIM and PERMANOVA were used to assess whether the distribution of species across stations was related to the fishing effort which was categorized as “low” (below median value) and “high”. The statistical significance of the ANOSIM statistic *R* was assessed by permuting the grouping vector to obtain the empirical distribution of *R* under null-model. In PERMANOVA, significance tests are done using F-tests based on sequential sums of squares from permutations of the raw data. Both tests were used here as they have been observed to give different results despite the similarity of the approaches (Walters & Coen 2006). If differences were significant, the species (or trait modality) accounting for the differences between “low” and “high” fishing effort hereafter referred to as “indicator species” and “indicator modality”, were identified by calculation of an index called the indicator value (Dufrene & Legendre 1997). “labdvs” package in R. The indicator value is the product of the relative frequency and relative average abundance in clusters. The index of species (or trait modality) i in cluster j is thus maximal if species (or trait modality) i is only found in cluster j and if species (or trait modality) i occurred in all the stations of cluster j. The statistical significance of the species indicator values was evaluated using a randomization procedure. This was done for the 15, 25, 35, and 45 pictures sub-samples and run 50 times. The top ten indicator species and indicator modalities contributing to the “low” and “high” clusters were recorded for each significant iteration. Results for the subsample of pictures that showed the highest ANOSIM and PERMANOVA statistics are presented.

4.3.5 Recovery of epifaunal communities

The recovery of abundance, richness or functional composition was described in relation to the estimated date of the last disturbance event. First, the correlation between fishing intensity and the time of the last disturbance event was tested to eliminate the possibility of confounding effects, as it was possible that the most intensively fished areas were also the ones with the shortest time since last disturbance. Then, in the absence of empirical data on the form of recovery dynamics, the logistic equation (Verhulst 1845) was used to fit the recovery curve (Pitcher et al. 2000):

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)\ (eq1)$$

where r is the intrinsic increase, K the carrying capacity, N the abundance (or richness) of benthic communities and t the time since last disturbance.

This equation describes an exponential increase of a population which slows as the carrying capacity of the environment is reached. We made the simplifying assumption that the community would behave as a population. In reality, the size and species composition of the community would change during recovery owing to the different intrinsic rates of increase of the component species.

The equation was integrated between $N_{(t=0)}$ and N to express the abundance N as a function of time since last disturbance t:

$$\int_{N_{t=0}}^{N} \frac{dN}{N(K-N)} = \int_{N_{t=0}}^{N} \frac{r}{K}\, dt \quad (eq2) \quad \Leftrightarrow \qquad N = \frac{N_{t=0} K e^{rt-\ln(K-N_{t=0})}}{1+N_{t=0}\, e^{rt-\ln(K-N_{t=0})}} \ (eq3)$$

The growth parameter r was expected to vary as a function of the environment and was therefore expressed in the model as a function of q covariates where

$$r = \alpha_0 + \alpha_1 x_1 + \cdots + \alpha_q x_q \ (eq4)$$

Two environmental covariates, tidal velocity and wave stress, were chosen because they are known to be important drivers of sessile epifauna abundance around the Isle of Man (Lambert et al. 2011). Further, it was expected that stations surrounded by a higher abundance or richness of epifauna would recover relatively faster. The characteristics of the surrounding communities were defined as the mean characteristics of the communities located within a 6km radius of the station. In effect this selected the closest stations because the sampling grid was spaced at ca. 5km.

The carrying capacity, K, would ideally be expressed as a linear function of environmental parameters prior to the fitting of the curve, to limit the number of parameters used to estimate in the model. However, this was not possible given the infrequent sampling of unfished stations and K was therefore fixed as being the maximum value recorded at any station where no 'last disturbance event' was found. These stations were more numerous than the unfished stations, since the last disturbance event was calculated on a 1km^2 grid and fishing effort on a 9km^2 grid.

The models were built by including covariates one at a time. The Akaike's Information Criterion (AIC) was calculated and used to identify the most parsimonious model (Venables & Ripley 2002). The models were tested on the 50 iterations of the 15, 25, 35 and 45 picture sub-samples.

The significant models were used to assess the recovery time of the communities. Recovery was assumed to have occurred when 90% of the carrying capacity, K, was reached since, by definition, K is never reached by the curve. Recovery (T) was estimated based on eq3:

$$t = \frac{1}{\mathrm{r}}\left(\ln\left(\frac{N}{N_{t=o}}\right) + \ln\left(\frac{K - N_{t=o}}{K - N}\right)\right) \quad (eq5)$$

$$\Leftrightarrow\ T = \frac{1}{\mathrm{r}}\left(\ln\left(\frac{0.9K}{N_{t=o}}\right) + \ln\left(\frac{K - N_{t=o}}{0.1K}\right)\right) \quad (eq6)$$

If the environmental covariates were found to significantly influence the growth parameter, r and T were subsequently defined as ranges.

4.4 Results

Fishing impact on epifaunal communities

Community species and trait compositions were significantly related to fishing intensity (table 4.2).

Table 4. 2 Significance of fishing impacts on species and trait composition. “Number” represents the number of relationships that were found at the level of significance indicated in the p-value column after 50 iterations. Significant corresponds to a p-value <0.05.

			ANOSIM		PERMANOVA	
	Pictures number	p-values	Global *R* (+- SE)	Number	Partial R^2	Number
Species composition	15	Significant	0.13 (±1.6x10^{-3})	50	0.05 (±3.8x10^{-4})	50
		Non significant	_	0	_	0
	25	Significant	0.16 (±1.1x10^{-3})	50	0.05 (±2.8x10^{-4})	50
		Non significant	_	0	_	0
	35	Significant	0.15 (±8.5x10^{-4})	50	0.06 (±1.7x10^{-4})	50
		Non significant	_	0	_	0
	45	Significant	0.14 (±4.9x10^{-4})	50	0.07 (±1.3x10^{-4})	50
		Non significant	_	0	_	0
Trait composition	15	Significant	0.06 (±1.9x10^{-3})	49	0.04 (±1.0x10^{-3})	49
		Non significant	_	1		1
	25	Significant	0.07 (±1.9x10^{-3})	50	0.05 (±1.0x10^{-3})	50
		Non significant	_	0		0
	35	Significant	0.09 (±2.7x10^{-3})	50	0.06 (±1.0x10^{-3})	50
		Non significant	_	0		0
	45	Significant	0.06 (±1.1x10^{-3})	31	0.05 (±3.7x10^{-4})	33
		Non significant	_	19	_	17

The analysis of species composition revealed a significant difference between lightly and heavily fished habitats. Amongst the species that consistently belonged to the group of "high" fishing intensity were the target species of the fishery, the queen scallop *Aequipecten opercularis* and the king scallop *Pecten maximus*, as well as some brittlestars *Ophiura spp*., some ascidians, the bryozoans *Cellaria spp*., the starfish *Leptasterias muelleri*, the bivalve *Palliolum tigerinum* and the hard cup coral *Caryophyllia smithii.* In the "low" fishing intensity group, a greater number of species contributed significantly to the species composition. Among those species were a variety of gastropods, crustaceans, echinoderms and mostly cnidarians, such as hydroids and the anemones *Urticina spp.* (figure 4.1).

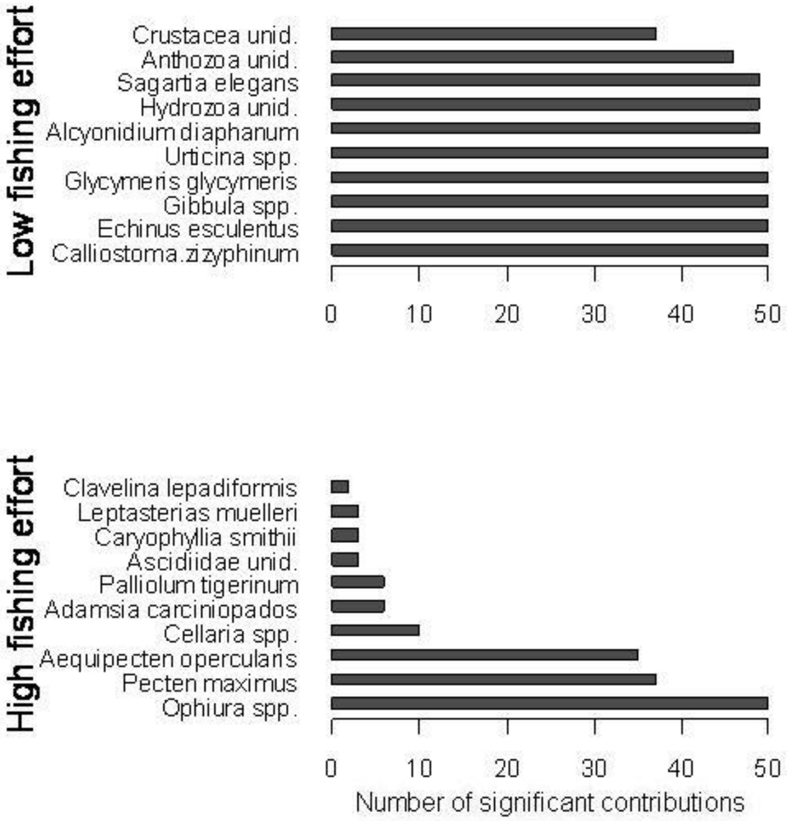

Figure 4. 1 Species contributing to the difference between low and high fishing effort as identified from the species indicator value. 50 iterations of 25 randomly selected pictures per station.

The difference in trait composition between stations attributed to “high” and low” fishing was mostly explained by the high number of indicator traits found in the “low” fishing intensity group. No trait contributed significantly to the “high” group, although those traits that were expected to characterise highly disturbed sites, such as short life span, high mobility and small size, were seldom identified as indicators (figure 4.2).

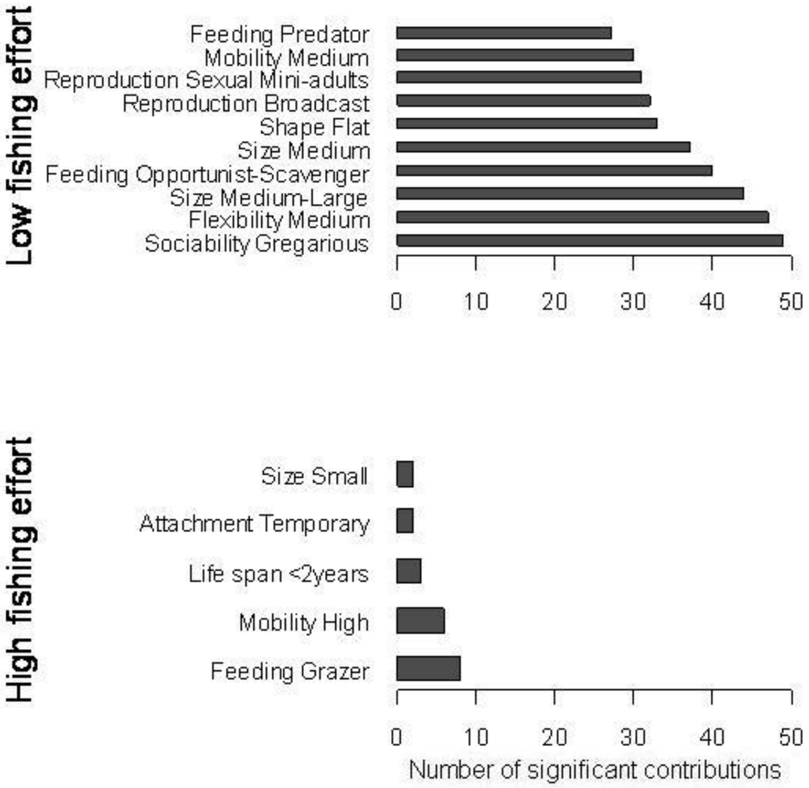

Figure 4. 2 Traits contributing to the difference between low and high fishing effort as identified from the trait indicator value. 50 iterations of 35 randomly selected pictures per station.

Since the indicator value was a combination of the relative abundance and frequency in a cluster compared with the alternative cluster, the results show that there was a higher diversity of trait modalities found at higher abundances in most of the stations that were only lightly impacted by fishing compared to the heavily impacted stations. The stations that were the most impacted had fewer trait modalities, which occurred at lower abundances and frequencies. Among the traits that characterised the lightly impacted stations, the first five were opportunist-scavenger feeding mode, gregarious social behaviour, 10°-45° flexibility, 10-20cm adult size and 21- 50cm adult size (figure 4.2).

Potential recovery during the first year after fishing impact

The time since the last disturbance significantly decreased with increasing fishing intensity when all stations were included in the analysis (Pearson's correlation coefficient = 0.25, df = 70, p = 0.031). This relatively weak relationship was not significant when soft substratum stations were removed (Pearson's correlation coefficient 0.19, df=44, p=0.205). Therefore, the effect of time since last disturbance on community characteristics was less likely to be an effect of fishing intensity but was considered to be a more representative estimate of recovery time.

The recovery time of species abundance, the abundance of gregarious species and species with medium body size depended on tidal velocity, with the modelled intrinsic rate of increase increasing with increasing tidal velocity (table 4.3, Annex).

If the communities were left undisturbed from fishing activities, the models predicted that post-disturbance recovery would occur between 349 and 1207 days, i.e. between ca. 11 months and 3.5 years, for species abundance and medium size species. Recovery would be faster for gregarious species, between 228 and 744 days, i.e. ca. 7.5 months to 2 years. This recovery rate was similar to the recovery of species with medium body flexibility for which no environmental covariate was significant, between 690 and 797 days.

Table 4. 3 Recovery time estimates and model parameters for each community descriptor that was affected by fishing activities. The model used was the logistic model as described in the method section (eq. 3). The significant environmental variables are given in the table. The range covered by the parameters is based on 50 iterations of selections of 15, 25, 35 and 45 pictures. The value of the response variable in unfished areas is given for comparison with the modeled carrying capacity K (further details are given in Annex)

Response variable	**Environmental parameter**	**Equation parameters**	**Range of equation parameters on environmental gradient**	**Carrying capacity from unfished areas**	**Recovery time (days)**
Abundance	Tidal velocity	r	$4.3\text{x}10^{-3}$ – $1.5\text{ x}10^{-2}$		349 – 1207
		K	117.3 – 122.1	8.4 – 88.7	
		No	4.9 – 5.6		
Richness	None	r	$7.1\text{x}10^{-4}$		3060
		K	24.7	9.5 – 17.7	
		No	12.5		
	Tidal velocity	r	$5.7\text{x}10^{-4}$ – $1.3\text{ x}10^{-4}$		217 – 4938
		K	31.4	9.5 – 21.0	
		No	11.0		
Gregarious *spp*.	Tidal velocity	r	$9.2\text{x}10^{-3}$ – $3.1\text{ x}10^{-2}$		228 – 744
		K	78.1 – 88.1	6.3 – 22.1	
		No	$5.9\text{x}10^{-1}$ – $8.9\text{x}10^{-1}$		
Medium size *spp*.	Tidal velocity	r	$5.2\text{x}10^{-3}$ – $1.7\text{x}10^{-3}$		381 – 1192
		K	103.6 – 110.2	7.9 – 29.9	
		No	1.5 – 1.9		
Medium-large size *spp*.	Local abundance	r	$9.6\text{x}10^{-4}$ – $2.6\text{ x}10^{-2}$		234 – 5922
		K	17.0 – 17.4	1.2 – 4.1	
		No	$2.4\text{x}10^{-1}$ – $5.1\text{x}10^{-1}$		
Medium flexibility *spp*.	None	r	$7.7\text{x}10^{-3}$ – $8.7\text{ x}10^{-2}$		690 – 797
		K	72.9 – 78.8	2.6 – 17.2	
		No	1.4 – 1.6		
Opportunist-scavenger *spp.*	Tidal velocity	r	$5.6\text{x}10^{-4}$ – $1.3\text{ x}10^{-2}$		319 – 7398
		K	6.4 – 8.5	1.4 – 3.2	
		No	0.7 – 0.8		

Recovery of medium-large adult size species depended on their local abundance and varied accordingly between 234 and 1076 days, i.e. between ca. 10 months and 3 years, as estimated based on 15 and 25 picture selections, and could take up to 5922 days (>15years) according to the results from the 35 picture selection (table 4.3, Annex). The number of significant relationships with tidal velocity at the 35 picture selection level was however lower than for 15 and 25 selected pictures. Furthermore, recovery was not significant when more pictures, i.e. less stations, were included in the analysis. For opportunistic-scavenger feeders recovery was more variable than for other groups and estimated to take from ca. 10 months up to 20 years (table 4.3, Annex). The model of richness recovery, as estimated from 15 pictures, was hardly better than the null model (ΔAIC=0.2), leading to a high recovery estimate of 3060 days. The fit was stronger with 25 pictures, with a range for recovery of 217 to 4938 days.

Examples of recovery trajectories for each significant variable are shown in figure 4.3. For species abundance, gregarious species, medium and medium-large species, the average values observed in unfished areas always occurred in the upper range of the values observed in fished areas; although they remained mostly below the ‘recovered’ values. This suggested that either most of the unfished stations had actually been impacted during the fishing season just prior to 2007-2008 or that the carrying capacity estimated from the least-impacted stations was actually higher than the carrying capacity anywhere else. For the other response variables however, species richness, medium flexibility and opportunist-scavenger species, the average values observed in unfished areas fell in the lower range of the values observed in fished areas (table 4.3, figure 4.3), suggesting a behaviour different than expected when released from fishing pressure.

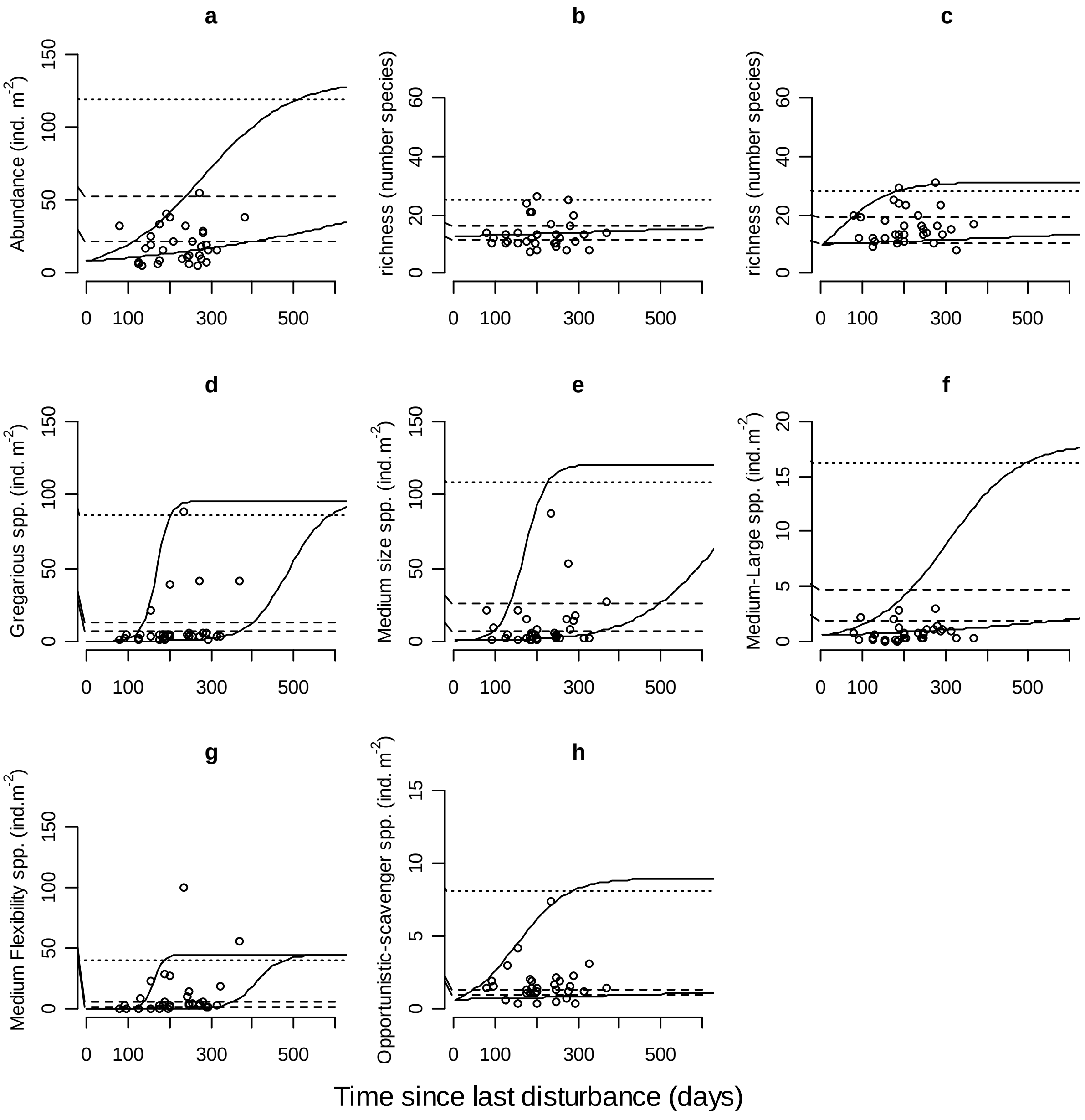

Figure 4. 3 Recovery of (a) benthic epifaunal abundance, (b) richness (15 pictures), (c) richness (25 pictures), (d) abundance of gregarious spp., (e) medium size spp., (f) medium-large spp., (g) medium body flexibility spp. and (h) opportunistic-scavenger spp. after fishing impact – Example of 1 iteration. The dash lines represent the average abundance (± standard error) of areas for which fishing intensity was equal to 0, i.e. areas likely to have remained unfished for over a year while the dotted lines represent

90% of the carrying capacity estimated from the maximum estimate observed across all unfished stations. The continuous lines are the modelled recovery trajectories for the minimum and maximum value of the covariate when there was one.

Total abundance – AIC null model = 269.19, AIC logistic model = 267.50
Gregarious *spp*. – AIC null model = 284.76, AIC logistic model = 228.36
Medium Size *spp*. – AIC null model = 274.80, AIC logistic model = 244.87
Medium large size *spp*. – AIC null model = 85.55, AIC logistic model = 78.98
Medium body fexibility *spp*. – AIC null model = 251.33, AIC logistic model = 235.41
Opportunist scavenger *spp*. – AIC null model = 106.16, AIC logistic model = 92.05
Richness – AIC null model = 269.17, AIC logistic model = 195.17
Richness – AIC null model = 269.20, AIC logistic model = 196.65

4.5 Discussion

The territorial waters of the Isle of Man have been fished for decades and yet, by combining information on fishing effort and the ecological properties of benthic communities, we show that the fishing grounds consist of a mosaic of communities at different stages of recovery from the last fishing event. Owing to the dynamics and patchiness of fishing effort, such patterns are expected on all fishing grounds, and taking account of these patterns provides a good opportunity to assess recovery at larger scales and with high levels of replication. In principle, the information on recovery trajectories would also allow the recovery status of benthic habitat to be mapped based on knowledge of the distribution of previous events.

Communities demonstrated clear signs of recovery between fishing events and the modeled trajectories (based on many individual recovery trajectories) suggest that recovery may occur between approximately 1 and 4 years if the seabed was left undisturbed. The exact time-scale depended mostly on the hydrodynamics of the area and the proximity of the fishing ground to less disturbed habitats. The latter is an important finding as it provides evidence for the benefits of reserves or unimpacted areas that provide sufficient adults to provide a supply of larvae or juvenile to surrounding impacted areas of the seabed. The results suggested however that large adult size organisms may take much longer to recover (>10 years). Inconsistencies between the state of the communities in unfished and fished areas suggested further that species richness and abundance of species with medium body flexibility or opportunist-scavenger behavior could not be related to fishing and their recovery trajectories leading to large recovery time scales might only be artifacts. Encouragingly, our measurements of recovery time based on this novel approach correspond to what is expected from meta-analyses and large-scale long-term studies, ranging from <3 years to 5-10 years (Cranfield et al. 2001, Blyth et al. 2004, Collie et al. 2005, Kaiser et al. 2006a) but they also provide insight into variation in recovery state within fishing grounds. Recovery from other human activities affecting similar habitats, such as industrial extraction, which are more destructive since they remove the substratum, can take from 2-4 years to up to >7years (Desprez 2000, Cooper et al. 2007).

The present study, together with the few studies that have followed the recovery of benthic communities after the cessation of long-term fishing impact, confirms the potential for heavily fished grounds to start recovering during the first years post fishing disturbance. For example, Blyth et al. (2004), showed that the benthic community of a mixed coarse substrata area impacted by towed gear was approaching the composition of an adjacent non-impacted area after 2 years of cessation of towed-gear activities but that biomass still remained lower. Collie et al. (2005) showed significant increases in abundance and biomass 2.5 years after the closure of a gravel sediment area of the Georges Bank, but increases in numbers and biomass of certain species were still observed up to 5 years after the closure.

The present study based its conclusion purely on abundance and species composition and does not consider the additional time necessary for biomass to recover which is an important ecological state indicator (Van Dolah et al. 1987, Newell et al. 2004, Collie et al. 2009). Therefore, it is very likely that the communities may need longer than 1 to 4 years to reach the maximum carrying capacity of the environment in terms of biomass. Further, in highly structured communities that directly compete for space there is likely to be some successional change with shifts from smaller to larger species through time. Biomass recovery could be estimated if biomass were estimated from the pictures. This has been achieved by Lambert et al. (2011) but was outside the scope of this study given the very high number of pictures used in the present analysis and the variety of organisms identified.

For the range of fishing intensities encountered in the present study, species richness did not show any consistent recovery from fishing, consistent with the different responses of biodiversity to trawling impacts reported in the literature (Collie et al. 1997, Veale et al. 2000, Bradshaw et al. 2001). Such trends tend to become more apparent when extremes of fishing intensity are encountered (e.g. Hinz et al. 2009). In addition, this may be a consequence of the existence of resilient species that would have had time to adapt to high levels of disturbance over the years. Relatively lightly and highly fished areas were however distinguished by their species and trait compositions. Even though richness did not seem to respond directly to fishing, there were more species and traits that were indicative of lightly fished stations compared to those that were highly fished. This is an important result in itself as the diversity in species traits has been highlighted as a key factor in maintaining the adaptive capacity and resilience of communities (Elmqvist et al. 2003). Some species responded to fishing as anticipated from their life history traits, such as sessile anemones and hydroids that were mostly present in lightly fished areas or the scavenger-predator *Leptasterias muelleri* that occurred in heavily fished areas (Ramsay et al. 1998, Tillin et al. 2006). However, the species and traits that were mostly found in the least impacted areas included some that were expected to be representative of heavily fished grounds and vice-versa. For instance, most opportunist-scavenger feeders and flat bodied species were found in lightly fished grounds while the upright bryozoa *Cellaria sp.* was indicative of heavily fished grounds (see Bradshaw et al. 2001). These counter-intuitive results suggest that changes in community composition under fishing pressure are not always easy to detect. For instance, some sessile upright species that are found in fished areas, such as *Cellaria sp.* here, might have similar distributions to the species targeted by the fishery although they remain affected by fishing gears within the fishing grounds (Lambert et al. 2011). Additionally, some species that have adapted to life in disturbed areas might be able to survive just as well in undisturbed areas and aggregations of scavengers after a fishing event may only be a transient (Ramsay et al. 1998, Thrush et al. 1998). Therefore, because opportunists-scavengers may not be representative of unimpacted or lightly impacted grounds, their recovery trajectory estimated in the present study may be an artifact as suggested earlier.

Among the other trait modalities that responded to fishing intensity, two belonged to the size trait and one to social behavior, with larger species and gregarious species being indicative of lightly fished areas. Large body size is known to be correlated to other life history traits, such as low intrinsic rates of increase and slow growth, and thus large species are usually more sensitive to a given rate of mortality. The decrease in size of biota with fishing has also been widely reported (Collie et al. 2000b, McConnaughey et al. 2005, Tillin et al. 2006, Robinson & Frid 2008). Species with gregarious behavior can be expected to be particularly sensitive to fishing gears, although those traits were different, but not incompatible, to those identified by Tillin et al. (2006). The potential for species characterized by these life history traits to recover between 1 and 4 years indicate that the recovery observed for total abundance of species is accompanied by a recovery of the structure of community in terms of functional composition. This is important as it suggests that the impacted communities on this fishing ground may thus not have flipped into an alternate steady state that would prevent their recovery to a pre-fished state (Scheffer et al. 2001, Birkeland 2004).

Estimates of recovery that focus on functional groups overlook individual species that may be important in terms of function or from a conservation perspective. Our methods could be used to look at the recovery of species, although this was not the focus of this study. A proportion of species will recover relatively slowly. For example, Hall-Spencer & Moore (2000) reported that live maerl thalli did not show any sign of recovery 4 years after being fished by a towed-gear while long-term historical studies suggest that some fragile taxa have been extirpated from the North Sea following intensive trawling and do not appear to be recovering (Philippart 1998, Robinson & Frid 2008).

Recovery has to be assessed in relation to a reference point (Thrush & Dayton 2010). Most studies use pre-impact values or values from neighbouring areas as recovery reference points (Newell et al. 2004, Kaiser et al. 2006a). Here, the recovered state was estimated from the community characteristics of the mixed to hard substratum grounds around the Isle of Man which did not appear to have been fished during the year. It is however possible that the potential carrying capacity was higher than shown by the data due to the long history of human impact around the island (Veale et al. 2000). Patches of *Modiolus modiolus* beds were observed around the island during the survey. These hotspots of biodiversity were not included in the present analysis since their underlying substratum type could not be identified as mixed to hard substratum. However, if *Modiolus modiolus* were able to colonize those substrata and were taken as reference for the recovered state of benthic communities, it is very likely that complete recovery would be close to impossible regarding the distance between certain fishing grounds and those remaining mussel beds or the long life span of *Modiolus modiolus* and the very high diversity and abundance of associated species (Sanderson et al. 2008). Careful considerations have thus to be made if such analysis was to be used to set management targets, whether the targets were to reach the recovered state or maximize the productivity of the system. As carrying capacity depends on primary production, it will generally depend on environmental conditions although it could not be verified here. Further data collected from unfished areas would therefore provide estimates of the recovered state and would help defining sensible management targets. Here we showed that the second parameter of the recovery model of species abundance, the intrinsic rate of increase, depended mostly on tidal velocity. Hydrodynamic regime has already been shown to affect recolonization rates by influencing both the adult and juvenile and larval stages in soft sediment communities (Dernie et al. 2003). Intrinsic rate of increase of species abundance could therefore be expected to depend on the surrounding assemblages (Allison 2004), but this was only observed for medium-large adult size species where recolonization might be helped by immigration and/or larval supply from relatively short distances.

The abundance of queen and king scallops stocks around the Isle of Man increased in recent years (Beukers-Stewart et al. 2005). However, epifaunal abundance at most fished sites is less than half of the recovered estimate (figure 4.3). While this implies high epifaunal production (Pitcher et al. 2000), scallop spat depend on sessile epifauna for settlement (Paul 1981, Lambert et al. 2011) and it is not known at what abundance the availability of epifauna might become limiting.

Our approach of calculating the time since last disturbance and describing subsequent recovery trajectories is particularly relevant to the Isle of Man scallop fishery. There, disturbance is applied in acute pulses, where a ground is intensively fished for a 2 week period and then the fleet moves on, potentially coming back onto the ground once more before the end of the season (Veale et al. 2000). This fleet behavior allows for a good approximation of the date at which the station might have been fished since the whole area is not continuously fished at variable intensities. This approximation was improved by the use of recently developed techniques to model the track of fishing vessels (Hintzen et al. 2010, Lambert et al. in press). However, to apply the method developed in this paper to other systems, VMS data at higher poll rates than the 2 hours that are characteristically used in European fisheries are needed. Furthermore, it has to be noted that, due to the limited accuracy of the fishing tracks, some strong assumptions had to be made to estimate the last disturbance event at each station. Ideally, the last disturbance event would be the latest date at which the sampled station had had a high probability to have been fished, e.g. when fishing intensity reached 0.5 in the cell that contained the station. However, the low fishing intensity around the Isle of Man for the period investigated (generally $<0.5y^{-1}$) did not allow us to use this approach. Here, we used as last disturbance event the date at which half of the effort applied during the year had been reached. Although this approach gave convincing results, studying the implications of the choice of the approach on the recovery estimates would be necessary in order to validate our conclusions.

By studying many locations in the fishing ground, our approach achieved uniquely high replication of recovery trajectories. The approach is valuable because it illustrates the extent of heterogeneity in recovery and provides a better overall assessment of recovery rates than the single experimental studies or studies of area closures that have supported previous assessments. Measurements of recovery time can be used to define the resilience of different habitat types to different types of fishing impact and will allow managers to estimate trawling frequencies that are consistent with sustainable impacts and/or to assess if the resilience of habitats is so low that fishing would be inconsistent with management objectives.

4.6 Annex

4 0 Annex. Recovery time estimates and model parameters for each community descriptor that was affected by fishing activities.

The model used was the logistic model of the form $N = \frac{N_{t=0} K e^{rt - \ln(K - N_{t=0})}}{1 + N_{t=0} e^{rt - \ln(K - N_{t=0})}}$,

where N is the response variable, t is the time since last disturbance and K, r and $N_{t=0}$ are the parameters to estimate. K is fixed at the maximum value amongst all stations where no last disturbance event has been found. r is expressed as linear combinations of environmental variables. The best models for each response variable calculated from 15, 25, 35 and 45 pictures are presented. They were chosen based on their AIC value. The most parsimonious model was the model with the lowest AIC. The significant environmental variables are given in the table along with the number of times this covariate was chosen compared to the number of times the logistic model (with or without covariate) was significantly better than the null model. ΔAIC gives the average difference (± standard error) in AIC between the selected logistic model and the null model. The null model was the model with intercept only. The value of the response variable in unfished areas is given for comparison with the carrying capacity K.

*Not presented in the result section of the paper (table 4.3) since the AIC estimates are not significantly different from the null model

Response variable	**Pictures Number**	**Environmental parameter (number significant)**	**Equation parameters**	**Parameter estimates**	**Range of equation parameter r on environmental gradient**	**Carrying capacity from unfished areas**	**ΔAIC**	**Recovery time (days)**
Abundance	15	Tidal velocity (50/50)	r	$\beta0= 4.5\ x10^{-3}\ (\pm 1.4x10^{-4})$	$4.6\ x10^{-3} - 1.5\ x10^{-2}$		20.94 (± 0.51)	349 - 1137
				$\beta1= 4.0x10^{-3}\ (\pm 1.5x10^{-4})$				
			K	122.1 (± 4.0)		18.2 - 63.1		
			No	$5.6\ (\pm 1.9x10^{-1})$	_			
	25	Tidal velocity (50/50)	r	$\beta0= 5.0\ x10^{-3}\ (\pm 8.5x10^{-5})$	$5.1\ x10^{-3} - 1.5\ x10^{-2}$		21.32 (± 0.38)	356 - 1046
				$\beta1= 3.7x10^{-3}\ (\pm 8.4x10^{-5})$				
			K	118.0 (± 2.0)		8.4 - 68.8		
			No	$4.9\ (\pm 1.1x10^{-1})$	_			
	35	Tidal velocity (50/50)	r	$\beta0= 4.1x10^{-3}\ (\pm 5.4x10^{-5})$	$4.3x10^{-3} - 1.4\ x10^{-2}$		20.51 (± 0.26)	371 - 1207
				$\beta1= 3.7x10^{-3}\ (\pm 4.3x10^{-5})$				
			K	117.3 (± 1.6)		9.4 - 88.7		
			No	$5.6\ (\pm 7.2x10^{-2})$	_			
	45	Tidal velocity (50/50)	r	$\beta0= 5.4x10^{-3}\ (\pm 4.1x10^{-5})$	$5.5x10^{-3} - 1.4\ x10^{-2}$		14.72 (± 0.16)	375 - 955
				$\beta1= 3.3x10^{-3}\ (\pm 3.1x10^{-5})$				
			K	118.2 (± 0.8)		10.1 - 84.3		
			No	$5.3\ (\pm 5.4x10^{-2})$	_			
Richness	15	None (34/50)	r	$7.1x10^{-4}\ (\pm 5.5x10^{-5})$	_		0.20 (± 0.03)	3060
			K	24.7 (± 0.3)		9.5 - 17.7		
			No	$12.5\ (\pm 5.8x10^{-2})$	_			
	25	Tidal velocity (38/50)	r	$\beta0= 4.2x10^{-3}\ (\pm 4.5x10^{-5})$	$5.7x10^{-4} - 1.3\ x10^{-2}$		9.7 (± 0.35)	217 - 4938
				$\beta1= 4.8x10^{-3}\ (\pm 1.3x10^{-5})$				
			K	31.4 (± 0.2)		9.5 - 21.0		
			No	$11.0\ (\pm 1.0x10^{-2})$	_			

Response variable	**Pictures Number**	**Environmental Parameter (number significant)**	**Equation parameters**	**Parameter estimates**	**Range of equation parameter r On environmental gradient**	**Carrying capacity from unfished areas**	**ΔAIC**	**Recovery time (days)**
Medium-large size *spp*.	15	Local abundance (43/50)	r	β0= 4.5x10^{-3} (± 2.6x10^{-4})	4.5x10^{-3} - 2.6x10^{-2}		10.1 (± 0.73)	234 - 1352
				β1= 1.3x10^{-3} (± 3.8x10^{-5})				
			K	17.4 (± 3.1x10^{-1})		1.5 - 4.1		
			No	3.5x10^{-1} (± 2.0x10^{-2})				
	25	Local abundance (47/50)	r	β0= 5.9x10^{-3} (± 2.5x10^{-4})	6.0 x10^{-3} - 2.0 x10^{-2}		11.6 (± 0.51)	323 - 1076
				β1= 1.4x10^{-3} (± 2.8x10^{-5})				
			K	17.2 (± 1.7x10^{-1})		1.4 - 3.9		
			No	2.4x10^{-1} (± 1.5x10^{-2})				
	35	Local abundance (27/50)	r	β0= 8.5x10^{-4} (± 1.0x10^{-4})	9.6 x10^{-4} - 1.5 x10^{-2}		34.70 (± 0.87)	379 - 5922
				β1= 1.3x10^{-4} (± 2.2x10^{-5})				
			K	17.0 (± 1.8x10^{-1})		1.5 - 3.9		
			No	5.1x10^{-1} (± 1.2x10^{-2})				
Medium size *spp*.	15	Tidal velocity (50/50)	r	β0= 7.0x10^{-3} (± 3.2x10^{-4})	7.2x10^{-3} - 1.7 x10^{-2}		9.57 (± 0.24)	381 - 900
				β1= 3.7x10^{-3} (± 3.0x10^{-4})				
			K	110.2 (± 4.4)		8.2 - 28.5		
			No	1.5 (± 7.3x10^{-2})	_			
	25	Tidal velocity (50/50)	r	β0= 6.4x10^{-3} (±1.7x10^{-4})	6.6x10^{-3} - 1.6x10^{-2}		8.55 (± 0.14)	397 - 962
				β1= 3.5x10^{-3} (± 1.1x10^{-4})				
			K	103.6 (± 2.7)		7.9 -24.4		
			No	1.6 (± 5.7x10^{-2})	_			
	35	Tidal velocity (50/50)	r	β0= 5.1x10^{-3} (± 8.3x10^{-5})	5.2x10^{-3} - 1.5x10^{-3}		7.95 (± 0.10)	413 - 1192
				β1= 3.6x10^{-3} (± 6.1x10^{-5})				
			K	105.8 (± 1.9)		9.2 - 24.3		
			No	1.9 (± 3.4x10^{-2})	_			
	45	Tidal velocity (50/50)	r	β0= 7.1x10^{-3} (± 4.9x10^{-5})	7.2x10^{-3} - 1.5 x10^{-2}		5.59 (± 0.07)	425 - 885
				β1= 3.1x10^{-3} (± 2.4x10^{-5})				
			K	105.9 (± 0.8)		9.2 - 29.9		
			No	1.6 (± 1.8x10^{-2})	_			

Response variable	**Pictures Number**	**Environmental parameter (number significant)**	**Equation parameters**	**Parameter estimates**	**Range of equation parameter r on environmental gradient**	**Carrying capacity from unfished areas**	**ΔAIC**	**Recovery time (days)**
Medium flexibility *spp*.	15	None (30/50)	r	7.9x10^{-3} (± 3.0x10^{-4})	_		3.22 (± 0.23)	777
			K	73.7 (± 4.9)		2.6 - 17.2		
			No	1.4 (± 9.1x10^{-2})	_			
	25	None (31/50)	r	7.7x10^{-3} (± 1.8x10^{-4})	_		2.4 (± 0.12)	797
			K	78.8 (± 3.4)		3.0 - 15.8		
			No	1.5 (± 6.5x10^{-2})	_			
	35	None (50/50)	r	8.5x10^{-3} (± 1.1x10^{-5})	_	3.3 - 15.6	2.74 (± 0.08)	721
			K	72.9 (± 1.9)				
			No	1.4 (± 3.5x10^{-2})				
	45	None (50/50)	r	8.7x10^{-3} (± 8.0x10^{-5})	_	3.2 - 15.8	1.71 (± 0.04)	690
			K	73.7 (± 9.4x10^{-1})				
			No	1.6 (± 3.2x10^{-2})				
Opportunistic-scavenger spp.	15	Tidal velocity (32/50)	r	β0= 5.7 x10^{-4} (± 1.1x10^{-4})	6.9 x10^{-4} - 1.1 x10^{-2}		18.2 (± 0.88)	396 - 6307
				β1= 4.0x10^{-3} (± 1.6x10^{-4})				
			K	8.5 (± 0.2)		1.4 - 3.2		
			No	0.8 (± 2.2x10^{-2})	_			
	25	Tidal velocity (47/50)	r	β0= 9.1 x10^{-4} (± 9.0x10^{-5})	1.0 x10^{-3} - 1.2 x10^{-2}		19.72 (± 0.64)	376 - 4514
				β1= 4.2x10^{-3} (± 8.1x10^{-5})				
			K	7.8 (± 0.2)		1.4 - 2.9		
			No	0.7 (± 1.6x10^{-2})	_			
	35	Tidal velocity (49/50)	r	β0= 1.0 x10^{-3}(± 7.5x10^{-5})	1.1 x10^{-3} - 1.2 x10^{-2}		19.41 (± 0.38)	385 - 4201
				β1= 4.3x10^{-3} (± 5.4x10^{-5})				
			K	7.6 (± 7.6x10^{-2})		1.5 - 2.9		
			No	0.7 (± 1.4x10^{-2})	_			
	45	Tidal velocity (37/40)	r	β0= 4.1x10^{-4} (± 5.0x10^{-5})	5.6x10^{-4} - 1.3x10^{-2}		11.04 (± 0.13)	319 - 7398
				β1= 4.8x10^{-3} (± 3.7x10^{-5})				
			K	6.4 (± 0.0)		1.6 - 2.7		
			No	0.8 (± 9.8x10^{-3})	_			

Response variable	Pictures Number	Environmental parameter (number significant)	Equation parameters	Parameter estimates	Range of equation parameter r on environmental gradient	Carrying capacity from unfished areas	ΔAIC	Recovery time (days)
Gregarious *spp.*	15	Tidal velocity (48/50)	r	β0= 1.5 x10^{-2} (±1.8x10^{-4})	1.5x10^{-2} - 3.1 x10^{-2}		7.42 (± 0.25)	228 - 472
				β1= 6.3 x10^{-3} (±8.8x10^{-4})				
			K	78.1 (± 3.4)		6.3 - 20.9		
			No	5.9x10^{-1} (± 6.2x10^{-2})	_			
	25	Tidal velocity (50/50)	r	β0= 1.0 x10^{-2} (± 8.8x10^{-4})	1.0x10^{-2} - 2.1 x10^{-2}		6.12 (± 0.17)	330 - 693
				β1= 4.2 x10^{-3} (±4.3x10^{-4})				
			K	88.1 (± 2.8)		6.9 - 21.5		
			No	7.7 x10^{-1} (± 4.8x10^{-2})	_			
	35	Tidal velocity (50/50)	r	β0= 9.0 x10^{-3} (± 9.1x10^{-4})	9.2x10^{-3} - 2.0 x10^{-2}		5.26 (± 0.09)	336 - 731
				β1= 4.1 x10^{-3} (±3.9x10^{-4})				
			K	83.6 (± 1.9)		7.9 - 22.1		
			No	8.9 x10^{-1} (± 4.0x10^{-2})	_			
	45	Tidal velocity (50/50)	r	β0= 9.2 x10^{-3} (± 5.6x10^{-4})	9.3x10^{-3} - 1.8 x10^{-2}		3.06 (± 0.02)	385 - 744
				β1= 3.3 x10^{-3} (± 3.5x10^{-4})				
			K	84.1 (± 0.7)		8.6 - 22.1		
			No	7.4 x10^{-1} (± 9.9x10^{-3})	_			

Testing the performance of laser-lines and photographic image processing to support large-scale cost-effective surveys of habitat complexity and the assessment of fishing impacts.

Chapter 5 – Habitat complexity

Lambert G. I., Hiddink J. G., Hinz H., Kaiser M. J., Murray L., Jennings S. (in prep). Testing the performance of laser-lines and photographic image processing to support large-scale cost-effective surveys of habitat complexity and the assessment of fishing impacts.

Authors' contribution:

I was responsible for the logistics in the laser line project. I wrote the programs, conducted all the analyses and wrote the manuscript.

Simon Jennings, Michel Kaiser and Jan Hiddink supervised the work and helped at different stages: discussing the ideas, structuring the manuscript, writing it up and proofreading it.

Simon Jennings had a strong input on the direction to take with the manuscript.

Hilmar Hinz was at the origin of the laser line project when we conducted the survey in 2008.

Hilmar Hinz and Lee Murray were both involved in the discussions on the best use of the laser line data and also helped taking the calibration pictures.

I also want to acknowledge two more people:

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- Lael Parrott who developed the method for the picture analysis with Raphael Proulx and who confirmed my interpretation of the results (although she has not read the manuscript). Here I wrote the code myself in R but Dr Parrott recently provided me with her and Dr Proulx's latest Matlab code so that I can use their version in any future research project.

5.1 Abstract

The monitoring and assessment of habitat distribution and status is needed to support existing and emerging environmental policy commitments. Traditional monitoring of species’ abundances in marine seabed ecosystems is costly and labour intensive and might usefully be complemented by cheaper and more readily automated methods that can be used at higher frequencies on larger spatial scales. We assess how information on seabed habitat complexity is linked to the abundance of habitat forming species and human pressure, in this case dredging and trawling disturbance. Two methods were used to measure seabed complexity. The first method was based on the use of a laser line that allowed the calculation of the deviations of seabed features to a straight line while the second method was based on the pixel value distribution of seabed pictures. The complexity index calculated from the laser line method provided the most reliable index of complexity across a range of habitat types as it showed a monotonic increase with coarseness of the substratum, from mixed sands to mixed rocks, and the abundance of sessile epifauna on a range of habitats. The photographs did not consistently pick up the increase in complexity due to sessile epifauna. The laser line complexity index also responded to the impacts of dredging and trawling, suggesting it would be suitable for monitoring habitat impacts and recovery. We recommend the laser line method for further development and application in monitoring. While we envisage that the scale and frequency of habitat monitoring and assessment could be increased using a laser line system, such monitoring and assessment would have to be linked to lower frequency and lower resolution assessments based on conventional biological sampling or photography to provide an overall description of habitat status.

5.2 Introduction

The requirement to protect marine habitats and biodiversity through habitat protection is articulated in national, regional and international guidelines and policies (e.g. Habitat Directive (EC 1992), Magnuson-Stevens Fishery Conservation and Management Act in the US (U.S. Congress 1996) and the Convention on Biological Diversity (UNEP/CBD 2010)). To support such guidelines and policies, both the distribution and status of different habitat types have to be monitored and reported. This information is used to assess human impacts and to determine the need for, and performance of, management measures.

The distribution and status of marine habitats is affected by human and environmental pressure. Bottom trawling is one of the most widespread human pressures (e.g. Eastwood et al. 2007) and modifies habitat structure and associated biodiversity (e.g. Auster & Langton 1999, Thrush & Dayton 2002). Changes in habitat owing to trawling pressure are usually quantified by intensive sampling to provide species identity, abundance and/or body size data (e.g. Jennings et al. 2001b, Blanchard et al. 2004) or by photographic methods that are used to derive metrics of species' abundance (e.g. Collie et al. 2000a, Lambert et al. 2011). Both approaches are relatively costly and labour intensive, require specialist taxonomic skills and are therefore challenging to use for frequent monitoring over large spatial scales.

The structural complexity of a habitat depends on the substrate type and the types of sessile fauna that are present (Auster & Langton 1999). Soft sediments are generally dominated by infauna (Snelgrove & Butman 1994) but can be stabilized by diverse communities of infaunal species or by the development of biogenic reefs, such as mussel beds (Probert 1984, Meadows et al. 1998). Sessile epifaunal communities on hard mineral substrates or biogenic reefs may create structurally complex environments which in turn increase the area available for settlement and provide shelter for a variety of organisms such as fish recruits and small crustaceans (Connell & Jones 1991, Beck 1997, Bradshaw et al. 2003). Structurally complex habitats modify the local environment in many ways, by changing the local hydrodynamics, the exchange of nutrients between the seabed and the water column and the flow of larvae to the seabed (e.g. Wildish et al. 1997, Bruno & Bertness 2001, Bolam et al. 2002). The complexity of the habitat structure influences further the interactions between the seabed and other parts of the ecosystem (Crowder & Cooper 1982, Bruno & Bertness 2001). Complexity is therefore an important component of the ecosystem.

Trawling and dredging in structurally complex environments can reduce habitat complexity by flattening the substratum, fragmenting rocks and damaging, removing or killing the sessile organisms growing on it (Kaiser et al. 2000b, Kaiser et al. 2002b, Lambert et al. 2011). The scale of modification depends on the intensity of fishing, the background levels of natural disturbance and the species composition and interactions in the community (e.g. Hall 1994, Thrush et al. 1998, Turner et al. 1999, Kaiser et al. 2000b).

While detailed assessments of the effects of trawling or dredging on species composition and abundance provide an accurate description of fishing effects, the demands for frequent monitoring of habitats and fishing effects on large spatial scales and for assessing the performance of management actions suggest that less costly and labour intensive methods might usefully complement existing approaches. Previously, there have been several attempts to describe habitat complexity in general terms, instead of focusing on the identity and abundance of species (McCormick 1994 and references therein). These are predicated on the assumption that more complex habitats support relatively higher biodiversity and/ or are indicative of lower levels of human impact. Methods for describing complexity have relied on direct measurement, for example by using a profile gauge or comparing linear distances with distances across a habitat surface (Luckhurst & Luckhurst 1978, McCormick 1994). These measurements are usually made by divers and are difficult to use over large-spatial scales. Acoustic methods can provide descriptions of habitat complexity at large spatial scales, but they do not describe the contribution of fauna with soft tissues to the habitat.

Here, we explore the performance of an alternate method for assessing habitat complexity. The method can potentially be used to describe habitat structure and to assess the impacts of fishing on habitat at large spatial scales. The first method is derived from the profile gauge and chain methods. It is based on the use of a line laser fitted on a sled that is towed along the seabed. It allows the replication of detailed vertical topographic measurements at scales of tens of kms. The laser line method has already been used once in a marine ecology study where the authors' objectives were different from the present study, i.e. they were measuring the physical impact of one fishing event of different gears on a range of sediment types (O'Neill et al. 2009). The second method is based on the use of seabed photographs to assess 2-dimensional heterogeneity within habitats. It calculates an index of complexity from the layout of the pixel values (Proulx & Parrott 2008). Both methods are cost effective as they do not require the collection and identification of fauna. We assessed the capacity of these methods to distinguish between habitats of different complexity by comparing trends in derived indices of complexity with detailed information on community structure that was collected at the same spatial scale.

5.3 Methods

5.3.1 Survey description

Seabed habitats around the Isle of Man were surveyed in August 2008. Photographs of the seabed were taken at 120 stations located on a regular grid with 5km spacing inside the 12 nautical mile territorial limit. A sledge, fitted with a still camera (high resolution Canon 400D digital camera) and a video camera, was towed on the seabed for 15min at each station. Every 9 s, a 10 megapixel still photograph was taken with the camera pointing perpendicularly towards the seabed (ca. 100 pictures per station); each photograph recorded an area of 0.14 m^2 (ca. 40x35cm) (adapted from Lambert et al.

2011). The video camera pointed forward at an angle of ca. 50° of the seabed and recorded throughout the tow. A cable-less line laser in a waterproof housing was fitted to the sledge pointing perpendicularly towards the seabed, at a distance of ca. 20 cm in front of the video camera, both at a height of ca. 60 cm. The so-called laser "line" is more precisely described as a laser "plane" that draws a line on the seabed which crosses the video screen from left to right (see figure 5.2). The laser was a Z-Laser model Z3A with a red wavelength of 635 nm and a line length of 1m when mounted at 50cm in the air. Deviations of the seafloor from flat surface could be observed on the video monitor. The position and deflections of the laser line were thus recorded on the video camera as the sled was towed. The red line could only be recorded if the lights on the sledge were off. Therefore, after recording for 15 minutes with lights on, the sled was towed for 2-3 minutes with lights off.

5.3.2 Data collection

To link descriptions of habitat complexity to the ecology of the habitat and fishing, data on species, substratum type and fishing intensity were required. The still photographs were used to identify and quantify the benthic epifauna present at each station to the lowest possible taxonomic level. Biomass of sessile epifauna was estimated based on analysis of 10 photographs per station as in Lambert et al. (2011).Additionally, species were identified and quantified in terms of abundance on 10 to 50 photographs per station; the number of photographs analyzed per station was limited by the quality of the pictures and by time constraints. The area sampled needed to be the same at each station to compare abundance and richness between stations, i.e. same number of photographs (Lambert et al. in prep.). Therefore, 15 photographs were randomly selected from all analysed photos for each station. The random sub-sampling was done 50 times in order to determine a more reliable average estimate of the abundance of mobile and sessile species and the richness of mobile species. Fish and worms were excluded as the photograph and video methods are not suitable for estimating abundance of infaunal, tube-dwelling or highly motile species. The photographs were also used to make a qualitative assessment of substratum type: as mud, sand, mixed sand (including shells), mixed gravel, mixed cobble or mixed rocks (when boulders were present). An overall category per station was chosen over a more detailed quantitative description per picture for several reasons, the main one being that it was not possible to determine the substratum type of the images recording the laser line in the dark. Therefore a general category for the overall station was needed.

The main towed fishing gears used in the territorial waters of the Isle of Man are scallop dredges and queen scallop otter trawls. All vessels fishing within the territorial waters are fitted with vessel monitoring systems (VMS). Data were available for the whole 2007-2008 fishing season prior to the sampling date. Cumulative fishing intensity at each station was calculated from positions recorded by a VMS within a 9km^2 area around each station (Lambert et al. in prep.).

5.3.3 Calculation of structural complexity indices

Complexity indices derived from the laser lines

Between 10 and 30 still images showing the laser lines were extracted from the videos at 20 stations with coarse substratum. The number of images used depended on the actual length of the tow and the quality of the video. The images were enhanced by increasing the contrast between the laser line and the surrounding environment and removing the noise (such as bubbles that would reflect the laser at random) and the coordinates of the laser lines extracted using Image J v.1.43 (National Institute of Mental Health) and R (R Development Core Team 2008, www.r-project.org). The laser lines coordinates were extracted as a series of points on the two-dimensional (x,y) plane.

Changes in the distance between the camera and the point at which the laser line illuminated the seabed, due to the lifting of the sled from the seabed, meant that the line did not appear at the same place on the recorded image. To ensure that the true length of the laser line could be determined, extracted lines had to be calibrated from pixels to cm. The calibration technique was based on that developed in soil sciences by (Darboux & Huang 2003) and applied to fisheries research by (O'Neill et al. 2009). A grid with 4cm graduations was placed underwater in the laser plan in front of the sledge (figure 5.1). The real coordinates of each intersection point (in cm) were then related to the (x,y) coordinates of the pixels in the image of the grid using 4th degree polynomial equations (figures 5.1 and 5.2):

(eq. 1) $$real\ x\,(cm) = \sum_{\substack{i,j=0 \\ 1+j\le 4}}^{4} A_{ij}\,x^i y^j$$

(eq. 2) $$real\ y\,(cm) = \sum_{\substack{i,j=0 \\ i+j\le 4}}^{4} B_{ij}\,x^i y^j$$ (adapted from O'Neill et al. 2009)

where A_{ij} and B_{ij} are the polynomial coefficients. More details on the calibration procedure can be found in (Darboux & Huang 2003) and (O'Neill et al. 2009).

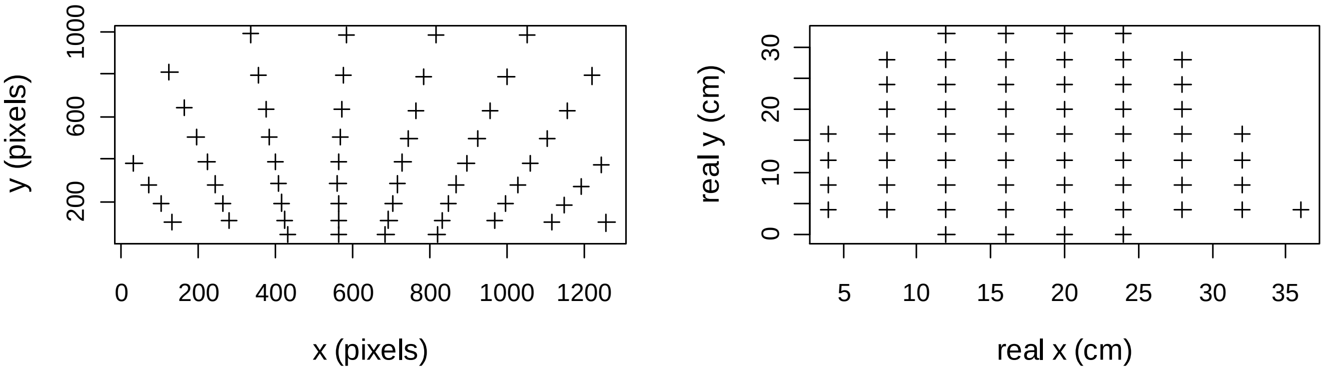

Figure 5. 1 Position of the calibration points of the grid recorded by the video camera in the (x, y) plan (left) and real position of the calibration points of the grid in the real system in cm (right).

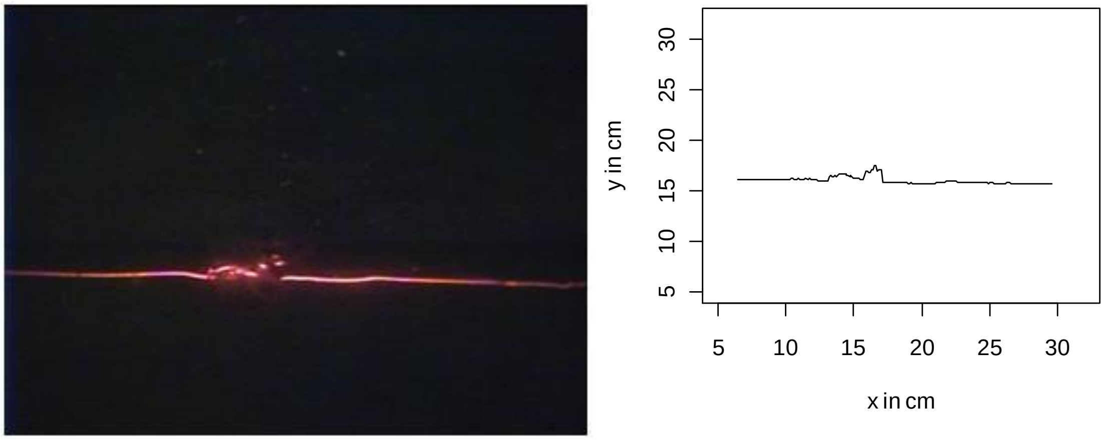

Figure 5. 2 Extraction of a laser line and calibration. Left: laser line as recorded from the video, right: calibrated laser line used to calculate complexity indices.

Along the real x-axis, the real value of y was extracted every 1mm in order to limit the noise around the width of the laser line. Three indices of complexity were then derived from the adjusted laser line: Chain and Tape (CT), which is the measure of the length of the line compared to a straight line (McCormick 1994); Vector Dispersion (VD), which is the variation in angles from one point to the next along the line (McCormick 1994); and deviation from a straight line, i.e. standard deviation of the residuals of the Linear Regression (LR).

Complexity indices derived from the still photographs

Complexity measurements were made from still photographs taken at 20 stations where laser line measurements were also available and a further 23 stations. Ten photographs per station were used to assess the biomass of sessile organisms and to calculate the seabed complexity. Individual photographs were replaced by the next available photograph when numerous or large mobile species were obscuring the seabed and therefore prevented calculation of the index of structural complexity.

Prior to analysis, photographs were enhanced using Image J software. To remove dark edges, photographs were cropped by removing 300 pixels from all edges. Cropped images were converted into black and white images. The pixels values, i.e. 0 for black and 255 for white pixels, and their coordinates in a two-dimensional (x,y) plane were extracted into text files to be processed with R software. The extracted data were used to calculate two indices of heterogeneity, based on the definition of disorder derived from the comparison of the Boltzmann-Gibbs-Shannon entropy (Andrienko et al. 2000). The two indices calculated were the Mean Information Gain (MIG) and the Mean Mutual Information (MMI) (as defined by Proulx & Parrott 2008). These indices are considered to provide a good mathematical description of habitat structural complexity (Proulx and Parrott, 2008). MIG and MMI are both calculated from the comparison between the amount of aspatial, $H[\gamma]$, and spatial, $H[\chi]$, heterogeneity in the pictures:

(eq. 3) $MIG = \frac{H[\gamma]-H[\chi]}{\log N^4 - \log N}$

(eq. 4) $MMI = \frac{4H[\gamma]-H[\chi]}{4\log N - \log N}$

with (eq. 5) $H[\gamma] = -\sum_{i=1}^{N} p(\gamma_i)\log p(\gamma_i)$

and (eq. 6) $H[\chi] = -\sum_{i=1}^{N^4} p(\chi_i)\log p(\chi_i)$ (from Proulx & Parrott 2008)

where $p(\gamma_i)$ is the probability of observing a pixel value independently of its location on the picture and N is the number of categories of pixels values, here N =2; $p(\chi_i)$ is the probability of finding a specific 2x2 black and white combination in the picture and N^4 is the number of theoretical 2x2 combinations, here N^4 = 16.

MIG and MMI values vary between 0 and 1. MIG equals 0 for uniform patterns and 1 for random ones while MMI equals 1 for uniform patterns and 0 for random ones (figure 5.3). Clustered patterns would have values between 0 and 1. The mean of MIG and MMI were calculated by station. Both indices were calculated to assess their auto-correlation. High correlation justified the use of a single index in the analyses. More details on the MIG and MMI indices can be found in (Proulx & Parrott 2008) and references therein.

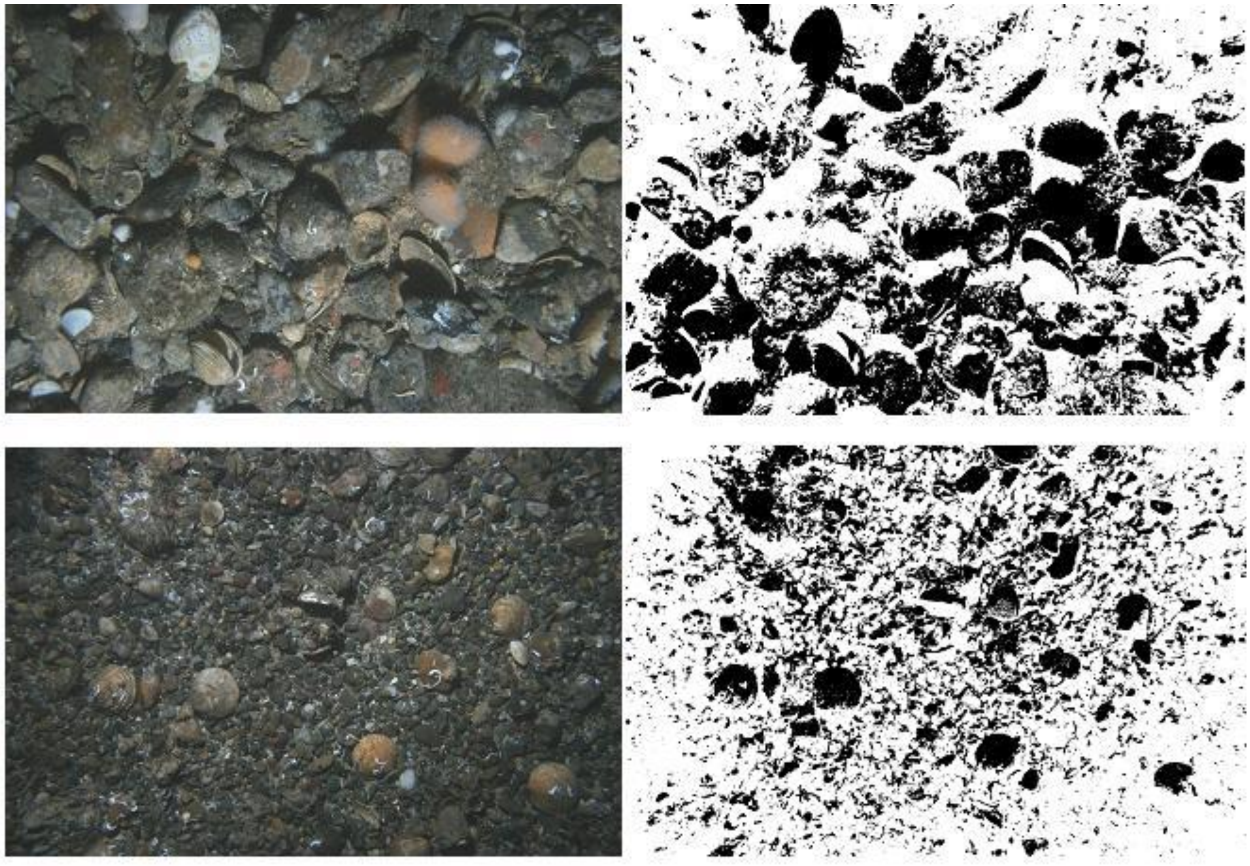

Figure 5. 3 Examples of pictures of 2 different habitats and their binary transformation for calculation of the Mean Information Gain (MIG) and the Mean Mutual Information (MMI) indices. Top pictures: mixed rock habitat and binary picture: MIG=0.14, MMI=0.84; bottom pictures: mixed gravel habitat and binary picture: MIG=0.17, MMI=0.67.

5.3.4 Statistical analyses

Collinearity between every pair of the five complexity indices was tested by calculating Spearman's rank correlation coefficients. Only independent indices were kept for analyses to avoid the problem of multiple comparisons (e.g. Benjamini & Hochberg 1995).

The potential for each selected index to capture the difference in structural complexity between different substratum types was analyzed by analysis of variance and multiple comparisons post hoc Tukey's HSD test. In order to test whether the indices captured the complexity due to sessile epifauna, substratum types that did not present a significantly different signature for a given complexity index were grouped together. Then, relationships between complexity index values and biomass or abundance of sessile epifauna within groups of habitats were tested by linear regressions or saturating curves, and the goodness of fit estimated after Student's t-tests.

The relationship between complexity indices and associated mobile epifauna was analyzed to verify the assumption that complexity increased associated diversity. Finally, we assessed how fishing effort distribution related to each complexity index to validate the use of habitat complexity indices as indices of fishing impacts on habitats.

5.4 Results

Correlations between habitat complexity indices

The complexity indices calculated from the binary photographs and the laser lines were all correlated, with highly significant correlations between the three laser line indices (figure 5.4). The two least correlated indices, one derived from the binary photographs and one from the laser lines were thence retained for the analyses: Mean Mutual Information (MMI) and standard deviation of the residuals of the Linear Regression (LR).

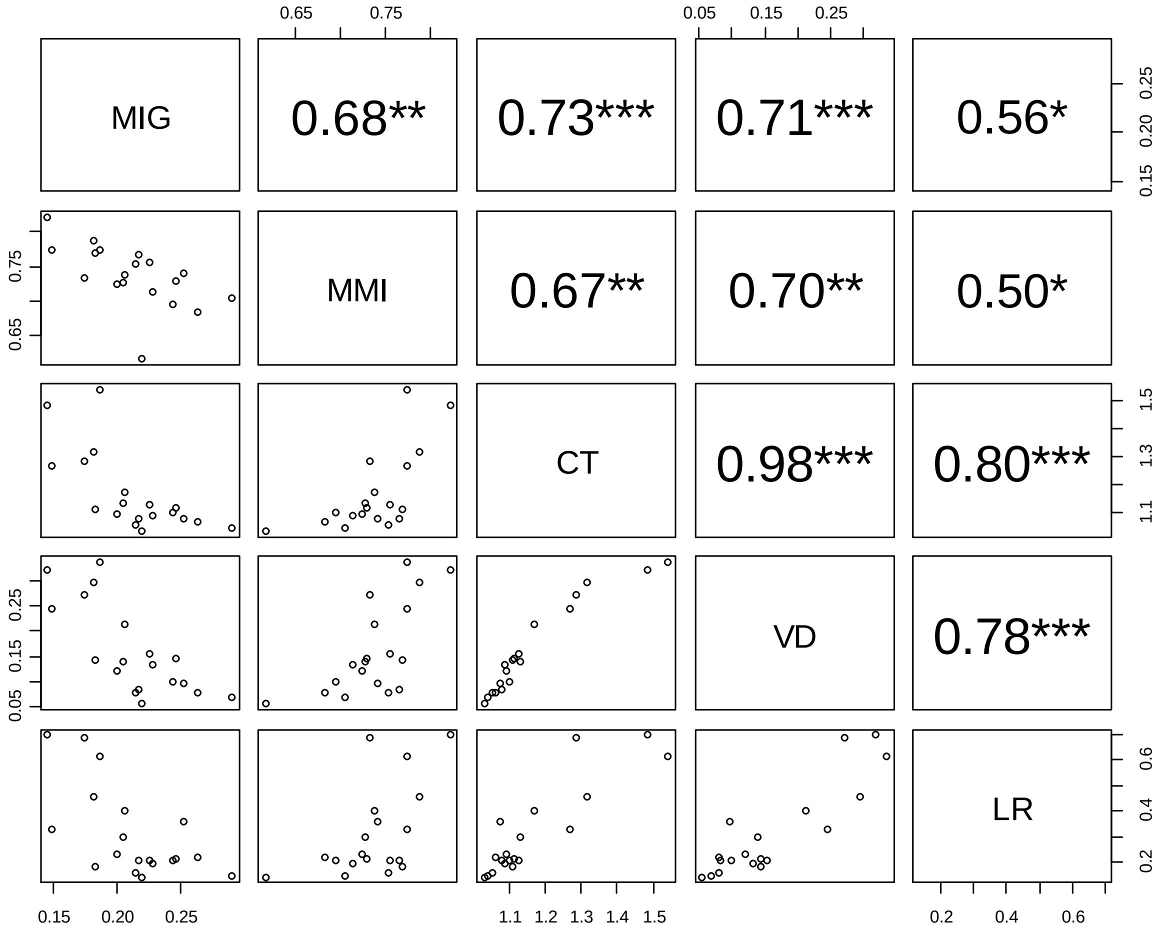

Figure 5. 4 Correlations between complexity indices. Panels under the diagonal show the correlations between indices while panels above the diagonal give the Pearson correlation coefficients and their significance. Significance levels: ***: p < 0.001, **: p < 0.01, *: p < 0.05.

Variation of habitat complexity indices with substratum type

Both MMI and LR indices showed an apparent increase with sediment coarseness, defined from the categorised substratum types, from sandy to rocky habitats (figure 5.5). MMI significantly differentiated mixed sand from all other substratum types but none of the other pairs of substrata were significantly different. LR significantly differentiated two substratum categories from the others, i.e. mixed cobble and mixed rock (table 5.1).

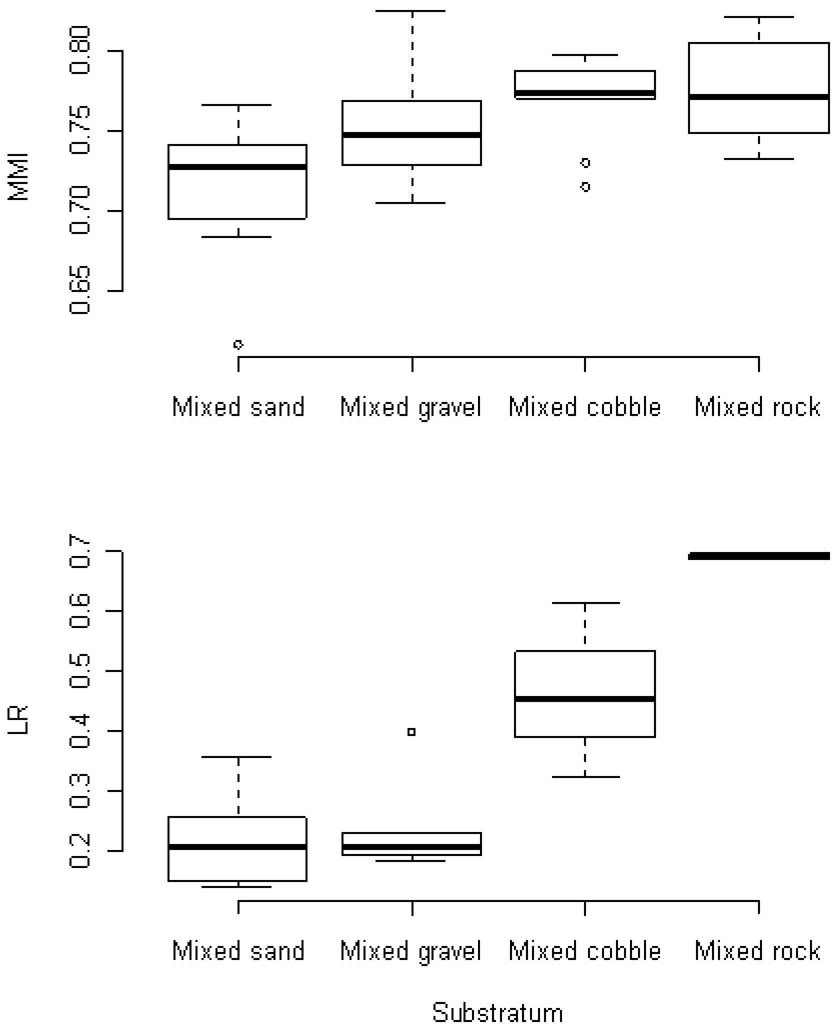

Figure 5. 5 Complexity indexes per substratum type. The substrata are ordered by level of coarseness. From top to bottom: MMI=Mean Mutual Information, LR=standard deviation of residuals from Linear Regression.

Table 5. 1 Results of the analyses of variance of complexity in relation to substratum type and significant comparisons between substratum types revealed by the Tukey test. MMI=Mean Mutual Information, MMIse= standard error MMI, LR= standard deviation of residuals to Linear Regression.

Response	Anova			Tukey test		
	df	F	p-value	Significant comparison	Difference	p-value
MMI	3	5.779	0.002***	Mixed gravel – Mixed sand	0.036	0.058
				Mixed cobble – Mixed sand	0.048	0.005
				Mixed rock – Mixed sand	0.054	0.007
LR	3	20.157	<0.001***	Mixed rock – Mixed sand	0.476	<0.001
				Mixed rock – Mixed gravel	0.456	<0.001
				Mixed rock – Mixed cobble	0.227	0.055
				Mixed cobble – Mixed gravel	0.228	0.011
				Mixed cobble – Mixed sand	0.249	0.004

Variation of habitat complexity indices with sessile epifauna

Since the complexity of mixed sand habitats was significantly different from all other substratum types, the effect of sessile epifauna on the MMI complexity index was tested independently in mixed sand and in all other substratum types, mixed gravel, cobble and rock. For the LR index, mixed sand and gravel were grouped together against mixed cobble and rock which were grouped according to their low significant difference. In mixed sand, MMI was significantly increasing with both abundance and biomass of sessile species (figure 5.6, table 5.2). However, this relationship was not evident in coarser habitats. LR increased with abundance in both mixed sand-gravel and mixed cobble-rock habitats but did not significantly increase with biomass of sessile species (figure 5.7, table 5.2).

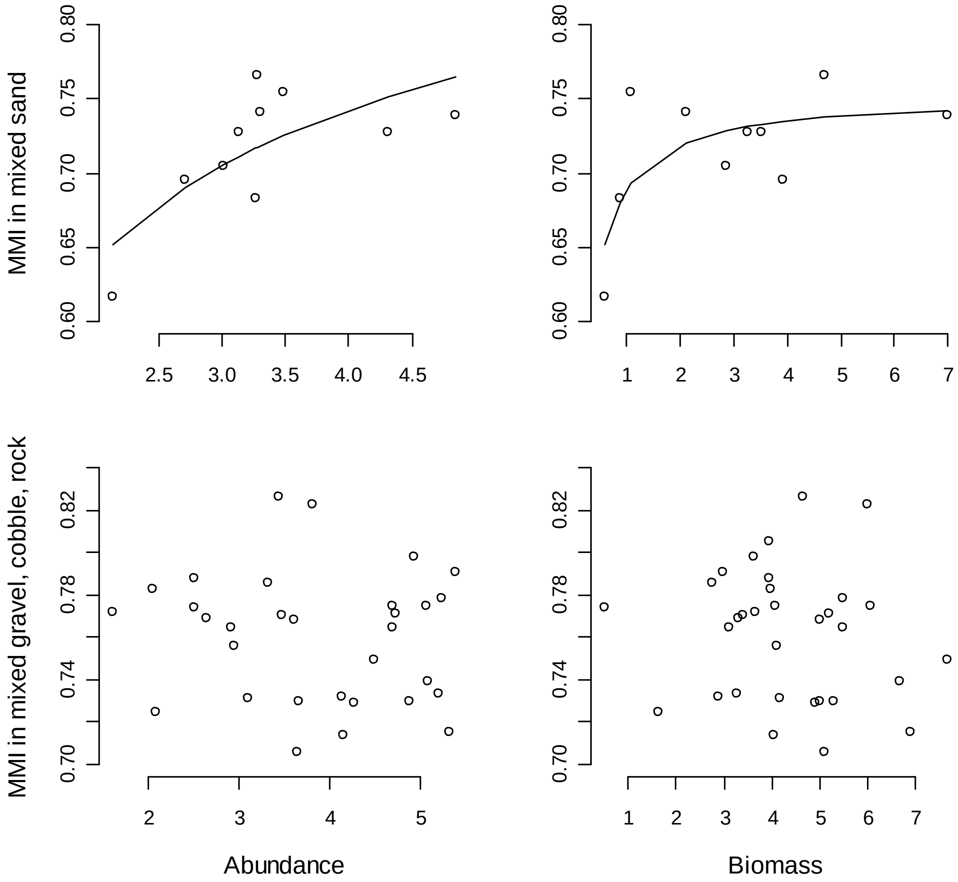

Figure 5. 6 Complexity calculated by Mean Mutual Information (MMI) in relation to sessile epifauna within groups of substrata. Top panels: mixed sand, bottom panels: mixed gravel, cobble and rock. Left panels= log-transformed abundance of sessile epifauna (ind.m^{-2}), right panels= log-transformed biomass of sessile epifauna (g.m^{-2}). The solid lines represent the significant models (statistics given in the text).

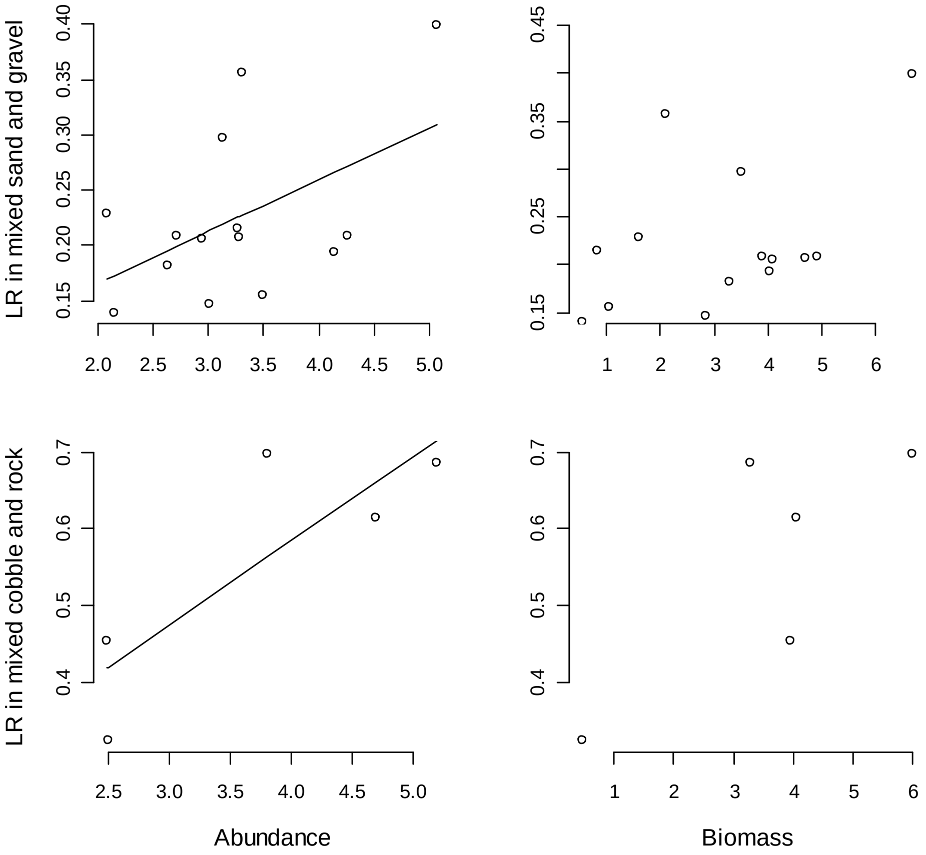

Figure 5. 7 Complexity calculated by standard deviation of residuals from Linear Regression (LR) in relation to sessile epifauna within groups of substrata. Top panels: mixed sand and gravel, bottom panels: mixed cobble and rock. Left panels= log-transformed abundance of sessile epifauna (ind.m^{-2}), right panels= log-transformed biomass of sessile epifauna (g.m^{-2}). The solid lines represent the significant models (statistics given in the text).

Table 5. 2 t-statistics of the significant relationships between complexity indices and sessile epifauna, mobile epifauna and fishing intensity as presented in the result section. MMI= Mean Mutual Information; LR= standard deviation of residuals to Linear Regression. Parameters a and b are the parameters of the saturating curve, $y = \frac{ax}{b+x}$, while intercept and slope are the parameters of the linear regression.

Response	Explanatory variable	df	Parameters	t-value	p-value	s.e.	r^2
MMI in mixed sand	Sessile abundance	8	a=0.886 b=0.769	12.411 2.389	<0.001 0.044	0.031	_
MMI in mixed sand	Sessile biomass	8	a=0.752 b=0.093	43.305 2.538	<0.001 0.035	0.032	_
LR in mixed sand- gravel	Sessile abundance	12	intercept=0.073 slope= 0.047	0.949 2.006	0.361 0.067	0.068	0.19
LR in mixed cobble- rock	Sessile abundance	3	intercept=0.147 slope= 0.109	0.917 2.649	0.427 0.077	0.102	0.6
Mobile abundance	MMI	39	intercept=-6.982 slope= 14.278	-2.144 3.290	0.038 0.002	1.064	0.19
Mobile abundance	LR	17	intercept=2.303 slope= 3.293	5.876 3.005	<0.001 0.008	0.837	0.31
Mobile richness	MMI	39	intercept=-11.727 slope= 26.661	-1.289 2.198	0.205 0.034	2.975	0.09
Mobile richness	LR	17	a=15.566 b= 0.298	3.641 1.741	0.002 0.099	2.408	_
MMI	Fishing intensity	40	a=0.766 b= -0.008	83.327 -2.216	<0.001 0.032	0.037	0.09
LR	Fishing intensity	17	a=0.552 b= -0.087	9.251 -4.582	<0.001 <0.001	0.124	0.53

Relation between habitat complexity indices and associated species and effect of fishing

Abundance and richness of mobile epifauna significantly increased with both MMI and LR (figure 5.8, table 5.2). Both indices could also detect and quantify the difference in complexity between habitats along the fishing gradient (figure 5.9). Across all habitats, MMI and LR complexity indices significantly decreased with fishing intensity (table 5.2).

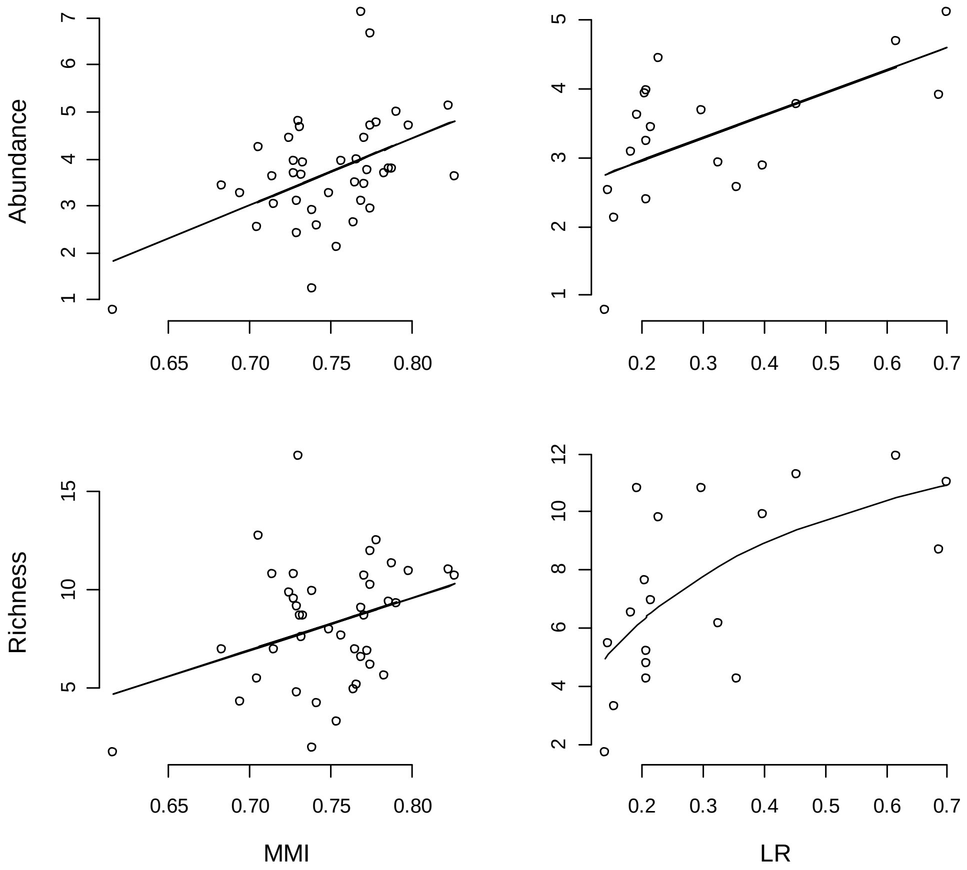

Figure 5. 8 Relationships between the indices of habitat complexity Mean Mutual Information (MMI) or standard deviation of residuals from Linear Regression (LR) and abundance (log-transformed (ind.m^{-2})) and richness of mobile species. The solid lines represent the significant model (statistics given in the text). The complexity indices are MIG= Mean Information Gain; MMI= Mean Mutual Information; CT= Chain and Tape; VD= Vector Dispersion; LR= standard deviation of residuals to Linear Regression.

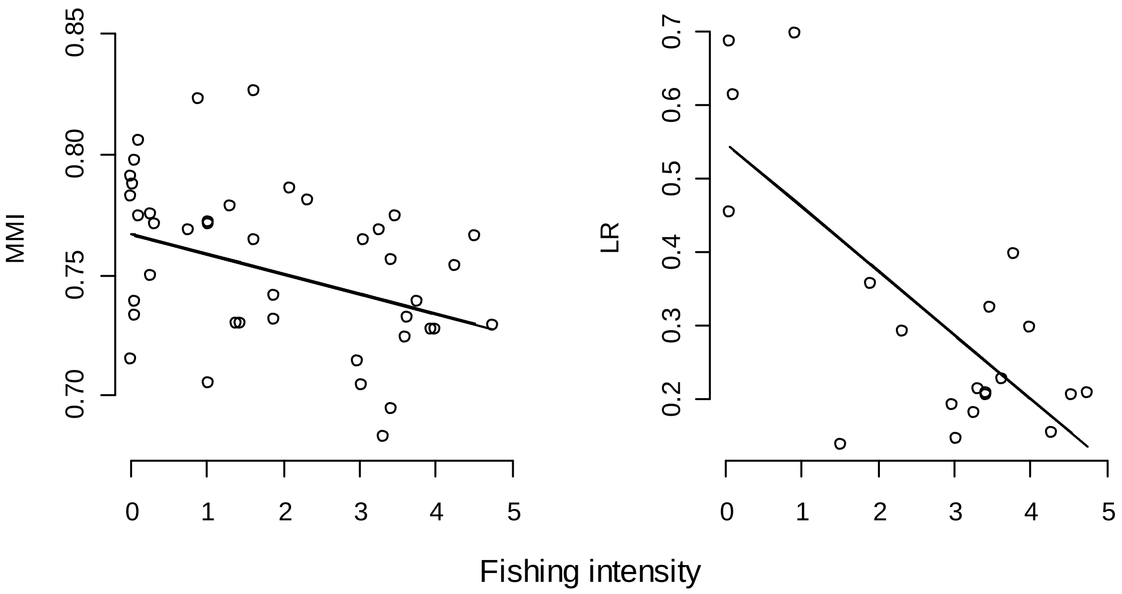

Figure 5. 9 Relationships between fishing intensity (log transformed (y^{-1})) and the indices of habitat complexity Mean Mutual Information (MMI) and standard deviation of residuals from Linear Regression (LR). The solid lines represent the significant models (statistics given in the text).

5.5 Discussion

Our results show how laser lines and processing of photographs can be used to measure seabed habitat complexity at scales that are relevant to the assessment of fisheries impacts. The two indices presented here, derived from binary photographs and laser lines, are straightforward to implement at large scales as a many stations and a high number of replicates per station can be obtain quickly and cost-effectively.

The mean information gain (MIG), which increases monotonically from uniformity to randomness, the direct opposite of MMI, has been assessed a good index of spatial heterogeneity and was related to increases in complexity and structural species diversity in an old-growth forest ecosystem (Proulx & Parrott 2008). However, at the scale of the present sampling unit, i.e. pictures recording an area of 0.14 m^2, complex habitats in coarse substrata appeared uniform rather than random. Indeed, an increase in the coarseness of the sediment, i.e. the presence on the pictures of stones and boulders and of large habitat-forming species, such as dead man's fingers *Alcyonium digitatum*, increased the uniformity of the pictures as opposed to gravel and sparse small sessile epifauna, which increased randomness (figure 5.3). MIG was thus decreasing with complexity at the present sampling scale while MMI was a more intuitive complexity index since it was increasing with sediment coarseness. However, while the index was indicative of an increase in complexity with sessile epifauna in mixed sand, i.e. an increase in apparent uniformity, this was not the case for mixed gravel, cobble and rock. This was probably because the presence of sessile epifauna on stones would have the opposite effect to that on mixed sand. Indeed, the presence of large biota on sand would add some homogeneity to the picture while it may add some patchiness, or randomness, to the photograph on large stones, leading to a conflicting increase in MMI with sediment grain size against a decrease with the presence of epifauna on stones. The laser line was in this respect a more reliable index of complexity across all habitat types since LR showed a monotonic increase with coarseness of the substratum and with abundance of sessile epifauna in both mixed sand and gravel and mixed cobble and rock. Since LR visually increased with biomass of sessile organisms but the number of points was low, the absence of significance of the relationship seemed to be due to the lack of replicates or the lack of precision of the biomass estimates rather than to a limitation of the index itself.

Despite the limited ability for MMI to measure an increase in complexity across substratum types, both LR and MMI indices could quantify how mobile species abundance and richness increased with habitat complexity. This effect of habitat complexity on associated biodiversity has been widely reported in the literature but the relationship was never quantified (e.g. Heck & Wetstone 1977, Bell & Westoby 1986, Beck 2000, Taniguchi & Tokeshi 2004, Gratwicke & Speight 2005). Whether abundance and richness increase due to actual complexity or increase in surface area is difficult to assess since surface area generally increases with greater surface complexity (Johnson et al. 2003).

Both methods detected a decrease in habitat complexity with increase in fishing pressure. Ideally, the statistical analyses should have been conducted within habitat rather than between habitats but there were not enough samples per habitat type to do so, so all stations had to be aggregated. This should not limit the validity of the results if fishing was proven to be partly responsible for the changes in habitat types as discussed thereafter.

There is a need to discern whether the decrease in complexity is due to fishing or if fishing occurs in initially less complex habitats. Since dredging and trawling kills epifauna and flattens the seabed it is very likely that the decrease in complexity is caused by fishing activities. Nevertheless, it can be argued that fishing occurs mostly in sandy and gravelly areas and that the decrease in complexity with fishing pressure reflects the habitat preference of the target species or the limited possibility for the gears to be towed over rocky grounds (Boulcott 2011). However, the laser line index not only captured variation in complexity due to substratum types but also due to sessile epifauna, which suggests that a decrease in complexity is probably not only a reflection of the substratum choices of the fishers. The increase in fishing activity over finer sediment grounds may also reflect changes in substratum types due to repeated trawling or dredging. Hall-Spencer and Moore (2000) reported that natural bottom features were eliminated along the tracks occasioned by scallop dredges, and that boulders up to $1m^3$ could be dragged along the sediment surface. The granulometric structure of the surface sediment was also found to shift in the tracks compared with adjacent, unfished areas (Hall-Spencer & Moore 2000). Hence, dredging and trawling might have an effect on the substratum comparable to aggregate extraction which changes substratum types from sandy gravels to gravelly sands (Caddy 1973, Rees et al. 2006). Furthermore, coarser substratum types may often be in close spatial association with prolific scallop grounds since scallop spat settlement is known to be enhanced by the presence of complex epifaunal turfs from which the surrounding areas might benefit (Paul 1981, Howarth et al. 2011). To conclude, a decrease in habitat complexity is to be expected as a consequence of fishing activities but the actual magnitude of the gear effects remains difficult to isolate. However, this limitation would not be an issue for temporal monitoring.

A current limitation to using laser lines to assess habitat complexity is that extraction of the laser lines from the video was only semi-automated for the present study. It required some operator time to enhance the images individually. There was an additional issue due to the shadow effect, phenomenon by which the line is interrupted because some part of the surface blocked the view of the laser. These two problems could be partly solved by using two lasers illuminating the surface with opposite incident angles (Darboux & Huang 2003) and developing software to extract the wavelength required at high frequencies so that the number of replicates would be high enough to appropriately represent complex surfaces (Frost et al. 2005).

Of the methods considered, the laser line gives more consistent information on habitat complexity and the effects of fishing. It has potential to support demands for frequent monitoring of habitats and fishing effects on large spatial scales (e.g. monitoring the performance of marine protected areas or the effects of changes in fishery management regulations). It is less costly and labour intensive than other approaches and can be deployed from vessels of many sizes. With some engineering expertise, it could even be used to create full 3D landscape if videos were analysed continuously and automatically. The laser model used in this study cost ca. £150. The housing was not included and was manufactured for the present study, complete models, including housing, are generally more expensive. The equipment could also be deployed by divers on habitats where the impacts of towing a sled over the seabed were not acceptable, such as coral reefs. Compared with other methods for assessing complexity discussed by (Frost et al. 2005): chains, profile gauges and stereo photography, the laser line is likely the most practical, precise and cost effective instrument for measuring subtidal habitat complexity. Two of its major advantages are that each measurement can be replicated at high frequencies on a particular habitat and at the highest level of precision possible. While the capacity to describe habitat complexity and fishing impacts on habitat at large spatial scales and at high resolution would add to existing monitoring and assessment, it is unlikely that it would entirely replace taxonomic assessment. We would envisage that the scale and frequency of monitoring and assessment might be increased by using a laser line system, but that this would be linked to a lower frequency and lower resolution assessment based on conventional biological sampling or photography.

General discussion

Chapter 6 – General discussion

In this thesis I have considered many aspects of the assessment and management of fishing impacts on benthic communities. In this general discussion I attempt to describe the relevance of the results to the ecosystem approach to fisheries management (EAFM).

6.1 Implementation of an ecosystem approach to fisheries management (EAFM) from an ecological perspective

Pikitch et al. (2004) summarize the objectives of an EAFM as follows: "(i) avoid degradation of ecosystems, as measured by indicators of environmental quality and system status; (ii) minimize the risk of irreversible change to natural assemblages of species and ecosystem processes; (iii) obtain and maintain long-term socioeconomic benefits without compromising the ecosystem; and (iv) generate knowledge of ecosystem processes sufficient to understand the likely consequences of human actions."

Here I propose a framework with the main objective to show how my results feed into the ecological aspect of an EAFM process that addresses the objectives outlined above. To do so, I describe the implementation of an EAFM as a six step process (figure 6.1) consisting of (1) describing the problem(s) that require(s) an action plan and gathering background knowledge on the issue; (2) understanding the underlying mechanisms of the system that requires specific management by gathering relevant empirical information; (3) quantifying the implications of human disturbance at the ecosystem level; (4) developing indicators and monitoring techniques that are representative and sensitive to changes in the system studied; (5) suggesting some management options for the system studied and evaluating scenarios; and (6) implementing management strategies, enforcing and monitoring.

More comprehensive EAFM frameworks, e.g. including the socio-economical aspect of the EAFM, have been described elsewhere (see ICES 2005).

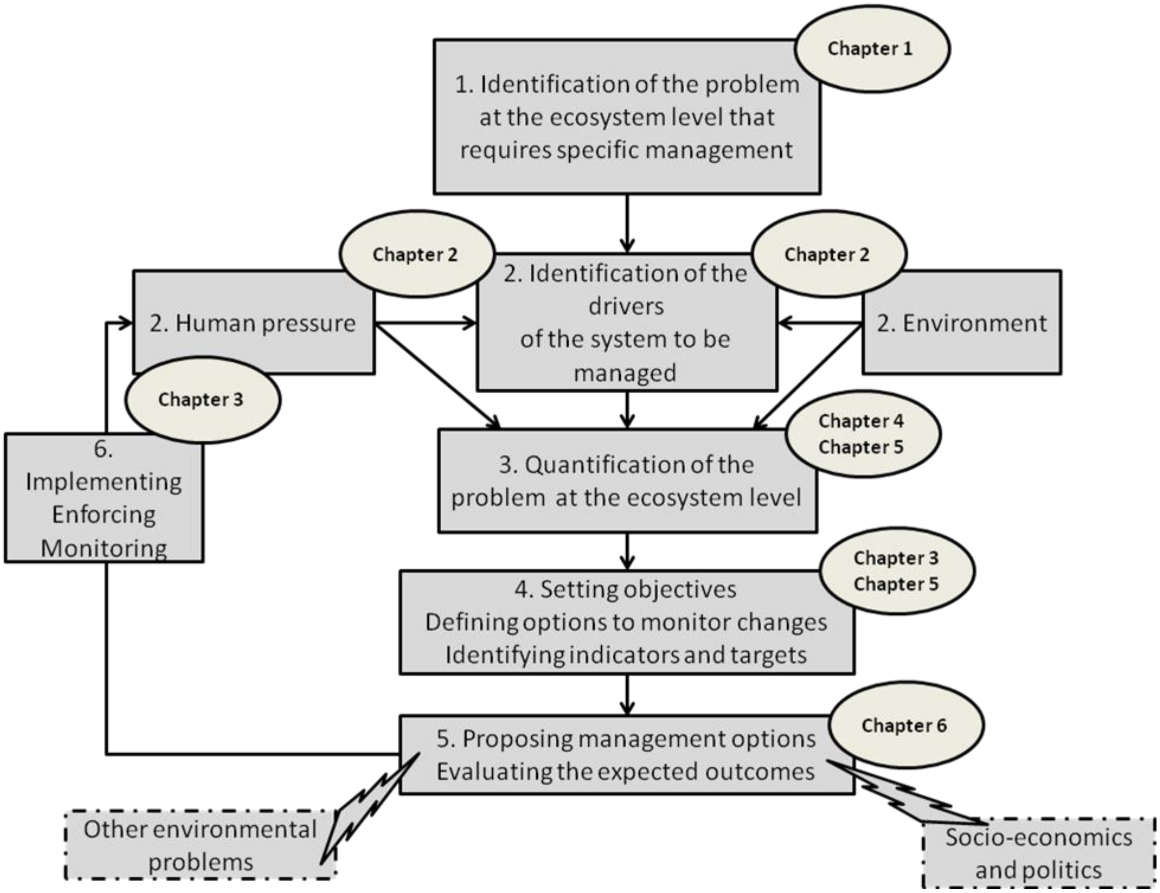

Figure 6. 1 Diagrammatic representation of the contribution of the results presented in this thesis to a framework designed for the implementation of an ecosystem approach to fisheries management (EAFM)

In the following sections, I elaborate on the EAFM process I propose and then describe the relevance of the results of this thesis in relation to this process.

6.1.1 Step 1: to describe the problem(s) that require(s) an action plan and to gather background knowledge on the issue.

The impacts of fishing on the marine ecosystem include bycatches (e.g. Currie & Parry 1999, Lewison et al. 2004), alteration of marine food webs (e.g. Jennings et al. 2001b, Pinnegar et al. 2002), reduction of biodiversity (e.g. Watling & Norse 1998, Thrush & Dayton 2002) and habitat damage (e.g. Kaiser et al. 2002b, Hiddink et al. 2007). These issues cannot be dealt with simultaneously and therefore require separate assessments that can be integrated subsequently to propose management options (figure 6.1).

This thesis focussed on the quantification and prediction of the impact of fishing on benthic species that attach and grow on harder substrata and create habitat (biogenic fauna) and their associated mobile fauna. The rationale and background research are presented in the introduction (Chapter 1). Briefly, biogenic fauna offer highly valuable services to the ecosystem such as providing shelter and food for numerous mobile species (e.g. Connell & Jones 1991, Beck 1997, Bradshaw et al. 2003). Biogenic fauna are expected to be particularly sensitive to the impacts of towed bottom-fishing gear and therefore require specific protection measures (e.g. Collie et al. 2000b, e.g. Kaiser et al. 2006a). These biogenic fauna may also have an important role in maintaining populations of target species. This is particularly true in the case of the territorial waters of the Isle of Man since the fishery targets scallops. Scallop spat are known to settle on a variety of organisms that provide a clean silt-free surface raised above the seabed (Brand et al. 1980). However, to date, these habitats have received inadequate attention in relation to understanding how fishing activities impact upon them and what the repercussions are at the ecosystem level. This is even more surprising given that such habitats often have high levels of diversity and tend to be considered as highly valuable from a habitat conservation perspective (e.g. Heck & Wetstone 1977, Bell & Westoby 1986, Beck 2000, Taniguchi & Tokeshi 2004, Gratwicke & Speight 2005). As a result, habitat-forming species that occur on harder substrata were the focal point of the present research.

6.1.2 Step 2: to understand the underlying mechanisms of the system that requires specific management by gathering relevant empirical information.

To be successful, EAFM should be built on a scientific rationale that links ecological processes to ecosystem-level patterns (Browman et al. 2004). The scientific bases behind the implementation of management strategies at the ecosystem level are however often limited by the lack of empirical knowledge to explain the observed patterns (e.g. Carr 2000, Hilborn et al. 2004). Indeed, if the relationships between the species or habitats that have been identified as requiring protection, their environment, other species, and human pressure are unknown, the planning of protection measures will be hampered (e.g. Olsson & Folke 2001, deYoung et al. 2004, Dobson et al. 2006, Greenstreet & Rogers 2006). The EAFM framework implemented here proposes to tackle this issue in two phases. In step 2, the focus is on the understanding of the drivers of the system studied. Then, the actual function of the system studied as set in the context of the overall ecosystem is quantified in step 3 of this EAFM framework.

The analyses in Chapter 2 quantified the responses of habitat-forming species to external forces, such as environmental factors and fishing pressure. Fishing and the hydrodynamics were identified as the main drivers of epifaunal biomass. Fishing and wave stress had negative effects on biomass while tidal velocity had a positive effect on biomass. In order to quantify the direct effect of fishing on benthic biota, it is necessary to understand precisely the spatial distribution and intensity of fishing activities. Despite advances in vessel monitoring system technology, the current polling rate used in VMS is sufficiently infrequent to introduce considerable error in the estimation of the distribution of direct impacts of fishing on the seabed. The models presented in Chapter 3 provided a means to correct for such errors in relation to scallop dredging.

The key conclusions drawn from the research in Chapter 3 indicated that if VMS data are used to estimate fishing effort, the temporal and spatial scale of aggregation have to be considered with care as they can change considerably the estimated impact of fishing on the benthos. It would be highly desirable for an implementation of high VMS poll rates to be able to monitor effectively mobile bottom fisheries and their impacts. The interpolation methods used to model fishing tracks did not prove very effective when fishing occurred over small scales and VMS pings were recorded only every 2h as currently used in the European Union.

6.1.3 Step 3: to quantify the implications of human disturbance at the ecosystem level.

In summary, steps 1 and 2 identified the role of the environment and fishing activities in shaping the system studied. In step 3, the wider spatiotemporal implications of the impact of fishing are assessed through the quantification of the contribution of the system to the rest of the ecosystem. To do so, it is necessary to define the poorly-understood relationships such as habitat attributes-species productivity or biodiversity-ecosystem functioning (Loreau et al. 2001, Browman et al. 2004, Dobson et al. 2006). After these first three steps, the key underlying mechanisms of the system that requires special management and of the impact of fishing will be quantified at the ecosystem level. This forms the basis for the implementation of adaptive management strategies and the effective monitoring of responses of the system to the implement management measures used to reach defined ecosystem targets.

In the thesis, the first two steps, presented in the introduction and in Chapters 2 and 3, identified the role of environmental parameters and fishing activity in shaping the benthic communities on harder substrata, and a mechanism to attribute fishing activity to specific areas of seabed was derived. In Chapters 4 and 5, some ecosystem implications of the effects of fishing on the benthos and their potential long term repercussions were quantified. Chapter 4 presented a novel approach to quantify recovery on fishing grounds across sea-basin areas. This research showed that recovery of benthic communities impacted by fishing might take from 1 to 4 years (or more) depending upon prevailing hydrodynamic conditions, which concurs with the predictions from other studies (Cranfield et al. 2001, Blyth et al. 2004, Collie et al. 2005, Kaiser et al. 2006a). Chapter 5 showed how habitat complexity determined the abundance and richness of local mobile epifaunal communities and how fishing had a negative impact on these communities through decreasing habitat complexity. Loss of habitat complexity due to fishing combined with low recovery rates means that the modification benthic communities have an overall negative impact on the functioning of the ecosystem. This suggests that the management measures to take should include preservation of habitat complexity and should consider habitat recovery rates at different locations.

6.1.4 Step 4: to set objectives and to develop indicators and monitoring techniques that are representative and sensitive to changes in the system studied.

Gislason et al. (2000) stated that a key challenge to incorporating ecosystem objectives within fisheries management was to define measurable indicators and cost-effective monitoring programs that relate to ecosystem objectives. A range of definitions of what a good indicator is can be found in the literature. To summarize, indicators used to support a decision-making process should be scientifically valid, simple and easy to communicate to non-specialists, show spatial and temporal trends, be sensitive, i.e. provide early warning of adverse effects and show progress towards meeting management objectives, be cost-effective and describe pressure upon and state of an ecosystem (Jennings 2005, Hiddink et al. 2006b, Rees et al. 2006). Relevant indicators for fisheries management can be defined based on the quantitative information gathered in the three previous steps of this EAFM framework.

The results of Chapter 5 suggest that habitat complexity would be a relevant state indicator of fishing impact on the seabed. Complexity increases with habitat-forming species abundance and biomass and with associated species and decreases with fishing pressure. Fishing pressure would naturally be used as a pressure indicator as described in Chapter 3. The use of the laser line method presented in Chapter 5 to monitor habitat complexity is a good example of how the habitat complexity indicator could be cost-effectively monitored. Recovery of benthic communities could thereby be monitored by combining the use of the laser with lower frequency biological sampling.

6.1.5 Step 5: to suggest some management options for the system studied and to evaluate the outcomes.

To meet management objectives a range of tools can be used depending on the fishery, the sensitivity of the ecosystem component or attribute that is impacted and the resources available for management. Tools to support management include management measures such as input controls, which aim at regulating the amount of human activity that is permitted; output controls, which aim at regulating the degree of perturbation of an ecosystem component that is permitted; spatial and temporal distribution controls, which aim at regulating where and when an activity is allowed to occur; and economic incentives, which aims at encouraging “good behaviour” of the stakeholders to help achieving ecological objectives. Other management tools that are not management measures exist, such as integrated planning tools, which can be used to ensure that management is coordinated, and remediation tools, which aim at restoring damaged components of the ecosystem. More details on these different tools and some examples are given in ICES (2005).

Use of Marine Protected Areas (MPAs) as management tools

Of the spatial and temporal distribution controls, those that define when and where an activity can occur, marine protected areas have assumed increasing prominence in the debate about how to ensure the sustainability of bottom fishing impacts.

An MPA refers to a management area in which usage is regulated by zoning for different activities (Sumaila et al. 2000). This means that a variety of activities can be restricted and these may be zoned such that there is a gradient from no-take zones to areas within which only certain activities are restricted. It is often identified as an appropriate tool for implementing EAFM (e.g. Agardy 1994, Kelleher 1999, Jones 2001, Browman et al. 2004, Kaiser 2005, Greenstreet et al. 2009). For habitats with very long recovery times then sustainable use may not be feasible at expected levels of fishing effort and closure may be the best option to meet a management objective for sustainable use. For other areas, the frequency and intensity of fishing might be matched to the potential for recovery.

Although ecosystem-level management objectives for the territorial sea of the Isle of Man are not specified, one possible objective would be to protect areas of high habitat complexity since they are expected to play an important role in supporting the functioning of the ecosystem (Chapter 5). These areas of high habitat complexity can be identified from the distributional maps presented in Chapter 2. Habitats may be less altered by fishing disturbance if they recover quickly and are therefore more likely to allow sustainable use that would also allow the fisheries to maintain economically viable catch rates (e.g. Hiddink et al. 2006a). Information on recovery rates can be used to identify areas which have a high likelihood to recover between fishing events, based either on theoretical assumptions about fishing rates or on data obtained from VMS analysis (Chapters 3 and 4). Habitats with faster recovery times would be considered to be areas where fishing with towed bottom-fishing gear is more sustainable.

The recovery rate estimates derived in Chapter 4 suggest that temporary closures for 1 to 4 years would be sufficient to allow habitats to recover to a state consistent with the prevailing natural environment. This is an interesting result as it suggests that chronically fished areas might be able to recover in a relatively short period of time and this had not been demonstrated before. Furthermore, areas that are rarely impacted by fishing (Chapter 3) and show a slow recovery (Chapter 4) are unlikely to support sustainable use and protection may be the favoured management option. Hiddink et al. (2006a) showed further that benthic communities would benefit from closures if fishing effort was initially low in the area that is being closed since it would lead to less effort displacement (see next section on “Assessing the risks of adverse effects of area closures”).

One of the reasons why habitat complexity should be preserved in the territorial waters of the Isle of Man is because it enhances settlement, and thereby recruitment success, of juvenile scallops (Howarth et al. 2011). Therefore, the main objective would be to create a network of protected areas that would enhance habitat complexity and thereby boosting scallop recruitment. If protected areas are used to support the sustainability of scallop fisheries and the environment that supports successful scallop recruitment then one of the main issues to consider is whether closures of a few large areas or many smaller areas provide the greater management benefits: the “single large or several small” (SLOSS) debate (e.g. Vaaland Burkey 1989, Lomolino 1994). The present study does not directly address this issue, but based on the life cycle of the target species and the known effects of the closed areas of the Georges Bank in enhancing scallop stocks I suggest that the implementation of a network of several small areas chosen based on the above consideration on recovery rates would be appropriate to the sustainable management of the scallop fishery around the Isle of Man. The reasons to my statement are listed below.

Scallops are sedentary species which can spread mostly through larval dispersal. The larval phase lasts 30-40 days before settlement (Tremblay et al. 1994). On Georges Bank, scallop larvae have been estimated to be spread over tens of kilometres during that time (Gell & Roberts 2003). There, the closure of three large areas, totalling 17000km^2, has proven highly beneficial to the scallop fishery, especially as they were instituted at the same time as a significant reduction in fishing effort (Murawski et al. 2000). These protected areas encompassed large gravel-cobble pavements where sessile epifauna rapidly developed after the closure, which led to an increase in the overall habitat suitability for scallop spat and hence recruitment success (Murawski et al. 2000, Collie et al. 2009). In these studies, fishing effort aggregated at the places that biophysical models suggested would have received most scallop larvae exported from the closed areas (Gell & Roberts 2003). Around the Isle of Man, the results of this thesis showed that sessile epifauna can grow wherever currents are strong enough, wave disturbance is limited and hard substratum is available. However, the presence of hard substrata around the island is very patchy. Recruitment is also very patchy and highly variable between years (N. Hold, unpublished data, Beukers-Stewart et al. 2003). Therefore, it is likely that a network of areas placed where hard substratum is available and connected through currents would be beneficial to the growth of epifauna and would thereby enhance the chances of successful scallop settlement and hence possible recruitment. Since hydrodynamics seem to control the distribution and growth rates of epifauna, hydrodynamic connectivity amongst protected areas might be more important than the absolute size of an area in terms of habitat recovery. It is difficult to say what size area should be recommended for protection, but evidence suggests that networks of reserves of moderate size and variable spacing should adequately protect and maintain the density and biodiversity of a large proportion of benthic organisms (Halpern & Warner 2003). Moderate size here would equate to a few km^2, which takes into account the relatively small area covered by the territorial waters (ca. 4000km^2) and the reported benefits derived in an existing closed area of 2km^2 located off the south west coast of the island where scallop densities have been observed to increase over the last 20 years (Beukers-Stewart et al. 2005). Dispersal patterns that would affect the self-sustainability of individual reserves and the connectivity within the network should be considered in relation to the exact placement of the reserves (Roberts et al. 2003). Conducting further research on the connectivity of the different scallop grounds around the island and determination of the sources and sinks of scallop spat would be highly advantageous (Beukers-Stewart et al. 2003).

Management options that maintain the patchy distribution of the fishery would maintain a higher proportion of complex seabed habitat in an unaltered state and would thereby enhance the productivity of the fishery. To an extent, the fishers on the Isle of Man already behave as such, which may explain why the fishery remains viable after > 60 years of exploitation. Because of the patchy distribution of scallops, fishers repeatedly tow a relatively small area (few kms in length) until they reach uneconomic levels of catch rate and then move onto another ground (Beukers-Stewart et al. 2003). This behaviour aggregates further the amount of seabed disturbance which has unintended (but positive) conservation effects. Irrespective of spatial management measures that might be used in this fishery, it remains clear that total fishing effort and/or scallop catches have also to be monitored in order not to decrease the scallop spawning biomass to levels that would not be sustainable.

Assessing the risks of adverse effects of area closures

Protecting areas of the sea from fishing activity induces reallocation of fishing effort if capacity reduction measures are not simultaneously taken. This can lead to both positive and negative predicted effects of area closures on benthic communities at regional scales (Rijnsdorp et al. 2001, Dinmore et al. 2003, Hiddink et al. 2006a, Greenstreet et al. 2009). These effects result from a trade-off between recovery in the closed areas and trawling impacts in the open areas that arose from displaced fishing activity (Hiddink et al. 2006a). Displacement of a large amount of fishing effort may not only increase pressure on already fished systems but might lead to the exploration of new areas which can be disproportionately detrimental since the first impact on pristine benthic communities is expected to be the greatest (Kaiser 2005, Hiddink et al. 2006c). However, preventing effort displacement to pristine or productive areas could be achieved by identifying areas for protection based on specific biomass and recovery rates using methods similar to those presented in Chapters 2 and 4. Conversely, increasing pressure on already heavily impacted habitats could lead to a shift of the benthic community into an alternate state (e.g. Scheffer et al. 2001, Mangel & Levin 2005). From the recovery analysis conducted in Chapter 4, it seems that chronically fished sites can still recover towards a state of unimpacted communities, therefore a precautionary approach should be advised and fishing pressure should not increase in sites that already are heavily fished. Because of these issues linked to effort reallocation, it is advised that the creation of protected areas often needs to be accompanied by a reduction in fishing effort or Total Allowable Catch (TAC) to meet management objectives (Greenstreet et al. 2009). Additionally, closing several small areas rather than few large ones would also probably limit effort displacement. Generally, there is a problem of enforcement associated with the choice of closing small rather than large areas for logistical and financial reasons (e.g. Agardy 2000). However, this would not be an issue in the present situation given the full VMS coverage of the Isle of Man territorial waters and the new methodologies available to reconstruct vessels tracks (such as the cubic Hermit spline method used in Chapter 3 (Hintzen et al. 2010)).

Temporary or rotating area closures can have further adverse effects if they do not allow sufficient time for recovery in between opening seasons. Such measures can lead to a greater homogeneity of trawling disturbance (Dinmore et al. 2003). Therefore, if areas are not to be protected permanently, care should be taken when implementing this type of management strategy and a precautionary approach should be preferred (e.g. protecting areas for longer than the recovery time expected, here we suggest that this is likely to be 1 to 4 years regarding epifaunal recovery but probably more regarding scallop recovery (Beukers-Stewart et al. 2005)) (but see Holland & Schnier 2006a).

Alternative strategies to marine protected areas to enforce habitat protection

In addition to closed areas, other management options summarised at section 6.1.5 could contribute to meeting management objectives for seabed habitats and the scallop fishery. Here I consider two incentive-based approaches that could help enforcing habitat protection in lights of the results of this thesis: a system of Individual Habitat Quotas (IHQ) (Holland & Schnier 2006a) and a spatiotemporal tariff-based system of credits called Real-Time Incentives (RTIs) (Kraak et al. 2011).

IHQs could be set with the objective to maintain a target habitat stock such that quotas would reflect the amount of habitat damage that fishers cause by trawling. Holland and Schnier's (2006a) simulation model did not take account of the spatial variation in habitat sensitivity to trawling (Hiddink et al. 2007). However, it is known that different habitats will have different responses to different fishing gears (Kaiser et al. 2006a). The method would therefore be enhanced through the integration of predictions on habitat sensitivity (Hiddink et al. 2007).

RTIs have a broader application since spatiotemporal tariffs would be based on any ecosystem management target, such as limiting discards, by-catches or habitat damage. The principle is that layers of spatially explicit tariffs can be superimposed and regularly updated to create a tariff map. The tariff maps can further differ for different gear types (Kraak et al. 2011). Therefore, although the impact of one metier compared to another has been estimated (Kaiser et al. 2006a), further studies would be needed to assess the exact impact of specific gears and their variants. Fishers would be attributed a certain credit and could spend it as they want, knowing that fishing in highly sensitive areas would use a large amount of credits. Protected areas could be included in this system by being attributed an infinite cost (Kraak et al. 2011).

In the present case study, it would be possible to provide spatially-explicit habitat sensitivity information based on the biomass predictions and recovery rates presented in Chapters 2 and 4. Both IHQ and RTIs methods could benefit from such information. In the case of the RTIs, a habitat-forming species-layer could be created where costs would be calculated based on the carrying capacity of the area and the recovery time. A habitat with a high carrying capacity and a very slow recovery rate would be the most expensive, while a habitat with low carrying capacity and fast recovery rate would be very cheap.

Evaluating the outcomes of different management scenarios

Understanding and predicting the real implications of proposed management strategies is complex, but provides managers with valuable insights into the possible consequences of their actions. As described in the introduction of the thesis, scientists and fisheries economists are working together to develop ecosystem models that could be used to inform managers about the consequences of alternate management actions (e.g. development of Management Strategy Evaluations (MSE) based on operational models such as Atlantis (Fulton and Smith 2004)). So-called end-to-end models are still lacking a large amount of the empirical information required for them to become operational (Travers et al. 2007, Rose et al. 2010, Moloney et al. 2011).

The findings in this thesis provide some quantitative information on the benthic compartment of the ecosystem, its drivers, its role in the ecosystem and the impact of fishing upon it. This is highly valuable information since most ecosystem models present a very simplified benthic compartment (Blackford 1997, Steele & Ruzicka 2011). All this information, i.e. responses to environmental factors, response to fishing gears, recovery rates and the relationship between habitat and associated species, could be used to inform ecosystem models from their conceptualization to the validation stage and thereby improve the management scenario evaluation stage of the EAFM framework.

6.1.6 Step 6: to implement management strategies, enforce and monitor.

The effectiveness of any ecosystem management strategy would be highly limited if it was not properly enforced and monitored (e.g. Agardy 2000).

Enforcement is not discussed in this thesis. However, some recommendations in relation to monitoring can be given. Monitoring can be done through the use of VMS data as presented and discussed in Chapter 3. Increasing VMS poll rate in combination to using interpolation techniques are suggested as an efficient way of monitoring fishing distribution and intensity.

6.2 General conclusion

The EAFM framework suggested here (figure 6.1) would provide some useful insights to fisheries researchers who are dealing with the issue of fishing impacts on the seabed and are looking for assessment methods and potential management frameworks to evaluate these impacts and set management targets for the fishery. The research provides a mechanism to evaluate a fishery such that it is possible to avoid degradation of the ecosystem, minimize the risk of irreversible change, and thereby maintain long-term socioeconomic benefit derived from a more sustainable fishery.

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