Clarke, Jo (2017) *The role of spatial measures in the management and conservation of marine fish and invertebrates*. PhD thesis.

The role of spatial measures in the management and conservation of marine fish and invertebrates


www.wildoceanphotography.com

Jo Clarke
MSc, University of Wales, Bangor
BSc (Hons), University of Wales, Cardiff

Submitted in fulfilment of the requirements for the Degree of Doctor of Philosophy

Institute of Biodiversity, Animal Health and Comparative Medicine
College of Medical, Veterinary and Life Sciences
University of Glasgow

December 2016

Abstract

Historically sea fish were thought to be an inexhaustible resource, in 1882 Thomas Huxley recognised that it was possible to extirpate some fisheries such as the UK oyster and salmon fishery, but he thought “in relation to our present modes of fishing” sea fish were so abundant that they were inexhaustible. Fishing causes impacts other than overfishing, such as bycatch of non-target and vulnerable species discarding and damage to habitats and ecological communities. Fishing intensity has been increasing since the industrial revolution through which technological advances have given fishing vessels the ability to go further and for longer. This has resulted in the need for an ecosystem focused method of management for fisheries, known as ecosystem based fisheries management (EBFM).

EBFM requires the development of indicators which represent the ecosystem with which thresholds can be set against fishing pressure. This was investigated for “Sea-pen and burrowing mud megafaunal communities”, which have been identified by OSPAR as a threatened or declining habitat in the North Sea and Celtic Seas. Baited cameras were used to monitor mobile megafauna communities across a gradient of fishing intensity to determine which species are sensitive to fishing pressure and could be used in metrics to monitor recovery in areas proposed for protection. Trawling had a negative effect on species richness of mobile megafauna, *Munida rugosa*, *Cancer pagurus* and *Liocarcinus depurator,* but no effect was found on deep burrowing species (*Nephrops norvegicus* and *Goneplax rhomboides*). This study identified species that demonstrated different trends with trawl intensity, the trends are related to the ability to burrow and the species mobility. This gives support to the use of biological traits as indicators to detect changes of communities to fishing pressure.

In addition to the development of indicators EBFM supports the use of spatial closures as a tool for fisheries management. This method of management is widely used yet remains controversial, often due to the lack of clear objectives and monitoring. Evidence is growing in support of their use but results are often seen after an extended period of long-term monitoring. Clear objectives for each spatial area closure are essential to be able to set relevant targets and reference points, this allows for robust monitoring and improves the ability to effectively manage the area. Although the use of experimental design and statistical analysis to monitor the effects of area closures throughout the world is increasing, there is still a lack of standardisation and the use of theoretically robust survey designs   The use of the Before-After, Control-Impact (BACI) design has been identified as the most robust method to monitor areas closed to fishing Few studies have been conducted using this method due to the difficulty in obtaining sufficient temporal and spatial data prior to the implementation of the area closure. There can also be difficulty in identifying suitable reference sites; monitoring begins after closures have already been established or there are limited funds to allow intense temporal and spatial replication. Area closures are particularly beneficial for species which have key life history stages that congregate, such as for spawning. Although the use of area closures are now common place in the UK, this management approach remains controversial due to the frequent lack of clear objectives, monitoring and impact studies. Providing evidence is therefore vitally important to support decision-making for future area closures and to evaluate whether existing closures are achieving their objectives. This was addressed by evaluating an existing seasonal area closure for Atlantic cod (*Gadus morhua*) in the Firth of Clyde off the Scottish West Coast. The study uses standardised scientific trawl data and a beyond-BACI approach to compare population trends of the Clyde spawning aggregations with two other sub-populations of the same stock. There was no evidence of local recovery in terms of abundance, biomass or reduced mortality in the Clyde more than a decade after the closure was established. Considering the severely depleted state the Clyde sub-population was in when the closure was implemented it appears that the measure was too little and too late.

The advantage of EBFM and using an area closure is when there is uncertainty with regard to the effects of fishing on environment and fish stocks, for example if the sensitivity of a habitat to fishing disturbance is unknown or there is not enough data to accurately assess a stocks biomass. This is applicable for deep-sea in the north east Atlantic where since the onset of deep-sea fishing in the 1970s there has been a decline in the abundance of commercial fish species. Management measures were introduced in 2003 which set Total Allowable Catch (TAC) and restricted days at sea, but this still did not allow for the recovery in biomass of commercial species. Also the fishery has high levels of bycatch, including vulnerable deep-sea sharks, which are estimated to have declined by up to 90%. There has been a recent global debate as to whether there is a depth beyond which fisheries cannot be expected to operate in an economically and ecologically sustainable way. The European Union is currently considering new legislation to manage deep-sea fisheries, including the introduction of a depth limit to bottom trawling. However, there is little evidence to suggest an appropriate depth limit. This was addressed using long-term scientific deep-sea trawl data and calculating important ecological and economical indices. The non-linear trend and first derivatives of these indices were calculated with depth. The results suggest that between 600 and 800 m the commercial benefits derived from fishing start to be outweighed by potentially negative ecological consequences.

In the marine environment uncertainty is a great impediment for the sustainable management of resources, this thesis demonstrates that with long-term commitments to monitoring, clear objectives and the development of novel techniques to interrogate data, strong evidence can be established to support policy and decision-making.

Table of Contents

List of Tables

Appendices:

List of Figures

Appendices:

Acknowledgements

It would not have been possible to complete the work undertaken in this thesis without the help of many, many people. Firstly, I would like to thank both my supervisors Dr. David Bailey (Institute of Biodiversity, Animal Health and Comparative Medicine (IBAHCM), School of Medical, Veterinary and Life Science (MVLS), University of Glasgow) and Dr. Peter Wright (Marine Scotland Science) for all their help, patience and support over the past four years. I would also like to thank Dr Ruedi Nager for being my Assessor for the duration of this project. This project was funded as part of the European Union's INTERREG IVA Programme (project 2859 "IBIS") managed by the Special EU programmes Body.

I am extremely grateful to the crew of the Aquarius who made data collection plain sailing and Marine Scotland Science for funding vessel time (Chapter 2). In particular I would like to thank Dr Sophie Elliot for being motivational, supportive and for all the help in the development of the camera systems, the fieldwork and the analysis of the data. Thank you to Kirsty Wright for assisting me at the start of the project and helping me to develop the camera systems. Thank you Howard Wood (COAST) for all your help. Thanks to Bob McLaren the use of your swimming pool to calibrate the cameras. I am very grateful for the training I received in Event Measure and CAL from Jim Seager (SeaGIS) and the continued support in using the software throughout the project.

The study of the Clyde cod closure (Chapter 3) was made possible by many years of data collection by the crew, officers and scientists of the FRV ''Scotia'' of the FRS and Marine Scotland Science. Also thanks to Fanyan Zeng from Marine Scotland Science for extracting the landings and effort data.

Chapter 4 would not have been possible without the collaboration and input from Dr Francis Neat of Marine Scotland Science. The analysis used multiple datasets, thank you to all who were involved in collecting, collating and managing these invaluable resources including the officers and crew of the FRV ''Scotia'' and all FRS and Marine Scotland Science staff involved in the surveys over the years. The Scottish Association for Marine Science and the ships parties of RRS Discovery and Challenger are gratefully acknowledged, with thanks to the other members of the trawling and catch-processing teams. Scotia surveys were funded by the Scottish Government under projects ECOSDEEP, OFFCON, and MOREDEEP. The early surveys by SAMS and IOS were supported directly by the Natural Environment Research Council, EU MAST contract MAS2-CT920033 1993–1995, and analysis is contributed to the EU-HERMES program. Later surveys were funded through the Natural Environment Research Council grant PSB GR3/12789. Thanks to Dr. Neil Campbell, Dr. Bill Turrell, Professor Monty Priede, and Dr. Martin Collins for useful comments on the manuscript. Thanks to Dr Rosanna Milligan for continuous sanity checks, extensive statistical support and infinite wisdom on all things deep-sea.

Finally, I would like to thank every one of my office mates, fellow IBIS students, collaborators, friends and family, for all their help. Particular thanks to Piero for keeping me calm and Dr Martina Quaggiotto

Author’s Declaration

I declare that, except where explicit reference is made to the contribution of others, that this dissertation is the result of my own work and has not been submitted for any other degree at the University of Glasgow or any other institution.

Signature ________________________________

Printed name ________________________________

Abbreviations

AIC: Akaike’s Information Criterion
ANOSIM: ANalysis Of SIMilarities
BACI: Before-After, Control-Impact
BRUV: Baited remote underwater video
BUC: Baited Underwater Camera
CBD: Convention on Biological Diversity
CFP: Common Fisheries Policy
CI: Confidence Interval
DF: Degrees of Freedom
EAFM: Ecosystem Approach to Fisheries Management
EBFM: Ecosystem Based Fisheries Management
EBM: Ecosystem Based Management
EEZ: Exclusive Economic Zone
EIA: Environmental Impact Assessment
EU: European Union
FAO: Food and Agriculture Organisation
GES: Good Environmental Status
GLM: Generalised Linear Model
GLMM: Generalized Linear Mixed Model
HTS: Hebrides Terrace Seamount
ICES: International Council for the Exploration of the Sea
IPCC: International Panel on Climate Change
IUCN: International Union for Conservation of Nature and Natural Resources
LM: Linear Model
MaxN: Maximum Number
MPA: Marine Protected Area
NB: Negative Binomial
NF: Near Field
nMDS: Non-metric Multi-Dimensional Scaling
NTU: Nepheloid Turbidity Units
ODE: Ordinary Differential Equation
OSPAR: The Convention for the Protection of the Marine Environment of the North-East Atlantic
P: Poisson
SD: Standard Deviation
SSB: Spawning Stock Biomass
SSBR: Spawning Stock Biomass per Recruit
SIMPER: SIMilarity PERcentages
TFAP: Time to First Arrival
UNCLOS: United Nations Convention on Law of the Sea
UTV: Underwater Towed Video
UVC: Underwater Visual Census
VME: Vulnerable Marine Ecosystems

Chapter 1: Introduction

The oceans cover 71% of the Earth's surface and have played a major role in shaping the Earth as we know it today. They form complex systems in which organisms are linked to one another and to the environment in intricate ways. We are beginning to understand that if we change a part of it there can be unexpected consequences in other parts. Human interactions with the ocean and the life it contains are extensive and increasing (Halpern *et al.*, 2015). Only through a better understanding of these interactions and the impact of human activities on the marine system will it be possible to develop wise management decisions to facilitate their coexistence. Marine ecosystems provide us with a variety of goods and services which can broadly be separated into two groups. Firstly there are the "fundamental services for maintaining ecosystem functioning", such as nutrient cycling, food web dynamics, the transport of nutrients, carbon and minerals (Holmlund and Hammer, 1999). These services are a prerequisite for human existence irrespective of whether any economic value is placed on it. For example, the oceans are fundamental in regulating atmospheric conditions, stabilising global temperature and therefore buffering the effects of climate change (IPCC, 2014). Secondly, they recognise "demand-derived services based on human values", such as food, flood defence, waste detoxification and cultural services (Holmlund and Hammer, 1999). Human population growth is putting increasing cumulative pressure on the marine environment (Halpern *et al.*, 2015) in the form of fishing, pollution, the introduction of invasive species (Molnar *et al.*, 2008), changes in temperature and pH due to climate change (IPCC, 2014), utilization of a growing proportion of the ocean's primary productivity which supports all marine life (Watson *et al.*, 2015). Fishing is one of the main pressures on the ocean, but it is also one of the most valuable activities to humans providing an important source of protein, particularly for developing countries (FAO, 2014).

1.1 Fishing impacts

The impacts from fishing include overfishing of target species, bycatch of non-target and vulnerable species (Jones *et al.*, 2005), discarding (Alverson *et al.*, 1994) and damage to habitats and ecological communities (Hall-Spencer, 2000; Hall-Spencer *et al.*, 2002; Hinz *et al.*, 2009). Historically sea fish were thought to be an inexhaustible resource. In 1882 Thomas Huxley recognised that it was possible to extirpate some fisheries such as the UK oyster (*Ostrea edulis*) and Atlantic salmon (*Salmo salar*), but he thought “in relation to our present modes of fishing” sea fish were so abundant that they were inexhaustible (Huxley, 1882). Retrospectively using historical records there is evidence that some fisheries have been in decline since the 1850s, due to the intensification of fishing (Jones *et al.*, 2015). Not only has fishing intensity increased but also after the industrial revolution technological advances have given fishing vessels the ability to travel further and for longer, increasing total fishing effort (Thurstan *et al.*, 2010), and allowing the footprint of fishing to expand geographically (Swartz *et al.*, 2010) and into deep-sea (Morato *et al.*, 2006). This resulted in global catches in the 1950s and 1960s to increase at a faster rate than human population growth (Pauly *et al.*, 2002). It has been suggested that the ability to explore new areas and exploit new stocks masked any initial declines in biomass from overfishing (Pauly *et al.*, 2005), until the1980s when the global limits of exploitation were reached (Worm and Branch, 2012). This period coincided with the conclusion of the 3rd United Nations Conference on the Law of the Sea which resulted in new legislation entitled The United Nations Convention on the Law of the Sea (UNCLOS, 1982). This convention set a framework in place for international cooperation and legal principles (Potts *et al.*, 2012). It enabled countries to claim Economic Exclusion Zones (EEZs) to 200 nautical miles from shore and therefore placed the responsibility of fisheries management on the maritime country (Pauly *et al.*, 2005). This legislation was important as recent analysis has determined that it has resulted in legally enforceable and tested harvest strategies, coupled with rights-based incentives required for a country to manage its fisheries successfully (Beddington *et al.*, 2007).

In recent decades sustainable levels of fishing have been achieved through improvements in fishery assessment (Hilborn, 2012), reductions in fishing capacity (Worm *et al.*, 2009) and setting allowable catch limits in line with scientific advice (Marchal *et al.*, 2016). However, there is a noticeable geographic divergence between regions achieving sustainable levels of exploitation, in some cases this is due to the level of data available to inform fisheries management (Worm and Branch, 2012; Halpern *et al.*, 2015). In developed countries where stocks are well-assessed, overfishing has been reduced and target stock biomass are typically increasing (for example in the UK, Fernandes and Cook, 2013). Other methods of improvements in fisheries management include reducing the incidental catch of unwanted individuals known as bycatch or discards. Bycatch is the non-commercial part of a catch that is not the target species but incidentally caught and discards are usually considered the commercial species that are disposed of at sea for regulatory reasons (e.g. insufficient quota) or for economic reasons (e.g. high-grading)

(Little *et al.*, 2014). Typically this part of the catch is not brought to shore, but now some countries have a ban on discarding (typically applied to just the commercial species) and this is currently being implemented by the European Union (EU) under the reformed Common Fisheries Policy (CFP) (The European Commission, 2013). Bycatch is particularly problematic for vulnerable, slow growing species, such as deep-sea sharks (Allain *et al.*, 2003) and for populations whose biomass is below a critical threshold, such as Northeast Atlantic cod (*Gadus morhua*) (Kelly *et al.*, 2006). Modifications to fishing gears are continuously being developed to overcome the problem of bycatch (Hall and Mainprize, 2005). Moreover, the introduction of real-time closures is being used in European and American fisheries. Real-time closures are a temporary spatial closure triggered by high catch rates of species which would be discarded if caught, they result in fishing effort being moved away from areas of high density and therefore reduce discarding (Little *et al.*, 2014).

Bottom fishing can cause physical and biological changes negatively affecting the benthic environment and its communities. Fragile, slow-growing species, such as cold-water coral (Hall-Spencer *et al.*, 2002) and calcareous algae (maerl) beds can be significantly impacted by dredging and trawling through burial and breakage (Hall-Spencer *et al.*, 2003). On soft sediments physical disturbance can cause geophysical changes directly altering the structure of the seabed (Humborstad, 2004) and hydrodynamic changes through the mobilisation of sediments into the water column (O'Neill and Ivanovic, 2015). This can lead to the homogenisation of habitats (Thrush *et al.*, 2001) and can negatively influence biogeochemical processes that occur at the sediment-water interface (Lohrer *et al.*, 2004). Biological changes due to bottom trawling include the reduction in biomass, diversity and size of benthic invertebrates (Hiddink *et al.*, 2006; Kaiser *et al.*, 2006); changes of benthic community composition (Tillin *et al.*, 2006; Hinz *et al.*, 2009), functioning (Clare *et al.*, 2015), and reduction in fish condition due to a reduction in prey availability (Hiddink *et al.*, 2011, 2016). These changes can affect ecosystem structure and function, reducing productivity (Bolam *et al.*, 2014). Such changes in state can make communities more susceptible to environmental fluctuations, for example oyster reefs degraded from dredging have been shown to have a greater rate of mortality during a period of anoxia compared to a healthy reef (Lenihan *et al.*, 1998). The impact of fishing is dependent on the type of fishing gear and the habitat type (Gray *et al.*, 2006). Recent research to determine the physical and ecological impact of trawling on different types of soft sediment in the sublittoral found that its impact is greatest on mud than on sand and the effect varied between functional groups (van Denderen *et al.*, 2015; Rijnsdorp *et al.*, 2016). The wider implications of the loss of biodiversity through fishing is the decrease in the ocean's ability to provide ecosystem services and recover from perturbations (Worm et al., 2006).

1.2 Fisheries Management

Under current fisheries management regimes that use single species stock assessments, exploitation rates are decreasing and biomass is improving for many stocks. However, this form of management has come under recent scrutiny because it does not address the additional ecosystem level problems caused by the fishery and its management. These environmental concerns have been raised at international forums and meetings (FAO, 2012) which has led to the consideration of the ecosystem within management and the development of regional policies (Froese *et al.*, 2016). There has been a variety of terminology developed to describe the management of fisheries within an ecosystem context and these terms have often been used interchangeably and to refer to different aspects of ecosystem management. Within this thesis the definitions described in Dolan *et al.*, (2016) that distinguish between the ecosystem approach to fisheries management (EAFM), ecosystem-based fisheries management (EBFM) and ecosystem-based management (EBM) will be used. EAFM is concerned with the management of a single stock and considers the influence of ecological and environmental factors on that stock. This may include multi-species modelling (Thorpe *et al.*, 2014), consideration of habitat (Clark and Dunn, 2012) and the use of area-based management strategies to achieve the successful management of that particular stock (Grüss *et al.*, 2013; Clarke *et al.*, 2015a; van Overzee and Rijnsdorp, 2015). EBFM moves away from the focus on a single stock and refers to the management of all fisheries within an ecosystem, looking at trade-offs between stocks to optimize the yield at an ecosystem level. EBM spans multiple sectors and is the management of the ecosystem considering sustainability, ecological status and human dimensions (Leslie and McLeod, 2007).

In the North east Atlantic the Common Fisheries Policy (CFP) (The European Commission, 2013) and Marine Strategy Framework Directive (MSFD) (The European Commission, 2008) are the main policy drivers behind the implementation of EBFM. The goal of the MSFD is to achieve Good Environmental Status (GES) by 2020. GES is defined in the directive (Article 3) as “The environmental status of marine waters where these provide ecologically diverse and dynamic oceans and seas which are clean, healthy and productive". There is a list of 11 descriptors each with a set of detailed criteria and quantitative indicators which will be assessed against reference levels to determine if progress towards the aim of GES is being made. MSFD and the CFP are closely linked as one of the indicators for Descriptor 3 (for commercially exploited fish and shellfish) within the MSFD requires that "the population age and size distribution is indicative of a healthy stock" to achieve GES. The attainment of this indicator of a healthy stock will rely on the measures undertaken by the CFP. The new CFP became effective from the 1st of January 2014 and supports the idea of EBFM because it is not solely concerned with the rebuilding of commercial fish stocks, but also requires that "negative impacts of fishing activities on the marine ecosystem are minimized" (Article 2.3).

Currently there is little consideration for the ecosystem within fisheries management in Europe and most fishery management considerations are based on single-species stock assessments. An exception is the current consideration for reforming how the deep sea is managed within the European EEZ. The major fishing area for deep-water bottom trawl fisheries in the North east Atlantic lies west of Scotland and Ireland out to the Rockall and Hatton Banks. This area was first exploited in the early 1970's, and the trawl fishery grew rapidly in the 1980s and 90s (Heymans *et al.*, 2010). In 2001 it was recognised that most target species fished in EU deep seas were exploited outside of safe biological limits (Large *et al.*, 2003) and several deep-sea sharks found in the Northeast Atlantic have been classified as vulnerable or near threatened under the IUCN criteria. Also areas of "Vulnerable Marine Ecosystems" have been identified and designated within Scottish Nature Conservation Marine Protected Areas. This combination of ecological uncertainty and possible negative impacts with fishing has resulted in the European Union considering the introduction of a depth limit to fishing. There was a lack of evidence and support for deciding upon an appropriate depth. In Chapter 3 first derivatives are calculated of non-linear trends in relevant ecological indices with depth to determine if there are any relevant depths where the indices are significantly increasing or decreasing (Clarke *et al.*, 2015b). The results suggest that between 600 and 800 m the commercial benefits derived from fishing start to be outweighed by potentially negative ecological consequences. The use of a depth limit determined by examining a trade-off between fishing and ecological indicators can be considered as a form EBFM.

There has been great debate about the difficulties involved with implementing EBFM and EAFM, from the complex management framework of legislation within which managers of the marine environment and fisheries have to work (Boyes and Elliott, 2014) to the lack of clear strategy and objectives (Jennings and Rice, 2011) and the data requirements and model complexity necessary to model ecosystems (Hilborn, 2011). Despite the complexity of the problem, progress is being made and theory is beginning to be put into practice. EAFM requires the simplification of information on complex systems into management objectives (Shin *et al.*, 2010). While it is possible to develop multiple ecosystem indicators, the main features that represent the health of an ecosystem can be captured in relatively few parameters (Fulton *et al.*, 2005), but these require development and testing. It is particularly important to identify thresholds where fishing and environmental pressures significantly influence ecological indicators (Large *et al.*, 2013b). This use of indicators within a EAFM context has been explored in relation to the Georges Bank finfish fishery where a guild based multispecies simulation model of the community was established and values of ecological indicators were assessed under different fishing scenarios. The response in the indicators could be used to determine limits on annual catches (Fay *et al.*, 2013).

An opinion raised by (Hilborn, 2011) is that single species management is relatively simplistic compared to EAFM, as the implementation of this management method has been unsuccessful in many cases. Therefore can we expect a new, more complex and more uncertain method to be successful? It is also suggested the EAFM will be more difficult for ecosystems that straddle stock boundaries, and that it might be more easily achieved at a local scale (Dolan *et al.*, 2016). This may be relevant to management of European waters, where fish and fisheries cross boundaries and the development of ecological indicators that represent a healthy ecosystem may be difficult to establish due to the extensively altered ecosystems after centuries of fishing (Thurstan *et al.*, 2010). Although there has been slow progression in the full implementation of EAFM, elements of the concept have been in use for several decades through the use of spatial closures for fisheries management. Spatial closures have been used in variety of ways for multiple objectives, but mainly in response to the difficulty of managing a multi-species fishery with limited data, by providing a form of insurance against management mistakes in predictions or unexpected environmental variation. They may also offer a relatively simplistic solution to the difficulty in managing multiple fisheries simultaneously and meeting conservation objectives.

1.2.1 Spatial regulations for fisheries management and conservation

Spatial closures as a tool for fisheries management are widely used yet they remain controversial often due to the lack of clear objectives and monitoring. Evidence is growing in support of their use but positive results are often seen only after an extended period of long-term monitoring (Vandeperre *et al.*, 2011). It has been suggested that the benefits of spatial closures are dependent on the species home range, ontogenetic migration, the size of the closure and the species metapopulation dynamics (Grüss *et al.*, 2011). The benefits of permanent spatial closures to fisheries include the spillover effect which is expected to occur when fish move out of a closure due to density dependent effects (Gell and Roberts, 2003; Russ *et al.*, 2004; Abesamis and Russ, 2005). Density dependent movement is only likely to occur when the population within the reserve has recovered to its carrying capacity (Russ and Alcala, 2004) and can be driven by a number of factors such as an increase in predation leading to avoidance behaviours and recruitment resource limitation (Abesamis and Russ, 2005). Other ways in which fisheries can benefit from permanent spatial closures is through the protection of critical life stages of target species, such as spawning aggregations and juvenile nursery areas (Grüss *et al.*, 2011). This protects older, larger, more fecund individuals and has been suggested to largely improve recruitment success (Birkeland and Dayton, 2005). It is very difficult to measure the contribution of MPAs to recruitment, methods that have been developed include genetic parental analyses and the examination of otolith chemistry. Using genetic parental analyses Harrison *et al.*, (2012) estimated that half of the total juvenile recruitment originated from within the local MPA even though the area of the reserve accounted for 28% of the total reef area investigated. Other studies have found high levels of self-recruitment within MPAs that was consistent over several years (Berumen *et al*., 2012). A study in the Mediterranean that examined otolith microchemistry found that juvenile *Diplodus vulgaris* were recruited into the fishery up to 165 km away from their natal MPA origins (Di Franco *et al*., 2015).

Juveniles are more vulnerable to predation, therefore are likely to utilise more complex substrata to hide and reduce their risk of predation (Lindholm *et al.*, 1999; Roberts and Sargant, 2002; Elliott *et al.*, 2016). Protecting areas favoured by juveniles in known nursery areas can benefit the long term population persistence (Fodrie *et al.*, 2009), and reduce fishing mortality by preventing bycatch (Diamond *et al.*, 2010). Most studies on the benefits of spatial closures have been conducted in tropical and warm temperate ecosystems where species movements are spatially contracted (Caveen *et al.*, 2012). Many knowledge gaps remain, particularly in temperate waters where commercially important fish tend to be highly mobile, demonstrating seasonal movements and with unclear population dynamics. The use of spatial closures can be divided into three broad categories which fit the objectives of the three types of ecosystem management previously mentioned: Type 1) for a single stock (EAFM); Type 2) for multiple fisheries and the ecosystem (EBFM); and Type 3) for conservation which can include commercial and non-commercial species, habitat and the wider ecosystem (EBM).

1.2.2 Type 1 – Single stock closures

Spatial closures intended to protect single species include spawning area closures (Sadovy and Domeier, 2005; Grüss *et al.*, 2014), nursery area closures (Pastoors, 2000; Fisher and Frank, 2002) and real-time closures (Little *et al.*, 2014). These types of closure would primarily be for the benefit of the fishery and the objective would be to improve long-term yield (Fisher and Frank, 2002). Closures may be seasonal or permanent dependent upon the distribution of the species and the distribution of the fishery in relation to the closure (Cuaig and Officer, 2007). Spatial fishery closures for spawning aggregations are commonly used but are rarely documented outside of the grey literature (van Overzee and Rijnsdorp, 2015). Spawning closures have been used for a long time in the tropics for example to manage fishing effort and reduce mortality on large groupers (Grüss *et al.*, 2013, 2014). Targeting spawning aggregations results in high catch rates, leading to higher fishing mortality of the breeding population (Halliday, 1988; van Overzee and Rijnsdorp, 2015) and the risk of overexploitation of the stock (Rose and Kulka, 1999; Erisman *et a*l., 2011). Therefore, a spatial closure protecting aggregated spawners can reduce fishing mortality but allow sustainable fishing outside of the spatial closure (Murawski *et a*l., 2000). This method does not always meet the intended objectives: for example, an area closure designed to protect spawning groupers (*Epinephelus fuscoguttatus* and *Plectropomus areolatus*) in Komodo National Park (Eastern Indonesia) was not associated with any change in length composition or trend in abundance (Pet *et al.*, 2005).

Spawning area closures are widely used in the UK (STECF, 2007) and the British fishing industry has shown support for seasonal spawning area closures (Jones, 2008), yet there have been few studies to investigate their effectiveness (Clarke *et al.*, 2015a). Nursery area closures have been limited and questions have been raised as to whether it is more beneficial to reduce mortality on adults rather than juveniles, as juveniles are already exposed to high levels of natural mortality. Some studies suggest that the proportion of juveniles that contribute to stocks can vary spatially and that areas with higher densities of juvenile fish could benefit from area closures (Wright *et al.*, 2010). However, empirical evidence for nursery area closures has also had variable and unexpected outcomes. For example, the "Plaice Box" in the North Sea was implemented to reduce fishing mortality on undersized and juvenile plaice (*Pleuronectes platessa*) by prohibiting large trawlers within a major nursery area (Beare *et al.*, 2013). Results showed that juvenile growth rate decreased within the closure and abundance decreased, likely due to juveniles moving into deeper waters. It is suggested this was consistent with a regional trend due to climate and nutrient changes, but results were confounded by the "Plaice Box" and support from the fishing industry for the use of spatial closures was lost (Beare *et al.*, 2013). By contrast, a nursery closure for haddock (*Melanogrammus aeglefinus*) on the Scotian Shelf had a positive effect on their abundance within the closure which supplemented the open area so benefitting the fishery (Fisher and Frank, 2002). The review of real-time closures in Europe and the United States by Little *et al.*, (2014) suggests that the main challenges are developing systems and technology that relay true real-time information, and the requirement for a policy to vary on a fishery by fishery basis as "one size fits all" management strategies are unlikely to be effective.

1.2.3 Type 2 – Multiple fisheries and the ecosystem

Spatial closures to manage multiple fisheries and consider ecosystem effects have been used widely in tropical reef systems where the movements of reef fish are limited and the benefits to fisheries are expected to occur via the spillover effect. An assessment of the Mona Island marine protected area (MPA) and no-take zone (NTZ) in the Caribbean Sea found a strong recruitment signal within the reserve and that this contributed to the stock outside the MPA which helped achieve the goal of fish stock restoration (Mateos-Molina *et al.*, 2013). The benefits of spatial closures are also dependent on compliance and enforcement by the local fishing community, which can change the benefits temporally and spatially (Advani *et al.*, 2015).

Spatial closures aimed at multiple fisheries have varied in success in temperate regions. For example, two spatial closures implemented off the east coast of Iceland to protect the existing demersal fish community had positive impacts on some species but no effect on others. Haddock (*Melanogrammus aeglefinnus)* increased in abundance and average size inside the closure suggesting that this could benefit the fishery through spillover. The change was detected in the overall ecosystem where species diversity and community composition did not differ between inside and outside the closures, but did vary temporally (Jaworski *et al.*, 2006). Spatial closures on the Georges Banks and off Southern New England (NW Atlantic) in 1994 were selected based on the seasonal spawning locations of the demersal fish and had objectives to protect spawning adults and juvenile demersal fish species. The closures met their objective of effectively reducing mortality on the demersal fish species but also provided benefits to wider elements of the ecosystem such as increasing the abundance of shallow-sedentary fish assemblages and scallops (*Plactopecten magellanicus*) (Murawski *et al.*, 2000). Results from a theoretical study using a spatially explicit dynamic population model suggests that the benefits of an area closure to a fishery is dependent on the current status of the fishery and the species being targeted, with closures for under exploited fisheries and mobile species providing the least benefit to the fishery (Quesne and Codling, 2009). Another theoretical study that modelled the effects of spatial closure to investigate the trade-off between different ecological or economic factors found that closures achieved their specific objective with regards to fisheries management but did not necessarily result in gains in broad-scale objectives (Dichmont *et al.*, 2013).

1.2.4 Type 3 – Marine Protected Areas for conservation (commercial and non-commercial species, habitat and wider ecosystem)

There has been an international drive to implement nature conservation Marine Protected Areas. The outcome of the Johannesburg World Summit on Sustainable Development (WSSD, 2002) established a binding deadline to reduce the rate of biodiversity loss by 2010 and to establish a network of Marine Protected Areas by 2012. This was followed by the Convention on Biological Diversity (CBD, 2004), which set a target to protect 10% of the global marine area by 2010. These aims have been translated into national laws, such as the Marine Strategy Framework Directive (The European Commission, 2008) in Europe which requires that MPAs should be designated in member states to contribute to the achievement of GES. Evidence of the benefits of MPAs as a conservation tool has been widely accepted in the scientific community and MPAs are used within the context of wider marine spatial planning (Agardy *et al.*, 2011), to reduce the loss of biodiversity and maintain (or allow the recovery of) the trophic structure of ecosystems (Babcock *et al.*, 1999). A meta-analysis of global studies found that no take marine reserves lead to the greatest increases in biomass and abundance of fish and invertebrate populations, and that even partially protected area closures can provide benefits compared to unprotected areas

(Sciberras *et al.*, 2013). A global synthesis of no-take reserves found that although reserve characteristics influenced the direction and magnitude of change within reserves, overall positive benefits are far more common than no differences and negative responses (Lester *et al.*, 2009).

1.2.5 Overview of area based management

Clear objectives for each spatial area closure are essential to be able to set relevant targets and reference points, this allows for robust monitoring and improves the ability to effectively manage the area. The use of area closures is not the answer to all problems (Dinmore *et al*, 2003) and should be used in combination with management measures within an Ecosystem Management framework. For example, area closures do not reduce the overall fishing effort, but just displace it outside of the closed area which may cause damage to other areas that were previously undisturbed by fishing (Parrish, 1998). Therefore examination of trade-offs between different management approaches is necessary prior to establishment of area closures and evaluation of alternative conservation efforts (Allison *et al*, 1998). Area closures are useful when there is uncertainty with regard to the effects of fishing on environment and fish stocks. For example, if the sensitivity (the time it takes to return to “normal” productivity) of a habitat to fishing disturbance is unknown then implementation of an area closure can prevent further degradation of the environment whilst studies can be conducted to determine if the resources in that area can be exploited sustainably.

Uncertainty is a great impediment to the management of sustainable resources in the marine environment due to the inability to directly observe population abundances (Botsford and Parma, 2005). It is proposed that area closures reduce uncertainty in the relationship between specified fishing regulations and mortality rate (Lauck *et al*, 1998) although Botsford and Parma (2005) state that they just switch sources of uncertainty from the effects of fishing to larval dispersal distance. Overall the use of the precautionary approach allows the management of marine systems to be more proactive rather than reactive, preventing damage rather than responding to it (Agardy *et al*, 2003). Another benefit to area closures is that they can improve a community’s ability to recover and increase its resilience to natural environmental fluctuations. Bevilacqua *et al* (2006) conducted an experiment to determine if a no-take marine reserve can facilitate the recovery of benthic assemblages impacted by a date mussel (*Lithophaga lithophaga*) fishery on rocky substrate in the SW Mediterranean Sea. It was found that there was a significant difference between the protected and control locations in patterns of assemblage recovery and that within the no-take reserve recovery was faster than at the unprotected control location.

1.3 Monitoring area closures

There has been an increase in the use of experimental design and statistical analysis to monitor the effects of area closures throughout the world (Claudet and Guidetti, 2010), but there has been a lack of standardisation and the use of theoretically robust survey designs (Claudet and Guidetti, 2010; Addison, 2011; Ojeda-Martinez *et al.*, 2011; Osenberg *et al.*, 2011; Fenberg *et al.*, 2012). A review of older MPAs with long term studies by Addison (2011) found there is little consistency of the type of statistical analyses used to study the effects of MPAs with a clear gap in the scientific literature in regards to a discussion about which statistical analysis for the study of MPAs is most appropriate. Of the 11 case studies only 4 conducted formal statistical analyses that accounted for changes over time between MPA and reference sites.

1.3.1 Before/After, Control/Impact (BACI) study design

Only recently has the use of BACI (Underwood, 1992) as a monitoring design been identified as being relevant to the monitoring of areas closed to fishing (Sale et al. 2005; Zeller et al. 2003; Francini-filho & Moura 2008; Willis et al. 2003; Guidetti 2010; Fenberg et al. 2012), where the area closure would be the impacted site, and other similar non-protected, “fished” locations would be the control sites. The “impact” is typically considered to represent the reduction in fishing within the area closure. BACI surveys have previously mostly been used by those involved in conducting Environmental Impact Assessments (EIA) where specific response variables (such as abundance or community composition) are monitored at an area that is proposed to be impacted (such as at a sewage outfall or harbour construction site) (Green, 1979; Bernstein and Zalinski, 1983; Stewart-Oaten *et al.*, 1986; Underwood, 1992).

The BACI experimental design was first put forward by Green (1979) who stated that to determine if a site has been impacted a sample needs to be taken once before the time of the disturbance at the “impact” site and at a control site, then once after the disturbance, at both these sites. It would be expected that if a disturbance has affected the population in question then a change would be detected at the impacted site but not at the control site.

However, this sample design is not statistically rigorous and is classed as pseudoreplication (Hurlbert, 1984). Bernstein & Zalinski, (1983) and Stewart-Oaten, Murdoch, & Parker, (1986) identified the need for additional temporal replication because most populations naturally fluctuate over time. By only sampling at one point in time the potential to detect the disturbance would be low as it could be confounded by natural variation in the population and therefore cannot be directly linked to the disturbance event. Bernstein & Zalinski, (1983) and Stewart-Oaten, Murdoch, & Parker, (1986) suggested monitoring the impacted site and one control site several times before the disturbance event and several times afterwards. They emphasise that the control site should be chosen with care so that it is sufficiently far enough away from the impact as not to be affected by it but close enough so that it is in range of any natural phenomenon that will influence long term changes in the biological populations and communities. This approach has been built upon by Underwood (1992) who commended the design for its replication in time, but suggested that spatial replication is just as important and needs to be incorporated into the BACI design too (this design is known as “beyond-BACI”). Ideally, this would include replicated impacted and control sites, but as Underwood (1992) states the probability of having more than one impacted site at one time is unlikely. By using several similar but randomly chosen control sites (asymmetrical design), the chance of detecting location-specific changes in the impacted site is reduced.

1.4 Methods for monitoring area closures

1.4.1 Scientific trawl and dredge surveys

Scientific trawls and dredge surveys are widely used to monitor commercial species by collecting measures of abundance, biomass, size distributions and other metrics of benthic fish and invertebrates. The gear and methodology are typically standardised within each nation, and in fisheries that cross EEZs attempts have been made to either standardise between nations or to calibrate between methods. This standardisation ensures that samples are comparable across large areas or time periods. For example ICES (International Council for the Exploration of the Sea) maintain a database that collates all the international bottom trawl surveys conducted in the North east Atlantic for the management of commercial fish stocks. The methodologies and results for each survey are standardised and have to pass a quality assessment before they can be uploaded to the database. The database is open access and allows scientists no directly involved with stock assessments and management to interrogate the data. There are disadvantages to the use of bottom trawling or dredging as a tool for monitoring area closures, and that can be if the closure is introduced to prevent the damage of vulnerable marine species or habitats by fishing.

1.4.2 Underwater Visual Census (UVC)

A common method for monitoring fish abundance over relatively small spatial scales is the use of self-contained underwater breathing apparatus (SCUBA) or snorkelling to complete a visual underwater census (Samoilys and Carlos, 2000; Smith *et al.*, 2011; Kruschel and Schultz, 2012). This can be done using the belt transect method, where divers swim along for a predetermined length and identify, count and estimate the size of all fish within the boundaries of the transect. Another method is the stationary point count where a buddy pair of divers remain in one location for a set time period and identify, count and estimate the length of all fish within a given area (usually determined by the accuracy of identifying fish at distance and visibility) (Watson and Quinn II, 1997; Smith *et al.*, 2011). There are advantages and disadvantages for using these methods. Advantages are that they are technically simple, and relatively cheap methods of measuring fish abundance, compared to conducting camera tows, using Remote Operated Vehicles (ROVs) or conducting acoustic surveys. They are also non-destructive compared to trawl, grab sampling and netting surveys designs. Disadvantages are that they are weather and visibility dependent; they also require experienced and qualified personnel. Divers are also restricted to physical limitations, such as depth and time spent underwater. Some studies have found that there is an influence from the diver on fish behaviour whilst conducting the surveys (Kulbicki, 1998; Dickens *et al.*, 2011), so that there is an over estimate of fish attracted to divers and an underestimate of fish that are more shy (Willis and Babcock, 2000; Dearden *et al.*, 2010). This can be compensated for by using more than one method of survey (Murphy and Jenkins, 2010), such as combining UVC with baited underwater cameras (BUC). There are advantages and disadvantages between using a point count method and belt transect method. The point count method is usually quicker than completing transects, the divers are stationary so that the disturbance to fish is minimised (Colvocoresses and Acosta, 2007), but as for the belt transect it is dependent on visibility remaining constant throughout the time period and between sites. The larger area surveyed using the transect method has been deemed better for assessing large expanses with diverse fish assemblages with non-random distributions (Kulbicki, 1998). Since the transect survey is always moving, the risk of duplicate counts is reduced, but in turn this may limit the ability to identify cryptic, less conspicuous species. Kruschel & Schultz (2012) introduced a lure to their snorkelling survey to improve the visibility of fish that are difficult to detect. If fish metrics other than abundance are also required from the UVC then there is another source of error from the diver estimates. For example visual estimates of fish length have been found to be significantly different from actual fish length, with divers underestimating larger fish and overestimating smaller fish (Bower *et al.*, 2011). Although accuracy was not good enough to predict changes in abundance between life stages with differences in length, precision was high enough to be able to compare the average length between populations and locations (Bower *et al.*, 2011). The use of calibration software for analysing recordings taken from diver operated stereo video has been found to provide more accurate length estimates of fish than diver estimates (Bower *et al.*, 2011).

1.4.3 Baited cameras

Baited remote underwater video (BRUV) is a method that has become more popular in the last decade for estimating fish abundance of carnivorous, herbivorous and planktivorous fish (Watson *et al.*, 2005). It is a method to measure relative abundance, typically by counting the maximum number of each species recorded at one time (MaxN), the time to first appearance for each species (TFAP) and/or the time to MaxN. These method can allow an understanding of fish assemblage structure, diversity, inter and intra-specific interactions and behavioural responses. BRUV methodology has often been compared to Underwater Visual Census (UVC) which is typically conducted by divers. The advantage of using BRUVs is that the depth is only limited by technology and not risk to personnel, and they can therefore be used in deeper waters (Jamieson *et al.*, 2006). The method also requires fewer personnel, the remote camera systems permit more than one to be deployed at any one time allowing a greater amount of data to be collected and there are generally fewer logistical concerns compared to UVC. BRUV has been demonstrated to record species richness consistently between sites unlike the results of UVC, although both recorded similar size distributions of species (Stobart *et al.*, 2007). A study by Stobart *et al.*, (2007) found that more cryptic species were detected by BRUV compared to UVC, although this contradicts other studies (Colton and Swearer, 2010; Lowry *et al.*, 2012).

Stereo BRUVs are systems of two cameras that can accurately measure distance and therefore the length of any focal object that is simultaneously within the field of view of both cameras. This method reduces inter-observer variability in size estimates when compared to traditional underwater monitoring methods when conducting underwater visual census. This system has been favoured by recent studies requiring a good estimate for length abundance data when comparing the effects of fishing between different areas (Watson *et al.*, 2009; Langlois *et al.*, 2012). Stereo-BRUVs have a higher statistical power to detect change in mean length of fish than UVC, especially where numbers are low (Harvey *et al.*, 2002). They have also been shown to have a lower selectivity, recording a wider range of lengths, higher species richness and higher number of individuals due the lower selectivity than fish trap gears (Harvey *et al.*, 2012). They are able to sample over a wider range of habitat types than other techniques such as otter trawls (Cappo *et al.*, 2004) and depths compared to divers.

A problem associated with the measurement of abundance using baited cameras is determining the spread of the bait plume. This has been overcome in some studies which use "time of first arrival" as a proxy for fish density. Martinez *et al*., (2011) found that the time of first arrival was related to current speed in some fish species but not in others, fish swimming speed, territorial and guarding behaviour, different olfactory capabilities (Bassett and Montgomery, 2011), and fish foraging behaviour (Bailey and Priede, 2002). Moreover, there are problems with the maximum number of individuals (MaxN) which can be affected by inter and intra-species behaviour. For example, smaller fish may avoid the BRUVs when there are larger predatory fish present and this may affect the observed average length of a sample when using the protocol of measuring length of all fish at the MaxN, (Watson *et al.*, 2009; McLean *et al.*, 2010). Guarding behaviour has been recorded from territorial species, guarding the bait against conspecifics and other species, which could lead to underestimates of species and densities on deployments where this behaviour occurs (Monk *et al.*, 2012). Langlois *et al*. (2010) found no significant difference in the biomass of herbivores between the use of BRUV and diver operated video but estimated a greater biomass (calculated from the length-weight relationship obtained from FishBase) and species richness of carnivores using the BRUV rather than the diver operated video.

The problem of measuring abundance using baited cameras has been overcome in deep-sea studies by using a theoretical estimate of density. Priede & Merrett (1998) conducted long term deployments of baited cameras on the abyssal plane and developed a theory which predicts that the number of fish visible at the bait is the result of equilibrium between arrivals and departures, and that the staying time at an exhaustible food source is inversely related to the probability of finding food. Therefore in areas of high food abundance the arrival time will be shorter because there is a higher abundance, but the MaxN will be low because they will leave the bait sooner due to the availability of alternative food sources.

The reverse is true for areas of poor food availability, the time to first arrival would be longer and the staying time would also be longer due to the lack of other feeding opportunities, resulting in a higher MaxN (Cappo *et al.*, 2005). Priede *et al.* (1990) determined a theoretical estimate of density using the inverse square law of the time to first arrival and a constant derived from fish swimming speed and current speed. This theory is for deep water ecosystems where density of fish is low, in shallower waters density is typically higher therefore the time to first arrival is much shorter and does not give reliable comparisons of density (Cappo *et al.*, 2005). Therefore, other methods to standardize the indices of relative abundance has been used, such as comparing to Underwater Visual Census (UVC) (Willis and Babcock, 2000) and non-baited video (Watson *et al.*, 2005). Advantages of stereo-BRUVs are that they are more cost effective than the use of diver operated cameras, results show less variance in the assemblage metrics (Watson *et al.*, 2005, 2010; Langlois *et al.*, 2010) allowing for greater statistical power in detecting spatial and temporal differences. Baited cameras may however be biased towards more predatory and scavenger species (Lowry et al. 2012; Dunlop et al. 2015).

1.5 Limitations to monitoring

Few studies have been conducted using Underwood's (1992) beyond-BACI design because of the difficulty in obtaining sufficient temporal and spatial data prior to the implementation of an area closure. There can also be difficulties in identifying suitable reference sites as area closures are usually designated because they are "special" in some way (such as a spawning site); because they are already established; or because there are limited funds to allow appropriate temporal and spatial replication (Claudet and Guidetti, 2010). Few studies of area closures to protect spawning aggregations have shown an increase in abundance of spawning fish with the limitations of success suggested as being due to ineffective survey design, implementation and sustained high fishing pressure outside the closure (Grüss *et al.*, 2013). The majority of previous studies have been conducted with the deconstructed sampling design of after-control-impact (Halpern, 2003; Claudet and Guidetti, 2010; Ojeda-Martinez *et al.*, 2011), but it is difficult to argue that the change in trajectory of the response variable measured is due to the area closure if there is no temporal data collected before the event (Underwood, 1992; Addison, 2011; Osenberg *et al.*, 2011). From this evaluation of the literature the conclusions that should be highlighted are that if a management plan is to be successful it needs to have well-defined objectives with clearly defined and transparent metrics that can be monitored over finite time-scales (Kraak *et al.*, 2013).

1.6 Aims and objectives

Area closures have been suggested as a tool to support fisheries management (particularly for areas where key life history stages congregate, such as spawning aggregations) and ecosystem-based conservation objectives. Although these two different objectives for using area closures are now commonplace in the UK, the use of area-based closures management approach remains controversial due to the frequent lack of clear objectives, monitoring and statistically robust impact studies. There can be negative impacts on the livelihoods of fishers who are displaced from fishing grounds due to the introduction of area closures. This has resulted in understandable opposition to their implementation. Providing good evidence regarding the effectiveness of area-based closures is therefore vitally important to support decision-making for future area closures and to evaluate whether existing closures are achieving their objectives. This thesis utilises three case-studies from UK waters to investigate the pressure-state relationship of fishing on demersal fish and invertebrate communities (EBFM); to evaluate the use of area-based management for EAFM; and to utilise evidence to assess the potential costs and benefits of applying a large-scale closure to restrict fishing in the deep sea by depth (EBM).

1.7 Structure of thesis

The introductory chapter (Chapter 1) is followed by three chapters describing the major studies undertaken (Chapters 2 – 4) and a concluding chapter (Chapter 5).

Chapter 2 uses stereo BRUVs to estimate the abundance of mobile megafauna on Burrowed Mud habitat that have been exposed to different levels of trawl intensity off the West Coast of Scotland. The aims of this study were to determine if baited cameras could be used effectively as a non-destructive method for monitoring mobile megafauna communities and to identify potential indicator species which may be sensitive to fishing pressure that could be used in future monitoring studies.

Chapter 3 evaluates the effectiveness of an existing spawning area closure for Atlantic cod (*G. morhua*) using a beyond-BACI design using standardised scientific trawl data. The study compares population trends of the Clyde spawning aggregation before and after the introduced area closure, using two other sub-population spawning grounds as control areas.

Chapter 4 uses a novel technique to show depths where ecological indices and the value of catch significantly change using long-term scientific deep-sea trawl data from the North east Atlantic. First derivatives are calculated of non-linear trends in ecological indices with depth.

Chapter 5 summaries the findings from these studies and provides a discussion of their relevance in the context of current research into the management of fisheries. Recommendations for future work are also considered.

Chapter 2: Identifying the effect of trawl intensity on mobile megafauna associated with Burrowed Mud

2.1 Abstract

Trawling has been identified as one of the main causes of human disturbance affecting benthic habitats, reducing the biomass and productivity of many benthic invertebrates and changing the benthic community structure. “Sea-pen and burrowing megafaunal communities”, also known as “Burrowed Mud” has been identified by OSPAR as a threatened or declining habitat in the North Sea and Celtic Seas. The condition of Burrowed Mud communities is ecologically significant because the burrowing benthic fauna act as ecosystem- engineers creating habitat for other organisms. A common burrowing species found on Burrowed Mud is *Nephrops norvegicus*, a commercially targeted species in the NE Atlantic. The overlap of this fishery with a habitat designated as threatened requires information on the habitat and its associated species to inform management decisions. In this study stereo baited remote underwater videos are used to estimate the abundance of mobile megafauna on Burrowed Mud habitat that have been exposed to different levels of trawl intensity off the West Coast of Scotland. The aim of this study was to determine if baited cameras could be used as a non-destructive method for monitoring mobile megafauna communities on Burrowed Mud and to identify species which are sensitive to fishing pressure that could be used in metrics for monitoring recovery in areas proposed for protection. Trawling intensity was negatively related to species richness of mobile megafauna, *Munida rugosa, Cancer pagurus* and *Liocarcinus depurator*, but no relationship was found on the species richness of deep burrowers (*Nephrops norvegicus* and *Goneplax rhomboides*). Hence, this study suggests that burrowing crustaceans are less vulnerable to the impacts of trawling than those that do not burrow. This gives support to the use of biological traits as indicators to detect changes of communities to fishing pressure.

2.2 Introduction

The regional sea of the North east Atlantic has been fished for centuries, but during the 20th Century there has been a notable increase in the use of bottom trawls (Greenstreet et al., 1999). Trawling has been identified as one of the main causes of human disturbance affecting the benthic habitats of the Northeast Atlantic shallow waters and continental shelf

(Thrush and Dayton, 2002; Jennings *et al*., 2012). Impacts from fishing can lead to physical and biological changes, by directly altering the structure of the seabed (Humborstad, 2004); reducing the biomass and production of benthic invertebrates (Hiddink *et al*., 2006, 2011; Kaiser *et al*., 2006; Reiss *et al*., 2009); changing the benthic community (Hinz *et al*., 2009) and functional composition (Tillin *et al*., 2006; Hinz *et al*., 2009); and affecting biogeochemical processes (Lohrer *et al*., 2004) and removing predatory fish (Heath and Speirs, 2012). Trawling, plus cumulative anthropogenic impacts in the marine environment has raised concerns for the diversity and functioning of ecosystems (Jennings and Kaiser, 1998; Large *et al*., 2013; Hiddink *et al*., 2015). Still a number of knowledge gaps still exist, such as what is the acceptable level of fishing that can continue without impacting on ecosystem services and what indicators can be used to assess against agreed reference points (Kaiser *et al*., 2015). The difficulty in answering these questions has led to the development of an ecosystems approach to management (EAM) (Hughes *et al*., 2005; Leslie and McLeod, 2007), which is a principal element of The Convention for the Protection of the Marine Environment of the North-East Atlantic (the ‘OSPAR Convention', OSPAR, 1992).

OSPAR identified “Sea-pen and burrowing megafaunal communities” as a threatened or declining habitat in the North Sea and Celtic Seas (OSPAR Regions II and III) (from here onwards termed “Burrowed Mud”; OSPAR, 2010). The OSPAR definition of this habitat is areas of fine mud, at water depths ranging from 15 to 200 m or deeper that are heavily bioturbated by burrowing megafauna such as *Nephrops norvegicus* (from here called by its genus *Nephrops*), *Goneplax rhomboides. Calocaris macandrae* and *Callianassa subterranean*. Burrows and mounds form a prominent feature at the sediment surface and sea-pens, typically *Funiculina quadrangularis*, *Virgularia mirabilis* and *Pennatula phosphorea* are present. Burrowed Mud is ecologically significant because the burrowing benthic fauna act as ecosystem-engineers through processes such as bioturbation and biodeposition (Rice *et a*l., 2012). These processes rework the substratum creating habitat and shelter for other organisms (Trenkel *et al*., 2007); reduce the risk of erosion and mix sediments changing physiochemical properties through the release of nutrients (Cadee, 2001; Laverock *et a*l., 2011; Rice *et al*., 2012). These processes are functionally important as it is estimated that up to 80% of the nitrogen needed by primary producers in shallow shelf seas is provided by benthic remineralisation reactions (Dale, 2002).

Nephrops norvegicus is a commercially targeted species in the NE Atlantic and is one of the main species commonly found in Burrowed Mud. 52 thousand tonnes were landed in the NE Atlantic in 2014, 30.5 thousand tonnes of which were landed in the UK (The European Commission, 2016). The value of this fishery to the UK is £98.2 million representing approximately 6% of the total value of fisheries landings in the UK (Marine Management Organisation, 2014). The legal requirement to sustainably manage Burrowed Mud in the NE Atlantic and the overlap of this habitat with the *Nephrops* fishery makes management options contentious. To overcome this in the UK, some areas of Burrowed Mud have been designated as protected features within English Marine Conservation Zones (MCZs; Marine and Coastal Access Act, 2009) and Scottish nature conservation Marine Protected Areas (ncMPAs; Marine (Scotland) Act, 2010). Within these areas the status of Burrowed Mud will have to be determined and whether this status needs to be maintained or improved. To do this appropriate metrics and methods will be required to monitor the status of this habitat and gain information on its ability to recover from fishing disturbance.

Beam trawl and grab sampling are standard monitoring methods that have been successfully used in trawling impact studies in the North Sea (Hiddink *et al*., 2006; Bolam *et al.*, 2014) and Celtic Sea (Hinz *et al*., 2009; van Denderen *et al*., 2015). However, for protected sites non-destructive methods are preferred to monitor the impact of protection. Also trawl sampling has been found to underestimate many non-target species such as sea-pens *Pennatula phosphorea* (Dyer *et al*., 1982; Greathead *et al*., 2007). Grab sampling is useful for assessing abundant infaunal invertebrates and the distribution of sediment particle size, but due to the small area sampled this method under samples larger invertebrate and does not effectively sample less abundant species (Bergman and van Santbrink, 1994). Towed video is another method used to monitor invertebrates that live on soft sediments such as *Nephrops* on Burrowed Mud and Scallops on gravel. Towed video has been used to provide stock assessments of *Nephrops* in Scottish and Irish waters since 1994 (Campbell *et al*., 2009). It is currently being trialled to estimate abundance of sea-pens and other burrowing megafauna (Greathead *et al*., 2011). ICES suggest that using this method on a wider scale in the NE Atlantic is technically feasible but it is not certain if the current surveys have appropriate coverage of the habitat to currently be assessed (ICES, 2011). Greathead *et al*. (2011) identified an additional nine species from the *Nephrops* surveys in the North Sea, six are anthozoa and three are polychaetes (Greathead *et al*., 2011). To get estimates of abundance for more mobile fish species associated with Burrowed Mud, such as *Lesueuriogobius friesii* is more difficult due to the natural responses of different species to disturbance from towed cameras (Stoner *et al*., 2008; McIntyre *et al*., 2015). Estimates of abundance from counting burrows from towed video surveys of species such as *Goneplax rhomboides* also needs to be validated to ensure the correct burrow is being assigned to the correct species and to determine if one burrow equates to one individual (Rice and Chapman, 1971). Therefore the choice of sampling techniques when monitoring Burrowed Mud is important as different techniques can lead to different biological interpretations being made about the results (Monk *et al*., 2012).

A non-destructive method that could be used to sample a range of mobile fauna is baited video underwater video (BRUV) (Unsworth *et al*., 2014). Baited cameras have been suggested as a statistically robust method for determining differences in abundance and community composition between habitat types (Bernard and Götz, 2012) and between space and time (Harvey *et al*., 2007). Recent baited camera studies have used two cameras set up in stereo, allowing for precise size estimates to be taken which are necessary to determine changes in community size structure and species stock structure over time. Monitoring studies using baited stereo-video found that areas of higher fishing intensity had a lower biomass of target species than areas of lower fishing intensity, but this difference was not detected for non-target species (Langlois *et al*., 2012). Baited stereo-video have also been shown to have a greater statistical power than divers at detecting differences in size distribution of fish species and show less variance in assemblage metrics (Watson *et al*., 2005, 2010; Langlois *et al*., 2010). Other benefits of using baited cameras compared to other methods is that they do not require any specialist vessels for deployment and recovery, also after they are deployed they can be left unattended and allow other work to be completed (Bailey *et al*., 2007).

In this study stereo-BRUVs were used to estimate the abundance of mobile megafauna on Burrowed Mud habitat that have been exposed to different levels of trawl intensity off the West Coast of Scotland. The aim of this study was to determine if baited cameras could be used as a non-destructive method for monitoring mobile megafauna communities on Burrowed Mud and to identify species which are sensitive to fishing pressure that could be used in metrics for monitoring change in MPAs. Changes in species richness, community composition and the distribution of individual species were examined in relation to trawl intensity, depth and distance from shore.

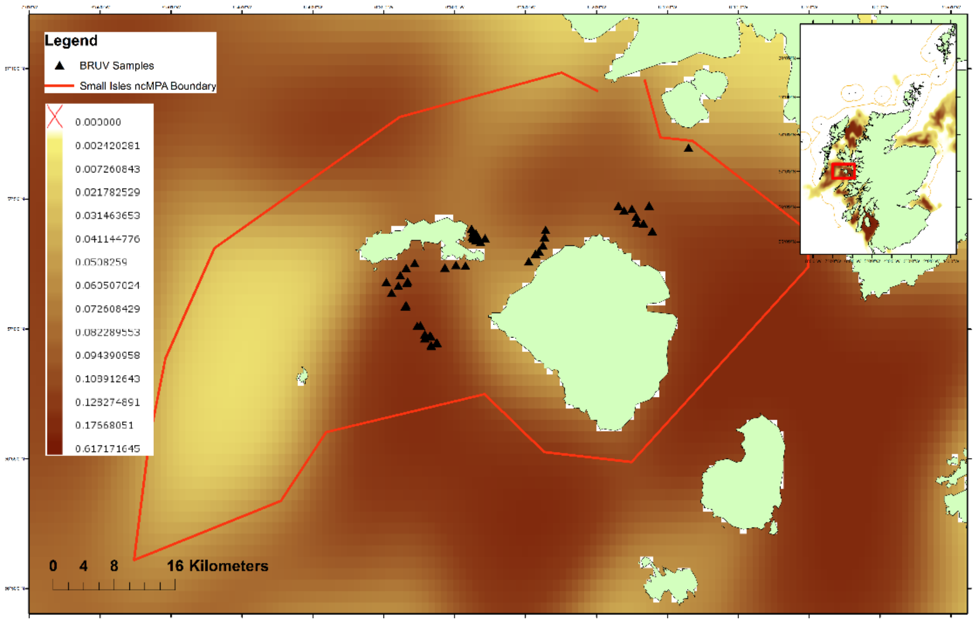

Figure 2-1 - Survey area within the Small Isles proposed MPA off the west coast of Scotland. Sample locations are indicated by black triangles. The range of colours yellow to orange represents fishing intensity of mobile *Nephrops* trawling (2009-2013) taken from the Scottish Government National Marine Plan Interactive website (Marine Scotland, 2015) © Crown copyright. The VMS layer represents fishing intensity (for vessels greater than or equal to 15m length) at a national scale, with darker areas representing higher activity (Kafas *et al*., 2012).

2.3 Methods

2.3.1 Survey Area

Mobile fauna were surveyed using BRUVs within the area of the Small Isles ncMPA over a period of two weeks in September 2013 (Figure 1). This area was chosen for the study because it is known to be an important area for Burrowed Mud and sea pens (Greathead *et al*., 2015) and because it has been exposed to a range of trawl intensity. The main fishery in this area is for *Nephrops* and the gear type used to catch *Nephrops* is classed within the TR2 category, which includes bottom trawls, Danish seines and other similar towed gear (excluding beam trawls) with mesh size greater than or equal to 70 mm and less than 100 mm (The European Commission, 2009). Although this area is in a proposed MPA when the survey was conducted it was prior to any restrictions to trawling, but in the future it will be subject to changes in management which will reduce trawling disturbance over some areas of Burrowed Mud (The Scottish Government, 2014a).

Depth (D), Trawl Intensity (TI) and Distance from Shore (DI) were the variables used in the analysis. Depth was measured at the time of deployment using the vessel's on-board echosounder. Distance from shore was calculated as the distance to the nearest shoreline using the "Join" function in ArcMap (v.10.1, ArcGIS), this parameter was chosen as a substitute to distance from complex substrata which was unknown and was hypothesised to influence the community structure. The trawl intensity data used in this analysis was modelled using "VMStools" package in R (Hintzen *et al.,* 2012) based on Vessel Monitoring System data of trawling vessels. Only vessels equal to or greater than 15 m in length carry VMS. Trawl intensity in this analysis was calculated as swept area per square kilometre for the period 2009-2013 and ranged from 0.48 to 14.87 times swept (mean = 6.26 ± 0.66). Permissions were not available to display the modelled data from the analysis to the public, therefore the representative data weighted to show just mobile *Nephrops* fishing was used in Figure 2.1. (Kafas *et al.*, 2012).

Fine scale environmental data modelled by Marine Scotland Science (MSS) such as % mud and slope were only available for 75% of the deployments therefore were not included in the analysis. Broad scale environmental data modelled by the Joint Nature Conservation Committee (JNCC; Cameron and Askew, 2011) was available for all drops but substrate type did not correspond to the substrate type viewed in a large proportion of video samples so was excluded (Figure 2-1)

2.3.2 Equipment

The BRUV configuration consisted of a frame (manufactured by Kiscadale Engineering Co.) (Figure 2-2) with a pair of calibrated stereo-video cameras (High Definition Canon Legria HFG10 in SeaGIS Pty Ltd housing) fixed at a set distance apart of 66 cm and converged at an angle of ~10º to gain an optimised field of view for conditions with limited visibility. A pair of W38VR dive lights (Xiware Technologies Ltd, Bulbs: White CREE XM-L U2 LED *2 (max 1400 Lumens); Colour temperature: 5000k) were mounted on the frame angled inwards towards the bait arm. The cameras were synchronised using a flashing diode (Beaver Sports Ltd, Electra Scuba dive strobe) facing towards the cameras situated on the bait arm (Figure 2-2). For each deployment new bait (200g of defrosted and chopped mackerel *Scomber scombrus*) was placed in an open container at the end of the bait arm. Two frames were used throughout the survey period, one was mounted with a Nortek AS Aquadopp current meter. The frame was set up with a bridle system of rope attached to a swivel and small buoy above the central point of the frame to stop the rope floating in front of the camera lens. The swivel was attached to mooring consisting of 160 m of polypropylene rope and a large A2 buoy, with an additional short length of rope and small pellet buoy to allow the easy recovery of the frame.

2.3.3 Video deployment and analysis

Frames were lowered to the seabed so that simultaneous deployments were at least 500 m apart, at stations ranging between 58 to 97 m in depth. The cameras were left recording on the seabed for approximately 60 min and with the current meter recording speed and direction of current every 3 seconds. Video length ranged from 49 to 88 minutes, with average length of 64 minutes (±1.2 SE, n = 47). Prior to start of the field season the cameras were calibrated following the procedure outlined in (Harvey and Shortis, 1996) using CAL^{TM} software (v2.2; www.seagis.com.au). The frame set-up ensured that the cameras remained in the same position in relation to each other throughout the survey period and the same camera was used in either the left or right side of the frame, with the focal length always set to infinity (∞). Video samples were interrogated using the software EventMeasure^{TM} (www.seagis.com.au), allowing stereo calibration to be verified whenever measurements were taken (Harvey and Shortis, 1996). Using the software all mobile fauna were recorded for each sample. The observer recorded the time each species was first seen and subsequently every time the maximum number for each species seen at one time increased. This results in collecting the maximum number (MaxN) of each species seen for each deployment and is a recognised method of collecting an index of relative abundance (Priede *et al.*, 1994; Cappo *et al.*, 2004), removing the chance of recording the same individual twice. Measurements were taken at MaxN of fork length for fish species, carapace length for *Nephrops* and *M. rugose* and carapace length for other crustaceans. Measurements were only able to be taken if individuals were present in both cameras, therefore analysis was limited to those species which were regularly recorded in both cameras and not used for community analysis.

2.3.4 Multivariate analysis

Multivariate analysis was conducted in the R programming environment using the package “vegan” (Oksanen et al., 2014). A Jaccard dissimilarity matrix was created using species data converted to presence or absence. Non-metric Multidimensional scaling (NMDS) was conducted using the metaMDS() function and the results were plotted in a 2-dimensional space and results from envfit() function were used to overlay environmental data. A permutational analysis of variance (PERMANOVA) was conducted using the adonis() function to determine the significance of the effects of the environmental variables, setting the maximum number of permutations to 999. Continuous environmental variables assessed were Depth (D), Trawl Intensity (TI) and Distance from Shore (DI). The betadisper() function was used to assess the homogeneity of each environmental variable.

2.3.5 Univariate analysis

Generalized Linear Mixed Models (GLMMs) were used to test for trends in Species Richness and the relative abundance of seven different species against the environmental variables Trawl Intensity (TI), Depth (D) and Distance from Shore (DI). Only species that were recorded in at least 10 out of 47 samples were modelled. This was due to the difficulty in determining if a recorded absence was a true absence or due to sampling error. Of the seven species that were modelled, six were typically observed as one individual in each sample and were therefore modelled as a binomial response with a logit link function. A Poisson distribution was found to be the distribution of best fit for species richness and a negative binomial distribution for the relative abundance of *M. merlangius*. Multicollinearity was examined for the explanatory variables by calculating the Variance Inflation Factor (VIF) for each (Zuur *et al.*, 2010) using the corvif() function in the package “AED” (Zuur *et al.*, 2009). Any variable with a VIF greater than 3 was removed (Zuur *et al.*, 2010). Video length (vl) was used as an offset in each model. The function glmer() was used for Poisson or binomial distributed data from the package “lme4” (Bates *et al.*, 2015) and the function glm.nb() was used for over-dispersed, negative binomial data from the package “MASS” (Ripley *et al.*, 2015).

2.4 Results

2.4.1 Descriptive

A total of 14 species of mobile fauna were identified from 13 families during 47 deployments around the Small Isles. Two species of sea pen which are Scottish Priority Marine Features (PMF) (SNH, 2016) were recorded, *Funiculina quadrangularis* was present at 3 sites and *Pennatula phosphorea* was present at 3 different sites all on mud substrate. The most abundant and most frequently observed species was whiting, *Merlangius merlangus,* which was present in 46 out of 47 drops (Table 2-1). The highest number of mobile species observed in a single sample over mud was 12 and on average 4.6 (±0.31 SE, n = 47).

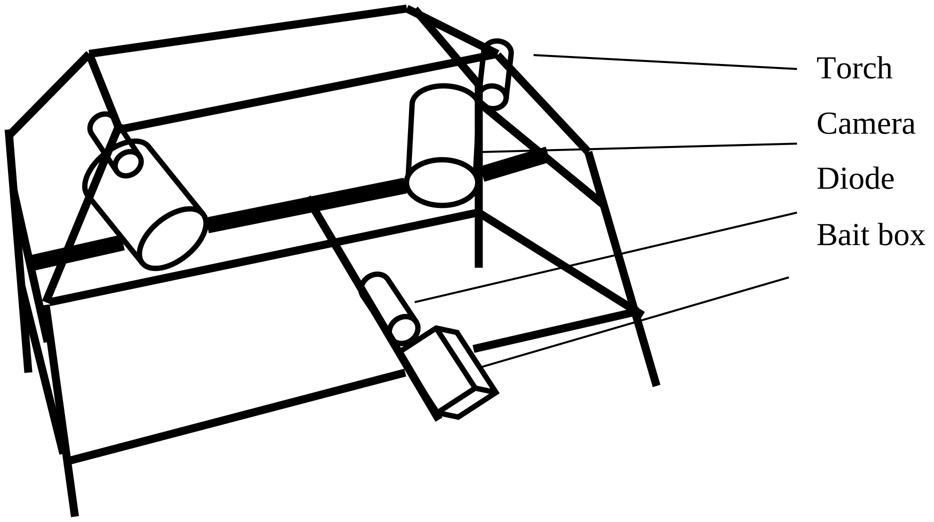

Figure 2-2 - Schematic of a stereo-video camera setup

Table 2-1 The highest number of mobile species observed in a single sample over mud was 12 and on average 4.6 (±0.31 SE, n = 47).

Species/Family	Frequency (n=47)	% Present
Atelecyclidae	2	4
Callionymus lyra	4	9
Cancer pagurus	10	21
Goneplax rhomboides	18	38
Lesueuriogobius friesii	16	34
Liocarcinus depurator	18	38
Melanogrammus aeglefinus	6	13
Merlangius merlangus	46	98
Munida rugosa	25	53
Nephrops norvegicus	37	79
Pagurus spp.	9	19
Pleuronectidae	8	17
Scyliorhinus canicula	5	11
Triglidae	10	21

2.4.2 Multivariate

The explanatory variables did not demonstrate multicollinearity (VIF<2; see Table A1). The nMDS plot of the community data shows that community similarity was influenced by a range of environmental variables (Figure 2-3), this was corroborated using PERMANOVA. Community composition was significantly related to trawl Intensity (PERMANOVA, F1,46 = 4.423, p = 0.001) and distance from shore (PERMANOVA, F1,46 = 2.160, p =0.028). No effect of depth was found on the community composition (PERMANOVA, F1,46 = 1.923, p =0.060). Figure 2-4 represents the similarity in community of each sample, but is overlaid with the species that are influencing these differences and the directional influence of trawl intensity.

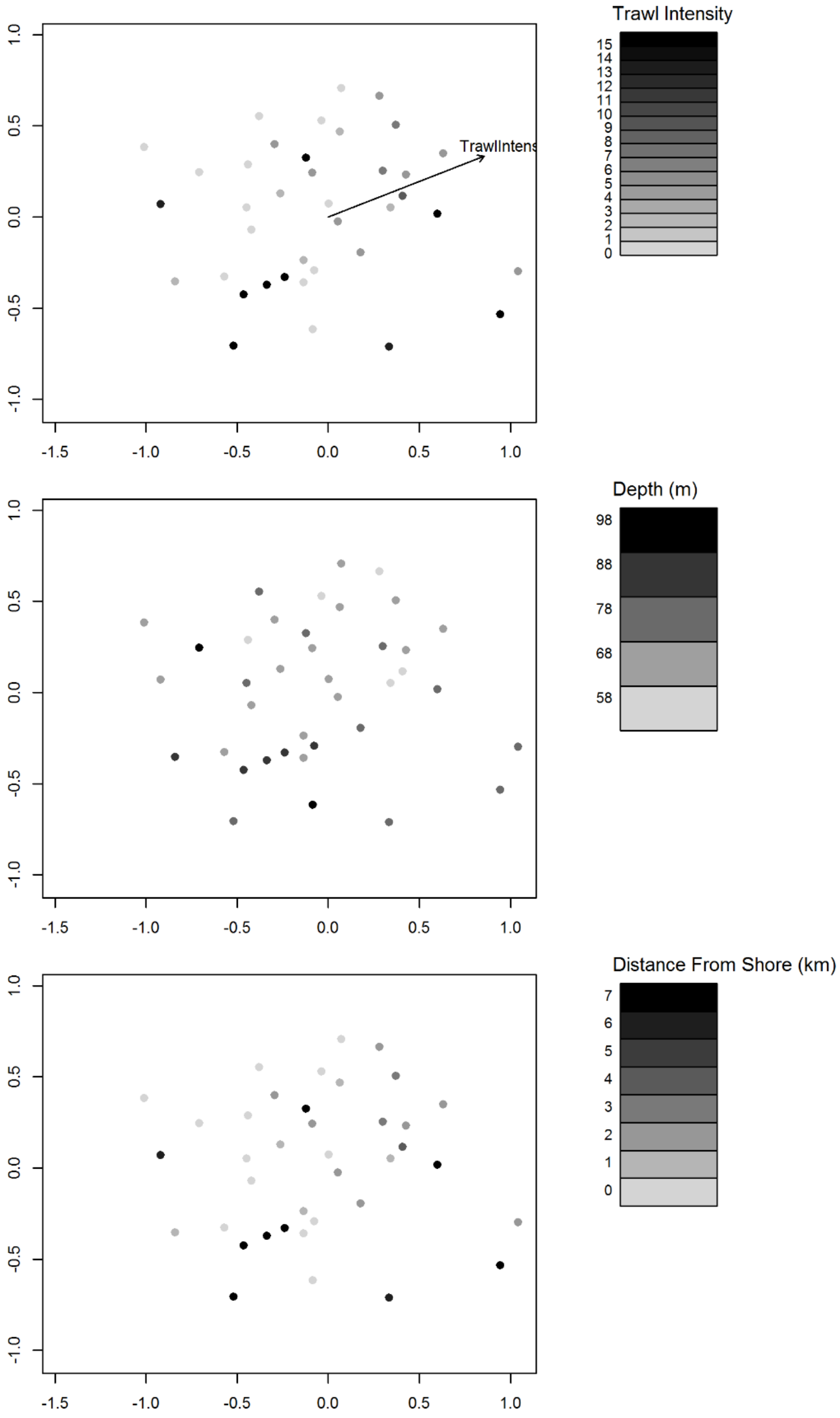

Figure 2-3 - A two dimensional visualisation of the relationship in the community structure between each sample using non-metric multidimensional scaling (nMDS), stress =0.205. Each graph is overlaid with a gradient for continuous variables of A) Trawl Intensity at each sample location; B) Depth at each sample location; C) Distance from shore of each sample location.

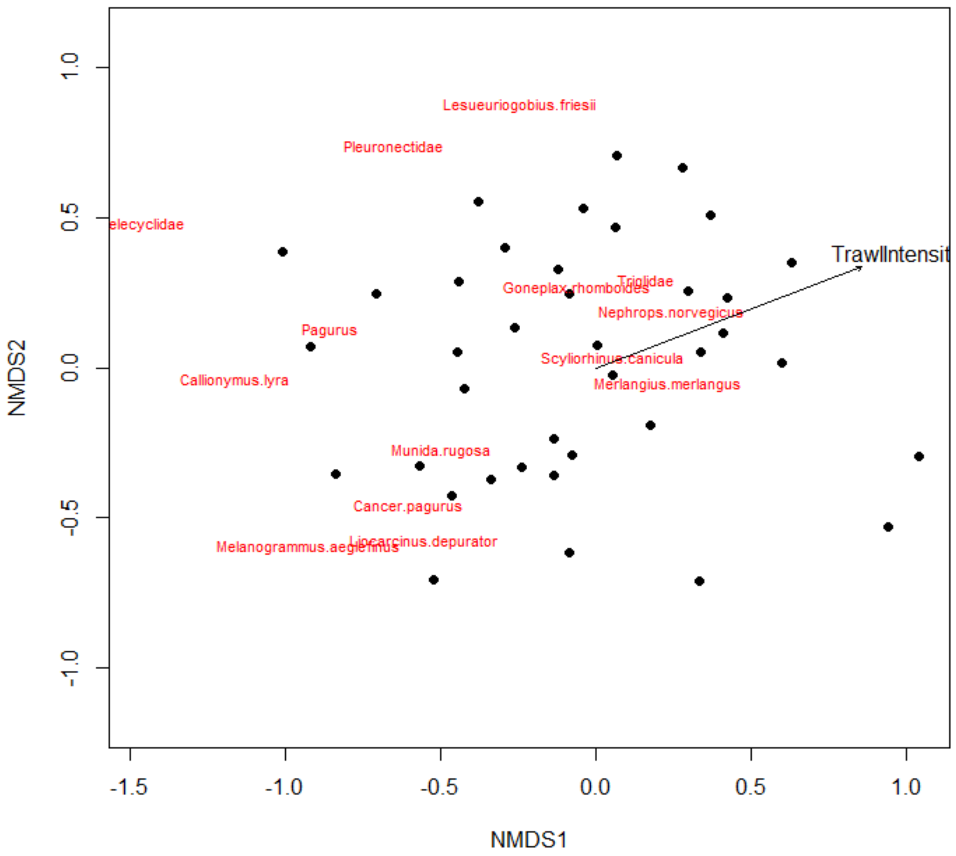

Figure 2-4 The black circles represent each sample in a two dimensional space as a visualisation of the relationship of community structure between each sample using non-metric multidimensional scaling (nMDS), stress =0.205. Overlaid is the centroid of each species as a weighted average of “site scores” that contribute most to the similarity between communities. Arrow represents the directional influence of trawl intensity.

2.4.3 Univariate

Species Richness and *M. rugosa* MaxN showed a significant negative relationship with Trawl Intensity (Poisson, $Z_{1,47}$= -3.782; p <0.001; Binomial, $Z_{1,47}$= -2.380; p =0.0173 respectively). *C. pagurus* and *L. depurator* MaxNs showed a significant negative relationship with Trawl Intensity (Binomial, $Z_{1,47}$= -2.228; p =0.026; Binomial, $Z_{1,47}$= -3.281; p =0.001 respectively) and *C. pagurus* a significant positive relationship with distance from shore (Binomial, $Z_{1,47}$= 2.623; p =0.009) and *L. depurator* a significant positive relationship with depth (Binomial, $Z_{1,47}$= 2.256; p =0.024) . *M. merlagius* showed a significant negative relationship with distance from shore (Neg.Bin, $Z_{1,47}$= -2.491; p <0.05).

For *G. rhomboides* , *Nephrops* and *L. friesii* no significant effect of Trawl Intensity (Binomial, $Z_{1,47}$= -0.817, p =0.414; Binomial, $Z_{1,47}$= -0.093, p =0.926; Binomial, $Z_{1,47}$= -0.564, p =0.572), Distance from shore (Binomial, $Z_{1,47}$= -1.860, p =0.063; Binomial, $Z_{1,47}$= --1.803, p =0.071; Binomial, $Z_{1,47}$= -1.314, p =0.189) or depth (Binomial, $Z_{1,47}$= -1.016, p =0.309; Binomial, $Z_{1,47}$= -0.068, p =0.946; Binomial, $Z_{1,47}$= -1.911, p =0.056) was found.

Table 2-2 Output from the model of best fit for each response variable a) to e). Fixed effects show treatment contrast coefficients and diagnostics (z- and p-values) indicate the effect of each parameter level on the reference level, denoted as intercept.

	Estimate	**Standard Error**	**Z value**	**p-value**
a) *Species Richness (Poisson, n=47)*				
Constant	1.798	0.106	17.024	<0.0001
Trawl Intensity	-0.059	0.016	-3.782	<0.001
b) *Munida rugosa (Binomial, n=47)*				
Constant	1.179	0.568	2.076	0.0379
Trawl Intensity	-0.176	0.074	-2.380	0.0173
c) *Cancer pagurus (Binomial, n=47)*				
Constant	-1.255	0.644	-1.948	0.051
Trawl Intensity	-0.399	0.179	-2.228	0.026
Distance From Shore	0.7361	0.281	2.623	0.009
d) *Liocarcinus depurator (Binomial, n =47)*				
Constant	-6.639	3.503	-1.895	0.058
Trawl Intensity	-0.451	0.137	-3.281	0.001
Depth	0.116	0.051	2.256	0.024
e) *Merlangius merlangus (Neg. Bin, n=47)*				
Constant	2.722	0.210	12.959	<0.0001
Distance From Shore	-0.175	0.070	-2.491	0.0127

2.5 Discussion

This study demonstrates a novel, non-destructive method to estimate abundance of mobile fauna over Burrowed Mud and shows that it can be used as a method to detect changes in community composition along a gradient of trawl intensity. The results in this study show that trawling has a negative effect on the species richness of mobile megafauna that live in Burrowed Mud. Whilst this study corroborates with other studies that have shown that trawling reduces species richness of infauna and epi-fauna in soft sediments (Hiddink *et al.*, 2006; Hinz *et al.,* 2009), it identifies mobile, non-burrowing crustaceans such as *M. rugosa, C. pagurus* and *L. depurator* to be sensitive to trawling pressure. Burrowing crustaceans, *Nephrops* and *G. rhomboides* and the burrow dwelling goby *L. friesii* were found to not be sensitive to trawl intensity. A study in the NW Mediterranean found similar trends in the epi-benthic community composition, where trawled areas were characterised by motile burrowing predators, and non-trawled areas were characterised by motile surface predators and sedentary filter feeders (De Juan *et al.*, 2007). Although in contrast, a study conducted in Bay of Biscay to sample megafauna in areas of high and low trawl intensity found that areas of high trawling disturbance were dominated by opportunistic scavengers including *L. depurator* and *M. rugosa (*Vergnon and Blanchard (2006). Differences were detected in community composition between two methods of sampling, using video and trawling which may be due to differences in selectivity of each method. The catch efficiency of beam trawls has been shown to under sample large invertebrates, particularly those that create burrows (Reiss *et al.*, 2006). Therefore if the efficiency of beam trawls to sample burrowing species is low, then it would be expected to have more variation in the abundance estimates, an incomplete picture of community composition and a reduced ability to detect trends with environmental or anthropogenic gradients. Whereas studies using towed cameras more accurately sample all of the mobile community, including those that create burrows as they are likely to be recorded before avoiding the towed camera. This source of error caused by disturbance is further reduced by using BRUVs which are stationary and allow time for more precautious species to emerge from their burrows. Although the sample area is small the frequency with which common species were recorded was high as would be expected if sampling efficiency was high, for example the most common species *M. merlangus* and *Nephrops* were recorded at 98 and 79% of the drops respectively.

Identifying which species are sensitive to different pressures is an important element when developing indicators for monitoring ecosystem health. Quantitative indicators and reference levels are required to determine if progress towards the aim of “Good

Environmental Status" is being made under the MSFD (Rijnsdorp *et al.*, 2016) and will be required for monitoring the status of protected features within the OSPAR Network of MPAs. There is currently no published data using a different methodology around the Small Isles to assess if the BRUVs were sampling the full range of motile species which would be a requirement to truly assess the efficiency of this methodology. A recent study using a limited number of deployments of BRUVs in the North Sea to assess the effect of wind turbines on benthic fauna found that species richness was lower than in other studies, particularly noting a low abundance of gobies (Griffin *et al.*, 2016). Some studies have suggested that BRUVs have limited capability to detect cryptic (i.e. difficult to see) species (Colton and Swearer, 2010; Lowry *et al.*, 2012), whilst others have shown a greater capacity to detect rare species (Dunlop *et al.*, 2014). In this study the most cryptic species was *L. friesii* and it was recorded at 34% of the deployments. Even though the species is relatively small, the habitat is fairly homogenous and *L. friesii* did not exhibit any avoidance behaviour or interspecies interaction to suspect that this methodology has a sampling bias.

The lack of impact on burrowing species by trawling such as *G. rhomboides* and *Nephrops* could be due to their ability to hide in their burrows when trawls pass with only the proportion of the population above ground caught. Although the otter boards of *Nephrops* trawls can penetrate soft sediment down to 35 cm (Lucchetti *et al.*, 2012), the main groundgear only impacts approximately the first 12cm (O'Neill *et al.*, 2009). As *Nephrops* can create burrows up to 30 cm in depth (Rice and Chapman, 1971) a proportion of the population is probably able to escape capture and the emergent time of female *Nephrops* is different to males as they spend a greater proportion of their time underground when berried in the autumn months (Rice and Chapman, 1971). Also *G. rhomboides* have burrows similar to those of *Nephrops* but are smaller descending only 10-15cm but may be deep enough to protect them getting caught (Rice and Chapman 1971; Atkinson 1974a). A reduced spatial overlap was found between species of *Nephrops* and *G. rhomboides* in the Bay of Biscay suggesting competition between the species for food and space (Trenkel *et al.*, 2007). This was not detected in this study as *Nephrops* was present at nearly every station, so any effect on the abundance of *G. rhomboides* could not be inferred. The decreased probability of *M. rugosa*, *L. depurator* and *C. pagurus* at sites of high fishing intensity makes sense, even if these species are mobile scavengers and can quickly recolonise a trawled area, if an area is regularly trawled and these species are not associated with a deep burrow then they would be susceptible to being caught by the fishery more so than species that create burrows.

Indicators that can demonstrate the relationship between pressure and natural state need to be developed along with appropriate methods that can adequately monitor change. This study identified the presence of a range of mobile benthic species found over Burrowed Mud and suggests that there is trawl intensity has no effect on the incidence of some characteristic species of Burrowed Mud communities (ie *Nephrops*, *G. rhomboides* and *L. friesii*. The species that did show a negative response to increased fishing intensity are all mobile and found on the surface of the substratum (ie *M. rugosa, C. pagurus* and *L. depurator).* These species are not considered characteristic of Burrowed Mud communities, but they do commonly occur in this habitat. It is important to discern what species are affected by trawling and which are not when developing a monitoring strategy. When the species of interest or elements of the community of interest are identified it is then also important to choose the correct monitoring method to ensure that you are accurately measuring changes to that species abundance or that component of the community. This study identified species that showed different trends with trawl intensity, with further validation against other methodologies baited cameras could be a potential future method for monitoring MPAs.

Chapter 3: Evaluating the effectiveness of a seasonal spawning area closure[1]

3.1 Abstract

Fish that aggregate at predictable locations and times to spawn are often vulnerable to over-exploitation. Seasonal closures have often been implemented in an attempt to alleviate such impacts but the effectiveness of these measures is rarely tested. This study evaluates the effectiveness of a spawning closure for Atlantic cod (*Gadus morhua*) in the Firth of Clyde off the Scottish West Coast (ICES area VIa). This closure was introduced in March 2001 as an emergency measure to allow as many cod as possible to spawn and avoid the build-up of displaced effort from another spawning closure. Genetic, tagging and otolith microchemistry investigations indicate that cod inhabiting the Clyde are reproductively isolated from other resident groups in the central and northern part of the Scottish West Coast stock. This study used a beyond-BACI (Before-After, Control-Impact) approach to compare population trends of the Clyde spawning aggregation before and after the introduced area closure, using two other sub-population spawning grounds as control areas. There was no evidence of local recovery in terms of abundance, biomass or reduced mortality in the Clyde more than a decade after establishing the closure. Mortality may have remained high because young cod are still caught as bycatch in the *Nephrops* fishery in the area and the predation rate may have increased due to an expanding whiting population. Considering the state of the already severely depleted Clyde sub-population when the closure was implemented the measure appears to have been too little and too late. The tendency to implement such spawning closures on nearly collapsed stocks may be why these measures often appear to have been ineffective.

---

[1] Clarke, J., Bailey, D. M., and Wright, P. J. 2015. Evaluating the effectiveness of a seasonal spawning area closure. ICES Journal of Marine Science, 72: 2627–2637.

3.2 Introduction

Catch control measures for commercial species are often at a spatial scale greater than that of local population dynamics, making individual spawning components vulnerable to extirpation (Stephenson, 1999; Hutchinson, 2008; Armstrong *et al.*, 2013). Area closures have been suggested as a tool to support fisheries management, particularly for areas where key life history stages congregate (Halliday, 1988; Murawski *et al.*, 2000; Pickett *et al.*, 2004), such as spawning aggregations. Spawning aggregations often occur at times and places that are predictable making them vulnerable to exploitation (Sadovy and Domeier, 2005). Aggregative behaviour can cause localised increases in catchability which can lead to higher fishing mortality (Halliday, 1988; van Overzee and Rijnsdorp, 2015). High catch rates during spawning can mask overall stock declines as the aggregation fisheries exhibit catch per unit (CPUE) hyperstability (Rose and Kulka, 1999; Erisman *et al.*, 2011). This is where catch rates remain high even when the actual stock abundance is in steep decline through the spatial concentration of fish and fishery (Hilborn and Walters, 1992). Consequently, many spawning aggregations have at first appeared inexhaustible and this has led to their depletion (Ames, 2004) and in some cases near extirpation (Beets and Friedlander, 1998; Aguilar-Perera, 2006; Erisman *et al*., 2011; Armstrong *et al.*, 2013). Therefore the introduction of a spawning area closure timed to the period when fish aggregate to spawn can reduce fishing mortality directly, whilst permitting sustainable exploitation outside of the spawning period (Murawski *et al.*, 2000). However, for a spawning closure to have a net benefit to population growth there should be a reduction in the annual fishing mortality (Heppell *et al.*, 2006). Hence, if fish are not particularly susceptible to capture during spawning or there is a change in fishing effort that negates the seasonal reduction in mortality, a spawning closure may have no effect (Grüss *et al.*, 2013; Grüss and Robinson, 2015).

If the catchability is greater during the spawning period than at other times of the year, then reducing overall fishing effort through the introduction of a spawning area closure can benefit the fish population by reducing fishing mortality (Grüss *et al.*, 2013; Grüss and Robinson, 2015) and also by reducing disturbance (Morgan *et al.*, 1997). Disturbance from fishing can alter spawning aggregation behaviour and interrupt the spawning process with some fish not returning to spawn until after the disturbance has stopped (Dean *et al.*, 2012). Loss of spawning areas may impact recruitment since the diversity and location of sites where eggs are released may help mitigate against the effects of local mortality events and promote favourable egg and larval transport (Marteinsdottir, 2000; Jonasson *et al.*, 2009). Re-colonisation of extirpated spawning grounds may take many generations in species where spawning migrations are related to social learning, as inexperienced recruits learn the routes to grounds by following older experienced individuals (Rose, 1993). High fishing mortality on spawning individuals will also lead to a size and age truncation, which can affect the viability of offspring produced and the timing of spawning (Birkeland and Dayton, 2005; Wright and Trippel, 2009). Ultimately, the removal of larger individuals during spawning may also create a strong selection pressure for fish that mature at a smaller size and younger ages and so may have evolutionary consequences (Law, 2007; Devine *et al.*, 2012). Therefore the cessation of fishing of spawning aggregations can lead to a recovery of demographic structure (Wright and Trippel, 2009), sex ratios (Beets and Friedlander, 1998), prevent the extirpation of distinct spawning components (Ames, 2004; Armstrong *et al.*, 2013) and reduce negative selection pressures (Law, 2007).

Despite theoretical models predicting potential benefits of spawning area closures for fish conservation (Sadovy and Domeier, 2005; Grüss *et al.*, 2014) this management approach remains controversial due to the frequent lack of clear objectives, monitoring and empirical impact studies (Sadovy and Domeier, 2005; STECF, 2007; Grüss *et al.*, 2014). Although many spawning area closures have been established, the effectiveness of this approach has rarely been evaluated (van Overzee and Rijnsdorp, 2015). Whilst potential impacts of spawning fidelity and effort redistribution have been examined there is still comparatively few empirical studies of spawning closures. The Before/After, Control/Impact (BACI) survey design has been widely accepted as an appropriate method of directly assessing the effects of area closures (Claudet and Guidetti, 2010; Ojeda-Martinez *et al.*, 2011; Osenberg *et al.*, 2011; Fenberg *et al.*, 2012). Of those studies that have examined the effect of area closures to protect spawning aggregations (Beets and Friedlander, 1998; Murawski *et al.*, 2000; Rhodes and Sadovy, 2002; Pet *et al.*, 2005), none have used a BACI survey design.

Atlantic cod, *Gadus morhua*, are particularly relevant to the debate about spawning area closures as this measure has been applied to many stocks (Murawski *et al.*, 2000; Hu and Wroblewski, 2009; Armstrong *et al.*, 2013). They are broadcast spawners (Hutchings *et al.*, 1999) that aggregate in high numbers to spawn (Rose, 1993; Rose and Kulka, 1999; Wright *et al.*, 2006a; Siceloff and Howell, 2013). Aggregations are persistent from year to year and form in specific locations for set periods of time. Cod exhibit a diversity of migratory behaviour associated with differing degrees of reproductive isolation among spawning aggregations (Knutsen *et al.*, 2003; Wright *et al.*, 2006b; Skjaeraasen *et al.*, 2011). Many resident populations often exhibit differences in life history traits over comparatively small spatial scales (Olsen *et al.*, 2004; Yoneda and Wright, 2004; Wright *et al.*, 2011).

Cod off the West Coast of Scotland in ICES Area VIa are managed as a single stock (ICES, 2013). However evidence on the connectivity between nursery and spawning areas from otolith microchemistry and home ranges based on tag-recapture experiments suggest that this stock is composed of three sub-populations; the Clyde, Minch and South West (Wright *et al.*, 2006a; 2006b). Cod from the Clyde were shown to be reproductively isolated having little detectable exchange with the northern spawning aggregations. Genetic evidence also supports this population structure as Clyde cod were found to have a greater affinity to those from the Irish Sea than the cod from the northern aggregations (Heath *et al.*, 2014). Different trends in spawning stock biomass (SSB) among the sub-populations further supports the existence of this population structure (Holmes *et al.*, 2014). A fishery closure was introduced to the Firth of Clyde in 2001 to coincide with the cod spawning period (6th March to 30th April) to allow as many cod as possible to spawn (Commission Regulation (EC) No 456/2001) and was subsequently continued by the Scottish Government (The Sea Fish (Prohibited Methods of Fishing) (Firth of Clyde) Order 2002) . The location was known as an important spawning area for cod identified by a high catch rate of mature individuals (age 3 and 4) (Armstrong *et al.*, 2006), and spawning individuals (Wright *et al.*, 2006a) and the area is vulnerable to increased fishing efforts during the spawning period (Hislop, 1986). In addition, the Clyde closure was intended to avoid an increase in local fishing mortality as a consequence of fishing effort being displaced from an Irish Sea closure (Commission Regulation (EC) No 304/2000). The closure has two zones (Figure 3-1), Area 2 prohibits gears that target fish and trawling for *Nephrops* (*Nephrops norvegicus*), but allows creeling and dredging for scallops (*Pecten maximus*) whilst Area 1 also prohibits gears targeting fish but permits trawling for *Nephrops*, creeling and scallop dredging.

Given the apparent reproductive isolation of Clyde cod, the seasonal closure was expected to reduce the sub-population mortality rate and aid the recovery of spawning stock biomass, although it was not expected to affect the other sub-populations within ICES Area VIa. The aim of this study was to investigate the rationale and effectiveness of the area closure. The rationale that the closure reduced catchability was examined from changes in commercial landings and fishing effort before and after the closure. Effectiveness, in terms of the closure allowing the recovery of the Clyde sub-population, was assessed by applying an asymmetric “beyond-BACI” design (Underwood, 1992) to analyse survey based indices of spawning stock biomass (SSB) and CPUE. The fine scale sub-population structure within the stock with a relatively long time series of standardised survey data, lends itself to a BACI analysis, by providing one sub-population with a putative impact (the area closure) and two comparable control spawning areas. To establish whether the closure had an effect on total mortality the same beyond-BACI methodology was applied to a linearised catch curve of the length composition for each sub-population, before and after the measure was introduced.

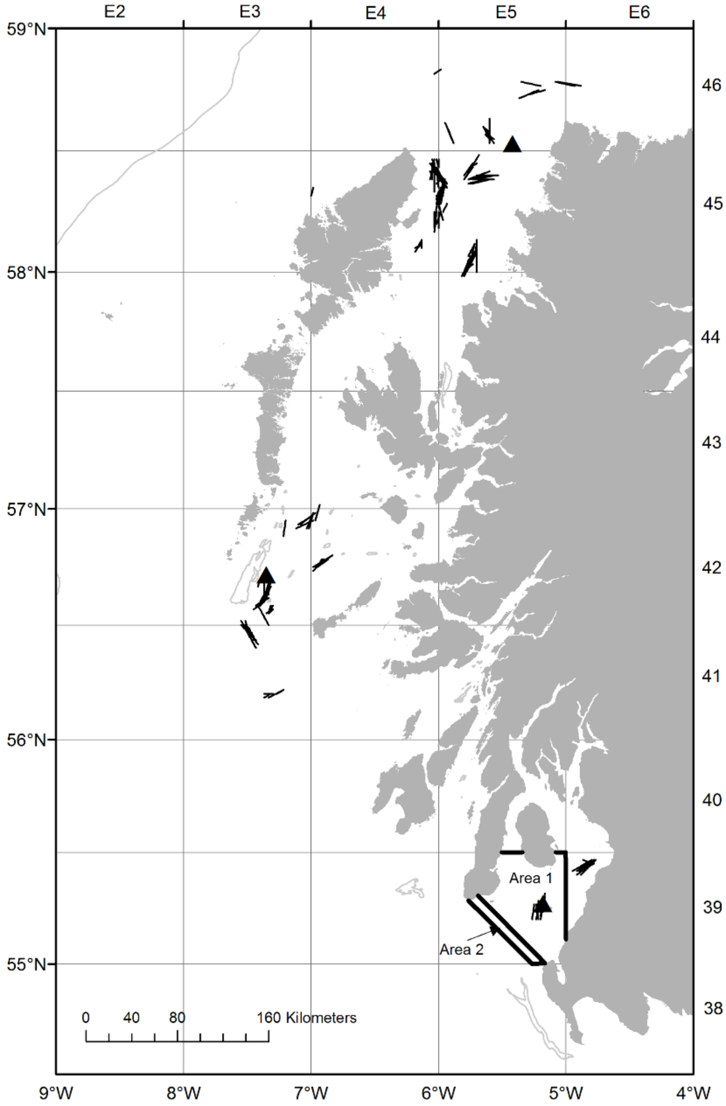

Figure 3-1 Map of survey area to the west of Scotland. Lines indicate all trawls conducted during the study period and used in the analysis. Black triangles indicate spawning locations taken from surveys conducted by (Wright et al., 2006a). The Clyde closure is split into two zones, Area 1 prohibits gear that targets fish and Area 2 prohibits gear that targets fish and *Nephrops* during the spawning period.

3.3 Methods

The three sub-populations and their associated spawning aggregations used in this study were identified from Wright *et al*. (2006b). Landings of cod and fishing effort (hours fished) data for each vessel type greater than 10m were extracted from the Marine Scotland FIN database by ICES rectangle (1° longitude x 0.5° latitude). Data were summed for multiple ICES rectangles corresponding to each of the three sub-populations (Table 3-1), then effort was displayed as monthly proportions for the period “Before” (1986-2000) and “After” (2001-2010) the Clyde cod closure was introduced. Landings per unit effort were calculated using a correction factor for each of the seven gear types based on that used by Wright *et al.*, (2006a) and displayed as corrected landings per unit effort (CLPUE) monthly total for each sub-population for each time period. The sum effort and landings for the two gears that accounted for most landings; light otter trawls (LTR) and *Nephrops* trawls (NTR) was calculated for each sub-population area for each year.

3.3.1 Seasonal and annual variation in catch rates

Data on catch per unit effort and length composition were obtained from the 1st quarter (February to April) Scottish West Coast Bottom Trawl Survey conducted by Marine Scotland Science from 1986 until 2010, during the March-April spawning period for cod. Due to a change in the survey design after this date later data were not used in the analysis. The surveys used a Grande Overture Vertical trawl with a high-headline bottom trawl fitted with a 20 mm cod end liner. The distance of the tow, wingspread and speed was recorded so that the catch per unit effort (CPUE) could be standardised to the number of cod caught at each 1 cm size class per hour. The surveys within ICES area VIa were replicated at a spatial scale of an ICES rectangle (1° longitude x 0.5° latitude). All trawls used in the Minch were within 65 km of the identified spawning site; 60 km of the SW spawning site and 35 km of the Clyde spawning site (Figure 3-1)**.** Sample sizes for each sub-population can be seen in Table 3-1.

3.3.2 Changes in CPUE and SSB from scientific trawls

Generalised Linear Models were used to test for different trends in both CPUE and SSB before (1986-2000) and after (2001–2010) the closure. As the closed area was expected to reduce fishing mortality of spawning cod, only mature sized cod were used in the analysis. The length at which 25% of cod off the West coast of Scotland are mature is 35 cm according to Yoneda and Wright (2004), and so this length threshold was used in the estimation of mature cod CPUE. 25 % length at maturity rather than 50 % was used due to the low abundance of larger sized cod during the after period, which would not have allowed for a robust analysis. SSB was calculated by using data on length and weight from ICES Area VIa extracted from the DATRAS website. A linear model was fitted to the natural logarithm (base e) of the length and weight of all cod sampled. The intercept (-1.9307) and slope (2.9831) from this model were then used to calculate the weight from the measured length of all mature fish. The SSB for each trawl was then calculated by summing the total biomass of mature fish for each trawl.

Analysis of both SSB and CPUE started with a saturated model, including all interaction terms based on *a priori* hypotheses for the inclusion of a third order interaction (β_7,spy) between period (p), sub-population (s) and year (y) (Equation 1).

$$\text{Log(Response)}= \beta_0 + \beta_1,s + \beta_2,p + \beta_3,y + \beta_4,sp + \beta_5,py + \beta_6,sy + \beta_7,spy \qquad (1)$$

Both sub-population and period were modelled as factors, where sub-population (s) included three levels: (i) Clyde closed area, (ii) Minch control area, and (iii) SW control area. Period (p) included two levels for the time period (i) “before” the area closure from 1986 until 2000; and (ii) “after” including 2001 until 2010. Year (y) was modelled as a continuous variable. Generalised linear models were implemented using the glm() function in the R package “nLME ”(Pinheiro *et al.*, 2013). The model of best fit was identified using backward model selection from the fully saturated model using likelihood ratio tests (Zuur *et al.*, 2009), and checking residual plots. If the model of best fit includes the third order interaction (spy) this would indicate that the trend in response variable differed for each sub-population, and the trend differed for each sub-population for each of the time periods, “before” and “after” the area closure. A difference in trend for the Clyde sub-population in the “after” period compared to the other sub-populations could then be inferred as an effect of the closure.

3.3.3 Changes in length composition and total mortality

Changes in length composition “Before” and “After” the closure in each sub-population were compared using a Kolmogorov-Smirnoff (K-S) test from the function clus.lf() from the R package “fishmethods” (Nelson, 2014) applied to calculated CPUE per 5 cm length bin. Total mortality (Z) before and after the closure was calculated from the slope of a linearised catch curve, modelling the relationship between the natural logarithm of CPUE and length (Jensen, 1984) implemented using the function glmer() in the R package “lme4” (Bates *et al.*, 2015). A general linear mixed model was used to analyse mortality using the following model structure:

$$Z = \beta_0 + \beta_1, s + \beta_2, p + \beta_3, l + \beta_4, sp + \beta_5, sl + \beta_6, lp + \beta_7, spl + b_0 + b_{1,}y + b_{2,}l \qquad (2)$$

Both sub-population (s) and period (p) were modelled as factors as in the preceding analysis. Length was modelled as a continuous variable between 45 cm and 70 cm. This range was chosen as the catch curve indicated that smaller sizes were not fully vulnerable to the fishing gear and larger fish were not regularly caught in all areas. A random intercept and slope effect was included in the model to account for different mortality rates each year. Year was modelled as a random factor with 25 levels. A significant interaction effect would imply that the CPUE of different size fish changes for different sub-populations during the different time periods. The model of best fit was identified using backward model selection from the fully saturated model using likelihood ratio tests (Zuur *et al.*, 2009), and checking residual plots. If the model of best fit includes the third order interaction and a positive coefficient for the Clyde sub-population then this would indicate a reduction in total mortality (Z) and could be inferred as an effect of the area closure.

3.4 Results

3.4.1 Seasonal and annual variation in catch rates

CLPUE and proportion of fishing effort varied significantly over the year in all three sub-population areas (Kruskall-Wallis; $p < 0.01$). In the Clyde and SW area there was a peak in the CLPUE and proportion of fishing effort related to spawning time during the “Before” period (Figure 3-2). In the “Before” period in the Clyde area, there was a 3 times difference in catchability (CLPUE) between the spawning and non-spawning period; 70% of annual landings were taken during these two months and 45% of the total annual effort for Light Otter Trawls in this area was accounted for during these two months (Figure 3-2). During the “After” period effort in the Clyde peaked in October although there was a small peak in cod landings during the spawning period. In the SW and Minch there was no peak in either landings or fishing effort around spawning time in the “After” period. Landings and effort by the light otter trawls decreased from the start of the study period until the end with a clear decline from the 1990s for all areas (Figure 3-3). Importantly, there was no redistribution of light otter trawl in the Clyde area following the closure, the effort was effectively removed from this area (Figure B-1). The effort of *Nephrops* trawls remained fairly constant throughout the study period (Figure B-2) although the landings of cod showed a decline in each of the areas, which was particularly steep after 2000. As a result, landings and effort by 2001 represented < 12% of the peak (Figure 3-3).

Table 3-1 List of ICES rectangles used for each sub-population. Values represent the number of trawl surveys conducted by Marine Scotland Science in quarter 1 within each sub-population area in each time period.

Sub-population	ICES Rectangle	Before	After	Total
Clyde	39E4 and 39E5	32	21	53
Minch	45E4, 45E3, 46E4	109	64	173
SW	42E3, 42E2, 41E2	41	39	80

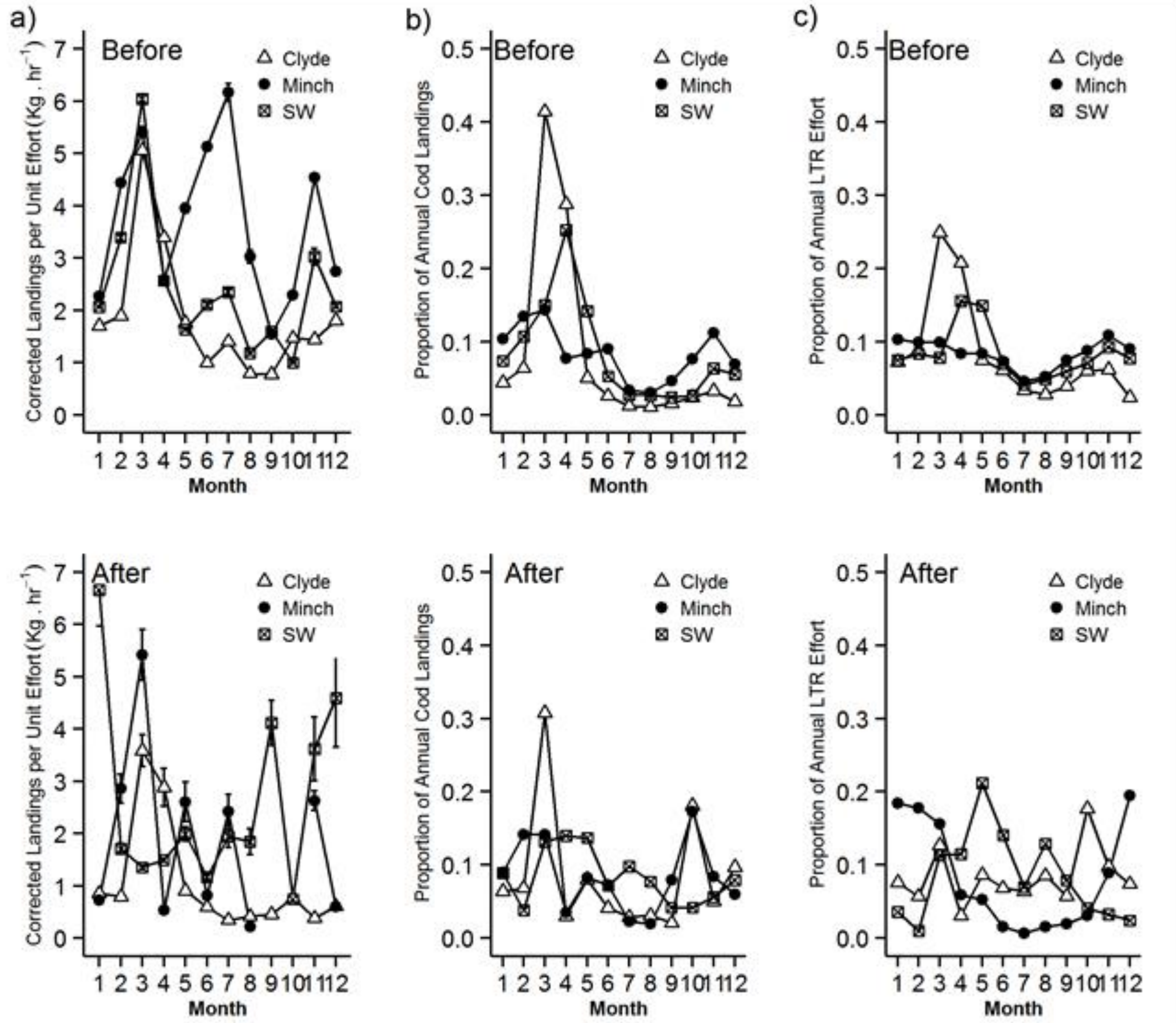

Figure 3-2 Solid lines show corrected landings per unit effort (CLPUE) (kg.h-1) for each location for each month during the “Before” time period (upper graph) and “After” (lower graph) for all vessel types. The dashed lines show the proportion of effort for each area, for each month for all gear types during the “Before” time period (upper graph) and “After” (lower graph).

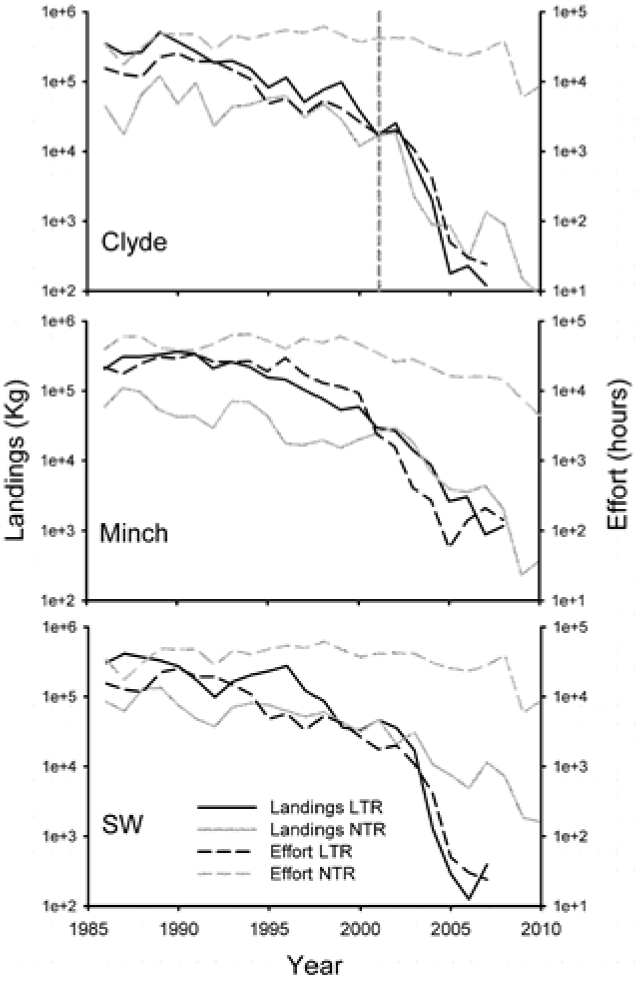

Figure 3-3 Solid lines indicates the sum landings of cod in kilograms and the dashed lines indicate the sum of the effort in number of hours fished for each location for each year. Black lines are the sum total for Light Otter Trawls (LTR) and the grey lines are the sum total for Nephrops Trawls (NTR). Vertical dashed line in the Clyde graph indicates the in the Clyde graph indicates the year the area closure was implemented

3.4.2 Changes in CPUE and SSB from scientific trawl

Model selection for estimating changes in CPUE and SSB did not support the three-way interaction term between year, time and sub-population. The absence of evidence supporting a three-way interaction indicates that there was no effect of the Clyde closure on CPUE or SSB. The model of best fit (Equation 3) for both CPUE and SSB supported interactions between time period and year, and sub-population and year (CPUE in Table 3-2 and SSB in Table 3-3). For the “Before” time period the gradient of the slope for CPUE (Figure 3-4) and SSB (Figure 3-5) was negative for all areas. For the “After” period the gradient of the slope was more negative, but the degree of decline was equal for each area, indicating no effect of the Clyde area closure.

$$Log(Response) = \beta 0 + \beta 1,s + \beta 2,p + \beta 3,y + \beta 4,py + \beta 5,sy \qquad (3)$$

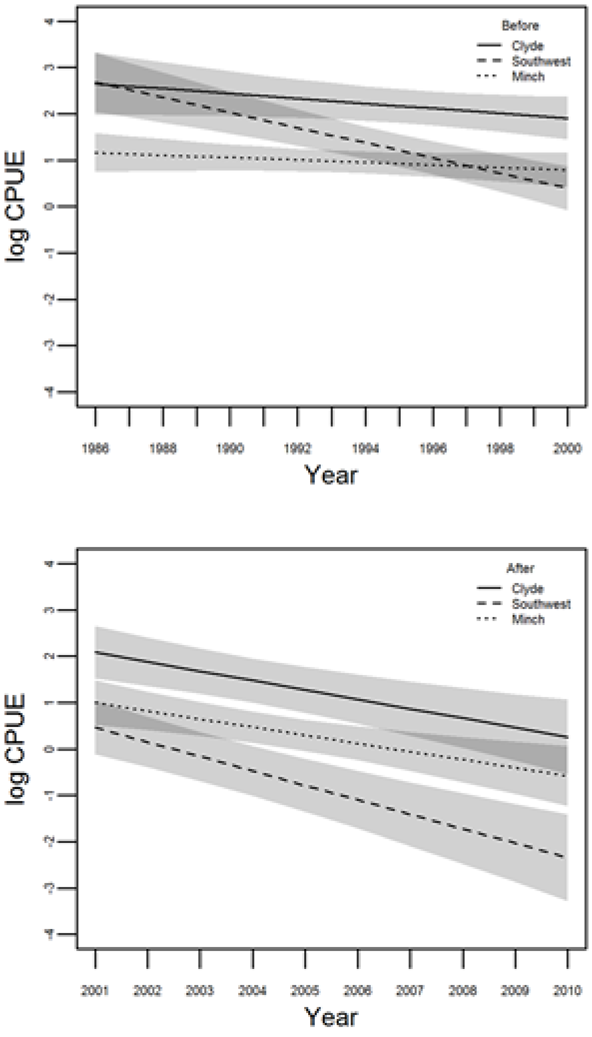

Figure 3-4 Fitted values taken from the model of best fit of the logarithm Catch per unit Effort (CPUE) for scientific trawls versus year for each sub-population with 95% confidence intervals shaded in grey. The upper figure is for the “Before” time period and the lower figure is for the “After” time period

Table 3-2 Output from the model of best fit for the response variable CPUE. Fixed effects show treatment contrast coefficients and diagnostics (z- and p-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference levels for each term are: Time, After and Sub-population, Clyde.

CPUE	Estimate	Standard Error	z value	p value
(Intercept)	2.085	0.289	7.222	<0.001
Time(Before)	-0.233	0.304	-0.765	0.444
Sub-population(Minch)	-0.202	0.054	-3.761	<0.001
Sub-population(SW)	-1.086	0.220	-4.929	<0.001
Year	-1.618	0.278	-5.81	<0.001
Time(Before) : Year	0.149	0.055	2.711	0.007
Year : Sub-population(Minch)	0.027	0.028	0.943	0.346
Year : Sub-population(SW)	-0.110	0.035	-3.098	0.002

Table 3-3 Output from the model of best fit for the response variable SSB. Fixed effects show treatment contrast coefficients and diagnostics (z- and p-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference levels for each term are: Time, After and Sub-population, Clyde

SSB	Estimate	Standard Error	z value	p value
(Intercept)	2.855	0.352	8.115	<0.001
Time(Before)	-0.582	0.367	-1.584	0.113
Sub-population(Minch)	-0.267	0.063	-4.229	< 0.001
Sub-population(SW)	-0.667	0.270	-2.471	0.013
Year	-1.697	0.335	-5.069	<0.001
Time(Before) : Year	0.180	0.064	2.832	0.004
Year : Sub-population(Minch)	0.066	0.035	1.884	0.060
Year : Sub-population(SW)	-0.165	0.044	-3.75	<0.001

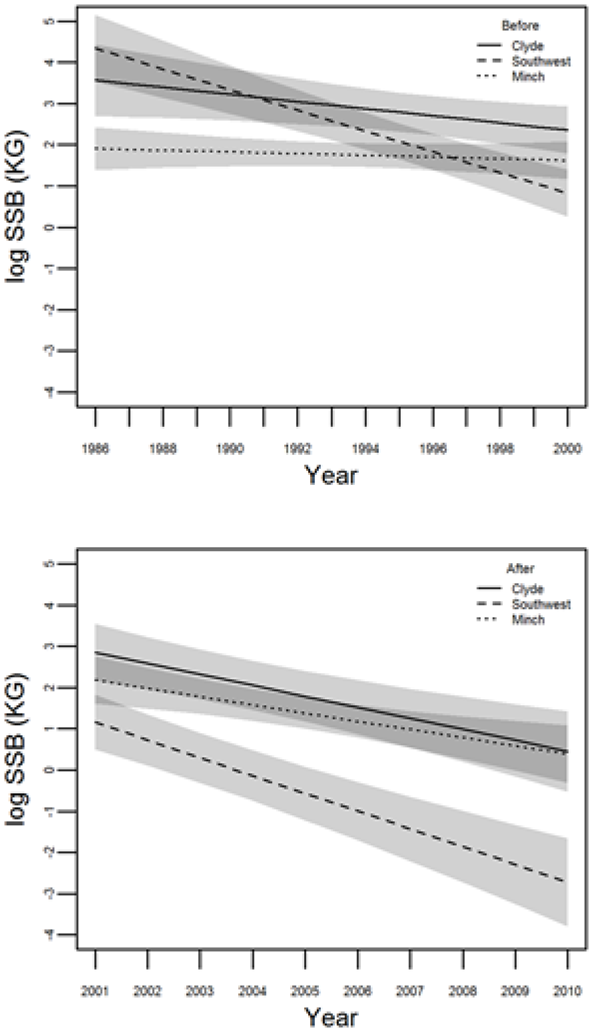

Figure 3-5 Fitted values taken from the model of best fit of the logarithm of Spawning Stock Biomass (SSB) versus year for each sub-population with 95% confidence intervals shaded in grey. The upper figure is for the "Before" time period and the lower figure is for the "After" time period.

3.4.3 Changes in length composition and total mortality

There was no significant change in length structure in any of the three sub-populations before and after the closure (Kolmogorov-Smirnov test, $p > 0.1$). In the Clyde population the most frequently caught length classes were 15-20 cm and 45-50 cm before and after the closure. The population did show signs of size truncation with no fish greater than 70 cm caught after 2001, whereas prior to 2001 cod up to the size of 100 cm were caught (Figure 3-6). Both the Minch and SW sub-populations also showed signs of size truncation and the most frequently caught size classes can be seen in Figure 3-6.

Model selection for the estimation of total mortality did not support the three-way interaction between sub-population, time and length. The model of best fit included the slope intercept random effect and both of the two way interactions between sub-population and period, and sub-population and length (Equation 4). Hence whilst there were different gradients for the slope for each sub-population, the gradient did not differ between the “Before” and “After” periods. This suggests that total mortality is different for each sub-population but that this did not change between the “Before” and “After” time period (Table 3-4). The steepest slope, which can be inferred as the highest rate of total mortality was for the Minch, followed by the Clyde and then the SW (Figure 3-7).

$$Z = \beta_0 + \beta_1,s + \beta_2,p + \beta_3,l + \beta_4,sp + \beta_5,sl + b_0 + b_{1,}y + b_{2,}l \qquad (4)$$

Table 3-4 Output from the model of best fit for the response variable estimating mortality (CPUE). Fixed effects show treatment contrast coefficients and diagnostics (t- and p-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level for each term are: Time, After and Sub-population, Clyde

Mortality	Value	Standard Error	t value	p value
(Intercept)	1.243	0.513	2.422	0.016
Length	-0.026	0.009	-3.074	0.002
Sub-population(Minch)	-1.227	0.588	-2.086	0.038
Sub-population(SW)	-2.153	0.615	-3.498	<0.001
Time(Before)	0.095	0.201	0.472	0.641
Length:Sub-population(Minch)	-0.002	0.010	-0.157	0.875
Length:Sub-population(SW)	0.022	0.011	2.032	0.043
Sub-population(Minch):Time(Before)	0.551	0.196	2.808	0.005
Sub-population(SW):Time(Before)	0.361	0.215	1.683	0.093

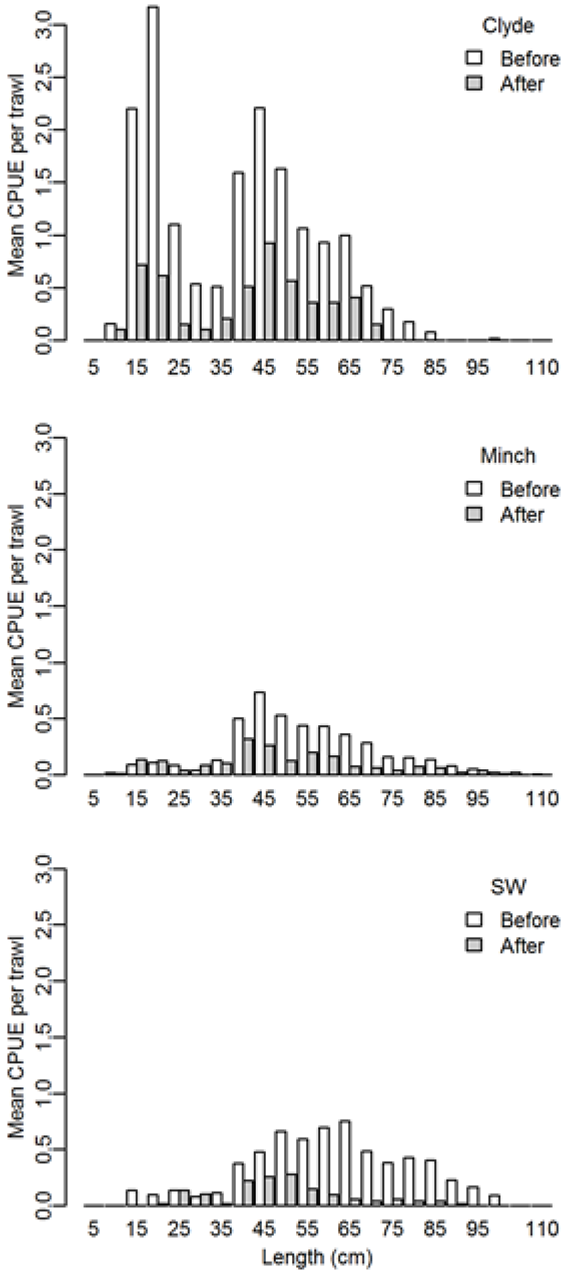

Figure 3-6 Length frequency plots of mean number of cod caught per trawl in 5cm length bins for each sub-population for each time period. The top figure is the Clyde, middle is the Minch and the bottom is the SW.

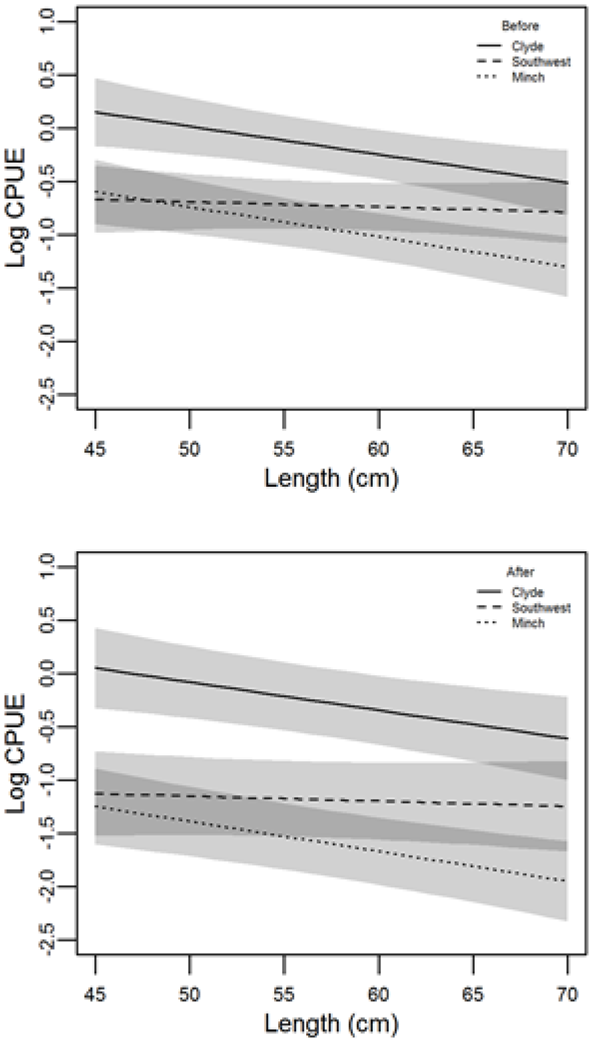

Figure 3-7 Fitted values taken from the model of best fit for the logarithm of Catch per unit effort (CPUE) for each sub-population across length from the time period “Before” (upper figure) and “After” (lower figure).

3.5 Discussion

The Clyde seasonal closure did stop the seasonal build-up of fishing effort on spawning cod and probably prevented a build-up that might have been even more intense given the concurrent displacement of fishing effort from a similar closure in the Irish Sea. Before the closure, there was a clear seasonal peak in effort corresponding to the spawning time of cod in this area (Yoneda and Wright, 2004; Wright *et al.*, 2006a). This peak in effort corresponded with an increase in catchability as evident from the elevated corrected landings per unit effort (CLPUE) during the spawning months of March and April. The closure stopped this seasonal build up in effort, although increased catchability could still be seen from the elevated CLPUE in March and April. Hence even with the marked decline in local population abundance, catch rates remained high consistent with aggregations exhibiting hyperstability (Rose and Kulka, 1999; Erisman *et al.*, 2011). The seasonal trend in monthly CLPUE was consistent with an earlier study by Hislop (1986), which showed a 10-fold increase in LPUE during March and April for the time period 1971-80. Many fishers are known to capitalize on the predictable nature and high catch rate of such spawning aggregations by concentrating their effort on spawning fish (Sadovy and Domeier, 2005; Erisman *et al.*, 2012). Management measures to reduce mortality on cod have often included spawning closures for this very reason. For example, in the Gulf of Maine a series of large “Rolling Closures” were introduced (Armstrong *et al.*, 2013). In the Irish Sea seasonal closures were introduced in 2000 (Kelly *et al.*, 2006) and temporary spawning closures have been applied in the North Sea (Holmes *et al.*, 2011). Consequently, the Clyde spawning closure seemed appropriate and would have been expected to benefit the local population of cod because this area encloses the major spawning component for this region (Wright *et al*., 2006b).

This is the first study that has used a beyond-BACI (Underwood, 1992) approach to compare the trends within a spawning aggregation before and after the introduction of an area closure. In the wider field of fisheries area closures and marine protected areas the beyond-BACI methodology has been identified as the most robust method to monitor the trajectory of populations over time (Sale *et al.*, 2005; Claudet and Guidetti, 2010; Fenberg *et al.*, 2012). In this study spawning areas of three distinct sub-populations were used for the analysis, each of which has a high level of self-recruitment (Wright *et al*., 2006b). Therefore any localised reduction in fishing mortality due to the spawning aggregation area closure would be expected to affect the local sub-population without influencing any of the control sub-populations. Particularly in spawning aggregation studies it is difficult to find representative control populations, which may be why other studies have been unable to take a similar approach to this study.

Despite the potential benefits of a seasonal closure there was no evidence of a local recovery on the Clyde cod sub-population more than a decade after its implementation. We can infer this because the beyond BACI approach (Underwood, 1992) allows us to account for before/after differences in both the area where management was implemented and other control sites that are likely to be exposed to the same natural drivers of change. There was a greater rate of decline in SSB and CPUE for all the three sub-populations after 2001 compared to before, but the change in rate of decline was the same for each of the three sub-populations. This implies that there was no detectable effect of the area closure on the Clyde sub-population of cod. Although spawning area closures have been used for a wide-range of species throughout the world's oceans, there have been few studies that have attempted to evaluate the effectiveness of this measure (see Van Overzee and Rinsdorp, 2015). Those empirical studies that have looked at the effects of spawning aggregation closures are mostly descriptive, comparing changes in length composition, sex ratios, abundance and biomass, but generally lack baseline and/or temporal data (Beets and Friedlander, 1998; Murawski *et al.*, 2000; Rhodes and Sadovy, 2002; Pet *et al.*, 2005; Heppell *et al.*, 2012).

Theoretical studies have suggested that a combination of spawning aggregation reserves and reduced fishing effort are required to maintain or promote the recovery of fish populations (Heppell *et al.*, 2006; Ellis and Powers, 2012), whilst others have suggested that the use of spawning aggregation closures over normal residence closures is dependent on the catchability during the spawning period (Grüss *et al.*, 2013; Grüss and Robinson, 2015). Model simulations show that redistribution of effort, particularly when it exceeds that which occurred prior to a closure, can negate any benefit of a spawning closure (Heppell *et al.*, 2006; Grüss *et al.*, 2013; Grüss and Robinson, 2015). However, for a highly exploited population where a seasonal closure removes a large proportion of fishing effort that targets spawners without redistribution of this effort this would be predicted to benefit population growth (Grüss *et al.*, 2013, 2014; Grüss and Robinson, 2015). This was expected to be the case for the Clyde spawning area closure where fishing effort was reduced and not redistributed, at least for the main gear targeting cod. Landings have similarly declined in all three sub-population areas although by 2006 estimated discards did exceed landings across the entire west of Scotland stock region (ICES, 2013).

As cod in the Clyde are largely self-recruiting (Wright *et al*., 2006b), recovery depends on the intrinsic population growth rate of this sub-population. Without any fishing mortality the median population growth rate of cod from the Scottish west coast has been estimated to be 26% per year (Wright, 2014). Based on such a rate of population growth and in the absence of density dependent recruitment or fishing mortality, the local sub-population may have been expected to recover to near 1980s levels within 10 years of closure. It would be expected that such a fast recovery rate would be evident well within the study period based on estimates of the power to detect changes in cod abundance from surveys (Maxwell and Jennings, 2005). The lack of recovery in the Clyde sub-population after the introduction of the area closure may therefore indicate a number of possibilities such as sustained fishing mortality, increasing natural mortality, reproductive failure and/or low recruitment.

Total mortality or length composition did not change in the Clyde after the area closure was introduced, although there was evidence of size truncation. Reductions in mortality would have been expected to lead to a recovery in the length composition, such as in the study by Beets and Friedlander (1998) who found a recovery of length composition of the grouper, *Epinephelus guttatus*, after the introduction of a seasonal spawning area closure. Cod are vulnerable to fishing gears outside of the seasonal area closure and as there was not a substantial change in effort and landings by light otter trawls (Figures B1 and B3) immediately associated with the Clyde closure and effort for the Nephrops trawls remained steady until 2009 (Figure B2), fishing mortality may not have been significantly reduced by this measure. Catchability remained high during the spawning period after the closure had been introduced, so it is likely that cod migrating to spawning sites still appeared particularly vulnerable. Whilst the demersal fishery ceased in the Clyde during the early 2000s there were still landings coming from the *Nephrops* trawl fishery, which has a derogation to fish all year in most of the closed area. Cod landings from the *Nephrops* fishery peaked in March and April both before and after the closed area was introduced indicating that some fishing induced mortality on spawning cod continued. Similarly reduced but continued fishing within a closure was not associated with any change in length composition or trend in abundance in an area closure designed to protect groupers (*Epinephelus fuscoguttatus* and *Plectropomus areolatus*) whilst aggregating to spawn in Komodo National Park, Eastern Indonesia (Pet *et al*., 2005).

Across the Scottish west coast cod catches were less than a tenth of the peak by 2000 and SSB was below Blim (ICES 2013). As there is strong evidence that cod at low SSB can be subject to depensation, i.e. the Allee effect (Keith and Hutchings, 2012) the apparent ineffectiveness of the closure may reflect the poor state of the Clyde sub-population by the time this measure was implemented. Several mechanisms have been hypothesized as to how the Allee effect impacts marine fishes such as altered food-web dynamics (“cultivation-depensation”) (Walters and Kitchell, 2001); increased predator mortality (Kuparinen and Hutchings, 2014) and reduced mating success (Rowe et al., 2004).

It is possible that the change in the Clyde fish community from highly diverse to one dominated by whiting (*Merlangius merlangus*) could have increased the natural mortality of an already depleted population of cod. Since 1995, whiting, a piscivorous gadoid, has dominated the biomass of fish within the Clyde (Heath and Speirs, 2012). Young of the year whiting have been shown to compete with other gadoids for food and through predation on smaller size classes (Bromley *et al.*, 1997) and adult whiting have also been shown to be a voracious predator of juvenile cod (Temming *et al.*, 2007). Hence a key predator and competitor of young cod may have impeded the recovery of cod. A recent study has also suggested that another key predator of cod, Grey seals (*Halichoerus grypus*) could be a contributing factor to the lack of recovery of cod off the west coast of Scotland (Cook *et al.*, 2015), although the population of this predator is relatively low in the Clyde.

Disturbance from fishing can change the behaviour of spawning fish compromising reproduction (Morgan *et al.,* 1997; Dean *et al.,* 2012). The reduction in targeted fishing on spawning cod is likely to have reduced the overall level of disturbance on the Clyde cod sub-population. However, whilst cod are unlikely to be spawning on the grounds targeted by *Nephrops* trawl fishing, as spawning cod tend to avoid mud (González-Irusta & Wright, in review), it is possible that shoals moving to those spawning sites could have continued to be disturbed. Recruitment success may have also decreased in Clyde cod as a result of poor environmental conditions and the combined effect of truncated size structure of the spawning stock (Stige *et al.*, 2006). A positive correlation between spawner mean age and offspring survival was found in the Irish Sea and North Sea cod (Wright, 2014). Possible reasons for an effect of spawner age on reproductive success include maternal effects on larval viability (Marteinsdottir and Steinarsson, 1998) and/or the potential for a mismatch between spawning and optimal conditions for larval survival (Wright and Trippel, 2009), as there are age related differences in the onset of cod spawning (Morgan *et al.*, 2013). The GOIS (Goals, Objectives, Indices and Success Criteria) approach has been used to provide a framework for objective setting, planning, and governance of closed areas (Rice *et al.*, 2012).

The goal of the Clyde closure was to protect adult cod during the spawning period, but no explicit objectives or indices of success were defined at the time of the closure. STECF (2007) suggested that the criteria to indicate that the Clyde closure had been a success was the extent of reduction in fishing mortality on mature cod and a local increase in SSB. Based on these criteria the closure has not been a success. Even though there has been no sign of recovery of cod in the Clyde, the rationale for an area closure to protect spawning cod appears justified on the basis that it did reduce targeted fishing effort on spawning cod and prevented additional fishing effort displaced from the Irish Sea Closure. Considering the state of the already severely depleted population when the closure was introduced, it could be argued that a) the area closure was implemented too late, b) the closure alone was not sufficient and c) that it did not go far enough to protect spawning cod. We cannot change the past but we can address the future by managing populations within an ecosystem context, like that being discussed through the Clyde 2020 project (The Scottish Government, 2014). Spawning area closures alone are not enough to manage populations when numbers are too low to withstand environmental fluctuations and additional sources of mortality. Other measures will be required to protect all life stages and prevent unintentional sources of fishing mortality. However, the current Clyde spawning area closure permits disturbance of aggregations with derogations allowing the continued use of some types of fishing gear with the possibility of incidental bycatch of spawning cod. Hence, whilst it is unclear what combination of factors are preventing the recovery of the local cod population, at the very least what can be done is to allow those remaining to spawn undisturbed to improve the chances of successful reproduction.

Chapter 4: Drawing a line under deep-sea fishing: A scientific basis for regulation by depth[2]

4.1 Abstract

The deep-sea is the world's largest ecosystem, with high levels of biodiversity, with many species that exhibit life history characteristics that make them vulnerable to high levels of exploitation. Many fisheries in the deep-sea have a track record of being unsustainable. In the north-east Atlantic there has been a decline in abundance of commercial fish species since deep-sea fishing commenced in the 1970s. Current management is by effort restrictions and Total Allowable Catch (TAC) but there remain problems with compliance and high levels of bycatch of vulnerable species such as sharks. The European Union are currently considering new legislation to manage deep-sea fisheries, including limiting bottom trawling by depth. However, to date there is little evidence to suggest an appropriate depth limit. Here we use survey data to show that biodiversity of the demersal fish community, the ratio of non-commercial to commercial biomass, and the ratio of Elasmobranchii (sharks and rays) to commercial biomass significantly increases between 600 and 800 m depth whilst commercial value decreases. These results suggest that limiting bottom trawling to a maximum depth of 600m could be an effective management strategy that would fit the needs of European legislations such as the Common Fisheries Policy (EC No 1380/2013) and the Marine Strategy Framework Directive (2008/56/EC).

4.2 Introduction

There has been a recent global debate as to whether there is a depth beyond which fisheries cannot be expected to operate in an economically and ecologically sustainable way. Stopping deep-sea fishing in the high seas (the areas beyond national jurisdiction) has been suggested to be more "equitable, and environmentally and economically sensible" (Sumaila *et al.*, 2015). In European deep-seas another report suggested that "sustainable levels of exploitation are probably too low to support an economically viable fishery" (The European Commission, 2012). On the other hand deep-water fisheries can provide

---

[2] Clarke, J., Milligan, R. J., Bailey, D. M., and Neat, F. C. 2015. A Scientific Basis for Regulating Deep-Sea Fishing by Depth. Current Biology, 25: 2425–2429.

regional socioeconomic benefits, most notably in remote areas. In the northeast Atlantic, the major fishing area for deep-water bottom trawl fisheries lies west of Scotland and Ireland out to the Rockall and Hatton Banks (ICES, 2014). Deep-water fish stocks were first exploited in this area in the early 1970s but the fishery only became regulated in 2003 after it was recognised that most target species were being exploited outside of safe biological limits (Large *et al.*, 2003). The introduced management measures included setting Total Allowable Catch (TAC) limits for listed commercial species, effort restrictions on days at sea, and required vessels to hold fishing licences. Despite this there have been difficulties: TACs were often not complied with (Villasante *et al.*, 2012) and high proportions of catches were being discarded (Allain *et al.*, 2003). Of particular concern were species with low-productivity, such as deep-sea sharks and rays (Elasmobranchii), some of which were estimated to have declined by up to 90 % (WGEF, 2010). In addition, incomplete information on fishing effort, landings and discards due to under-reporting (The European Commission, 2007) and limited scientific surveys (Large *et al.*, 2013a) generates much uncertainty in the scientific advice for management. With EU regulations such as the Common Fisheries Policy (CFP; EC No 1380/2013) and Marine Strategy Framework Directive (MSFD; 2008/56/EC) now requiring the implementation of an ecosystem approach to marine management, the question has been raised as to whether a better management strategy would be to impose a maximum fishing depth limit. Such a limit might reflect the depth at which the commercial benefits derived from fishing start to be outweighed by potentially negative consequences for sustainable management, ecosystem health and the preservation of biodiversity.

In this study we examined the trends of catch composition indices taken from scientific trawls with depth to determine if any consistent patterns could be found. The data were collected from trawl surveys between the depths of 240 and 1500 m in the north-east Atlantic (Figure 3-1). Surveys used different gear types, at different locations and spanned different periods of time between 1978 and 2013 (for details see Supplementary Information). The indices calculated from the trawl data were: a) Simpson’s diversity index; b) the ratio of “discarded” to commercially valuable biomass; c) the ratio of Elasmobranchii to commercially-valuable biomass; and d) the value per km^2 of each trawl in Euros. Generalized additive mixed models (GAMMs) were used to determine the relationship between each index and depth, with depth included as a smoother term. As the surveys were conducted in different locations and with four different gear types, “survey” was included as a random effect. The first derivatives of the modelled trends were then calculated to identify depth ranges where the rate of change of the smoother was significantly different to zero.

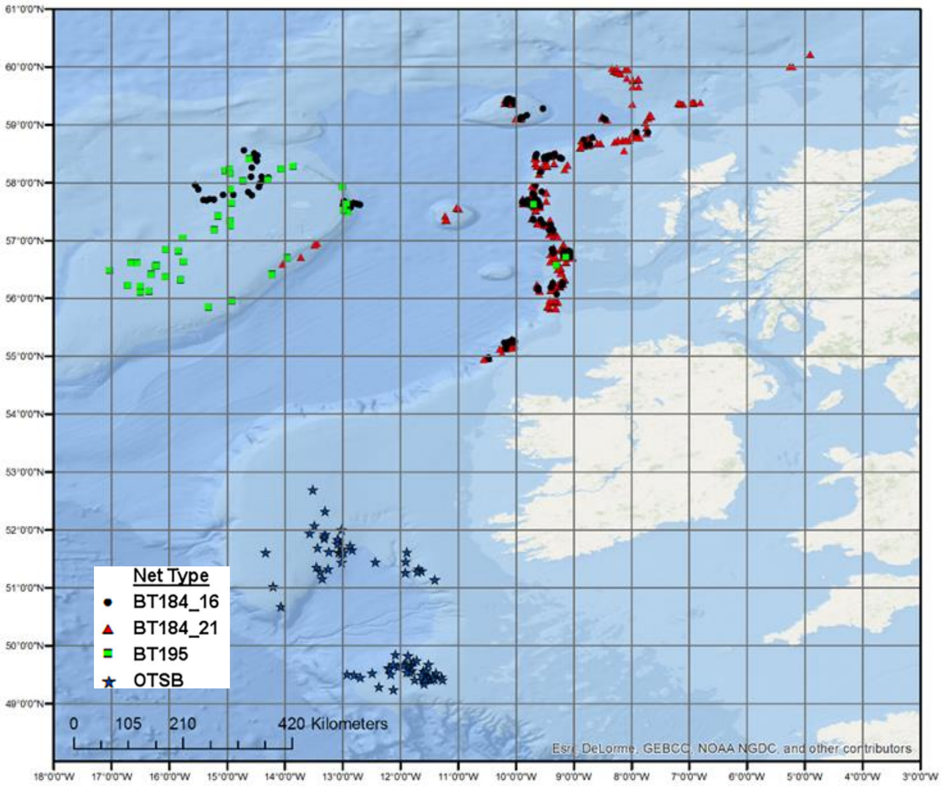

Figure 4-1 Map of the west coast of the UK and Ireland. Different coloured symbols indicate locations of trawls conducted by each gear type.

4.3 Methods

Details on each of the four survey methodologies can be found in the references provided in Table C1 in the appendix. For all surveys all fish were identified to species level wherever possible. Using the Fishbase (Froese and Pauly, 2014) database all species were classified as demersal or bathypelagic. Only demersal species were used in the analysis. Individual lengths were measured to the closest 1.0 or 0.5 cm accuracy. For the Outer Hebrides surveys the total weight of each species for each catch was recorded to within 0.1 kg and subsamples of individuals were weighed to an accuracy of one gram. For the Porcupine Seabight surveys, no weights were obtained in the earlier surveys (1979-1989) while in the later period (1997-2002) surveys all animals were wet weighed to a precision of 1.0 g (Godbold *et al.*, 2013). Length-weight relationships were calculated by fitting a linear model to the logarithm (base 10) of length and weight for each species separately from the West coast of Scotland and the West coast of Ireland surveys. Using the output from these models the weights for all other individual fish were calculated from their known length. Simpson's diversity metric ($1-\lambda'$) was calculated for each trawl and used in the analysis (Simpson, 1949).

Data on the value of each fish species landed in the UK, Ireland, France and Spain were aggregated from the EuroStat website (The European Commission, 2015). The value for each species in Euros per tonne was taken as an average value for the four countries UK, Ireland, France and Spain, taken over a ten year period between 2003 and 2012. If a fish species was landed and identified as having a value it was classed as being commercial (see Table C3 in the appendix). All species not found to have an attached value were deemed non-commercial or "discarded". An exception was made for the species *Alepocephalus bairdii* which although landed in some parts of the Atlantic is discarded by the main fisheries operating in the Rockall Trough area (Allain *et al.*, 2003). Elasmobranchii were all classed as non-commercial as these fisheries have been closed since 2010. Due to the known vulnerability of Elasmobranchii to exploitation we assessed changes in the ratio of their biomass to commercial biomass with depth.

The weights of all demersal fish species were aggregated to give a total biomass per trawl. Then the weight for all commercial species, non-commercial species and Elasmobranchii were aggregated per trawl. The following metrics were calculated: the ratio of discarded to commercially-valuable fish biomass, the ratio of Elasmobranchii to commercially-valuable fish biomass and the value of commercially-valuable fish biomass per km^2. Very few Elasmobranchii were caught in the Porcupine Seabight trawls, so these were excluded from the analysis. It should be noted that most of the data used in this study were collected after deep-sea fisheries had commenced and therefore does not reflect a pristine ecosystem, abundances and biomass have been depleted (Bailey *et al.*, 2009). Therefore indices used are representative of the current state of the ecosystem and could change in the future.

Generalized Additive Mixed Models (GAMMs) were used to model the relationship between the selected metrics and depth, with depth included as a smooth term (Equation 1). As trawls were conducted in different locations and with four different gear types, "Survey" was included as a random effect.

$Y_i = \beta_0 + f_1(\text{depth}_\text{i}) + \varepsilon_\text{i}, + a_i$; $\varepsilon = N(0, \sigma^2)$; $a_i = N(0, \sigma_\text{a}^2)$ Equation 1

Where: Y_i = the response variable (the individual catch metrics), depth_i = depth in metres (200m to 1500m). β_0 = a constant term and ε_i = model's residuals. All catch metrics were modelled using the Gaussian distribution with an identity link function. Model validation was carried out by visually examining plots of the normalized residuals versus the fitted values from each of the models. Any models that violated assumptions of homogeneity of variance were refitted with different variance structures using the "VarFunc" command. Model selection was conducted using Akaike's Information Criterion (AIC) (Table C2 in the appendix). The depth smoother and number of degrees of freedom was calculated during model fitting using penalised splines and generalised cross validation (GCV). This was conducted using the "gamm" function from the Mixed GAM Computation Vehicle (mgcv) package (Wood, 2013) in R statistical software (R Core Development Team, 2015). Penalised splines using GCV allowed for model selection to be selected back to a single degree of freedom equalling a linear trend if that was determined to be the best fit.

To interpret the fitted trends and identify if there were any depth ranges which showed significant rates of change, first derivatives were calculated along with 95% simultaneous confidence intervals. When the 95% confidence intervals of the first derivatives do not include zero, this indicates a significant increase or decrease in the rate of change of the response variable. 95% confidence intervals of the first derivative were calculated by estimating the slope of the spline at multiple points, for multiple posterior simulations. This was done for each fitted smoother by estimating the fitted values at 200 equally spaced points. The point was moved by a very small amount (1×10^{-7} m) and again the fitted values of the trend were determined. The difference between the two sets of fitted values was divided by the difference in depth to give a predictor matrix of the slope of the spline at the 200 equally spaced points. This predictor matrix was then multiplied by the coefficients of 10000 random simulations from the posterior distribution of the model. This method of sampling from the posterior distribution producing simultaneous confidence intervals for the entire trend is a more rigorous assessment of uncertainty than using pointwise confidence intervals. From these the 95% confidence interval of the first derivatives was calculated by taking the two extreme quantiles of the distribution.

4.4 Results

Fish biodiversity increased between depths of 400-1000m (Figure 4-2a) suggesting that the deeper that trawls are deployed the greater the potential impact on biodiversity. Based on estimates of depth distribution for each species, Table 4-1 shows that approximately 18 additional species are encountered for every 100 m increment in depth. Over the range of 600-800 m, the proportion of discarded non-target species (Figure 4-2b) increased. The ratio of “discard” to commercially-valuable biomass significantly increased with depth from 1:1 at c. 600-800 m to a peak of 1.6:1 at c. 1300 m (Figure 4-2b). The commercial value per unit effort significantly decreased between depths of 400-500m indicating decreasing returns per unit effort of fishing over this depth range. The value per trawl then remained constant between 900 m before rising again at c. 1300 m (Figure 4-2d) reflecting the dominance of the commercial species (*Coryphaenoides rupestris*) at these depths (Neat and Burns, 2010). Over the range of 600-800 m, the ratio of Elasmobranchii biomass to commercial biomass significantly increased with depth (Figure 4-2c) eventually peaking at 1300m

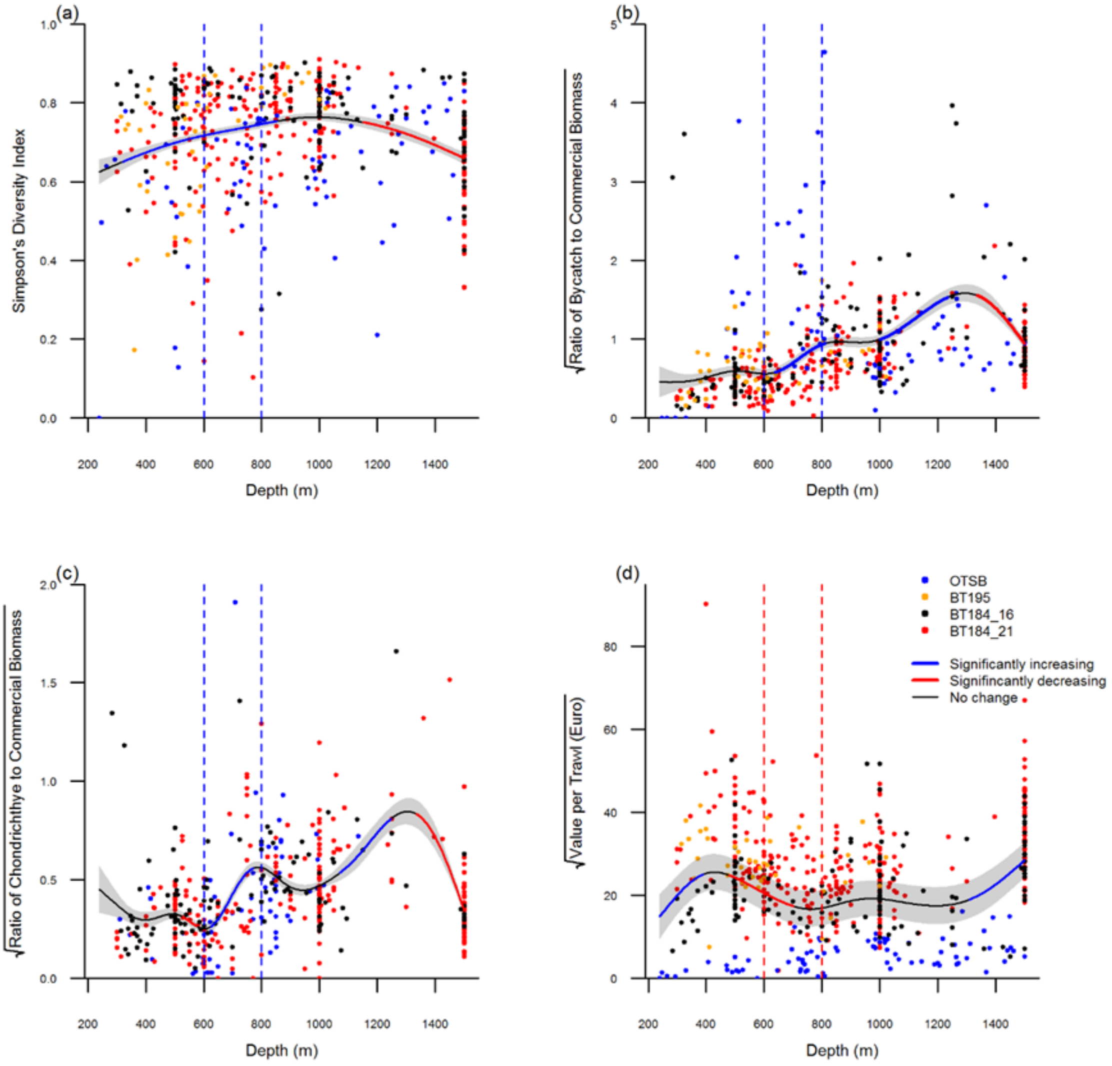

Figure 4-2 a) Simpson’s diversity; b) Square root of the ratio of non-commercial to commercial biomass; c) Square root of the ratio of chondrichthye to commercial biomass; d) Square root of the value of each trawl in Euros. Each response variable is fitted with a general additive mixed effect model versus depth. The fitted line is black with 95% confidence intervals shaded in grey. First derivatives were calculated and significant increases are coloured blue and significant decreases are coloured red. Each point is a trawl and the different gear types are coloured differently: blue is OTSB; orange is BT195; black is BT184_16; red is BT184_21.

The number of demersal fish species whose minimum depth of occurrence fell within the stated depth ranges. These are the numbers of fish species that would no longer fall within the trawled area if this type of fishing was restricted to shallower depths. E.g. a trawl depth limit of 600 m would be expected to remove all 25-77 species whose minimum depths of occurrence fall between 600 and 1500 m from the range of trawling.

Table 4-1 The first column indicates the total number of demersal fish species that were caught within the depth range of the study. The second column indicates the number of species whose minimum depth of occurrence fall within 600 to 1500 m and would therefore be out of range of fishers if no fishing occurs deeper than 600m. The third column indicates the number of species whose minimum depth is 800 m.

	200- 1500 m	600- 1500 m	800-1500 m
DWTS	175	77	41
Monkfish Survey	65	25	11
Rockall	84	54	39
PSB	78	48	34
Average	100	51	31

4.5 Discussion

The increase of biodiversity to 100m and the increase in number of species encountered with every 100 m depth increment is clearly relevant to the EC's Marine Strategy Framework Directive that requires fishing activity to be managed to meet conservation objectives, one of which is "the maintenance of biodiversity". Even though a recent study in the north-east Atlantic suggested that there has been no detectable impact of deep-sea fishing on fish diversity (Campbell *et al.*, 2010), there have been significant declines in abundances of some commercially-important species (Devine *et al.*, 2006; Bailey *et al.*, 2009) leading to commercial extinction in some cases (Dransfeld *et al.*, 2013). When interpreting the lack of effect of deep-sea fishing on biodiversity (Bailey *et al.*, 2009; Campbell *et al.*, 2010; Godbold *et al.*, 2013), caution should be taken as it may take a longer time period (decades) for the effects of fishing to become fully apparent.

The high proportion of "discard" biomass caught by all net types in this study corroborates with other studies where scientific observers on commercial fishing vessels recorded discard biomass was almost equal to landings biomass, and discard rates increased with depth (Allain *et al.*, 2003). In these studies the increase in discard rate with increasing depth was driven by a change in the length-frequency distribution of the commercial catch, as smaller commercial fish were caught and subsequently discarded (Lorance *et al.*, 2008). There is no legal minimum landing size for any deep-sea commercial species, but for economic reasons small individuals of commercial species are discarded to maximise the total value of the landings (high-grading). Within the present study, commercial fish of all sizes were classed as "commercial biomass" and our estimates of commercial biomass in this study are therefore likely to be conservative as in reality the landed biomass of commercially valuable fish would be lower. Three of the 4 trawl nets (OTSB, BT184_16, BT184_21) used in this analysis were scientific nets, with a smaller mesh size and smaller width than commercial nets raising the issue of how representative these results are of commercial fishing operations. However, the fourth net used was a commercial fishing gear and the catch ratios derived from the scientific nets were similar (Figure 4-2) suggesting this potential issue is not of major concern.

The conservation of the deep-sea sharks taken as bycatch is a specific management concern of deep-water fisheries and these results suggest that there is an increase in ratio of Elasmobranchii biomass to commercial biomass caught with increasing depth. Deep-sea species of sharks are extremely vulnerable to exploitation (Norse *et al.*, 2012), and have been documented to typically exhibit more "K-dominated" life history traits with increasing depth (Rigby and Simpfendorfer, 2015). Surveys conducted in the late 1990's showed that catch rates of Elasmobranchii had decreased by an order of magnitude since the start of the fishery to the west of Scotland (Jones *et al.*, 2005). A zero TAC was introduced for sharks in 2010 (ICES, 2014), but that does not prevent them getting caught as bycatch in a mixed fishery (Connolly and Kelly, 1996). Overall these results highlight a rise in the ecological impacts of bottom trawling and reduced commercial gain per unit effort at depths greater than 600 m until c. 1300 m.

4.6 Conclusions

In the EU attempts have been made to overcome the problems of discards and reduce the exposure of vulnerable fish and habitats to deep-sea fisheries. However, while the introduction of management measures for deep-sea fish stocks may have prevented further stock declines, they have not allowed for recovery (Neat and Burns, 2010). New measures to protect deep-water ecosystems from fishing are currently being considered by the EU. One of the most controversial proposals calls for a ban on trawling at depths greater than 600 m. The present study suggests that fishing deeper than 600 m results in decreasing economic gains per unit effort at increasing detriment to the ecosystem. Prohibition of trawling at depths > 600 m may therefore help meet the criteria of multiple European legislations. These include achieving Good Environmental Status (GES) for three descriptors (biological diversity, marine food webs and sea-floor integrity) required under the Marine Strategy Framework Directive and the implementation of an ecosystem approach to fisheries management under the Common Fisheries Policy. Progress has been made in the management of our shelf seas in the north-east Atlantic, resulting in the majority of fish stocks now providing a sustainable and secure food source (Fernandes and Cook, 2013). In order to achieve a similar status for Europe’s deep-sea fish stocks, a restriction of bottom-trawling to less than 600m could be a solution that now has a stronger scientific basis. While the depth ranges identified in this study as being indicative of an appropriate depth limit to trawling may be particular to the NE Atlantic, the methodology could be applied globally to generate region specific management advice.

Chapter 5: Discussion

The consideration of the ecosystem within fisheries management is now mainstream throughout the world's oceans and support for its implementation through global declarations is widespread (FAO, 2014). However, progression of its implementation has been a little slower as it has been perceived as something desirable but pragmatically unachievable (Patrick and Link, 2015). These difficulties stem from the idea that the ecosystem is too complex to model and requires copious amounts of data (Hilborn, 2011). It is true that ecosystems are very complex and we do not fully understand all the dynamics and interactions, but we should still continue to account for as much as we can in models and consider the impact of fishing on the wider ecosystem (Dolan *et al.*, 2016). What is required is a basic understanding of which processes are important and a method to integrate these into a model. This can be through the simplification of elements into an indicator. This has been demonstrated in the Northeast Shelf Large Marine Ecosystem (Large *et al.*, 2013; Fay *et al.*, 2013). The effect of fishing pressure will differ between ecosystems, therefore the development of indicators should be specific to the ecosystem and/or community. The primary aim of Chapter 2 was to determine if there was a relationship between fishing intensity and the benthic community of Burrowed Mud, for which there is currently little understanding. The results found that the probability of a burrowing species being present on Burrowed Mud is not affected by trawl intensity within the range examined in this study. This suggests that using them as indicators to determine the effect of trawling on the wider community will not be very effective and it is the mobile species that live on the surface of the seabed that may be the most useful indicator of trawl intensity. In Chapter 3 the effectiveness of a spawning area closure for Atlantic cod was evaluated over a decade after its implementation. Spatial closures are a part of the toolset within the use of EAFM and EBFM, they have been widely used for many year and their applicability are more accepted (Jones, 2008). Their success is rarely evaluated due to the difficulty in collecting long-term data and finding suitable control sites. A component of EAFM is the development of models that recognise multiple factors such as biological, physical, economic and social trade-offs for managing fisheries. This was explored in Chapter 4 where indices of economic and ecological value were assessed against depth with the aim to determine whether there was any rationale for prohibiting fishing beyond a certain depth. The results gained from these studies have added to our wider knowledge on ecological trends in the deep-sea and improved the scientific basis to make informed managerial decisions.

5.1 Justification of methodology and limitations

Sea-pen and burrowing megafaunal communities are a habitat type designated as threatened and in decline in the Northeast Atlantic region by OSPAR and for which Scotland contains a large proportion of the total within EU waters. It has been incorporated into the Scottish ncMPA network, designated as Burrowed Mud but there has been much difficulty in designating areas with any meaningful conservation measures due to conflicting demands for the same habitat by the *Nephrops* fishery. In addition there is a lack of information on the impact of trawling to Burrowed Mud communities. Common sense would suggest that trawling would remove sea pens and affect their distribution. But this was not the case (Greathead *et al*., 2011). Long sea pen has not been influenced and the short sea pen is capable to pull itself into the mud. A recent analysis on the impact of bottom trawling by Rijnsdorp *et al.,*(2016) found that of the three general types of sublittoral soft sediment habitat (Eunis classification A5.1, Sublittoral coarse sediment; A5.2, Sublittoral sand and A5.3, Sublittoral mud) Sublittoral mud was the most negatively affected by trawling. This was due to the high intensity of fishing and large proportions of long-lived taxa.

Monitoring methods are currently being considered for Burrowed Mud to determine the effectiveness of management in relation to recently implemented MPAs and to gain a better understanding of general condition for the reporting of GES under the MSFD. A large proportion of Burrowed Mud is currently assessed but only in relation to the abundance of *N. norvegicus*, which is the second most valuable commercial species in UK waters (£98.2 million in 2014, MMO). The stock is assessed using underwater towed video (UTV) and counting the number and density of burrows of different stocks. It has been suggested that these towed videos could be used to evaluate MPA management effectiveness and GES and videos have been interrogated for presence of sea pens (Greathead *et al.*, 2007) and other burrowing species, notably *Cerianthus lloydi* and *Maxmuelleria lankesteri* (Greathead *et al.*, 2011). The method is still in development and could benefit from a comparative study of the invertebrate megafauna with baited cameras. The results from Chapter 2 suggest that it is the mobile invertebrate megafauna that live on the seabed that are most affected by trawl intensity and the presence of these species is not currently monitored by the UTV survey for *N. norvegicus*. The use of towed video to monitor mobile benthic megafauna may not be the most appropriate method because the disturbance caused by the sled can cause them to move away from the field of view of the camera. Grab samples are also used to estimate abundance of infauna but they are not at a suitable scale for sampling larger invertebrates. This suggests that baited cameras may be the most appropriate method for monitoring the benthic invertebrate community of Burrowed Mud. Although this technique would need to be developed and used on a wider scale to validate the results found in this study. If expanded to examine the relationship between community metrics of Burrowed Mud and fishing on a wider scale then the inclusion of spatial variables and examination of Particle Sediment Analysis (PSA) is recommended.

The baited camera systems used in Chapter 2 were stereo-BRUVs, these types of camera systems have becoming more commonly used throughout the world (Watson *et al.*, 2009; Unsworth *et al.*, 2014) since their development in Australia (Watson *et al.*, 2005). The camera systems have typically been used for gaining indices of abundance for fish populations, there are very few studies where they have been used to assess invertebrates (Jamieson *et al.*, 2009; Dunlop *et al.*, 2014). The present study recorded very few species of fish and those recorded were predominantly juvenile (whiting (*Merlangius merlangus*), Pleuronectidae and haddock (*Melanogrammus aeglefinus*). This is likely to be an accurate representation of the density and fish community structure for this region, which is part of ICES subarea VIa and not showing the signs of recovery demonstrated in other areas of the Northeast Atlantic (Fernandes and Cook, 2013). In this study rarely more than one individual of each species of the benthic invertebrate community was recorded within the field of view at any one time, therefore length frequency data could not be collected. Individuals were measured for interest, but could not be presented in a way of any value to be included in this thesis. Although the ability to collect measurement data from stereo-cameras is a very useful tool, acquisition of the data does present some challenges. To be able to measure an object using the cameras, the object must be in the overlapping field of view of both cameras. When the fish are very small or a strong current is present, the fish tend to be in just one field of view swimming into the current, which prevents measurements to be taken. Having now trialed the systems in this environment and understanding the community that is present this could be overcome easily by positioning the cameras closer together to increase the overlap in the field of view of both the cameras. This benefit would have to be weighed against the cost of sampling a smaller area and possibly not recorded some of the burrowing species distributed at low densities.

In Chapter 3 multiple metrics are used to assess the status of Atlantic cod in this study, including SSB, CPUE, mortality and changes to the length frequency distribution before and after the closure was implemented. These metrics were used as they were deemed the most representative of the status of the sub-populations accounting for the scale at which the data were collected. Other studies have investigated the effects of area closures using per-recruit models and spawning-stock-biomass-per-recruit (SSBR) (Grüss *et al.*, 2013). This type of model requires knowledge of total fishing effort and the proportion of the fishing effort directed at the spawning aggregation. The analysis by Gruss *et al*., (2013) was conducted on a subsistence, small-scale fishery whose total fishing effort of 169 boat days per year, 12 occurring during the spawning period. They modelled different scenarios to evaluate which would improve the SSBR and fishery yield. They found that no effect of spawning area closures on SSBR and suggest that reducing overall fishing effort may be more effective. Although the application of the analysis to the Clyde spawning cod would be of interest for future investigation, the analysis will not be so straightforward due to the low resolution that fishing effort and biomass is recorded. Currently data on fishing effort and abundance is collected at the scale of an ICES rectangle, which equates to 1° longitude x 0.5° latitude. With the mandatory requirement in 2012 that all vessels over 12 m must carry VMS, the data collected from these vessels combined with logbook records of landings has allowed for more refined information on what is being caught and where. Unfortunately, the majority of vessels working inshore waters around Scotland are less than 12 m and the information gathered on the spatial distribution of fishing effort for these vessels is still very coarse. However, with regard to the cod spawning area in the Clyde using data at the scale of ICES rectangles, prior to the closure 45% of total annual effort and 70% of annual landings occurred during the two months that cod were spawning and after the introduction of the closure this fishing effort was removed it was expected to benefit population growth. There is still very little data on bycatch and discarding in Scotland, information is collected from a few observers who accompany fishing vessels for a few days per year. The results from this are then extrapolated to represent the rest of the fishery, although this may not represent the true extent of bycatch.

The deep-sea ecosystem off the west coast of Scotland is one of the most studied in time and detail yet there is still a lack of data on some factors with which to construct ecosystem models (Heymans *et al.*, 2011). In particular there is little information on the rate of discarding and there is difficulty in estimating stock biomass, this makes it difficult to conduct EAFM. In addition, it has recently been discovered that there is a continuum of life history characteristics with depth (Drazen and Haedrich, 2012) and therefore species become less resilient to exploitation with increasing depth. This has prompted the question as whether a depth limit to fishing would be a suitable alternative to EAFM and if there is a depth beyond which fisheries cannot be expected to operate sustainably. A recent study conducted an economic analysis of the impact of depth limit at 400 m on the UK fishing fleet, they found that it would affect 40 UK vessels and equate to the loss of 9 jobs (Mangi *et al.*, 2016). The results suggest that a depth limit would be more beneficial to smaller vessels than previously discussed legislation which included the introduction of target and bycatch species permits with limits on vessel numbers. This concurs with the results found in Chapter 4 that indicate the value of the catch decreases with increasing depth. The loss of value in the catch comes with an increase in expense of fishing deeper (requiring longer and stronger wires) and further from shore (greater fuel expense) which is expected not to be compatible with smaller vessels. Although this was not considered in the economic index in Chapter 4 due to the figures not being readily available, it would be an interesting addition to the study to incorporate the cost of fishing deeper. The recent debate surrounding the depth limit to fishing in European waters has highlighted the concerns of the fishery which include the removal of fishing ground of commercial species that are assessed and do not meet the criteria of being classed as deep-sea fish, such as ling (*Molva molva*), conger eel (*Conger conger*) and monkfish (*Lophius piscatorius*). An addition to the analysis in Chapter 4 would be to separate out these species and compare their trends with depth and also the ratio of their biomass to the biomass of non-commercial species versus depth.

5.2 Implications, applications and future investigations

Trialling new methodologies in new habitats can improve our understanding of community structure. Baited cameras are a non-destructive form of sampling therefore could be used within MPAs. The results of Chapter 2 suggest that baited cameras can be a useful tool to monitor the invertebrate megafauna of Burrowed Mud and could be used to detect changes due to fishing intensity. It would be expected that if an area closure was implemented to prevent fishing on Burrowed Mud then over time the benthic invertebrate community would change to have more mobile non-burrowing species present and species richness would increase. The results from this study could feed into the long-term monitoring strategies of the Scottish Government to determine if the conservation objectives of ncMPAs have been met.

The findings of Chapter 3 provide a novel contribution to the knowledge on the implications of seasonal area closures on spawning aggregations. This is a widely used but understudied management measure and will therefore be of interest to academics, policy makers and others working in fisheries conservation and management globally. Most studies in this field have been conducted in tropical waters where fishing pressure is different, typically from subsistence line fisheries not trawlers and use theoretical models. Chapter 3 is the first study to use a beyond-BACI approach to compare temporal trends of biomass and abundance within a spawning aggregation before and after the introduction of a closure, with comparable temporal trends of spawning aggregations without any area-based protective measures. The results are particularly relevant now at a time when stocks of Atlantic cod are recovering due to a combination of reduced fishing pressure and changing climatic conditions, yet the west coast of Scotland stock is not showing the same trends. There was a recent review of the Clyde cod closure by the Scottish Government for which the analysis of Chapter 3 was used to demonstrate the changes that have occurred in the abundance, biomass, mortality and length frequency of the Clyde cod sub-population prior to the closure and after. The evidence was used to determine whether the seasonal closure should continue, it was renewed for the spring of 2016. The methods used in Chapter 3 can be applied to any long term data set that has an understanding of the metapopulation dynamics of the stock.

First derivatives have been used to identify when bird populations have significantly changed over time (Fewster *et al.*, 2000) and also to determine thresholds at which fishing pressure significantly alters the response of ecological indicators (Large *et al.*, 2013). In Chapter 4 they were used in a novel way to look at trends of deep-sea ecological and economic indicators with depth. Similar analyses could be used in other deep-sea ecosystems that have systematically surveyed the benthic community across depth contours to identify depths at which the costs of fishing to the ecosystem outweigh the benefits. There is increasing pressure from policy to provide advice for management based on evidence, therefore the ability to clearly determine thresholds is important. In addition there is also the requirement to translate complex information on ecosystems into appropriate indicators. Advances are being made in the Northeast Shelf Large Marine Ecosystem where they have identified reference levels where environmental forces and fishing pressure result in ecosystem changes (Large *et al.*, 2013) and have used these reference levels to limit catch thresholds in multispecies simulations to examine trade-offs between catch and environmental impacts (Fay *et al.*, 2013). Comparable analyses and examinations could be conducted in the north east Atlantic for the mixed fishery in the North Sea.

5.3 Conclusions

The results of this thesis demonstrate that baited cameras are a useful tool in identifying the pressure state relationship of fishing on demersal fish and invertebrate communities. The development and validation of this technique could allow indicators to be developed for the use in applying EAFM. Applying EAFM and spatial measures should not be considered as a last resort after an ecosystem has been altered or a population has reached the point of near collapse. The spawning closure for the sub-population of Atlantic cod in the Clyde was implemented after the numbers were severely depleted, the observations from this thesis demonstrate that this was too little and too late. Although the biomass of deep-sea elasmobranchs and other commercial deep-sea fish have severely declined and not shown any signs of recovery since the onset of fishing, there is a chance to stop things getting any worse. The EU is currently considering imposing a depth limit to fishing in the deep-sea, conclusions from this thesis have joined a body of literature to provide a stronger scientific basis on which to make the decision. Considering the EAFM has been fundamental in the development of the research within this thesis and the results will provide preliminary evidence to support future policy making decisions.

Appendix A: Chapter 2 model selection and outputs

Table A-1 The Variance Inflation Factors (VIF) for each of the explanatory variables

Explanatory Variable	Variance Inflation Factor (VIF)
Trawl Intensity	1.583269
Depth	1.140324
Distance From Shore	1.653325

Table A-2 Likelihood ratio tests of the full models with and without the inclusion of the third order interaction; Df = degrees of freedom, AIC = Akaike Information Criterion; logLik = log likelihood score of model.

	Model Comparison	Df	AIC	logLik	D	p-value
	a) Species Richness (Mud, n=47)					
1	TI+DI+D	4	197.99	-94.99		
2	TI+DI	3	197.12	-95.56	-1.138	0.286
3	TI	2	195.41	-95.71	-0.287	0.592
4	Null	1	208.23	-103.11	-14.814	<0.001
	b) Merlangius merlangus					
1	TI+DI+D	5	326.87	-158.43		
2	TI+DI	4	325.25	-158.63	0.384	0.536
3	TI	3	328.80	-161.40	5.551	0.018
4	DI 2vs4	3	324.07	-159.03	0.816	0.366
5	Null	1	326.97	-161.48	4.900	0.027
	c) Nephrops					
1	TI+DI+D	4	50.41	-21.21		
2	TI+DI	3	49.62	-21.81	-1.199	0.274
3	TI	2	51.73	-23.86	-4.111	0.043
4	DI 2 vs 4	2	48.44	-22.22	-0.822	0.365
5	Null	1	49.74	-23.87	-3.297	0.069
	d) Munida rugosa					
1	TI*D+TI+D	4	64.93	-28.46		
2	TI+DI	3	63.79	-28.89	-0.862	0.353
3	TI	2	63.58	-29.79	-1.800	0.180
5	Null	1	68.00	-33.00	-6.413	0.011
	e) Goneplax rhomboides					
1	TI+DI+D	4	66.53	-29.27		
2	TI+DI	3	67.15	-30.57	-2.614	0.106

3	TI	2	66.32	-31.16	-1.176	0.278
5	Null	1	65.00	-31.50	-0.68	0.41
f)	*Cancer pagurus*					
1	TI+DI+D	4	46.86	-19.43		
2	TI+DI	3	44.99	-19.49	-0.127	0.722
3	TI	2	52.14	-24.07	-9.153	0.002
4	DI	2	51.63	-23.81	-8.645	0.003
5	Null	1	53.27	-25.13	-11.285	0.004
g)	*Liocarcinus depurator*					
1	TI+DI+D	4	46.23	-19.12		
2	TI+DI	3	48.74	-21.37	-4.506	0.034
3	TI+D	3	44.24	-19.12	-0.003	0.955
4	TI	2	48.50	-22.25	-6.269	0.012
5	D	2	63.02	-29.51	-20.78	<0.001
6	Null	1	65.52	-31.76	-25.28	<0.001
h)	*Lesueuriogobius friesii*					
1	TI+DI+D	4	63.00	-27.50		
2	TI+DI	3	64.05	-29.02	-3.043	0.081
3	TI	2	63.69	-29.84	-1.643	0.200
5	Null	1	62.01	-30.01	-0.321	0.375

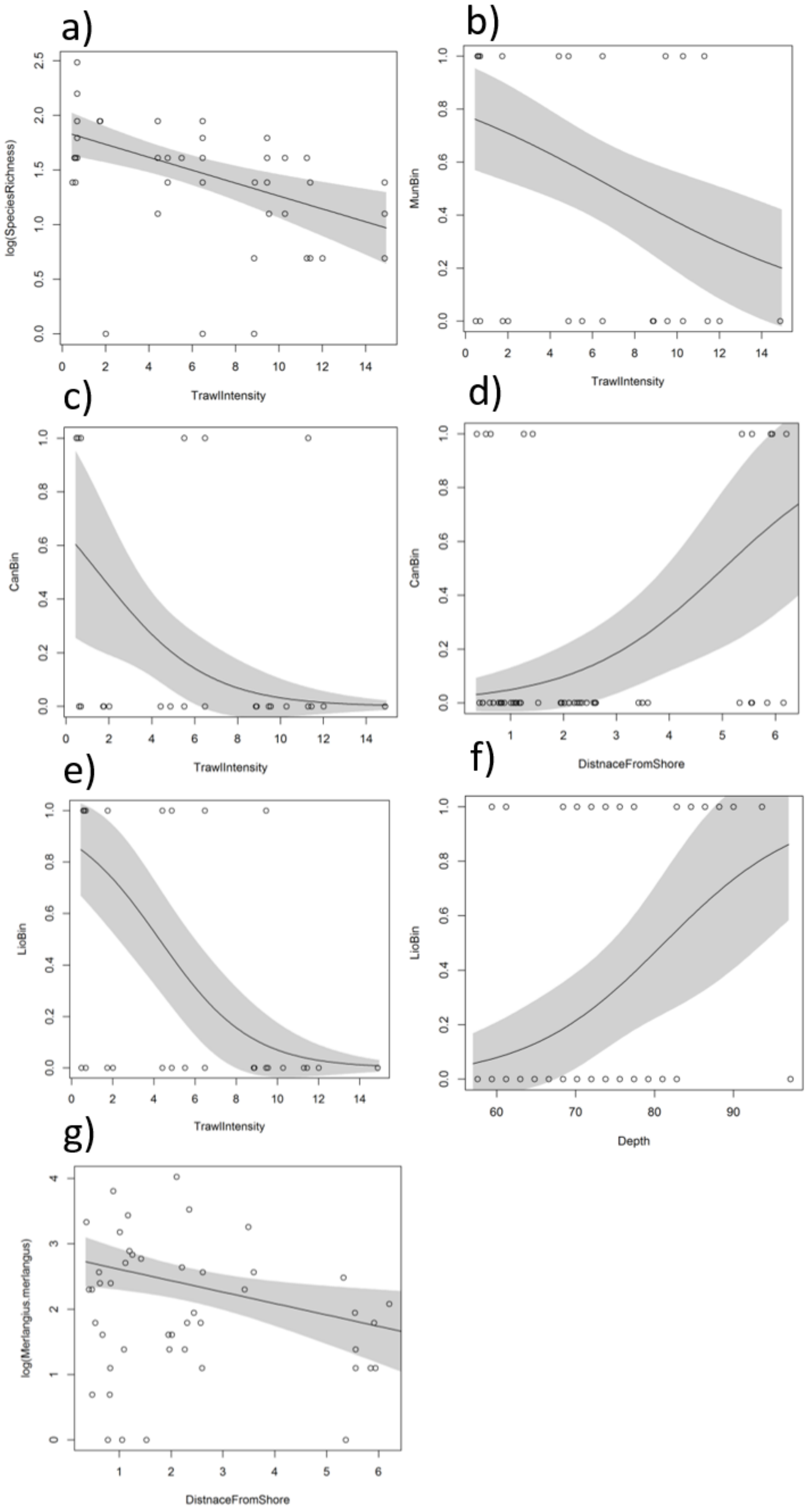

Figure A-1 Fitted values taken from the model of best fit of a) species richness versus trawl intensity; the binomial presence data of b) *Munida rugosa* versus trawl intensity; c) *Cancer pagurus* vesus trawl intensity; d) *Cancer pagurus* versus distance from shore; e) *Liocarcinus depurator* versus trawl intensity; f) *Liocarcinus depurator* versus depth and abundance indices of *Merlangius merlangus* versus distance from shore

.

Appendix B: Chapter 3 model selection and outputs

Table B-1 Likelihood ratio tests of the full models with and without the inclusion of the third order interaction; Df = degrees of freedom, AIC = Akaike Information Criterion; logLik = log likelihood score of model

	Model Comparison	Df	AIC	logLik	Test	Likelihood ratio test p-value
	a) CPUE					
1	3-way interaction	13	1273.094	-623.547		
2	3* 2-way interactions (S:T+S:Y+T:Y)	11	1270.558	-624.279	1 vs 2	0.481
3	2*2-way interaction (S:T+S:Y)	10	1275.359	-627.680	2 vs 3	<0.01
4	2*2-way interaction (S:T+T:Y)	9	1275.803	-628.901	2 vs 4	<0.01
5	2*2-way interaction (S:Y+T:Y)	9	1267.017	-624.509	2 vs 5	0.795
6	1*2way interaction (S:T)	8	1281.251	-632.325	5 vs 6	<0.001
7	1*2way interaction (S:Y)	8	1272.169	-628.055	5 vs 7	<0.01
8	1*2way interaction (Y:T)	7	1283.738	-634.869	5 vs 8	<0.001
9	Null	2	1364.133	-680.066	5 vs 9	<0.001
	b) SSB					
1	3-way interaction	13	1620.484	-797.242		
2	3* 2-way interactions (S:T+S:Y+T:Y)	11	1617.299	-797.650	1 vs 2	0.665
3	2*2-way interaction (S:T+S:Y)	10	1621.998	-800.999	2 vs 3	<0.01
4	2*2-way interaction (S:T+T:Y)	9	1626.546	-804.273	2 vs 4	<0.01
5	2*2-way interaction (S:Y+T:Y)	9	1613.529	-797.764	2 vs 5	0.892
6	1*2way interaction (S:T)	8	1632.897	-808.448	5 vs 6	<0.001
7	1*2way interaction (S:Y)	8	1618.77	-801.385	5 vs 7	<0.01
8	1*2way interaction (Y:T)	7	1648.652	-817.326	5 vs 8	<0.001
9	Null	2	1698.462	-847.231	5 vs 9	<0.001

.

Table B-2 Likelihood ratio tests of the full models with and without the inclusion of the third order interaction; Df = degrees of freedom, AIC = Akaike Information Criterion; logLik = log likelihood score of model.

	Model Comparison	Df	AIC	logLik	Test	Likelihood ratio test p-value
	a) Mortality					
1	3-way interaction	16	695.91	-331.96		
2	3 * 2-way interaction (S:T)+(L:T)+(S:L)	14	694.97	-333.49	1 vs 2	3.061, p= 0.216
3	2 * 2-way interaction (L:S)+(L:T)	13	693.02	-333.51	2 vs 3	0.048, p= 0.827
4	2 * 2-way interaction (L:T)+(T:S)	12	698.91	-337.45	3 vs 4	7.886, p= 0.005
5	2 * 2-way interaction (T:S)+(L:S)	12	697.15	-336.57		
6	Null model	5	799.21	-394.60	5 vs 6	116.059, p <.0001

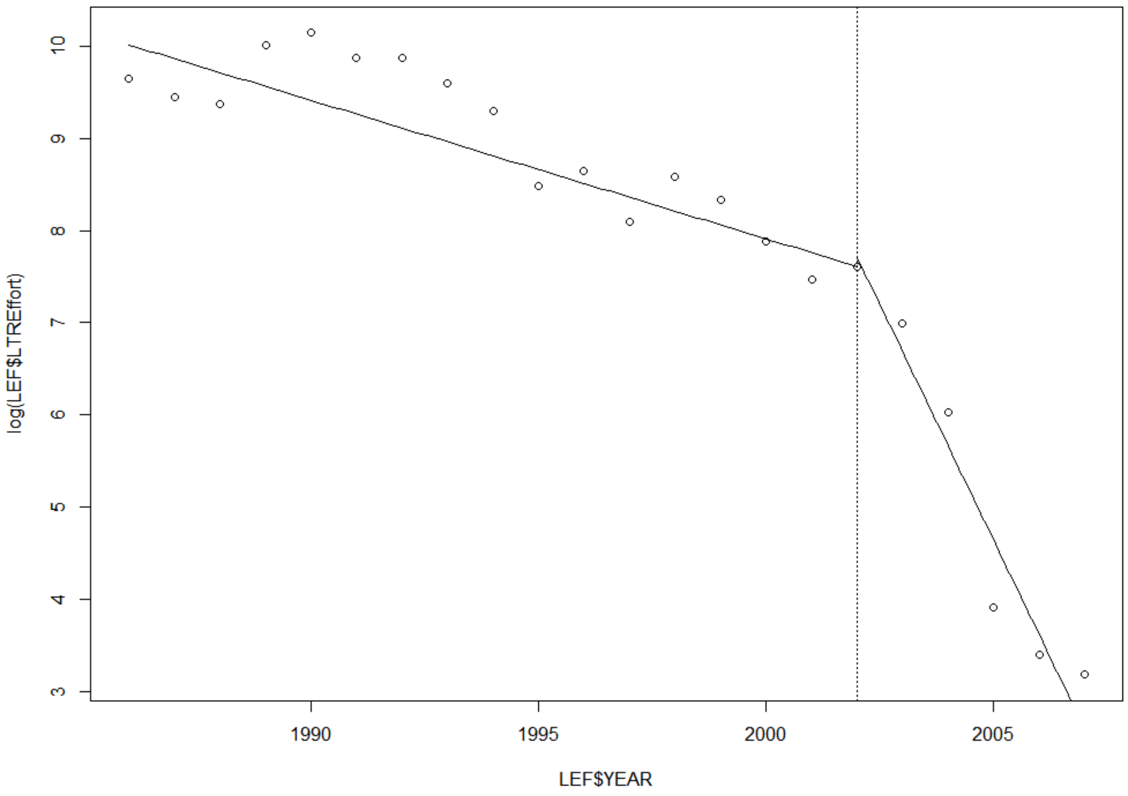

Figure B-1 Output from Piecewise regression of the natural logarithm of light trawl effort in hours versus year for the Clyde area. Piecewise regression estimates breakpoint of the data by estimating the lowest residual Mean Square Error of fitting two lines. This shows that from 2003 until 2010 there is a greater decline in effort compared to the period prior to 2003.

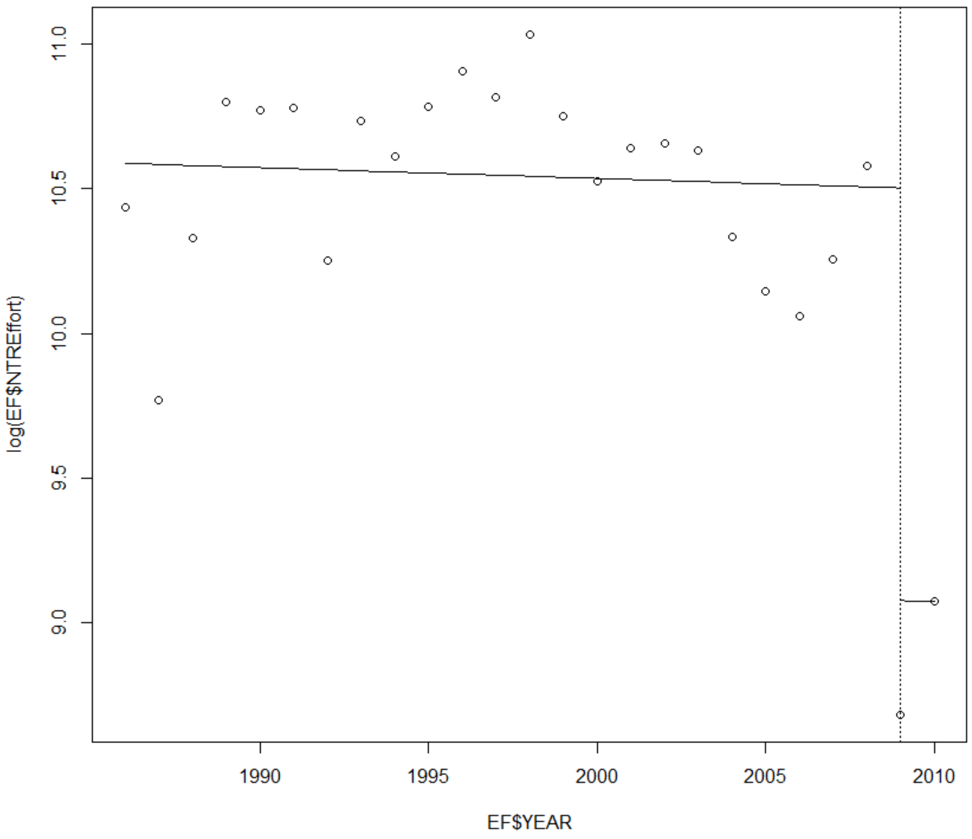

Figure B-2 Output from Piecewise regression of the natural logarithm of *Nephrops* trawl effort in hours versus year for the Clyde area. Piecewise regression estimates breakpoint of the data by estimating the lowest residual Mean Square Error of fitting two lines. This shows that until 2008 effort was relatively stable.

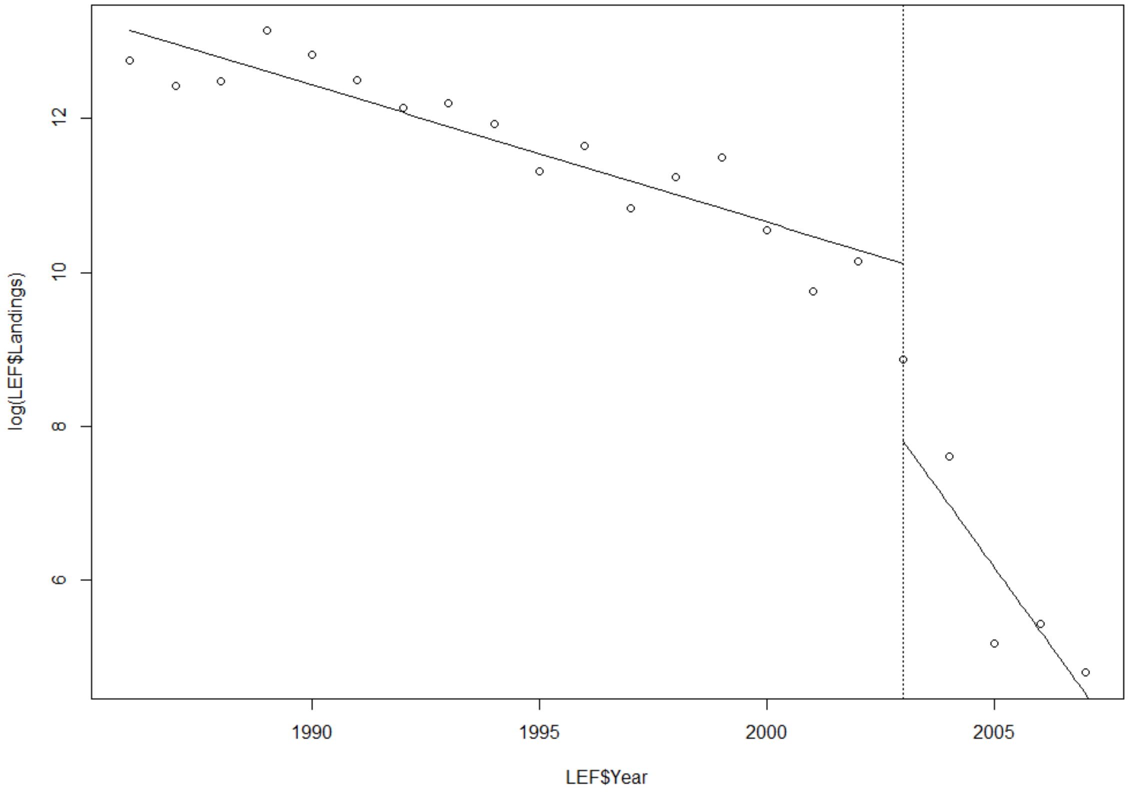

Figure B-3 Output from Piecewise regression of the natural logarithm of Light Otter trawl cod landings in tonnes versus year for the Clyde area. Piecewise regression estimates breakpoint of the data by estimating the lowest residual Mean Square Error of fitting two lines. This shows that until 2003 landings were declining, but that this decline was steeper after 2003.

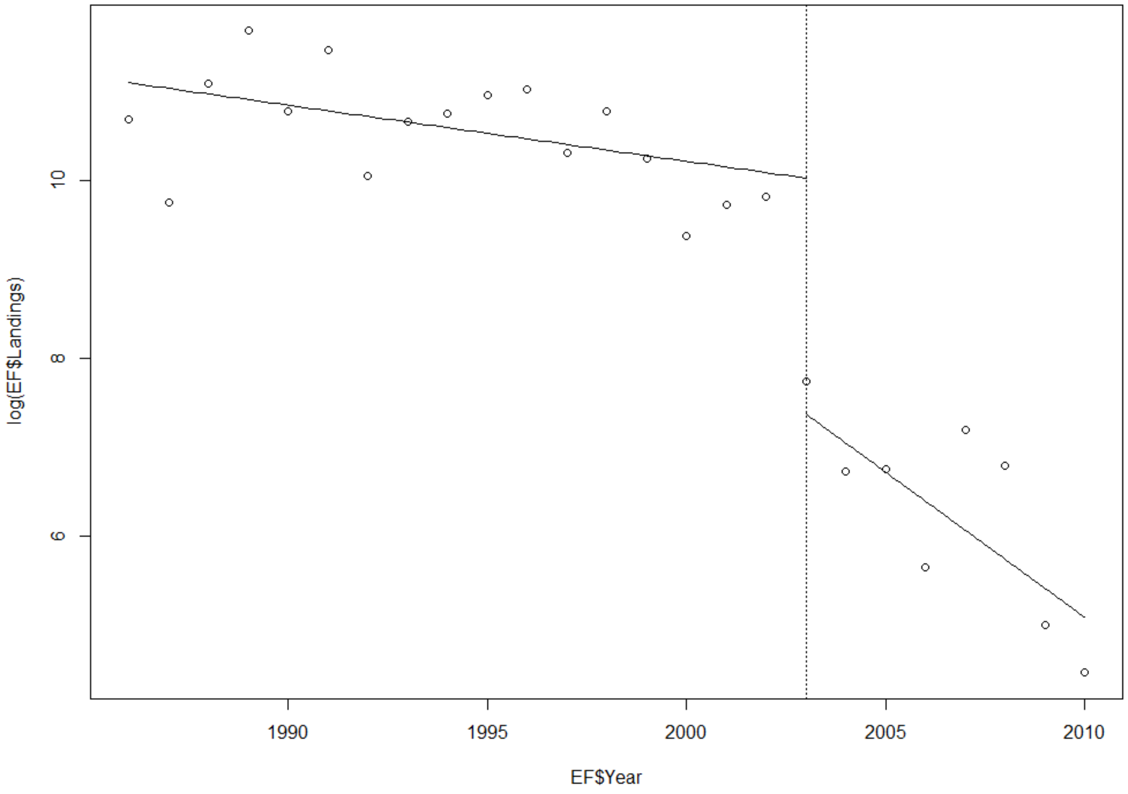

Figure B-4 Output from Piecewise regression of the natural logarithm of *Nephrops* trawl cod landings in tonnes versus year for the Clyde area. Piecewise regression estimates breakpoint of the data by estimating the lowest residual Mean Square Error of fitting two lines. This shows that until 2003 landings were declining but relatively stable. After 2003 this decline was steeper.

Appendix C: Chapter 4 supplemental information

Table C-1 Overview of trawl surveys used in analysis with references to detailed description of survey methodology

Gear type	Reference	Time range	Depth range	Number of Trawls
OTSB	Bailey, D. M., Collins, M. a, Gordon, J. D. M., Zuur, a F. & Priede, I. G. Long-term changes in deep-water fish populations in the northeast Atlantic: a deeper reaching effect of fisheries? *Proc. Biol. Sci.* **276,** 1965–1969 (2009).	1978-2002	240-1500	79
BT195	ICES. 2009. Report of the Workshop on Anglerfish and Megrim (WKAGME), 23–27 February 2009, Aberdeen, UK. ICES CM 2009/ACOM:28. 112 pp	2008-2014	315-1015	42
BT184_21	Neat, F. C., Kynoch, R., Drewery, J. & Burns, F. *Marine Scotland Science Report 03/10: Deepwater Trawl Survey Manual*. (2010).	1996-2009	300-1500	294
BT184_16	Neat, F. C., Kynoch, R., Drewery, J. & Burns, F. *Marine Scotland Science Report 03/10: Deepwater Trawl Survey Manual*. (2010).	2009-2013	300-1500	133

Table C-2 Description of variance structure that was determined as best fit from model selection

	Residual	Intercept	Slope (estimated degrees of freedom)	AIC
Simpson's Diversity	No Random effect for gear type	0.720595	3.328	-600.49
Proportion of Commercial fish biomass	Random effect for gear type plus VarPower variance structure with depth	0.62349	6.953	-256.36
Ratio of Elasmobranch and Ray to Commercial fish biomass	No Random effect for gear type	15.7626	7.61	-51.43
Commercial Value	Random effect for gear type plus VarPower variance structure with depth	20.994	6.448	3897.92

Table C-3List of commercial species used in analysis and value for each species per tonne

Scientific Name	**Common Name**	**Value (Euro per Tonne)**
Anarhichas denticulatus	Jelly Cat	3060
Anarhichas lupus	Catfish	1942.35
Anguilla	Eels	207798.3
Antimora rostrata	Antimora	3281
Aphanopus carbo	Black Scabbardfish	2550.58
Argentina silus	Greater Argentine	223.5
Argentina sphyraena	Lesser Argentine	1783.58
Beryx decadactylus	Beryx decadactylus	6569.7
Beryx decadactylus	Alfonsino	6569.7
Brosme brosme	Torsk	1398.38

Callionymus lyra	Dragonet	454
Capros aper	Boar Fish	175.33
Chimaera monstrosa	Rabbit Ratfish	1672.25
Clupea harengus	Herring	619.87
Conger conger	Conger Eel	1558.4
Coryphaenoides rupestris	Round Nosed Grenadier (Rat tail)	1888.05
Epigonus telescopus	Bullseye	1694.07
Eutrigla gurnardus	Grey Gurnard	918.46
Gadus morhua	Cod	2610.15
Gaidropsarus argentatus	Silvery Rockling	564.04
Gaidropsarus macrophthalmus	Big-eyed Rockling	564.04
Gaidropsarus vulgaris	Three-bearded Rockling	564.04
Glyptocephalus cynoglossus	Witch	2234.88
Helicolenus dactylopterus dactylopterus	Blackbelly rosefish/Blue-Mouth	2665.61
Hippoglossoides platessoides	Long Rough Dab	2632.17
Hippoglossus hippoglossus	Halibut	5808.34
Hoplostethus atlanticus	Orange Roughy	4279.57
Lepidorhombus boscii	Four-spot Megrim	15309.67
Lepidorhombus whiffiagonis	Megrim	3512.8
Limanda limanda	Common Dab	1679.67
Lophius budegassa	Black-bellied Angler	5275
Lophius piscatorius	Angler (Monk fish)	4830.75
Macrourus berglax	Rough Rat tail	1711.45
Merluccius merluccius	European hake	3267.77
Microchirus variegatus	Thickback sole	4555.26
Microstomus kitt	Lemon Sole	3246.4
Molva dypterygia	Blue Ling	2085.33
Molva macrophthalma	Spanish ling	999
Molva molva	Ling	1966.8
Mora moro	Mora	1479.47
Nezumia aequalis	Smooth Rat tail	3060

Petromyzon marinus	Sea Lamprey	4379.33
Phycidae	Rocklings (unidentified)	2236.43
Phycis blennoides	Greater Forkbeard	2236.43
Pleuronectes platessa	Plaice	2723.18
Pollachius virens	Saithe	1204.16
Polyprion americanus	Wreckfish	11750.75
Reinhardtius hippoglossoides	Greenland Halibut	3503.17
Sebastes viviparus	Norway Haddock	2041.92
Spectrunculus grandis	Spectrunculus grandis	2177.33
Trachyscorpia cristulata echinata	Spiny scorpionfish	6535.74
Trisopterus esmarkii	Norway Pout	338.63
Trisopterus minutus	Poor Cod	1745.32

.

References

Abesamis, R. A., and Russ, G. R. 2005. Density-dependent spillover from a marine reserve: Long term evidence. Ecological Applications, 15: 1798–1812.

Addison, P. 2011. A global review of long-term Marine Protected Area monitoring programmes: The application of a good framework to marine biological monitoring. A report prepared for the Joint Nature Conservation Committee.

Advani, S., Rix, L. N., Aherne, D. M., Alwany, M. A., and Bailey, D. M. 2015. Distance from a fishing community explains fish abundance in a no-take zone with weak compliance. PLoS ONE, 10: 1–17.

Agardy, T., di Sciara, G. N., and Christie, P. 2011. Mind the gap: Addressing the shortcomings of marine protected areas through large scale marine spatial planning. Marine Policy, 35: 226–232.

Aguilar-Perera, A. 2006. Disappearance of a Nassau grouper spawning aggregation off the southern Mexican Caribbean coast. Marine Ecology Progress Series, 327: 289–296.

Allain, V., Biseau, A., and Kergoat, B. 2003. Preliminary estimates of French deepwater shery discards in the Northeast Atlantic Ocean. Fisheries Research, 60: 185–192.

Alverson, D. L., Freeberg, M. H., Murawski, S. A., and Pope, J. G. 1994. A global assessment of fisheries bycatch and discards. FAO Fisheries Technical Paper No. 339. Rome.

Ames, E. P. 2004. Atlantic Cod Stock Structure in the Gulf of Maine. Fisheries Research, 29: 10–28.

Armstrong, M., Dann, J., Garrod, C., and Shaw, S. 2006. Programme 3: Irish sea Roundfish. Fisheries Science Partnership Report: 1–44.

Armstrong, M. P., Dean, M. J., Hoffman, W. S., Zemeckis, D. R., Nies, T. a., Pierce, D. E., Diodati, P. J., *et al.* 2013. The application of small scale fishery closures to protect Atlantic cod spawning aggregations in the inshore Gulf of Maine. Fisheries Research, 141: 62–69.

Babcock, R. C., Kelly, S., Shears, N. T., Walker, J. W., and Willis, T. J. 1999. Changes in community structure in temperate marine reserves. Marine Ecology Progress Series, 189: 125–134.

Bailey, D. M., Collins, M. A., Gordon, J. D. M., Zuur, A. F., and Priede, I. G. 2009. Long-term changes in deep-water fish populations in the northeast Atlantic: a deeper reaching effect of fisheries. Proceedings of the Royal Society B: Biological sciences, 276: 1965–1969.

Bailey, D. M., and Priede, I. G. 2002. Predicting fish behaviour in response to abyssal food falls. Marine Biology, 141: 831–840.

Bassett, D. K., and Montgomery, J. C. 2011. Investigating nocturnal fish populations in situ using baited underwater video: With special reference to their olfactory capabilities. Journal of Experimental Marine Biology and Ecology, 409: 194–199.

Bates, D., Martin, M., Ben, B., Steven, W., Christensen, R. H. B., Singmann, H., and Dai, B. 2015. Package ‘lme4’.

Beare, D., Rijnsdorp, A. D., Blaesberg, M., Damm, U., Egekvist, J., Fock, H., Kloppmann, M., *et al.* 2013. Evaluating the effect of fishery closures: Lessons learnt from the Plaice Box. Journal of Sea Research: 1–12..

Beddington, J. R., Agnew, D. J., and Clark, C. W. 2007. Current problems in the management of marine fisheries. Science, 316: 1713–6.

Beets, J., and Friedlander, A. M. 1998. Evaluation of a conservation strategy: a spawning aggregation closure for red hind, Epinephelus guttatus, in the U.S. Virgin Islands. Environmental Biology of Fishes, 55: 91–98.

Bernstein, B. B., and Zalinski, J. 1983. An optimum sampling design and power tests for environmental biologists. Journal of Environmental Management1, 16: 35–43.

Birkeland, C., and Dayton, P. K. 2005. The importance in fishery management of leaving the big ones. Trends in ecology & evolution, 20: 356–8.

Berumen, M. L., Almany, G. R., Planes, S., Jones, G. P., Saenz-Agudelo, P. and Thorrold, S. R. (2012), Persistence of self-recruitment and patterns of larval connectivity in a marine protected area network. Ecology and Evolution, 2: 444–452. doi:10.1002/ece3.208

Bolam, S. G., Coggan, R. C., Eggleton, J., Diesing, M., and Stephens, D. 2014. Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: A biological trait approach. Journal of Sea Research, 85: 162–177.

Bower, M. R., Gaines, D. B., Wilson, K. P., Wullschleger, J. G., Dzul, M. C., Quist, M. C., and Dinsmore, S. J. 2011. Accuracy and Precision of Visual Estimates and Photogrammetric Measurements of the Length of a Small-bodied Fish. North American Journal of Fisheries Management, 31: 138–143.

Boyes, S. J., and Elliott, M. 2014. Marine legislation - The ultimate ‘horrendogram’: International law, European directives & national implementation. Marine Pollution Bulletin, 86: 39–47.

Bromley, P. J., Watson, T., and Hislop, J. R. G. 1997. Diel feeding patterns and the development of food webs in pelagic 0-group cod (*Gadus morhua* L .), haddock (*Melanogrammus aeglefinus* L .), whiting (*Merlangius merlangus* L .), saithe (*Pollachius virens* L .), and Norway pout (*Trisopterus esmarkii* Nilsso. ICES Journal of Marine Science, 54: 846–853.

Cameron, A., and Askew, N. 2011. EUSeaMap - Preparatory Action for development and assessment of a European broad-scale seabed habitat map final report. A report prepared for the Joint Nature Conservation Committee.

Campbell, N., Neat, F. C., Burns, F., and Kunzlik, P. 2010. Species richness , taxonomic diversity , and taxonomic distinctness of the deep-water demersal fish community on the Northeast Atlantic continental slope (ICES Subdivision VIa). ICES Journal of Marine Science, 68: 365–376.

Cappo, M., Harvey, E. S., and Shortis, M. 2005. Counting and measuring fish with baited video techniques - an overview: 101–114.

Cappo, M., Speare, P., and De’ath, G. 2004. Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. Journal of Experimental Marine Biology and Ecology, 302: 123–152.

Caveen, A. J., Sweeting, C. J., Willis, T. J., and Polunin, N. V. C. 2012. Are the scientific foundations of temperate marine reserves too warm and hard? Environmental Conservation, 39: 199-203.

CBD. 2004. Decisions adopted by the Conference of the Parties to the Convention on Biological Diversity at its seventh meeting.

Clare, D. S., Robinson, L. a., and Frid, C. L. J. 2015. Community variability and ecological functioning: 40 years of change in the North Sea benthos. Marine Environmental Research, 107: 24–34.

Clark, M. R., and Dunn, M. R. 2012. Spatial management of deep-sea seamount fisheries: balancing sustainable exploitation and habitat conservation. Environmental Conservation, 39: 204–214.

Clarke, J., Bailey, D. M., and Wright, P. J. 2015a. Evaluating the effectiveness of a seasonal spawning area closure. ICES Journal of Marine Science, 72: 2627–2637.

Clarke, J., Milligan, R. J., Bailey, D. M., and Neat, F. C. 2015b. A Scientific Basis for Regulating Deep-Sea Fishing by Depth. Current Biology, 25: 2425–2429.

Claudet, J., and Guidetti, P. 2010. Improving assessments of marine protected areas. Aquatic Conservation-Marine and Freshwater Ecosystems, 20: 239–242.

Colton, M., and Swearer, S. 2010. A comparison of two survey methods: differences between underwater visual census and baited remote underwater video. Marine Ecology Progress Series, 400: 19–36.

Colvocoresses, J., and Acosta, A. 2007. A large-scale field comparison of strip transect and stationary point count methods for conducting length-based underwater visual surveys of reef fish populations. Fisheries Research, 85: 130–141.

Connolly, P. L., and Kelly, C. J. 1996. Catch and discards from experimental trawl and longline fishing in the deep water of the Rockall Trough. Journal of Fish Biology, 49: 132–144.

Cook, R. M., Holmes, S. J., and Fryer, R. J. 2015. Grey seal predation impairs recovery of an over-exploited fish stock. Journal of Applied Ecology.

Cuaig, M. Ó., and Officer, R. 2007. Evaluation of the benefits to sustainable management of seasonal closure of the greencastle codling (*Gadus morhua*) fishery. Fisheries Bulletin No 27/2007.

De Juan, S., Thrush, S. F., and Demestre, M. 2007. Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). Marine Ecology Progress Series, 334: 117–129.

Dean, M. J., Hoffman, W. S., and Armstrong, M. P. 2012. Disruption of an Atlantic Cod Spawning Aggregation Resulting from the Opening of a Directed Gill-Net Fishery. North American Journal of Fisheries Management, 32: 124–134.

Dearden, P., Theberge, M., and Yasué, M. 2010. Using underwater cameras to assess the effects of snorkeler and SCUBA diver presence on coral reef fish abundance, family richness, and species composition. Environmental monitoring and assessment, 163: 531–8.

Devine, J. a, Baker, K. D., and Haedrich, R. L. 2006. Fisheries: deep-sea fishes qualify as endangered. Nature, 439: 29.

Devine, J. A., Wright, P. J., Pardoe, H. E., and Heino, M. 2012. Comparing rates of contemporary evolution in life- history traits for exploited fish stocks. Canadian Journal of Fisheries and Aquatic Sciences, 1120: 1105–1120.

Diamond, S. L., Kleisner, K. M., and Duursma, Daisy Englert Wanga, Y. 2010. Designing marine reserves to reduce bycatch of mobile species: a case study using juvenile red snapper (Lutjanus campechanus). Canadian Journal of Fisheries and Aquatic Sciences, 67: 1335–1349.

Dichmont, C. M., Ellis, N., Bustamante, R. H., Deng, R., Tickell, S., Pascual, R., Lozano-Montes, H., *et al.* 2013. Evaluating marine spatial closures with conflicting fisheries and conservation objectives. Journal of Applied Ecology, 50: 1060–1070.

Dickens, L. C., Goatley, C. H. R., Tanner, J. K., and Bellwood, D. R. 2011. Quantifying relative diver effects in underwater visual censuses. PloS one, 6: e18965.

Di Franco, A., Calo, A., Pennetta, A., De Benedetto, G., Planes, S. and Guidetti, P. 2015. Dispersal of larval and juvenile seabream: Implications for Mediterranean marine protected areas. Biological Conservation. 192:361-368.

Dolan, T. E., Patrick, W. S., and Link, J. S. 2016. Delineating the continuum of marine ecosystem-based management: a US fisheries reference point perspective. ICES Journal of Marine Science, 73: 1042–1050.

Dransfeld, L., Gerritsen, H. D., Hareide, N. R., and Lorance, P. 2013. Assessing the risk of vulnerable species exposure to deepwater trawl fisheries : the case of orange roughy Hoplostethus atlanticus to the west of Ireland and Britain. Aquatic Living Resources, 26: 307–318.

Drazen, J. C., and Haedrich, R. L. 2012. A continuum of life histories in deep-sea demersal fishes. Deep Sea Research Part I: Oceanographic Research Papers, 61: 34–42.

Duineveld, G. C. a, Bergman, M. J. N., and Lavaleye, M. S. S. 2007. Effects of an area closed to fisheries on the composition of the benthic fauna in the southern North Sea. ICES Journal of Marine Science, 64: 1–10.

Dunlop, K. M., Barnes, D. K. A., and Bailey, D. M. 2014a. Variation of scavenger richness and abundance between sites of high and low iceberg scour frequency in Ryder Bay, west Antarctic Peninsula. Polar Biology, 37: 1741–1754.

Dunlop, K. M., Marian Scott, E., Parsons, D., and Bailey, D. M. 2014b. Do agonistic behaviours bias baited remote underwater video surveys of fish? Marine Ecology: 1-9.

Elliott, S. A. M., Ahti, P. A., Heath, M. R., Turrell, W. R., and Bailey, D. M. 2016. An assessment of juvenile Atlantic cod distribution and growth using diver operated stereo-video surveys. Journal of fish biology.

Ellis, R. D., and Powers, J. E. 2012. Gag grouper, marine reserves, and density-dependent sex change in the Gulf of Mexico. Fisheries Research, 115-116: 89–98.

Erisman, B., Aburto-Oropeza, O., Gonzalez-Abraham, C., Mascareñas-Osorio, I., Moreno-Báez, M., and Hastings, P. a. 2012. Spatio-temporal dynamics of a fish spawning aggregation and its fishery in the Gulf of California. Scientific reports, 2: 284.

Erisman, B. E., Allen, L. G., Claisse, J. T., Ii, D. J. P., Miller, E. F., and Murray, J. H. 2011. The illusion of plenty : hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. Canadian Journal of Fisheries and Aquatic Sciences, 68: 1705–1716.

FAO. 2012. Report of the Reykjavik Conference on Responsible Fishing. Rome. 103 pp.

FAO. 2014a. The State of World Fisheries and Aquaculture 2014. 223 pp.

FAO. 2014b. Essential EAFM. Ecosystem Approach to Fisheries Management Training Course. RAP Publication 2014/13.

Fay, G., Large, S. I., Link, J. S., and Gamble, R. J. 2013. Testing systemic fishing responses with ecosystem indicators. Ecological Modelling, 265: 45–55.

Fenberg, P. B., Caselle, J. E., Claudet, J., Clemence, M., Gaines, S. D., Antonio García-Charton, J., Gonçalves, E. J., *et al.* 2012. The science of European marine reserves: Status, efficacy, and future needs. Marine Policy, 36: 1012–1021.

Fernandes, P. G., and Cook, R. M. 2013. Reversal of fish stock decline in the northeast atlantic. Current biology : CB, 23: 1432–7. Elsevier Ltd.

Fewster, R. M., Buckland, S. T., Siriwardena, G. M., Baillie, S. R., and Wilson, J. D. 2000. Analysis of Population Trends for Farmland Birds Using Generalized Additive Models. Ecological Society of America, 81: 1970–1984.

Fisher, J., and Frank, K. 2002. Changes in finfish community structure associated with an offshore fishery closed area on the Scotian Shelf. Marine Ecology Progress Series, 240: 249–265.

Fodrie, F., Levin, L., and Lucas, A. 2009. Use of population fitness to evaluate the nursery function of juvenile habitats. Marine Ecology Progress Series, 385: 39–49.

Francini-filho, R. B., and Moura, R. L. 2008. Evidence for spillover of reef fishes from a no-take marine reserve : An evaluation using the before-after control-impact (BACI) approach. Fisheries Research, 93: 346–356.

Froese, R., and Pauly, D., Editors. 2000. FishBase 2000: concepts, design and data sources. ICLARM, Los Baños, Laguna, Philippines. 344 p.

Froese, R., Winker, H., Gascuel, D., Sumalia, U. R., and Pauly, D. 2016. Minimizing the impact of fishing. Fish and Fisheries:

Fulton, E. A., Smith, A. D. M., and Punt, A. E. 2005. Which ecological indicators can robustly detect effects of fishing? ICES Journal of Marine Science, 62: 540–551.

Gell, F. R., and Roberts, C. M. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. Trends in Ecology & Evolution, 18: 448–455.

Godbold, J. a., Bailey, D. M., Collins, M. a., Gordon, J. D. M., Spallek, W. a., and Priede, I. G. 2013. Putative fishery-induced changes in biomass and population size structures of demersal deep-sea fishes in ICES Sub-area VII, Northeast Atlantic Ocean. Biogeosciences, 10: 529–539.

Gray, J. S., Dayton, P., Thrush, S., and Kaiser, M. J. 2006. On effects of trawling, benthos and sampling design. Marine pollution bulletin, 52: 840–3.

Greathead, C., Demain, D., Dobby, H., Allan, L., and Weetman, A. 2011. Quantitative assessment of the distribution and abundance of the burrowing megafauna and large epifauna community in the Fladen fishing ground, northern North Sea. Scottish Marine and Freshwater Science or Marine Scotland Science Report Vol 2 No 2.

Greathead, C. F., Donnan, D. W., Mair, J. M., and Saunders, G. R. 2007. The sea pens Virgularia mirabilis, Pennatula phosphorea and Funiculina quadrangularis: distribution and conservation issues in Scottish waters. Journal of the Marine Biological Association of the UK, 87: 1095–1103.

Green, R. H. 1979. Sampling design and statistical methods for environmental biologists.

Griffin, R. a., Robinson, G. J., West, A., Gloyne-Phillips, I. T., and Unsworth, R. K. F.

2016. Assessing Fish and Motile Fauna around Offshore Windfarms Using Stereo Baited Video. Plos One, 11: e0149701.

Grüss, A., Kaplan, D. M., Guénette, S., Roberts, C. M., and Botsford, L. W. 2011. Consequences of adult and juvenile movement for marine protected areas. Biological Conservation, 144: 692–702.

Grüss, A., Kaplan, D. M. M., and Robinson, J. 2013. Evaluation of the effectiveness of marine reserves for transient spawning aggregations in data-limited situations. ICES Journal of Marine Science.

Grüss, A., and Robinson, J. 2015. Fish populations forming transient spawning aggregations: should spawners always be the targets of spatial protection efforts? ICES Journal of Marine Science, 69: 1205–1217.

Grüss, A., Robinson, J., Heppell, S. S., Heppell, S. A., and Semmens, B. X. 2014. Conservation and fisheries effects of spawning aggregation marine protected areas: Whatwe know, where we should go, and what we need to get there. ICES Journal of Marine Science.

Hall, S. J., and Mainprize, B. M. 2005. Managing by-catch and discards: how much progress are we making and how can we do better? Fish and Fisheries, 6: 134–155.

Halliday, R. G. 1988. Use of Seasonal Spawning Area Closures in the Management of Haddock Fisheries in the Northwest Atlantic. NAFO Scientific Council Studies, 12: 27–36.

Hall-Spencer, J. 2000. Scallop dredging has profound, long-term impacts on maerl habitats. ICES Journal of Marine Science, 57: 1407–1415.

Hall-Spencer, J., Allain, V., and Fosså, J. H. 2002. Trawling damage to Northeast Atlantic ancient coral reefs. Proceedings. Biological sciences / The Royal Society, 269: 507–511.

Hall-Spencer, J. M., Grall, J., Moore, P. G., and Atkinson, R. J. a. 2003. Bivalve fishing and maerl-bed conservation in France and the UK?retrospect and prospect. Aquatic Conservation: Marine and Freshwater Ecosystems, 13: S33–S41.

Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications, 13: S117–S137.

Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., Lowndes, J. S., *et al.* 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. Nature Communications, 6: 7615. Nature Publishing Group.

Harrison HB, et al. 2012. Larval export from marine reserves and the recruitment benefit for fish and fisheries. Current Biology 22: 1023–1028.

Harvey, E. S., Fletcher, D., and Shortis, M. 2002. Estimation of reef fish length by divers and by stereo-video A first comparison of the accuracy and precision in the field on living fish under operational conditions. Fisheries Research, 57: 255–265.

Harvey, E. S., Newman, S. J., McLean, D. L., Cappo, M., Meeuwig, J. J., and Skepper, C. L. 2012. Comparison of the relative efficiencies of stereo-BRUVs and traps for sampling tropical continental shelf demersal fishes. Fisheries Research, 125-126: 108–120. Elsevier B.V.

Harvey, E. S., and Shortis, M. 1996. A System for Stereo-Video Measurement of Sub-Tidal Organisms. Marine Technology Society Journal, 29.

Heath, M. R., Culling, M. a., Crozier, W. W., Fox, C. J., Gurney, W. S. C., Hutchinson, W. F., Nielsen, E. E., *et al.* 2013. Combination of genetics and spatial modelling highlights the sensitivity of cod (Gadus morhua) population diversity in the North Sea to distributions of fishing. ICES Journal of Marine Science.

Heath, M. R., and Speirs, D. C. 2012. Changes in species diversity and size composition in the Firth of Clyde demersal fish community (1927 − 2009) Changes in species diversity and size composition in the Firth of Clyde demersal fish community (1927 – 2009): 543–552.

Heppell, S. S. A., Heppell, S. S. A., Coleman, F. C., and Koenig, C. C. 2006. Models to compare management options for a protogynous fish. Ecological Applications, 16: 238–249.

Heymans, J. J., Howell, K. L., Ayers, M., Burrows, M. T., Gordon, J. D. M., Jones, E. G., and Neat, F. 2010. Do we have enough information to apply the ecosystem approach to management of deep-sea fisheries? An example from the West of Scotland. ICES Journal of Marine Science, 68: 265–280.

Heymans, J. J., Howell, K. L., Ayers, M., Burrows, M. T., Gordon, J. D. M., Jones, E. G., and Neat, F. C. 2011. Do we have enough information to apply the ecosystem approach to management of deep-sea fisheries ? An example from the West of Scotland, 68: 265–280.

Hiddink, J. G., Jennings, S., Kaiser, M. J., Queirós, A. M., Duplisea, D. E., and Piet, G. J. 2006. Cumulative impacts of seabed trawl disturbance on benthic biomass , production , and species richness in different habitats, 736: 721–736.

Hiddink, J. G., Johnson, A. F., Kingham, R., and Hinz, H. 2011. Could our fisheries be more productive? Indirect negative effects of bottom trawl fisheries on fish condition. Journal of Applied Ecology, 48: 1441–1449.

Hiddink, J. G., Moranta, J., Balestrini, S., Sciberras, M., Cendrier, M., Bowyer, R., Kaiser, M. J., *et al.* 2016. Bottom trawling affects fish condition through changes in the ratio of prey availability to density of competitors. Journal of Animal Ecology, in press: 1–18.

Hilborn, R. 2011. Future directions in ecosystem based fisheries management: A personal perspective. Fisheries Research, 108: 235–239. Elsevier B.V.

Hilborn, R. 2012. The evolution of quantitative marine fisheries management 1985 - 2010. Natural Resource Modeling, 25: 122–144.

Hilborn, R., and Walters, C. J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.

Hintzen, N. T., Bastardie, F., Beare, D., Piet, G., Ulrich, C., Deporte, N., Egekvist, J., et al. 2012. VMStools: open-source software for the processing, analysis and visualization of fisheries logbook and VMS data. Fisheries Research, 115-116: 31–43.

Hinz, H., Prieto, V., and Kaiser, M. J. 2009. Trawl disturbance on benthic communities: chronic effects and experimental predictions. Ecological applications : a publication of the Ecological Society of America, 19: 761–73.

Hislop, J. R. G. 1986. The demersal fishery in the Clyde Sea Area. Proceedings of the

Royal Society of Edinburgh. Section B. Biological Sciences, 90: 423–437.

Holmes, S. J., Bailey, N., Campbell, N., Catarino, R., Barratt, K., Gibb, a., and Fernandes, P. G. 2011. Using fishery-dependent data to inform the development and operation of a co-management initiative to reduce cod mortality and cut discards. ICES Journal of Marine Science, 68: 1679–1688.

Holmes, S. J., Millar, C. P., Fryer, R. J., and Wright, P. J. 2014. Gadoid dynamics: differing perceptions when contrasting stock vs. population trends and its implications to management. ICES Journal of Marine Science, 71.

Holmlund, C. M., and Hammer, M. 1999. Ecosystem services generated by fish populations. Ecological Economics, 29: 253–268.

Hu, L., and Wroblewski, J. S. 2009. Conserving a subpopulation of the northern Atlantic cod metapopulation with a marine protected area, 193: 178–193.

Humborstad, O. 2004. RoxAnn bottom classification system, sidescan sonar and video-sledge: spatial resolution and their use in assessing trawling impacts. ICES Journal of Marine Science, 61: 53–63.

Hurlbert, S. H. 1984. PSEUDOREPLICATION AND THE DESIGN OF ECOLOGICAL FIELD EXPERIMENTS. Ecological Monographs, 54: 187–211.

Hutchings, J. a, Bishop, T. D., and McGregor-Shaw, C. R. 1999. Spawning behaviour of Atlantic cod, Gadus morhua : evidence of mate competition and mate choice in a broadcast spawner. Canadian Journal of Fisheries and Aquatic Sciences, 56: 97–104.

Hutchinson, W. F. 2008. The dangers of ignoring stock complexity in fishery management: the case of the North Sea cod. Biology letters, 4: 693–5.

Huxley, T. H. H. 1882. Inaugural address. Fisheries exhibition, London. http://aleph0.clarku.edu/huxley/SM5/fish.html.

ICES. 2013. ICES Advice for 2014 for Cod in Division VIa (West of Scotland). 1-11 pp.

ICES WGDEEP REPORT 2014 Assessment of Deep-sea Fisheries Resources Report of the Working Group on Biology and (WGDEEP) International Council for the Exploration of the Sea. 2014. : 4–11.

IPCC. 2014. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, United Kingdom and New York, NY, USA. 1820 pp.

Jamieson, A. J., Bailey, D. M., Wagner, H. J., Bagley, P. M., and Priede, I. G. 2006. Behavioural responses to structures on the seafloor by the deep-sea fish Coryphaenoides armatus: Implications for the use of baited landers. Deep-Sea Research Part I: Oceanographic Research Papers, 53: 1157–1166.

Jamieson, A. J., Fujii, T., Solan, M., Matsumoto, A. K., Bagley, P. M., and Priede, I. G. 2009. First findings of decapod crustacea in the hadal zone. Deep-Sea Research Part I: Oceanographic Research Papers, 56: 641–647.

Jaworski, A., Solmundsson, J., and Ragnarsson, S. 2006. The effect of area closures on the demersal fish community off the east coast of Iceland. ICES Journal of Marine Science, 63: 897–911.

Jennings, S., and Rice, J. 2011. Towards an ecosystem approach to fisheries in Europe: A perspective on existing progress and future directions. Fish and Fisheries, 12: 125–137.

Jensen, A. L. 1984. Non-linear catch curves resulting from variation in mortality among subpopulations. ICES Journal of Marine Science, 41: 121–124.

Jonasson, J. P., Gunnarsson, B., and Marteinsdottir, G. 2009. Abundance and growth of larval and early juvenile cod (Gadus morhua) in relation to variable environmental conditions west of Iceland. Deep Sea Research Part II, 56: 1992–2000.

Jones, E., Beare, D., Dobby, H., Trinkler, N., Burns, F., Peach, K., and Blasdale, T. 2005. The potential impact of commercial fishing activity on the ecology of deepwater chondrichthyans from the west of Scotland. ICES CM 2005/N:16. ICES Annual Science Conference; Elasmobranch Fisheries Science.

Jones, P., Catchcart, A., and Speirs, D. C. 2015. Early evidence of the impact of preindustrial fishing on fish stocks from the mid-west and southeast coastal fisheries of

Scotland in the 19th century. ICES Journal of Marine Science.

Jones, P. J. S. 2008. Fishing industry and related perspectives on the issues raised by no-take marine protected area proposals. Marine Policy, 32: 749–758.

Kafas, A., Jones, G., Watret, R., Davies, I., Scott, B., 2013.2009 - 2013 amalgamated VMS intensity layers, GIS Data. Marine Scotland, Scottish Government. doi: 10.7489/1706-1

Kaiser, M. J., Clarke, K., Hinz, H., Austen, M., Somerfield, P., and Karakassis, I. 2006. Global analysis of response and recovery of benthic biota to fishing. Marine Ecology Progress Series, 311: 1–14.

Kelly, C. J., Codling, E. a., and Rogan, E. 2006. The Irish Sea cod recovery plan: some lessons learned. ICES Journal of Marine Science, 63: 600–610.

Knutsen, H., Jorde, P. E., André, C., and Stenseth, N. C. 2003. Fine-scaled geographical population structuring in a highly mobile marine species: the Atlantic cod. Molecular ecology, 12: 385–94.

Kraak, S. B. M., Bailey, N., Cardinale, M., Darby, C., De Oliveira, J. a. a., Eero, M., Graham, N., *et al.* 2013. Lessons for fisheries management from the EU cod recovery plan. Marine Policy, 37: 200–213.

Kruschel, C., and Schultz, S. T. 2012. Use of a lure in visual census significantly improves probability of detecting wait-ambushing and fast cruising predatory fish. Fisheries Research, 123-124: 70–77. Elsevier B.V.

Kulbicki, M. 1998. How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. Journal of Experimental Marine Biology and Ecology, 222: 11–30.

Langlois, T., Harvey, E. S., Fitzpatrick, B., Meeuwig, J., Shedrawi, G., and Watson, D. 2010. Cost-efficient sampling of fish assemblages: comparison of baited video stations and diver video transects. Aquatic Biology, 9: 155–168.

Langlois, T. J. J., Harvey, E. S., and Meeuwig, J. J. J. 2012. Strong direct and inconsistent indirect effects of fishing found using stereo-video: Testing indicators from fisheries closures. Ecological Indicators, 23: 524–534. Elsevier Ltd.

Large, P. A., Agnew, D. J., Ángel, J., Pérez, Á., Froján, C. B., Cloete, R., Damalas, D., *et al.* 2013a. Strengths and Weaknesses of the Management and Monitoring of Deep- Water Stocks, Fisheries, and Ecosystems in Various Areas of the World—A Roadmap Toward Sustainable Deep-Water Fisheries in the Northeast Atlantic? Reviews in Fisheries Science, 21: 157–180.

Large, P. a., Hammer, C. ., Bergstad, O. a., Gordon, J. D. M., and Lorance, P. 2003. Deep-water fisheries of the northeast Atlantic: II. Assessment and management approaches. Journal of Northwest Atlantic Fishery Science, 31: 151–163.

Large, S. I., Fay, G., Friedland, K. D., and Link, J. S. 2013b. Defining trends and thresholds in responses of ecological indicators to fishing and environmental pressures. ICES Journal of Marine Science, 70: 755–767.

Law, R. 2007. Fisheries-induced evolution: present status and future directions. Marine Ecology Progress Series, 335: 271–277.

Leslie, H. M., and McLeod, K. L. 2007. Confronting the challenges of implementing marine ecosystem-based management. Frontiers in Ecology and the Environment, 5: 540–548.

Lester, S., Halpern, B., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B., Gaines, S., Airamé, S., *et al.* 2009. Biological effects within no-take marine reserves: a global synthesis. Marine Ecology Progress Series, 384: 33–46.

Lindholm, J. B., Auster, P. J., and Kaufman, L. S. 1999. Habitat-mediated survivorship of juvenile (0-year) Atlantic cod Gadus morhua. Marine Ecology Progress Series, 180: 247–255.

Little, A. S., Needle, C. L., Hilborn, R., Holland, D. S., and Marshall, C. T. 2014. Real-time spatial management approaches to reduce bycatch and discards : experiences from Europe and the United States. Fish and Fisheries.

Lohrer, A. M., Thrush, S. F., and Gibbs, M. M. 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions, 431: 2–5.

Lorance, P., Large, P. A., Bergstad, O. A., and Gordon, J. D. M. 2008. Grenadiers of the Northeast Atlantic – Distribution, biology, fisheries, and their impacts, and developments in stock assessment and management. *In* Grenadiers of the world oceans: biology, stock assessment and fisheries, pp. 365–397.

Lowry, M., Folpp, H., Gregson, M., and Suthers, I. 2012. Comparison of baited remote underwater video (BRUV) and underwater visual census (UVC) for assessment of artificial reefs in estuaries. Journal of Experimental Marine Biology and Ecology, 416-417: 243–253.

Lucchetti, A., Sala, A., and Jech, J. M. 2012. Impact and performance of Mediterranean fishing gear by side-scan sonar technology. Canadian Journal of Fisheries and Aquatic Sciences, 69: 1806–1816.

Mangi, S. C., Kenny, A., Readdy, L., Posen, P., Ribeiro-Santos, A., Neat, F. C., and Burns, F. 2016. The economic implications of changing regulations for deep sea fishing under the European Common Fisheries Policy: UK case study. Science of The Total Environment, 562: 260–269..

Marchal, P., Andersen, J. L., Aranda, M., Fitzpatrick, M., Goti, L., Guyader, O., Haraldsson, G., *et al.* 2016. A comparative review of fisheries management experiences in the European Union and in other countries worldwide: Iceland, Australia, and New Zealand. Fish and Fisheries: n/a–n/a.

Marine Scotland. 2015. Interactive VMS layers. http://www.gov.scot/Topics/marine/seamanagement/nmpihome/Productive/VMSAmalgamated.

Marteinsdottir, G. 2000. Spatial variation in abundance, size composition and viable egg production of spawning cod (Gadus morhua L.) in Icelandic waters. ICES Journal of Marine Science, 57: 824–830.

Marteinsdottir, G., and Steinarsson, A. 1998. Maternal influence on the size and viability of Iceland codGadus morhuaeggs and larvae. Journal of fish biology, 52: 1241–1258.

Martinez, I., Jones, E. G., Davie, S. L., Neat, F. C., Wigham, B. D., and Priede, I. G. 2011.

Variability in behaviour of four fish species attracted to baited underwater cameras in the North Sea. Hydrobiologia, 670: 23–34.

Mateos-Molina, D., Schärer-Umpierre, M. T., Appeldoorn, R. S., and García-Charton, J. a. 2013. Measuring the effectiveness of a Caribbean oceanic island no-take zone with an asymmetrical BACI approach. Fisheries Research, 150: 1–10.

Maxwell, D., and Jennings, S. 2005. Power of monitoring programmes to detect decline and recovery of rare and vulnerable fish. Journal of Applied Ecology, 42: 25–37.

McLean, D., Harvey, E. S., Fairclough, D., and Newman, S. 2010. Large decline in the abundance of a targeted tropical lethrinid in areas open and closed to fishing. Marine Ecology Progress Series, 418: 189–199.

Molnar, J. L., Gamboa, R. L., Revenga, C., and Spalding, M. D. 2008. Assessing the global threat of invasive species to marine biodiversity. Frontiers in Ecology and the Environment, 6: 485–492.

Monk, J., Ierodiaconou, D., Harvey, E. S., Rattray, A., and Versace, V. L. 2012. Are we predicting the actual or apparent distribution of temperate marine fishes? PloS one, 7: e34558.

Morato, T., Watson, R., Pitcher, T. J., and Pauly, D. 2006. Fishing down the deep. Fish and Fisheries, 7: 24–34.

Morgan, M. J., DeBlois, E. M., and Rose, G. a. 1997. An observation on the reaction of Atlantic cod (Gadus morhua) in a spawning shoal to bottom trawling. Canadian Journal of Fisheries and Aquatic Sciences, 54: 217–223.

Morgan, M. J., Wright, P. J., and Rideout, R. M. 2013. Effect of age and temperature on spawning time in two gadoid species. Fisheries Research, 138: 42–51.

Murawski, S. A., Brown, R., Lai, H.-L., Rago, P. J., and Hendrickson, L. 2000. Large-scale closed areas as a fishery-management tool in temperate marine systems: The Georges Bank Experience. Bulletin of Marine Science, 66: 775–798.

Murphy, H. M., and Jenkins, G. P. 2010. Observational methods used in marine spatial monitoring of fishes and associated habitats: a review. Marine and Freshwater Research, 61: 236–252.

Neat, F. C., and Burns, F. 2010. Stable abundance, but changing size structure in grenadier fishes (Macrouridae) over a decade (1998–2008) in which deepwater fisheries became regulated. Deep Sea Research Part I: Oceanographic Research Papers, 57: 434–440.

Nelson, G. A. 2014. fishmethods: Fishery Science Methods and Models in R.

Norse, E. a., Brooke, S., Cheung, W. W. L., Clark, M. R., Ekeland, I., Froese, R., Gjerde, K. M., *et al.* 2012. Sustainability of deep-sea fisheries. Marine Policy, 36: 307–320. Elsevier.

O’Neill, F. G., and Ivanovic, A. 2015. The physical impact of towed demersal fishing gears on soft sediment. ICES Journal of Marine Science, 69: 380–388.

O’Neill, F. G., Summerbell, K., and Breen, M. 2009. An underwater laser stripe seabed profiler to measure the physical impact of towed gear components on the seabed. Fisheries Research, 99: 234–238.

Ojeda-Martinez, C., Bayle-Sempere, J. T., Sanchez-Jerez, P., Salas, F., Stobart, B., Goni, R., Falcón, J. M., *et al.* 2011. Review of the effects of protection in marine protected areas: current knowledge and gaps. Animal Biodiversity and Conservation, 34: 191–203.

Olsen, E. M., Knutsen, H., Gjøsaeter, J., Jorde, P. E., Knutsen, J. A., and Stenseth, N. C. 2004. Life-history variation among local populations of Atlantic cod from the Norwegian Skagerrak coast. Journal of Fish Biology, 64: 1725–1730.

Orr, H. G., Simpson, G. L., des Clers, S., Watts, G., Hughes, M., Hannaford, J., Dunbar, M. J., *et al.* 2014. Detecting changing river temperatures in England and Wales. Hydrological Processes, 29: 752–766.

Osenberg, C. W., Shima, J. S., Miller, S. L., and Stier, A. C. 2011. Assessing effects of marine protected areas: confounding in space and possible solutions. *In* Marine Protected Areas. A multidisciplinary approach, pp. 143–167.

Pastoors, M. 2000. Effects of a partially closed area in the North Sea (‘plaice box’) on stock development of plaice. ICES Journal of Marine Science, 57: 1014–1022.

Patrick, W. S., and Link, J. S. 2015. Myths that Continue to Impede Progress in Ecosystem-Based Fisheries Management. Fisheries, 40: 155–160.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., Watson, R., *et al.* 2002. Towards sustainability in world fisheries, 418: 689–695.

Pauly, D., Watson, R., and Alder, J. 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 360: 5–12.

Pet, J. S., Mous, P. J., Muljadi, A. H., Sadovy, Y. J., and Squire, L. 2005. Aggregations of Plectropomus areolatus and Epinephelus fuscoguttatus (groupers, Serranidae) in the Komodo National Park, Indonesia: Monitoring and Implications for Management. Environmental Biology of Fishes, 74: 209–218.

Pickett, G., Kelley, D, and Pawson, M. 2004. The patterns of recruitment of sea bass, Dicentrarchus labrax L. from nursery areas in England and Wales and implications for fisheries management. Fisheries Research, 68: 329–342.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Team. 2013. nlme: Linear and Nonlinear Mixed Effects Models.

Pitcher, T. J., and Cheung, W. W. L. 2013. Fisheries: Hope or despair? Marine pollution bulletin: 1–11.

Potts, T., O'Higgins, T., and Hastings, E. 2012. Oceans of opportunity or rough seas? What does the future hold for developments in European marine policy? Philosophical transactions. Series A, Mathematical, physical, and engineering sciences, 370: 5682–700.

Priede, I. G., Bagley, P. M., and Smith, K. L. 1994. Seasonal Change in Activity of Abyssal Demersal Scavenging Grenadiers Coryphaenoides (Nematonurus) armatus in the Eastern North Pacific Ocean. Limnology and Oceanography, 39: 279–285.

Priede, I. G., and Merrett, N. 1998. The relationship between numbers of fish attracted to baited cmaeras and population density: studies on demersal grenadiers Coryphaenoides

(Nematonurus) armatus in the abyssal NE Atlantic Ocean. Fisheries Research, 36: 133–137.

Priede, I. G., Smith, K. L., and Armstrong, J. D. 1990. Foraging behavior of abyssal grenadier fish: inferences from acoustic tagging and tracking in the North Pacific Ocean. Deep-Sea Research, 37: 81–101.

Quesne, W. J. F. Le, and Codling, E. A. 2009. Managing mobile species with MPAs : the effects of mobility , larval dispersal , and fishing mortality on closure size: 122–131.

R Development Core Team (2015). R: a language and environment for statistical computing (R Foundation for Statistical Computing). https://www.r-project.org/.

Reiss, H., Kröncke, I., and Ehrich, S. 2006. Estimating the catching efficiency of a 2-m beam trawl for sampling epifauna by removal experiments. ICES Journal of Marine Science, 63: 1453–1464.

Rhodes, K. L., and Sadovy, Y. 2002. Temporal and spatial trends in spawning aggregations of camouflage grouper , Epinephelus polyphekadion , in Pohnpei , Micronesia. Environmental Biology of Fishes, 63: 27–39.

Rice, A. L., and Chapman, C. J. 1971. Observations on the burrows and burrowing behaviour of two mud-dwelling decapod crustaceans, Nephrops norvegicus and Goneplax rhomboides. Marine Biology, 20: 330–342.

Rice, J., Moksness, E., Attwood, C., Brown, S. K., Dahle, G., Gjerde, K. M., Grefsrud, E. S., *et al.* 2012. The role of MPAs in reconciling fisheries management with conservation of biological diversity. Ocean and Coastal Management, 69: 217–230.

Rigby, C., and Simpfendorfer, C. A. 2015. Patterns in life history traits of deep-water chondrichthyans. Deep-Sea Research Part II: Topical Studies in Oceanography, 115: 30–40.

Rijnsdorp, A. D., Bastardie, F., Bolam, S. G., Buhl-Mortensen, L., Eigaard, O. R., Hamon, K. G., Hiddink, J. G., *et al.* 2016. Towards a framework for the quantitative assessment of trawling impact on the seabed and benthic ecosystem. Ices Journal of Marine Science, 73: 127–138.

Ripley, B., Venables, B., Bates, D. M., Firth, D., Hoernik, K., and Gebhardt, A. 2015. Package ‘ MASS ’.

Roberts, C. M., and Sargant, H. 2002. Fishery benefits of fully protected marine reserves : why habitat and behavior are important. Natural Resource Modeling, 15:487-507.

Rose, G. a. 1993. Cod spawning on a migration highway in the north-west Atlantic. Nature, 366: 458–461.

Rose, G. a., and Kulka, D. W. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (Gadus morhua) declined. Canadian Journal of Fisheries and Aquatic Sciences, 56: 118–127.

Russ, G. R., and Alcala, A. C. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. Oecologia, 138: 622–7.

Russ, G. R., Alcala, A. C., Maypa, A. P., Calumpong, H. P., and White, A. T. 2004. Marine Reserve Benefits Local Fisheries. Ecological Applications, 14: 597–606.

Sadovy, Y., and Domeier, M. 2005. Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs, 24: 254–262.

Sale, P. F., Cowen, R. K., Danilowicz, B. S., Jones, G. P., Kritzer, J. P., Lindeman, K. C., Planes, S., *et al.* 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology & Evolution, 20: 74–80.

Samoilys, M. A., and Carlos, G. 2000. Determining methods of underwater visual census for estimating the abundance of coral reef fishes. Environmental Biology of Fishes, 57: 289–304.

Sciberras, M., Jenkins, S. R., Kaiser, M. J., Hawkins, S. J., and Pullin, A. S. 2013. Evaluating the biological effectiveness of fully and partially protected marine areas. Environmental Evidence, 2: 4-35.

Shin, Y. J., Bundy, A., Shannon, L. J., Simier, M., Coll, M., Fulton, E. A., Link, J. S., *et al.* 2010. Can simple be useful and reliable? Using ecological indicators to represent and compare the states of marine ecosystems. ICES Journal of Marine Science, 67: 717–731.

Siceloff, L., and Howell, W. H. 2013. Fine-scale temporal and spatial distributions of Atlantic cod (Gadus morhua) on a western Gulf of Maine spawning ground. Fisheries Research, 141: 31–43.

Simpson, E. H. 1949. Measurement of Diversity. Nature, 163.

Skjaeraasen, J. E., Meager, J. J., Karlsen, O., Hutchings, J. a., and Ferno, A. 2011. Extreme spawning-site fidelity in Atlantic cod. ICES Journal of Marine Science, 68: 1472–1477.

Smith, S. G., Ault, J. S., Bohnsack, J. a., Harper, D. E., Luo, J., and McClellan, D. B. 2011. Multispecies survey design for assessing reef-fish stocks, spatially explicit management performance, and ecosystem condition. Fisheries Research, 109: 25–41.

SNH. 2016. Scottish Natural Heritage Commissioned Report No. 406. Descriptions of Scottish Priority Marine Features (PMFs). http://www.snh.org.uk/pdfs/publications/commissioned_reports/406.pdf

STECF. 2007. Evaluation of Closed Area Schemes (SGMOS-07-03).

Stephenson, R. L. 1999. Stock complexity in fisheries management : a perspective of emerging issues related to population sub-units. Fisheries Research, 43: 247–249.

Stewart-Oaten, A., Murdoch, W. W. ., and Parker, K. R. 1986. Environmental Impact Assessment: ‘Pseudoreplication’ in Time? Ecology, 67: 929–940.

Stige, L. C., Ottersen, G., Brander, K., Chan, K. S., and Stenseth, N. C. 2006. Cod and climate: Effect of the North Atlantic Oscillation on recruitment in the North Atlantic. Marine Ecology Progress Series, 325: 227–241.

Stobart, B., García-Charton, J. a., Espejo, C., Rochel, E., Goñi, R., Reñones, O., Herrero, A., *et al.* 2007. A baited underwater video technique to assess shallow-water Mediterranean fish assemblages: Methodological evaluation. Journal of Experimental Marine Biology and Ecology, 345: 158–174.

Sumaila, U. R., Lam, V. W. Y., Miller, D. D., Teh, L., Watson, R., Zeller, D., Cheung, W. W. L., *et al.* 2015. Winners and losers in a world where the high seas is closed to fishing. Scientific Reports, 5: 8481.

Swartz, W., Sala, E., Tracey, S., Watson, R., and Pauly, D. 2010. The spatial expansion and ecological footprint of fisheries (1950 to present). PLoS ONE, 5: 3–8.

Temming, A., Floeter, J., and Ehrich, S. 2007. Predation Hot Spots: Large Scale Impact of Local Aggregations. Ecosystems, 10: 865–876.

The European Commission. 2007. Communication from the Commission to the Council and the European Parliament on Review of the Management of Deep-sea Fish Stocks.

The European Commission. 2008. Directive 2008/56/EC of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). Official Journal of the European Union.

The European Commission. 2009. Council Regulation (EC) No 43/2009 of 16 January 2009 fixing for 2009 the fishing opportunities and associated conditions for certain fish stocks and groups of fish stocks, applicable in community waters and, for community vessels, in waters where catch l. Official Journal of the European Union, L22: 1–205.

The European Commission. 2012. Proposal for a regulation of the European Parliament and of the council establishing specific conditions to fishing for deep-sea stocks in the North-East Atlantic and provisions for fishing in international waters of the North-East Atlantic and repealing .

The European Commission. 2013. REGULATION (EU) No 1380/2013 on the Common Fisheries Policy, amending Council Regulations (EC) No 1954/2003 and (EC) No 1224/2009 and repealing Council Regulations (EC) No 2371/2002 and (EC) No 639/2004 and Council Decision 2004/585/EC. Official Journal of the European Union.

The European Commission. 2015. Eurostat Fisheries database. http://ec.europa.eu/eurostat/web/fisheries/data/da

The Scottish Government. 2014a. Small Isles Nature Conservation Marine Protected Area Order. Scottish Ministerial Order.

The Scottish Government. 2014b. Clyde 2020 Summit. Report published by Marine Scotland.

Thorpe, R. B., Dolder, P. J., Reeves, S., Robinson, P., and Jennings, S. 2014. Assessing fishery and ecological consequences of alternate management options for multispecies fisheries. ICES Journal of Marine Science, 71: 236–240.

Thrush, S. F., Hewitt, J. E., Funnell, G. a, Cummings, V. J., Ellis, J., Schultz, D., Talley, D., *et al.* 2001. Fishing disturbance and marine biodiversity: role of habitat structure in simple soft-sediment. Marine Ecology-Progress Series, 221: 255–264.

Thurstan, R. H., Brockington, S., and Roberts, C. M. 2010. The effects of 118 years of industrial fishing on UK bottom trawl fisheries. Nature communications, 1: 15

Tillin, H., Hiddink, J., Jennings, S., and Kaiser, M. J. 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Marine Ecology Progress Series, 318: 31–45.

Trenkel, V. M., Le Loc'h, F., and Rochet, M.-J. 2007. Small-scale spatial and temporal interactions among benthic crustaceans and one fish species in the Bay of Biscay. Marine Biology, 151: 2207–2215.

UNCLOS. 1982. United Nations Convention on the Law of the Sea, signed at Montego Bay, Jamaica, on 10 December 1982.

Underwood, a. J. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. Journal of Experimental Marine Biology and Ecology, 161: 145–178.

Unsworth, R. K. F., Peters, J. R. R., McCloskey, R. M. M., and Hinder, S. L. L. 2014. Optimising stereo baited underwater video for sampling fish and invertebrates in temperate coastal habitats. Estuarine, Coastal and Shelf Science, 150: 1–7.

van Denderen, P., Bolam, S., Hiddink, J. G., Jennings, S., Kenny, a, Rijnsdorp, A. D., and van Kooten, T. 2015. Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. Marine Ecology Progress Series, 541: 31–43.

van Overzee, H., and Rijnsdorp, A. D. 2015. Effects of fishing during the spawning period: implications for management. Reviews in Fish Biology and Fisheries, 25: 65–83.

Vandeperre, F., Higgins, R. M., Sánchez-Meca, J., Maynou, F., Goñi, R., Martín-Sosa, P., Pérez-Ruzafa, A., *et al.* 2011. Effects of no-take area size and age of marine protected areas on fisheries yields: a meta-analytical approach. Fish and Fisheries, 12: 412–426.

Vergnon, R., and Blanchard, F. 2006. Evaluation of trawling disturbance on macrobenthic invertebrate communities in the Bay of Biscay, France: Abundance biomass comparison (ABC method). Aquatic Living Resources, 19: 219–228.

Villasante, S., Morato, T., Rodriguez-Gonzalez, D., Antelo, M., Österblom, H., Watling, L., Nouvian, C., *et al.* 2012. Sustainability of deep-sea fish species under the European Union Common Fisheries Policy. Ocean & Coastal Management, 70: 31–37.

Watson, D., Anderson, M., Kendrick, G., Nardi, K., and Harvey, E. S. 2009. Effects of protection from fishing on the lengths of targeted and non-targeted fish species at the Houtman Abrolhos Islands, Western Australia. Marine Ecology Progress Series, 384: 241–249.

Watson, D. L., Harvey, E. S., Anderson, M. J., and Kendrick, G. a. 2005. A comparison of temperate reef fish assemblages recorded by three underwater stereo-video techniques. Marine Biology, 148: 415–425.

Watson, D. L., Harvey, E. S., Fitzpatrick, B. M., Langlois, T. J., and Shewdrawi, G. 2010. Assessing reef fish assemblage structure: how do different stereo-video techniques compare. Marine Biology, 157: 1237–1250.

Watson, R., Nowara, G. B., Hartmann, K., Green, B. S., Tracey, S. R., and Carter, C. G. 2015. Marine foods sourced from farther as their use of global ocean primary production increases. Nature Communications, 6: 7365.

Watson, R., and Quinn II, T. J. 1997. Performance of transect and point count underwater visual census methods. Ecological Modelling, 104: 103–112.

WGEF, I. 2010. ICES WGEF REPORT 2010 Report of the Working Group on Elasmobranch Fishes (WGEF). 22-29 pp.

Willis, T. J., and Babcock, R. C. 2000. A baited underwater video system for the determination of relative density of carnivorous reef fish. Marine and Freshwater Research, 51: 755–763.

Willis, T. J., Millar, R. B., and Babcock, R. C. 2003. Protection of exploited fish in temperate regions: high density and biomass of snapper Pagrus auratus (Sparidae) in northern New Zealand marine reserves. Journal of Applied Ecology, 40: 214–227.

Wood, S. N. 2013. Package ‘ mgcv ’.

Worm et al., B. 2006. Impacts of Biodiversity Loss on Ocean Ecosystem Services. Science, 314: 787–790.

Worm, B., and Branch, T. A. 2012. The future of fish. Trends in ecology & evolution, 27: 594–9.

Worm, B., Hilborn, R., Baum, J. K., Branch, T. a, Collie, J. S., Costello, C., Fogarty, M. J., *et al.* 2009. Rebuilding global fisheries. Science (New York, N.Y.), 325: 578–85.

Wright, P. J. 2014. Are there useful life history indicators of stock recovery rate in gadoids? ICES Journal of Marine Science.

Wright, P. J., Galley, E., Gibb, I. M., and Neat, F. C. 2006a. Fidelity of adult cod to spawning grounds in Scottish waters. Fisheries Research, 77: 148–158.

Wright, P. J., Millar, C. P., and Gibb, F. M. 2011. Intrastock differences in maturation schedules of Atlantic cod, Gadus morhua. ICES Journal of Marine Science, 68: 1918–1927.

Wright, P. J., Neat, F. C., Gibb, F. M., Gibb, I. M., and Thordarson, H. 2006b. Evidence for metapopulation structuring in cod from the west of Scotland and North Sea. Journal of Fish Biology, 69: 181–199.

Wright, P. J., Tobin, D., Gibb, F. M., and Gibb, I. M. 2010. Assessing nursery contribution to recruitment: relevance of closed areas to haddock Melanogrammus aeglefinus. Marine Ecology Progress Series, 400: 221–232.

Wright, P. J., and Trippel, E. A. 2009. Fishery-induced demographic changes in the timing of spawning : consequences for reproductive success : 283–304.

WSSD. 2002. United Nations Report on the World Summit on Sustainable Development. , South Africa.. Johannesburg. 74 pp.

Yoneda, M., and Wright, P. J. 2004. Temporal and spatial variation in reproductive investment of Atlantic cod Gadus morhua in the northern North Sea and Scottish west coast. Marine Ecology Progress Series, 276: 237–248.

Zeller, D., Stoute, S. L., and Russ, G. R. 2003. Movements of reef fishes across marine reserve boundaries : effects of manipulating a density gradient. Marine Ecology Progress Series, 254: 269–280.

Zuur, A. F., Ieno, E. N., and Elphick, C. S. 2010. A protocol for data exploration to avoid common statistical problems: 3–14.

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. a., and Smith, G. M. 2009. Mixed effects models and extensions in ecology with R. Statistics for Biology and Health. Springer New York, New York, NY.