Elliott, Sophie Ann Marie (2016) *Exploring the role of coastal environments for gadoid fish using stereo-video imagery*. PhD thesis.

Exploring the role of coastal environments for gadoid fish using stereo-video imagery

Sophie Anne Marie Elliott

MSc, The Autonomous University of Madrid

BSc, University of Leeds

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

August 2016

Abstract

With increasing pressures on marine ecosystems and little recovery being observed in commercially important fish, it is essential to understand ecosystem effects on species. Unfortunately, in many cases the habitat requirements of commercially important species are not well understood. Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) were of commercial importance within the Firth of Clyde, west coast of Scotland prior to the late 20th century. However, over fishing and other anthropogenic impacts led to declines in all three species. Despite the prohibition of targeted fishing for these gadoids in much of the Firth of Clyde, they have still not recovered and scientific bottom trawl surveys have shown that 90% of the biomass is made up of small *M. merlangus*.

With increased concern regarding the state of the world's marine environment, efforts to implement ecosystem based fisheries management and restore ecosystems through spatially explicit management measures have developed. The array of ecosystem based research, management and monitoring initiatives has led to the use of a range of habitat-related terminology with different interpretations of the terms. Inconsistencies in terminology not only cause confusion between studies, but also make it difficult to understand the ecological requirements of fish. The second chapter of this PhD reviews the current terminology and sets the scene for the major habitat-related concepts used throughout the thesis.

Photogrammetric techniques were used to collect data on gadoid distribution, abundance and size from June to September in 2013 and 2014. The study site was a recently designated Marine Protected Area (MPA) within the Firth of Clyde, west coast of Scotland. The two photogrammetric techniques used were stereo-video SCUBA transects and Stereo Baited Remote Underwater Video (SBRUV) deployments. 31 SCUBA transects were conducted in 2013 and a total of 258 SBRUV deployments were conducted over the two data collection periods. SBRUV deployments were chosen as the main technique to collect demersal fish and benthos related data due to the ability to collect an increased number of deployments at higher resolution, in addition to avoiding logistical constraints with SCUBA methods.

From both SCUBA transects and SBRUV deployments, a higher abundance of *G. morhua* was observed in gravel-pebble substratum containing maerl and medium density algae, than boulder-cobble substratum with high algal cover or sandy areas with little or no macrophyte cover. A higher relative abundance of *G. morhua* was also observed in shallow and sheltered environments. Both *M. aeglefinus* and *M. merlangus* were observed in higher relative abundance in deeper sand and mud substratum types. All three species were observed in higher relative abundance in areas of increased benthic and demersal species diversity. On average *G. morhua* were smaller than *M. aeglefinus* and *M. merlangus* and exhibited the lowest growth rates.

Seabed ground-truthed data from the stereo-video methods in combination with a range of observed environmental variables were used to predict substratum type, distribution and extent within the MPA. The predicted seabed map was used to understand landscape effects on gadoid distribution. *G. morhua* were observed in more heterogeneous landscapes than *M. aeglefinus* or *M. merlangus*. An increase in *M. merlangus* relative abundance was also observed with increasing substratum extent.

The stereo-video photogrammetric methods in combination with the predicted substratum mapping have provided us with a better understanding of gadoid fish habitat requirements. This study has also provided fish and benthos baseline data within the MPA, trialled the use of non-damaging and extractive fisheries independent monitoring methods, and contributed evidence to support potential fisheries management options. The techniques used in this thesis could be rolled out on a larger scale across the UK to support sensitive seabed and fish monitoring and management measures.

Table of contents

List of tables

List of figures

Acknowledgements

This thesis would not have been possible without the help and support from those around me. Firstly I would like to thank David Bailey for his support and encouragement throughout the thesis and during fieldwork data collection. Thanks to my other supervisors, Bill Turrell for his support and encouragement in the production of my chapters and Mike Heath for his advice and contribution. Thanks to Jason Matthiopoulos, my assessor for his critique and guidance to help me pull together a cohesive thesis. Thanks also to those from the University of Glasgow spatial group, especially Paul Johnson, James Grecian and Grant Hopcraft for their guidance and support in the realms of statistical modelling and Elena Argaña Pérez for GIS support.

I am extremely thankful to the funders of my PhD, including the ClimateXChange centre for providing me with my scholarship, Marine Scotland (Clyde 2020) and Scottish Natural Heritage who generously supported my fieldwork funding. In particular I would like to thank David Donnan and Bill Turrell who supported this process and encouraged me throughout my thesis and prior to. Thanks also to the dive team at SAMS, in particular Martin Sayer and NERC National facility for Scientific Diving (Grant NFSD/13/01) for helping me improve my dive techniques and achieve CMAS level 3*. Thanks to Hanumant Singh and Yogesh Girdhar for showing me the world of automated imagery analysis and making me feel welcome at Wood Hole Oceanographic Institute. I would also like to thank Peter Auster who independently reviewed Chapter 2 prior to publication, Martin Sayer and Richard Unsworth who independently reviewed Chapter 3 prior to publication and the editors Phil Smith and Kath Sloman who edited these two papers.

I am extremely thankful to COAST and Millport staff who supported me in field work data collection. Especially Howard Wood from COAST, helping in all tasks from splicing ropes, collecting data, providing ground-truthed data on seabed types around South Arran, taking me out on COAST's RIB and encouragement throughout the thesis. Thanks to Russ Cheshire for also taking me out on his RIB, and always making me smile. Thanks to Bob McLaren for letting us use his swimming pool on Arran for calibration of the cameras. Thanks to the staff at

Millport especially Tom Stevenson and Duncan waking up at ridiculous hours of the morning to be able to steam us to South Arran in time for a day's data collection and always with a joke or story to tell.

I would also like to thank Rosanna Milligan who contributed to the paper for Chapter 2 and Paullina Ahti who contributed to video analysis and the paper for Chapter 3. Thanks to Brooke Allan who supported in data collection for 2014 and video analysis for Chapter 4. Thanks to Katie Thomson and Hannah Walkinshaw who supported with CPC analysis for the baited camera work. Thanks also to all those who support in data collection in particular Jo Clarke, Connor Willmott, Charlotte Hopkins and Debbie McNeil. Thanks to Alessandro Sabatino for providing modelled point data on tidal speed information. Thanks to Nosrat Mirzai for support with electrical equipment malfunctions and encouragement. Thanks to Jo Clarke, Sonya Auer, Jose Noguera and Dan Haydon for advice on certain chapters, encouragement and support. A special thanks to my family in particularly my father John Elliott. Finally, I would like to thank my partner Kike Gil Lariño for always being there for me and encouraging me.

Author's Declaration

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

Sophie Elliott

Abbreviations and acronyms

AGP: Algal-gravel-pebble

AIC: Akaike's Information Criterion

ANOSIM: ANalysis Of SIMilarities

ANOVA: Analysis Of Variance Analysis

AUC: Area Under the Curve

AUV: Autonomous Underwater Vehicle

BACI: Before/After and Control/ Impact survey

CBD: Convention on Biological Diversity

CFP: Common Fisheries Policy

BGS: British Geological1 Survey

COAST: Community Of Arran Seabed Trust

CPC: Coral Point Count

DATRAS: DAtabase of TRAwl Surveys

d.f.: Degrees of Freedom

EBFM: Ecosystem Based Fisheries Management

EEZ: Exclusive Economic Zone

EFH: Essential Fish Habitat

EU: European Union

FAO: Food and Agriculture Organization

FVCOM: Finite-Volume Community Ocean Model

GES: Good Environmental Status

GIMP: GNU Image Manipulation Program

GIS: Geographical Information System

GL(M)M: Generalised Linear (Mixed) Model

GMT: Greenwich Mean Time

GPS: Global Positioning System

ICES: The International Council for the Exploration of the Sea

IUCN: International Union for Conservation of Nature

JD: Julian Day **JDg:** Grouped Julian day

JPEG: Joint Photographic Experts Group

JNCC: Joint Nature Conservation Committee

L: likelihood
LM(M): Linear (Mixed) Model

MaxN: The maximum number of individuals of the same species appearing in a frame at the same time

MMO: Marine Management Organisation

MPA: Marine Protected Area

MSFD: Marine Strategy Framework Directive

MSY: Maximum Sustainable Yield

NBN: Negative Binomial

NCMPA: Nature Conservation Marine Protected Area

nMDS: Non-metric Multi-Dimensional

OMBAR: Oceanography and Marine Biology: An Annual Review

OSPAR: The Convention for the Protection of the Marine Environment of the North-East Atlantic

***P*:** Probability

PCA: Principal Component Analysis

PERMANOVA: PERMutation Analysis Of Variance Analysis

PMF: Priority Marine Feature

PRIMER: Plymouth Routines in Multivariate Ecological Research

RIB: Rigid Inflatable Boat

RMS: Root Mean Square

ROC: Receiver Operating Characteristic

ROV: Remotely Operated Vehicle

SAMS: The Scottish Association for Marine Science

SBRUV: Stereo Baited Remote Underwater Video

SCUBA: Self-Contained Underwater Breathing Apparatus

S.D.: Standard Deviation

SFA: Sustainable Fisheries Act

SIMPER: SIMilarity PERcentages

SNH: Scottish Natural Heritage

SSB: Spawning Stock Biomass

TFA: Time to First Arrival

UK: United Kingdom

UN: United Nations

USA: United States of America

UVC: Underwater Visual Census

VIF: Variance Inflation Factor

VME: Vulnerable Marine Ecosystems

WGS: World Geodetic System

Chapter 1. General introduction

The human population is now greater than seven billion and is causing ever increasing pressure on the natural resources that we depend upon (Costanza 1999; Sanderson et al. 2002; Halpern et al. 2008; Worldmeters 2015). The increase in human population combined with growing demands on the world's resources, affects our wildlife populations through direct mortality of target species and land or seabed transformation (Dobson et al. 1997; Sanderson et al. 2002; Foley et al. 2005; FAO 2014). Land and seabed transformation causes indirect mortality and reduces reproductive success by removing or inhibiting access to essential habitat components (Box 2.3.1, Chapter 2) for the survival of individuals and species (Turner 1996; Dobson et al. 1997; Sanderson et al. 2002). Habitat components may include food resources for survival or refuges from predation or environmental pressures (Hammer et al. 1993; Sodhi et al. 2004, Beaumont et al. 2007; Chapter 2). Land and seabed transformation has been cited as the single greatest threat to species diversity (Sanderson et al. 2002; Lotze 2006; Crain et al. 2009). Reductions in population sizes from hunting or harvesting, or from land or seabed transformation can also cause imbalances to community structures and ecosystem functioning, exacerbating extinction rates (Hammer et al. 1993; Dobson et al. 1997).

Marine ecosystems are the most harvested and economically important wild ecosystems on earth (Costanza et al. 1997; Costanza 1999; FAO 2014). They have also received little attention (Costanza 1999; Dulvy et al. 2003), causing difficulties in identifying anthropogenic impacts and extinction rate (Dulvy et al. 2003). Marine ecosystems not only provide us with important sources of food worldwide but also raw materials such as fertiliser from seaweed, fishmeal for aquaculture and farming, and increasingly the basis for pharmaceuticals products (Holmlund and Hammer 1999; Beaumont et al. 2008; Crain et al. 2009). The oceans and their biodiversity are vital for climate regulation and their biogenic structures have been found to be essential in alleviating damage from flooding and storms (Costanza 1999; Beaumont et al. 2008). Maintaining species diversity has been observed to enhance ecosystem productivity, stability, goods and services including food resources (Holmlund and Hammer 1999; Worm et al. 2006; Beaumont et al. 2008). Consequently there is a large concern regarding the effects of biodiversity loss on ecosystems and human well-being (Hammer et al. 1993; Liquete et al. 2016).

1.1. Anthropogenic pressures on marine ecosystems

Some of the most important anthropogenic pressures on marine ecosystems include climate change and commercial fishing activity (Worm et al. 2006; Halpern et al. 2007; 2008). Physiological and biological effects of climate change and ocean acidification on fish include phenological changes, productivity effects and distribution changes (Heath et al. 2012). For fish occupying coastal areas or shallow waters there may also be changes in rainfall and storminess and reduced availability of calcifying species such as corals and bivalves (Cheung et al. 2012; Heath et al. 2012). Indirect impacts from climate change may occur through the displacement of fishing effort away from offshore areas and towards coastal areas, should storms inhibit offshore fishing activities (Pinnegar et al. 2010; Cheung et al. 2012).

Harvest rates by large fisheries may have profound impacts on the targeted species they catch but may also impact non-target species and benthos (Hammer et al. 1993; Holmlund and Hammer 1999; Crain et al. 2009). Intense fishing over the years has led to changes in the reproductive age of adult gadoids and today, spawning stocks consist of smaller, younger adults (Hislop 1996; Hutchings and Reynolds 2004; Ottersen et al. 2006). Since spawning-stock biomass is made up of smaller-sized cohorts, there may be changes in the quantity and quality of eggs produced, particularly since fecundity of younger females is generally lower than that of mature females (Hislop 1996; Scott et al. 1999). In addition, the reduction of older larger spawners may influence the timing of the spawning season and also lead to shorter seasons (Hislop 1996; Scott et al. 1999). Indirect effects of fishing can however have more important impacts on ecosystem structure and function than the removal of fish (Hammer et al. 1993; Holmlund and Hammer 1999; Lotze 2006).

Certain fishing gear technologies can impact upon marine benthos through physical disturbance, abrasion and bycatch (Auster et al. 1996; Jennings and Kaiser 1998; Kaiser et al. 2006; Perry et al. 2010). Demersal trawling and dredging can also have severe consequences on benthos structure, reducing the structural rugosity and heterogeneity (Box 2.3.1, Chapter 2) of the seafloor (Auster et al. 1996; Jennings and Kaiser 1998; Freese et al. 1999; Kaiser et al. 2006). The combined effects can lead to overall reduced benthic productivity (Hammer et al. 1993; Jennings and Kaiser 1998). Such changes could also potentially alter the suitability of substrata for species within the area (Auster 1998; Jennings and Kaiser 1998; Ryan and Bailey 2012). Thurstan & Roberts (2010) have also implicated the opening of nearshore waters (< 3 nm) to trawling as the cause of a collapse in fish landings due to benthic impacts from the fishing gear.

1.2. The importance of coastal areas

To date some 30,000 different fish species have been identified (Froese & Pauly, 2015). Global catch (reported and estimated unreported) of both finfish and marine invertebrates peaked in 1996 at 130 million tonnes, but have since declined at a mean rate of 1.22 million tonnes per year (Pauly and Zeller 2016). Global discards are estimated to be 10.3 million tons/year (Pauly and Zeller 2016). Costanza et al. (2014) estimated the global value of coastal areas as one of the most important ecosystems, providing approximately $27.7 trillion US$/year. Coastal areas are also thought to contain some of the most heterogeneous and biodiverse ecosystems (Airoldi and Beck 2007; Rogers et al. 2014). Nonetheless, coastal areas are subject to particularly high anthropogenic pressures since most of the world’s population live near and depend on coastal ecosystems (Costanza 1999; Halpern et al. 2007, 2008; Beaumont et al. 2008).

Coastal areas are also known to be important nursery areas for a variety of marine organisms e.g. gag grouper (*Mycteroperca microlepis*, Goode and Bean, 1879), herring (*Clupea harengus*. L) and Atlantic cod (*Gadus morhua*. L) (Beck et al. 2001; Seitz et al. 2014; Liquete et al. 2016). Nursery areas are defined as areas that contribute more than average production of individuals that recruit to an adult population (Beck et al. 2001). However, understanding what makes these nursery areas important, where these areas are, and the condition they need to be in to provide these vital services, can be quite difficult when considering highly mobile species such as gadoid fish (Hammer et al. 1993; Langton et al. 1996; Gaillard et al. 2010).

1.3. Towards good environmental status

Since the United Nations 1992 Convention on Biological Diversity (CBD), efforts have been put in place to try and recover and protect species and their habitats (Sinclair et al. 2002; Potts et al. 2012). One of the major initiatives which have been used to protect species and their habitats has been by the use of spatial management measures such as Marine Protected Areas (MPAs) (Dobson et al. 1997). Significant efforts have been put in place to develop MPAs. However, for these to be of benefit to fish, an understanding of their life cycles and habitat is essential (Rice 2005; Johnson 2012). Current methods to regulate fish stocks in Europe are primarily through the Common Fisheries Policy (CFP). Efforts to regulate fishing via the CFP largely include setting total allowable catches, controlling fishing effort and setting rules on fishing gear adaptations to reduce bycatch, in addition to the introduction of some fisheries closures (EC 2009; Hilborn 2011; Fernandes and Cook 2013). An assessment of the effectiveness of a seasonal spawning area protection in the Firth of Clyde showed that it had no effect on trends in the relevant *G. morhua* stock compared to other stocks without protection (Clarke et al. 2015). Rijnsdorp et al. (2001) observed a similar trend with another *G. morhua* fisheries closures in the North Sea. While little is known about how much MPAs and fishery closures are doing for fish populations it is clear that many were implemented without sufficient knowledge of the habitat requirements of fish (Pikitch et al. 2004; Rice 2005).

Conventional fisheries management mechanisms are recognised to be insufficient (Pikitch et al. 2004; Hilborn 2011) to recover fish stocks. More ecosystem based, multisector and multi-objective management methods are now required (Sinclair et al. 2002; Crain et al. 2009; Potts et al. 2012; Chapter 2), as proposed through Ecosystem Based Management (Pikitch et al. 2004; Hilborn 2011; Potts et al. 2012). The relatively new Marine Strategy Framework Directive (MSFD) brings together different pieces of European legislation with the aim to achieve Good Environmental Status (GES) by 2020 and implement more of an

Ecosystem Based Management (EU 2008). Under the MSFD, achievement of a wide range of Descriptors is required to demonstrate GES (EU 2008). Some descriptors of the relevant to fish and their habitat (Box 2.3.1, Chapter 2) include maintaining biological diversity (D1) and seafloor integrity (D6), and reducing pollution (D8 - 11). For each of these descriptors a set of relevant indicators and targets need to be established so that progress towards GES can be assessed (Borja et al. 2013). Nonetheless, there are still many gaps with regard to the current understanding of human activities and pressures on marine ecosystems. Particular problems include our lack of knowledge of pre-disturbance conditions from which GES could be defined and how to combine the indicators and descriptors into an assessment of environmental status holistically (McQuatters-Gollop 2012; Borja et al. 2013).

1.4. Gadoid fish stocks and their decline

Throughout the North Atlantic, many fisheries have declined, largely due to intensive fishing activities over the last few centuries (Myers et al. 1996; Hutchings and Reynolds 2004; Thurstan and Roberts 2010). Particularly affected are gadoid species (Hutchings and Reynolds 2004). In the UK the majority of fish are landed in Scottish waters (Thurstan and Roberts 2010; MMO, 2015). In recent years gadoid fish stocks have been reduced and, unlike some gadoid stocks in the North Sea which have been better studied (Bailey et al. 2011), some stocks of commercial importance to the west coast of Scotland (i.e. *G. morhua*) have shown no recovery (Fernandes and Cook 2013).

Specifically, within the Firth of Clyde, southwest coast of Scotland, gadoid fishing was once an important fishery (Thurstan and Roberts 2010). However, overexploitation and improved methods of demersal fishing led to crashes in gadoid stocks and other demersal fish stocks (Thurstan & Roberts 2010). Since 1984 the predominant fishery taking place in the Firth of Clyde is for the Norway lobster (*Nephrops norvegicus* L.) (Thurstan & Roberts 2010). Scientific bottom trawl surveys have however shown that 90% of the biomass is made up of small whiting (*Merlangius merlangus* L.) (Heath and Speirs 2012). The EU cod recovery plan introduced in the early 2000s, implemented various fisheries closures (including a spawning closure in the outer Firth of Clyde) and measures to promote the conditions of *G. morhua* stocks (Anon 2001; Kraak et al. 2013). Nonetheless, stocks around the west coast of Scotland, including the Firth of Clyde have not recovered (Fernandes & Cook 2013; Clarke et al. 2015; ICES 2015a-c).

There are various possible reasons for the lack of recovery in gadoid stocks throughout the Atlantic. The latter includes very large scale factors across the northern hemisphere such as climate change effects driving key larval food (*Calanus finmarchicus*, Gunnerus, 1770) further north (Beaugrand et al. 2003; Heath and Lough 2007). This change in abundance may be associated with the warming of seas (Beaugrand et al. 2003; Bundy and Fanning 2005; Heath and Lough 2007). The increase in grey seal (*Halichoerus grypus*, Fabricius, 1791) abundance preying on young *G. morhua* has also been discussed (e.g. O'Boyle & Sinclair 2012; Smout et al. 2014; Cook et al. 2015). Other possible causes for lack of recovery in gadoid fish stocks include mortality from bycatch and misreporting (Thurstan & Roberts 2010; ICES 2015a - c). It is also likely that centuries of fishing pressure have fundamentally altered the ecosystem (Jackson et al, 2001) and the characteristics of the fish in ways that are not automatically redress by reducing fishing activity (Dunlop et al. 2009; Enberg et al. 2009). For instance, while fishing may provide a strong selective pressure towards smaller and earlier reproduction (Heino and Godø 2002; Probst et al. 2013), its cessation does not necessarily provide an equally strong pressure towards later reproduction within the same time period (Enberg et al. 2009).

The three gadoid species studied within this thesis are *G. morhua,* haddock (*Melanogrammus aeglefinus*. L) and *M. merlangus*. All three species are commercially important and valuable species in the UK (MMO; 2014; Barreto & Bailey 2015). During their juvenile stages they are known to occupy coastal areas on the west coast of Scotland and have been subject to overfishing (ICES 2015a – c). *G. morhua* are also listed as a vulnerable species on IUCN red list (IUCN 2015) and both *G. morhua* and *M. merlangus* are listed as a Priority Marine Feature (PMF) to protect under the Scottish Marine Act (SNH 2016). Neither species was chosen as an MPA Search Features (Tyler-Walters et al, 2012) and therefore no MPAs were consequently designated to take into account *G. morhua* or *M. merlangus*. In the case of *G. morhua* this was because they were considered too mobile (SNH 2010) despite closed areas being shown to benefit *G. morhua* in the USA and Norway (Murawski et al. 2000; Moland et al. 2013).

In addition to CFP measures to regulate gadoid fishing activity, the International Council for the Exploration of the Sea's (ICES) provide specific yearly management advice for fish stocks. Advice for 2016 *G. morhua* stocks on the west coast of Scotland (ICES area VIa), is that landings should remain at zero and that bycatch and discards should be minimised (ICES 2015a). The latter is a result of low Spawning Stock Biomass (SSB) and recruitment (ICES 2015a). ICES' management advice on *M. aeglefinus* on the west of Scotland (VIa) is combined with the North Sea (IV) and Skagerrak (IIIa) area since 2014 and states that catches should be no more than 74,854 tonnes (ICES 2015b). However, there is no current agreed management plan for this area, and recruitment and SSB remain low (ICES 2015b). ICES' advice for *M. merlangus* on the West Coast of Scotland (division VIa) for 2016 states that there should be "no directed fisheries and all catches should be minimised" (ICES 2015c). This is as a result of SSB being below the precautionary and limit reference point (B_{pa} and B_{lim}) (ICES 2015c).

1.5. Gadoid life cycle in the west coast of Scotland

1.5.1. Atlantic cod, *Gadus morhua*

G. morhua VIa stocks are distributed widely throughout the west coast of Scotland (Wright et al. 2006a; Barreto & Bailey 2015). Upon reaching maturity between two and four years of age, *G. morhua* aggregate to spawn in large groups (Barreto & Bailey 2015; Clarke et al. 2015). Spawning areas have been documented as occurring in the Hebrides (particularly the Outer) and close to the entrance of the Firth of Clyde from February to June (Wright et al. 2006a; Wright et al. 2006b; Bailey et al. 2011), with peak spawning periods on the west coast thought to be in March (Wright et al. 2006a; Barreto & Bailey 2015). *G. morhua* have pelagic egg and larval stages, which float on the subsurface for several weeks, drifting towards the coast before developing into young pelagic age-0 (commercial fish in their first year of life cycle) *G. morhua* and then settling on the seabed (total length between 30 and 60 mm) in nearshore areas as of late June to July (Magill & Sayer 2004; Juanes 2007; Bastrikin et al. 2014; Chapter 3 and 4). Movement of larvae and pelagic juveniles is thought to be associated with onshore larval transport and settlement during downwellings with retention of juveniles in coastal areas during upwellings (Ings et al. 2008).

Gibb et al. (2007), undertook a study to identify *G. morhua* nursery grounds around Scottish waters. Although the density of 0-age *G. morhua* was generally scarce around much of Scotland’s coast, elevated densities were found within 60 km of the coast, in particular around the Firth of Clyde (100 *G. morhua*.km^{-2}) and isolated areas off Mull (Gibb et al. 2007). The study further confirmed that nursery areas for juvenile *G. morhua* are in shallow areas in depths less than 20 m (Gibb et al. 2007). It is thought that juvenile *G. morhua* remain in such shallow (< 9 m depth), sheltered and structurally rugose substrata (such as maerl and eelgrass) all year round, but are most abundant during late summer through to early autumn (Fromentin et al. 1997; Magill and Sayer 2004; Kamenos 2004).

On the west coast of Scotland juvenile *G. morhua* are thought to begin moving out of shallow waters after their first winter (Magill and Sayer 2004; Bailey et al. 2011) to coarser substrata and areas of high bathymetric relief at depths of 15-120 m (Gregory and Anderson 1997; Cote et al. 2003; Bailey et al. 2011). Movement out of shallow water does how seem to vary between stocks (Bailey et al. 2011). Adults have rich and complex spatial structures which are only partly understood. Nonetheless, adults are thought to remain relatively close to spawning areas all year round (Wright et al. 2006a, Galley et al. 2006). Other studies have shown they migration to natal spawning areas (Wright et al. 2006a; Heath et al. 2008). Although a few studies have been undertaken looking at juvenile *G. morhua* nursery areas around Scotland (e.g. Gibb et al. 2007; Ware 2009), little information exists on fine scale distributions within these nursery areas around the west coast of Scotland (Gibb et al. 2007, Ryan and Bailey 2012) as is available in Canada and the USA e.g. (Lough et al. 1989; Tupper and Boutilier 1995a; 1995b; Gregory and Anderson 1997; Laurel et al. 2003b; Lough 2010).

Important food sources for larvae and juvenile fish include zooplankton such as *C. finmarchicus* (Drinkwater 2005; Heath and Lough 2007; Demain et al. 2011). As juvenile fish develop their diet expands to include crustaceans and polychaetes, and small fish such as plaice (*Pleuronectes platessa*. L) (Ware 2009, Demain et al. 2011; Bastrikin et al. 2014). Foraging in juvenile fish is thought to mostly occur at night to avoid predators (Gibson et al. 1996; Linehan et al. 2001). Mature *G. morhua* primarily feed on capelin (*Mallotus villosus*, O. F. Müller, 1776), *C. harengus* and crustaceans such as *N. norvegicus* (Bundy and Fanning 2005; Lilly et al. 2008). In the absence of other prey, cannibalism has been observed to increase (Uzars 2000; Lilly et al. 2008). Thought to be a crucial factor to population recruitment is the carrying capacity of the environment, particularly since *G. morhua* stocks indicate a high degree of spawning fidelity among repeat spawning fish (Wright et al. 2006a; Heath et al. 2008).

1.5.2. Haddock, *Melanogrammus aeglefinus*

M. aeglefinus are widely distributed around the west coast of Scotland (Barreto and Bailey 2015). *M. aeglefinus* aggregate to spawn between January to May, with peak times between February and March, and at a depth of about 100 m (Gibb et al. 2004; Bailey et al. 2011; Barreto and Bailey 2015). Spawning aggregations have been identified in mid waters to the west of the Outer Hebrides (Heath and Gallego 1998; Gibb et al. 2004; Ware 2009). *M. aeglefinus*, like *G. morhua*, have pelagic eggs which are produced in batches and have been found in the Clyde area, probably as a result of drifting with currents (Gibb, 2004; Ware 2009; Casaretto et al. 2014). Larvae hatch after 90 days (depending on temperature), where they remain pelagic until they settle on the seabed as juveniles (total length 40 - 80 mm) from June to August (Wright et al. 2010). Following settlement juveniles have been observed to demonstrate site fidelity for many weeks (Wright et al. 2010; Demain et al. 2011). They can however, occupy the entire water column (Olsen et al. 2010). Juvenile *M. aeglefinus* have been observed over a range of substrata including sand and gravel (Lough et al. 1989)

Otolith microchemistry studies undertaken by Wright et al. (2010) indicate that relatively small regions (assessed at ICES rectangles scales) may act as important nurseries and that *M. aeglefinus* appear to show site fidelity for many weeks following settlement. Wright et al. (2010) also confirmed that although adult *M. aeglefinus* in offshore west of Scotland waters appear to be derived from inshore juveniles in the west of Scotland; eggs and pelagic larvae from the west coast contribute to the North Sea stock (Heath and Gallego 1997; Wright et al. 2010).

Pelagic *M. aeglefinus* larvae have been observed to begin arriving at coastal areas as of late April and begin occupying demersal areas in June (Bastrikin et al. 2014). *M. aeglefinus* have been associated with inshore areas on the west coast of Scotland and the Clyde Sea, changing depths according to preferred temperature ranges (Perry and Smith 1994; Heath and Gallego 1997). As *M. aeglefinus* mature (September onwards) they have been associated to increasingly deep and relatively less rugose substrata with smaller size particles (Ware 2009; Olsen et al. 2010; Chapter 4). Adult *M. aeglefinus* can reproduce from two years of age, however maturation is usually between 4 - 7 years (40 - 60 cm) (Olsen et al. 2010; Barreto & Bailey, 2015).

The diet of adult *M. aeglefinus* varies with size and time of year but mainly consists of sandeels (*Ammodytes tobianus* L.), Norway pout (*Trisopterus esmarkii*, Nilsson, 1855), and invertebrates such as molluscs and urchins (Demain et al. 2011; Keltz & Bailey 2012). Studies by Demain et al. (2011) and Bastrikin et al. (2014) showed that age-0 *M. aeglefinus* mainly preyed upon crustaceans such as copepods, decapods and fish species such as *Ammodytes* spp.

1.5.3. Whiting, *Merlangius merlangus*

M. merlangus is not a particularly valuable species compared to *M. aeglefinus* and *G. morhua*, they are however caught in high numbers and even discarded as a bycatch species (Barreto and Bailey 2015). West coast *M. merlangus* stocks are widely distributed along the west coast, with higher abundances to the north (Barreto and Bailey 2015). Spawning periods are closely associated with temperature changes around January to June (at depths ranging from 36 – 80 m), as the sea temperature begins to rise (Wright & Trippel, 2009; Bailey et al. 2011). At two years of age females are usually able to spawn and spawning periods can last 14 weeks from February to May, where batches of eggs are produced (Fromentin et al. 1997; Gibb et al. 2004; Barreto and Bailey 2015).

Like *G. morhua* and *M. aeglefinus*, *M. merlangus* spend their first few months in the upper pelagic zones feeding on zooplankton before migrating to sheltered, inshore demersal areas at lengths 30 - 60 mm from June to December (Fromentin et al. 1997; Bailey et al. 2011). Juvenile *M. merlangus*, like the other gadoids are thought to begin moving to more exposed offshore areas from January to the summer period (Hall et al. 1990; Fromentin et al. 1997; Bailey et al. 2011). Little is known about the habitat of *M. merlangus*. However, *in situ* studies by Atkinson et al. (2004) have shown age-1 juveniles are though to select structurally more rugose substrata in response to risk of predation with larger individuals (age-2) aggregating over sand and gravel. In Scotland, adult *M. merlangus* displacement ranges can vary however can be greater than 500 km (Tobin et al. 2010). Age-0 *M. merlangus* substratum association has not been well studied however it is thought that they may not have a particular association other than to seek shelter (Hislop 1996; Fromentin et al. 1997; Bailey et al. 2011). Juvenile *M. merlangus* feed on crustaceans and as they develop they feed increasingly on other fish (Temming et al. 2007; Demain et al. 2011; Bastrikin et al. 2014).

1.6. Juvenile gadoid habitat

Fisheries research has largely concentrated on the target fish populations and only recently has more attention been given to important fish habitat components (Langton et al. 1996; Lindholm et al. 2001; Box 2.3.1, Chapter 2). Potential recovery of gadoid species on the west coast of Scotland depends on an understanding of important habitat components for all life stages (Langton et al. 1996; Cote et al. 2003) which is currently unknown. Numerous studies have been undertaken to understand substrata association of gadoids, particularly in Canada, the USA and Scandinavian countries. However, fine scale distribution and substrata association observations in the UK are few and far between (Gibb et al. 2007; Ryan and Bailey 2012). Studies have also demonstrated varying results with different stocks demonstrating different behavioural traits (Bailey 2011). Further, most current studies have only investigated one or two habitat components (e.g. substrata and depth association), failing to take into consideration a range of abiotic and in particular biotic variables which may affect where a species inhabits (Darwin, 1972; Hall et al. 1997; Gaillard et al. 2010; Chapter 2).

Studies of fish habitat provide a useful insight into the ecology of species (Rice 2005), revealing factors such as predator avoidance, feeding, habitat component association or selection (Box 2.3.1, Chapter 2) and population dynamics (e.g. Cote et al. 2003; Renkawitz et al. 2011; Ryan et al. 2012). Understanding juvenile fish habitat could be particularly important since studies by Olsen & Moland (2010), showed that 75% of juvenile gadoids (*G. morhua*) died in their first year (50% caught by fishers). Understanding habitat information could therefore be important to help managers gain a better understanding of possible areas to protect which is currently being sort around the UK.

A recruitment bottleneck may be occurring where environmental conditions do not facilitate high survival at early life stages and favour conditions for older fish (Svåsand et al. 2000; Fodrie et al. 2009). Insufficient important habitat components at early life stages which is currently unknown, may inhibit the recovery of gadoid populations. Additionally, changes in habitat component quantity and quality (Box 2.3.1, Chapter 2) caused by natural or anthropogenic events, could be used to predict the effects on recruitment (Gibson 1994). Most studies of gadoids in the UK have taken place using commercial catch and standardized trawl surveys (e.g. Ware 2009; Wright et al. 2010). The latter has not resulted in the spatially resolved data needed for detailed understanding of important juvenile gadoid habitat components, which may affect density, growth and survival to adult populations (Langton et al. 1996; Wright et al. 2010).

1.7. Techniques to collect data on juvenile gadoids

A wide variety of methods exist to collect data on fish habitat, these include traditional mechanisms such as trawling which is commonly used for stock assessments, trapping techniques such as the use of seine and fyke nets. Non-traditional techniques include the use of acoustic surveys, egg surveys for plankton, diver underwater visual census and the use of imagery techniques such as Remotely Operated Vehicles (ROV), drop down cameras, video transects and Baited Remote Underwater Video (BRUV) deployments (Murphy and Jenkins 2010).

Survey techniques for demersal fish species have traditionally used trawl techniques. Since use of landings and trawling data is well established, long time series can be accessed e.g. Heath and Speirs 2012. However, such extractive methods are inherently destructive to the benthos and can alter the structure and function of benthic communities (Jennings and Kaiser 1998, Holmlund and Hammer 1999, Thrush and Dayton 2002). These techniques are therefore not suitable within protected areas or vulnerable substrata such as coral, sponges and maerl or where seagrass may occur. Use of trawl techniques is also not possible in highly structurally rugose substrata and shallow waters where juvenile gadoids are known to inhabit (Cappo et al. 2006). Additionally trawl techniques fail to provide detailed information of the interactions between substrata and benthic communities and the species of interest (Gregory and Anderson 1997, Harvey et al. 2007, Fitzpatrick et al. 2012; Chapter 4).

Other trapping techniques commonly used to assess juvenile gadoid populations include seine netting methods and fykenets (e.g. Laurel et al. 2007 and Kamenos et al. 2004). Although these techniques enable areas to be quantified as with trawl techniques, biological interactions between species which may affect the distribution and abundance of the focal species of interest are difficult to quantify. It is also difficult to access highly rugose substrata using beach seine nets and deeper regions further from shore (Laurel et al. 2007).

Hydro acoustic instruments are commonly used by research vessels and commercial fishermen to detect fish populations. The different sound frequencies enable the detection and quantification of species (ICES, 2007). Acoustic methods are however less accurate in detecting demersal and juvenile fish population in shallower waters due to the disturbance of the signal with the seafloor, bubbles from the vessel in the water column and the small size of the fish (ICES, 2007; Murphy and Jenkins 2010; Mallet and Pelletier 2014). Furthermore, detailed quantification of fish with their environment and other species is not possible using acoustic methods. Various fish tagging methods also exist (e.g. Lucas and Baras 2000) which can provide useful information on the movement, migration, use of space and distribution (Murphy and Jenkins 2010). However, unless detailed seabed mapping has been undertaken in the area and numerous arrays of acoustic receivers are fixed, substratum association of fish is not possible (Murphy and Jenkins 2010). *In situ* acoustic tagging studies of age-0 gadoids can be difficult due to their small size and previous tagging studies have demonstrated low recapture rates (Ware, 2009).

Visual survey methods can provide an effect solution to access vulnerable, shallow, topographically rugose and protected areas whilst enabling the interactions between species and substrata to be quantified (Cappo et al. 2003, Harvey et al. 2007, Fitzpatrick et al. 2012). Such multifaceted information cannot be obtained using traditional fisheries techniques or any of the techniques described above. Visual surveys also enable a more complete picture of the habitat of demersal fish to be obtained albeit smaller scale assessments. Problems facing visual census techniques include quality of imagery (particularly in temperate and turbid waters) and the ability to accurately identify species and measure species (Shortis et al, 2009). Stereo-video imagery techniques, which uses two cameras to record pairs of frames with a calibration procedure, have enable accurate length measurements and 3-dimentional images to be obtained of objects in front of the cameras and the area sampled can be quantified (Harvey et al. 2002; Harvey et al. 2010; Langlois et al. 2010; Murphy and Jenkins 2010). The provision of a stable platform (from drop down frames) or controlled movement from ROVs and imaging software can also help to improve image quality.

Use of imagery techniques can help improve miss-identification errors by providing a permanent record (Cappo et al. 2003; Langlois et al. 2010; Boutros et al. 2015). Visual surveys also facilitate accurate and repeatable fish surveys to take place (Harvey and Shortis 1995; Boutros et al. 2015). Imaging techniques are also thought to be more accurate than trapping and trawling techniques (Spencer et al. 2005; Cappo et al. 2003) and could complement abundance estimates of fish (Priede and Merrett 1996). Cappo et al (2004) undertook a comparative analysis comparing BRUVs with prawn trawls to assess fish biodiversity. Significantly different fauna were recorded, where trawls caught smaller sedentary and demersal species, whereas BRUVs recorded larger, more mobile species from a larger range of sizes and families. Accurate comparative analysis of such techniques should however include approximations of the area sampled which for BRUV is currently not fully applicable (Cappo et al. 2003; Dunlop et al. 2015; Chapter 6).

In shallow waters, diver operated imagery techniques is possible (e.g. Harvey and Shortis, 1995). However, SCUBA methods are restricted to depth limits (Boutros et al. 2015). Drop down, towed cameras, stereo or simply (S)BRUV deployments are also commonly used(Watson et al. 2005; Hunter and Sayer 2009; Murphy and Jenkins 2010; Easton et al. 2015). In deep waters, Remotely Operated Vehicles (ROV), manned vehicles and Autonomous Underwater Vehicles are used to gain a better understanding of the rocky and fragile benthos and demersal species (e.g. Isaacs and Schwartzlose 1975; Costello et al. 2005; Friedman et al. 2012; Morris et al. 2014).

Lowry et al. (2012) undertook a comparative study between BRUV deployments and Underwater Visual Census (UVS) and found UVS methods recorded a greater number of species including better estimates of rare and cryptic species than BRUVs on reefs in southeast Australia. However, such comparative methods can be biased since BRUV methods of collecting data are passive whereas with UVS methods the divers can search within the substrata to identify and count species (Lowry et al. 2012).Certain species may also be diver averse (Harvey et al. 2007, Lowry et al. 2012). Conversely, comparative surveys between stereo-video diver operated transects and SBRUV undertaken in western Australia have indicated that SBRUV are more cost and time-efficient (Langlois et al. 2010). Baited cameras (used to attracted species) are commonly used to decrease zero counts, increase similarity and repeatability between surveys (Murphy and Jenkins 2010; Mallet and Pelletier 2014). Baited cameras may however be biased towards more predatory and scavenger species (Lowry et al. 2012; Dunlop et al. 2015). Bernard and Gotz 2012 also performed a comparative analysis between BRUVs and RUVs and found that BRUVs were more efficient at surveying entire communities (including demersal fish and benthic invertebrates). RUVs on the other hand were found to be more effective and surveying micro-invertebrates. Murphy and Jenkins (2010) and Mallet and Pelletier (2014), provide a detailed overview of observational methods used to monitor fish and their association to benthos.

1.7.1. Use of stereo-video cameras to collect *in situ* data on juvenile gadoids

Underwater, stereo-video imaging techniques have been around since the 1960s with synchronised cameras first used in the 1980s enabling length measurements of mobile species to be obtained in addition to size, density and structure of schools to be measured (Shortis et al. 2009). For accurate and precise measurements, stereo-video systems require rigid camera housings with a bar connecting the two cameras to ensure that the optical path is consistent for all measurements based on the calibration (Shortis et al. 2009, Shortis 2015). The relationship between the camera and the housing port must be consistent to ensure changes in position when removing and replacing the cameras from the housing is kept consistent (Shortis et al. 2009, Shortis 2015).The optical characteristics of the cameras and their orientation must also be determined during the calibration process (Harvey and Shortis 1995, Shortis 2015). Additionally, the left and right cameras must be synchronised, this is facilitated by placing a Light Emitting Diode within the field of view of both cameras (Mallet and Pelletier 2014). For calibration to take place the dimensions of the calibration object (usually a cube) must be known (Shortis et al. 2009, Shortis 2015). The calibration procedure involves rotating the cube whilst within the field of view of the camera in different angles so that measurements can be made. Calibrations must be undertaken within a controlled environment such as a swimming pool. Length measurements are then independently calibrated using a scale bar to calculate the accuracy of the calibration (refer to Harvey and Shortis et al 1995;1998).

Various methods exist to calculate the calibration to be able acquire accurate measurements. Shortis et al. (2009), provide a comprehensive review of underwater stereo-image measurements. Boutros et al. (2015) compares calibration techniques to configure stereo-video systems. Automation of measurement process in recent years has however enabled non-technical specialists to use stereo-video imagery for a wider range of purposes such as to further the understanding of marine biological systems and ecology.

Stereo imagery analysis can however increase costs, the bulk of equipment and lengthen information processing time unless automated or semi-automated imaging techniques are used (Shortis et al, 2009).The additional benefits of stereo-video imagery is however thought to outweigh the costs. Most work using stereo-video cameras to study fish populations and the ecology of fish have taken place in tropical and subtropical environments (e.g. Langlois et al. 2010; Misa et al. 2013; Goetze et al. 2015). The use of stereo-video cameras in temperate waters to study fish populations, nursery areas and behaviour has rarely been studied. However, this methodology could provide an important monitoring technique with the growing number of MPAs and other area closures.

1.8. Thesis aims and objectives

To understand the reasons for unrecovered gadoid stocks, the high biomass of juvenile *M. merlangus* in the Firth of Clyde, and to provide advice on possible management measures, knowledge of the full life cycle of gadoids is required. Sparse research exists on different aspects of gadoid life cycles on the west coast of Scotland and anthropogenic impacts on gadoid habitat. However, the cohort size of marine fish is thought to be determined during the first year of piscine life (Campana et al. 1989; Myers and Cadigan 1993; Ings et al. 2008). Understanding what variables affect juvenile gadoid distribution could therefore help recruitment and protection from anthropogenic activities.

Consequently the overall aim of this thesis is to improve our knowledge of juvenile gadoid habitat. Chapters 3 - 5 address this aim. The second main aim of this thesis was to trial the use of two stereo-video SCUBA transects and SBRUV deployments as photogrammetric monitoring methods of collecting data on juvenile gadoid, demersal fish and benthos. Chapter 3 and 4 address this aim. The third main aim, addressed in chapters 3 - 5 was to provide baseline data on seabed type within a recently designated MPA -South Arran Nature Conservation MPA (NCMPA) (SNH 2014), and potential management and monitoring information for the conservation of juvenile gadoids. All research undertaken for this thesis was carried out within South Arran NCMPA which was designated August 2014. Data collection during 2013 took place before designation and data collection during both years took place before management measures were implemented.

To begin understanding gadoid habitat, chapter 2 provides a background to the terminology related to demersal fish habitat. The objective of this chapter was to disentangle the various uses of habitat and habitat related terminology, provide clear definitions for habitat related concepts discussed and examples of how to assess the fish habitat for conservation and management purposes.

Chapter 3 trials the use of stereo-video SCUBA transects as a means of collecting abundance and length on age-0 *G. morhua*. Data were collected within South Arran Nature Conservation MPA (NCMPA), within the Firth of Clyde between June and the end of September 2013. Abiotic and biotic variables influencing the distribution and length of juvenile *G. morhua* in shallow (4.5 – 23 m) subtidal waters were explored. An assessment of the stereo-video SCUBA transects is made.

Chapter 4 trials the use of SBRUV surveys as a method to collect relative abundance and length measurements on juvenile gadoid within South Arran NCMPA. Data were collected between June and the end of September 2013 and 2014. Abiotic and biotic variables influencing juvenile *G. morhua, M. aeglefinus* and *M. merlangus* distribution and length in subtidal waters between 4 and 47 m were explored. An assessment of the use of SBRUV surveys is made.

Chapter 5 explores a range of environmental variables in combination with the ground-truthed data using the stereo-video techniques to improve the substratum predicted map within South Arran NCMPA. The predicted maps were used to understand seabed landscape effects (substratum heterogeneity and extent) on juvenile gadoid distribution.

Chapter 6 summarises the findings from these studies and discusses their use in the context of fisheries independent monitoring and management methods. This chapter also explores possible future applications of the findings of this work and the new methods developed.

Chapter 2. Disentangling habitat concepts for demersal marine fish management[1]

2.1. Abstract

Fishing and other anthropogenic impacts have led to declines in many fish stocks and modification of the seabed. As a result, efforts to restore marine ecosystems have become increasingly focused on spatially explicit management methods to protect fish and the habitats they require for survival. This has led to a proliferation of investigations trying to map ‘habitats’ vulnerable to anthropogenic impacts and identify fish resource requirements in order to meet conservation and management needs.

A wide range of habitat-related concepts, with different uses and understandings of the word ‘habitat’ itself has arisen as a consequence. Inconsistencies in terminology can cause confusion between studies, making it difficult to investigate and understand the ecology of fish and the factors that affect their survival. Ultimately, the inability to discern the relationships between fish and their environment clearly can hinder conservation and management measures for fish populations.

This review identifies and addresses the present ambiguity surrounding definitions of ‘habitat’ and habitat-related concepts currently used in spatial management of demersal marine fish populations. The role of spatial and temporal scales is considered, in addition to examples of how to assess fish habitat for conservation and management purposes.

---

[1] NB: This chapter has been accepted as a paper: Elliott, S. A. M., Milligan, R. J, Heath, M. R., Turrell, W. R. & Bailey, D. M. 2016. Disentangling habitat concepts for demersal marine fish management. Oceanography and Marine Biology: An Annual Review, 54: 171-188.

2.2. Introduction

Fish represent a highly diverse group of animals (Eschmeyer et al. 2010). They are known to play important roles in ecosystem structuring and provide essential resources for humans through the provision of food, regulation of food web dynamics and carbon cycling (Holmlund & Hammer 1999; Baum & Worm 2009). However, fishing and other anthropogenic pressures have led to declines in many fish species and modification of the seafloor (Jennings & Kaiser 1998; Crain et al. 2009). As a result, much effort has been expended on identifying management mechanisms to protect, sustain and restore depleted fish stocks. There has also been an increasing emphasis on the application of ecosystem-based fisheries management (EBFM) (Box 2.3.1), in addition to species-by-species assessment and fisheries management (Schmitten 1999; Sinclair et al. 2002, Gavaris 2009).

The transition to EB(F)M has led to a proliferation of investigations to identify fish ‘habitats’ for fisheries management purposes, ‘habitat’ mapping for seabed conservation purposes, and ‘habitat’ characterisation to explain ecosystem (Box 2.3.1) functioning (Christensen et al. 1996; Diaz et al. 2004; Francis et al. 2007). In many cases, the term ‘habitat’ is not well defined and can have different meanings or implications, which may lead to confusion when interpreting the results of different studies, as reviewed by Block & Brennan (1993) and Hall et al. (1997). The use of ‘habitat’ to refer to seabed characteristics for mapping purposes and ecosystem functioning has been formalised through legislation that requires habitats to be classified and protected; e.g. the European Union Habitats Directive (92/43/EEC, CEC 1992) and the Marine Strategy Framework Directive (2008/56/EC, EU 2008). These uses of ‘habitat’ have become synonymous with descriptions of physical characteristics of the seabed, such as substratum type (e.g. seagrass, coral reefs or maerl beds) (Box 2.3.1) or marine biotopes (Box 2.3.1) (Olenin & Ducrotoy 2006; Dauvin et al. 2008a). These definitions of ‘habitat’ are fundamentally different from Darwin’s definition, which relates to the place in which a species lives (Dauvin et al. 2008b).

Since the definition of ‘habitat’ is not standardised, further confusion has been caused by terms for certain characteristics of habitat (e.g. habitat complexity, habitat heterogeneity or quality) (Box 2.3.1), which also have often lacked clear explanation (Block & Brennan 1993; McCormick 1994; Hall et al. 1997). Part of the difficulty is that much of the terminology is entirely dependent on spatial and temporal scales (Levin 1992; Chave 2013). For example, a demersal fish might utilise distinct substrata for feeding or protection at different times or during a particular stage in its ontogeny (e.g. Laurel et al. 2009; Grol et al. 2014). Equally, the type of substratum required to provide physical protection will depend on the size of the demersal fish (Chave 2013; Figure 2.3.2). A substratum's 'complexity' is therefore entirely dependent on the size and morphology of the species.

Misused or undefined terminology could lead to misinterpretation of the role of a particular substratum type for individual species, or to the use of inappropriate methodologies when analysing the role of a 'habitat' or substratum type to a fish. For instance, if species' abundance is greater around one substratum type than another, is that species displaying 'habitat selection' based on a particular 'preference' (Box 2.3.1), or is that observation related to other environmental or life-history parameters that were not measured? Could the substratum type be considered 'essential' to the fish if other habitat components (e.g. appropriate depth range or other substrata) were not present? If definitions of habitat are unclear, variables which could affect fish distribution or abundance may not be recorded. Ultimately, the inappropriate use of 'habitat' and related terminology could have implications for the effectiveness of EB(F)M, especially where different fields of marine science use the same term with different implications.

The present review paper, while not exhaustive, addresses the current ambiguity surrounding habitat and habitat-related concepts currently used in the spatial management of demersal marine fish. Particular attention is therefore paid to the role of the seabed. For each concept discussed, a conceptual definition is provided, followed by examples of how to assess fish habitat for conservation and management purposes. These definitions provide a possible conceptual framework for consideration of demersal fish-environment relationships, which could equally be applied to other areas of ecology.

2.3. Concepts and definitions

2.3.1. Habitat

The first use of the term ‘habitat’ discussed here, referred to hereinafter as Interpretation I, is derived from Darwin’s (1872) definition, describing the place in which a plant or animal lives (Box 2.3.1). This encompasses the resources and environmental conditions that determine the presence, survival and reproduction of a species (Hall et al. 1997; Gaillard et al. 2010). Interpretation I therefore encompasses the physical (e.g. depth, substratum type, wave exposure), chemical (e.g. oxygen concentration, pH, salinity) and biological characteristics (e.g. predator prey dynamics, competition and fauna providing structure to the seabed) of the environment (Hall et al. 1997; Kaiser et al. 1999; Diaz et al. 2004). Figure 2.3.1 illustrates schematically how the habitat of a demersal fish can be considered as the intersection of appropriate substratum type, physicochemical parameters and biological characteristics.

For quantitative purposes, this interpretation of habitat (Interpretation I) has been explained as the ‘environmental space’ that a species is found within (e.g. Aarts et al. 2008; Matthiopoulos et al. 2015). However, many studies of fish habitat have often only described one or two habitat components, which may concern either the seabed type (Figure 2.3.1A), the physicochemical properties of the water column (Figure 2.3.1B), or both, with no mention of biological characteristics (Figure 2.3.1C) (Kaiser et al. 1999). Examples include seagrass or coral reef substratum types that a particular fish is found over, around or among (Costello et al. 2005; Seitz et al. 2014), or the depth and temperature ranges (e.g. Smale et al. 1993; Perry & Smith 1994). As stated by Lima & Dill (1990) and Able (1999), the lack of studies incorporating biological characteristics and interactions in the identification of fish habitat is most likely due to the difficulties of quantifying these aspects and collecting the required data *in situ*.

The second use of habitat (Interpretation II), follows arbitrary classifications of the seabed or features based on differences obvious to human observers (e.g. different types of sediment, macroalgal beds, or biogenic reefs; Figure 2.3.1A) (Fraschetti et al. 2008). Interpretation II does not explicitly consider the ecological requirements of a particular species; however, it has been used to identify associations of some species with particular substrata (e.g. Seitz et al. 2014). Kenny et al. (2003) provides an overview of seabed mapping technologies available for classification purposes.

The third use of habitat (Interpretation III) encompasses an ecosystem- or a marine biotope-based view of habitat (Olenin & Ducrotoy 2006; Airoldi & Beck 2007; Dauvin et al. 2008a). Descriptions under Interpretation III typically include seabed properties (Figure 2.3.1A), physicochemical properties of the water column (Figure 2.3.1B) and the fauna found in that specific area, though interactions between those fauna are not considered. Interpretation III is typically characterised in terms of the community of flora and fauna present, rather than a particular focal species (Olenin & Ducrotoy 2006; Dauvin et al. 2008a).

Interpretations II and III derive from conservation and planning requirements to classify and map habitats in measurable geographical units for national and international management and monitoring purposes (Airoldi & Beck 2007; Fraschetti et al. 2008; Galparsoro et al. 2012). Classification of seabed types and their associated communities facilitates the implementation of policies to assess, maintain or restore marine environments subject to anthropogenic impacts (Airoldi & Beck 2007; Fraschetti et al. 2008; Galparsoro et al. 2012), but legal definitions of habitat can be inconsistent. For instance, the EU Habitats Directive (92/43/EEC) defines “natural habitats” as “terrestrial or aquatic areas distinguished by geographic, abiotic and biotic features”, but confusingly also defines the “habitat of a species” as “an environment defined by abiotic and biotic factors in which a species lives at any stage of its biological cycle” (CEC 1992, Dauvin et al. 2008b). Examples of “natural habitats” defined under the Habitats Directive include reefs, *Posidonia* beds and estuaries (CEC 1992). The same word is therefore used to describe geological, biological and geographical entities at spatial scales varying from metres to many kilometres (Dauvin et al. 2008b). Similarly, the Vulnerable Marine Ecosystem (VME) concept (FAO 2009) refers to classifications of the seabed and includes associated species, but has no clear description of what an ecosystem or habitat is (FAO 2009; Auster et al. 2010). Such classification systems move away from the traditional definitions of habitat by focusing only on certain habitat components without considering biological or physicochemical linkages. Interpretations II and III also instigate and perpetuate confusion in terminology across different fields of marine science and policy (Dauvin et al. 2008a, b; Galparsoro et al. 2012). Further, if the classified seabed types or identified fish habitats are used for conservation and management purposes without taking due account of varying temporal and spatial scales, efforts to protect and restore fish stocks and their habitats may be ineffective (Hilborn et al. 2004b; Guarinello et al. 2010). For example, a poorly planned *G. morhua* fisheries closure established in the North Sea in 2001 not only had negligible effects on *G. morhua* stocks, but also displaced fishing activity, increased discarding and negatively impacted vulnerable populations of skate (*Dipturus batis*) (Rijnsdorp et al. 2001; Hilborn et al. 2004b).

Identifying and collecting data on fish habitat is by no means straightforward, since habitats vary not only among species, but can also vary between sexes of the same species, life history stages and among different stocks. Investigations conducted over different temporal and spatial scales will also produce different outcomes when identifying a particular species' habitat. Managers are therefore faced with daunting tasks of managing and monitoring stocks, often with little prior information on fish distribution and abundance, and insufficient funds (Bailey 1982; Langton et al. 1996). Loose definitions can therefore be beneficial for managers trying to implement measures to conserve and restore stocks with little baseline information (Fletcher & O'Shea 2000; Elliott & McLusky 2002). However, if simplified managerial definitions are adopted in the scientific literature, ecological meanings can become lost or confused, partly due to a lack of consensus within the scientific community itself (Dauvin et al. 2008a). As a result, habitats frequently lack metrics, threshold values or analytical approaches for their identification, monitoring and management (Murphy & Noon 1991; Auster et al. 2010) and end up becoming separated from their theoretical roots (Dauvin et al. 2008b).

In an attempt to reduce the confusion surrounding the term 'habitat', the present review uses Interpretation I, which refers to the combination of the types of substrata, biological characteristics and physicochemical properties required by a species during a particular stage in its ontogeny (Figure 2.3.1D) (Hall et al. 1997; Kaiser et al. 1999). A species' habitat can therefore be applied both to individuals and to populations or stocks. Appropriate scales of time and space will vary according to the hierarchical level in question. ‘Substratum type’ (Box 2.3.1) will be used to define seabed characteristics (Figure 2.3.1A). If only physicochemical properties of water and substrata are taken into account when identifying a species’ habitat, this will be referred to as ‘physicochemical space’ (Box 2.3.1; Figure 2.3.1E), a term modified from the “environmental space” of Aarts et al. (2008). The incorporation of biotic communities into the classification of substratum types (Interpretation III) will be referred to as a species’ ‘biotope’ (Olenin & Ducrotoy 2006; Dauvin et al. 2008a).

The use of Interpretation II or III rather than Interpretation I is thought to have contributed to underperformance of fisheries management through lack of consideration of variables that might have an effect on fish abundance and spatial distribution (Degnbol et al. 2006). When trying to protect a certain species’ habitat, understanding the variables affecting its distribution and abundance is more likely to provide benefits to that focal species than using artificial constructs of substratum categories. Marine Protected Areas (MPAs), for example, are commonly designed to limit or exclude fishing and other damaging activities within a defined area (Halpern et al. 2010). Nonetheless, there is often a mismatch between the objectives of MPAs and ecosystem-based goals arising from different biological disciplines and specialisms (Degnbol et al. 2006; Halpern et al. 2010). In the UK for example, the majority of MPAs have been designated for the protection of benthic features, with little understanding of whether these features are of value to commercial fish species, and may therefore miss potential EBFM benefits (Hilborn et al. 2004b; Hilborn 2011). It should be noted that clarification of terminology and more widespread adoption of EBFM will not solve all fisheries management problems (Degnbol et al. 2006; Marasco et al. 2007). There are no blanket solutions to all fisheries management problems (Degnbol et al. 2006; Beddington et al. 2007; Hilborn 2007). Nonetheless, addressing discrepancies in language to facilitate cross-sector collaboration can only be beneficial.

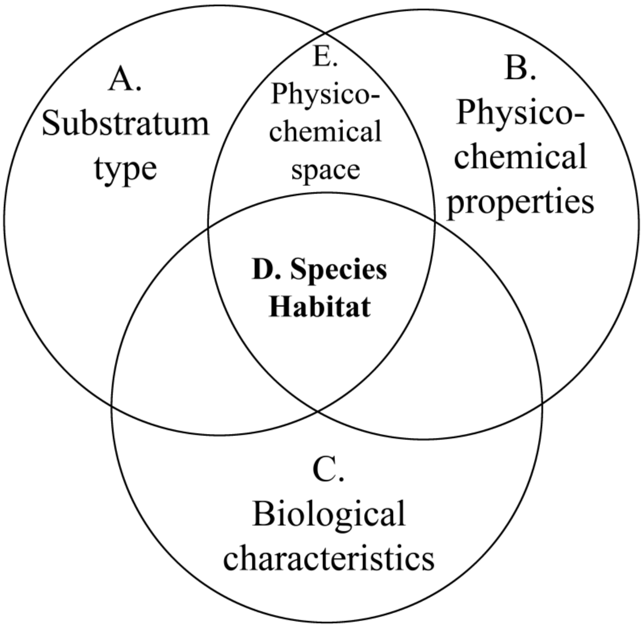

Figure 2.3.1 - The three major components making up a species habitat. These include the substratum type (A), physicochemical properties of the water column (B), and biological characteristics (C), which together comprise a species' habitat (D; Interpretation I). Circle A on its own encompasses interpretation II; the intersection of circles A and B (area E) is referred to as physicochemical space. Interpretation III of habitat would also be represented by area D, but considers communities rather than individual species (a biotope).

2.3.2. Habitat complexity'

McCoy & Bell (1991) highlight three structural variables in relation to the ecological significance of 'habitats' (defined here as 'substrata'): complexity, heterogeneity and scale. 'Habitat complexity' has been used to refer to the rugosity (Box 2.3.1) of the seafloor (e.g. Friedlander & Parrish 1998a; Wilding & Sayer 2002), the type and density of vegetation (e.g. McCoy & Bell 1991; Jackson et al. 2001), the presence and diversity of biota on the seabed (e.g. Kovalenko et al. 2012), as well as to substrata that provide vertical relief (e.g. Bohnsack 1991; Santos et al. 2012). At larger spatial scales, 'complexity' has been used in relation to the diversity or 'heterogeneity' of substratum types available within a benthic 'landscape' (Box 2.3.1) (e.g. Dutilleul 1993; Kovalenko et al. 2012). The catch-all term 'complexity' has become a convenient shorthand despite the diverse measures used and the variety of scales at which it is quantified

(McCormick 1994; Bartholomew et al. 2000). Although habitat complexity and heterogeneity are well-established concepts, few policy documents address or define them. Within the international guidelines for deep-sea fisheries management (FAO 2009), structural complexity is characterised “by complex physical structures created by significant concentrations of biotic and abiotic features”. Although the FAO (2009) separates vulnerability and species diversity, their definition of complexity is circular and based on anthropocentric’ perceptions rather than being framed in terms of the resource requirements of particular focal species, and has no reference to scale or how complexity should be measured.

‘Complex habitats’ are considered important to the survival of many fishes, since the interstices that characterise them may provide refugia from predators, currents and strong wave surges, and could potentially lead to reduced mortality (Sebens 1991). Some substrata, such as rock, calcareous shells of sessile invertebrates, macroalgae and seagrass, can also provide areas of attachment for other biota that may in turn form new substrata (e.g. algae, hydroids and bryozoans) (Sebens 1991; Gratwicke & Speight 2005). Such biotic substrata can lead to increased rugosity and heterogeneity, which may provide a wider range of refugia, biological diversity and food resources than an area of seabed with fewer types of substrata (Auster et al. 1996; Kaiser et al. 1999; Kovalenko et al. 2012). Rugosity may also cause heterogeneity in aspect and flow regime, leading to a wider range of conditions suitable to more species (Sebens 1991; Kovalenko et al. 2012). Numerous studies that have investigated the roles of different marine substrata for fish species highlight the importance of structurally ‘complex’ substratum types (e.g. maerl or coral reefs), raising their profile in terms of management priorities (e.g. Almany 2004; Kamenos 2004; Kutti et al. 2015). Yet a combination of sediment grain sizes such as boulders with sparse coral may provide functionally equivalent rugosity for a particular species as a dense coral reef (Auster 2005). The use of ‘complexity’ to refer to ‘important’ biotic substrata has been reinforced because many are themselves vulnerable to anthropogenic impacts, such as trawling and dredging (Jennings & Kaiser 1998; Halpern et al. 2008).

The diverse ways in which substratum complexity can be measured, has made the term difficult to apply in practice and compare between studies. To be able to measure and define the role of substrata, the present review adopts the terms substratum 'rugosity' and 'heterogeneity' (Box 2.3.1), which can be applied regardless of the scale at which they are measured, but the appropriate scale of measurement will depend on the size and mobility of the species in question (McCoy & Bell 1991; Levin 1992). Rugosity is the measure of corrugation of a substratum and the degree of angulation that together provide a three-dimensional space (McCormick 1994) that a fish may occupy, during a particular stage in its ontogeny. This can therefore include interstices and interstructural spaces of relevance to the species in question (Bartholomew et al. 2000). The rugosity of a substratum may therefore affect the availability (Box 2.3.1) of refugia and possible food resources (Figure 2.3.2) (Bartholomew et al. 2000). On a larger scale, substratum heterogeneity refers to the frequency, composition and pattern of substratum types and patches (Box 2.3.1; Figure 2.3.2) within a benthic landscape (Sebens 1991; Dutilleul 1993; Tews et al. 2004). The different types of substrata that occur within a particular species' habitat will depend on the size, longevity, and mobility of the respective fish.

There is usually a variety of different factors or gradients generating substratum rugosity or heterogeneity from a fish's perspective (Sebens 1991; Gratwicke & Speight 2005; Du Preez 2015). For example, substratum height, height variation and interstitial space will affect the rugosity, while diversity of substratum, composition, areal extent and spatial distribution will affect the heterogeneity (Gratwicke & Speight 2005; Wilson et al. 2006). It is also important to be aware that substrata and community composition of the habitat may vary over time following successional processes or anthropogenic impacts (Sale 1991; Friedlander & Parrish 1998b; Kamenos et al. 2003). Table 2.3.2 gives some examples of methodological studies in which substratum rugosity and heterogeneity have been measured.

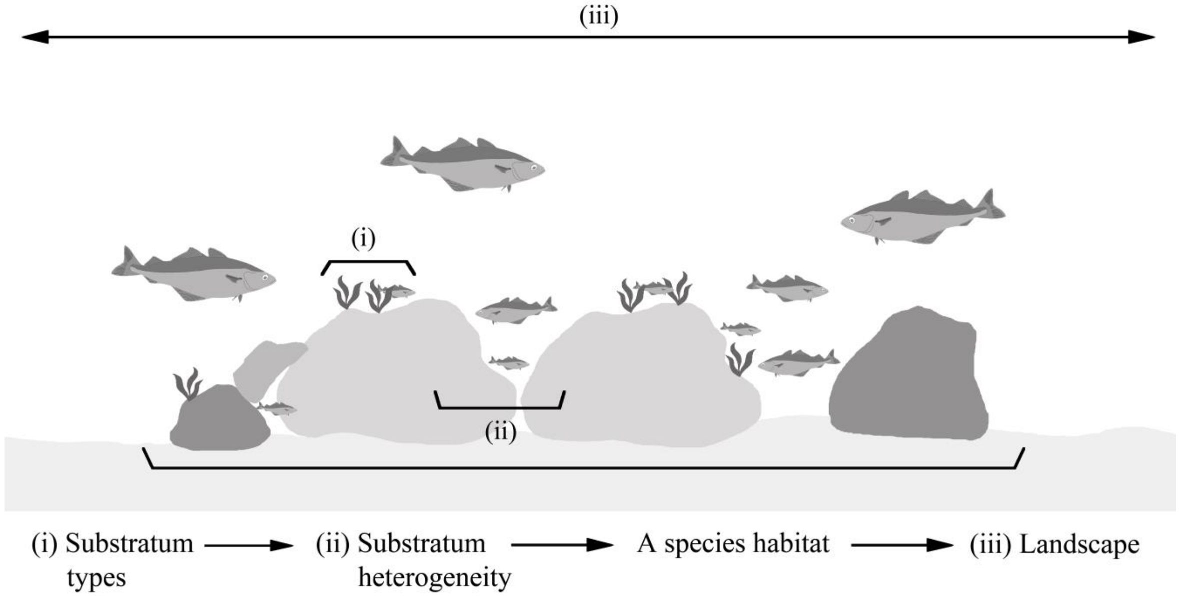

Figure 2.3.2 - Substratum rugosity and heterogeneity relative to the size of fish. A species' habitat during a particular stage in its ontogeny may encompass rugose or heterogeneous substrata. Over the course of its life cycle, an individual may occupy different parts of the submarine 'landscape'.

2.3.3. Habitat association, selection and preference'

To relate species to habitat components, terms such as 'habitat association', 'selection' and 'preference' are frequently used to identify environmental variables of relevance to the individual organism, population or stock. Theoretical and modelled applications in this field seem to be well established (e.g. Johnson 1980; Aarts et al. 2008; 2013), but both field and laboratory studies have frequently lacked clarity, and the terms 'association', 'selection' and 'preference' have been used interchangeably (e.g. Atkinson et al. 2004; Laurel et al. 2007; Misa et al. 2013). This interchangeable use of terms may arise from the overlapping definitions of association, selection and preference (e.g. Krausman 1999 and Morris 2003). To support implementation of the Essential Fish Habitat (EFH) concept under the United States Sustainable Fisheries Act (SFA) (USDOC 1996), the National Marine Fisheries Service considered four levels of information on fish populations in different substrata that could be used (following Able 1999). These levels are: (1) species presence-absence data, (2) population densities, (3) information derived from estimated growth, reproduction or survival rates, and (4) estimates of fish production (Able 1999).

The different options for the identification of EFH is beneficial to managers when considering data-poor ecosystems, but can lead to further lack of clarity in the terminology used to describe the role of a particular substratum for an individual fish.

The present review focuses primarily on interactions with substrata, so for clarity ‘substratum’ rather than another habitat component is considered in relation to association, selection and preference. This terminology could, however, be applied to other habitat components (e.g. depth or temperature ranges) in a similar way. Specifically, substratum association has been defined as the substratum type(s) that a fish is observed to occupy during particular time and place (Box 2.3.1) (Hall et al. 1997). This has typically been measured by comparing relative abundances or densities of individuals in, on, or over different substratum types (e.g. Nickell & Sayer 1998; Misa et al. 2013). Here, substratum association refers to all the substrata that the fish occupies during a particular stage in its life cycle without any consideration as to whether an active choice was made to reside in the given substrata.

Substratum selection refers to the process by which fish actively choose to occupy a particular substratum type at a given time, and therefore results from voluntary movements that cannot be attributed to passive transport (Box 2.3.1) (Johnson 1980; Kramer et al. 1997). Factors affecting substratum selection may include individual preference, the availability or condition of substrata in the landscape, or predation risk (Johnson 1980; Kramer et al. 1997; Gaillard et al. 2010). Selection has been measured as the disproportionate use of one substratum type with respect to its availability (Aarts et al. 2013).

Substratum preference (Box 2.3.1) is defined as a substratum type that an individual would associate with given a free choice (i.e., in the absence of predators or competitors) at a given time (Gaillard et al. 2010). Confusingly, ‘preference’ has also been measured as the relative abundances of the focal species in the areas of different substrata in relation to their relative availability (Johnson 1980; Aarts et al. 2008). The latter would only measure a species’ innate preference after it has been modified by other, presumably unmeasured effects, such as predator-prey or competitive dynamics. Arguably, this usage concerns the realised substratum selection. Laboratory experiments or field enclosures may be a more appropriate test for preference (Kramer et al. 1997).

A practical problem when measuring substratum association, preference or selection by only comparing one or a few substratum types is that patches are rarely a uniform shape, size and condition. These aspects may have a strong influence on the extent, spatial distribution and refuge value of habitat for a particular species (Morrison et al. 1992; Block & Brennan 1993). For example, in a field experiment to investigate the significance of eelgrass patches for survival of juvenile *G. morhua*, Laurel et al. (2003) found that predation rates were negatively correlated with patch size. Methods to measure substratum preference are not always straightforward. Laboratory techniques usually simplify the environment to one or a few variables from complex natural marine systems (Kramer et al. 1997). Studies using a combination of field and laboratory methods may lead to more reliable conclusions (e.g. Stoner et al. 2008; Laurel et al. 2009). Table 2.3.2 provides examples of studies that use quantitative methods to study preference and selection for habitat components by demersal fish.

2.3.4. Important habitats’

The ultimate aim of spatial management for the protection of fish species is often to protect ‘important’, ‘critical’ or ‘essential’ habitats. Essential Fish Habitat is defined under the US SFA as “those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity” (USDOC 1996). A key element of the EFH concept is the identification of existing and potential threats to habitat components, and conservation measures that may improve the quality of the habitat and eliminate or minimise anthropogenic threats (Schmitten 1999). The provision of EFHs through the SFA enabled a significant step towards EBFM (Fletcher & O’Shea 2000; Marasco et al. 2007). Unfortunately, although the SFA provided a platform to better understand EFH and a capacity to protect fish habitat through spatial management measures, the SFA’s definition of what EFH actually meant, is quite limited in scope (Sarthou 1999; Fletcher & O’Shea 2000), as reviewed and applied by Able (1999).

Similar terms to EFH include ‘important’ and ‘critical habitats’ (Box 2.3.1), which are typically defined as areas required by fish to carry out key life history processes, such as reproduction, foraging and migration (Langton et al. 1996; Able 1999; Bradbury et al. 2008). These habitats may include nursery areas, defined by Beck et al. (2001) as areas whose “contribution per unit area to the production of individuals that recruit to the adult population is greater, on average, than production from other habitats in which juveniles occur”. Jackson et al. (2001) pointed out that assessing the importance of a substratum type to a fish species should include consideration of whether the substratum type is needed to sustain their populations. In the present review, an ‘important’ or ‘critical’ habitat component is considered to be a property of the environment (e.g. a type of substratum or temperature range) which, if altered or reduced in availability, could adversely affect survival rate of an individual, population or stock. This definition is linked to habitat quality (Box 2.3.1) but focuses on certain components of the habitat rather than its entirety (Krausman 1999). At a population level, an important habitat component would therefore affect the long-term viability of a population (Murphy & Noon 1991). It should be noted that different population subunits (e.g. stocks) may utilise different but functionally equivalent habitat components. Isolating important habitat components rather than important habitats (which include substratum, physicochemical and biological characteristics) allows usable definitions to be developed for decision-making and policy implementation (Langton et al. 1996). Attempts to achieve this in a cost-effective and practicable manner are likely why management strategies often rely on identifying apparent associations between species and particular substrata.

The identification of EFH or important habitat components for spatial management measures have similar issues as described above for habitats, in that managers are tasked with identifying areas for protection with little baseline information and minimal resources (Langton et al. 1996; Rubec et al. 1999). The lack of detail in the SFA about how to identify EFHs can therefore be beneficial in enabling management authorities to identify EFH with little baseline information or by using the best available evidence. However, in some cases, using the best available evidence may amount to basing decisions on apparent selection for, or even just simple association with, certain habitat components, rather than identifying genuinely essential fish habitats, and in the worst cases this could lead to ineffective or counterproductive management measures (Able 1999; Fletcher & O’Shea 2000). Gaillard et al. (2010) proposed that for conservation and management purposes, attention should be focused on habitats that “increase average individual fitness”. This approach would require measurement of parameters such as survival, future reproductive potential and growth rate, which can be difficult to quantify. Langton et al. (1996) and Able (1999) recommended focusing on critical life phases that determine cohort size. The present authors recommend that when examining important fish habitat components, habitat quality should be assessed and linked to population demographics over different temporal and spatial scales (Gibson 1994; Able 1999; Gaillard et al. 2010). These sorts of studies require an understanding of the type, quantity and range of conditions required for the fish’s survival at each major life-history stage (Gibson 1994; Langton et al. 1996; Able 1999). Most demersal marine fishes, including most commercially exploited species, are highly mobile and occupy different substrata and depth ranges during different life history phases and according to varying environmental conditions. Spatial and temporal processes, such as diel, seasonal and ontogenetic movements between habitats must therefore be taken into consideration when identifying important fish habitat components and applying EBFM (Hilborn et al. 2004b). Table 2.3.2 highlights papers that provide quantitative methods for identifying important habitat components for species and management applications of this information.

Box 2.3.1 - A suggested glossary of terms used within the present review that relate to habitat conservation for demersal marine fish.

Biotope:

The definition of what a biotope consists of has evolved through time, as reviewed by Olenin & Ducrotoy (2006). The present review adopts the modern definition which describes the “physical environment and the community” (Olenin & Ducrotoy 2006) and therefore encompasses a biocoenosis (group of organisms found living together) rather than focusing on the habitat requirements of an individual species or “the ecosystem linkages between abiotic and biotic components” (Olenin & Ducrotoy 2006).

Ecosystem:

An ecosystem consists of biotic (community of organisms) and abiotic (physical, chemical and biogeochemical) features, processes and interactions in a defined space at a given time (Dauvin et al. 2008a; Curtin & Prellezo 2010) and may encompass many (potentially overlapping) biotopes. Dauvin et al. (2008a) provide an overview of the development of the term ecosystem.

Ecosystem-Based Fishery Management (EBFM):

There is a variety of definitions and interpretations of EBFM (Hilborn et al. 2004a; Marasco et al. 2007). The present review adopts the definition of Marasco et al. (2007): “Ecosystem-based fishery management recognises the physical, biological, economic, and social interactions among the affected components of the ecosystem and attempts to manage fisheries to achieve a stipulated spectrum of societal goals, some of which may be in competition.” Not all aspects of EBFM have been touched upon in this review.

Habitat:

The required types of substrata, physicochemical parameters and biological characteristics of an area occupied by a species during a particular stage of its ontogeny. A species’ habitat can therefore be applied to individuals and populations or stocks. Variables making up a species’ habitat can be dynamic or static (e.g., predator or prey density, or depth; Beyer et al. 2010). A habitat will have spatial and temporal scales relevant to the body size and mobility of the study organism (Hall et al. 1997; Diaz et al. 2004).

Habitat components:

The individual features and their properties that constitute a habitat; i.e., types of substratum, and physicochemical and biotic conditions (Figure 2.3.1) (Langton et al. 1996; Kaiser et al. 1999).

Habitat quality:

The degree to which a habitat directly influences the growth, survival and future reproductive potential of an individual fish depending on the condition and range of the individual habitat components (Gibson 1994; Hall et al. 1997). Factors affecting a habitat's quality include the quantity and nutritional value of food available for the organism in question, the optimality of the ranges of physicochemical parameters, and the degree of protection afforded (Gibson 1994). Nonetheless, habitat quality should be measured by the habitat's ability to promote growth and survival and reproduction (Gibson 1994; Able 1999).

Habitat component availability:

The areal extent of a habitat component that could be occupied by an additional individual fish, taking account of prior occupation, as a proportion of the total areal extent of that habitat component. For example, a fish's choice of substratum will depend on both its preferences and the availability of preferred substrata (Johnson 1980; Laurel et al. 2004).

Important or critical habitat component:

A habitat component for which a change in its condition or availability has the ability to directly affect the success (survival, growth and reproduction) of an individual or metapopulation. At a population level, a critical habitat component is essential for the long-term viability of the population (Murphy & Noon 1991).

Landscape:

The composition, distribution and topography of (abiotic and biotic) substratum types within a given area or volume of water (Saab 1999). A landscape typically encompasses several species' habitats and one habitat will occupy only part of the landscape (Figure 2.3.2). The spatial characteristics (size, shape, orientation, arrangement of components) of a landscape may influence the ecological function of the area, such as acting as a corridor for migration (Zajac 1999).

Physicochemical space:

A space bounded by the limits of the tolerable ranges of the abiotic variables that influence where an individual can live. These may include variables such as current velocity, depth, temperature, salinity, oxygen concentration, pH, etc. The physicochemical space may vary over an individual's lifespan and between sexes.

Substratum association:

The substratum type that is occupied by a fish during a particular stage in its life cycle.

Substratum heterogeneity:

The diversity and pattern of substratum types and patches within a habitat or a landscape, and the level of substratum rugosity (Dutilleul 1993; Tews et al. 2004). Substratum heterogeneity should be measured on the same spatial scale as the home range of the life stage in question.

Substratum patch:

A continuous or homogeneous area of unbroken substratum type (Morrison et al. 1992) e.g., an extent of seagrass or sand. The patch size should be measured at a scale appropriate to the life stage of interest.

Substratum preference:

The type of substratum that an individual would associate with given an unconstrained choice at a given time; for example, in the absence of predators and competitors (Johnson 1980; Hall et al. 1997).

Substratum rugosity:

The degree of corrugation and angulation of a substratum, which together provide a three-dimensional space (McCormick 1994) that a fish may occupy during a particular stage in its ontogeny. This includes interstitial and interstructural spaces of appropriate size and shape for the life stage in question (Bartholomew et al. 2000). Substratum rugosity should be measured at the scale appropriate to the focal species.

Substratum selection:

The active choice made by a fish to associate with a particular substratum type. This may be affected by behavioural responses such as preference, inter- or intra-specific competition, the availability or quality of other substrata or resources in the immediate surroundings, or predator presence. Selection is therefore indicated by the substratum type a species resides in at a particular time, taking into account the aforementioned behavioural responses (Johnson 1980; Hall et al. 1997; Kramer et al. 1997; Gaillard et al. 2010).

Substratum type:

A class of seabed of distinctive character composed of abiotic or biogenic material, or a combination, used to characterize sediment, algae, flora or biogenic reef, for conservation and explanatory purposes. Examples include seagrass, mud or maerl which may be found in an area. The appropriate degree of specificity will depend on the requirements of the study.

Table 2.3.2 - Examples of methodological papers relevant to habitat related terminology. Examples include peer-reviewed papers which encompass a range of different methodological and quantitative applications to concepts outlined within the present review. NB terminology in the selected papers may not be consistent with definitions used within this review.

Habitat related terminology	Summary description	Species / life stage	Habitat component	Geographic zone /location	Reference
Substratum rugosity and heterogeneity	A method to assess substratum complexity using 'habitat' assessment scores to take into account different aspects of substratum structure and composition.	Species richness and general fish abundance	Sandy, algal, seagrass and reef substrata	Tropical – British Virgin Islands	Gratwicke & Speight 2005
	A comparison of methods to measure and quantify substratum topography for reef fish.	Tropical reef fish	Coral and rocky reefs	Tropical – Australia	McCormick 1994
	A review of the relationship between species diversity and heterogeneity, looking at different spatial scales. Includes measurements of heterogeneity.	Generic, terrestrial	Generic	Generic	Tews et al. 2004

Habitat component preference and selection	A review of regression models for analysis of space use and 'habitat' preference using telemetry data and applied to tagged grey seals, *Halichoerus grypus*.	Generic, but applied to grey seals	Generic applied to sediment type, depth and distance from haul out	Generic, temperate, Scotland	Aarts et al. 2008
	Methods to quantify the effects of 'habitat' availability on species distribution to measure and apply 'habitat' selection functions.	Generic, applied to model simulations	Generic, using continuous and discrete covariates	Generic	Aarts et al. 2013
	Methods and application of habitat component usage and availability to understand selection and preference.	Generic but applied to mallards, *Anas platyrhynchos*	Terrestrial, wetland and open water areas	Generic, temperate, USA	Johnson 1980
Habitat component importance	A review and application for the identification of essential fish habitats (EFHs).	Juvenile estuarine fish	Estuaries; oxygen, pH, salinity and temperature	Temperate, USA	Able 1999

A conceptual framework for understanding ‘habitat’ performance relationships using long-term telemetry information from animals and indices of habitat quality at different spatial scales.	Generic	Generic	Generic	Gaillard et al. 2010
Advice to managers on prioritising information for the identification of EFHs, taking into account fisheries impacts.	Generic	Generic	Generic, temperate, USA	Langton et al. 1996
Modelling fitness to link habitat availability to density-dependent population growth rates of mobile species.	Generic, mobile species	Generic	Generic	Matthiopoulos et al. 2015

2.4. Discussion and recommendations

With the continued decline in many fish stocks and anthropogenic pressure on marine ecosystems, there is a clear need to identify habitat components of importance to marine fishes and to introduce effective management mechanisms (Parma et al. 2006). Considerable effort has been spent on substratum mapping, ecosystem conservation and identification of fish habitat components (Diaz et al. 2004; Francis et al. 2007), yet an integrated approach to EB(F)M is required for its successful implementation (Francis et al. 2007; Curtin & Prellezo 2010; Guarinello et al. 2010). The effects of fishing gear impacts on substrata and on fish have been described, but the effects of substrata and loss of benthic fauna on fish stocks are rarely included in demersal stock assessments (Auster & Langton 1999; Armstrong & Falk-Petersen 2008). For spatial management to be effective for fish, protection of important components of their habitat is clearly essential (Schmitten 1999; Francis et al. 2007). Throughout the world, there has been increased use of spatial management measures to manage fish populations, promote biodiversity, and improve ecosystems as a whole. However, benefits from such spatial management measures have not always been evident (Hsu & Wilen 1997; Hilborn et al. 2004a, b) and spatial management measures should not be seen as the only option to restore depleted stocks (Hilborn 2011). In endeavouring to protect important habitat components, careful planning and consideration of spatial and temporal scales are essential, in addition to adaptive management and monitoring (Hilborn 2011). Temporal and spatial scales are particularly important when managing fishing activities, to help reduce and resolve conflicts between different sea user groups through zoning (Marasco et al. 2007). Such consideration may also avoid unintended consequences of increased fishing prior to the implementation of spatial management (Hsu & Wilen 1997) and displacement of fishing effort to other areas with potentially harmful effects (Murawski et al. 2000; Hilborn et al. 2004b).

Language in science has changed over time and differs between disciplines; however, at a minimum, clarity in the use of language is necessary (Murphy & Noon 1991; Olenin & Ducrotoy 2006). The term habitat has been used in different ways and has become synonymous with ‘substratum type’ and in some cases with ‘biotope’ or even ‘ecosystem’, through its adoption into policy and legislation (Hall et al. 1997; Olenin & Ducrotoy 2006). Habitat-related terminology has become confused through widespread use for different purposes without clear definitions, and through inconsistent usage in scientific research (Murphy & Noon 1991; Hall et al. 1997). To be able to manage marine resources, terminology must be ‘operational’, so that concepts can be realised and accurately measured (Murphy & Noon 1991; Hall et al. 1997). Papers focusing on reasons for the failure to properly manage marine resources consistently point to the need for improved clarity, transparency and clearly defined management objectives (Hsu & Wilen 1997; Fletcher & O’Shea 2000; Parma et al. 2006).

Many of the terms relating to a species’ habitat are inherently scale dependent (Levin 1992; Hall et al. 1997; Chave 2013). The terms proposed in this review are scale-independent insofar as they can be applied to any spatial or temporal scale deemed relevant to a particular study species. This avoids the need for additional, unnecessary terms (e.g. ‘microhabitats’). Nonetheless, scale must be carefully considered in the design and interpretation of any investigation of habitat and should be explicitly stated to allow meaningful comparison between studies. When using the term habitat from the point of view of the individual, population or species, it is essential to consider the temporal and spatial scales relevant to the needs of the organism(s) in question, and for the concept to be biologically meaningful (Hall et al. 1997; Diaz et al. 2004; Guarinello et al. 2010).

The present review has identified some of the causes of confusion in use of the term habitat and habitat-related terminology, and provides a conceptual framework for managers to work with and apply to spatial management programmes. It is widely agreed that the different specialisms within marine or even terrestrial science and policy have not been well integrated, and better integration is required, particularly to achieve EBM (Degnbol et al. 2006; Marasco et al. 2007). With the increasing number of studies relating to fish habitat, standardised and consistent terminology is a prerequisite for developing clear hypotheses and carrying out comparable research (Murphy & Noon 1991; Levin 1992; Hall et al. 1997). By reviewing habitat-related concepts and re-emphasising existing definitions for researchers and managers to work with, some standardisation may be possible. This could help align language used in different fields of marine science and management, and help improve interdisciplinary collaboration, enabling a more coherent and effective implementation of EBM.

Chapter 3. An assessment of juvenile *Gadus morhua* distribution and growth using diver operated stereo-video surveys[2]

3.1. Abstract

Protecting juvenile fish habitat is of particular importance for their survival. However, in many cases fish habitat requirements are poorly understood. Stereo-video methods can provide non-destructive quantitative information on fish abundance and size in relation to their surrounding environment. Stereo-video SCUBA transects were conducted during daylight hours from June to September 2013 within a proposed Marine Protected Area (MPA) in the Firth of Clyde, west of Scotland. More juvenile Atlantic cod (*Gadus morhua)* of size range 6 – 11 cm were observed in substrata containing mixed gravel, including maerl, than in boulder-cobble substrata with high algal cover, or sand with low density seagrass. Community composition was significantly different between substratum types. A decrease in *G. morhua* abundance was observed over the period of data collection. Over time, mean and variance in fish size increased, indicating multiple recruitment events. Protecting mixed gravel substrata could be a beneficial management measure to support the survival and recruitment of juvenile *G. morhua,* other substrata might be important at night given their diel migratory behaviour. Stereo-video cameras provide a useful non-destructive fisheries independent method to monitor species abundance and length measurements.

---

[2] NB: This chapter has been accepted as a paper: Elliott, S. A. M., Ahti, P. A., Heath, M. R., Turrell, W. R. & Bailey, D. M. 2016. An assessment of juvenile Atlantic cod distribution and growth using diver operated stereo-video surveys. Journal of Fish Biology. doi:10.1111/jfb.12998

3.2. Introduction

With increasing concern over the state of the marine environment much attention has been paid to the development of Marine Protected Areas (MPAs) as an ecosystem-based approach to protect vulnerable substrata and restore species and their habitats (Roberts et al. 2005; Seitz et al. 2014). However, in many cases factors affecting the survival of temperate marine fish are not well understood (Langton et al. 1996). This is of particular relevance within European waters where measures to restore fish stocks have focused primarily on reducing fishing effort, fishing gear adaptations to reduce bycatch, and fisheries closures (Hilborn 2011; Fernandes & Cook, 2013). While improvements in some stocks have been observed in the European Union (e.g. European anchovy *Engraulis encrasicolus* L. and *M. merlangus*), West of Scotland *G. morhua* stocks remain depleted (Fernandes & Cook, 2013; ICES 2015a).

The Firth of Clyde was once a productive fishery. However, commercially important *G. morhua* stocks declined sharply around the 1980s (Thurstan & Roberts, 2010; Heath & Speirs, 2012). Since the first phase of the *G. morhua* recovery plan was introduced (early 2000s) (Anon 2001; Kraak et al. 2013), measures have been implemented to try and restore stocks, including the prohibition of targeted fishing and a seasonal spawning area closure implemented in the outer Firth of Clyde (Anon 2001; 2002; Clarke et al. 2015). Today the predominant fishery occurring in the Firth of Clyde is the Norway lobster *N. norvegicus* fishery, with smaller amounts of scallop dredging and creel fishing occurring (Thurstan & Roberts, 2010; McIntyre et al. 2012). There are various possible reasons for the lack of recovery in *G. morhua* stocks. However in the UK, little attention has been paid to key habitat requirements for juveniles in comparison to Canada, the USA and Scandinavian countries (Bailey et al. 2011).

To avoid confusion, within the present paper habitat refers to resources and conditions required by a species to live in during a particular stage of its ontogeny (Hall et al. 1997). Habitat therefore includes the types of substrata (e.g. sediment and algae type), physiochemical parameters and biological characteristics required by a species (Gaillard et al. 2010; Chapter 2). A substratum type is considered important where a change in its conditions or availability has the ability to directly affect the survival of fish (Langton et al. 1996; Able 1999). All terminology used in this chapter is in line with chapter 2.

Age-0 *G. morhua* are known to migrate into and inhabit shallow (< 20 m) nearshore waters between June and October following pelagic larval stages (Magill & Sayer, 2004; Gibb *et al.* 2007). It is particularly important to understand the habitats of juveniles since cohort size of marine fish may be determined during their first year (Campana *et al.* 1989; Myers & Cadigan, 1993; Able 1999). Juvenile demersal fish are also thought to occupy a narrower range of substrata than adults (Gibson 1994; Able 1999). Higher densities of *G. morhua* have been observed around rocky reefs and eelgrass substrata (Tupper & Boutilier, 1995; Bertelli & Unsworth, 2014), as well as in more exposed areas (Lekve *et al.* 2006).

Monitoring of fish in shallow coastal areas containing rocky reefs and boulders is not possible using fisheries dependent mechanisms such as demersal trawling gear. Fishing and gear restrictions may also inhibit access in managed areas. SCUBA transect methods can be advantageous, reducing damage and mortality to benthos and fish, and being able to provide greater detail about the association of individual fish with the morphology of the seabed (Gregory & Anderson, 1997). To produce accurate comparative surveys, undertaking standardised diver surveys and minimising disturbance to fauna can improve precision and reduce bias (Sayer & Poonian, 2007). Stereo-video cameras are particularly advantageous since they enable accurate measurements to be made (Harvey *et al.* 2002). Stereo-video systems have previously been used in tropical sea environments (e.g. Cappo *et al.* 2006; Fitzpatrick *et al.* 2012) but their application to identify fish substratum association in the UK has only recently been trialled through baited camera techniques (i.e. Unsworth *et al.* 2014). Such methods might be a valuable means of collecting information for spatial planning and for monitoring to see whether management is effective.

The aims of the present study were two-fold: firstly, to determine the effectiveness of stereo-video SCUBA belt transects to assess the diversity, abundance and length of different epibenthic and demersal fish species in UK waters; and secondly, to assess abiotic and biotic variables influencing the distribution and abundance of juvenile *G. morhua* in shallow subtidal waters. Data were collected between June and September 2013 around the south of the Isle of Arran, Firth of Clyde. All study sites fell within the South Arran Nature Conservation MPA (NCMPA) (SNH 2014), but took place before designation and any new management measures were implemented. By understanding abiotic and biotic variables affecting age-0 *G. morhua* abundance and distribution, targeted management measures within the South Arran NCMPA could be implemented to support their survival and apply a more ecosystem-based management.

3.3. Materials and methods

3.3.1. Study location

Data were collected at depths of 4.5 - 23 m around South Arran NCMPA (Figure 3.3.1). South Arran NCMPA encompasses an area of 250 km^2 and was designated in 2014 for its internationally important seagrass and maerl beds in addition to other substrata (burrowed mud, kelp and seaweed communities) and epibenthic fauna (SNH 2014). The MPA contains within its boundaries the Lamlash Bay No Take Zone (NTZ), designated in 2008 and prohibiting all fishing within its boundaries under the Inshore Fishing (Scotland) Act of 1984 (Axelsson *et al.* 2009).

3.3.2. Camera set up

A SeaGIS underwater stereo-video camera system (SeaGIS 2013) which consisted of two high-definition (HF G25, Canon) video cameras in waterproof housings, attached to a custom made diver-portable steel frame (Figure 3.3.2). The system was set up similar to prototype described in Harvey and Shortis (1995; 1998), however, this system was optimised for smaller bodied fish. Distances between cameras were therefore configured with a base separation of 66 cm and an inward calculated angle of view of ~10° in sea water visibility of < 6 m distance. Each camera was set to manual mode with the focal length set to infinity (∞). Two underwater LED W38VR Archonlight (1400 lumen) torches were mounted on the frame, facing at an angle to the middle of the stereo-camera field of view. Prior to in-field data collection the mounted cameras were calibrated within a controlled environment using methods outlined within Harvey & Shortis (1998) and using the program and user guide CAL (version 2.11, SeaGIS 2013). A calibration cube (1 x 1 x 0.5 m) containing 85 targets was filmed with the stereo-video camera system in 20 different orientations (SeaGIS 2013). Individual camera calibrations were produced using the CAL software and physical camera parameters, camera separation and orientation parameters were computed to allow accurate photographic measurements to be taken (SeaGIS 2013).

3.3.3. Data collection

Deployment locations were determined according to existing information collected on substratum types around the pre-designated MPA (COAST 2012; SNH 2014). Stratified random points were identified within five zones (Figure 3.3.1) with samples collected within each zone over the period of data collection. The zones were created according to prior information on substratum type and wave fetch, using Generate Stratified Random Points with Geospatial Modelling Environment software (Spatial ecology 2013) in Arc Geographic Information System (GIS) version 10.1. These zones were created to provide independent replicates of each substratum type and collect data across a representative range of substrata, depths and wave fetch values. Repeat transects within the same location were not undertaken. Survey work was not conducted in strong tides (measured using tide timetables) and bad weather (heavy rain and wind speed and gusts > 15 km/hour), because of difficulties in equipment and Rigid Inflatable Boat (RIB) handling. It has been previously observed that tidal conditions can cause variability in *G. morhua* counts (Sayer & Poonian, 2007).

The abundance of *G. morhua* around South Arran NCMPA was recorded along 100 m strip transects between 5 June and 20 September 2013 (Figure 3.3.1). Since juvenile *G. morhua* had not yet arrived during data collection days in June (5 - 13), data analysis used 31 transect videos, taken after the first observation of *G. morhua*. Strip transects were chosen as a standard and accurate technique for assessing fish abundance (Kimmel 1985; Hunter & Sayer, 2009). A leaded line transect was laid perpendicular to the shore line to keep survey depth consistent within the transect. Following a 10 minute wait for any disturbance to the seabed or fauna to dissipate (Dickens *et al*. 2011), the divers descended and swam at a slow constant speed along the transect. Transects were carried out by SCUBA divers swimming approximately one metre above the seabed with cameras held at an oblique angle to capture fauna in front of the field of view and the substratum. An index of maximum horizontal visibility was measured using a Secchi disk attached to the end of the leaded line. The maximum distance at which it could be distinguished was measured in the stereo-video recordings. An LED diode was used to synchronise the video footage prior to surveys and following transect completion (Harvey & Shortis, 1995). To reduce diel effects on species, data collection took place between 0800 and 1500 hours (GMT), a minimum of three hours after sunrise and before sunset. As a result of logistical complications night sampling did not take place.

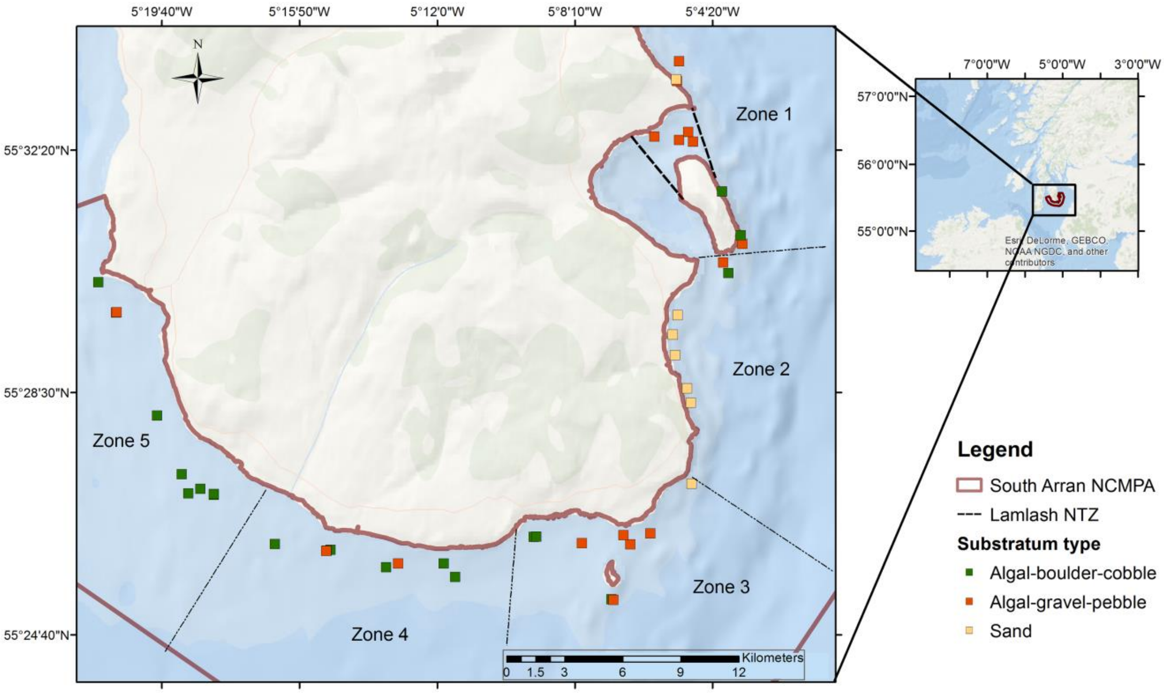

Figure 3.3.1 - South of Arran NCMPA with dive site locations and substratum categories.

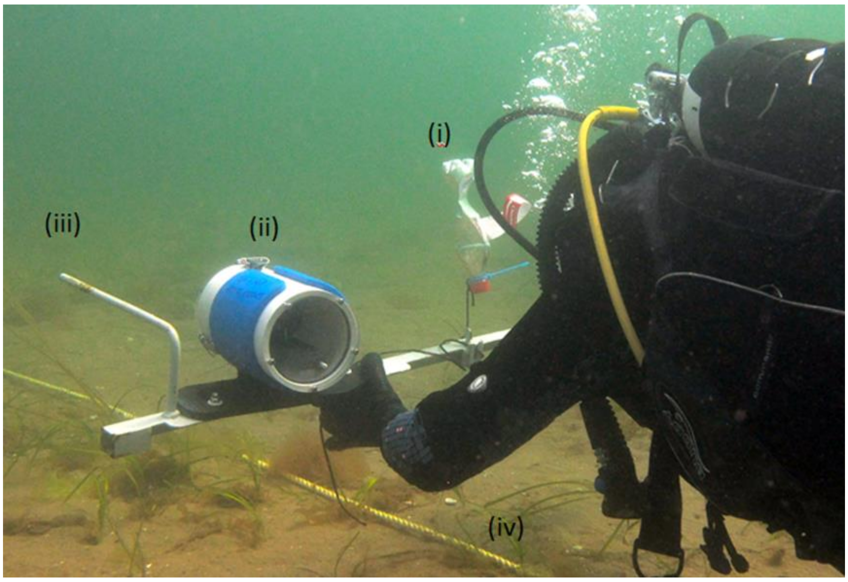

Figure 3.3.2 - Image of stereo-video camera and line set-up showing i) float for frame buoyancy ii) stereo-video cameras in housing iii) custom made bar to attach LED lights iv) leaded line.

3.3.4. Video analysis

Each transect video was analysed twice by two observers using Event Measure software (version 3.61, SeaGIS 2013) to reduce observer bias. The first analysis focused on substratum characterisation, the second on fauna identification, abundance and length measurements. In the absence of acoustically mapped substrata around South Arran, substratum categories were visually classified according to the most abundant combination of sediment grain sizes and macrophyte types observed together (Table 3.3.1), similar to Gregory & Anderson (1997) and Cote *et al.* (2001 and 2003). Since transects had a uniform combination of sediment and algae type, transects were assigned a single overall transect substratum type using the two most common divisions on the Wentworth scale sediment (Wentworth 1922; Connor *et al.* 2004) and broad algae type and density (estimated by percentage cover; Table 3.3.1). Seagrass was not treated separately to sand because of the low density and spatial extent within the area, and the small sample size of the dataset. Equally, maerl was not treated separately from gravel-pebble substratum type because of its gravel-pebble sized form around south of Arran. In addition impacted maerl has been demonstrated to be more similar to gravel than live maerl (Kamenos et al. 2003). As a result of insufficient prior knowledge of the substratum types of the area, the experimental design was unbalanced. Fourteen algal-boulder-cobble substratum type transects were carried out compared to 12 algal-gravel-pebble and five for the sand substratum category.

Table 3.3.1 - Substratum type characterisation. Substratum types characterised according to dominant sediment type and macrophyte type and density.

Substratum type	**Sediment composition**	**Algae and seagrass type and density**
Algal-boulder-cobble (ABC)	Sediments composed of mixed boulders and cobbles (particles > 6.4 cm).	Sediment covered in a mixture of kelp and red algae (> 60 % algae cover). Examples of algae species include *Laminaria spp.* and *Ceramium spp.*
Algal-gravel-pebble (AGP)	Mixed gravel (stone, shell and maerl *Phymatolithon calcareum (*Adey & McKibbin, 1970) and pebble (particles 0.4 to 6.4 cm).	Between 20 and 50 % of sediment covered by algae.
Sand	Sandy sediments which may contain some gravel (consisting of broken shell) (particles < 0.4 cm)	< 25 % algae or seagrass *Zostera marina* L. cover.

Sections of the video recordings where the camera angle was incorrect and the substratum was not visible were removed and the transect length adjusted in subsequent calculations. Any further distance lost from transect length caused by large boulders or slack line was deducted from the total length of the transect. One entire transect was removed from the analysis because of inappropriate field of view. For each transect, the width of the field of view of the video camera was measured by identifying recognisable points on the seabed on both cameras. Horizontal visibility along the transect was measured in the video recordings as the greatest distance at which the Secchi disk was visible.

Fauna were identified to the lowest taxonomic level possible, usually to species. The fish fork length measurements were taken (measuring from the nose to the fork). To undertake length measurements, each individual observed had to be visible in both cameras. Length measurements of all *G. morhua* observed, were therefore not possible. All length measurements with a Root Mean Square (RMS) error above 2 cm and with a precision of length measurements > 0.5 cm were removed from analysis (SeaGIS 2013).

3.3.5. Data analysis

To understand community composition differences between substratum types, a one factor PERMutation Analysis Of Variance Analysis (PERMANOVA) in PERMANOVA 6 software as described in Anderson *et al*. (2008) was undertaken. PERMANOVA was used in order to overcome distributional and homoscedasticity restrictions of ANOVA. The standardised abundance of benthic and demersal fauna was square root transformed, to reduce the influence of dominant species. A Bray-Curtis similarity coefficient was used prior to applying PERMANOVA. Posterior pair-wise tests were used to compare the difference between the groups of samples. The PERMANOVA was run with 9999 permutations to draw inferences at the P (perm) < 0.001 level. Visualisation of the matrices was achieved using non-metric Multi-Dimensional Scaling (nMDS) plots which provide values of stress (stress increases with reduced dimensionality or the ordination). SIMilarity PERcentages (SIMPER) analysis was used to determine which species contributed most to the dissimilarity between the different substratum types (Clarke and Warwick, 2001).

The effect of abiotic variables on age-0 *G. morhua* abundance included: substratum type, depth (m), distance from coast (m), Julian day (JD, days) and wave fetch (km). Wave fetch values for a 200 m coastline grid (downloaded from http://www.sams.ac.uk/michael-burrows) were used as described in Burrows *et al*. (2008). For each transect location, wave fetch for the closest grid was obtained. Distance from coast was calculated using Arc GIS version 10.1. Biotic variables explored included: Hill diversity N_2 (reciprocal of Simpson's index) and N_∞ (reciprocal of the proportional abundance of the commonest species) (Hill 1973) for epibenthic fauna (e.g. tunicates, echinoderms and crustaceans).

Difficult to identify fauna, e.g. hydroid, bryozoan and *Majidae* spp. (Samouelle, 1819) could not always be identified to species level. For continuity of analysis such fauna were quantified in total visible hydroid and bryozoan or *Majidae* abundance (e.g. Unsworth *et al.* 2014).

To condense multivariate variability into fewer dimensions and identify habitat variables affecting the distribution of *G. morhua*, a Principal Component Analysis (PCA) was performed using R software (version 3.03, R Core Team, 2015). Explanatory variables observed to have a stronger effect on *G. morhua* abundance from the PCA were used in a Generalised Linear Model (GLM) to understand *G. morhua* abundance, removing collinear variables. An offset for transect area (m^2) was incorporated into the GLM. A negative binomial distribution was used to account for over dispersion. Explanatory variables included substratum type (three levels), Hill diversity index for epibenthic fauna (continuous), wave fetch (continuous) and JD (treated as a continuous variable to reduce the number of parameters used in the model). The model of best fit was:

$$log(Y_i) = \beta_0 + \beta_1, S_{ij} + \beta_2, JD_i + Offset\ (transect\ area)_i \tag{3.1}$$

where Y_i is *G. morhua* abundance, β are the coefficients, S_{ij}, substratum type and JD_i, Julian day. A random effect for zone using R package “glmmADMD” (Skaug *et al.* 2014) was tested for but was not significant. Tukey tests using R package “multcomp” (Hothorn *et al.* 2008) were used to test the difference between categorical variables. Backwards stepwise model selection was implemented (Bolker *et al.* 2009; Zuur *et al.* 2009) and a log likelihood ratio test was used to test model significance against the null hypothesis in addition to checking residual plots.

A Linear Mixed Model (LMM) using R package “nlme” (Pinheiro *et al.* 2014) was used to model length measurements. The best model fit included JD as a fixed effect with an offset for the transect area, and a random effect for zone:

$$Y_i = \beta_0 + \beta_1, JD_i + Offset\ (transect\ area)_i + z_{ij} \tag{3.2}$$

where Y_i is *G. morhua* fork length, β are the coefficients, JD_i, Julian day and z_{ij}, the random effect for zone. A large outlier identified by Cleveland dotplot was removed from analysis since it was considered that the individual could have been of age-1.

Length variation over the period of data collection was analysed by subtracting the maximum length from the minimum length from each day of data collection.

$$Y_i = \beta_0 + \beta_1, JD_i \qquad (3.3)$$

where Y_i is *G. morhua* fork length variation.

3.4. Results

Thirty one stereo-video SCUBA transects were analysed, covering an area of 4093.14 m^2 (mean transect length = 95.56 m, S.D. = 10.23 m and mean transect width = 1.38 m, S.D. = 0.18 m) (Figure 3.3.1). A total of 496 *G. morhua* were identified with a mean of 11.41 (S.D. ± 19.47) per transect and within four of the 31 (13%) transects no *G. morhua* were observed. 45 taxonomic groups were identified from 34 different families. 90% (9327) of the fauna identified were classed as epibenthic fauna. The maximum distance *G. morhua* were able to be identified and measured accurately was 2.86 m from the cameras (mean = 1.52 m, S.D. ± 0.39) and the minimum distance objects were measured was 0.85 m. The maximum distance the Secchi disk was seen from the cameras varied between 4 – 5.5 m. It is therefore unlikely that varying underwater visibility affected identification and measurement analysis.

Differences in community composition between substratum types were observed (pseudo-F = 2.33, P (perm) < 0.001). Pair-wise tests between substratum type showed significant differences between AGP and ABC (t = 1.63, P (perm) < 0.001) and ABC and sand substratum type (t = 1.99, P (perm) < 0.001). No significant difference between AGP and sand substratum type was observed (t = 0.91, P(perm) > 0.05). The nMDS plot (Figure 3.4.1) shows relatively good ordination (stress 0.16), with some overlap between substratum types. SIMPER analysis showed 22 species were required to explain dissimilarity between substratum types with 80% dissimilarity between AGP and sand, 79% between AGP and ABC and 94% between ABC and sand. Hydroids and poor cod (*Trisopterus minutus* L.) featured in the top species causing the largest dissimilarity between AGP and sand and AGP and ABC. Burrowing anemones (*Ceriantheopsis lloydii*, Gosse, 1859) and the common sea urchins (*Echinus esculentus* L.) led to greatest dissimilarity between ABC and sand (cumulative dissimilarity of 19%).

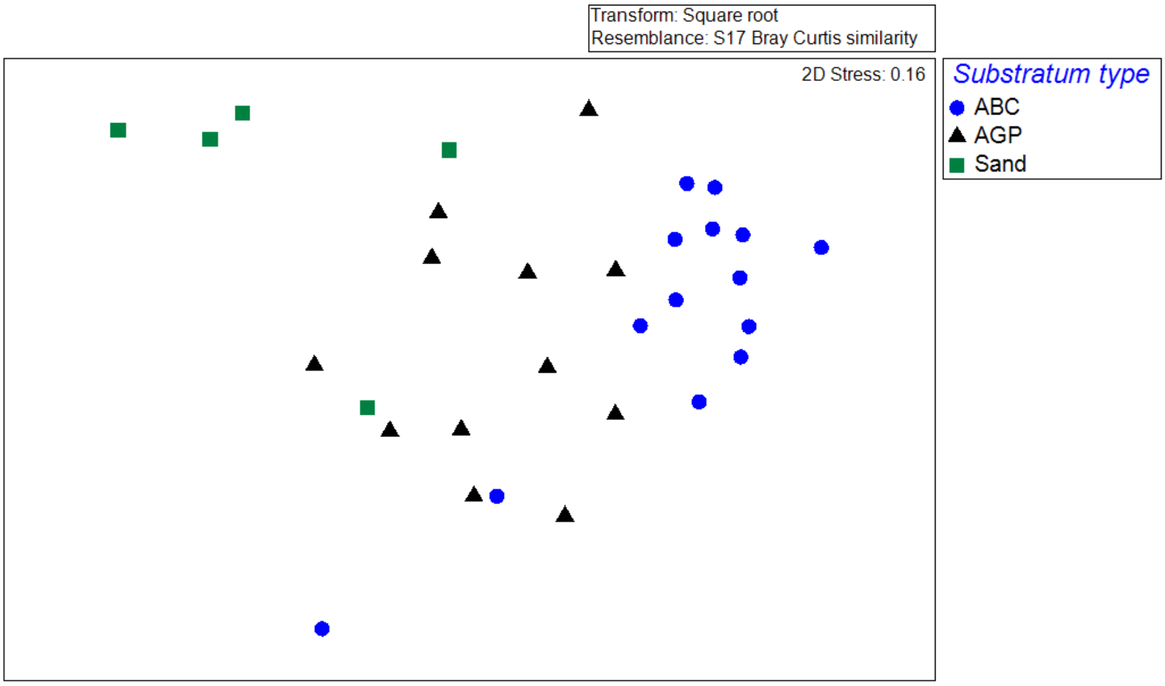

Figure 3.4.1 - nMDS plot of the community composition of all fauna observed between substratum types. Significant effects of substratum type on assemblage structure are observed (PERMANOVA: $P < 0.001$).

3.4.1. Abiotic and biotic effects on *G. morhua* abundance

The PCA was conducted on seven variables. Two components had eigenvalues over Kaiser’s (1960) criterion of 1, and in combination explained 57% (PC1 35%, PC2 22%) of the variance. PC1 was most negatively correlated with Hill diversity indices followed by substratum type and positively correlated with wave fetch.

PC2 correlated most strongly with distance from coast with a negative correlation with substratum type (Table 3.4.1). These results indicate that N_2, substratum type, distance from coast and wave fetch had stronger trends than other variables and were therefore used as explanatory variables to understand the abundance and distribution of *G. morhua*.

Table 3.4.1 - Eigenvectors of the standardised first and second principal component from the PCA of seven *G. morhua* habitat variables.

Variable	PC1	PC2
Depth	0.240	0.268
Distance from coast	0.258	0.568
JD	-0.175	0.265
N_2	-0.539	0.360
N_∞	-0.512	0.410
Substratum type	-0.448	-0.261
Wave fetch	0. 301	0.409

Analysis of the explanatory variables independently, only substratum type and JD had an effect on the abundance of juvenile *G. morhua* (L = 95.32, d.f. = 5, theta = 0.48, $P < 0.01$). The highest abundance of juvenile *G. morhua* was observed within AGP substratum type, and the lowest abundance was observed in sand substratum type. Intermediate values were observed in ABC (Figure 3.4.2 and Appendix Table E.1 – Table E.2). A decrease in the abundance of *G. morhua* was observed over the period of data collection (Figure 3.4.3 and Appendix Table E.1).

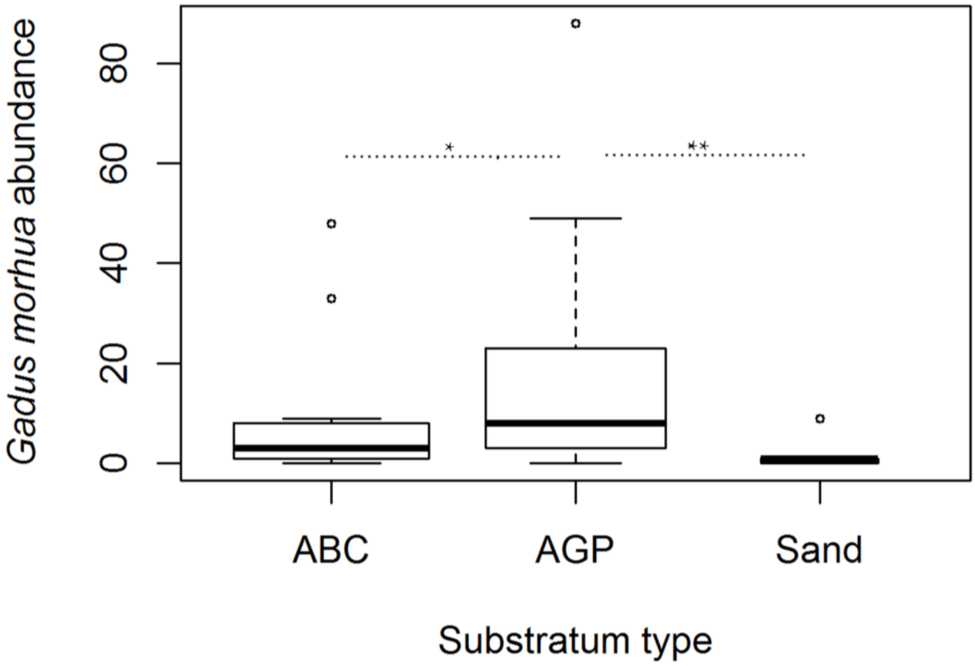

Figure 3.4.2 - Substratum type association of age-0 group *G. morhua* observed around south Arran NCMPA. More juveniles were found in relation to substratum type algal-gravel-pebble than algal-boulder-cobble or sand. No significant difference was observed between algal-boulder-cobble and sand. The varied width boxplots, proportional to the square root of the sample sizes, indicate the 25th and 75th percentiles of the total number of G. morhua observed within the different substrata. The upper bars indicate the 10th and the lower bars the 90th percentiles. The thick line indicates the median abundance. Open circles indicate the outliers. Dashed horizontal lines between substratum types with * refers to Tukey test P value significance (* = $P < 0.05$ and ** = $P < 0.01$).

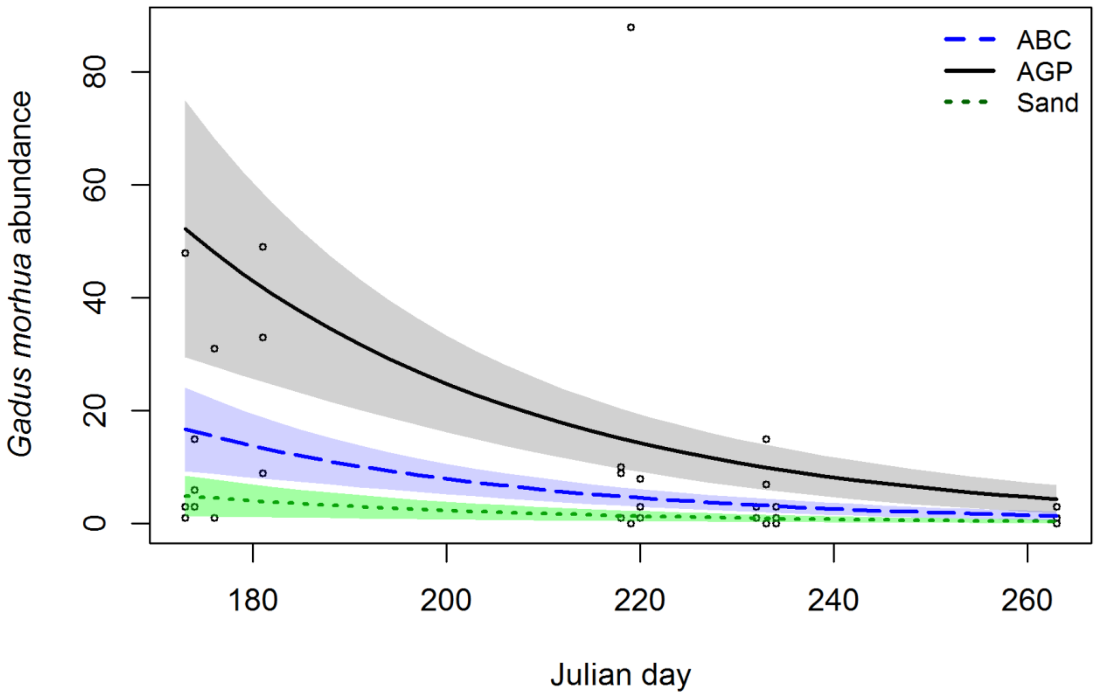

Figure 3.4.3 - Fitted values ± 95% confidence intervals from the model of best fit for *G. morhua* abundance for each substratum type over the course of data collection. Open circles represent abundance of *G. morhua* from 22 July to 20 September 2013. A decline in *G. morhua* abundance was observed over the course of data collection (P < 0.01).

3.4.2. Length Analysis

121 *G. morhua* length measurements were made with the average length of 6.3 cm (S.D. ± 1.4 cm). The largest *G. morhua* observed was 11.4 cm and the smallest 3.2 cm. The largest individual (2 cm larger than the second largest individual) was excluded from analysis as it could have been a small age-1 individual following exploration of Marine Scotland Science quarter three (July – September) scientific bottom trawl data. All other *G. morhua* analysed were deemed to be age-0 (Dalley & Anderson, 1997; Marty *et al.* 2014). An increase in length was observed over the course of data collection (L = -470.50, d.f. = 4, *P* < 0.01; Figure 3.4.4 and Appendix Table E.3). No other variables were significant in explaining *G. morhua* length. An increase in length variation was also

observed over this time period (LM, $F_{1,118} = 9.18$, $P < 0.01$) (L = -547.30, d.f. = 3, $P < 0.01$; Appendix Table E.4).

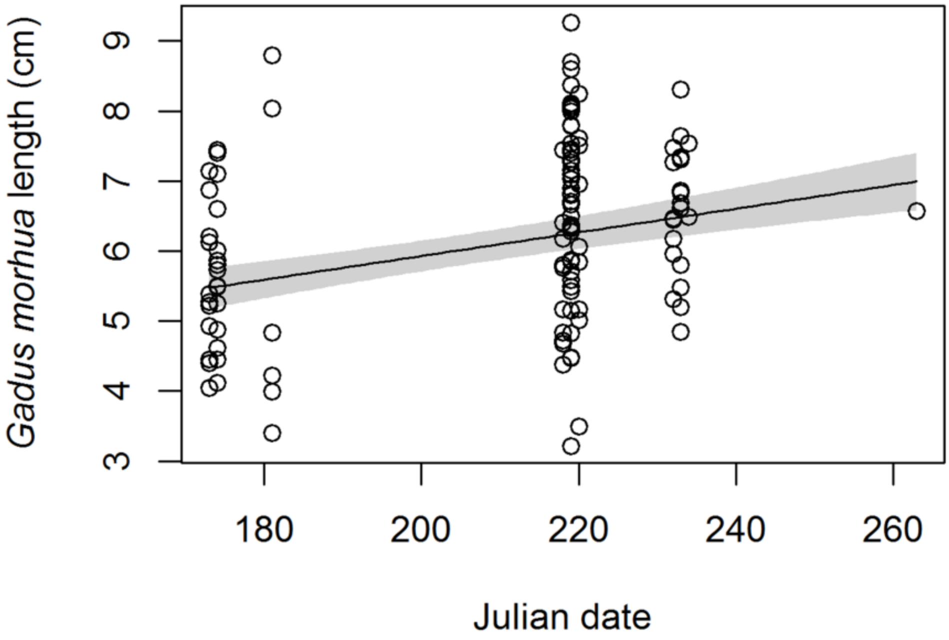

Figure 3.4.4 - *G. morhua* length frequency (cm) over the course of data collection. Data points represent lengths of *G. morhua* measured from 22 July to 20 September 2013. The solid line indicates the GLMM fitted line, the shaded area indicates ± 95 % confidence intervals. An increase in age-0 *G. morhua* length was observed over the course of data collection (P < 0.01).

3.5. Discussion

As far as the authors are aware, this is the first study using stereo-video SCUBA transects in the North Atlantic and builds upon existing single camera and Underwater Visual Census (UVC) studies (e.g. Schneider *et al.* 2008; Hunter & Sayer, 2009). Stereo-video SCUBA transects permit accurate, fisheries independent, three-dimensional measurements of fauna and transect dimensions to be made (Harvey *et al.* 2002). Data collected has enabled fine-scale abundance and distribution information to be gathered for the first time on *G. morhua* during daylight hours within the Firth of Clyde.

Community composition differences of benthic and demersal species observed between the different substrata categories. Some overlap between substratum categories was observed. The latter may be due to overlaps in species substrata association and given there was a certain amount of overlap in sediment grain sizes between substrata. Predictor variables such as wave fetch and depth are known to affect substrata which in turn affect the distribution of species (Burrows et al. 2008; 2012; Reiss et al. 2015; Chapter 5).

The abundance of juvenile *G. morhua* varied with substratum type, with more *G. morhua* observed in algal-gravel-pebble substrata than algal-boulder-cobble or sand. Juvenile *G. morhua* exhibit a light brown and white checkerboard pattern which on gravel-pebble surfaces makes them relatively difficult to distinguish from their background, obscuring their movement from predators (Gregory & Anderson, 1997). The combination of colouration and substrata of sufficient rugosity to seek refuge within, suggests age-0 *G. morhua,* of the size ranges observed, may choose to spend a greater proportion of their time on algal-gravel-pebble substratum type. Similarly, Lough *et al.* (1989) observed juvenile *G. morhua* in high abundance on pebble-gravel substrata. The high variability associated with these observations (Figure 3.4.2) is likely to be a consequence of the small sample size and some variability in juvenile *G. morhua* substratum selection.

Transects within Lamlash Bay NTZ were algal-gravel-pebble substratum type. The effect of the NTZ on juvenile *G. morhua* abundance was not explored since data on juvenile gadoid abundance was not available prior to its establishment to perform a Before/After and Control/Impact (BACI) survey (Underwood, 1992; Sale *et al.* 2005). A study undertaken by Howarth *et al.* (2015) found no difference in fish abundance within and out with Lamlash Bay NTZ. The latter may be a result of the reserve's small size (2.67 km^2) and its young age (Howarth *et al.* 2015). Previous research on juvenile *G. morhua* does however show limited movement (Grant & Brown, 1998) but this may vary depending on substratum type (Laurel *et al.* 2004).

Seagrass beds have previously been observed to be nursery grounds for age-0 *G. morhua* (Linehan *et al.* 2001; Bertelli & Unsworth, 2013; Lilley & Unsworth, 2014) with some studies showing increased nocturnal association (Anderson *et al.* 2007; Bertelli and Unsworth 2014). However, because of the sample size and low density of *Z. marina* sampled within the area, this substratum was merged with sand. Low density seagrass areas have been related to be more similar to sandy sites (Jackson *et al.* 2001; McCloskey & Unsworth 2015), particularly when patchy with low shoot density and area coverage (Jackson *et al.* 2001; Gorman et al, 2009). Mixed diurnal behaviour has also been observed with age-0 *G. morhua*, with some experiments showing more active behaviour during daylight hours (Keats & Steele, 1992; Sayer & Poonian, 2007). Differential aggregation behaviour has also been observed depending on light levels, predator presence, and seagrass patch size (Laurel *et al.* 2003a; Laurel *et al.* 2004; Anderson *et al.* 2007).

Gotceitas and Brown (1993) observed that juvenile *G. morhua* within an experimental tank selected cobble substrata in the presence of predators whilst selecting sand and gravel-pebble substrata in the absence of predators. It is possible that the juveniles identified during data collection did not feel threatened by the diver, and the low abundance of larger piscivores (Heath & Speirs, 2012) may have led to higher abundances on algal-gravel-pebble substratum type. In the present study, no predator prey interactions were observed. It is thought that some gravel substrata, specifically containing maerl, may contribute to higher benthopelagic diversity, structural rugosity (relative to the size of *G. morhua*) and heterogeneity, and that these factors are of importance to the survival of juvenile *G. morhua* (Hall-Spencer *et al.* 2003; Kamenos 2004; Lough 2010).

A decline in *G. morhua* abundance and an increase in juvenile size and size variation were detected over the course of data collection. *G. morhua* have been observed to arrive in recruitment pulses to coastal areas during downwelling events (Ings *et al.* 2008). The increase in size variation is most likely caused by pulse recruitment occurring over this time period, or one continued long pulse recruitment (Bastrikin et al. 2014) from July to August 2013. The decline in abundance is unlikely to have been caused by fish moving into deeper waters within such a narrow time span since previous studies show that this migration occurs after their first winter or first year (Magill & Sayer, 2004).

Fewer length measurements than counts were made (24% of the total number of *G. morhua*), owing to a combination of not being able to distinguish individual juveniles within schools in both cameras and a blind spot between the cameras where the fish were too close to the cameras to be measured (Unsworth *et al.* 2014). This latter problem could have been reduced by having the cameras closer together, but at the expense of reduced accuracy at distance (Boutros *et al.* 2015). Precision in the mid Z direction (towards and away from camera) is affected by the distance between cameras, affecting all measurements of objects which are not angled normal to the camera axis (SeaGIS 2013; Boutros *et al.* 2015).

Future temperate water studies should take water visibility and fish size into account in order to maximise the number of fish measured. Stereo-video SCUBA transects can provide detailed and valuable information on fish assemblage and population structure in rocky and sensitive substrata which would otherwise be inaccessible. Use of semi-closed or closed circuit rebreather apparatus, or Autonomous Underwater Vehicles (AUV) may further reduce observer bias (Sayer & Poonian, 2007; Clarke *et al.* 2009). With the rise in MPAs and spatial restrictions to manage substrata and species around the UK, this technique provides important information for fisheries management and information for possible future monitoring.

Despite measures in place to recover stocks, the already low numbers of *G. morhua*, small length index and isolation of the Firth of Clyde in comparison to neighbouring areas are likely to cause it to be more susceptible to local fishing impact (Heath & Speirs, 2012). Much debate exists on the value of MPAs for the protection of fish, particularly in temperate environments (Roberts *et al.* 2005; Takashina & Mougi, 2014; Fernández-Chacon *et al.* 2015). However, if an MPA can protect important substrata of value to juvenile *G. morhua*, bottle neck recruitment may be avoided, thus increasing the survival of individuals at this critical stage in their life cycle (Lough 2010). Management measures have recently (December 2015) been established to recover maerl beds found within the NCMPA (Scottish Government 2015). On the basis of the data presented here it appears that such management measures could have benefits for juvenile *G. morhua*. In the meantime, further investigations are recommended to strengthen habitat related observations of juvenile *G. morhua* abundance and distribution. Better understanding and protection of important habitat components could support juvenile *G. morhua* survival and recruitment.

Chapter 4. Habitat and growth related changes in juvenile gadoids using stereo-video baited cameras

4.1. Abstract

Demersal gadoid fishes such as Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) have been commercially important in the UK since the early 19th century. These species differ greatly in how well their stocks have fared in recent decades, with loss of juvenile habitat being a possible reason why some species and stocks are below safe limits.

Non-destructive Stereo-video Baited Remote Underwater Video (SBRUV) surveys were conducted across a recently designated Marine Protected Area within the Firth of Clyde between June and September in 2013 and 2014. Abiotic and biotic variables affecting the relative abundance and length of these gadoids during daylight hours were explored. *G. morhua* were observed in higher relative abundance in sheltered areas composed of gravel-pebble substrata containing maerl, than over sand and mud, and more exposed areas. Ontogenic shifts and density dependence effects on substratum association were also observed. *M. aeglefinus* and *M. merlangus* were observed in higher relative abundance in deeper sand and mud substratum types. Relative abundances of all three species were positively related to benthopelagic species diversity. On average, *M. aeglefinus* and *M. merlangus* were larger and also grew at a faster rate than *G. morhua*.

This work demonstrates the potential of SBRUV surveys as a non-destructive survey tool under northern-temperate conditions, allowing possible links between differences in the behaviour of different species and stock trends to be explored. The results also suggest that efforts to protect fish and enhance stocks must take into account the quality of the seabed, as indicated by benthopelagic diversity, and not just the presence of particular substratum types.

4.2. Introduction

Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) (Appendix A) are of considerable economic importance throughout the North Atlantic (Cote et al. 2003; MMO 2015). However, stocks of all three species declined in the late 20th century with historic lows for *G. morhua* and *M. merlangus* in the early 2000s (Holmes et al. 2014; ICES 2014; ICES 2015d). Subsequently efforts have been put in place to recover these stocks but little progress has been observed in much of the west coast of the UK and recruitment remains low for all three species (Fernandes & Cook 2013; ICES, 2014; Barreto & Bailey 2015). Specifically within the Firth of Clyde, southwest Scotland, demersal fishing was an important sector, today the predominant fishery occuring is that of *N. norvegicus* trawling (Thurstan and Roberts 2010; Heath and Speirs 2012). A change has also been observed in the Firth of Clyde from an area of high species eveness to one with high biomass of juvenile *M. merlangus* as of the later 20th century (Heath and Speirs 2012).

The recovery of commerical fish species depends not only on reductions in targeted fishing and bycatch but ensuring they have the food resources and shelter required to minimise natural mortality and maximise individual growth. Understanding habitat variables affecting fish distribution and abundance could also help reduce by-catch during this vulnerable stage in their life cycle if measures to protect these areas are implemented (Langton et al. 1996; Cote et al. 2003; Vasconcelos et al. 2014). Such measures were implemented on Georges Bank (Southern New England, USA) and along the Norwegian Skageerak coast. In both cases improved recruit survival was observed in demersal fish including *G. morhua* and *M. aeglefinus* (Murawski et al. 2000; Moland et al. 2013). Studies of habitat components of importance can provide useful information on the ecology of species, such as behavioural requirments for shelter use, important feeding areas and resource partioning (Kramer et al 1997). Habitat information can also provide valuable information for spatial management methods of protection (Vasconcelos et al. 2014). Unfortunately detailed analysis of habitat variables affecting species distirbution is often missing (Cote et al. 2003).

G. morhua, M. aeglefinus and *M. merlangus* (from here on referred to as gadoids) are known to have relatively similar life cycles, migrating to coastal areas following pelagic larval stages (Gibb et al. 2007; Olsen et al. 2010; Wright et al. 2010; Bailey et al. 2011). Higher densities of juvenile *G. morhua* have been observed around shallow (<20 m) rocky reefs and eelgrass substrata (Tupper and Boutilier 1995a; Gibb et al. 2007; Bertelli and Unsworth 2014), as well as in more exposed areas (Lekve et al. 2006). Few studies have been carried out on *M. aeglefinus* and *M. merlangus* habitat component associations, but juveniles are known to inhabit shallow coastal areas for the first year of their life cycle before migrating back into deeper waters as they undergo ontogenetic shifts (Heath and Gallego 1997; Ware 2009; Wright et al. 2010). Additionally, most studies that have looked at the habitats of these gadoids have not considered biological characteristics which may affect abundance observations.

The majority of fish distribution and abundance surveys around the UK and more widely have taken place through trawl and larval surveys (Vasconcelos et al. 2014) e.g. Gibson et al. 1996; Ware 2009; Wright et al. 2010; Bastrikin et al. 2014. Such methods provide little information on fine-scale substratum associations which may affect juvenile gadoid distribution. Photogrammetric techniques can provide a useful means of collecting non-damaging and non-extractive data on associations of fish with types of substratum and benthopelagic diversity (Harvey et al. 2007; Fitzpatrick et al. 2012). Data collection using imaging enables access to shallow and structurally rugose seabed types, and protected areas which would otherwise be inaccessible using trawl or seine netting methods (Cappo et al. 2006). Stereo systems are particularly advantageous since they enable accurate measurements to be made from stills or video (Harvey et al. 2002). Baited cameras are commonly presumed to be biased towards larger predators and scavengers (Lowry et al. 2012; Dunlop et al. 2015). However, comparisons between baited and unbaited cameras have shown higher relative abundances and species diversity in baited camera observations (Watson et al. 2005; Harvey et al. 2007; Bernard and Gotz 2012).

Stereo-video Baited Remote Underwater Video (SBRUV) deployments can avoid biases from the presence of divers on more cryptic species and enable a larger range of depths to be surveyed (Harvey et al. 2007). SBRUV deployments have also been discussed as the most effective way to collect data for fisheries and biodiversity monitoring and management (Murphy and Jenkins 2010; Bernard and Gotz 2012). Stereo-video systems have previously been used in tropical and deep sea environments (e.g. Cappo et al. 2006; Fitzpatrick et al. 2012) but their application to identify fish substratum association in the UK has only recently been trialled through baited camera techniques (i.e. Unsworth et al. 2014). SBRUV may be part of the solution to the survey and monitoring requirements of spatial management in the UK, but the method needs to be proven under the challenging conditions often found in British waters.

The aims of this study were to: firstly, identify what environmental variables gadoid association to be able to describe their habitat requirements; secondly, to understand whether there were any growth and arrival differences; and three assess the use of SBRUV surveys to monitor commercial fish species. Data were collected between June and September 2013 and 2014 within the south of the Isle of Arran, Firth of Clyde. All study sites fell within the South Arran Nature Conservation MPA (South Arran NCMPA) (SNH 2014), but took place before management measures were implemented. By understanding habitat variables affecting the distribution and growth of juvenile gadoids, multi-purpose protection measures can be proposed protecting not only vulnerable benthos of conservation importance, but also commercially valuable gadoids.

4.3. Method and materials

4.3.1. Study location

Within South Arran NCMPA data were collected at depths of 4.0 m – 47.2 m, (Figure 4.3.1). The MPA was designated in 2014 for its seagrass and maerl beds in addition to burrowed mud, kelp and seaweed communities and epibenthic fauna (SNH 2014), and encompasses an area of 250 km^2. Lamlash Bay No-Take-Zone (designated in 2008) covering an area of 2.67 km^2 also exists within the MPA prohibiting all commercial and recreational fishing within its boundaries (Axelsson *et al.*, 2009; Thurstan & Roberts, 2010).

4.3.2. Data collection

In the sampling design, the MPA was divided into five zones of approximately equal size (Figure 4.3.1), but which differed in exposure and other characteristics. These zones formed the strata of a stratified random design. Sampling location points within each zone were generated using Geospatial Modelling Environment software (version 10.1, Spatial ecology 2013). The effect of this was to allow interspersed patches of different substrata to be surveyed, with the exception of seagrass, for which only a single patch was available. Deployment locations varied slightly between years due to logistical reasons. During summer 2013 cameras were deployed from a 6.5 m RIB whilst summer 2014 a 10.8 m research vessel (RV Actinia) was used. During 2014 data were not collected around the southwest side of the island due to the slower steaming speed of the vessel used.

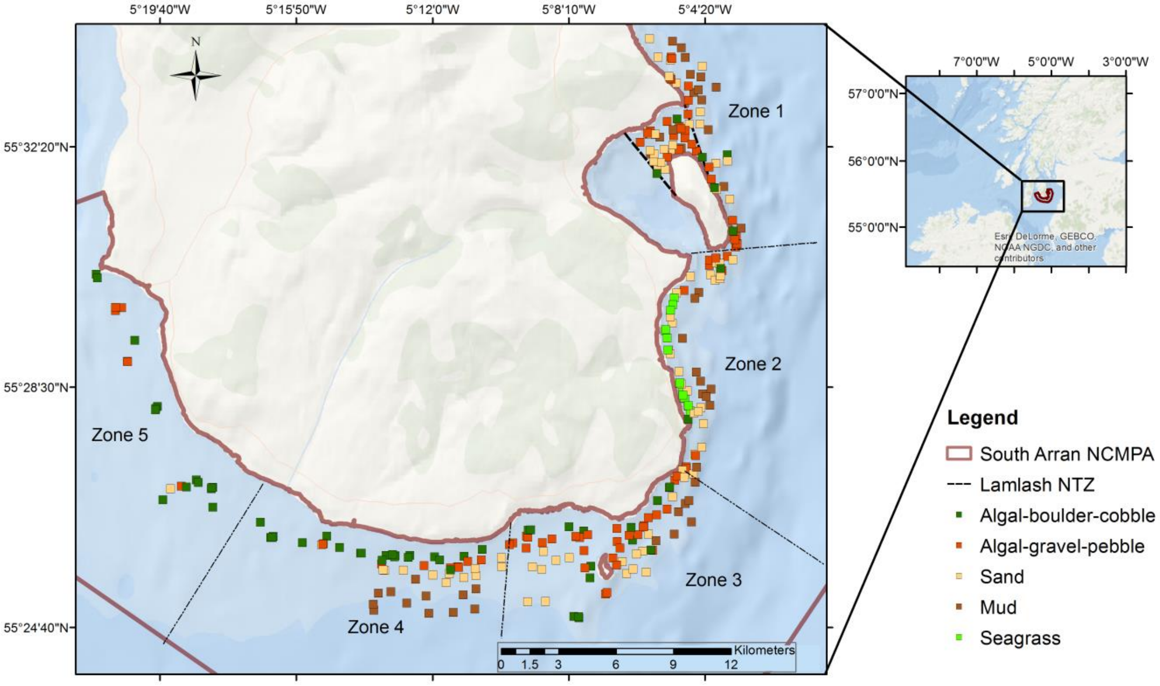

Figure 4.3.1 - SBRUV data collection locations within South Arran NCMPA over the course of 2013 and 2014. Different coloured squares represent different substratum types observed.

For 2013, sampling was conducted between 5th June – 29th September. However, data was used from 15th July due to the late arrival of gadoids. During 2014, sampling was conducted from 30th June – 18th September. Three baited camera systems were used, each consisting of a pair of high-definition Canon (HF G25) video cameras in waterproof housings (SeaGIS Pty, Australia).

The cameras were mounted on a custom made steel frame (Figure 4.3.2). The cameras were angled at an oblique view angle to have a partial view of the seabed (approximately half the image), and an inward angle of approximately 8° with a basal separation of 66 cm during year one and 58 cm during year two. The cameras were brought closer together during the second year to reduce the blind spot between the cameras where the fish were too close to the cameras to be measured (Unsworth et al. 2014). Each camera was set to manual mode with the focal length set to infinity (∞). Two underwater, LED W38VR Archonlight (1400 lumen) torches were mounted on the frame, facing at an angle to the middle of the stereo-camera field of view. A flashing strobe and bait box was attached on a 91 cm long bait arm situated in front of the camera (Figure 4.3.2). The strobe was used to synchronise the stereo-video images. The SBRUV frame was tethered to a rope for deployment and retrieval.

The system was set up in a similar way to the prototype described in Harvey & Shortis (1995; 1998). However, this system was optimised for smaller bodied fish in sea water visibility of < 6 m distance by bringing the cameras closer together than the 80 cm basal separation recommended by Boutros et al. (2015). Bait consisted of 500 g of cut Atlantic mackerel (*Scomber scombrus*). *S. scombrus* was used since this is oily, relatively inexpensive, and has frequently been used to study bait attraction in temperate waters (e.g. LØkkeborg 1998; Dunlop et al. 2015; Howarth et al. 2015). Prior to and over the course of field data collection, the mounted cameras were calibrated within a controlled environment using methods outlined within Harvey & Shortis (1998) and CAL software (version 2.11, SeaGIS 2013; Chapter 3).

To reduce vessel noise disturbance from affecting species behaviours recorded, the first three minutes after camera landing and last five minutes before camera recovery were not analysed. Camera systems were deployed for a minimum of 55 minutes on the seabed. This deployment length provided the best compromise between sufficient bait soak time as tested by Unsworth et al. (2014), and the need to bait and redeploy each camera multiple times on each sampling day. To minimise the possibility of deployments affecting each other, SBRUV deployments on the same day were a minimum distance of 500 m apart. This distance was chosen taking into account maximum current speeds around Arran and information on gadoid swimming speeds upon bait detection obtained from Blaxter & Dickson (1959). Greater distances were not possible due to the low speed of the vessel used in 2014 which would compromise the ability to obtain sufficient samples. Samples were collected between 9:00 and 15:00 (GMT), so that all deployments would be a minimum of three hours after sunrise and three hours before sunset to avoid crepuscular variation in fauna behaviour.

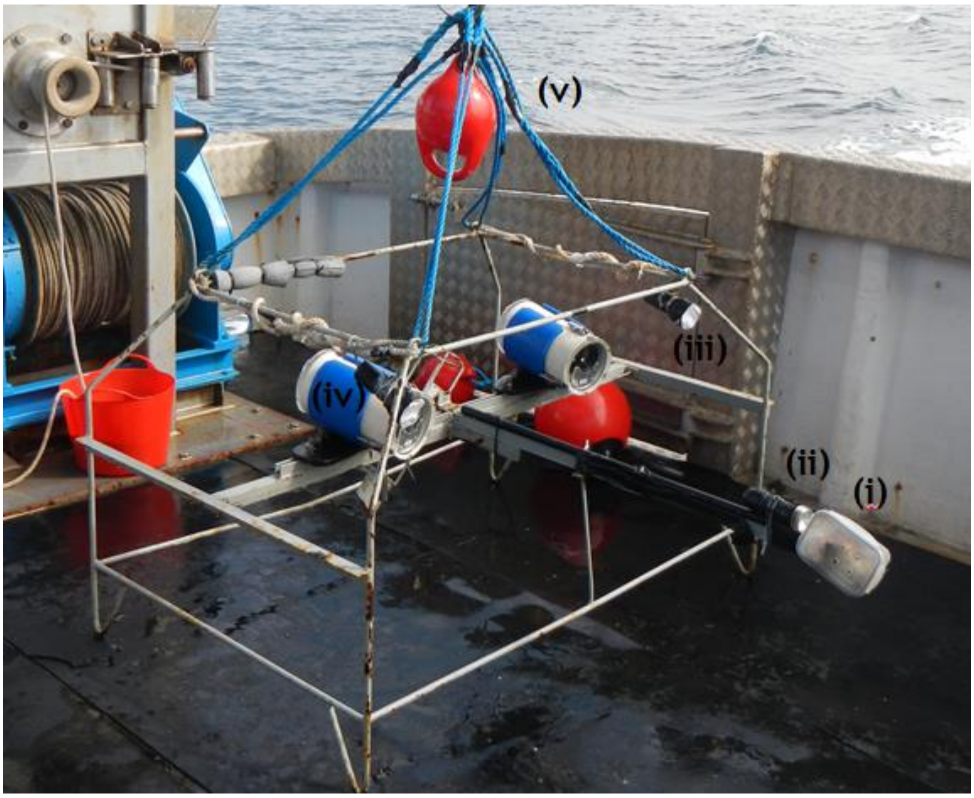

Figure 4.3.2 - Stereo Baited Remote Underwater Video system showing (i) bait box (ii) strobe to synchronise cameras (iii) torches (iv) water-proof housing containing video cameras (v) float and ropes to deploy the frame to the seabed from the vessel.

4.3.3. Video analysis

Prior to analysing the videos transects, the AVI videos were converted to high definition XVid files which are compatible with EventMeasure software (version 3.61, SeaGIS 2013). Each deployment was analysed using Event Measure software and a sample of 48 deployments were analysed by two separate observers to check for observer bias. To prevent any further observer bias, transects were assigned a random number before analysis and the resulting data were reconciled with location and depth information once analysis was complete. Benthopelagic fauna were used for community composition and diversity analysis, this included all epibenthic fauna observed (e.g. Echinoderms, crustaceans, tunicates etc.) and demersal species (e.g. gadids, blennies, dog fish, etc.). Benthopelagic fauna identified were quantified to the lowest taxonomic level possible. The maximum number of individuals of the same species appearing in a frame at the same time (MaxN) was used as a measure of relative abundance (Priede et al. 1994; Watson et al. 2005; Cappo et al. 2006). MaxN avoids repeat counts of individual fish re-entering the field of view (Priede et al. 1994; Watson et al. 2005). Time to First Arrival (TFA) was measured to understand whether gadoids observed were already within the vicinity of the SBRUV or travelled to the SBRUV. TFA is the elapsed time from camera settlement on the seabed to the first sighting of each species (Priede et al. 1990, 1994; Stoner et al. 2008).

For gadoid length and position measurements, each individual observed had to be visible in both cameras. Fish fork length measurements were taken at one time point per deployment, when the maximum number of measurable fish was present. This was typically at MaxN. Taking measurements at one time only, prevents repeat measurements of the same individual. All length measurements with a RMS error >2 cm and with a precision of length measurements >0.5 cm were removed from analysis (SeaGIS 2013).

To undertake seabed type categorisation, ten minutes after landing on the seabed still images (JPEG) were extracted from the video recordings and manipulated in GIMP (version 2.8.6, GIMP 2013) to reduce the effects of backscatter and light attenuation. Coral Point Count analysis (Kohler & Gill 2006; version 4.1, CPC 2013) was used to record sediment and macrophyte type from the still images taken of the seabed. Two divisions of Wentworth grain scale (Wentworth 1922) was used to classify sediment type (Connor et al. 2004) and algae type was classified into broad categories according to order and colour (Chapter 3). A total of 66 (11x6) randomly stratified points were overlaid on the image during CPC analysis. This number of points was based on a pilot study where six images were sampled five times with increments from 10 to 100 points with random stratified and uniform points. Stratified random points proved to be the optimum sampling procedure in terms of time taken to complete sampling and increasing rarer sediment and algae types detected within the image (Walkinshaw 2014). An optimum number of points to use were not found (Walkinshaw 2014). However, taking into account a similar investigation by Deter et al. (2012) and the time it took to complete sampling, 66 points were used for each image.

Using the outputs from the CPC analysis, substratum categories were made from the most dominant substrata occurring within each sample (

Table 4.3.1). Use of raw percentages was not possible due to high numbers of zero values. The European Union Nature Information System (EUNIS) classifications of substratum type were not used due to the difficulty in assigning fish substrata observations into such classes which would not be of relevance to the fish (Galparsoro et al. 2012).

Table 4.3.1 - Substratum type characterisation.

Substratum type	Sediment composition	Macrophyte type and density
Algal-boulder-cobble (ABC)	Mixed boulders and cobbles (particles > 6.4 cm).	Sediment covered in a mixture of kelp and red algae (> 60% algae cover). Examples of algae species include *Laminaria spp.* and *Ceramium spp.*
Algal-gravel-pebble (AGP)	Mixed gravel (stone, shell and maerl *Phymatolithon calcareum (*Adey & McKibbin, 1970) and pebble (particles 1.6 to 6.4 cm).	Between 20 and 50 % of sediment covered by algae.
Sand	Sandy sediments (particles 0.1to 0.4 cm)	Absence of macrophytes
Seagrass	Sandy sediment (particles 0.1to 0.4 cm)	Presence of seagrass, *Zostera marina*
Mud	Mud and sandy mud sediment grain size (particles < 0.1 cm)	Absence of algae

4.3.4. Data analysis

4.3.4.1. Community composition substratum differences

PERMutation Analysis Of Variance Analysis (PERMANOVA) was performed in PERMANOVA 6 software (Anderson et al. 2008), to understand whether there were community composition differences in benthopelagic species within and between substratum types. The MaxN of species were square root transformed, to reduce the influence of dominant species. Prior to applying PERMANOVA a Bray-Curtis similarity coefficient was performed. Posterior pair-wise tests were used to compare the difference between substratum categories. PERMANOVA was run with 9999 permutations to draw inferences at the *P* (perm) < 0.001 level. Non-metric Multi-Dimensional Scaling (nMDS) plots were used to visualise the matrices which provide values of stress. Zone and grouped data collection day were tested for as random factors.

4.3.4.2. Gadoid habitat identification

Abiotic habitat variables explored included: substratum type (categorical, 5 levels), depth (m), distance from coast (m), current speed (m/s), wave fetch (km) and year (categorical, 2 levels). Biotic variables explored included: Hill diversity indices N_1 (exponential of Shannon), N_2 (the inverse of Simpson's index) and N_∞ (inverse of Berger-Parker dominance index) (Berger and Parker 1970; Hill 1973), for benthopelagic fauna (e.g. tunicates, echinoderms, crustaceans and demersal fish). Continuous explanatory variables were standardised by dividing the mean by the standard deviation prior to statistical analysis. Random effects used included the effect of the zones (five levels) and grouped days of data collection (seven levels over the period of 2013 and 2014). Depth data were obtained from vessel echosounders. A Lowrance Elite-5X-DSI with a 455 and 800 kHz transducer was used on board the RIB during 2013 and Furuno FCV-295 with 28 and 200 kHz transducers was used for Actinia during 2014. Latitude and longitude were recorded via the vessels Global Positioning System (GPS) plotter, the RIB used a Cobra Marine, MC600Ci EU and Actinia used a Furuno GP-37 DGPS. Both boats used Admiralty Raster Charts, datum World Geodetic System (WGS) 1984. Distance from coast was calculated using the GPS fix made at time of deployment and ArcGIS v. 10.1 (EDINA digimap, datum WGS 1984, British National Grid 1984). Current speed was obtained from a tidal model developed by Sabatino et al (in review), which modelled the average current speed over the 55 minutes deployment at the time and location of each data collection point. Wave fetch values for a 200 m coastline grid (SAMS 2013) were used as described in Burrows et al. (2008).

All statistical analysis was performed with the software R (version 3.1.2; R Development Core Team 2009). Data exploration followed recommendations from Zuur et al. (2010). Homogeneity and potential outliers were analysed with Cleveland dotplots (Cleveland 1993), and boxplots. Spatial independence was evaluated with variograms. Variance Inflation Factor (VIF) analysis and Spearman's rank correlations were used to test for collinearity. Covariates with a VIF higher than three were removed stepwise and the analysis repeated until all values were below this cut-off level. A pair-wise correlation of P < −0.5 and > 0.5 was considered high for this study, and resulted in removal of one of the correlated covariates.

Following data exploration (testing for zero inflated and non-linear patterns) the model of best fit for all count data was a negative binomial distribution (NBN) to account for over dispersion, using R package “glmmADMD” (Skaug et al, 2012) . Backwards stepwise model selection was implemented (Bolker et al. 2009; Zuur et al, 2009) looking for potential interactions. Model selection was tested using the difference between Akaike’s Information Criteria (AIC). Analysis Of Variance was used to test for model term significance, dropping variables which were not significant. Pearson’s residuals were compared between models fitting a model with the highest level of heteroscedasticity. A log likelihood ratio test was used to test model significance against the null hypothesis. Tukey tests using R package “multcomp” (Hothorn et al, 2008) were performed to test for differences between categorical variables.

Equation 4.1 provides the model structure used for juvenile gadoid MaxN.

$$log(Y_i) = \beta_0 + \beta_1, X_{ij} + \beta_2, X_i + \beta_3, X_i \ldots\ldots + z_{ij} + t_{ij} \qquad (4.1)$$

where Y_i is gadoid MaxN, β are the coefficients, X_{ij}, categorical explanatory variables and X_i, continuous explanatory variables, z_{ij} and t_{ij} the random effects (zone and day of collection).

4.3.4.3. Gadoid substrata association differences between years

Differences in substratum association between years was analysed independently via equation 4.2.

$$log(Y_i) = \beta_0 + \beta_1, S_{ij} * \beta_2, Y_{ij} + z_{ij} \qquad (4.2)$$

where S_{ij}, is substratum type and Y_{ij}, year.

4.3.4.4. Seasonal relative abundance and length variation

SBRUV datasets were also analysed individually by year to understand relative abundance and changes in age-0 gadoids size over the period of data collection. For length measurements, linear mixed models were employed using the R package “nlme” (Pinheiro et al., 2014), testing for the significance of random effects. Data exploration and model selection was undertaken following the same steps outlined within the Gadoid habitat identification section p. 99). Equation 4.3 provides the model structure used to explore relative abundance of gadoids over the course of data collection for each year.

$$log(Y_i) = \beta_0 + \beta_1, X_{ij} + \beta_1, X_i ... + \beta_2, JD_{i/j} + z_{ij} \tag{4.3}$$

Where $JD_{i/j}$, is Julian day, treated as a continuous variable for 2013 and categorical for field season 2014 (data collection week).

Equation 4.4 provides the model variables used to explore recruitment and growth related changes for age-0 gadoids over the period of data collection. To reduce the likelihood of observing age-1 gadoids, all individuals larger than 15 cm were removed from analysis following DAtabase of TRAwl Surveys (DATRAS) ALK (product for standard species only) quarter 4 (October - December) data for the Clyde area (DATRAS 2015). A Linear Mixed Model (LMM) was used to model length measurements (taken at MaxN or when the maximum number of individuals could be measured), exploring habitat variables in addition to JD as a fixed effect and zone as a random effect:

$$Y_i = \beta_0 + \beta_1, JD_{i/j} + \beta_1, X_i + z_{ij} \tag{4.4}$$

Where Y_i is gadoid fork length.

LMM length variation over the period of data collection for each field season was also analysed by subtracting the minimum length from the maximum for each day of collection where a measurement was obtained.

$$Y_i = \beta_0 + \beta_1, JD_{i/j} \tag{4.5}$$

Where Y_i is *G. morhua* fork length variation

4.3.4.5. Gadoid size and bait attraction

To understand gadoid size and bait attraction differences around the SBRUV, length, position and TFA differences between the gadoids were analysed. Linear and Linear Mixed Models were used to explore size differences and gadoid 'mid Y' and 'mid Z' (relative to the mid-point of the camera system) positions in the water column. Where, mid Z values are the distance from the camera system and mid Y values are approximate to height above and below the cameras (Shortis et al. 2009; SeaGIS 2013, EventMeasure user guide).

To understand whether gadoids observed were already within the vicinity of the SBRUV or travelled to the SBRUV, a beta-binomial distribution GLMM was used to analyse TFA differences using R package "hglm" (Ronnegard et al. 2010), to allow random effects for time and zone to be incorporated into the model. Time was converted to proportions since it was bound between five and 55 minutes, lending to the need to use a beta distribution model (Faraway 2006; Crawley 2012). Equation 4.5 provides the model of best fit to explore these gadoid SBRUV observation differences.

$$Y_i = \beta_0 + \beta_1, G_{ij} + \beta_2, Y_{ij} + z_{ij} \tag{4.5}$$

Where G_{ij}, gadoid species.

4.4. Results

4.4.1. Community composition substratum differences

Significant differences in community composition between substratum types were observed (pseudo-F = 13.663, *P*(perm) < 0.0001). Table 4.4.1 show significant pair-wise test differences between substratum types and SIMPER percentage dissimilarity between substratum types. The nMDS plot (Figure 4.4.1), with a stress value of 0.21 illustrates some clear differences between the substratum types as outlined in Table 4.4.1 but also some overlap which was to be expected.

Table 4.4.1 - Pairwise tests between substratum type. Running PERMANOVA 9999 times to draw inferences at the *P*(perm)<0.001. Blanks indicate a non-significant result as shown using PERMANOVA software.

Substratum types	**t statistic**	***P* (perm)**	**Unique perms**	**Dissimilarity %**
AGP, sand	2.62	0.001	997	79
AGP, seagrass				77
AGP, ABC				81
AGP, mud	3.43	0.001	999	85
Sand, ABC	3.68	0.001	998	92
Sand, seagrass				72
Sand, mud				70
ABC, seagrass				89
ABC, mud	4.07	0.001	999	95
Seagrass, mud	3.42	0.001	999	81

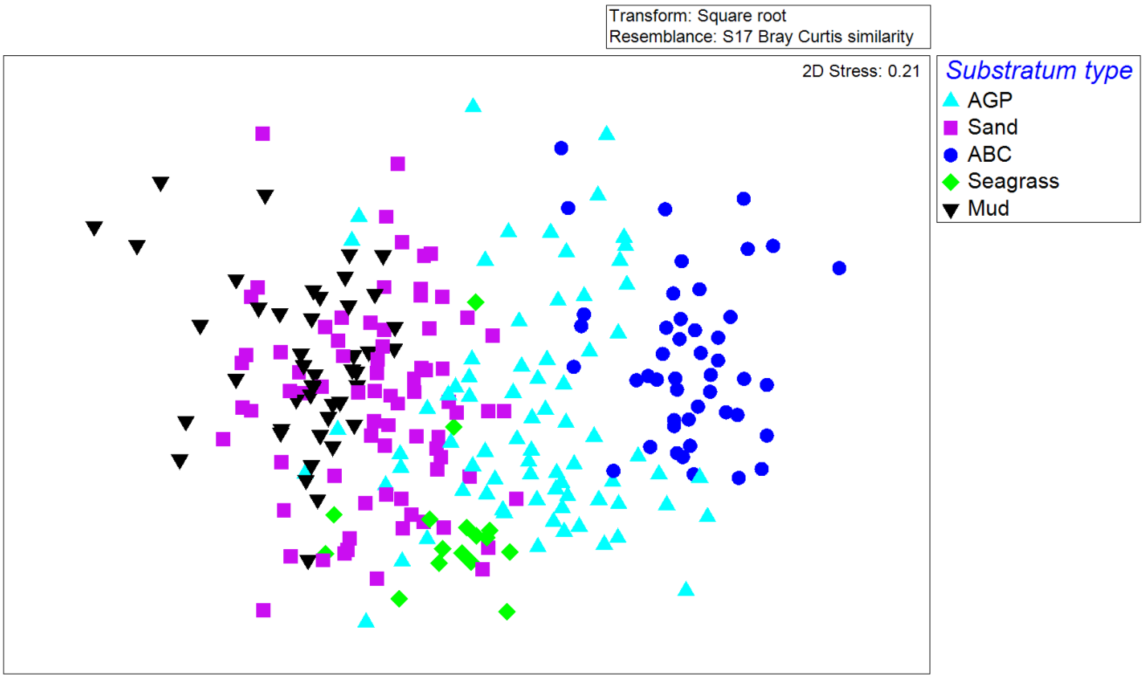

Figure 4.4.1- nMDS plot of the community composition of all demersal fauna observed between substratum types. Significant effects of substratum type on assemblage structure are observed (PERMANOVA: *P* < 0.001)

4.4.2. *G. morhua* relative abundance

A total of 542 *G. morhua* were identified over the course of data collection periods 2013 and 2014 (mean = 2.09, S.D. ± 7.86), and were observed in 84 of the 214 SBRUV deployments. More *G. morhua* were observed in 2013 (13% zero observations) than 2014 (54% zero observations). The maximum distance *G. morhua* were able to be identified and measured accurately was 2.79 m from the video (mean = 1.76 m, S.D. ± 0.30;

Figure **4.4.25**). To see whether the ability to identify and measure juvenile *G. morhua* decreased with increasing depth (and therefore possibly reduced light), an ANOVA test between range (the distance between the camera and the *G. morhua*) and depth was modelled. Depth had no effect on the mid Z distance at which juvenile *G. morhua* were measured (F(1,223) = 0.72, *P* > 0.05; Appendix Table F.1).

4.4.2.1. *G. morhua* habitat

No *G. morhua* were observed over the mud, this category was therefore removed from analysis to improve logistic model convergence. The highest MaxN was observed over AGP followed by ABC and Seagrass with lowest MaxN observed over sand (Figure 4.4.2; Appendix Table F.2 and Table F.3). A decrease in MaxN was observed with increasing N_∞. This shows how the dominance of species had a negative effect on the relative abundance of *G. morhua* MaxN. A decrease in MaxN was also observed with increasing wave fetch and a decline in MaxN was observed between years (L = -314.13, d.f. = 8, theta = 0.84, $P < 0.001$; Figure 4.4.3; Appendix Table F.2).

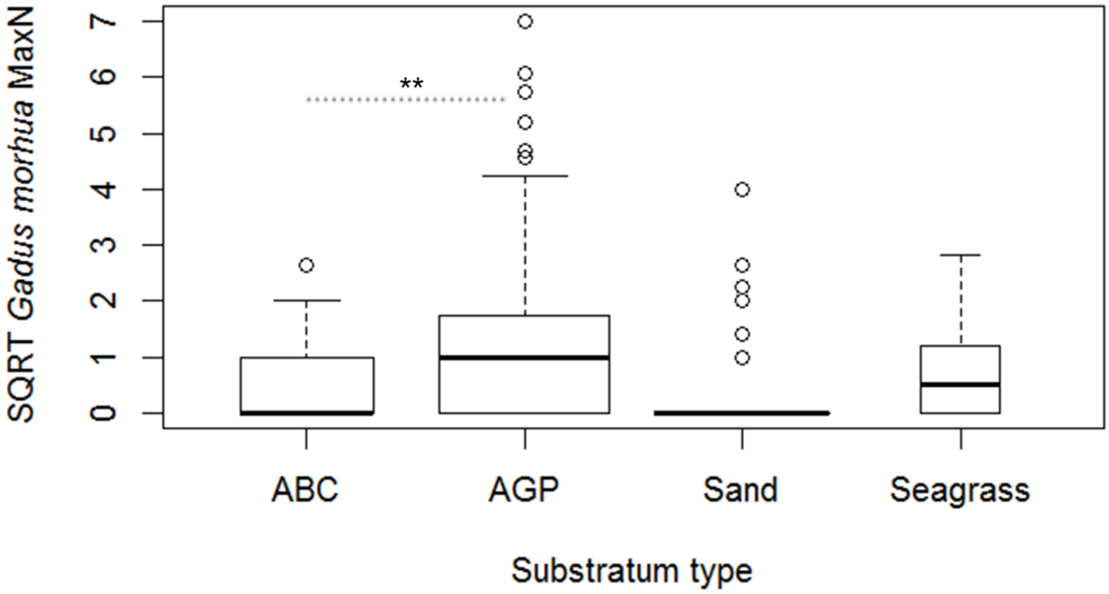

Figure 4.4.2 - Substratum type association of juvenile *G. morhua* observed within South Arran NCMPA. More juveniles were found in relation to substratum type AGP with no *G. morhua* observed over mud and few over sandy seabed types. Varied width boxplots proportional the square root of the sample sizes indicate the 25th and 75th percentiles of *G. morhua* MaxN observed between different substrata. The upper bars indicate the 10^{th} percentile. The thick line indicates the median MaxN. Open circles indicate the outliers. Dashed horizontal lines with * refers to Tukey test *P* value significance ** = $P < 0.01$).

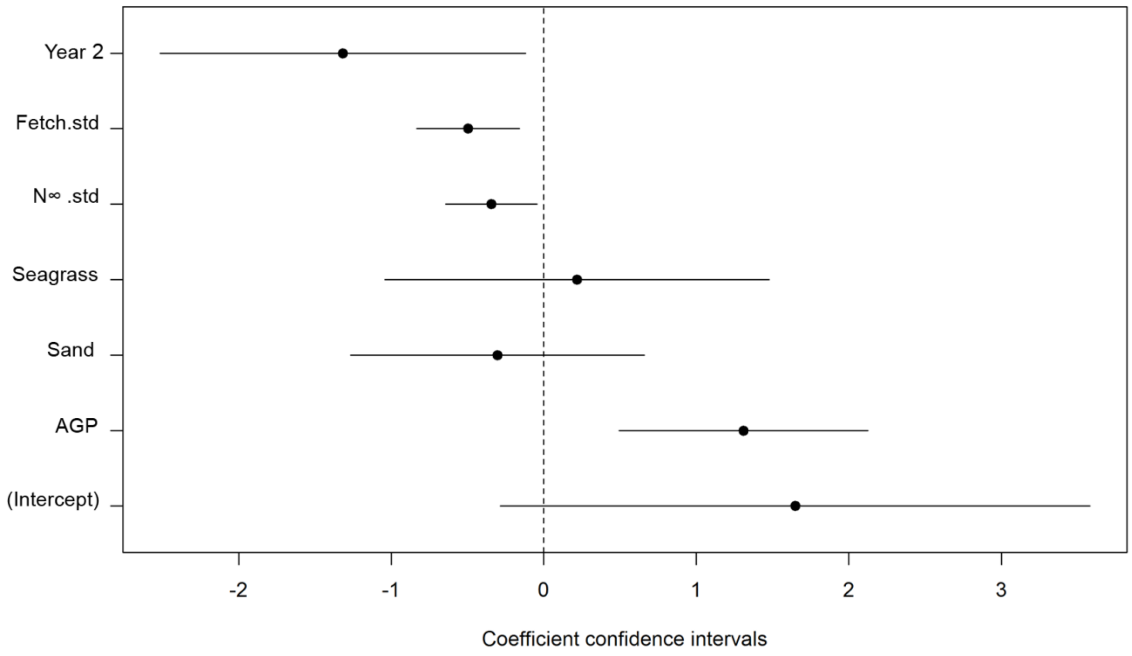

Figure 4.4.3 – Coefficient plot for model of best fit for *G. morhua* habitat variables. Lines contain 95% confidence intervals for each of the explanatory variables. The verticle dashed line is the reference line enabling us to see which coefficients are significantly different from zero. The intercept represents ABC and Year 1 of data collection.

4.4.2.2. *G. morhua* substrata association differences between years

When only exploring differences between year and substratum type, a significant difference was observed (L = -331.36, d.f. = 10, theta = 1.09, $P < 0.001$;

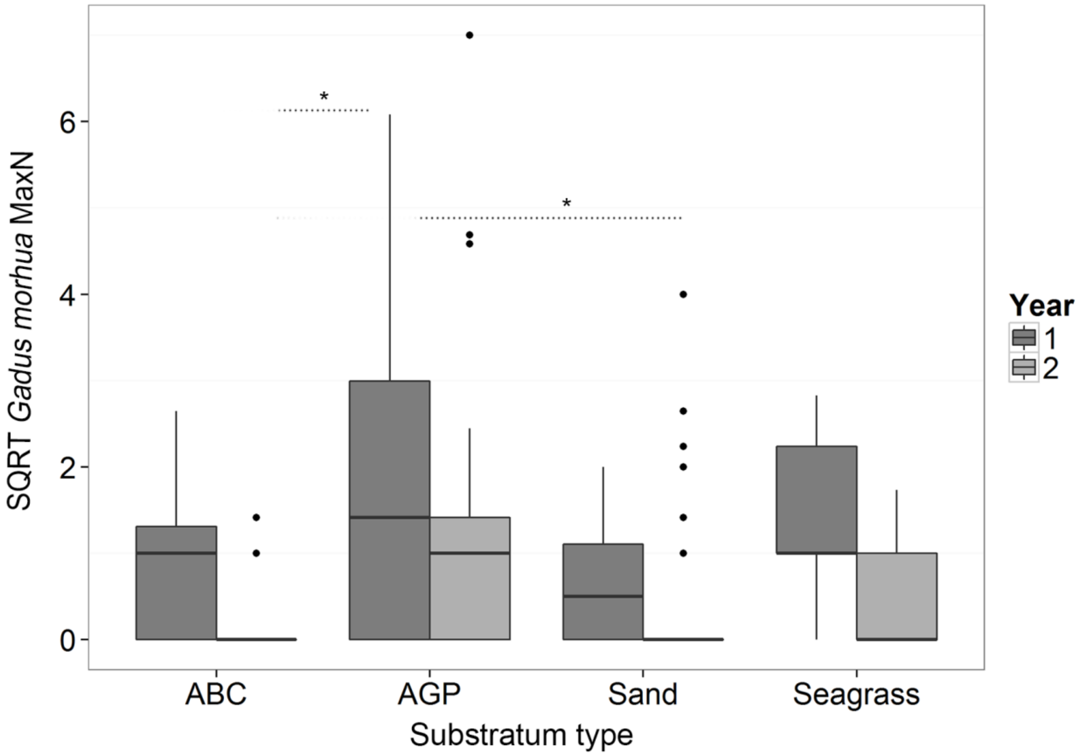

Figure 4.4.4; Appendix Table F.4 and Table F.5). Specific differences between substratum type and year showed, a decrease in *G. morhua* relative abundance over sand substratum type in year two relative to the MaxN over AGP in year one, and a decrease in *G. morhua* relative abundance over ABC in year two in comparison to AGP in year one.

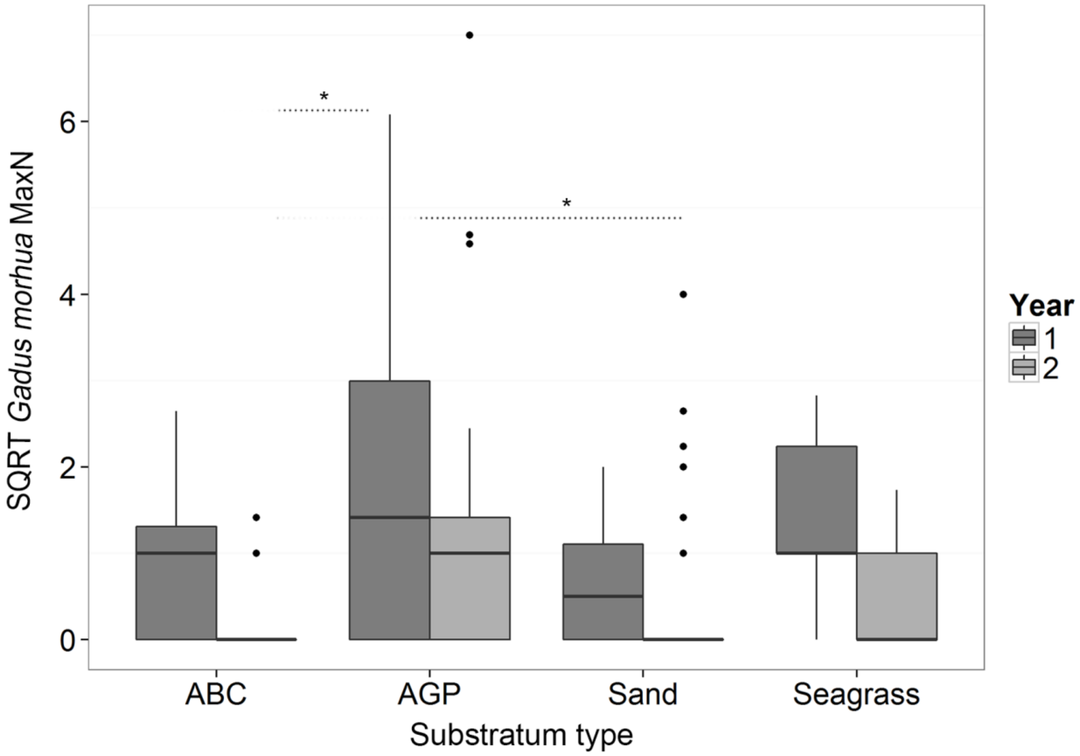

Figure 4.4.4 - Substratum association between summer of 2013 and 2014 for juvenile *G. morhua* observed within South Arran NCMPA. Tukey test significant differences between substratum association were observed between AGP in year 1 and Sand in year 2 and ABC in year 2 and AGP in year 1 (* = $P < 0.05$).

4.4.2.3. *G. morhua* seasonal relative abundance and length variation

From 15 July to 28 September 2013, a decline in *G. morhua* relative abundance was observed ($P < 0.001$)(L = -157.18, d.f. = 4, theta = 1.01, $P < 0.05$; Figure 4.4.5; Appendix Table F.6).

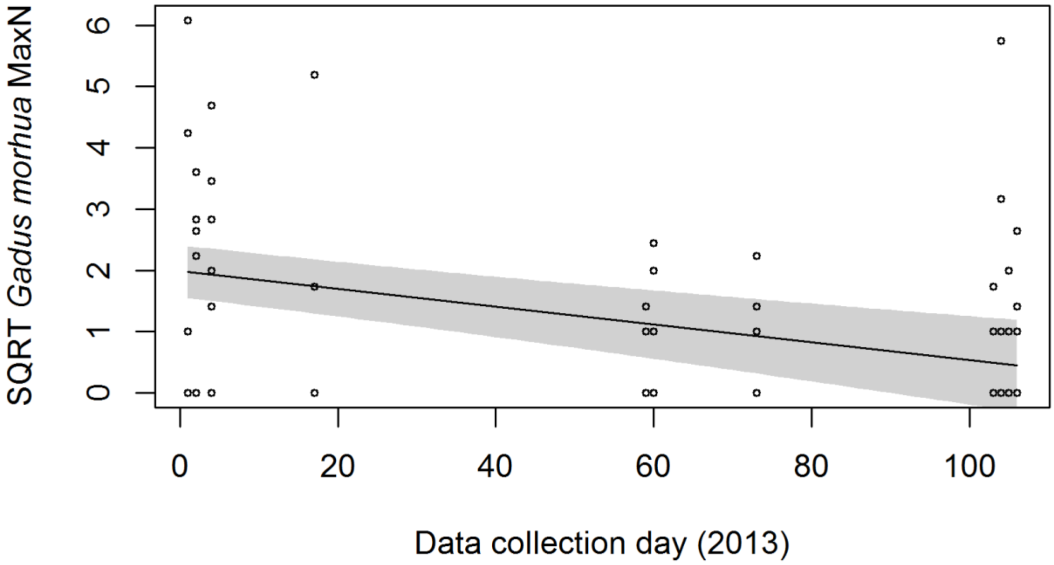

Figure 4.4.5 - Fitted values, ± 95% confidence intervals from the model of best fit for *G. morhua* MaxN over the period of data collection used for analysis (15 July – 28 September 2013). A decline *G. morhua* relative abundance was observed over the course of data collection ($P < 0.05$).

Over the course of summer 2014 from when *G. morhua* were observed (01 July – 18 September 2014), a significant increase in MaxN was observed following the first week of data collection (Tukey test P < 0.01; Appendix Table F.8), followed by a non-significant decline in *G. morhua* relative abundance (L = -175.07, d.f. = 6, theta = 1.17, $P < 0.001$; Figure 4.4.6; Appendix Table F.7 and Table F.8). This indicates a probable recruitment pulse shortly after the first week of July 2014.

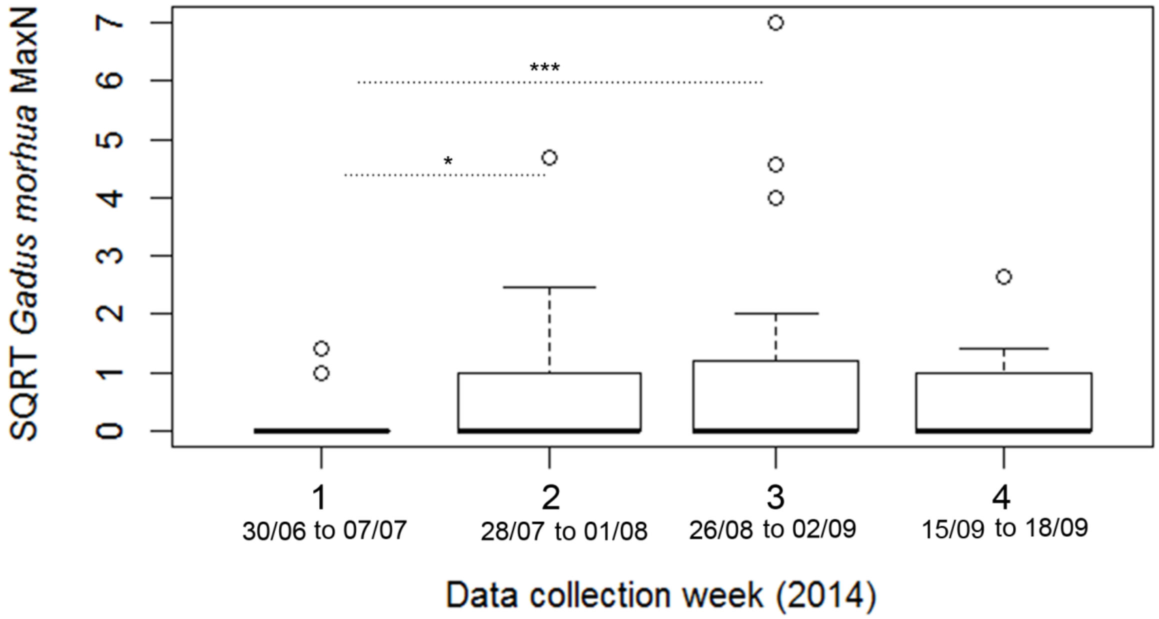

Figure 4.4.6 - *G. morhua* MaxN (square root transformed) during data collection weeks from 01 July to 18 September 2014. An increase in *G. morhua* relative abundance was observed from the end of June through to July. Dashed horizontal lines with * refers to Tukey test P value significance (* = $P < 0.05$, ** = $P < 0.01$).

From the length data collected, a total of 228 *G. morhua* length measurements were made in 87 SBRUV deployments. Average *G. morhua* size was 8.2 cm (S.D. ± 2.8 cm), the largest individual observed measured 21.2 cm and the smallest individual observed was 2.4 cm. All individuals larger than 15 cm were removed from analysis as they were likely to be age-1 individuals (Dalley & Anderson 1997; DATRAS 2014; Marty et al. 2014).

During field season 2013, 126 *G. morhua* length measurements were analysed. The average length of *G. morhua* was 7.4 cm (S.D. ± 1.8 cm). An increase in length was observed from 15th July to 28th September during 2013 ($P < 0.001$;

Figure **4.4.7**), in addition to an increase in length with increasing N_2 ($P < 0.05$) (L = -224.81, d.f. = 7, $P < 0.001$; Appendix Table F.9 and Table F.10). Significantly larger *G. morhua* were also observed in AGP (7.4 cm, S.D. ± 1.8 cm) than Sand

(5.7 cm, S.D. ± 1.7 cm) (L = -188.33, d.f. = 5, $P < 0.05$;

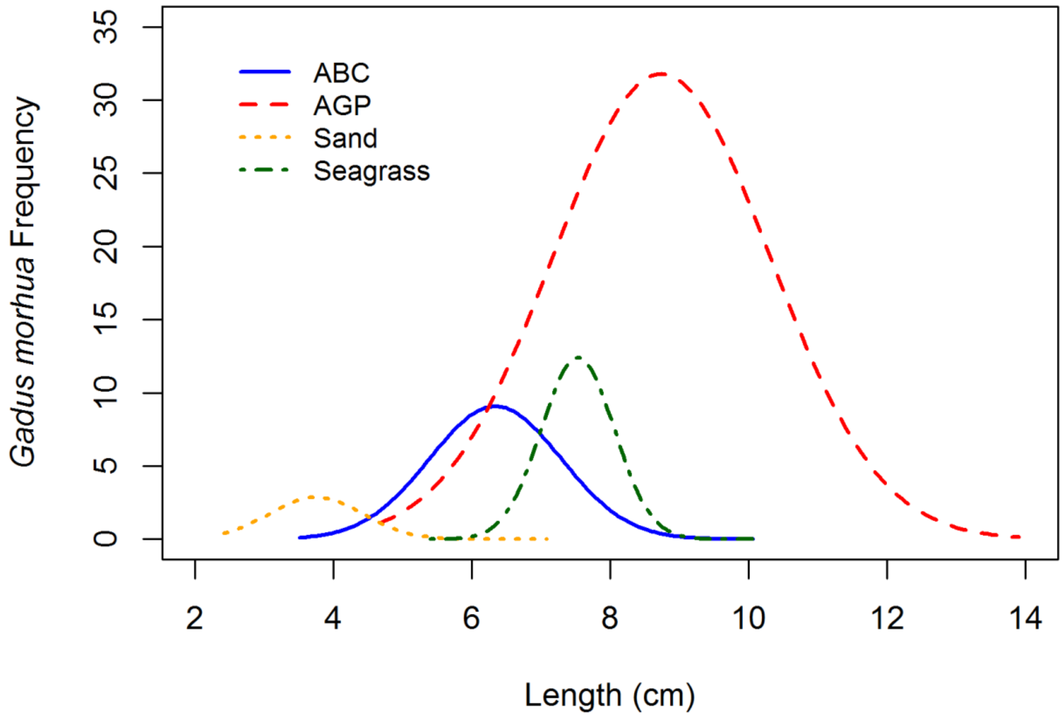

Figure **4.4.8**; Appendix Table F.10). Although an increase in length variation was observed for 2013, there was no significant effect of JD. This is most likely due to small sample size (n = 11 data collection day differences).

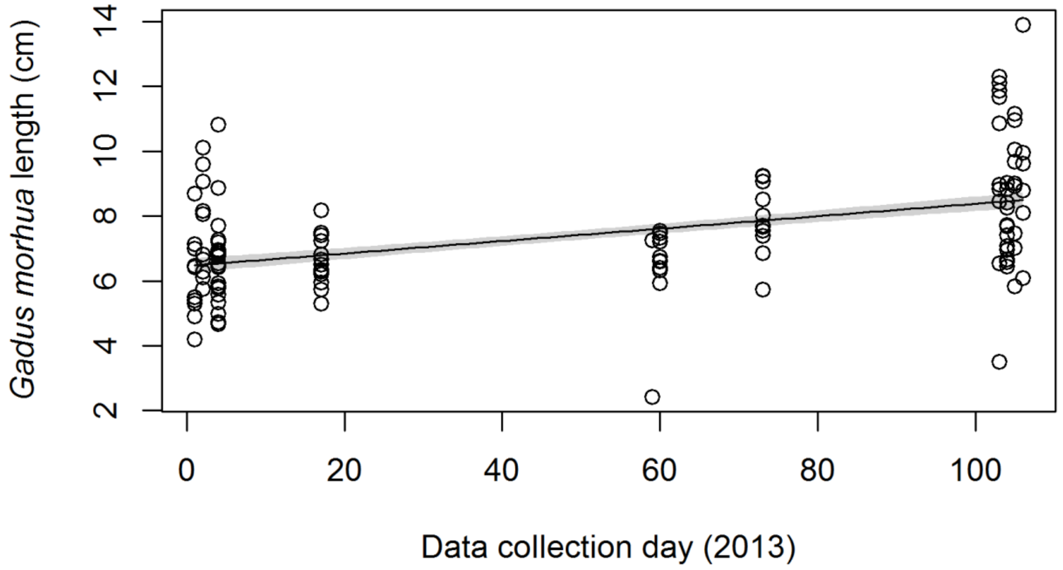

Figure 4.4.7 - Fitted values, ± 95% confidence intervals from the model of best fit for *G. morhua* length over the period of data collection used for analysis (15 July – 28 September 2013). An increase in *G. morhua* length was observed over this period ($P < 0.001$).

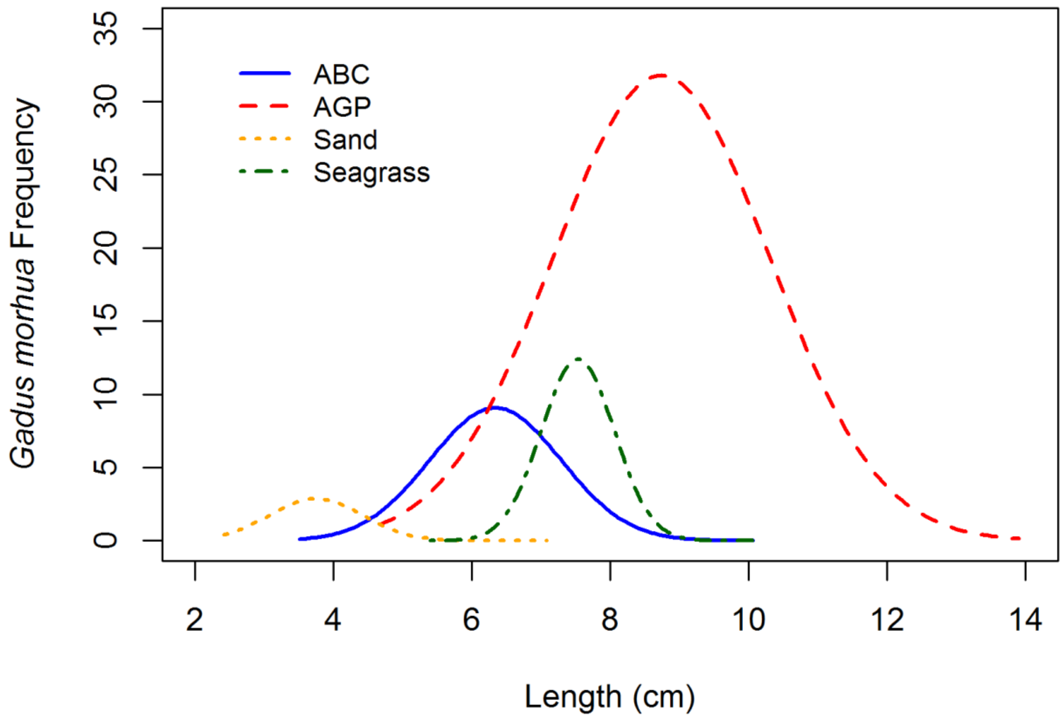

Figure 4.4.8 - Length-frequency distributions by substratum for *G. morhua* during 2013, illustrating that *G. morhua* are significantly larger over AGP substrata than sand ($P < 0.05$).

During field season 2014, 96 *G. morhua* length measurements were analysed. The average size of *G. morhua* observed during 2014 measured 8.3 cm (S.D. ± 1.8 cm). A significant increase in length was observed over the period of data collection for 2014 (

Figure **4.4.9**). There was also significant differences between substratum type with *G. morhua* of larger sizes over seagrass (10.2 cm, S.D. ± 2.5 cm) than that of AGP (7.8 cm, S.D. ± 1.7 cm) (L = -188.33, d.f. = 5, *P* < 0.05;

Figure 4.4.10; Appendix Table F.11 – Table F.13). No significant increase or decrease in length variation was observed for 2014. This is likely to be due to the small sample size (n = 12 data collection day differences).

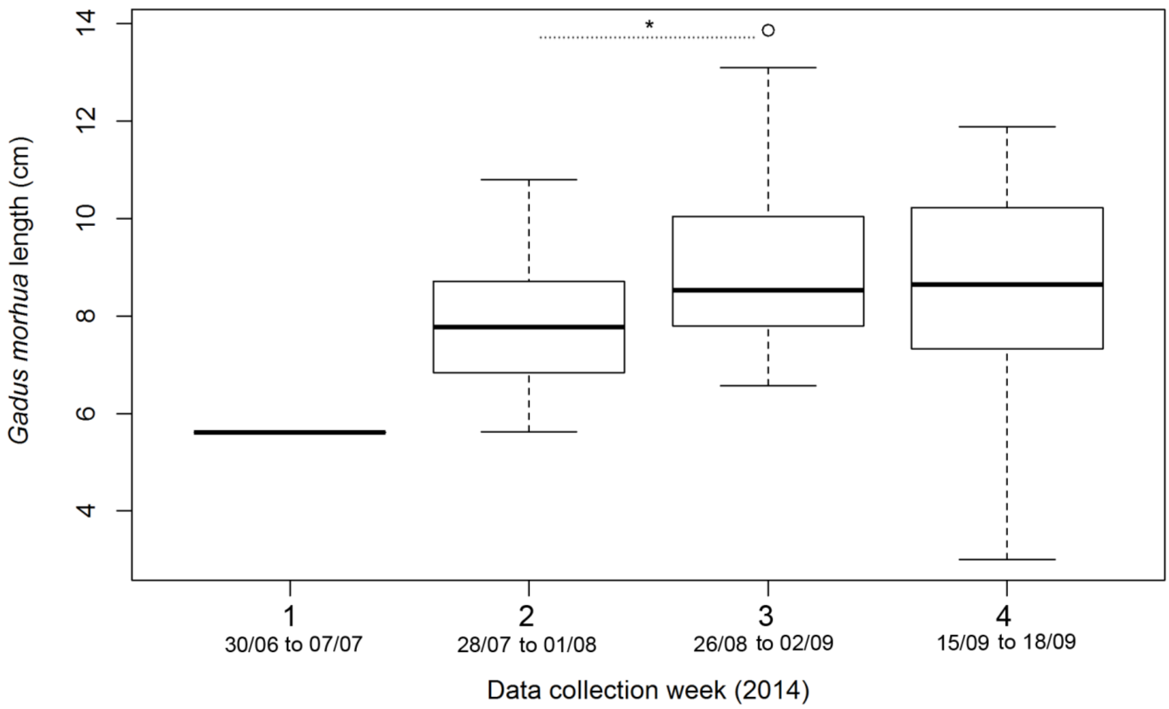

Figure 4.4.9 - *G. morhua* length change over the period of data collection weeks, from 01 July to 18 September 2014. Dashed horizontal lines with * refers to Tukey test *P* value (* = *P* < 0.05), an increase in *G. morhua* length was observed between week 2 and week 3.

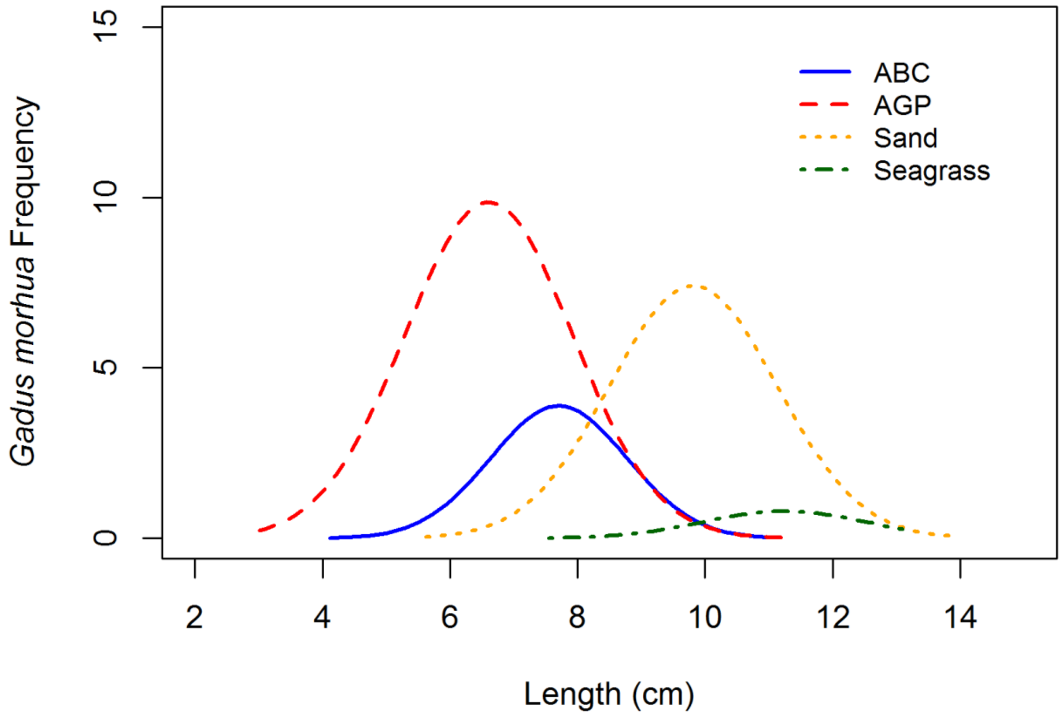

Figure 4.4.10 - Length-frequency distribution by substratum for *G. morhua* during 2014, illustrating that *G. morhua* are significantly larger over seagrass substrata than AGP ($P < 0.05$).

4.4.3. *M. aeglefinus* relative abundance

A total of 254 *M. aeglefinus* were identified between 2013 and 2014 (mean = 0.98, S.D. ± 2.35) in 81 of the 259 deployments. Relatively more *M. aeglefinus* were observed in 2013 than 2014 (24% zero observation in 2013 and 44% in 2014). The maximum distance at which *M. aeglefinus* were able to be identified and measured accurately was 3.01 m from the SBRUV (mean = 1.52 m, S.D. ± 0.40 m;

Figure 4.4.25). To see whether the ability to identify and measure juvenile *M. aeglefinus* decreased with increasing depth, an ANOVA test between mid Z and depth was modelled. Depth had no effect on the distance at which juvenile *M. aeglefinus* were measured (F(1,200) = 0.77, $P > 0.05$; Appendix Table F.14).

4.4.3.1. *M. aeglefinus* habitat

The highest average MaxN for *M. aeglefinus* was observed over the sand substratum type followed by mud with lowest MaxN observed over ABC (Figure

4.4.11; Appendix Table F.15 and Table F.16). An increase in MaxN was observed with decreasing N_∞ and wave fetch, and an increase in *M. aeglefinus* MaxN was observed with increasing depth (L = -278.98, d.f. = 10, theta = 1.31, $P < 0.001$; Figure 4.4.12; Appendix Table F.15).

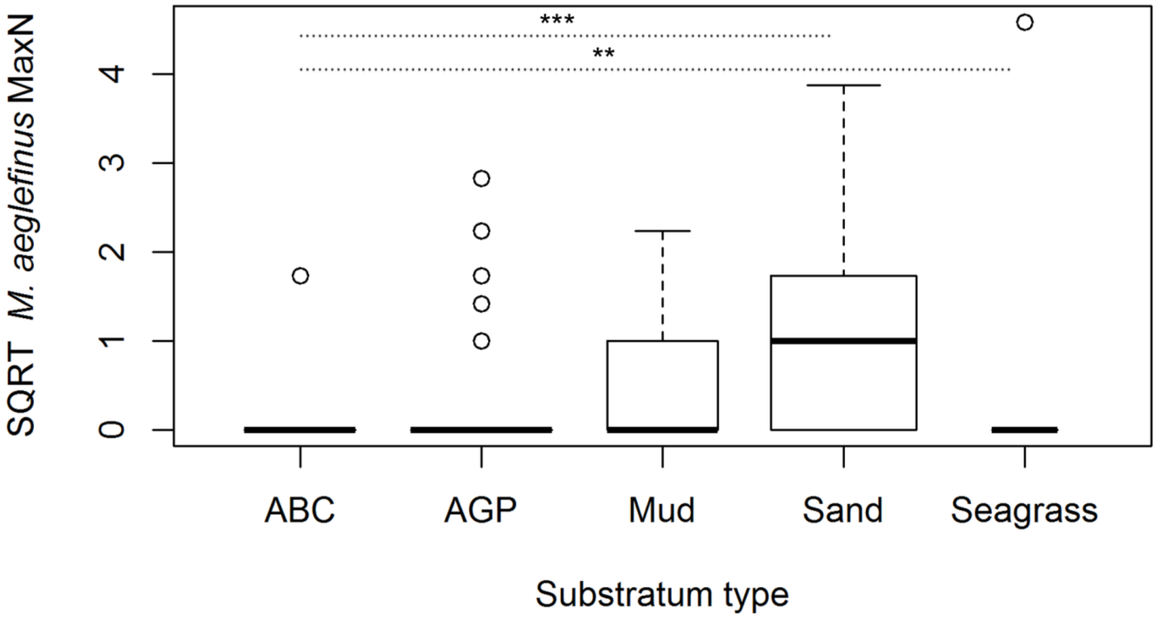

Figure 4.4.11 - Substratum type association of juvenile *M. aeglefinus* observed within South Arran NCMPA. More juveniles were found in relation to substratum type sand and mud with lowest MaxN observed on ABC substratum type. Dashed horizontal lines with * refers to Tukey test *P* value significance (** = $P < 0.01$, *** = $P < 0.001$).

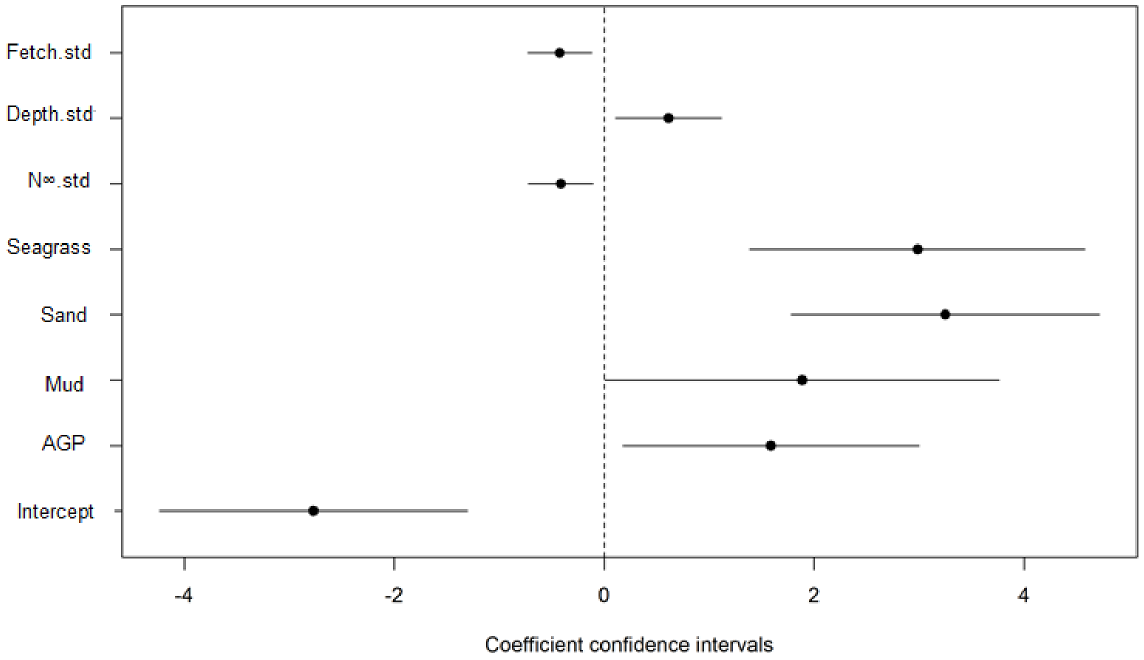

Figure 4.4.12 - Coefficient plot for model of best fit for *M. aeglefinus* habitat variables. Lines contain 95% confidence intervals for each of the explanatory variables. The verticle dashed line is the reference line enabling us to see which coefficients are significantly different from zero. The intercept is represented as ABC.

4.4.3.2. *M. aeglefinus* substrata association differences between years

Due to differences in data collection between years it was not possible to undertake statistical analysis comparing *M. aeglefinus* MaxN between substratum type since no data were collected in deeper water containing mud in year one. Figure 4.4.13 shows consistently higher MaxN over sand substrata than the other substrata over the two years of data collection.

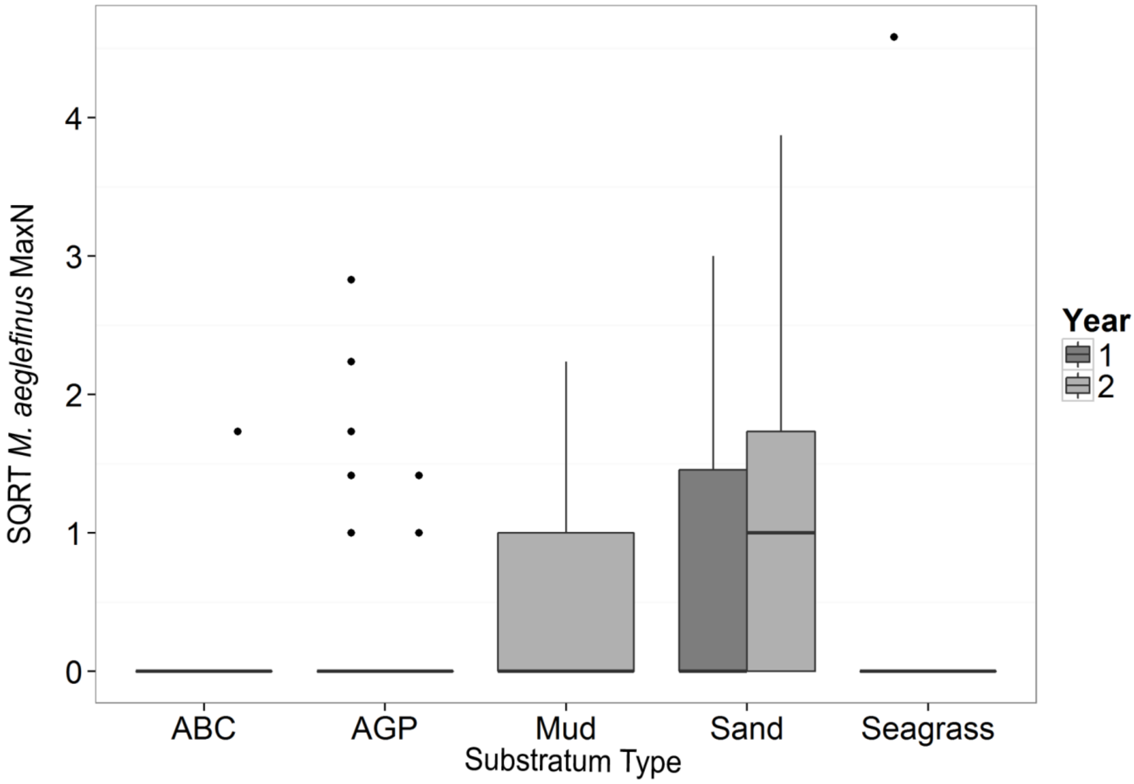

Figure 4.4.13 - Substratum association between summer of 2013 and 2014 for juvenile *M. aeglefinus* observed within South Arran NCMPA.

4.4.3.3. Seasonal relative abundance and length variation

During summer 2013 from 15 July – 28 September, no significant difference in *M. aeglefinus* relative abundance was observed (L = -59.10, d.f. = 3, theta = 0.76, $P > 0.05$). Over the course of between 30 June to 18 September 2014, a significant increase in MaxN was observed following the first week’s data collection ($P < 0.001$) (L = -233.42, d.f. = 5, theta = 0.93, $P < 0.001$; Figure 4.4.14, Appendix Table F.17 and Table F.18). This indicates a probable recruitment pulse shortly after the first week of July.

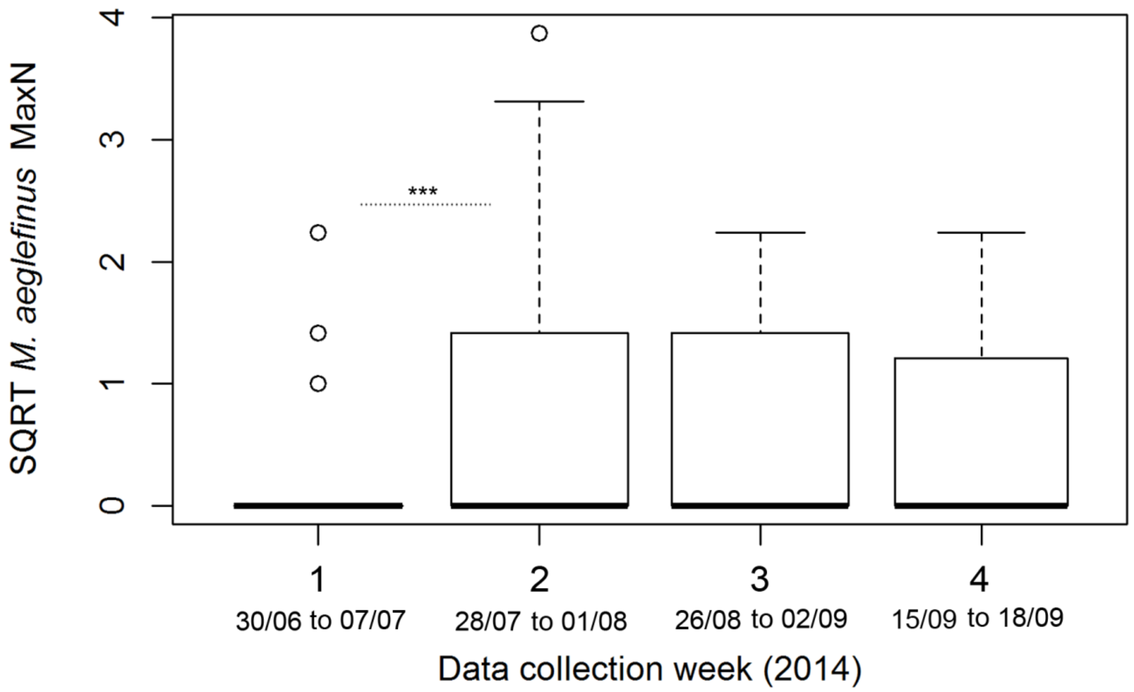

Figure 4.4.14 - *M. aeglefinus* MaxN (square root transformed) during data collection weeks from 01 July to 18 September 2014. An increase in *M. merlangus* relative abundance was observed from the first week's data collection period at the end of June. Dashed horizontal lines with * refers to Tukey test *P* value significance (*** = $P < 0.001$).

From the length data, a total of 208 *M. aeglefinus* length measurements were made in 72 of the 259 SBRUV deployments. Of the 81 SBRUV deployments *M. aeglefinus* were observed in, length measurements were not obtained in nine deployments. Average *M. aeglefinus* size was 12 cm (S.D. ± 3 cm), the largest individual observed measured 22 cm and was most likely an age-1 or 2 individual and the smallest individual observed was 6.8 cm. To understand recruitment and growth of age-0 *M. aeglefinus*, all individuals larger than 15 cm were removed from the dataset.

During field season 2013, 50 *M. aeglefinus* length measurements were analysed at MaxN in 10 deployments. The average length of *M. aeglefinus* was 12.3 cm (S.D. ± 1.8 cm). A significant increase in length was observed over the course of data collection (15th July – 28th September) during 2013 ($P < 0.001$) (L = -88.19, d.f. = 3, $P < 0.001$;

Figure **4.4.15**; Appendix Table F.19). Exploration of length variation of the period of data collection showed a non-significant increase in length variation for 2013. This is most likely due to small sample size (n= 6 data collection day differences).

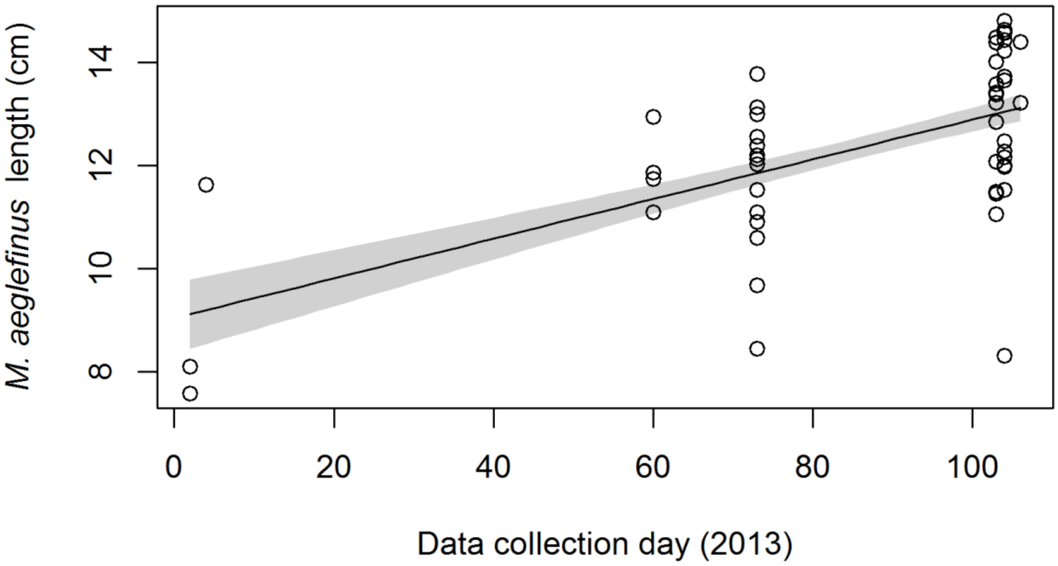

Figure 4.4.15 - Fitted values ± 95% confidence intervals from the model of best fit for *M. aeglefinus* length change over the period of data collection used for analysis (16 July – 28 September 2013). An increase in *M. aeglefinus* length was observed over the course of data collection (P < 0.001).

During field season 2014, 131 *M. aeglefinus* length measurements were analysed at MaxN from 50 SBRUV deployments. The average size of *M. aeglefinus* measured 10.6 cm (S.D. ± 1.9 cm). A significant increase in length was observed for 2014 over the course of data collection (*P* < 0.001) (L = -221.93, d.f. = 7, *P* < 0.001;

Figure **4.4.16**; Appendix Table F.20 and Table F.21). A significant increase in length was also observed with depth (*P* < 0.001) and a decrease in length with wave fetch (*P* < 0.05) was also observed. No significant increase or decrease in length variation was observed for 2014. This might be due to the small sample size (n=15 data collection day differences).

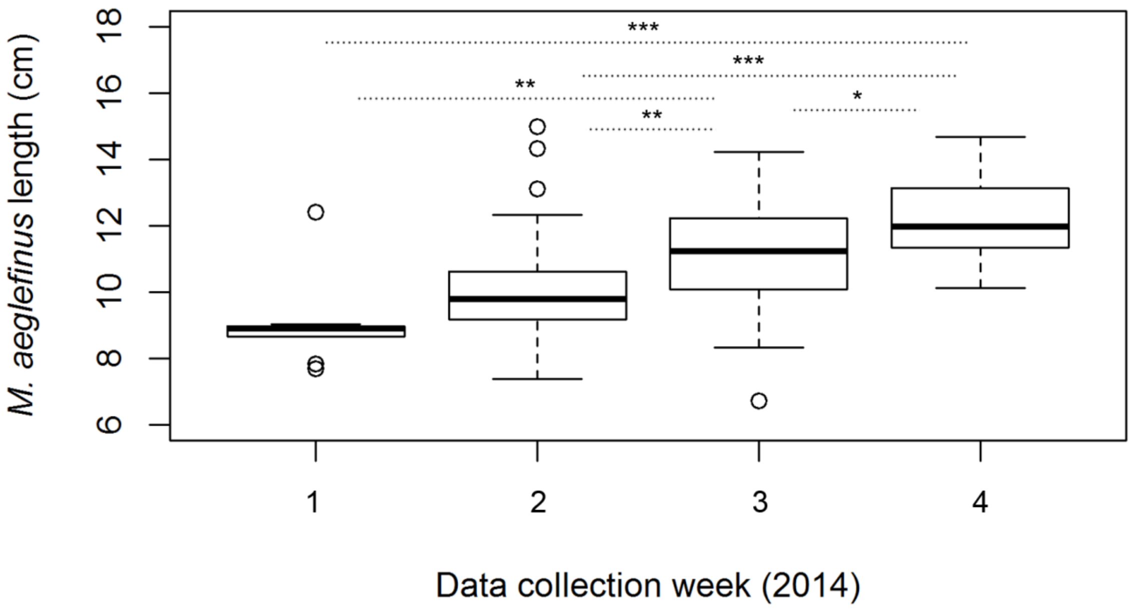

Figure 4.4.16 - *M. aeglefinus* length change over the period of data collection from 30 June to 18 September 2014. An increase in *M. aeglefinus* length was observed over the weeks of data collection. Dashed horizontal lines with * refers to Tukey test *P* value significance (* = $P < 0.05$, ** = $P < 0.01$ and *** = $P < 0.001$).

4.4.4. *M. merlangus* relative abundance

A total of 302 *M. merlangus* were identified between 2013 and 2014 (mean = 1.16, S.D. ± 5.28) in 82 out of the 259 SBRUV deployments *M. merlangus* were observed in. Relatively more *M. merlangus* were observed in 2013 (23% zero observations) than 2014 (45% zero observations). The maximum distance *M. merlangus* were able to be identified and measured accurately was 2.74 m from the video (mean = 1.24 m, S.D. ± 0.29 m;

Figure **4.4.25**). To see whether the ability to identify and measure juvenile *M. merlangus* decreased with increasing depth, an ANOVA test between range and depth was modelled. With increasing depth an increase in range was observed (F(1,135) = 4.24, $P < 0.05$; Appendix Table F.22). This will however have been due to the positive relationship between *M. merlangus* observations and depth rather than increasing visibility with depth (refer to section 4.4.4.1) since all individuals were observed within 274 cm of the cameras (mean 127.6, S.D. ± 29.1 cm).

4.4.4.1. *M. merlangus* habitat

The highest MaxN for *M. merlangus* was observed over sand with lowest MaxN observed over ABC (Figure 4.4.17; Appendix Table F.23 and Table F.24). An increase in MaxN was observed with increasing N_1 and depth. A decrease in MaxN was observed with increasing current velocity (L = -272.63, d.f. = 10, theta = 1.11, $P < 0.001$; Figure 4.4.18; Appendix Table F.23).

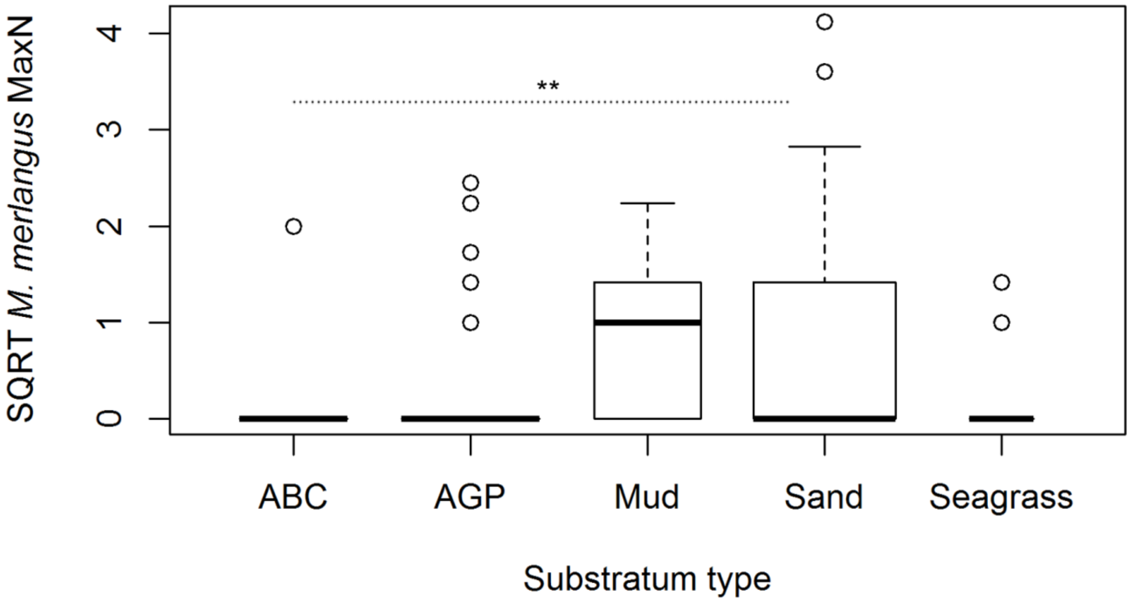

Figure 4.4.17 - Substratum type association of juvenile *M. merlangus* observed within South Arran NCMPA. More juveniles were found in relation to substratum type sand and mud with lowest MaxN observed on ABC substratum type. Dashed horizontal lines with * refers to Tukey test *P* value significance (** = $P < 0.01$).

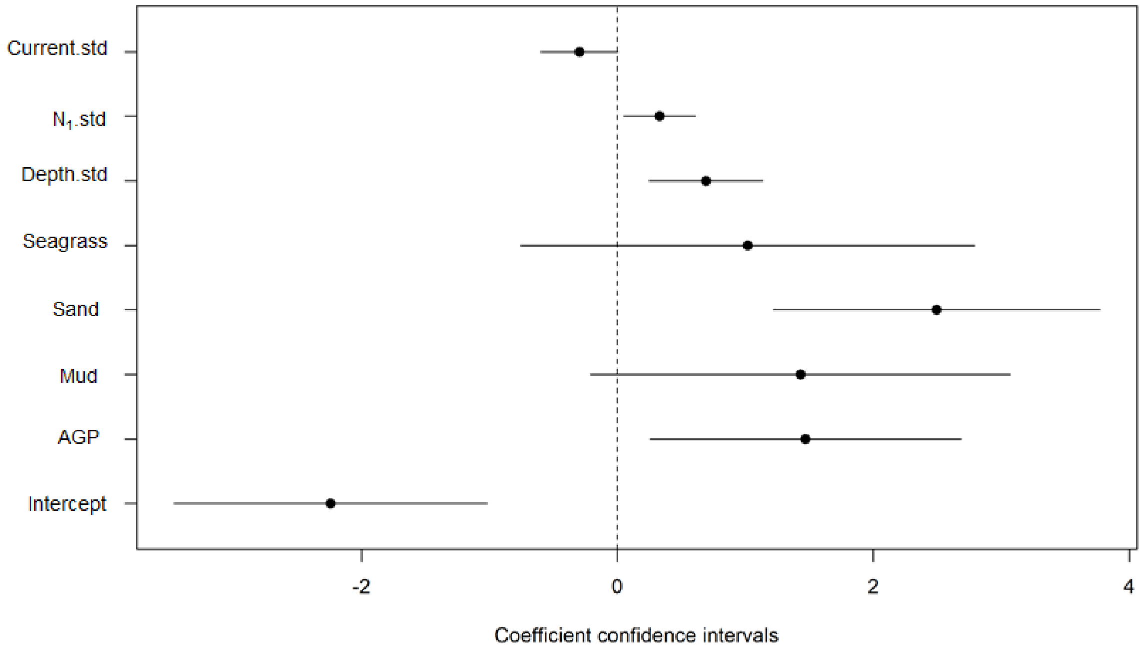

Figure 4.4.18 - Coefficient plot for model of best fit for *M. merlangus* habitat variables. Lines contain 95% confidence intervals for each of the explanatory variables. The verticle dashed line is the reference line enabling us to see which coefficients are significantly different from zero. The intercept is represented as ABC.

4.4.4.2. *M. merlangus* substrata association differences between years

Due to differences in data collection between years it was not possible to undertake statistical analysis comparing *M. merlangus* MaxN between substratum type since no data were collected in deeper water containing mud in year one.

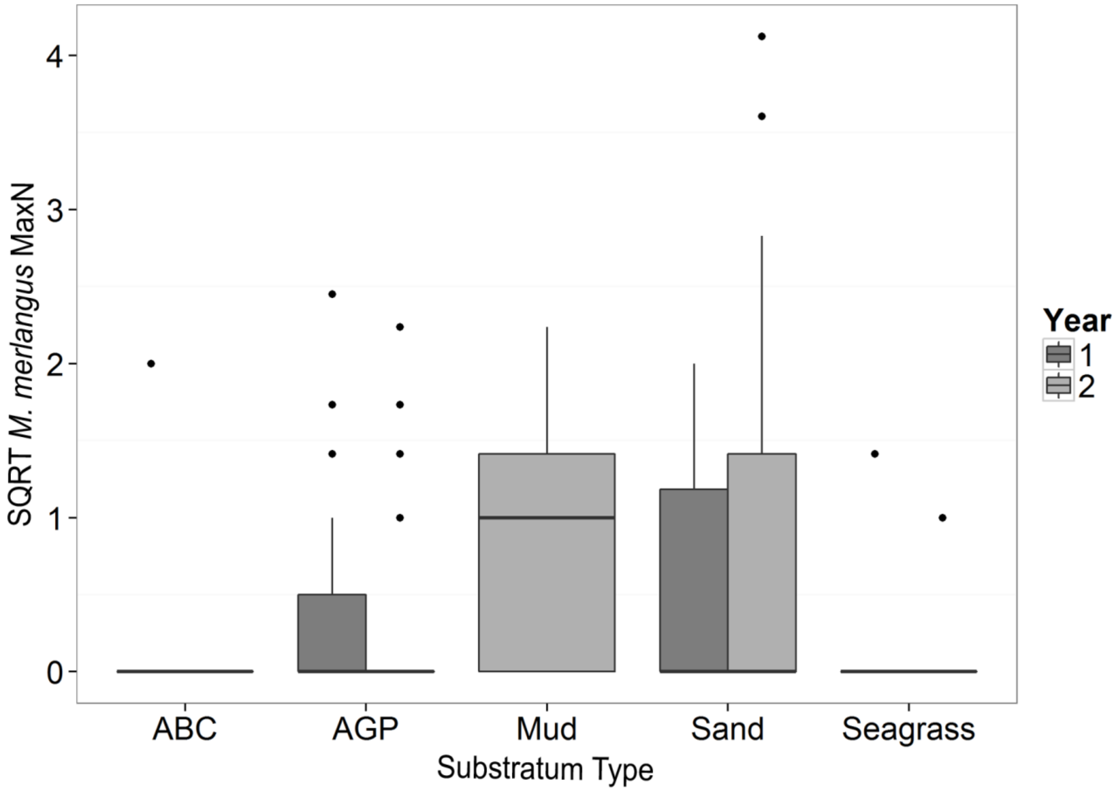

Figure 4.4.19, however, shows consistently high MaxN over sand substrata than the other substrata over the two years of data collection.

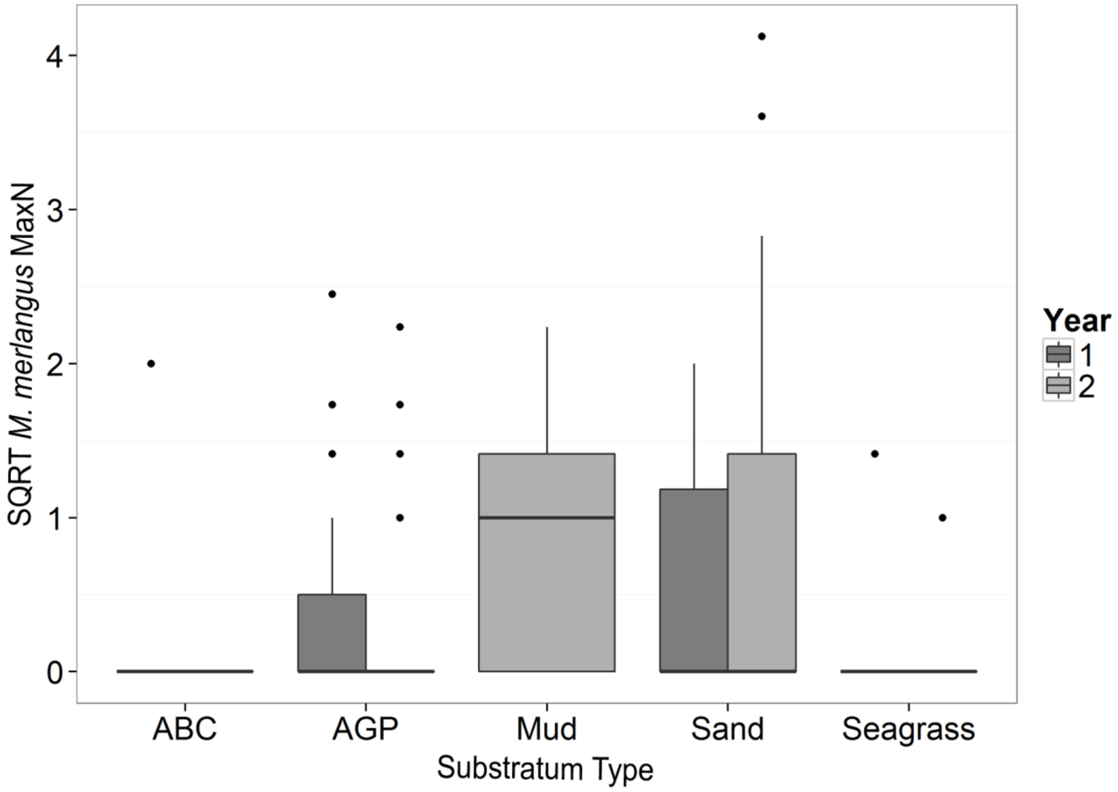

Figure 4.4.19 - Substratum association between summer of 2013 and 2014 for juvenile *M. merlangus* observed within South Arran NCMPA.

4.4.4.3. *M. merlangus* seasonal relative abundance and length variation

During field season 2013 (15 July – 28 September) no significant difference in MaxN was observed. During field season 2014 (30 June to 18 September 2014) the relative abundance of *M. merlangus* varied over the course of data collection with a decrease in MaxN observed during the third week (26 August - 2 September) followed by an increase in MaxN in the last week of data collection (15 – 18 September) (L = -229.30, d.f. = 5, theta = 1.08, *P* < 0.001;

Figure **4.4.20**; Appendix Table F.25 and Table F.26).

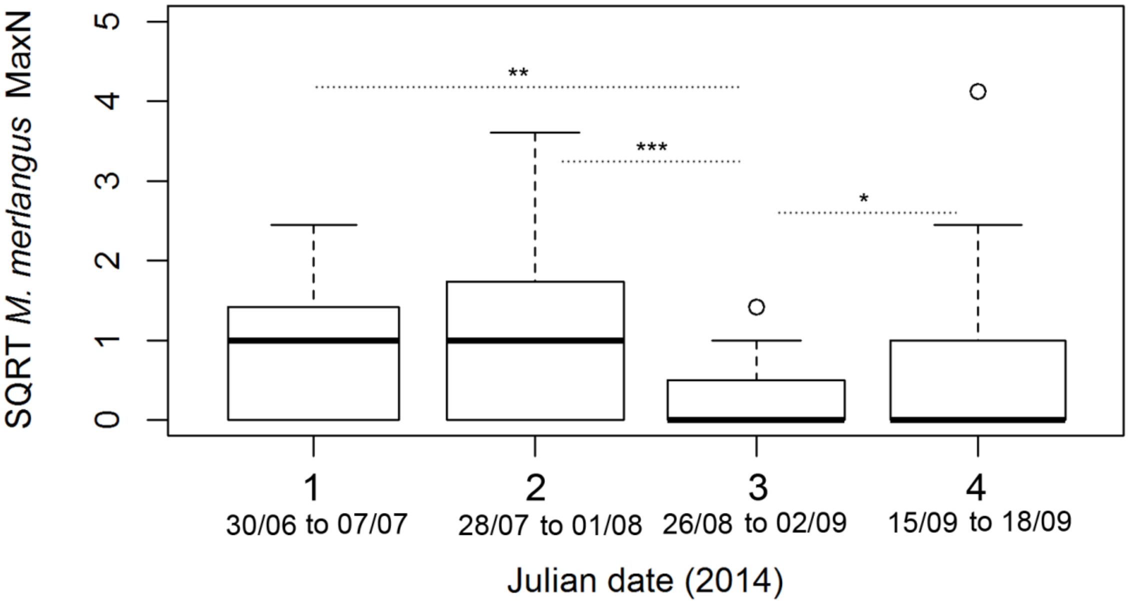

Figure 4.4.20 - *M. merlangus* MaxN (square root transformed) during data collection weeks from 30 June to 18 September 2014. A decline in *M. merlangus* relative abundance was observed during week three following by an increase in MaxN. Dashed horizontal lines with * refers to Tukey test *P* value significance (* = *P* < 0.05, ** = *P* < 0.01, *** = *P* < 0.001).

A total of 152 *M. merlangus* length measurements were made in 59 of the 259 SBRUV deployments. Of the 82 SBRUV deployments *M. merlangus* were observed in, length measurements were not obtained in 23 deployments. Average *M. merlangus* size was 14 cm (S.D. ± 4.3 cm), the largest individual observed measured 35.5 cm and was most likely an age-2 individual (DATRAS 2015) and the smallest individual observed was 6.3 cm.

During field season 2013, nine *M. merlangus* length measurements of individuals less than 15 cm were analysed at MaxN comprising of five deployments. The average length of *M. merlangus* was 10.7 cm (S.D. ± 2.2 cm). A significant increase in length was observed over the course of data collection (16th July – 27th September) during 2013 and a non-significant increase in length was observed with increasing depth (L = -15.56, d.f. = 4, $P < 0.05$;

Figure **4.4.21**; Appendix Table F.27). Exploration of length variation was not undertaken due to the limited dataset available for *M. merlangus* length measurements during 2013.

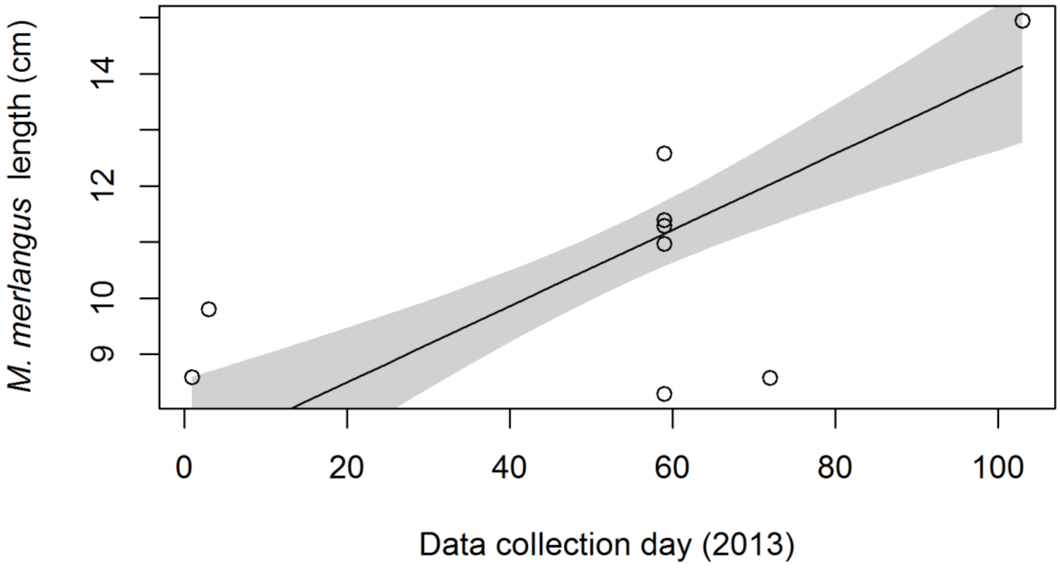

Figure 4.4.21 - Fitted values ± 95% confidence intervals from the model of best fit for *M. merlangus* length change over the period of data collection used for analysis (16 July – 28 September 2013). An increase in *M. merlangus* length was observed over the course of data collection ($P < 0.01$).

During field season 2014, 83 *M. merlangus* length measurements of juveniles smaller than 15 cm were made at MaxN from 37 SBRUV deployments. The average size of *M. merlangus* measured 11.3 cm (S.D. ± 2.3 cm). A significant increase in length was observed with depth during 2014 ($P < 0.01$) (L = -188.29, d.f. = 3, $P < 0.01$;

Figure **4.4.22**; Appendix Table F.28). No significant difference in size was observed in relation to data collection week. No significant increase or decrease in length variation was observed for 2014. This might be due to the small sample size (n=14 data collection day differences).

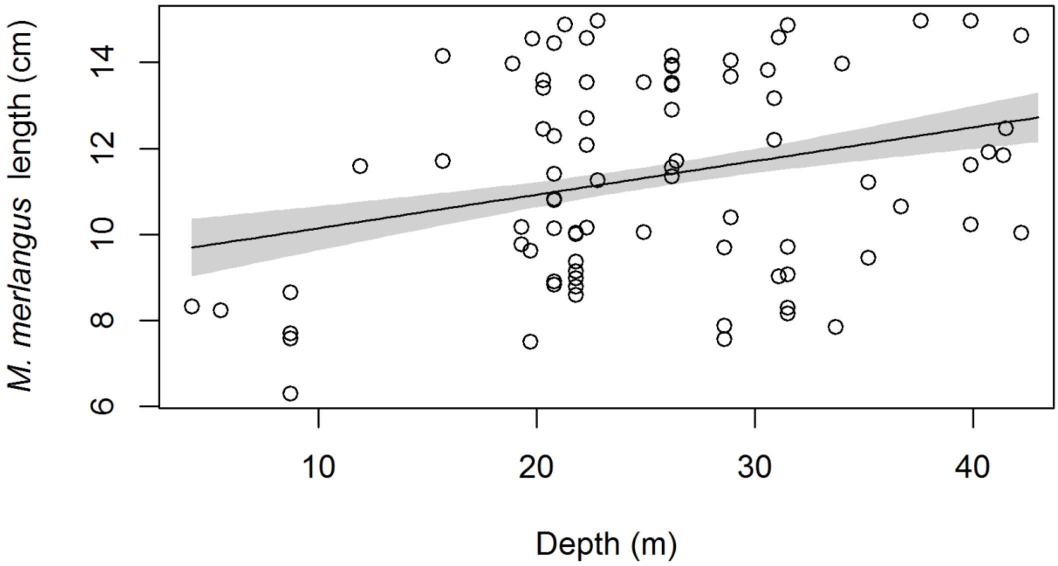

Figure 4.4.22 - *M. merlangus* length change with depth during field season 2014. Fitted values ± 95% confidence intervals from the model of best fit for *M. merlangus* length change with depth during field season 2014. A significant increase in length was observed with depth (*P* value; * = $P < 0.01$).

4.4.5. Gadoid size and bait attraction differences

4.4.5.1. Gadoid length differences

During field season 2013, significant difference in length were observed between species, with *G. morhua* smaller than *M. aeglefinus* and *M. merlangus* (L = -342.56, d.f. = 5, $P < 0.001$, $R^2 = 0.69$;

Figure **4.4.23**; Appendix Table F.29 and Table F.30).

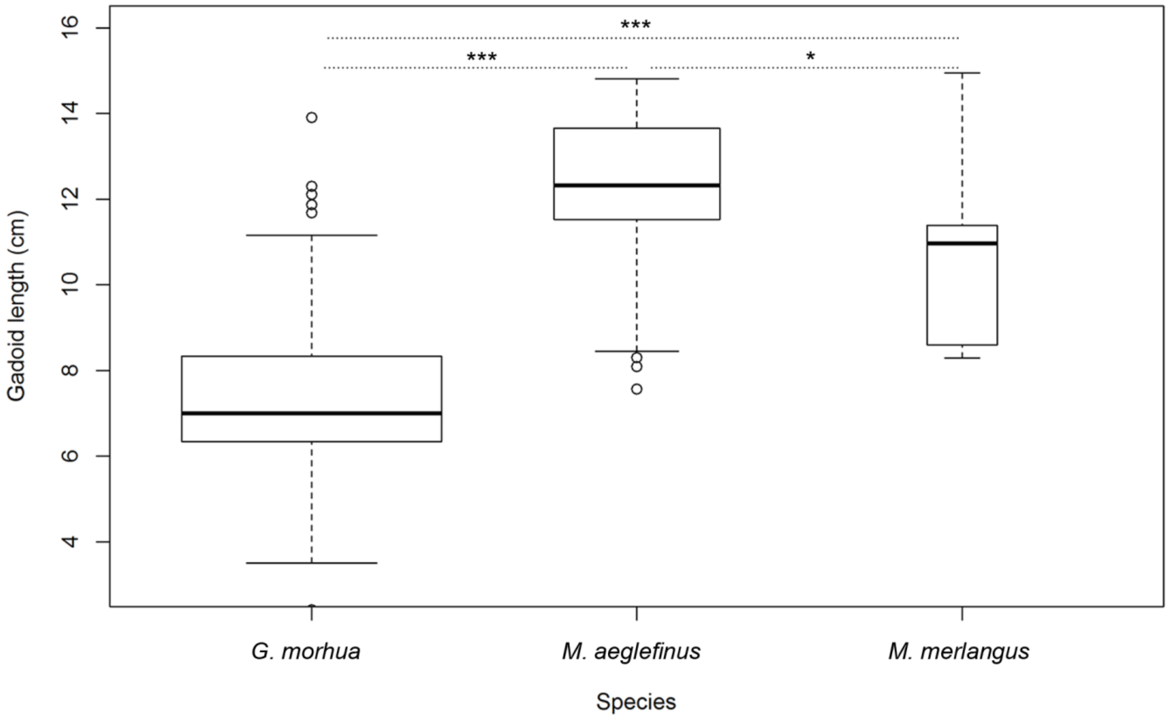

Figure 4.4.23 - Differences in folk length between gadoid species during field season 2013. *G. morhua* were significantly smaller than *M. aeglefinus* and *M. merlangus* and *M. merlangus* larger than *M. aeglefinus*. Dashed horizontal lines with * refers to Tukey test *P* value significance (*** = $P < 0.001$, * = $P < 0.05$).

During 2014 significant differences in length were observed between gadoids with *M. merlangus* larger than *G. morhua* and *M. aeglefinus* and *G. morhua* smaller than *M. aeglefinus* (L = -1337.11, d.f. = 5, $P < 0.001$, $R^2 = 0.37$;

Figure 4.4.24; Appendix Table F.31 and Table F.32).

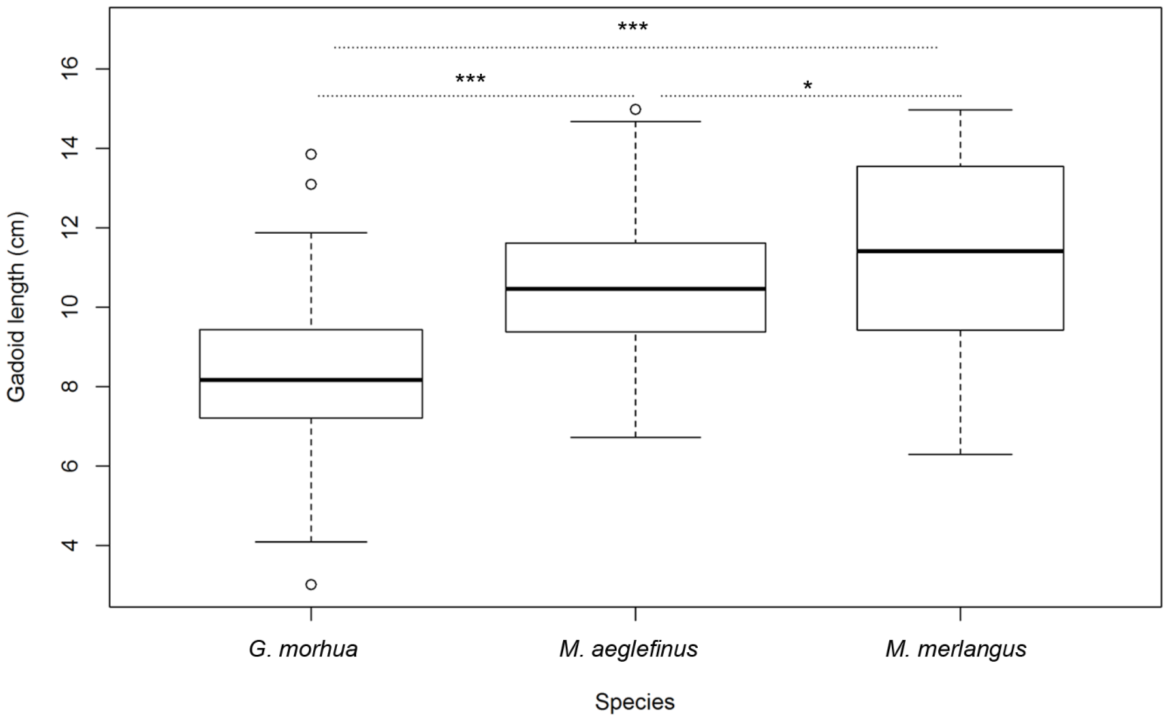

Figure 4.4.24 - Differences in folk length between gadoid species during field season 2014. *M. merlangus* were significantly larger than *M. aeglefinus* or *G. morhua*. Dashed horizontal lines with * refers to Tukey test *P* value significance (* = $P < 0.05$, *** = $P < 0.001$).

4.4.5.2. Gadoid mid Y and mid Z positioning

Significant differences in positioning between gadoids were observed. *G. morhua* positioning themselves on average closer to the seabed (mean mid Y = -6.8 cm, S.D. ± 14.3 cm) and further from the cameras (mean mid Z = 172.2 cm, S.D. ± 38 cm). *M. merlangus* average position was closer to the cameras in terms of height and distance off the seabed (mean mid Y = -3.2 cm, S.D. ± 12.3 cm, mean mid Z = 127.6 cm, S.D. ± 29.1 cm), for mid Y (L = -2359.36, d.f. = 6, $P < 0.001$; Appendix Table F.33 and Table F.34) and for mid Z (L = -2934.83, d.f. = 6, $P < 0.001$; Table 4.4.2;

Figure **4.4.25**; Appendix Table F.35 and Table F.36). *M. aeglefinus* were positioned at intermediate distances from the cameras relative to *G. morhua* and *M. merlangus* (mean mid Z = 152.2 cm, S.D. ± 40.1 cm and mean mid Y = -2.2 cm, S.D. ± 13.5 cm).

Table 4.4.2 - Tukey test differences in mid Y and mid Z positioning between gadoids.

Species differences	**Mid Y**	**Mid Z**
G. morhua – M. aeglefinus	$P < 0.001$	$P < 0.001$
G. morhua – M. merlangus	$P < 0.001$	$P < 0.001$
M. aeglefinus – M. merlangus	$P < 0.001$	$P < 0.001$

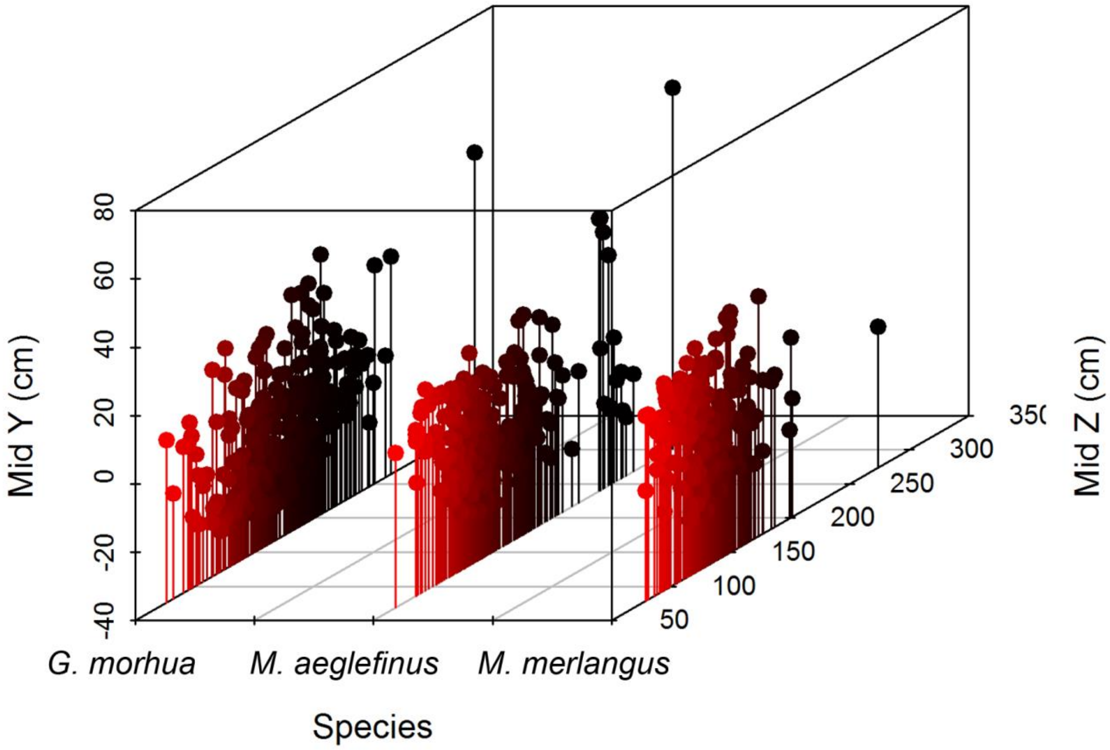

Figure 4.4.25 - Gadoid mid Y and mid Z positioning for 2013 and 2014. Measurements closer to the camera are shown in red and further from the camera in black. On average *G. morhua* positioned themselves further from the camera (mid Z) and closer to the seafloor (mix Y) than *M. aeglefinus* and *M. merlangus*, with *M. merlangus* positioning themselves closest to the camera in both mid Y and mid Z measurements.

4.4.5.3. Gadoid TFA

A significant difference in TFA for both years combined together was observed between gadoid species with *G. morhua* entering the field of view earlier than *M. merlangus* and the first *M. aeglefinus* arriving shortly after *G. morhua* (*P* < 0.001;

Figure **4.4.26**; Appendix Table F.37). Log likelihood ratio tests were not possible using the hglm package for this model. However, data exploration was undertaken to validate the results by Arcsin transforming the data to a Gaussian distribution and testing for significant differences. The same results were obtained. The Arcsin transformed model outputs were not used since logistic regressions have greater interpretability and higher power than arcsine-transformed response variables (Warton and Hui 2011).

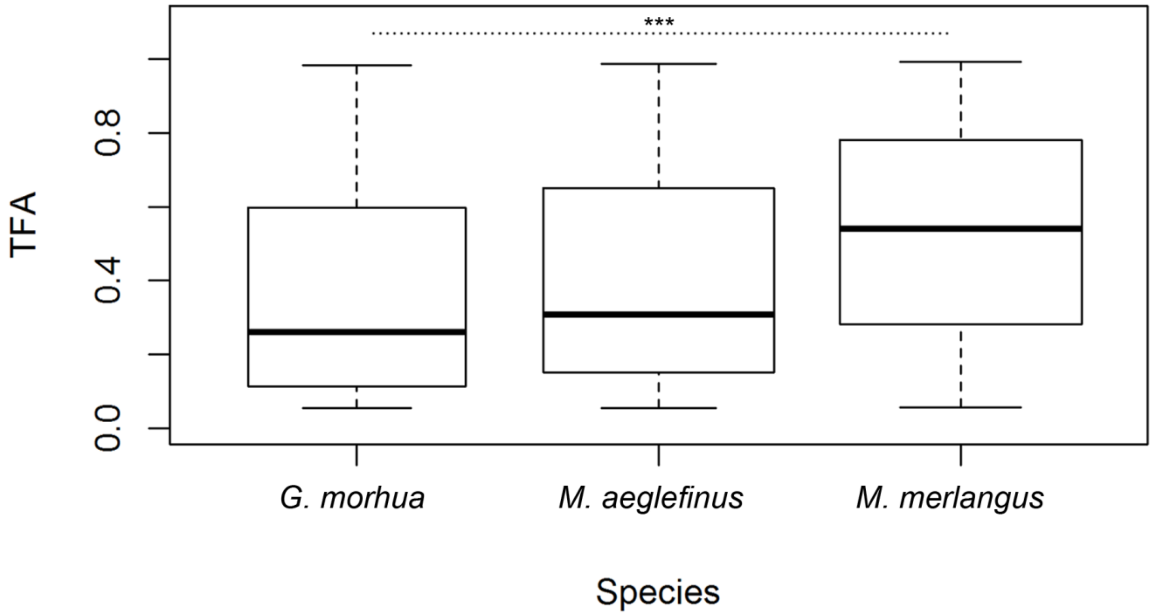

Figure 4.4.26 - TFA between the different gadoid species for both 2013 and 2014. *G. morhua* were observed in the field of view significantly earlier than *M. merlangus*. Dashed horizontal lines with * refers *P* value significance (*** = *P* < 0.001).

4.5. Discussion

Robust methods to assess fish distribution and abundance are essential for both fisheries management and conservation (Vasconcelos et al. 2014). With the increasing number of spatial management proposals being developed, non-extractive and non-damaging fisheries independent mechanisms are becoming indispensable. There is a paucity of data on gadoid habitat as defined in Chapter 2. This is unfortunate given the poor state of many stocks and their economic importance (Worm et al. 2009; FAO 2009; EEA 2011). Few studies in the northern hemisphere have used SBRUV surveys as a method to collect fish habitat data. This study provides habitat information on *G. morhua*, *M. aeglefinus* and *M. merlangus* in addition to behavioural, recruitment and growth observations from data collected during daylight hours.

Previous research demonstrated that *G. morhua* have been associated with a variety of substratum types including rocky reef areas, seagrass and maerl beds (Tupper and Boutilier 1995a; Laurel et al. 2004; Kamenos 2004; Chapter 3). However, most studies only compare a few different substratum types to one another (e.g. Laurel et al. 2004; Bertelli & Unsworth 2014). Here association to a variety of substratum types were analysed in addition to other abiotic and biotic variables. Higher relative abundance of *G. morhua* was observed over the algal-gravel-pebble substratum type, with no individuals observed over mud and the next fewest individuals observed occupying sand. These results support previous observations collected by stereo-video SCUBA transects (Chapter 3), where higher relative abundance of *G. morhua* were observed over algal-gravel-pebble substratum types.

It is likely that fewer *G. morhua* were observed over seagrass areas due to the patchy, low density and small area of seagrass (Jackson et al. 2001; Gorman et al. 2009, McCloskey and Unsworth 2015) around south Arran. Surveys by local conservation volunteers (COAST 2013) in addition to data collected over the course of this thesis, estimate that the area of seagrass within Whiting Bay (South Arran) is less than 1 km^2. Fewer *G. morhua* may have been observed over algal-boulder-cobble substrata since other potential predatory fish were observed around these areas e.g. adult pollack, *pollachius pollachius*, L and saithe, *Pollachius virens* L.

It is improbable that fewer individuals were observed in algal-boulder-cobble and seagrass substrata due to difficulties in observing the individuals since the static nature of SBRUV meant that any animals moving within the field of view were almost certain to be observed over the deployment period. Algal-gravel-pebble substrata may provide a sufficient level of protection for the size ranges of *G. morhua* observed. Gravel-pebble substrata may also be selected as an anti-predator technique, since *G. morhua* were more difficult to distinguish when over gravel-pebble surfaces (Lough et al. 1989; Gregory and Anderson 1997; Lough 2010). Much of the gravel around South Arran contained maerl which is thought to contribute to higher species diversity and heterogeneity and may be of importance to juvenile *G. morhua* (Hall-Spencer et al. 2003; Kamenos 2004; Lough 2010).

Ontogenetic shifts in substratum association were observed, with higher *G. morhua* MaxN were observed over more rugose substrata (relative to their size). *G. morhua* ontogenetic shift movement from sand to algal-gravel-pebble over the course of data collection period 2013 and algal-gravel-pebble to seagrass areas within 2014 was observed. This indicates that ontogenic shift in substratum use may be occurring within the size ranges (3 cm - 15 cm) observed. Similar results were observed by Keats & Steele (1992), Laurel et al. (2007) and Tupper & Boutilier (1995b), where ontogenic shifts to more rugose substrata were observed with increased size. Such behaviour has been suggested to reduce agonistic interactions (such as from competition for resource or predation) between individuals (Keats and Steele 1992; Tupper and Boutilier 1995b). Ontogenic shifts within this size range also highlights the importance of substrata of sufficient rugosity relative to the size of the individual and that multiple substratum types are needed by the same species (Nagelkerken et al. 2013; Chapter 3 - 5).

Significant differences in *G. morhua* relative abundance were observed between years, with significantly fewer individuals observed during 2014. During both summers (2013 and 2014), relative abundances observed over algal-gravel-pebble were higher than on other substrata. In addition, during data collection period 2014, *G. morhua* relative abundance dramatically reduced in all substrata, where as in algal-gravel-pebble substratum type, *G. morhua* mean MaxN only halved. The latter indicates a selection for algal-gravel-pebble substratum type as opposed to other substrata, and density dependent substrata association given *G. morhua* relative abundances during 2014 were significantly less than 2013. This result also indicates that algal-gravel-pebble may be an important habitat component affecting juvenile *G. morhua* survival. Density dependent substrata association in *G. morhua* has previously been observed by Laurel et al. (2004), with individuals moving to less productive substrata with increasing abundance. These results should however be treated with caution, since when incorporating an interaction with year and substratum type in the *G. morhua* habitat model (*G. morhua* habitat – p. 102), the interaction was not significant. This is likely to be due to the small effect of this interaction.

Although previous research has suggested *M. aeglefinus* and *M. merlangus* do not seem to have a particular nursery grounds (Hislop 1996), significant substratum associations were observed. For both species, higher relative abundances were observed over sand and mud substratum types with the fewest individuals observed over algal-boulder-cobble substratum types. Higher MaxN over sand was also observed over both years of data collection for both species, indicating a possible selection for this substratum type. These results match laboratory studies undertaken with *M. merlangus,* where juveniles selected sand when no external stimulus was present (Atkinson et al. 2004). Auster et al. (2001) and Brickman (2003) also found higher abundances of juvenile *M. aeglefinus* over sand-gravel surfaces in the western Atlantic.

Similarities in substratum association between *M. aeglefinus* and *M. merlangus* may be because, on average *M. aeglefinus* and *M. merlangus* were more similar in size and significantly larger than *G. morhua* (Figure 4.4.23 and

Figure **4.4.24**). Substratum and depth differences between species indicate size (Bastrikin et al. 2014) and/or species specific segregation, with *G. morhua* in shallower and relatively more rugose substrata than *M. aeglefinus* and *M. merlangus*. Species specific segregation potentially reduces predation (Myers and Cadigan 1993; Fromentin et al. 1997) and minimises competition, most likely as a result of different resource needs (Fromentin et al. 1997; Bastrikin et al. 2014).

M. aeglefinus and *M. merlangus* were also observed to occupy significantly higher heights off the seabed than *G. morhua* (

Figure **4.4.25**; Table 4.4.2). *G. morhua* are known to be more benthic species relative to *M. aeglefinus* and *M. merlangus* with a better developed chin barbel containing taste buds (Harvey & Batty, 2002). The sand and mud substrata may have a higher abundance and diversity of *M. aeglefinus* and *M. merlangus* preferred prey types. Such results demonstrate that measures to protect juvenile substrata must be tailored to the species and life-history stages under consideration and that there may not be general rules which apply even within groups of closely-related fish (Nagelkerken et al. 2013).

The relative abundances of all three species were positively correlated with the benthopelagic diversity. Increased N_∞ (species dominance) was linked to decreased *G. morhua* and *M. aeglefinus* relative abundance. However, increased N_1 (exponential of Shannon-wiener's index) was linked to increased *M. merlangus* relative abundance. The same Hill number may not have been significant for each species due to the high proportion of zeros in observations of gadoids and the variation in numbers of samples between the different substratum types. N_1 is also more sensitive to sampling imbalances (Soetaert and Heip 1990; Buckland et al. 2005, 2011). Benthic species observed were unlikely to have been prey food for the gadoids due to their larger sizes (Demain et al. 2011; Bastrikin et al. 2014). Key prey food for all three species with size ranges of 3 cm – 15 cm overlap to a certain extent. Stomach analysis on smaller individuals have shown consumption of a mixture of pelagic copepods and benthic invertebrates, to primarily invertebrates and juvenile fish at the larger age-0 size ranges (Demain et al. 2011; Bastrikin et al. 2014).

Species diversity can provide a range of function for fish from seabed-surface topography and structural rugosity, provision of substratum heterogeneity and food sources to gadoids, to ecosystem functioning (Folke et al. 2004; Sherwood & Grabowski, 2016; Worm et al. 2006; Thrush et al. 2016). Species diversity can also be an indicator of seabed disturbance (Thrush and Dayton 2002).

Maintaining species biological diversity is a well-known mechanism in maintaining ecosystem services on which we depend (Worm et al. 2006; Beaumont et al. 2008; Gamfeldt et al. 2008). Declines in species diversity are largely caused by anthropogenic impacts such as exploitation, physical damage to substrata, pollution and climate change (Dulvy et al. 2003; Lotze 2006; Worm et al. 2006). Shallower gravel type substrata where G. morhua were found in greater abundance are more vulnerable to demersal mobile fishing gear, in particular to dredging which has greater benthic impacts than trawling (Collie et al. 2000, Hiddink et al. 2006, Kaiser et al. 2006). Sand and mud substrata where M. merlangus and M. aeglefinus were found in greater relative abundance which is subject to higher levels of trawling (Collie et al. 2000; Hiddink et al. 2006; Kaiser et al. 2006). Protecting more diverse areas or improving the state of areas with lower species diversity may therefore support the survival of commercial fish (Worm et al 2006; Beaumont et al, 2008).

Wave exposure has previously been identified as having a strong influence on the local distribution of coastal species and food distribution (Burrows et al. 2008; Burrows 2012). For both *G. morhua* and *M. aeglefinus* there was a negative relationship between their relative abundance and wave fetch. Fromentin et al. (1997) observed higher abundances of *G. morhua* and *M. merlangus* in more sheltered areas within fjords as opposed to more exposed areas outside fjords. Mark recapture experiments undertaken by Rogers et al. (2014) have shown that distance travelled by juveniles is lower in more sheltered areas (Rogers et al. 2014). The results found here may differ from Lekve et al. (2006) who found increased abundance of *G. morhua* in more exposed areas, since the level of exposure may be quite different. Within Lekve et al. (2006), exposure was not quantified on a continuous scale as used in this investigation (Burrows et al. 2008), but instead categorically according to a more sheltered area and a more exposed areas.

Although juvenile gadoids were more abundant in more sheltered areas, increased exposure has previously been observed to help drive larvae to coastal areas (Huwer et al. 2014). Various hypotheses exist regarding how fish larvae and fry arrive at coastal areas, all of which include oceanic processes supporting the transport of larvae (Ings et al. 2008; Huwer et al. 2014). These hypotheses include being carried by shoreward moving tidal forces (Pineda 1994), active migration (Staaterman and Paris 2014) and arrival by up and downwellings (Ings et al. 2008). In all three species higher MaxN was observed during July and August with signs of possible pulse or extended recruitment from late June through to late September, due to the size ranges observed. The latter was particularly evident for *M. merlangus*. Significant differences in length variation indicating multiple recruitment cohorts were not observed. However, this is likely to be largely due to the small sample size.

In all three species, higher relative abundance was observed in July with declines in August and September. *G. morhua* were unlikely to have moved to deeper waters during this period of time since none were observed in the deeper waters (> 30 m). Additionally, migration to deeper waters is thought to occur after their first winter or first year (Magill & Sayer 2004). An increase or in gadoid relative abundance was expected over the period of data collection because of pulse recruitment observed and expected over the period of data collection (Ings et al. 2008). The decline in *G. morhua* relative abundance may therefore indicate that habitats of sufficient quality to provide food and refuge may have been a limiting factor to their survival (Tupper and Boutilier 1995b; Vasconcelos et al. 2014). For both *M. aeglefinus* and *M. merlangus* a positive relationship between depth and size was observed. Additionally, for both years *G. morhua* were smaller than *M. aeglefinus* and *M. merlangus*, this may have been due to later recruitment to coastal areas. A smaller size range and latter arrival not only puts *G. morhua* at a competitive disadvantage in comparison to *M. aeglefinus* and *M. merlangus* but potentially makes them more vulnerable to predation (Werner and Gilliam 1984; Ellis and Gibson 1995; Renkawitz et al. 2011). Studies undertaken by Heath & Speirs (2012) have shown that the biomass within the Firth of Clyde is largely made up of juvenile *M. merlangus*. Spawning earlier and multiple times throughout the year may give *M. merlangus* a competitive advantage over to *G. morhua* (Hislop 1975; McEvoy and McEvoy 1992; Wright & Trippel, 2009).

4.5.1. Management, considerations and future work

Few studies have been undertaken using SBRUV as a mechanism to collect fisheries independent data in the UK. Few studies have previously looked at how a range of abiotic and biotic habitat variables can affect gadoid abundance and length. Although measures have been put in place to recover gadoid stocks little improvement has been observed in west coast of UK stocks (Fernandes & Cook 2013; ICES, 2014; Barreto & Bailey 2015). Links to substratum types have previously been undertaken, but substratum fish size related studies are few and far between (Seitz et al. 2014; Vasconcelos et al. 2014). Future research should focus on trying to quantify the carrying capacity of important nursery areas to facilitate targeted management measures to try and improve survival and recruitment (Heath et al. 2008; Bailey et al. 2011).

A problem with using SBRUV is the limited view of substrata able to be observed around the cameras (approximately 2.5 – 3 m^2) and the unknown distance a fish may have travelled if attracted to the cameras to calculate absolute abundance (Chapter 6) and understand wider seabed landscape effects. From TFA analysis and gadoid mid Y and Z positions, it appears as if *M. merlangus* were attracted to the bait given the time it took to arrive at the bait and since their mid Y and Z positions were closer to the SBRUV than *G. morhua* which were already within the vicinity. At the time this data was collected, acoustic information on the seabed was not available around the south of Arran to be able to understand any possible landscape affects which could have affected gadoid distribution. Chapter 5, however, considers such substratum heterogeneity and landscape effects.

The findings on SBRUVS effectiveness under UK coastal waters should have wide relevance across the region. With the increasing number of spatial closures being designated within UK waters, SBRUV surveys could be used as a monitoring method. The biological results are specific to the area studied but would ideally be replicated elsewhere, or verified with several smaller-scale studies (see Chapter 6).

4.6. Conclusion

This study clearly demonstrates the importance of habitat variables on gadoid fish around the south of Arran. By understanding the range of conditions suitable to gadoid species, adequate protection measures can be implemented to try and recover stocks and mitigate against climate change and other anthropogenic impacts. Substrata were clearly of relevance to juvenile *G. morhua, M. aeglefinus* and *M. merlangus* and more specifically a range of substratum types were required by *G. morhua* from arrival to coastal areas as they increased in size. Further, this study highlights the importance of benthic and demersal species diversity for all three of these species throughout the range of substrata that they were observed over. The latter has significant management implications since not only are certain substratum types of particular importance but potentially their quality as indicated by benthopelagic diversity. This is particularly relevant given Sherwood and Grabowski (2016) found older, larger and fatter G. morhua within MPAs than out with. This study not only highlights habitat variables which should be considered for gadoid fish management but has MPA and Marine Strategy Framework Directive (MSFD) management and monitoring implications. This research is particularly relevant to the MSFD descriptors relating to biodiversity (D1), seafloor integrity (D6), commercially exploited fish (D3) and elements of the food web (D4) (EU 2008). Links between descriptors 1, 3 and 6 have not been addressed (OSPAR 2014) and in general interactions between biodiversity, the quality of the seafloor and commercial fisheries management is increasingly separated (Pauly 1995, Auster and Langton 1999, Armstrong and Falk-Petersen 2008). We recommend adopting such strategies to understand commercially exploited fish during critical life phases to habitat variables is essential to support the recovery of depleted fish stocks and implement a more ecosystem based management.

Chapter 5. Substratum prediction modelling to investigate landscape effects on juvenile gadoids

5.1. Abstract

Successful spatial and zonal management for conservation purposes requires a good understanding of the distribution of species and their habitats. Protecting nursery areas for juvenile demersal fish has been proposed as a measure to conserve or recover fish stocks. However, there has been few studies on the role of heterogeneity at a landscape level and so the importance of variability in substratum types across an area inhabited by fish remains poorly understood. This is of particular relevance for commercially important gadoid fish on the west coast of Scotland which have been subject to intense fishing activities for decades with little sign of recovery.

Data on gadoid relative abundance, size and substratum type were collected using fisheries independent, non-damaging SBRUV deployments within a recently designated MPA in the Firth of Clyde, southwest of Scotland. Factors correlating with the presence of different substratum types were determined, allowing substratum type to be predicted within the MPA. The predicted seabed map was used to understand the relationship between substratum type, extent (the area of each substratum type) and heterogeneity (diversity and pattern of substratum types and patches within a landscape), and gadoid relative abundance within a radius of 1500 m. The predicted substratum model performed well with an area under the curve score of 0.87 (rated as excellent). Atlantic cod (*Gadus morhua*) was associated with relatively more rugose substrata and heterogeneous landscapes, than haddock (*Melanogrammus aeglefinus*) or whiting (*Merlangius merlangus*). An increase in *M. merlangus* relative abundance was also observed with increasing substratum extent.

This is the first study to look at the effects of landscape heterogeneity and substratum extent on gadoid distribution. Results from this study suggest that heterogeneous landscapes should be considered for the protection of juvenile *G.*

morhua, rather than simply choosing areas with the highest proportion of the substrata with which *G. morhua* has the strongest association. The approach used in this study has benefits for MPA, fisheries management and monitoring advice, supporting a more ecosystem-based management.

5.2. Introduction

Protecting species and their habitats requires a good understanding of species distribution and the role of their habitat. Unfortunately in many cases the latter is not well understood due to the difficulties in collecting such data (Brown et al. 2011; Seitz et al. 2014; Sundblad et al. 2014). With the increase in spatial protection measures, understanding the distribution of species and their habitat is increasingly important (Howell et al. 2011; Moore et al. 2016). An understanding of seabed type and distribution can influence maritime spatial planning required under European Union’s 2014 directive (EU 2014) and reduce spatial conflict from multiple sea-users (White et al. 2012; Evans et al. 2015; Reiss et al. 2015). Knowledge of substratum distribution can also influence management measures for MPAs (Reiss et al. 2015). It is well recognised that substratum type is of importance to demersal fish (e.g. Seitz et al. 2014; Sundblad et al. 2014). However there is often a lack of knowledge of landscape (Box 2.3.1, Chapter 2) effects on fish abundance and survival (Mangel et al. 2006; Armstrong and Falk-Petersen 2008; Sundblad et al. 2014). This is of particular importance given that landscape analysis can provide a more complete understanding of how seabed type and distribution can effect demersal fish populations (Moore et al. 2011).

Fisheries affect fish populations through direct mortality as catch or bycatch but also through indirect effects on the success of individual fish (Auster et al. 1996; Jennings and Kaiser 1998; Armstrong and Falk-Petersen 2008). Such effects might include disruption or disturbance to spawning areas (Clarke et al. 2015) or damage to resources used by the fish such as food sources or shelter (Auster et al. 1996; Auster and Langton 1999). Direct mortality can be reduced by a reduction in fishing effort, modifications to gear or by avoiding times and places where there is high density of the species in question (Fernandes and Cook 2013; Clarke et al. 2015). Avoidance of indirect effects on the resources needed by fish is most commonly achieved through spatial measures such as MPAs or fisheries closures (Worm et al. 2009; Halpern et al. 2010).

Protecting areas important to fish still remains a less common approach to conserving fish than reducing fishing effort or modifying gear impact (Armstrong and Falk-Petersen 2008). This is mainly because of the difficulties in understanding which habitat components are important to fish and how the extent (area of each substratum type) and heterogeneity (diversity and pattern of substratum types and patches within a landscape) of substrata (Box 2.3.I, Chapter 2) within a landscape affect fish populations (Moore et al. 2010, 2011; Sundblad et al. 2014). Further, species will relate to their environment differently according to their size, behaviour and mobility (Buhl-Mortensen et al. 2012). More focus has therefore been placed in species abundance and distribution modelling than on modelling landscape effects on fish (e.g. Elith et al. 2006; Elith & Leathwick 2009). Environmental variability such as exceptionally warm or cold winters, can however cause fluctuations in fish abundance and distribution (e.g. Planque & Fox 1998; Planque & Frédou 1999; Magill & Sayer 2004) affecting species distribution models. Understanding substratum type and distribution of relevance to demersal and benthic species may therefore be more beneficial than modelling species distribution (Howell et al. 2011; Ross and Howell 2013). To protect substrata from anthropogenic impacts and understand how complex landscape responses affect species distribution, detailed full coverage seabed maps are required (Holmes et al. 2008; Moore et al. 2011).

Within coastal areas mapping has been derived from aerial and satellite images. Use of optical imaging techniques in high visibility waters can provide useful information, unfortunately such techniques are less useful in more turbid waters (Sundblad et al. 2014). Acoustic methods can also provide detailed maps of the seabed type (Brown et al. 2011), but can be resource intensive and prohibitively expensive (Reiss et al. 2015; Schubert et al. 2015). Predictive methods can therefore be an important tool to overcome such issues (Guisan and Zimmermann 2000). A wide range of predictive modelling methods exist (e.g. Guisan & Zimmermann 2000; Barry & Elith 2006; Elith & Leathwick 2009) and method-specific differences can yield varying performance (e.g. Elith et al. 2006; Reiss et al. 2011). In addition, predictive outcomes will vary largely on the spatial scales used (Levin 1992; Elith and Leathwick 2009; Chave 2013). For example, broad scale predictive maps already exist within the Firth of Clyde (i.e. Ross et al. 2009; McIntyre et al. 2012) and rock, gravel and sand substrata have been predicted within 12 km of the coastline the south of Arran coastline. However, ground-truthed data within the same area collected in chapters 3 and 4 demonstrated that there was a broader range of substrata with different distribution. For individual MPAs and other spatial management plans to be effective, adequate spatial scales need to be used (Levin 1992; Crain et al. 2009; Chave 2013). Therefore, rather than using broad scale predicted maps which have been undertaken on a country-wide scale to implement management measures within an MPA, higher resolution mapping should be undertaken at the scale of the MPA.

Given the need for higher resolution seabed maps to implement adequate spatial management measures and the lack of knowledge of landscape effects on fish abundance and distribution, the aims of this study were two-fold. Firstly a range of environmental variables were explored to undertake fine-scale predictive mapping of substrata within south Arran NCMPA (SNH 2014; Figure 5.3.1). The predicted seabed map was then used to understand how substratum type, extent and heterogeneity affected juvenile *G. morhua M.* and *aeglefinus M. merlangus* relative abundance. Fisheries independent SBRUV recordings were used to collect substratum and gadoid data within the MPA as a quantitative, non-destructive and non-extractive method of data collection. SBRUV surveys were undertaken since they are a useful technique that overcome depth and seafloor rugosity sampling limitations inherent of SCUBA and fisheries dependent techniques (Cappo et al. 2004; Harvey et al. 2007; Moore et al. 2010). Understanding the effect of the wider landscape on gadoid distribution was particularly important using SBRUV deployments since the field of view of SBRUV measurements are relatively small within temperate waters (~2 m^2 depending on visibility).

5.3. Method

5.3.1. Study Location

Research was conducted from June to September 2013 and 2014 within South Arran NCMPA, located within the Firth of Clyde, southwest coast of Scotland (Figure 5.3.1), covering an area of 250 km^2 (SNH 2014; refer to Chapter 3 and 4 for more information).

5.3.2. Data collection

Gadoid sampling was undertaken using three SBRUV frames as described in Chapter 4. SBRUV and stereo-video SCUBA transect substratum classifications were also used to undertake substratum prediction modelling. Refer to Chapter 3 and 4 for a detailed description of SCUBA and SBRUV substratum categorisation. A total of 289 ground-truthed data points were therefore used for substratum prediction analysis consisting of 74 SBRUV deployments from 2013, 184 SBRUV deployments from 2014 and 31 SCUBA transects (Figure 5.3.1).

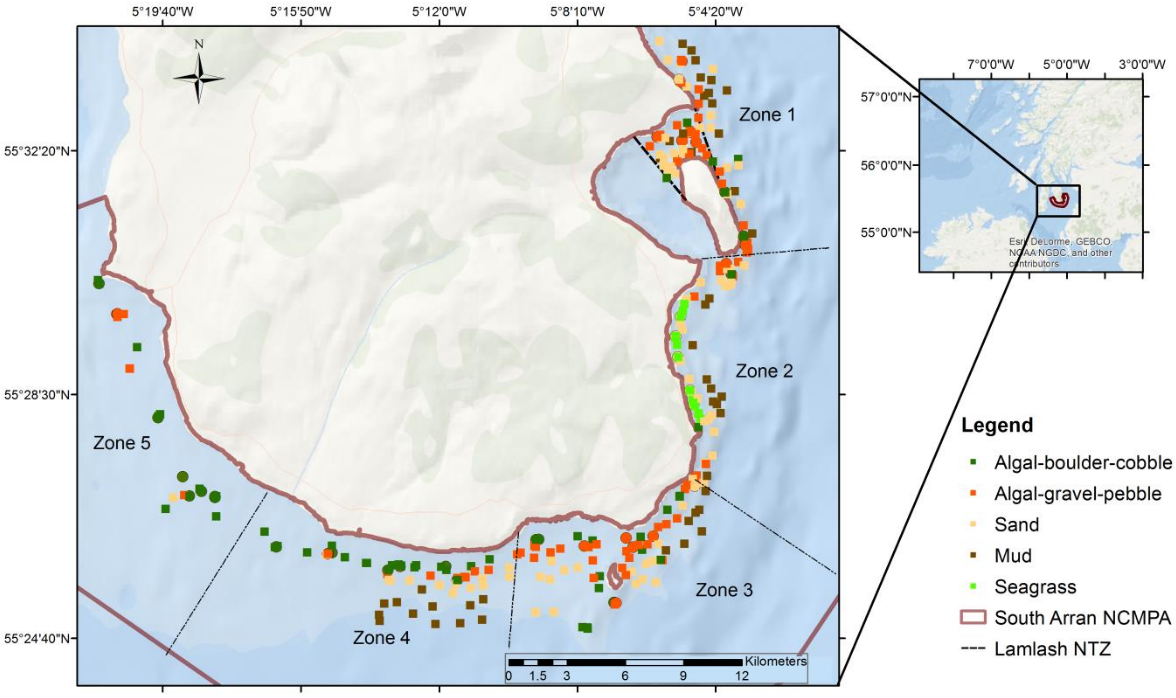

Figure 5.3.1 - South of Arran NCMPA with SBRUV 2013 and 2014 site locations and substratum classification. Circles represent dive site locations and squares represent SBRUV deployment locations

5.3.3. Substratum modelling

Five abiotic predictor variables were used for predictive substratum modelling (Table 5.3.1). These included depth, distance from coast, maximum current speed, wave fetch and underlying geology. Depth data were obtained from vessel echosounders (Chapter 4). Distance from shore was calculated using the GPS fix made at time of deployment and ArcGIS version 10.1 (EDINA digimap, British National Grid 1984). Maximum current speed was obtained from a hydrodynamic model of tidal elevations and current velocities developed by Sabatino et al (in review). The maximum current speed evaluated over a whole year was modelled at the location of each data collection point. Wave fetch values (downloaded from SAMS 2013) were used as described in Burrows et al. (2008). Information on the underlying geology of the MPA were obtained from British Geological Survey (BGS) was downloaded from EDINA (2015).

Table 5.3.1 - Summary of environmental predictors.

Predictor	Description	Unit	Range
Depth	Water depth	Metres	4.0 - 47.2
Wave fetch	A measure of exposure of a shore (the distance which wind-driven waves can build from the closest land point)	Kilometres	193 - 2877
Distance to coast	Distance of SBRUV from the shore	Metres	73- 2295
Maximum current speed	Maximum current speed at spring tides	Metres/second	0.11 - 0.91
Geology	Dominant rock type found to occur in the area	Categorical	2 levels: Permian rock and Triassic rock

A multinomial distribution was selected to understand predictor variables affecting substratum distribution, since five possible discrete outcomes restricted between zero and one were plausible (Faraway 2005; Hosmer et al. 2013). “nnet” R package (Venables & Ripley, 2002) in R software (version 3.03, R Core Team, 2015) was used for the multinomial model.Prior to statistical analysis, continuous variables were standardised to enable the predictor variables to be of comparable units. Principles outlined within Zuur et al. (2010) to check for collinearity and influential observations. One SBRUV sample was removed as a result of erroneous depth reading. One SCUBA transect was removed as described in Chapter 3. Automated model selection was undertaken using the stepwise function to find the model of best fit, selecting the best model using the difference between AIC scores. A log likelihood ratio test was used to test model significance against the null hypothesis. Equation 5.1, provides the model of best fit for substratum prediction.

$$Y_i = \beta_1, Distance_i + \beta_2, Depth_i + \beta_3,\ Max\ Current_i + \beta_4, Fetch_i + \beta_5, Geology_{ij} + \beta_6, Distance_i * + \beta_7, Depth_i + \beta_8, Fetch_i * \beta_9, Distance_i \qquad (5.1)$$

Where Y_i is the response variable and β are the modelled coefficientsfor sample i.

The multinomial model performance was tested on 25% of the dataset, by randomly splitting the combined 289 data points containing substratum classification and environmental variables into 217 samples (75%) to fit the data and 72 samples (25%) to validate the data. A confusion matrix and Area Under Curve (AUC) analysis and was run for the multiple class responses as outlined by Cullmann (2015) to assess the accuracy of the model. The confusion matrix was used as it allows visualisation of the performance of the model. Confusion matrices work by representing predicted classes against actual classes and so reporting the number of true positives (sensitivity) and true negatives (specificity) (Fielding & Bell 1997; Hosmer et al, 2013). AUC analyses provides a single measure of model performance by indicating the ability of a model to discriminate between the presence of substratum types, providing a score of how well the model discriminates between sensitivity (Fielding and Bell 1997; Hand and Till 2001; Leathwick et al. 2006). Both measures were used to help explain how well substrata were predicted. The threshold-independent Area

Under the Receiver Operating Characteristic (ROC) Curve was not implemented since it is deemed unsuitable for multiclass analysis as used in this analysis, as it measures the differences between two distributions (Hand and Till 2001). Interpretation of AUC range from: ≥ 0.9 = outstanding, ≥ 0.8 - < 0.9 = excellent, ≥ 0.7 - < 0.8 = acceptable, > 0.5 and < 0.7 = poor discrimination and ≤ 0.5 = no discrimination (Hosmer et al, 2013). In addition to overall model AUC and confusion matrix scores, correct classification for the individual substratum categories was also calculated to understand sensitivity of the model's predicted substratum types. "ROCR" R package (Sing et al, 2005) was used to understand how well each of the variables explained the presence of the modelled substrata.

To create a continuous map of the substrata, predictor variable values on a 400 and 600 m grid resolution were obtained within the South Arran NCMPA down to a depth of 50 m. This varied grid resolution was used since one of the main sources of predictor variables was a hydrodynamic model of tidal elevations and current velocities developed by Sabatino et al (In review). This hydrodynamic model was an implementation of the Finite-Volume Community Ocean Model (FVCOM) code, developed for simulating complex shelf and estuarine water circulation. FVCOM adopts an unstructured grid approach with triangular elements to better represent the coastline and provide increased resolution within the Firth of Clyde (Sabatino et al, in review).

The modelled maximum current speed and depth data were obtained from Sabatino et al's current model. Sabatino et al's depth data were originally sourced from General Bathymetric Chart of the Oceans (GEBCO) overlapped with SeaZone (version 1.1; GEBCO 2014; SeaZone 2014). The point data were imported into ArcGIS and converted into shapefiles to be able extract wave fetch, distance from coast and geological information values for the same coordinates. Depth down to 50 m was used to predict substratum distribution to improve model prediction accuracy and avoid spatial extrapolation issues (Reiss et al. 2015). The explanatory variables were then imported into R, standardised, and the multinomial model of best fit was used to predict substratum type. The resulting data frame containing substratum predictions was imported back into ArcGIS, converted into a point shapefile and validated with ground-truthed substratum types. Polygons were then created joining the ground-truthed and predicted substratum data points to create a smooth continuous surface for each substratum type across the predicted area (Figure 5.4.1).

5.3.4. Gadoid landscape calculations

Very little information exists on *in situ* juvenile gadoid movement patterns due to the difficulties in using acoustic tags on such small fish (< 10 cm) (Campana 2001; Chapter 4) and difficulties in tracking marked, recaptured individuals (Laurel et al. 2004; Olsen et al. 2004; Wright et al. 2006a). Approximations of the distance the juvenile gadoids move were estimated using the SBRUV data in addition to using existing literature on gadoid swimming speeds and home ranges. The two methods were used since fish behaviour around baited cameras is not usually classed as normal; whereas existing literature on juvenile gadoid movement is sparse and varied.

To calculate gadoid movement, their behaviour was first classified into four categories (Table 5.3.2). Only cruising behaviour - when the gadoids were moving in a straight line away from the bait, was taken into account to try and reduce bait bias. Cruising speed of ten individuals of each gadoid species of less than 20 cm were calculated (Appendix, Table G.1). The distance each gadoid could travel within an hour was then calculated (Appendix, Table G.2). Individuals of < 20 cm instead of < 15 cm as in the previous chapter were sampled since it was difficult to find and measure sufficient number of gadoids (particularly *M. merlangus*) undertaking the cruising behaviour. Current speed and direction were not taken into account.

Mark-recapture experiments undertaken by Grant & Brown (1998) showed that juvenile *G. morhua* remain relatively localised - within a few hundred meters, following pelagic larval stages through to their first winter. However, Laurel et al. (2004) demonstrated that such movement behaviour may be spatially and temporally variable and that *G. morhua* may demonstrate substratum specific movement behaviour. Existing studies on larger *G. morhua* (age 2+ / > 20 cm) (DATRAS 2015) have also demonstrated relatively limited movement (e.g. Løkkeborg et al. 2002; Cote et al. 2004; Wright et al. 2006a). Literature on *in situ M. aeglefinus* and *M. merlangus* movement behaviour is even scarcer. Distance calculations were therefore verified from laboratory literature on swimming speeds (e.g. Blaxter & Dickson 1959; Breen et al. 2004; Onsrud et al. 2005). From the combined distance and speed calculations and existing literature on gadoid speed and movement behaviour, three different radii created in ArcGIS around the gadoid point data collection were trialled. These included a radii of 500, 1000 and 1500 m (covering an area of 0.78, 3.14, 7.07 km^2).

Table 5.3.2 - Gadoid behaviour observed within the field of view of the SBRUV.

Behaviour observed	**Explanation**
Cruising	Gadoids observed moving at a steady speed away from the SBRUV, over a distance of >1.5 m for a period of time > 30 seconds.
Darting	Brief (< 3 seconds) short (< 0.5 m) period of movement to attack a con-specific or prey.
Turning	Frequent turning behaviour within a short period of time in an alert or feeding manner.
Feeding	Gadoids observed feeding attempting to feed on the bait, something in the water column or on the seafloor.

Using the predicted substratum point data, landscape heterogeneity was calculated using Hill numbers (Hill 1973). Substratum richness was the number of types of substrata within the radius, and evenness the frequencies of the substrata within the radius. Hill number N_1, N_2 and N_∞ (Hill 1973; Chapter 4), were used to understand how landscape heterogeneity affected gadoid relative abundance. The Hill numbers were used since they are inclusive of well-known indices (Jost 2015) and they are expressed as the effective number of species rather than probabilities as in Shannon-Wiener and Simpson’s (Maguran 2004; Jost 2006; Jost 2015). The extents of each substratum polygon within the radii were calculated in ArcGIS.

Fish counts were over-dispersed and therefore modelled with a NBN error distribution (log link function) using R package “glmmADMD” (Skaug et al, 2012) to enable random effects to be used. Random effects to account for varying location and data collection day were incorporated into the NBN models where significant. Zero inflated and non-linear patterns were explored but not significant. Starting with the full model, stepwise backwards selection, exploring for potential interactions, was used for model selection by AIC minimisation. Tukey tests were performed to test for differences between substratum categories using R package “multcomp” (Hothorn et al, 2008). Pearson’s residuals were compared between models fitting a model with the highest level of heteroscedasticity. Model selection was confirmed by log likelihood ratio tests against the null hypothesis.

Equation 5.2 provides the model structure used for juvenile gadoid MaxN landscape effects.

$$log(Y_i) = \beta_0 + \beta_1, X_{ij} + \beta_2, X_i + \beta_3, X_i \ldots\ldots + z_{ij} + t_{ij} \qquad (5.2)$$

where Y_i is gadoid MaxN, β are the coefficients, X_{ij}, categorical explanatory variables (substratum type) and X_i, continuous explanatory variables (landscape heterogeneity and or substratum extent), z_{ij} and t_{ij} the random effects (zone and grouped day of collection).

Spatial autocorrelation between gadoid SBRUV deployments was visually inspected using semivariograms of the residuals of the models fit as a function of distance, using R package “geoR” (Ribeiro & Diggle, 2015). Spatial autocorrelation is represented by increased semi-variance at shorter distances. No spatial autocorrelation was observed.

5.4. Results

5.4.1. Substratum distribution model

Evaluation of the multinomial model using the validation dataset indicated ‘excellent’ predictive power (AUC score of 0.88) and a confusion matrix correct classification of 61% (L = -131.21, d.f. = 32, *P* < 0.001; Appendix Table G.3). Correct classification for seagrass was 100%, followed by mud with 89%. Algal-gravel-pebble, sand and algal-boulder-cobble accurate classification received scores of 70%, 69% and 68% respectively. Predictor variable individual AUC scores were particularly strong for wave fetch and depth (0.71 and 0.69 respectively). Distance from coast and maximum current speed had AUC scores of 0.66 and 0.62. An AUC score for geology was not possible since categorical AUC values are not possible to evaluate.

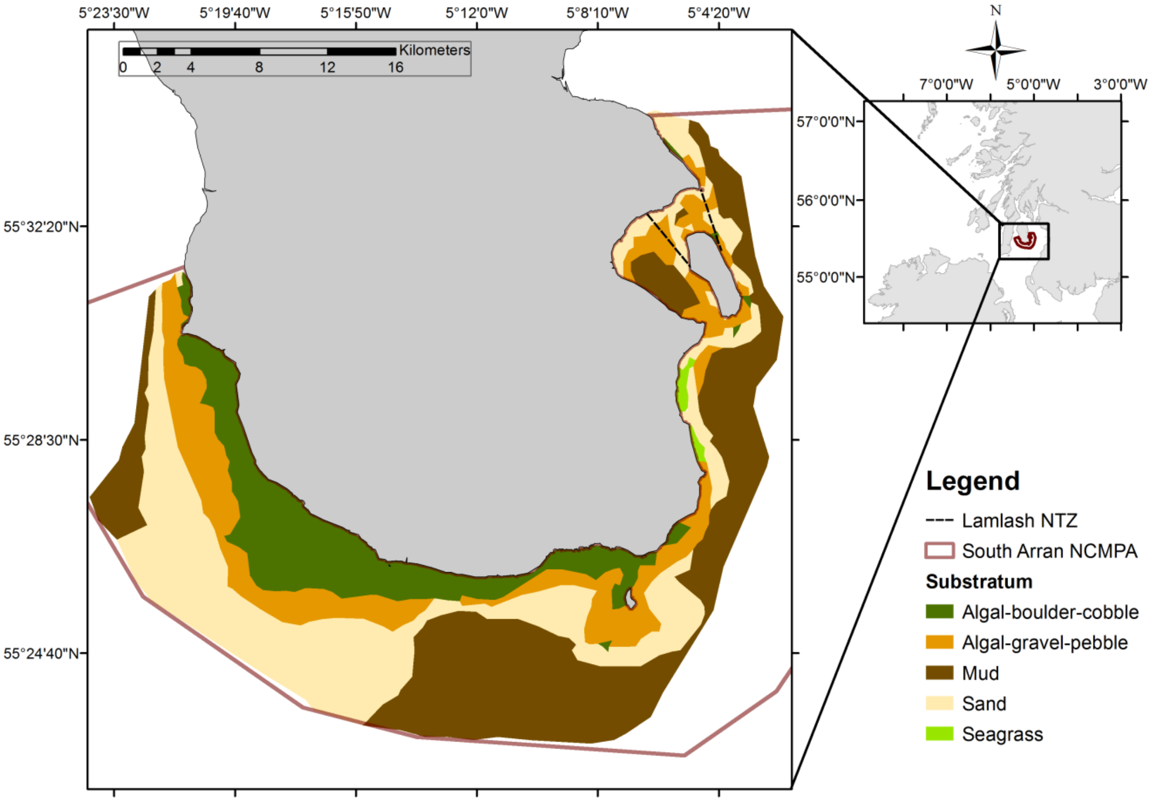

Figure 5.4.1 - Polygons of substratum types within South Arran NCMPA using substratum predictions in combination with ground-truthed data.

5.4.2. Landscape effects on *G. morhua*

G. morhua highest (mean and median) MaxN was observed over AGP substratum type with the lowest average MaxN observed over sand. Tukey test results between substrata demonstrated that significantly more G. morhua were observed in AGP than ABC (*P* < 0.01)(Figure 5.4.2; Appendix Table G.4 - Table G.5). No *G. morhua* were observed over mud, this category was therefore removed from analysis to improve logistic model convergence. A decrease in MaxN was observed with increasing N_{∞} (increase in dominance of substratum type) with a 1500 m radius (Figure 5.4.2; Figure 5.4.3; Appendix Table G.4). A significant decline in *G. morhua* was also observed between years with less *G.*

morhua in year two (2014) (L = -312.112, d.f. = 9, theta = 0.86, $P < 0.001$; Appendix Table G.4). Extent had no effect on *G. morhua* MaxN.

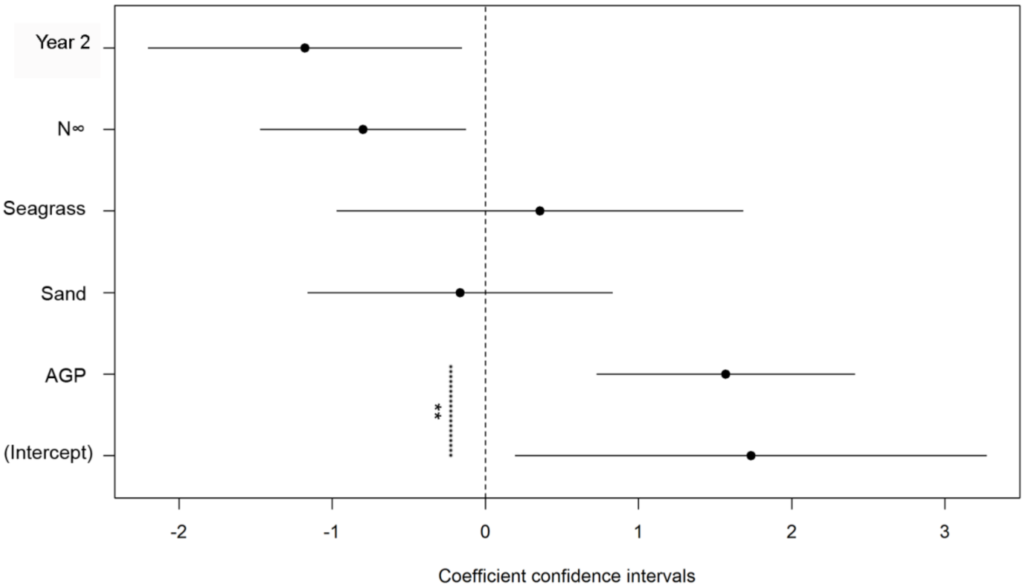

Figure 5.4.2 - Coefficient plot for model of best fit for *G. morhua* substratum landscape effects. Lines contain 95% confidence intervals for each of the explanatory variables. The verticle dashed line is the reference line enabling us to see which coefficients are significantly different from zero. The intercept represents ABC and Year 1 of data collection. Dashed vertical lines with * refers to Tukey test p value significance: ** $P < 0.01$).

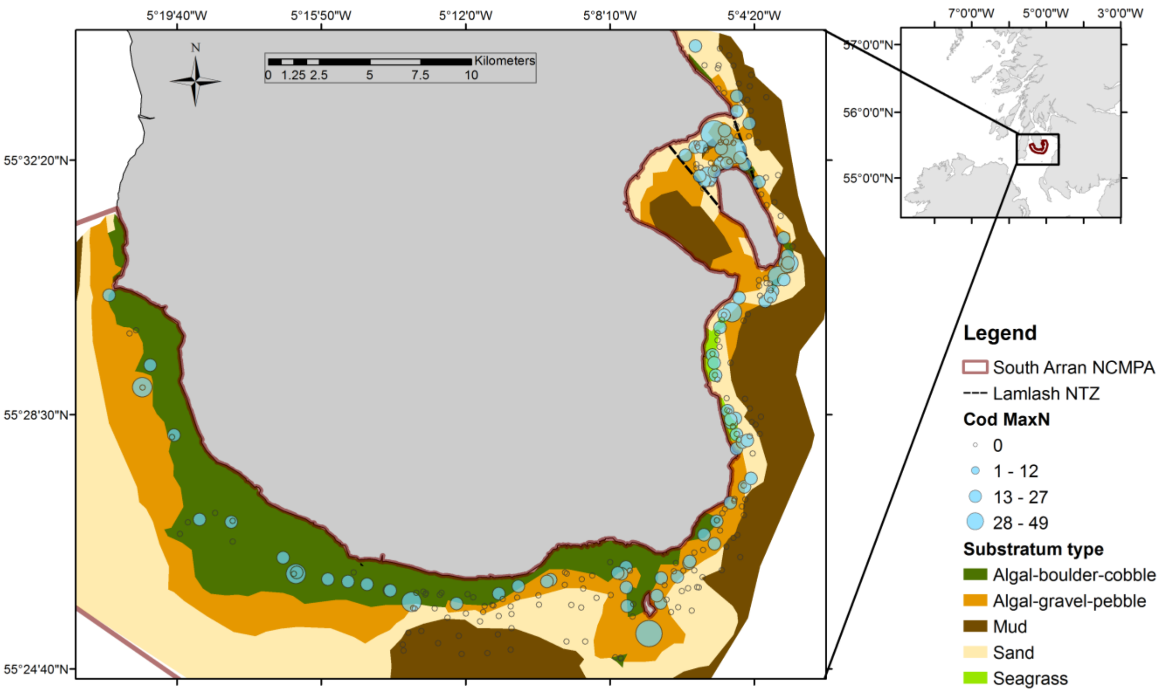

Figure 5.4.3 - Predicted substratum map with bubble plots showing the relative abundance of *G. morhua*

5.4.3. Landscape effects on *M. aeglefinus*

M. aeglefinus highest MaxN was observed over sand, followed by mud with lowest MaxN observed over ABC (Figure 5.4.4; Appendix Table G.6 and Table G.7). Significantly more *M. aeglefinus* were observed over sand and mud than ABC ($P < 0.001$). An increase in *M. aeglefinus* MaxN was observed with increasing substratum N_∞ and N_2 (tested independently) with a 1500 m radius (Figure 5.4.4 and

Figure **5.4.5**). When comparing models, N_∞ had a lower AIC (L = -282.749, d.f. = 9, theta = 0.88, $P < 0.001$; Appendix Table G.6).

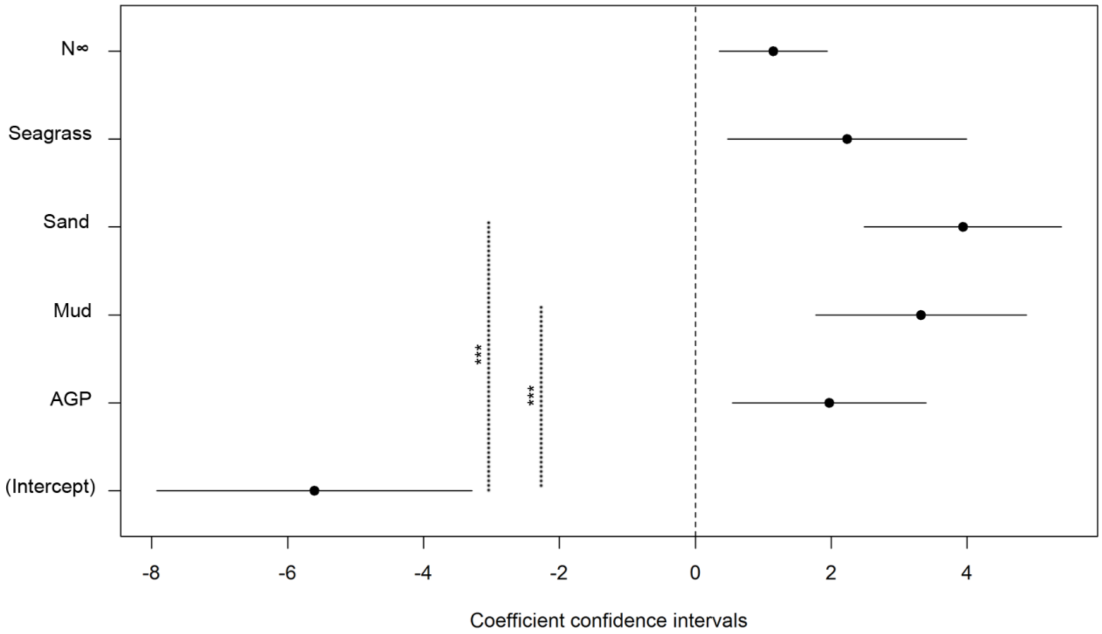

Figure 5.4.4 - Coefficient plot for model of best fit for *M. aeglefinus* substratum landscape effects. Lines contain 95% confidence intervals for each of the explanatory variables. The verticle dashed line is the reference line enabling us to see which coefficients are significantly different from zero. The intercept represents ABC. Dashed vertical lines with * refers to Tukey test *P* value significance: *** $P < 0.001$).

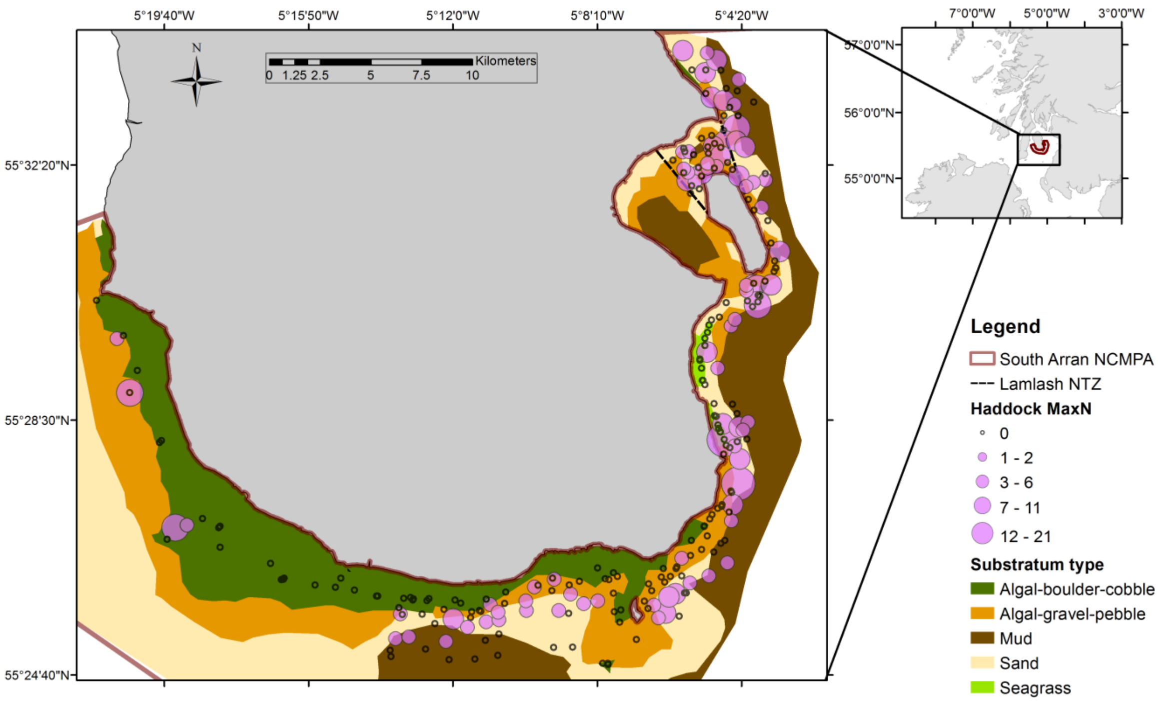

Figure 5.4.5 - Predicted substratum map with bubble plots showing the relative abundance of *M. aeglefinus*.

5.4.4. Landscape effects on *M. merlangus*

The highest MaxN (including mean and median) for *M. merlangus* was observed over sand with lowest MaxN observed over ABC and seagrass. A significantly higher *M. merlangus* MaxN was observed over mud, sand ($P < 0.001$) and AGP ($P < 0.05$) than ABC (Figure 5.4.6; Appendix Table G.8 and Table G.9). An increase in *M. merlangus* MaxN was observed with increasing substratum dominance (N_∞) at 1500 m and increasing substratum extent at 1500 m (L = -272.595, d.f. = 10, theta = 0.88, $P < 0.001$; Figure 5.4.6; Figure 5.4.7; Appendix Table G.8).

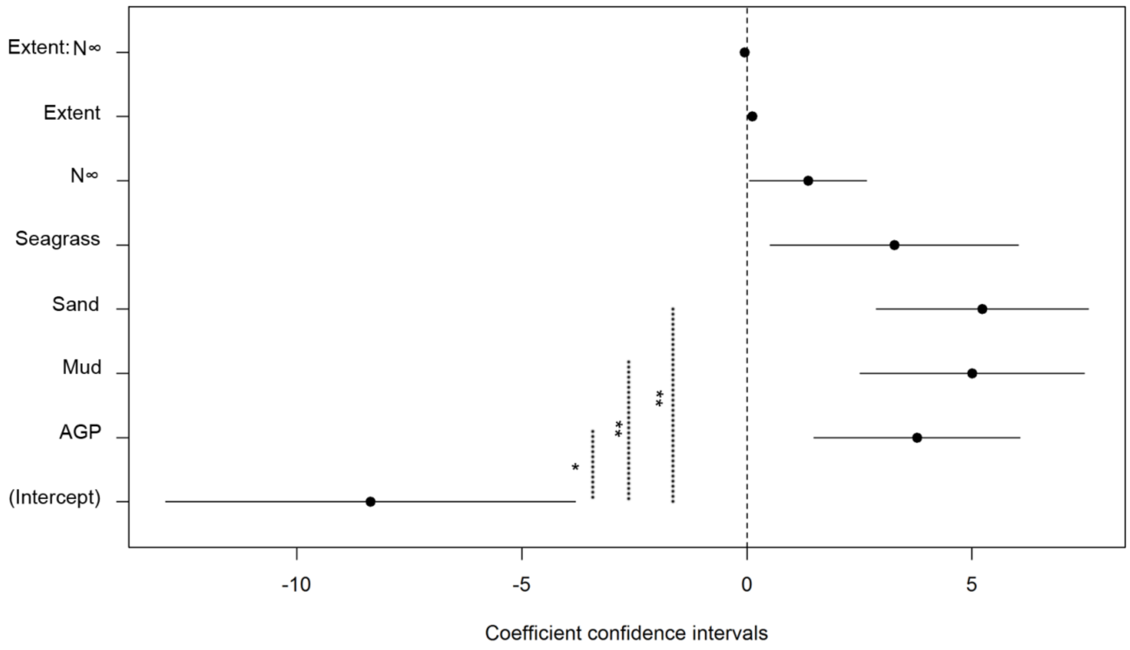

Figure 5.4.6 - Coefficient plot for model of best fit for *M. merlangus* substratum landscape effects. Lines contain 95% confidence intervals for each of the explanatory variables. The verticle dashed line is the reference line enabling us to see which coefficients are significantly different from zero. The intercept represents ABC. Dashed vertical lines with * refers to Tukey test *P* value significance: * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$).

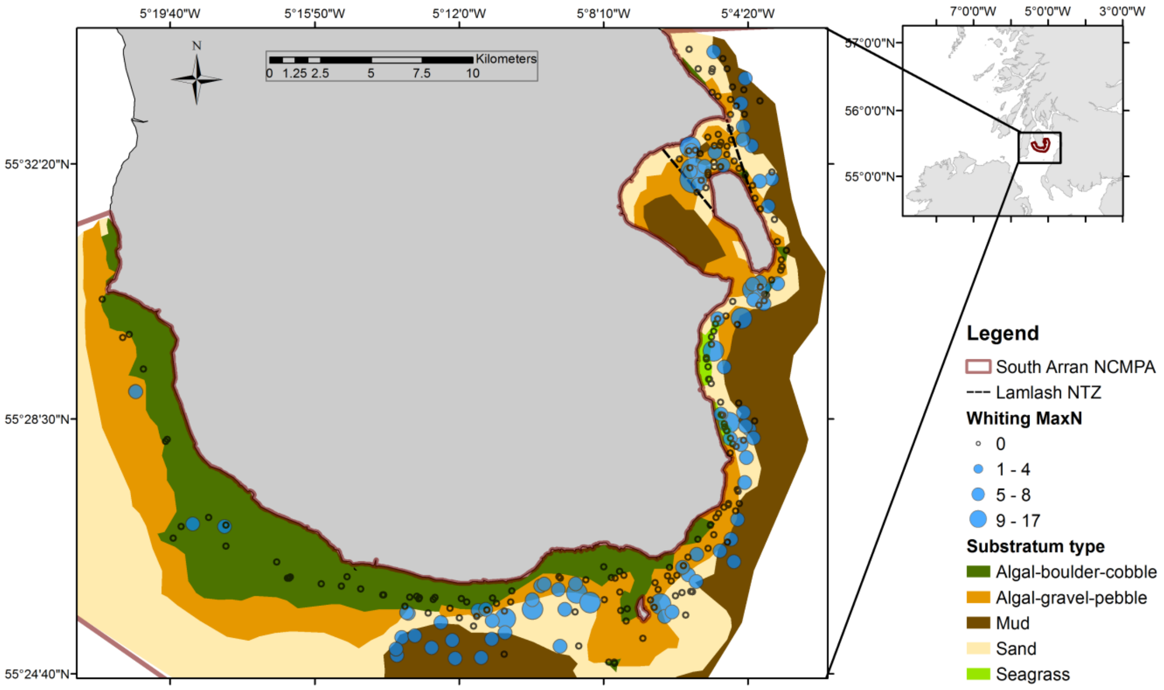

Figure 5.4.7 - Predicted substratum map with bubble plots showing the relative abundance of *M. merlangus*.

5.5. Discussion

This work had two main findings; firstly that a statistical model produced a map of substratum types within an area where ground-truthed data was collected. This is important because this method enabled a higher resolution and a more accurate map than previously existed to be obtained within the area (refer to Ross et al. 2009; McIntyre et al. 2012). The predictive model also enabled the drivers of substratum distribution to be explored and the resulting map could support South Arran NCMPA management and help with the design of monitoring. The second main finding was that diversity and extent of different substratum types, at ranges of up to 1500 m around gadoid data collection locations were related to the relative abundance of the gadoids. Such landscape effects on demersal fish has rarely been studied and could be beneficial to good fisheries management and MPA planning and monitoring (Sundblad et al. 2014, Vasconcelos et al. 2014; Reiss et al. 2015).

Overall the multinomial model used for substratum prediction performed well. Depth and wave fetch had the strongest relationships with the substratum types in comparison with the other predictor variables. Depth affects many species and is commonly used as a surrogate stressor for light, temperature and benthic shear stress from ocean swell (Holmes et al. 2008; Reiss et al. 2015). Wave fetch will also have an effect on benthic shear stress and light attenuation through varying levels of exposure and turbidity (Edwards 1980; Burrows 2012; Schubert et al. 2015). Maximum current speed will have acted as a surrogate for benthic shear stress in addition to providing actual point-specific information of hydrodynamic regimes within the area (Reiss et al. 2015). Depth, wave fetch and current are also proxies for a range of factors which affect demersal fish such as food availability and shear stress (Chapter 4). The geodiversity around Arran includes a wide variety of rock types and formations which partly arise from a geological fault bringing together contrasting geological features (Ross et al. 2009; COAST 2012; BGS 2015). The two main geological rock formations found within South Arran NCMPA include Permian rock (formed 286-248 million years ago), predominantly made up of sand stone and limestone, and Triassic rock (formed 248-213 million years ago) predominantly made up of siltstone and mudstone (EDINA, 2015). Together the above environmental variables (depth, wave fetch, distance from coast, maximum current speed and the underlying geology) enabled an accurate, high resolution map of substratum types to be predicted within South Arran NCMPA.

Although confusion matrix correct classification were only “acceptable” (Hosmer et al, 2013), confusion matrices can make the often erroneous assumption that the costs of the different kinds of misclassification are equal (Fielding and Bell 1997; Hand and Till 2001). Confusion matrices can also lead to unreliable metrics of the performance of classifiers if the dataset is unbalanced which was the case for the number of different substratum categories collected (Fielding & Bell 1997; Hand & Till, 2001). Individual substratum correct classification showed that seagrass and mud substrata had the highest classification accuracy. Seagrass only grows in shallow areas where sufficient light can penetrate, and mud only existed within deeper or more sheltered areas (Schubert et al. 2015; Figure 5.4.1). Algal-boulder-cobble substratum type also occurs at shallower depths (< 20 m) and more exposed areas composed of larger sediment grain sizes where the macro-algae can grow and anchor itself (Holmes et al. 2008; Burrows 2012; Christie et al. 2009). Algal-gravel-pebble substratum type largely consisted of varying percentages of maerl, which together with red algae requires a lesser degree of light penetration (≤ 30 m) (Hall-Spencer et al. 2003).

A maximum of approximately 30% live maerl was found within any SBRUV deployment. This is most likely due to heavy anthropogenic impacts from fishing activity (Hall-Spencer et al. 2003) which took place around Arran from the early 19th century (Thurstan and Roberts 2010). The combined factors of degraded maerl quality and displacement, may have led to reduced prediction accuracy for algal-gravel-pebble substratum. Sand substratum can be found within a broad range of environmental conditions which may have led to sand having a lower prediction accuracy (Reiss et al. 2011).

The predicted substratum map demonstrates how, from ground-truthed data and a range of environmental predictor variables, high resolution maps can be modelled saving on expensive and resource intensive acoustic methods. To increase accuracy of substratum prediction more accurate depth data would have been beneficial. Depth inaccuracies were observed using the modelled

SeaZone and GEBCO topographic data. The latter will most likely be due to the high variability in depth around the south of Arran.

Using the predicted full coverage map, seabed landscape effects on gadoid relative abundance were modelled at ranges relevant to the movement behaviour of the gadoids studied. This is particularly important since seabed types have been observed to have important effects on the abundance and even survival of juvenile gadoids (e.g. Tupper & Boutilier 1995a; Laurel et al. 2007; Lough 2010). Furthermore, experimental studies have shown that substratum patch size can affect the behaviour and predation rate of juvenile *G. morhua* (Laurel et al. 2003b, Ryan et al. 2012). *In situ* landscape effects on commercially important gadoid fish have however rarely been explored. Other studies measuring landscape heterogeneity effects on species using the use of diversity entropies include Freemark & Merriam (1986) and Brown (2003). Freemark & Merriam (1986) measured plant heterogeneity as an index of Shannon within forests. Brown (2003) measured substratum heterogeneity within a stream using a range of diversity entropies. Diversity entropies are, however, harder to compare against each other since they not are normalised as Hill diversity indices are. Moore et al. (2011) also explored landscape heterogeneity on demersal reef fish distribution and relative abundance within a 200 m radius of SBRUV deployments. From hydroacoustic surveys, Moore et al, (2011) explored 23 indices of landscape heterogeneity were explored including patch density, shape, extent and Shannon's diversity index.

In conjunction with results from Chapter 4 on habitat component association and behavioural observations, distinct niche occupation between *G. morhua* and that of *M. aeglefinus* and *M. merlangus* appears evident. *G. morhua* MaxN was observed in higher relative abundance over algal-gravel-pebble, whereas *M. aeglefinus* and *M. merlangus* were observed in higher relative abundance over sand and mud. Possible reasons for gadoid substratum association are outlined within Chapter 4. *G. morhua* were also on average significantly smaller than the *M. aeglefinus* or *M. merlangus* (Chapter 4). Smaller fish are not only at a competitive disadvantage but more vulnerable to predation (Tupper and Boutilier 1995b; Juanes 2007). Few demersal species are associated to a single seabed type, but instead use a combination of substrata according to foraging, shelter and tidal behaviours (Gorman et al. 2009; Nagelkerken et al. 2013). For example, Tupper and Boultier (1995a) found juvenile *G. morhua* to be associated to a range of substrata from sand, seagrass to rocky reefs. Growth rates were also observed to vary between substrata. As proposed by Nagelkerken et al. (2013), attempts to identify fish nursery areas are frequently static processes identifying individual homogeneous seabed types. However, seascapes are often dynamic and varied and the focal species may also undergo ontogenetic shifts as a result of changing resource needs (Laurel et al. 2009; Nagelkerken et al. 2013; Grol et al. 2014; Chapter 4). Such behaviour (ontogenetic shifts in resource and available substrata), may have explained why all three gadoids were observed over the range of substratum types.

A decrease in *G. morhua* relative abundance was observed with increasing N_∞ (Figure 5.4.2). This trend indicates that juvenile *G. morhua* are associated with more heterogeneous landscapes. However, for *M. aeglefinus* an increase in relative abundance was observed with increasing N_2 and N_∞. N_2 and N_∞ infinity are similar indices, particularly with a richness of five since Simpson’s index is sensitive to the abundance of the more abundant species in the sample and can therefore be regarded as a measure of dominance (Hill 1973; Buckland et al. 2005). *M. merlangus* were also observed in higher relative abundance with increasing substratum dominance (N_∞) but in combination with substratum extent. The N_∞ dominance indices might have been more significant than N_2 or N_1 for all three species since these other two Hill numbers are more sensitive to varying sample size (Soetaert and Heip 1990; Buckland et al. 2005, 2011).

The increase in *G. morhua* observed with increasing landscape heterogeneity may enable *G. morhua* to access areas with possibly increased food availability and areas with sufficient refugia (Kamenos et al. 2003; Moore et al. 2011; Nagelkerken et al. 2013). An experimental study undertaken by Laurel et al. (2003b) demonstrated that juvenile *G. morhua* seem to differentiate between substratum types, selecting areas where growth and survival were highest. Additionally, substratum type boundaries are thought to be important foraging and refuge areas for fish depending on the extent of the patches (Laurel et al. 2003b; Gorman et al. 2009). The increase in *M. aeglefinus* and *M. merlangus* observed with increasing substratum dominance, and extent for *M. merlangus,* may be an indication of how these gadoids are better adapted to prey found within sand and mud substrata.

Demain et al. (2011) observed greatest similarity between juvenile *M. aeglefinus* and *M. merlangus*, which concur with the results observed here. Demain et al. (2011) also observed an overlap between small to medium *G. morhua* and larger *M. merlangus* which may be disadvantageous to *G. morhua* as larger individuals would be expected to be more efficient predators (Demain et al. 2011). Juvenile *G. morhua* have previously been observed to be prey themselves to larger *M. merlangus* (Temming et al. 2007). The size differences between the *G. morhua* and, *M. aeglefinus* and *M. merlangus* (Chapter 4) may explain the differentiation between the gadoid distribution differences. More rugose substrata relevant to the size of *G. morhua* observed and more heterogeneous landscapes may provide smaller *G. morhua* with more prey in addition to refuge from predators (Brown 2003; Laurel et al. 2003b). Whereas, larger *M. aeglefinus* and *M. merlangus* prey may occur in greater abundance in the deeper sand and mud substrata, where these two gadoids were observed in greater relative abundance. Additionally, their increased size and mobility (Blaxter and Dickson 1959) may enable them to travel further in search of preferred prey as well as avoid predation.

Trialling of larger radii for all three species may have led to increased understanding of wider landscape effects on gadoid relative abundance. Juvenile gadoid (> age-2) movement data is limited for all three species. However, movement is likely to be greater for *G. morhua* than previously observed by Grant & Brown (1998) and subject to substratum type (Lindholm et al. 2001; Laurel et al. 2003b). A study by Gorman et al. (2009) found that predation risk of *G. morhua* was a parabolic function of patch size up to 80 m^2 with greatest risk at intermediate patch size. Only the larger radius of 1500 m may have been significant since the gadoids are relative mobile within short periods of time. In addition, the substrata around the south of Arran can be quite varied, and may lead to possibly increased movement (Lindholm et al. 2001; Laurel et al. 2003b).

5.5.1. Considerations, management and future work

Predictive substratum mapping provided a cost effective method to understand landscape effects on juvenile gadoid fish (Howell et al. 2011, Schubert et al. 2015). If combined with climate change scenarios, distribution modelling may be able to provide estimations of protection efficiency for MPAs (Beyer et al. 2010;

Reiss et al. 2015). Further refinements to this modelling approach would have been to trial other modelling methods such as Multivariate Adaptive Regression Splines (MARS), Maximum Entropy or Random Forest, since comparative approaches have shown that models can vary (Elith et al. 2006; Phillips et al. 2006; Reiss et al. 2011, 2015). A multinomial model was used due to the multiple class nature of substratum presence absence and since general linear models have a strong statistical foundation and ability to model ecological relationships realistically (Barry and Elith 2006; Elith et al. 2006). Other predictor variables such as light and wave action were not incorporated into the model since these data were not available at the appropriate resolution. The aforementioned predictor variables may also have been collinear with depth and wave fetch. .

Classifying substrata into categories, can lead to over simplification of actual seabed morphology and therefore difficulties in understanding its role for demersal species (Gaillard et al. 2010). However, quantifying substratum rugosity on a continuous scale as per McCormick (1994); Bartholomew et al. (2000) and Wilding et al. (2007) was not possible. Future considerations of structural rugosity could be advantageous to understand how substratum rugosity affects fish relative to their size. To take into account substratum rugosity on a continuous scale, several scales may need to be considered relative to the size of the study species (Chapter 2). Additionally a three-dimensional photographic mapping technique would be advantageous to take into account the multiple aspects of rugosity (Sebens 1991, Gratwicke & Speight 2005; Du Preez 2015). If substratum rugosity were possible to quantify on a continuous scale and combined with anthropogenic impacts, a better understanding of substratum patch and edge effects could be possible which are currently not well understood. The latter would be as a result of understanding spatial scales of substrata in relation to the species of interest, in addition to seabed's quality (Gorman et al. 2009 Gaillard et al. 2010).

5.6. Conclusion

The use of a range environmental variables enabled the prediction of substrata and the creation of a fine scale map. This fine scale map demonstrates how detailed maps are possible with simple field tools and often readily available data e.g. depth, geological information, distance from coast, etc. and should be used more widely. This study also demonstrates the importance of incorporating measures of landscape analysis in demersal fish distribution given that landscape heterogeneity had differing effects on the gadoids studied here. The different gadoid species studied here responded to landscape heterogeneity differently, demonstrating that both the diversity of substrata and contiguous substrata can be of benefit or disadvantageous to different species. The methods trialled in this study could be applied on a larger scale for the selection of areas for stock improvement. More detailed research into juvenile gadoid survival is recommended to better understand the importance of substrata for these gadoid fish for fisheries management and conservation prioritisation. The protection of important substrata could eliminate bottle neck recruitment which may be occurring.

Chapter 6. General discussion

With improvements in underwater technology, developing a better understanding of our marine environment is becoming increasingly possible and higher resolution data can be collected. The use of high-definition stereo-video imagery has provided *in situ*, fine-scale data on abundance, size, behaviour and the ecology of marine wild life that would not be possible using static and mobile gear or single camera techniques. The techniques used in this thesis have enabled progress towards an understanding of juvenile gadoid habitat within coastal waters. Notwithstanding, there is still a need for improved knowledge of the ecology of fish, their environment and factors affecting their survival, to be able to improve stocks.

The overall aim of this project was to 1) improve understanding of juvenile gadoid habitat. 2) Trial use of stereo-video imagery techniques in temperate waters to collect fish abundance, size and benthos data. 3) Collect baseline data within a recently designated MPA, and contribute to management and monitoring currently being discussed for demersal fish.

6.1. Exploring the role of coastal environments for juvenile gadoid

The primary aim of this thesis was to improve our knowledge of juvenile gadoid habitat requirements. It is hoped that this could help support the establishment of management measures to try to contribute to stock regeneration. While detailed studies have been carried out on juvenile gadoids in Canada, the USA and Scandinavian countries (Bailey et al. 2011), there was a set of major information gaps for UK waters. The present study only uses a single stretch of coastline in the Firth of Clyde. However, its variable geology, topographic exposure, and aspect made it an excellent model system in which to test these ideas.

When commencing this project it became clear that there were many confusions, ambiguities and inconsistencies in the way habitats and habitat-related terminology was described. Reviewing existing literature and terminology related to habitat concepts and assessing their application (Chapter 2), improved understanding of how to investigate juvenile gadoid habitat more holistically (Chapters 3 to 5).

Many studies of juvenile gadoid ‘habitat’ only consider a few variables such as substratum type and depth, rather than considering the range of abiotic and biotic characteristics which may affect fish abundance and distribution. In addition, few studies have looked at wider landscape effects on fish. This could be a result of the widespread understanding that the term ‘habitat’ only referring to seabed types, as opposed to the range of abiotic and biotic variables and the wider landscape affecting the spatial pattern of species.

Upon exploring the data to identify the habitat of juvenile gadoids, distinct niche differentiation between *G. morhua* and that of *M. aeglefinus* and *M. merlangus* was evident, since different relative abundance in substratum type, depth, water column occupancy, landscape heterogeneity, bait attraction and growth rates were observed (Allan 2014; Chapter 4 and 5). These observations have important implications for the management of these gadoid fish given the species-specific spatial measures that would be required.

Interestingly, all three species were found in higher relative abundance with increasing benthopelagic diversity (Chapter 4). Although a seemingly obvious result, species diversity effects on gadoid abundance have rarely been studied. Loss of biodiversity causes imbalances to community structures and ecosystem functioning, exacerbating extinction rates (Hammer et al. 1993; Dobson et al. 1997). The increased relative abundance with higher benthopelagic diversity is therefore an important driver for future ecosystem management considerations to protect and recover seabeds for commercially valuable species. A link which has not yet been made within the MSFD (Chapter 4).

In the three gadoids studied, a decline in relative abundance was observed over the period of data collection following recruitment (Chapter 3 and 4). This was a surprise since an increase in abundance is expected given pulse recruitment of juveniles to coastal areas is supposed to take place from June to end of September (Ings et al. 2008; McEvoy & McEvoy, 1992). It would be expected that pulse recruitment would lead to increased abundance at least until pulse recruitment ended. The observed decline in abundance may indicate that a density-dependent survival bottle neck exists in which good quality habitat is limiting (Svåsand et al. 2000; Fodrie et al. 2009). Although the mechanisms for the timing were not investigated in this thesis, collecting data from June to September enabled an indication of pulse recruitment to be observed through the size ranges of gadoids over the period of data collection. Discerning habitat components of relevance to juvenile gadoids in addition to timing of recruitment to coastal areas provides useful information on when to protect relevant coastal areas from anthropogenic pressures.

The predictive substratum mapping permitted landscape effects on juvenile gadoids to be observed for the first time (Chapter 5) and is one of only a small number of studies to have investigated landscape effects on fish. The different response of *G. morhua* in comparison to *M. aeglefinus* and *M. merlangus,* demonstrates how associated substrata, a diversity of substrata and contiguous substrata, can be of benefit to these gadoids. Gadoids are not currently protected under the present network of UK MPAs. Nonetheless, MPAs have been designated around the UK to protect seabed types and species of conservation importance (JNCC 2016), which may be of benefit to gadoid species. Further, the current UK MPA mechanism does not prioritise heterogeneous landscapes which are of benefit to *G. morhua*.

Large areas of the Firth of Clyde are made up of homogenous substratum types (largely mud and sandy substrata)(Ross et al. 2009; McIntyre et al. 2012). The higher relative abundance of *M. merlangus* and *M. aeglefinus* with increasing substratum dominance (particularly sand and mud), may partly explain why these two juvenile gadoids (especially *M. merlangus*) are more abundant in the Firth of Clyde (Heath and Speirs 2012).

Collecting data in the same location (within South Arran NCMPA), not only enabled more data to be collected to strengthen the understanding of the results against environmental variability (Chapter 4), but also permitted relative abundance differences between years to be examined. The latter results revealed density dependent selection of *G. morhua* for algal-gravel-pebble to be observed as opposed to an association, given the large difference in relative abundance between years (Chapter 4). A selection for sand substrata was also observed for *M. aeglefinus* and *M. merlangus* (Chapter 4).

It is recommended that more studies should be undertaken looking at how a variety of abiotic and biotic factors affect fish of commercial importance. Methods used in Chapters 3 and 4 could also be trialled during night hours to improve understanding of juvenile gadoid nocturnal behaviour. Improved knowledge of fish habitat during their various ontogenetic stages could facilitate more focused and better planned protection measures to be put in place. As previously highlighted, a number of fisheries closure exist around the UK to protect gadoids (e.g. Firth of Clyde seasonal spawning closure and the “windsock” closure north of Scotland). However, little improvements in stocks have been observed (Jaworski & Penny, 2009; Clarke et al. 2015). It is unlikely that improvements will be observed for many years given the variety of pressures facing fish (e.g. predation, direct and indirect capture from fishing activities, degradation of habitat quality, effects from climate change, etc.) (Chapter 1). However, being able to understand factors affecting their abundance, distribution and length, using methods undertaken in this thesis would enable better planned area closures to be put in place. The latter would be through understanding habitat variables affecting the abundance and distribution of gadoids, during critical stages of their ontogeny that determine cohort size (Auster et al. 1996; Able 1999; Chapter 2).

6.2. Trialling stereo-video photogrammetric methods to study juvenile gadoids in temperate waters

The second main aim of this thesis was to trial stereo-video photogrammetric techniques in temperate waters (Chapters 3 and 4). Use of such methods to explore fish habitat (as per reviewed in Chapter 2) have rarely taken place and SBRUV deployments has only recently been trialled in the UK (Unsworth et al. 2014). Both stereo-video SCUBA transects and SBRUV methods provided useful data to understand juvenile gadoid association with benthos. Additionally, both methods showed similar results with regard to *G. morhua* substrata association. *M. aeglefinus* and *M. merlangus* could not be compared due to the low frequency of observations in the year in which stereo-video SCUBA transects were used. The latter may be a result of shallow depths surveyed using SV-SCUBA transects, or the effects from diver presence. SBRUV surveys were the preferred method in the second year of data collection due to their ability to collect an increased number of deployments with less human resource in the same period of time. In addition, use of SBRUV deployments avoids decompression and depth constraints imposed by SCUBA techniques. These results observed are in line with Langlois et al. (2010).

Baited cameras are criticised as being biased towards predatory and scavenging species (Lowry et al. 2012; Dunlop et al. 2015). The latter was not tested for in this thesis, but was not considered a problem since the gadoids studied within this thesis are predatory, and large piscivores (> 25 cm) were rarely observed and generally not attracted to the cameras. It was observed that *M. Merlangus* was more attracted to the bait, with *G. morhua* the least attracted (Allan 2014; Chapter 4). This attraction did not affect *G. morhua* observations since they were still able to be observed within the field of view of the cameras. Statistical analysis between stereo-video SCUBA transects and SBRUV deployments was not undertaken. The latter was as a result of the limited SCUBA dataset collected, and since SBRUV deployments and SCUBA transects were rarely undertaken in the same location within the same time period (within a few weeks) due to logistical constraints (weather and divers support). In addition, it is difficult to compare such techniques quantitatively (Langlois et al. 2010) when the area species are drawn to by the bait is unknown as a result of unknown plume dispersal.

The use of baited cameras has also been criticised since they do not measure the absolute abundance of species due to the inability to calculate how far fish travelled to the cameras (Dunlop et al. 2015). Dunlop et al. (2015) developed a model to measure absolute abundance of species in shallow waters using BRUV systems, applying information from current speeds and existing published literature on species swimming/movement speeds. However, the model developed by Dunlop et al. (2015) did not take into account the fluid dynamics of bait plume dispersal. With the development of such a combined model, including juvenile gadoid speed calculations from the stereo-video cameras, absolute abundance could be calculated for juvenile gadoids.

6.3. MPA and commercial fish management and monitoring implications

The present thesis was part funded by Marine Scotland Science (MSS) and Scottish Natural Heritage (SNH), as a source of research contributing to the discussion of possible management plans within the Firth of Clyde (Scottish Government 2015; Clyde Forum 2016). Results from chapters 3 and 4 provided baseline ground-truthed data of benthos and fish abundance around South Arran NCMPA which fed into and could influence future management measure discussions within the MPA. The results from chapter 5 provided an up to date full coverage map of substrata within the MPA down to a depth of 50 m. Results from chapter 3 to 5 also demonstrated habitat variables that should be taken into consideration when considering juvenile gadoid habitat protection measures i.e. substratum type and heterogeneity, benthopelagic diversity, wave fetch and depth. Using this information on habitat variables where a higher abundance of juveniles were observed within, a carefully planned area closure, restricting benthic impacts and taking into account possible negative effects from displacement activities, could be implemented. A BACI survey could then be used to investigate the effects of the area closure on gadoid fish. The latter would help understand whether improvements to the quality of the seabed have an impact on gadoid abundance.

In addition, the results from the present thesis have demonstrated how *G. morhua* are more vulnerable to anthropogenic pressures than *M. aeglefinus* and *M. merlangus*. The latter is as a result of the smaller size, later arrival and slower growth of *G. morhua* relative to *M. aeglefinus* and *M. merlangus*. In addition *G. morhua* were found to occupy shallower substrata more vulnerable to climate change effects (seagrass and maerl) (Hiscock et al 2004) and dredging for which such substrata and their associated biota are more vulnerable to anthropogenic impacts (Collie et al. 2000; Hiddink et al. 2006; Kaiser et al. 2006).

The stereo-video imagery methods trialled here could be used as a fish or benthos monitoring technique on a wider scale in spatially restricted or sensitive seabed types around the UK. Other fish and benthos monitoring techniques that could be trialled would be the use of an AUV (Clarke et al. 2007; Morris et al. 2014). Use of AUVs permits precise area coverage to be calculated, in addition to being able to cover much larger areas without depth, time constraints imposed by SCUBA techniques (Clarke et al. 2007). AUVs also enable height above the seabed and the angle of the cameras to be controlled more precisely which could facilitate automated imagery processing (Girdhar 2014). Nonetheless installing a stereo-video system on an AUV has not yet taken place. In addition, applying a forward facing oblique view on AUVs which is useful for fish identification, understanding of the wider seabed, and controlling for more rugose topography is not currently possible using AUVs. The use of semi-closed or closed circuit rebreather apparatus, reducing noise disturbance from bubble exhalations could be another option (Sayer and Poonian 2007).

6.4. Recommendations

Despite considerable advances in understanding juvenile gadoid habitat through the use of imaging technology, there is plenty of scope for future improvement. It is still not possible to state whether any habitat component is important to the gadoid species studied. A key investigation to understand the importance of a habitat component is whether the use of particular substrata (or combinations thereof) results in higher survival, faster growth or reduced mortality.

An area of particular value to forward this thesis would therefore be to understand habitat components affecting the survival of juvenile gadoids through their first year to recruitment. Due to the difficulties in tagging such small juveniles a modelling approach would most likely be the best method to forward knowledge of juvenile gadoid survival (e.g. Campana et al. 1989; Myers and Cadigan 1993; Bjørnstad et al. 1999; Persson et al. 2012). An infield approximation of habitat component importance would be through experimental studies. For example, changes to the availability or quality of the environment could be used to understand changes in relative abundance between areas or through the use of tethering techniques (e.g. Laurel et al. 2003a; Gorman et al. 2009; Warren et al. 2010). Although not ideal such a method would enable the possibility to quantify habitat quality (Box 2.3.1, Chapter 2) of juveniles to support recruitment (Gibson 1994; Gaillard et al. 2010).

Over the course of the two years of data collection, and through looking at ICES recruitment data on gadoids, it is evident that fish populations fluctuate significantly between years (DATRAS 2015; Chapter 4). Long term monitoring is therefore highly recommended in order to gauge whether any improvement in stock is being observed and identify possible causes for recruitment success. Applying the techniques used within this thesis on a larger scale is recommended. Mapped coastal areas could be randomly selected within the Firth of Clyde, and even west coast of Scotland within similar depth ranges, with a range of substratum types. Monitoring juvenile gadoid abundance, distribution and benthopelagic diversity would then be required over a minimum of five years with at least two years prior to area closure. Gadoid length measurements would also be of benefit as an indicator for gadoid health (growth) (Borja et al. 2013; Probst et al. 2013), if monitoring within each area took place over a similar time frame (i.e. beginning of July - to the end of September). In Norway, *G. morhua* are known to remain in coastal waters and have not had selective pressure from trawling (within 12 nm) for over a 100 year (Hermansen et al. 2012). The techniques trialled in this thesis could therefore also be applied in Norwegian coastal water in order to investigate potential differences in juvenile gadoid habitat component association.

MPAs in the UK have largely been designated for specific features of conservation importance (JNCC 2016). However, managed areas with reduced benthic impact could improve benthopelagic diversity, benefiting juvenile gadoids. There is also a need for better planned and managed fisheries closures (Hilborn et al. 2004b). The methods used in this thesis (understanding habitat component association and substratum mapping for landscape effects) could be applied to establish or adapt fisheries closures to help improve stocks. For example identifying areas where higher fish abundance occurs, understanding the abiotic and biotic variable ranges within these areas and applying a BACI survey, are all actions that can help support the development of targeted management measures.

There are plenty of other fish stocks that have faced a similar situation to gadoids in the Firth of Clyde throughout the world e.g. Orange roughy (*Hoplostethus atlanticus* Collett, 1889) and Greenland halibut (*Reinhardtius hippoglossoides* Walbaum, 1792) (Moore et al. 2016). Trialling the methodologies undertaken within this thesis (use of SBRUV surveys and stereo-video SCUBA transects to identify fish habitat), and even trialling the use of AUVs or rebreather apparatus on other fish stocks to forward understanding of their habitat at the various stages in their ontogeny would be of value.

6.5. Concluding remarks

Despite the known importance of understanding species distribution and abundance, in particular commercially important species, there is a surprisingly large amount that is not known in the field of marine fish habitat. Research presented in this thesis enabled juvenile gadoid behaviour, distribution and sizes to be measured, alongside information about the benthos and the landscape. Comprehending fish habitat is increasingly important, especially given the increasing anthropogenic pressures exerted on the marine environment and increasing emphasis to put in place ecosystem-based management.

This thesis provides novel data on juvenile gadoid habitat and monitoring techniques in temperate waters. Improvements in the understanding of juvenile gadoid habitat has been made, and stereo-video SBRUV and SCUBA transects have been trialled to understand gadoid habitat for the first time in temperate waters. This work highlights the role of benthic diversity in supporting commercial fish stocks, at scales of meters to km. These concepts need further testing over a wider range of coastal areas, but if similar results are found they will have a vital role in the future management of fish populations.

Appendix A: Juvenile gadoids species investigated

Figure A.1 provides visual images of the three gadoid species observed in their juvenile form.

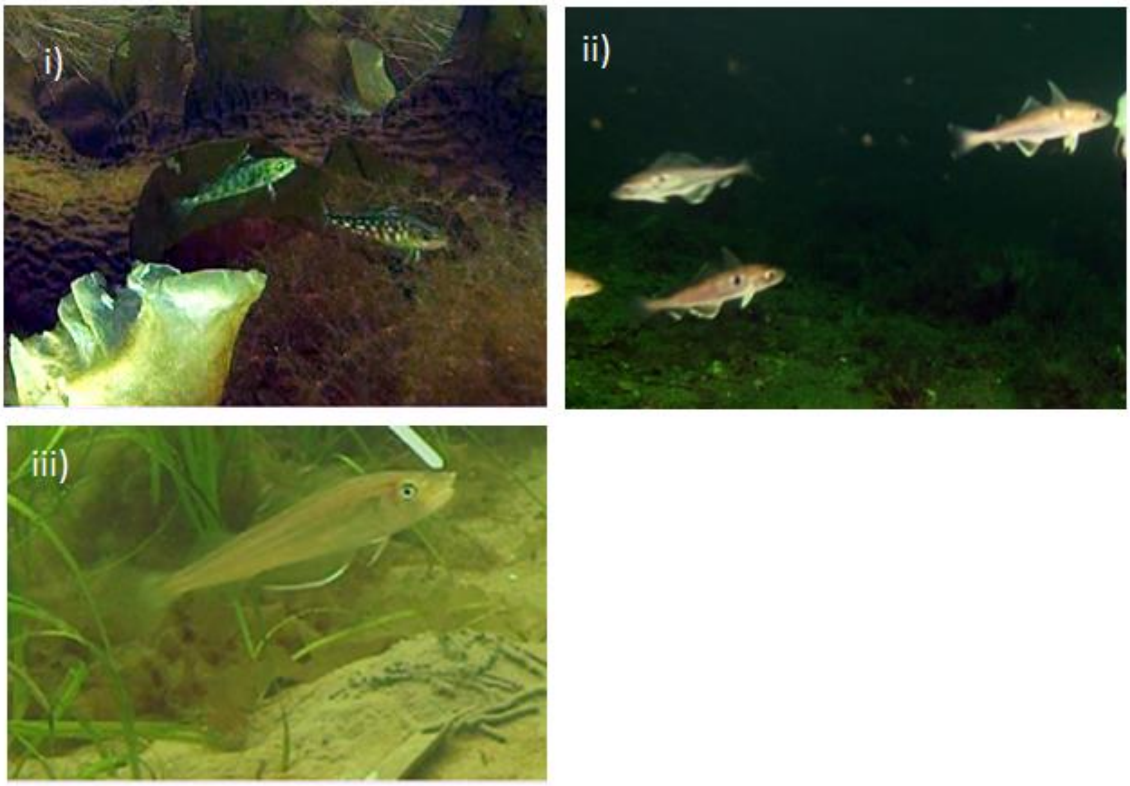

Figure A.1- Image of juvenile gadoid study species i) *G. morhua* ii) *M. aeglefinus* iii) *M. merlangus.*

Appendix B: Stereo-video SCUBA transect substratum types

Figure B.1 provides examples of each substratum categories used to analyse stereo-video SCUBA transects.

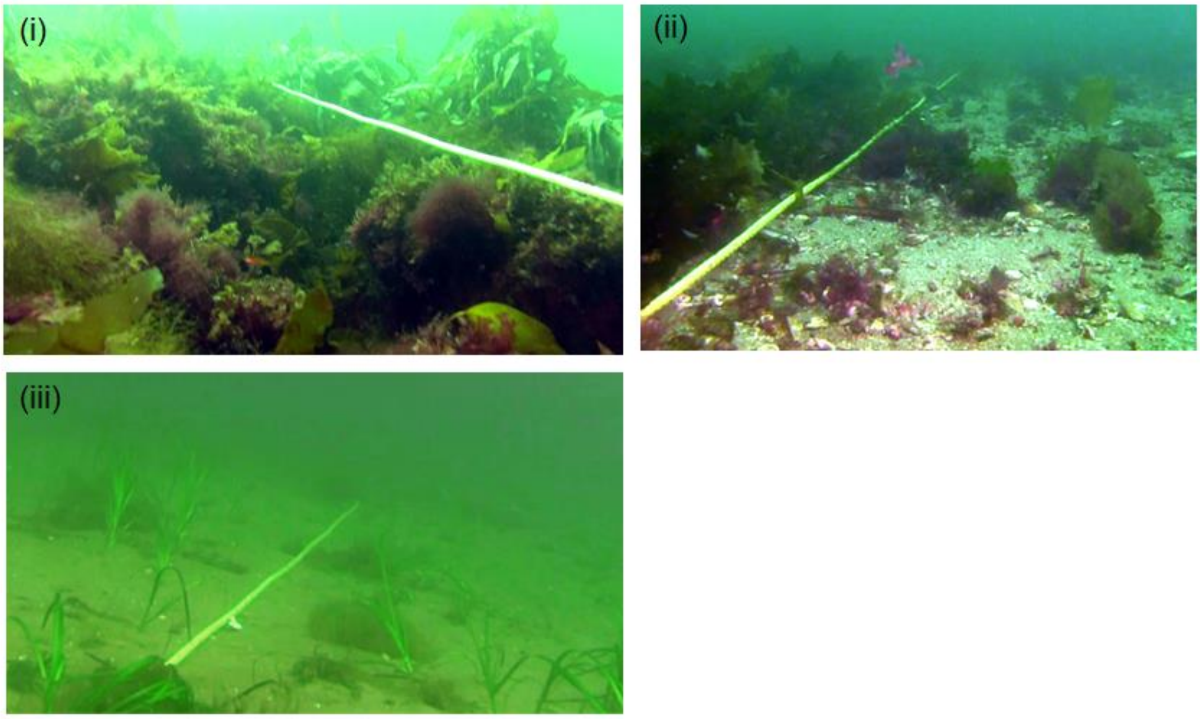

Figure B.1 - Examples of each substratum type i) Algal-boulder-cobble , ii) Algal-gravel-pebble, iii) Sand.

Appendix C: SBRUV substratum types

Figure C.1 provides examples of each substratum category used to analyse SBRUV surveys.

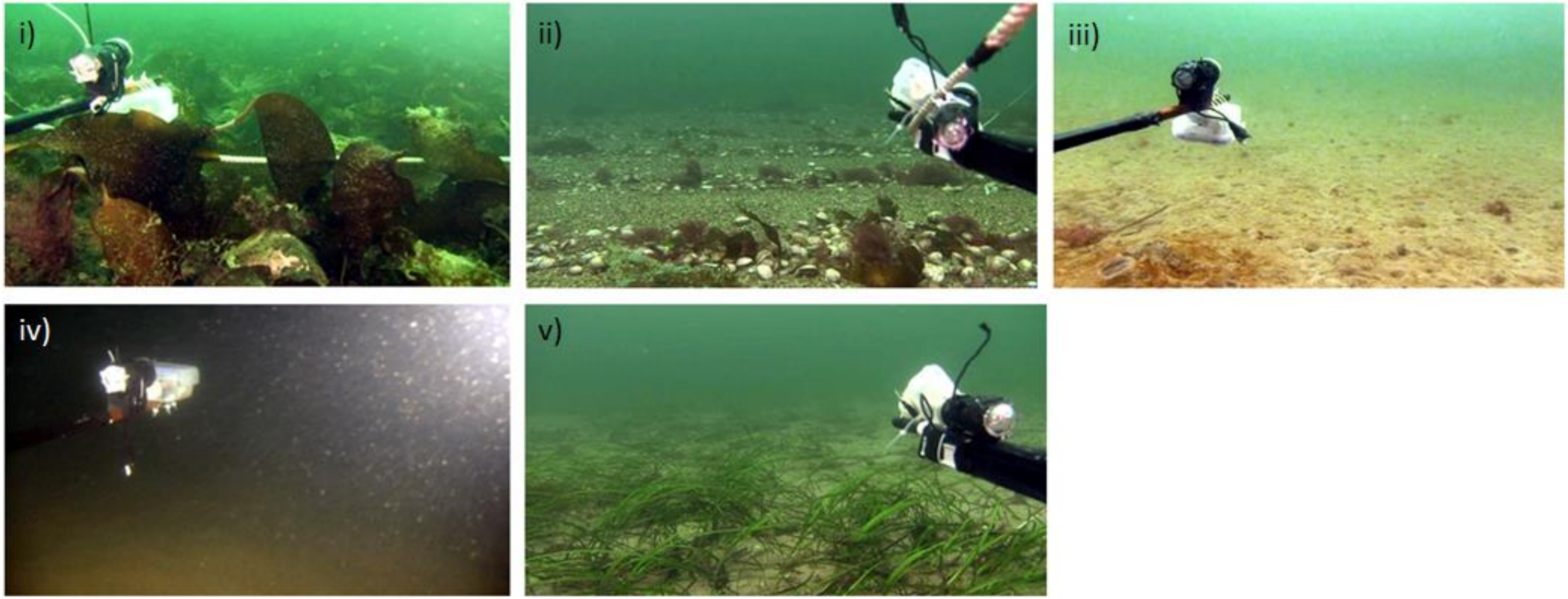

Figure C.1 - Examples of each substratum type i) Algal-boulder-cobble , ii) Algal-gravel-pebble, iii) Sand, iv) Mud, v) Seagrass.

Appendix D: Description of mathematical functions

Shannon-Wiener entropy

$$H^{i} = -\sum p_i \operatorname{In}(p_i)$$

Here, P_i, is the proportion of species *i*.

Simpson's diversity indices

$$1/D = 1/\sum_{i=1}^{S} P_i^2$$

Where the probability that a second individual drawn from a population should be of the same species as the first. *S* is the number of species (Simpson 1949).

Berger-Parker dominance index

$$d = \frac{N}{N_{max}}$$

Where N is the number of species and N_{max} is the maximum proportion of any one species in a sample (Berger & Parker, 1970).

N_1 diversity indices (exponential of Shannon index)

$$N_1 = In(N_i)$$

N_2 diversity indices (inverse of Simpson's index)

$$N2 = 1/SI$$

Where *SI* is Simpson's index.

N_∞ diversity indices (inverse of the proportional abundance of the commonest species)

$$N_\infty = 1/P_{max}$$

Were P_{max} is the maximum proportion of any one species in the sample.

Bray-Curtis similarity coefficient

$$S_{jk} = 100\left\{1 - \frac{\sum_{i=1}^{p} |y_{ij} - y_{ik}|}{\sum_{i=1}^{p}(y_{ij} + y_{ik})}\right\}$$

Where y_{ij} represents the species abundance in the *i*th row and the *j*th column of the data matrix and y_{ik} is the count for the *i*th species in the kth sample. |…| represents the absolute value of the differences.

Appendix E: Chapter 3 statistical output

G. morhua model coefficients and diagnostics

Table E.1 - Results from the model of best fit for the response variable *G. morhua* abundance. Explanatory variables show substratum type and JD with an offset of transect area (m^2). Coefficients and diagnostics (z- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level is substratum type, ABC. *P* value significance (* = *P* < 0.05 and *** = *P* < 0.001).

Variables	Estimate	Std. Error	*z* value	*P*-value	
(Intercept)	3.103	1.694	1.832	0.067	
AGP	1.152	0.472	2.441	0.015	*
Sand	-1.249	0.745	-1.678	0.093	
JD	-0.028	0.008	-3.537	0.001	***

Table E.2 - Results from the Tukey test performed between substratum type categories for the response variable *G. morhua* abundance. *P* value significance (* = *P* < 0.05 and ** = *P* < 0.01).

Variables	Estimate	Std. Error	*z* value	*P*-value	
AGP - ABC	1.139	0.476	2.393	0.042	*
Sand – ABC	-1.223	0.755	-1.620	0.230	
Sand – AGP	-2.361	0.759	-3.109	0.005	**

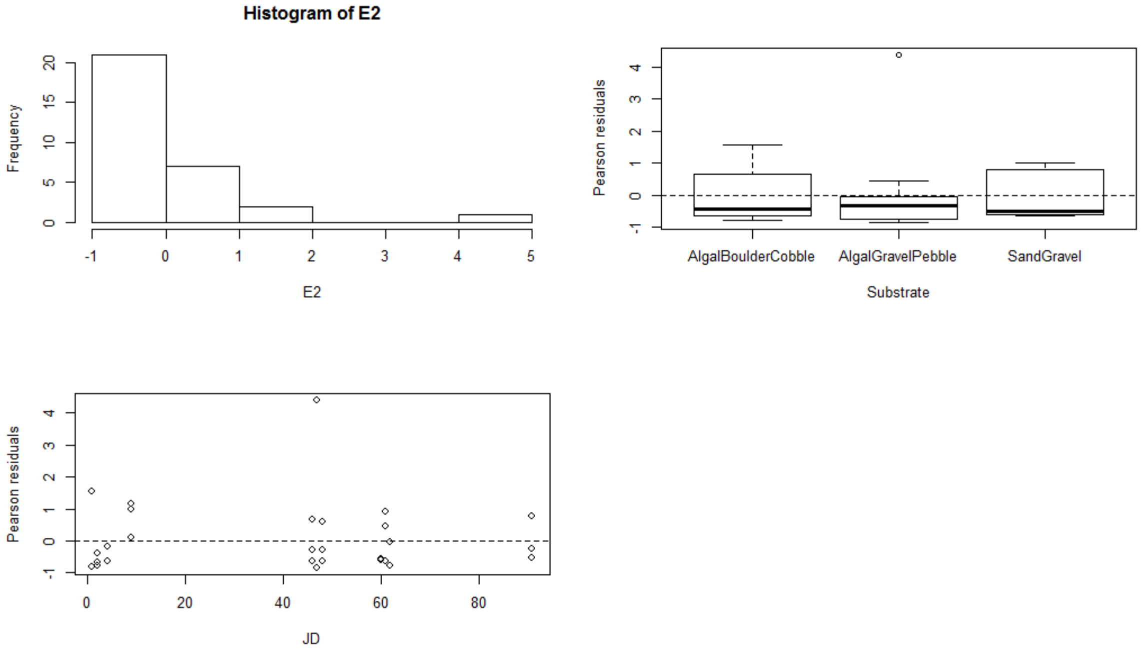

Figure E.1 - A histogram of the residuals for the optimal NBN model for *G. morhua* and residuals versus habitat variables.

Table E.3 - Results from the model of best fit for the response variable *G. morhua* length. Fixed effects show JD with an offset of transect area (m^2). *P* value significance (** = $P < 0.01$).

Variables	Estimate	Std. Error	*t*-value	*P*-value	
(Intercept)	23.30671	12.51339	1.862542	0.0652	
JD	0.182449	0.059287	3.077398	0.0026	**

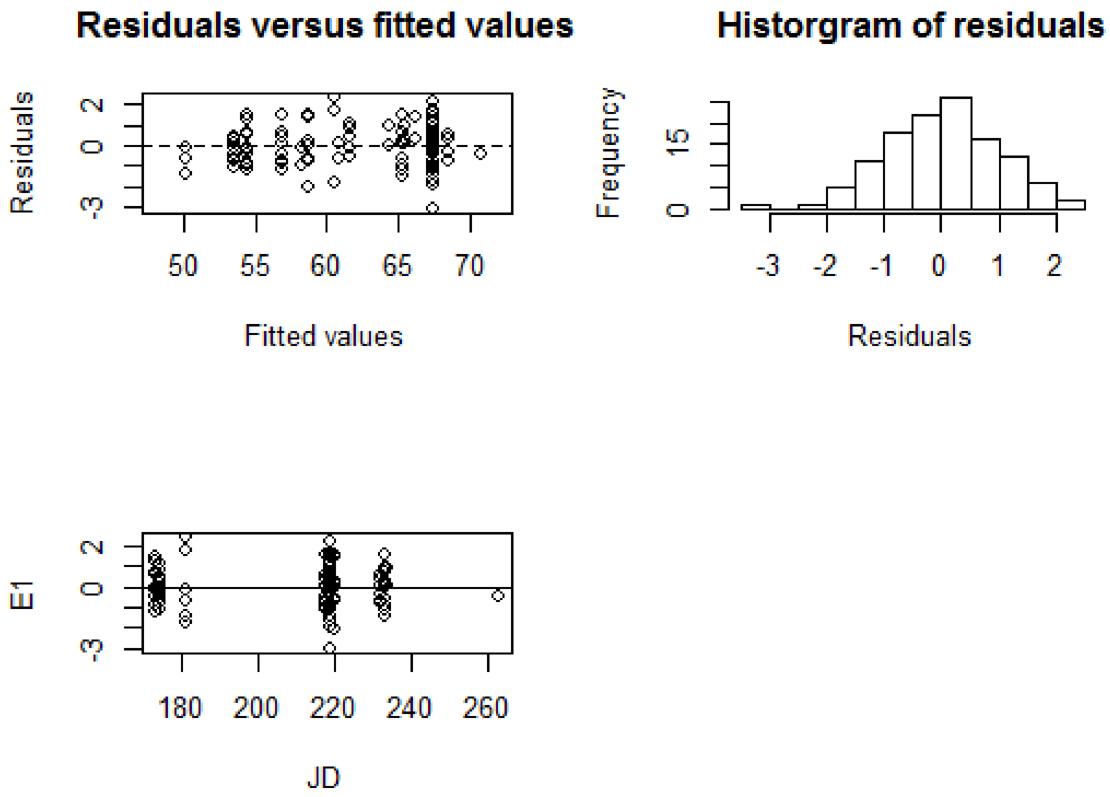

Figure E.2 - Residuals versus fitted values for *G. morhua* length, a histogram of the residuals for the optimal NBN model and residuals versus JD.

Table E.4- Results from the model of best fit for the response variable *G. morhua* length variation over the period of data collection. *P* value significance (** = *P* < 0.01).

Variables	Estimate	Std. Error	*t*-value	*P*-value	
(Intercept)	-9.603	20.488	-0.469	0.640	
JD	0.295	0.097	3.030	0.003	**

Appendix F: Chapter 4 statistical outputs

Results from Table F.1 to Table F.37 provide coefficient and diagnostics for the models of best fit within this chapter. Caution should be taken with respect to *P*-values provided since negative binomial mixed models are approximates (Zuur et al. 2009).

G. morhua model coefficients and diagnostics

Table F.1- Results from the ANOVA test for the response variable *G. morhua* MaxN with depth. Coefficients and diagnostics (F- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept.

Variables	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Depth	1	1838	1838	0.013	0.91
Residuals	217	31272997	144115		

Table F.2 - Results from the model of best fit for the response variable *G. morhua* MaxN. Explanatory variables show substratum type, N_∞, wave fetch and year. Coefficients and diagnostics (z- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level is substratum type, ABC and Year 1. *P* value significance: * = $P < 0.05$, ** = $P < 0.01$.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	0.33	0.50	0.66	0.51	
AGP	1.31	0.42	3.14	0.00	**
Sand	-0.30	0.49	-0.62	0.54	
Seagrass	0.22	0.64	0.34	0.74	
Ninf.std	-0.34	0.15	-2.24	0.02	*
Fetch.std	-0.50	0.17	-2.88	0.00	**
Year2	-1.32	0.61	-2.15	0.03	*

Table F.3- Results from the Tukey test performed between substratum type categories for the response variable *G. morhua* MaxN, *P* value significance: ** = *P* < 0.01.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
AGP – ABC	1.309	0.416	3.144	0.008	**
Sand - ABC	-0.303	0.491	-0.617	0.917	
Seagrass - ABC	0.217	0.643	0.338	0.985	
Sand – AGP	-1.612	0.694	-2.321	0.083	.
Seagrass - AGP	-1.092	0.789	-1.384	0.479	
Seagrass - Sand	0.520	0.701	0.742	0.866	

Table F.4 - Results from *G. morhua* Substratum association between summer of 2013 and 2014. Coefficients and diagnostics (z- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level is substratum type, ABC and Year 1. *P* value significance: ** = *P* < 0.01.

Variables	Estimate	Std.Error	z value	Pr(>|z|)	
(Intercept)	0.43	0.49	0.87	0.39	
AGP	1.56	0.52	3.01	0.00	**
Sand	-0.62	0.88	-0.70	0.48	
Seagrass	0.22	1.03	0.21	0.83	
Year2	-1.31	0.79	-1.65	0.10	.
AGP:Year2	0.13	0.90	0.14	0.89	
Sand:Year2	0.66	1.12	0.59	0.56	
Seagrass:Year2	-0.26	1.33	-0.19	0.85	

Table F.5 - Results from the Tukey test performed between substratum type categories and year for the response variable *G. morhua* MaxN, *P* value significance: * = $P < 0.05$.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
2xABC - 1xABC	-1.31	0.79	-1.65	0.68	
1xAGP - 1xABC	1.56	0.52	3.01	0.05	*
2xAGP - 1xABC	0.38	0.57	0.66	1.00	
1xSand - 1xABC	-0.61	0.88	-0.70	1.00	
2xSand - 1xABC	-1.27	0.59	-2.16	0.34	
1xSeagrass - 1xABC	0.22	1.03	0.21	1.00	
2xSeagrass - 1xABC	-1.35	0.89	-1.51	0.77	
1xAGP - 2xABC	**2.87**	**0.90**	**3.18**	**0.03**	*****
2xAGP - 2xABC	1.69	0.97	1.75	0.61	
1xSand - 2xABC	0.69	1.17	0.59	1.00	
2xSand - 2xABC	0.04	1.02	0.04	1.00	
1xSeagrass - 2xABC	1.53	1.34	1.14	0.93	
2xSeagrass - 2xABC	-0.04	1.26	-0.03	1.00	
2xAGP - 1xAGP	-1.18	0.76	-1.54	0.74	
1xSand - 1xAGP	-2.18	1.01	-2.15	0.34	
2xSand - 1xAGP	**-2.83**	**0.85**	**-3.32**	**0.02**	*****
1xSeagrass - 1xAGP	-1.34	1.21	-1.11	0.94	
2xSeagrass - 1xAGP	-2.91	1.13	-2.58	0.14	
1xSand - 2xAGP	-0.99	1.05	-0.95	0.97	
2xSand - 2xAGP	-1.65	0.81	-2.04	0.41	
1xSeagrass - 2xAGP	-0.16	1.15	-0.14	1.00	
2xSeagrass - 2xAGP	-1.73	1.05	-1.65	0.68	
2xSand - 1xSand	-0.65	1.07	-0.61	1.00	

1xSeagrass - 1xSand	0.83	1.36	0.61	1.00
2xSeagrass - 1xSand	-0.73	1.27	-0.58	1.00
1xSeagrass - 2xSand	1.48	1.10	1.35	0.85
2xSeagrass - 2xSand	-0.08	0.99	-0.08	1.00
2xSeagrass - 1xSeagrass	-1.56	1.24	-1.26	0.89

Table F.6 - Results from *G. morhua* MaxN over the period of data collection for 2013. Coefficients and diagnostics (z- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept. *P* value significance: *** = *P* < 0.001.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	1.30	0.24	5.36	0.00	***
JD	-0.01	0.00	-6.26	0.00	***

Table F.7 - Results from *G. morhua* MaxN over the period of data collection for 2014. Coefficients and diagnostics (z- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level is JDg 1. *P* value significance: * = *P* <0.05, ** = *P* < 0.01, *** = *P* < 0.001.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-2.04	0.73	-2.78	0.01	**
JDg 2	2.11	0.82	2.57	0.01	*
JDg 3	3.18	0.82	3.86	0.00	***
JDg 4	1.55	0.84	1.86	0.06	.

Table F.8 - Results from Tukey test performed between grouped JD for the response variable *G. morhua* MaxN over the period of data collection for 2014. *P* value significance: * = *P* <0.05, *** = *P* < 0.001.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
JDg 2 – 1	2.11	0.82	2.57	0.05	*
JDg 3 - 1	3.18	0.82	3.86	<0.001	***
JDg 4 – 1	1.55	0.84	1.86	0.24	
JDg 3 – 2	1.08	1.07	1.01	0.74	
JDg 4 – 2	-0.55	1.07	-0.52	0.95	
JDg 4 – 3	-1.63	1.04	-1.58	0.38	

Table F.9 - Results from *G. morhua* length over the period of data collection for 2013. Coefficients and diagnostics (t- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level is substratum type, ABC. *P* value significance (* = *P* < 0.05, *** = *P* < 0.001).

Variables	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	5.08	0.54	9.40	0.00	***
JD	0.02	0.00	6.00	0.00	***
AGP	0.74	0.41	1.82	0.07	.
Sand	-1.15	0.73	-1.58	0.12	
Seagrass	0.58	0.51	1.14	0.26	
N_2	0.21	0.08	2.56	0.01	*

Table F.10 - Results from the Tukey test performed between substratum type categories for 2013 for the response variable *G. morhua* length. *P* value significance: * = $P < 0.05$.

Variables	Estimate	Std. Error	t value	Pr(>|t|)	
AGP - ABC	0.74	0.41	1.82	0.26	
Sand - ABC	-1.15	0.73	-1.58	0.38	
Seagrass - ABC	0.58	0.51	1.14	0.65	
Sand - AGP	-1.89	0.65	-2.89	0.02	*
Seagrass - AGP	-0.16	0.41	-0.38	0.98	
Seagrass - Sand	1.73	0.74	2.34	0.09	

Table F.11 - Results from *G. morhua* length over the period of data collection for 2014. Coefficients and diagnostics (t- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level is substratum type, ABC and grouped JD (JDg) week 1. *P* value significance: *** = $P < 0.001$.

Variables	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	6.60	1.77	3.73	0.00	***
JDg 2	1.78	1.73	1.03	0.31	
JDg 3	2.94	1.74	1.69	0.09	.
JDg 4	2.05	1.76	1.17	0.25	
AGP	-0.99	0.51	-1.95	0.05	.
Sand	-0.50	0.55	-0.92	0.36	
Seagrass	1.24	0.91	1.36	0.18	

Table F.12 - Results from the Tukey test performed between grouped JD for 2014 for the response variable *G. morhua* length. *P* value significance: * = $P < 0.05$.

Variables	Estimate	Std. Error	t value	Pr(>|t|)	
JDg 2 - 1	1.78	1.73	1.03	0.71	
JDg 3 - 1	2.94	1.74	1.69	0.30	
JDg 4 - 1	2.05	1.76	1.17	0.62	
JDg 3 - 2	1.16	0.42	2.80	0.03	*
JDg 4 - 2	0.27	0.49	0.56	0.94	
JDg 4 - 3	-0.89	0.51	-1.76	0.27	

Table F.13 - Results from the Tukey test performed between substratum type for 2014 for the response variable *G. morhua* length. *P* value significance: * = $P < 0.05$.

Variables	Estimate	Std. Error	t value	Pr(>|t|)	
AGP - ABC	-0.99	0.51	-1.95	0.20	
Sand - ABC	-0.50	0.55	-0.92	0.79	
Seagrass - ABC	1.24	0.91	1.36	0.51	
Sand - AGP	0.49	0.41	1.21	0.61	
Seagrass - AGP	2.23	0.83	2.68	0.04	*
Seagrass - Sand	1.74	0.84	2.06	0.16	

M. aeglefinus model coefficients and diagnostics

Table F.14 - Results from the ANOVA test for the response variable *M. aeglefinus* MaxN with depth. Coefficients and diagnostics (F- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept.

Variables	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Depth	1	96576	96576	0.789	0.376
Residuals	179	21921217	122465		

Table F.15 - Results from the model of best fit for the response variable *M. aeglefinus* MaxN. Explanatory variables show substratum type, N_∞, depth and wave fetch. The reference level is substratum type, ABC. *P* value significance: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Variables	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	
(Intercept)	-2.771	0.748	-3.710	0.000	***
AGP	1.588	0.721	2.200	0.028	*
Mud	1.887	0.959	1.970	0.049	*
Sand	3.251	0.750	4.330	0.000	***
Seagrass	2.986	0.815	3.670	0.000	***
Ninf.std	-0.413	0.158	-2.620	0.009	**
Depth.std	0.615	0.257	2.390	0.017	*
Fetch.std	-0.422	0.155	-2.720	0.007	**

Table F.16 - Results from the Tukey test performed between substratum type categories for the response variable *M. aeglefinus* MaxN. *P* value significance: ** = *P* < 0.01, *** = *P* < 0.001.

Variables	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	
AGP - ABC	1.588	0.721	2.204	0.170	
Mud - ABC	1.887	0.959	1.967	0.270	
Sand - ABC	3.252	0.750	4.334	< 0.001	***
Seagrass – ABC	2.986	0.815	3.666	0.002	**
Mud - AGP	0.298	1.157	0.258	0.999	
Sand - AGP	1.663	0.920	1.809	0.355	
Seagrass – AGP	1.398	0.933	1.498	0.549	
Sand - Mud	1.365	0.825	1.654	0.448	
Seagrass - Mud	1.100	1.039	1.058	0.819	
Seagrass – Sand	-0.265	0.791	-0.335	0.997	

Table F.17 - Results from *M. aeglefinus* MaxN over the period of data collection for 2014. Coefficients and diagnostics (z- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level is grouped JD (JDg) week 1. P value significance: * = *P* < 0.05, ** = *P* < 0.01, *** = *P* < 0.001.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.01	0.34	-2.92	0.00	**
JDg 2	1.66	0.42	3.95	0.00	***
JDg 3	1.05	0.43	2.42	0.02	*
JDg 4	0.96	0.44	2.18	0.03	*

Table F.18 - Results from the Tukey test performed between grouped JD for 2014 for the response variable *M. aeglefinus* MaxN. *P* value significance: *** = *P* < 0.001.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
JDg 2 – 1	1.66	0.42	3.95	<0.001	***
JDg 3 – 1	1.05	0.43	2.42	0.07	.
JDg 4 – 1	0.96	0.44	2.18	0.13	
JDg 3 – 2	-0.62	0.36	-1.72	0.31	
JDg 4 – 2	-0.71	0.37	-1.94	0.21	
JDg 4 – 3	-0.09	0.38	-0.24	1.00	

Table F.19 - Results from *M. aeglefinus* length over the period of data collection for 2013. Coefficients and diagnostics (t- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept. *P* value significance: *** = *P* < 0.001.

Variables	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	9.04	0.69	13.11	< 2e-16	***
JD	0.04	0.01	5.00	0.00	***

Table F.20 - Results from *M. aeglefinus* length over the period of data collection for 2014. Coefficients and diagnostics (t- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level is grouped JD (JDg) week 1. *P* value significance: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Variables	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	8.55	0.57	15.08	< 2e-16	***
Depth	0.05	0.02	3.13	0.00	**
JDg 2	0.70	0.49	1.44	0.15	
JDg 3	1.74	0.53	3.32	0.00	**
JDg 4	2.91	0.57	5.06	0.00	***
Wave Fetch	0.00	0.00	-2.13	0.04	*

Table F.21 - Results from the Tukey test performed between grouped JD for 2014 for the response variable *M. aeglefinus* MaxN. *P* value significance: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Variables	Estimate	Std. Error	t value	Pr(>|t|)	
JDg 2 - 1	0.70	0.49	1.44	0.46	
JDg 3 - 1	1.74	0.53	3.32	0.01	**
JDg 4 - 1	2.91	0.57	5.06	< 0.001	***
JDg 3 - 2	1.04	0.29	3.61	0.00	**
JDg 4 - 2	2.21	0.37	6.03	< 0.001	***
JDg 4 - 3	1.16	0.39	3.01	0.02	*

M. merlangus model coefficients and diagnostics

Table F.22 - Results from the ANOVA test for the response variable *M. merlangus* MaxN with depth. Coefficients and diagnostics (F- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept. *P* value significance: ** = $P < 0.01$.

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Depth	1	409893	409893	7.445	0.00765	**
Residuals	90	4955185	55058			

Table F.23 - Results from the model of best fit for the response variable *M. merlangus* MaxN. Explanatory variables show substratum type, N_1, depth and current. The reference level is substratum type, ABC. *P* value significance: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-2.243	0.625	-3.590	0.000	***
AGP	1.470	0.621	2.370	0.018	*
Mud	1.431	0.837	1.710	0.087	.
Sand	2.496	0.652	3.830	0.000	***
Seagrass	1.018	0.904	1.130	0.260	
Depth.std	0.691	0.227	3.040	0.002	**
N1.std	0.330	0.145	2.280	0.022	*
Current.std	-0.296	0.154	-1.920	0.054	.

Table F.24 - Results from the Tukey test performed between substratum type categories for the response variable *M. merlangus* MaxN. *P* value significance: ** = $P < 0.01$.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
AGP - ABC	1.470	0.621	2.367	0.116	
Mud - ABC	1.431	0.837	1.710	0.410	
Sand - ABC	2.496	0.652	3.829	0.001	**
Seagrass - ABC	1.018	0.904	1.126	0.781	
Mud - AGP	-0.039	0.991	-0.039	1.000	
Sand - AGP	1.026	0.790	1.298	0.677	
Seagrass - AGP	-0.452	1.048	-0.431	0.992	
Sand - Mud	1.065	0.769	1.384	0.621	
Seagrass - Mud	-0.413	1.124	-0.368	0.996	
Seagrass - Sand	-1.478	0.969	-1.525	0.528	

Table F.25 - Results from *M. merlangus* MaxN over the period of data collection for 2014. Coefficients and diagnostics (z- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level is grouped JD, week 1. *P* value significance: ** = $P < 0.01$.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	0.30	0.27	1.11	0.27	
JDg 2	0.30	0.37	0.80	0.42	
JDg 3	-1.42	0.44	-3.22	0.00	**
JDg 4	-0.21	0.38	-0.55	0.59	

Table F.26 - Results from the Tukey test performed between grouped JD for 2014 for the response variable *M. merlangus* MaxN, *P* value significance: * = *P* < 0.05, ** = *P* < 0.01, *** = *P* < 0.001.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
JDg 2 - 1	0.30	0.37	0.80	0.85	
JDg 3 - 1	-1.42	0.44	-3.22	0.01	**
JDg 4 - 1	-0.21	0.38	-0.55	0.95	
JDg 3 - 2	-1.72	0.43	-3.98	< 0.001	***
JDg 4 - 2	-0.50	0.37	-1.36	0.52	
JDg 4 - 3	1.21	0.44	2.74	0.03	*

Table F.27 - Results from *M. merlangus* length over the period of data collection for 2013. Coefficients and diagnostics (t- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept. *P* value significance: * = *P* < 0.05.

Variables	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	2.42	3.85	0.63	0.55	
Depth	0.49	0.29	1.68	0.14	
JD	0.07	0.02	2.75	0.03	*

Table F.28 - Results from *M. merlangus* length with depth for 2014. Coefficients and diagnostics (t- and P-values) indicate the effect of each parameter level on the reference level, denoted as intercept. *P* value significance ** = *P* < 0.01, *** = *P* < 0.001.

Variables	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	9.36	0.79	11.90	< 2e-16	***
Depth	0.08	0.03	2.65	0.01	**

Gadoid size and behavioural differences

Table F.29 - Results from 2013 data collection period gadoid length differences. Explanatory variables show gadoid species. The reference level is *G. morhua*. *P* value significance: *** = $P < 0.001$.

Variables	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	7.39	0.17	44.83	< 2e-16	***
M. aeglefinus	4.94	0.31	16.10	< 2e-16	***
M. merlangus	3.32	0.63	5.26	0.00	***

Table F.30 - Results from the Tukey test performed between gadoid species for 2013 for the response variable length, *P* value significance: * = $P < 0.05$, *** = $P < 0.001$.

Variables	Estimate	Std. Error	t value	Pr(>|t|)	
M. aeglefinus - *G. morhua*	4.94	0.31	16.10	<0.001	***
M. merlangus - *G. morhua*	3.32	0.63	5.26	<0.001	***
M. merlangus - *M. aeglefinus*	-1.62	0.66	-2.45	0.04	*

Table F.31 - Results from 2014 data collection period gadoid length differences. Explanatory variables show gadoid species. The reference level is *G. morhua*. *P* value significance: *** = $P < 0.001$.

Variables	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	8.28	0.20	42.13	<2e-16	***
M. aeglefinus	2.34	0.26	9.04	<2e-16	***
M. merlangus	3.06	0.29	10.61	<2e-16	***

Table F.32 - Results from the Tukey test performed between gadoid species for 2014 for the response variable length, *P* value significance: * = *P* < 0.05, *** = *P* < 0.001.

Variables	Estimate	Std. Error	t value	Pr(>|t|)	
M. aeglefinus - *G. morhua*	2.34	0.26	9.04	<1e-04	***
M. merlangus - *G. morhua*	3.06	0.29	10.61	<1e-04	***
M. merlangus - *M. aeglefinus*	0.72	0.27	2.68	0.02	*

Table F.33 - Mid Y differences between gadoid species. Explanatory variables show gadoid species and data collection year. The reference level is *G. morhua* and year 1. *P* value significance: *** = *P* < 0.001.

Variables	Value	Std.Error	DF	t-value	p-value	
(Intercept)	-6.82	1.30	580.00	-5.26	0	***
M. aeglefinus	4.66	1.35	580.00	3.46	0.001	***
M. merlangus	10.51	1.54	580.00	6.84	0	***
Year 2	-0.76	1.35	580.00	-0.56	0.574	

Table F.34 - Results from the Tukey test performed between gadoid species for the response variable mid Y, *P* value significance: *** = *P* < 0.001.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
M. aeglefinus - *G. morhua*	4.66	1.35	3.46	0.002	**
M. merlangus - *G. morhua*	10.51	1.54	6.84	< 1e-04	***
M. merlangus - *M. aeglefinus*	5.85	1.47	3.98	0.001	***

Table F.35 - Mid Z differences between gadoid species. Explanatory variables show gadoid species and data collection year. The reference level is *G. morhua* and Year 1. *P* value significance: ** = *P* < 0.01, *** = *P* < 0.001.

Variables	Value	Std.Error	DF	t-value	p-value	
(Intercept)	166.67	4.15	580.00	40.20	0	***
M. aeglefinus	-22.74	3.61	580.00	-6.31	0	***
M. merlangus	-49.45	4.12	580.00	-12.02	0	***
Year 2	9.81	3.68	580.00	2.67	0.007	**

Table F.36 - Results from the Tukey test performed between gadoid species for the response variable mid Z, *P* value significance: *** = *P* < 0.001.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
M. aeglefinus - *G. morhua*	-22.74	3.61	-6.31	<1e-09	***
M. merlangus - *G. morhua*	-49.46	4.12	-12.02	<1e-09	***
M. merlangus - *M. aeglefinus*	-26.71	3.95	-6.76	<1e-09	***

Table F.37 - TFA differences between gadoid species. Explanatory variables show gadoid species and data collection year. The reference level is *G. morhua* and Year 1. *P* value significance: ** = *P* < 0.01, *** = *P* < 0.001.

Variables	Estimate	Std. Error	t-value	Pr(>|t|)	
(Intercept)	-0.94	0.29	-3.24	0.00	**
M. aeglefinus	0.11	0.14	0.80	0.43	
M. merlangus	0.53	0.15	3.60	0.00	***
Year 2	0.58	0.30	1.93	0.05	.

Appendix G: Chapter 5 statistical outputs

Gadoid swimming speed calculations

Table G.1 - Juvenile gadoid swimming speeds during cruising behaviour calculated from distance moved over time

Trial	Gadoid	Length (cm)	Distance (m)	Time (s)	Speed (m/s)
1	*G. morhua*	6.78	0.78	8	0.10
2	*G. morhua*	7.64	1.11	5	0.22
3	*G. morhua*	7.19	1.13	5	0.23
4	*G. morhua*	8.64	0.73	5	0.15
5	*G. morhua*	8.92	0.90	11	0.08
6	*G. morhua*	7.74	1.35	5	0.27
7	*G. morhua*	9.48	1.65	7	0.24
8	*G. morhua*	7.90	0.39	3	0.13
9	*G. morhua*	7.67	0.49	5	0.10
10	*G. morhua*	6.89	0.37	3	0.12
11	*M. aeglefinus*	10.80	1.12	5	0.22
12	*M. aeglefinus*	9.95	0.69	4	0.17
13	*M. aeglefinus*	9.84	0.65	4	0.16
14	*M. aeglefinus*	11.10	0.85	4	0.21
15	*M. aeglefinus*	11.97	0.53	3	0.18
16	*M. aeglefinus*	11.39	0.51	2	0.25
17	*M. aeglefinus*	9.46	0.81	4	0.20
18	*M. aeglefinus*	11.02	0.85	4	0.21
19	*M. aeglefinus*	10.42	0.54	4	0.14
20	*M. aeglefinus*	10.94	1.63	11	0.15
21	*M. merlangus*	15.46	0.90	2	0.45

22	*M. merlangus*	16.52	1.15	4	0.29
23	*M. merlangus*	15.35	0.35	1	0.35
24	*M. merlangus*	13.13	0.54	2	0.27
25	*M. merlangus*	14.86	0.43	1	0.43
26	*M. merlangus*	14.53	1.00	3	0.33
27	*M. merlangus*	13.59	0.85	2	0.42
28	*M. merlangus*	14.02	0.58	2	0.29
29	*M. merlangus*	14.99	0.26	4	0.06
30	*M. merlangus*	13.26	0.40	1	0.40

Table G.2 - Gadoid average swimming speed and length from Table G.1.

Gadoid	Average length (cm)	SD	SE	Speed (m/s)	SD	SE	Speed (m/hr)
G. morhua	78.86	8.38	2.65	0.16	0.07	0.02	586.99
M. aeglefinus	106.90	7.30	2.31	0.19	0.04	0.01	685.08
M. merlangus	152.50	10.24	3.24	0.33	0.11	0.03	1,190.90

Substratum prediction model outputs

Table G.3 - Results from the model of best fit for the multinomial substratum prediction model. Coefficients and the standard error indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level is substratum type ABC.

Coefficients	(Intercept)	Current.std	Fetch.std	Distance.std	Depth.std	Geology2	Distance.std: Depth.std	Fetch.std: Distance.std
AGP	5.00	0.92	-0.45	-0.22	2.47	-3.56	0.33	-0.86
Sand	5.67	-0.02	-0.27	0.37	6.85	-4.75	4.77	-1.49
Mud	1.33	-2.25	1.63	-0.38	13.62	-10.38	7.83	-4.72
Seagrass	-23.14	-1.39	-13.11	-27.61	-13.66	-56.14	-10.28	-25.82

Std.Error	(Intercept)	Current.std	Fetch.std	Distance.std	Depth.std	Geology2	Distance.std: Depth.std	Fetch.std: Distance.std
AGP	1.56	0.34	0.32	0.59	0.91	1.44	1.17	0.47
Sand	1.63	0.48	0.48	0.71	1.32	1.64	1.57	0.69
Mud	2.24	1.20	1.48	1.81	2.31	3.12	2.15	1.50
Seagrass	27.75	1.88	18.27	30.57	19.57	0.00	21.01	22.16

G. morhua statistical model outputs

Table G.4 - Results from the model of best fit for the response variable *G. morhua* MaxN. Explanatory variables show substratum type, heterogeneity (N_∞) and Year. Coefficients and diagnostics (z- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level is substratum type, ABC and Year 1. *P* value significance: * = *P* < 0.05, *** = *P* < 0.001.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	1.73	0.79	2.21	0.03	*
AGP	1.57	0.43	3.66	0.00	***
Sand	-0.17	0.51	-0.33	0.74	
Seagrass	0.36	0.68	0.53	0.60	
N_∞	-0.80	0.34	-2.33	0.02	*
Year 2	-1.18	0.52	-2.26	0.02	*

Table G.5 - Results from the Tukey test performed between substratum type categories for the response variable *G. morhua* MaxN. *P* value significance: ** = *P* < 0.01.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
AGP – ABC	1.57	0.43	3.66	0.00	**
Sand - ABC	-0.17	0.51	-0.33	0.99	
Seagrass - ABC	0.36	0.68	0.53	0.95	
Sand - AGP	-1.74	0.70	-2.47	0.06	.
Seagrass - AGP	-1.21	0.81	-1.49	0.42	
Seagrass - Sand	0.52	0.73	0.72	0.88	

Figure G.1 shows model outputs from the GLMM models looking at the effect of substratum type, heterogeneity and year on *G. morhua*.

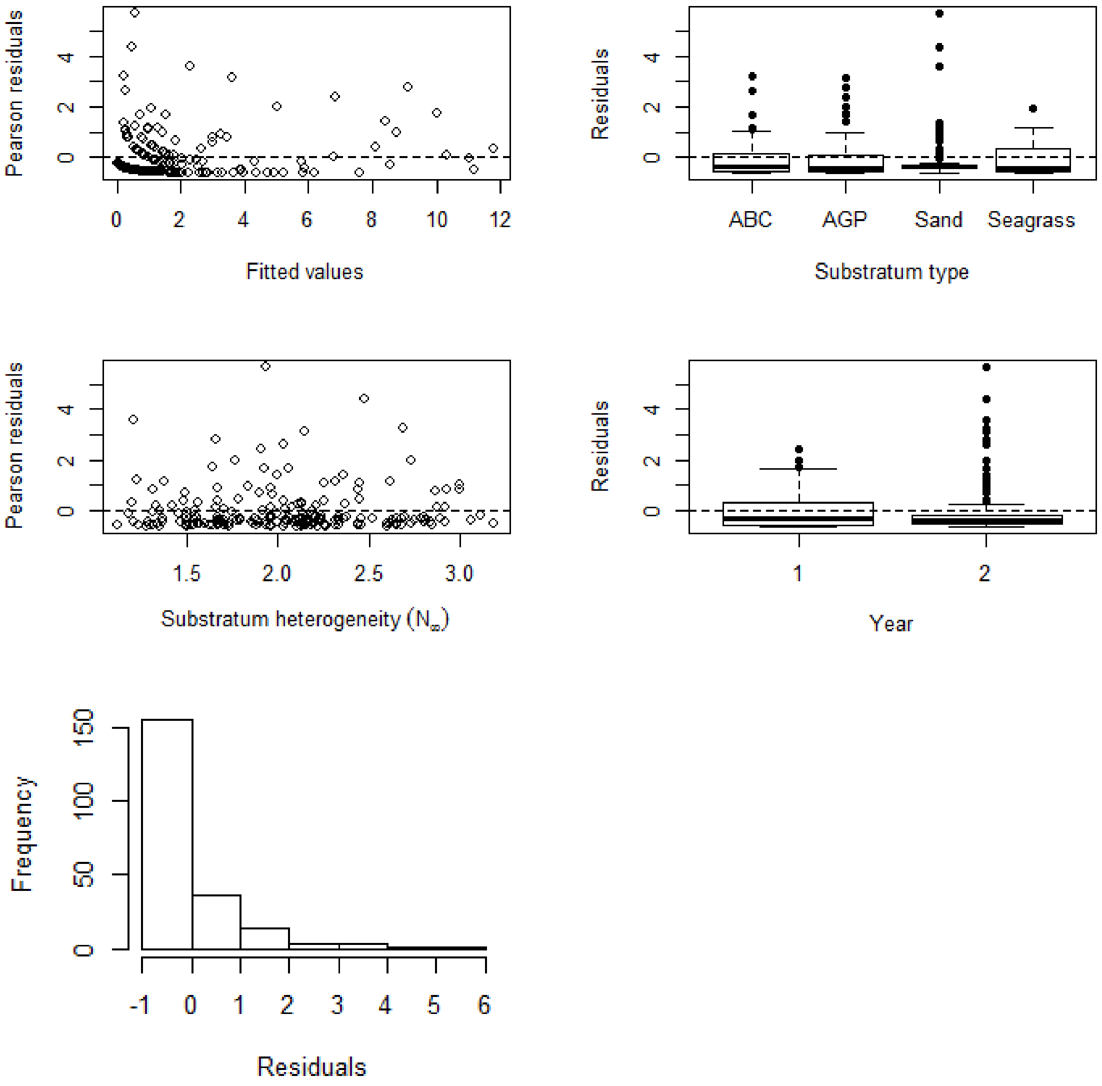

Figure G.1 - Residuals versus fitted values for *G. morhua* relative abundance and residuals substratum type, heterogeneity (N_∞) and year and a histogram of the residuals for the optimal NBN model.

M. aeglefinus statistical model outputs

Table G.6 - Results from the model of best fit for the response variable *M. aeglefinus* MaxN. Explanatory variables show substratum type and landscape heterogeneity (N_∞). Coefficients and diagnostics (z- and *P*-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level is substratum type ABC. P value significance: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-5.61	1.19	-4.73	0.00	***
AGP	1.97	0.73	2.71	0.01	**
Mud	3.32	0.79	4.20	0.00	***
Sand	3.94	0.74	5.32	0.00	***
Seagrass	2.23	0.90	2.49	0.01	*
N_∞	1.15	0.41	2.83	0.00	**

Table G.7 - Results from the Tukey test performed between substratum type categories for the response variable *M. aeglefinus* MaxN. P value significance: *** = $P < 0.001$.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
AGP – ABC	1.97	0.73	2.71	0.05	.
Mud - ABC	3.32	0.79	4.20	<0.001	***
Sand - ABC	3.94	0.74	5.32	<0.001	***
Seagrass – ABC	2.23	0.90	2.49	0.09	.
Mud – AGP	1.35	1.03	1.32	0.67	
Sand - AGP	1.97	0.90	2.19	0.18	
Seagrass – AGP	0.26	1.01	0.26	1.00	
Sand - Mud	0.62	0.71	0.86	0.91	
Seagrass - Mud	-1.09	0.98	-1.11	0.80	
Seagrass - Sand	-1.71	0.86	-1.98	0.27	

Figure G.2 show model outputs from the GLMM models looking at the effect of substratum type and heterogeneity on *M. aeglefinus*.

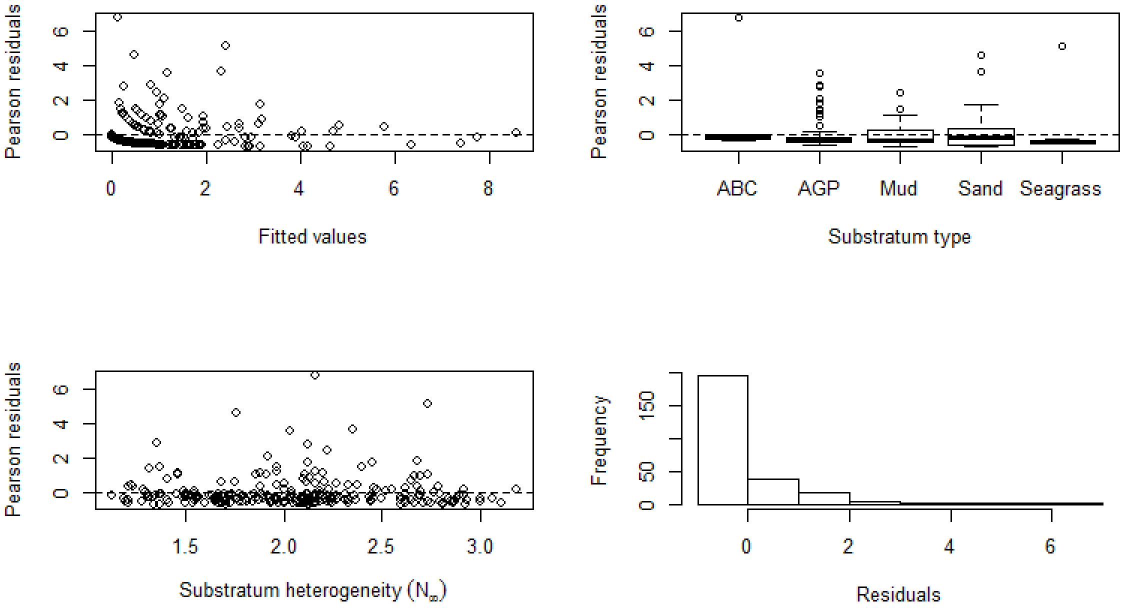

Figure G.2 - Residuals versus fitted values for *M. aeglefinus* MaxN, residuals substratum type and landscape heterogeneity (N_∞) and a histogram of the residuals for the optimal NBN model..

M. merlangus statistical model outputs

Table G.8 - Results from the model of best fit for the response variable *M. merlangus* MaxN. Explanatory variables show substratum type, heterogeneity (N_{∞}) and extent with a 1500 m radius. Coefficients and diagnostics (z- and P-values) indicate the effect of each parameter level on the reference level, denoted as intercept. The reference level is substratum type ABC. *P* value significance: * = *P* < 0.05, ** = *P* < 0.01, *** = *P* < 0.001.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-8.36	2.32	-3.60	0.00	***
AGP	3.78	1.17	3.23	0.00	**
Mud	5.01	1.27	3.94	0.00	***
Sand	5.23	1.20	4.35	0.00	***
Seagrass	3.27	1.41	2.33	0.02	*
N_{∞}	1.36	0.66	2.05	0.04	*
Extent	0.00	0.00	2.74	0.01	**
N_{∞}:Extent	0.00	0.00	-2.20	0.03	*

Table G.9 - Results from the Tukey test performed between substratum type categories for the response variable *M. merlangus* MaxN. *P* value significance: * = *P* < 0.05, *** = *P* < 0.001.

Variables	Estimate	Std. Error	z value	Pr(>|z|)	
AGP – ABC	3.78	1.17	3.23	0.01	*
Mud - ABC	5.01	1.27	3.94	<0.001	***
Sand - ABC	5.23	1.20	4.35	<0.001	***
Seagrass – ABC	3.27	1.41	2.33	0.13	
Mud – AGP	1.23	1.32	0.93	0.88	
Sand - AGP	1.45	1.12	1.29	0.69	
Seagrass – AGP	-0.51	1.41	-0.36	1.00	
Sand - Mud	0.23	0.94	0.24	1.00	
Seagrass - Mud	-1.73	1.35	-1.29	0.69	
Seagrass - Sand	-1.96	1.17	-1.68	0.44	

Figure G.3 show model outputs from the GLMM models looking at the effect of substratum type, heterogeneity and extent on *M. merlangus*.

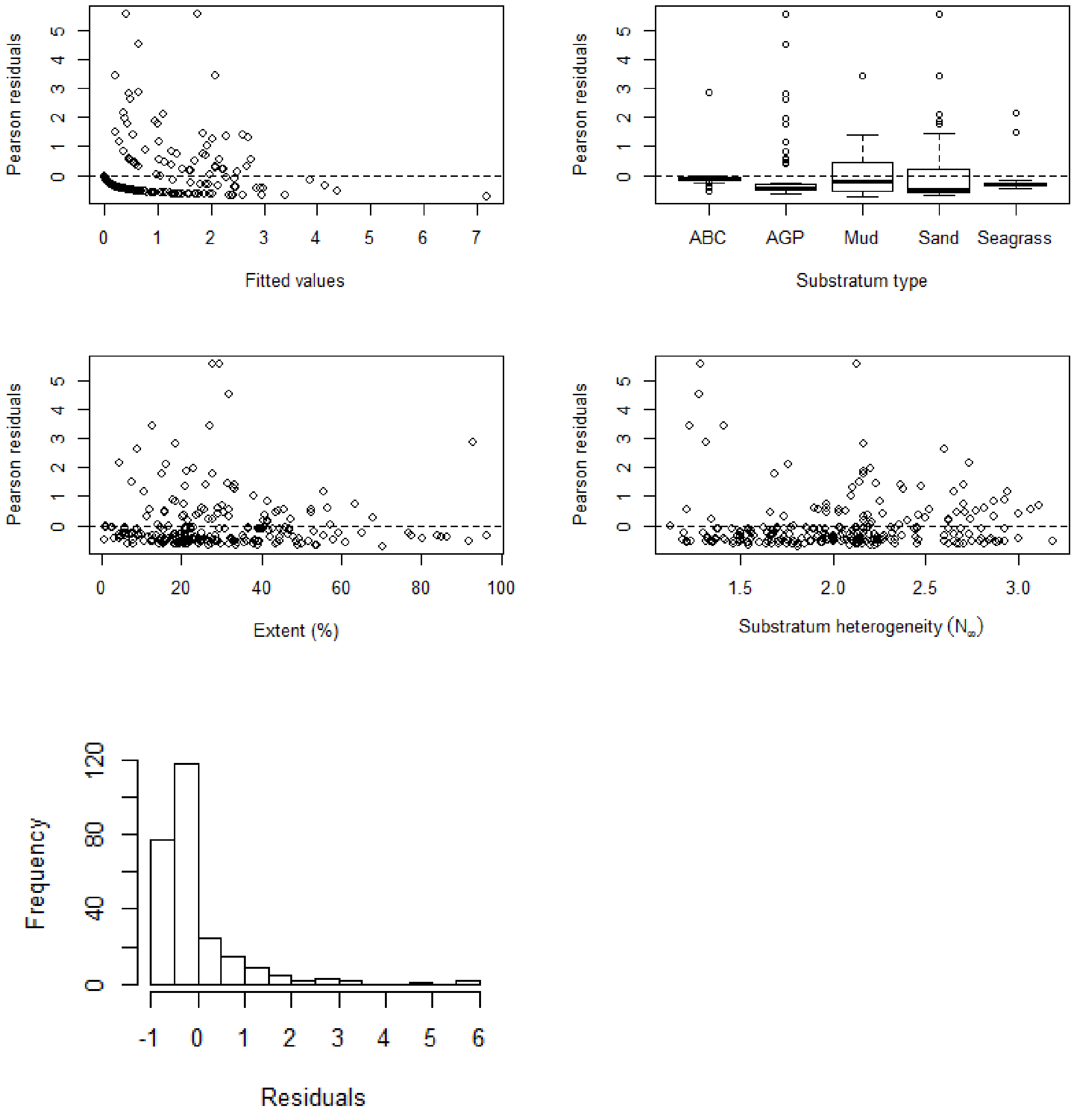

Figure G.3 - Residuals versus fitted values for *M. merlangus* MaxN, residuals substratum type, extent and heterogeneity (N_∞) and a histogram of the residuals for the optimal NBN model.

References

Aarts, G., J. Fieberg, S, Brasseur, and J. Matthiopoulos. 2013. Quantifying the effect of habitat availability on species distributions. Journal of Animal Ecology 82:1135–1145.

Aarts, G., M. MacKenzie, B. McConnell, M. Fedak, and M. Matthiopoulos. 2008. Estimating space-use and habitat preference from wildlife telemetry data. Ecography 31:140–160.

Able, K. W. 1999. Measures of juvenile fish habitat quality: examples from a National Estuarine Research Reserve. In Fish Habitat: Essential Fish Habitat and Habitat Rehabilitation, L.R. Beneka (ed.). American Fisheries Society Symposium 22 Maryland: 134–147.

Airoldi, L., and M. W. Beck. 2007. Loss, Status and Trends for Coastal Marine Habitats of Europe. Oceanography and Marine Biology: An Annual Review 45:345–405.

Allan, B. 2015. Estimating differences in attraction between cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) with stereo baited remote underwater video systems (SBRUVs). University of Glasgow, BSc dissertation.

Almany, G. 2004. Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. Oecologia 141:105–113.

Anderson, J. L., B. J. Laurel, and J. A. Brown. 2007. Diel changes in behaviour and habitat use by age-0 Atlantic cod (*Gadus morhua* L.) in the laboratory and field. Journal of Experimental Marine Biology and Ecology 351:267-275.

Anderson, M., R. Gorley, and K. Clarke. 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E: Plymouth, UK.

Anon. 2001. Commission Regulation (EC) No. 456/2001 of 6 March 2001 Establishing measures for the recovery of the stock of cod to the west of Scotland (ICES Division VIa) and associated conditions for the control of activities of fishing vessels. Official Journal of the European Communities, L65/13. Available at http://stecf.jrc.ec.europa.eu/documents/43805/44876/07-09_SG-MOS+07-03+-+Evaluation+of+closed+areas+II.pdf (accessed 23 February 2015).

Anon. 2002. The sea fish (prohibited methods of fishing) (Firth of Clyde) order 2002. Scottish statutory instrument 2002. HMSO, No. 58. Available at http://faolex.fao.org/docs/html/uk36239.htm (accessed 23 February 2015).

Armstrong, C. W., and J. Falk-Petersen. 2008. Habitat-fisheries interactions: a missing link? ICES Journal of Marine Science 65:817–821.

Atkinson, C., M. Bergmann, and M. Kaiser. 2004. Habitat selection in whiting. Journal of Fish Biology 64:788–793.

Auster, P. J. 1998. A conceptual model of the impacts of fishing gear on the integrity of fish habitats. Conservation Biology 12:1198–1203.

Auster, P. J. 2005. Are deep-water corals important habitats for fishes? In Cold-Water Corals and Ecosystems, A. Freiwald and J.M. Roberts (eds). Berlin: Springer, 747–760.

Auster, P. J., K. Gjerde, E. Heupel, L. Watling, A. Grehan, and A. D. Rogers. 2010. Definition and detection of vulnerable marine ecosystems on the high seas: problems with the “move-on” rule. ICES Journal of Marine Science 68:254-264.

Auster, P. J., K. Joy, and P. C. Valentine. 2001. Fish species and community distributions as proxies for seafloor habitat distributions: The Stellwagen Bank National Marine Sanctuary example (Northwest Atlantic, Gulf of Maine). Environmental Biology of Fishes 60:331–346.

Auster, P., and R. Langton. 1999. The effects of fishing on fish habitat. American Fisheries Society Symposium 22:150–187.

Auster, P. J., R. J. Malatesta, R. W. Langton, L. Watting, P. C. Valentine, C. L. S. Donaldson, E. W. Langton, A. N. Shepard, and W. G. Babb. 1996. The impacts of mobile fishing gear on seafloor habitats in the gulf of Maine (Northwest Atlantic): Implications for conservation of fish populations. Reviews in Fisheries Science 4:185–202.

Axelsson, M., S. Dewey, L. Plastow, and J. Doran. 2009. Mapping of marine habitats and species within the Community Marine Conservation Area at Lamlash Bay. Scottish Natural Heritage Commissioned Report No. 346.Available at http://www.snh.gov.uk/publications-data-and-research/publications/search-the-catalogue/publication-detail/?id=1508 (accessed 19 June 2014).

Bailey, J. 1982. Implications of ‘muddling through’ for wildlife management. Wildlife Society Bulletin 10:363–369.

Bailey, N., D. M. Bailey, L. Bellini, P. G. Fernandes, C. Fox, S. Heymans, S. Holmes, J. Howe, S. Hughes, S. Magill, F. McIntryre, D. McKee, M. R. Ryan, I. Smith, G. Tyldsely, R. Watret, and W. R. Turrell. 2011. Marine Scotland Science Report 0911:1-292. The West of Scotland Marine Ecosystem : A Review of Scientific Knowledge. Marine Scotland Science, Aberdeen, UK. Available at http://www.gov.scot/resource/doc/295194/0123085.pdf (accessed 03 March 2014).

Barreto, E., and N. Bailey. 2015. Marine Scotland Science: Fish and Shellfish Stocks: 2015 Edition. Marine Scotland Science. Available at: http://www.gov.scot/Publications/2015/05/4861/downloads (accessed 11 November 2016).

Barry, S., and J. Elith. 2006. Error and uncertainty in habitat models. Journal of Applied Ecology 43:413-423.

Bartholomew, A., R. J. Diaz, and G. Cicchetti. 2000. New dimensionless indices of structural habitat complexity: Predicted and actual effects on a predator’s foraging success. Marine Ecology Progress Series 206:45–58.

Bastrikin, D. K., A. Gallego, C. P. Millar, I. G. Priede, and E. G. Jones. 2014. Settlement length and temporal settlement patterns of juvenile cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and whiting (*Merlangius merlangus*) in a northern North Sea coastal nursery area. ICES Journal of Marine Science 71:2101–2113.

Baum, H.K. and B. Worm. 2009. Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology 78: 699–714.

Beaugrand, G., K., K. M. Brander, J. A. Lindley, S. Souissi, and P. Reid. 2003. Plankton effect on cod recruitment in the North Sea. Nature 426:661-664.

Beaumont, N. J., M. C. Austen, J. P. Atkins, D. Burdon, S. Degraer, T. P. Dentinho, S. Derous, P. Holm, T. Horton, E. van Lerland, A. H. Marboe, D. J. Starkey, M. Townsend, and T. Zarzycki. 2007. Identification, definition and quantification of goods and services provided by marine biodiversity:

Implications for the ecosystem approach. Marine Pollution Bulletin 54:253-265.

Beaumont, N. J., M. C. Austen, S. C. Mangi, and M. Townsend. 2008. Economic valuation for the conservation of marine biodiversity. Marine Pollution Bulletin 56:386-396.

Beck, M. W., K. L. Heck, L. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. 2001. The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates. BioScience 51:633-641.

Beddington, J.K., D. Agnew, and C. Clark. 2007. Current problems in the management of marine fisheries. Science 316:1713-1716.

Berger, W. H., and F. L. Parker. 1970. Diversity of planktonic foraminifera in deep-sea sediments. Science 168:1345-1347.

Bernard, A. T. F., and Gotz, A. 2012. Bait increases the precision in count data from remote underwater video for most subtidal reef fish in the warm-temperate Agulhas bioregion. Marine Ecological Progress Series 471:235-252.

Bertelli, C. M., and R. K. F. Unsworth. 2014. Protecting the hand that feeds us: Seagrass (*Zostera marina*) serves as commercial juvenile fish habitat. Marine Pollution Bulletin 83:425-429.

Beyer, H. L., D. T. Haydon, J. M. Morales, J. L. Frair, M. Hebblewhite, M. Mitchell, and J. Matthiopoulos. 2010. The interpretation of habitat preference metrics under use-availability designs. Royal Society of London B-: Biological Sciences 365:2245-2254.

BGS (British Geological Survey). 2016. Map record details. Available at: http://www.bgs.ac.uk/data/maps/maps.cfc?method=viewRecord&mapId=10648 (accessed 28 January 2016).

Bjørnstad, O. N., J. M. Fromentin, N. C. Stenseth, and J. Gjøsaeter. 1999. Cycles and trends in cod populations. Proceedings of the National Academy of Sciences of the United States of America 96:5066-5071.

Blaxter, J. H. S., and W. Dickson. 1959. Observations of swimming speeds of fish. ICES Journal of Marine Science 24:472-479.

Block, W.M., and L. A. Brennan. 1993. The habitat concept in ornithology. Current Ornithology 11:35-91.

Bohnsack, J. A. 1991. Habitat structure and the design of artificial reefs. In Habitat Structure: the Physical Arrangement of Objects in Space, S.S. Bell et al. (eds) London: Chapman and Hall, 412-426.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127-35.

Borja, A., M. Elliott, J. H. Andersen, A. C. Cardoso, J. Carstensen, J. G. Ferreira, A. S. Heiskanen, J. C. Marques, J. M. Neto, H. Teixeira, L. Uusitalo, M. C. Uyarra, and N. Zampoukas. 2013. Good Environmental Status of marine ecosystems: What is it and how do we know when we have attained it? Marine Pollution Bulletin 76:16-27.

Boutros, N., M. R. Shortis, and E. S. Harvey. 2015. A comparison of calibration methods and system configurations of underwater stereo-video systems for applications in marine ecology. Limnology and Oceanography: Methods 13:1-13.

Bradbury, I. R., B. J. Laurel, D. Robichaud, G. A. Rose, P. V. R. Snelgrove, R. S. Gregory, D. Cote, and M. J. S. Windle. 2008. Discrete spatial dynamics in a marine broadcast spawner: Re-evaluating scales of connectivity and habitat associations in Atlantic cod (*Gadus morhua* L.) in Coastal Newfoundland. Fisheries Research 91:299–309.

Breen, M., J. Dyson, F. G. O'Neill, E. Jones, and M. Haigh. 2004. Swimming endurance of haddock (*Melanogrammus aeglefinus* L.) at prolonged and sustained swimming speeds, and its role in their capture by towed fishing gears. ICES Journal of Marine Science 61:1071–1079.

Brickman, D. 2003. Controls on the distribution of Browns Bank juvenile haddock. Marine Ecology Progress Series 263: 235-246.

Brown, B. L. 2003. Spatial heterogeneity reduces temporal variability in stream insect communities. Ecology Letters 6:316–325.

Brown, C. J., S. J. Smith, P. Lawton, and J. T. Anderson. 2011. Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. Estuarine, Coastal and Shelf Science 92:502–520.

Buckland, S. T., A. E. Magurran, R. E. Green, and R. M. Fewster. 2005. Monitoring change in biodiversity through composite indices. Philosophical transactions of the Royal Society B 360:243–254.

Buckland, S. T., A. Studeny, A. E. Magurran, J. Illian, and S. Newson. 2011. The geometric mean of relative abundance indices: a biodiversity measure with a difference. Ecosphere 2:1–15.

Buhl-Mortensen, L., P. Buhl-Mortensen, M. F. J. Dolan, J. Dannheim, V. Bellec, and B. Holte. 2012. Habitat complexity and bottom fauna composition at different scales on the continental shelf and slope of northern Norway. Hydrobiologia 685:191–219.

Bundy, A., and L. Fanning. 2005. Can Atlantic cod (*Gadus morhua*) recover? Exploring trophic explanations for the non-recovery of the cod stock on the eastern Scotian Shelf, Canada. Canadian Journal of Fisheries and Aquatic Science 1489:1474–1489.

Burrows, M. T. M., R. Harvey, and L. Robb. 2008. Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. Marine Ecology Progress Series 353:1–12.

Burrows, M. T. 2012. Influences of wave fetch, tidal flow and ocean colour on subtidal rocky communities. Marine Ecology Progress Series 445:193–207.

Campana, S. E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59:197–242.

Campana, S. E., K. T. Frank, P. C. F. Hurley, P. A. Koeller, F. H. Page, and P. C. Smith. 1989. Survival and Abundance of Young Atlantic Cod (*Gadus morhua*) and Haddock (*Melanogrammus aeglefinus*) as Indicators of Year-class Strength. Canadian Journal of Fisheries and Aquatic Sciences 46:171–182.

Cappo, M., E. Harvey, and M. Shortis. 2006. Counting and measuring fish with baited video techniques - an overview. Australian Society for Fish Biology 101–114.

Cappo, M., P. Speare, and G. De'ath. 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.

Casaretto, L., M. Picciulin, K. Olsen, and A. D. Hawkins. 2014. Locating spawning haddock (*Melanogrammus aeglefinus*, Linnaeus, 1758) at sea by means of sound. Fisheries Research 154:127-134.

CEC (Council of the European Communities). 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Official Journal of the European Communities, L 206, 22/07/1992, 7-50. Available at: http://eur-lex.europa.eu/legal-content/EN/AUTO/?uri=uriserv:OJ.L_.1992.206.01.0007.01.ENG&toc=OJ:L:1992:206:TOC (accessed 30 December 2015).

Chave, J. 2013. The problem of pattern and scale in ecology: what have we learned in 20 years? Ecology letters 16:4-16.

Cheung, W. W. L., J. Pinnegar, G. Merino, M. C. Jones, and M. Barange. 2012. Review of climate change impacts on marine fisheries in the UK and Ireland. Aquatic Conservation: Marine and Freshwater Ecosystems 22:368-388.

Christensen, N. L., A. M. Bartuska, J. H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J. F. Franklin, J. A. MacMohon, R. F. Noss, D. J. Parsons, C. H. Peterson, M. G. Turner, and R. Woodmansee. 1996. The Report of the Ecological Society of America Committee on the Scientific Basis for Ecosystem Management. Ecological Applications 6:665-691.

Christie, H., K. M. Norderhaug, and S. Fredriksen. 2009. Macrophytes as habitat for fauna. Marine Ecology Progress Series 396:221-233.

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

Clarke, K., and R. Warwick. 2001. Change in Marine Communities: An approach to statistical analysis and interpretation, 2nd edition. Plymouth, PRIMER-E, 1-144.

Clarke, M. E., N. Tolimieri, and H. Singh. 2009. Using the seabed AUV to assess populations of groundfish in untrawlable areas. In The future of fisheries science in North America. Beamish R. J. and B. J. Rothschild (eds.). Fish and Fisheries Series. Springer Netherlands. : 357-372.

Clyde Forum. 2016. Firth of Clyde Forum. Available at: http://www.clydeforum.com/index.php (accessed 14 February 2016).

COAST (Community of Arran Seabed Trust. 2012. Proposed marine protected area south coasts of Arran. Community of Arran Seabed Trust. Available at http://arrancoast.com/website_pdf/COAST_Arran_South_MPA_proposal_9May_FinalP.pdf (accessed 19 May 2015).

Collie, J. S., S. J. Hall, M. J. Kaiser, and I. R. Poiner. 2000. A quantitative analysis of fishing impacts shelf-sea benthos. Journal of Animal Ecology 69:785-798.

Connor, D. W., J. H. Allen, N. Golding, L. Kerry, L. M. Lieberknecht, K. O. Northen, and J. B. Reker. 2004. The Marine Habitat Classification for Britain And Ireland. version 04.05. JNCC, Peterborough. Available at http://jncc.defra.gov.uk/marinehabitatclassification (accessed 15 April 2015).

Cook, R. M., S. J. Holmes, and R. J. Fryer. 2015. Grey seal predation impairs recovery of an over-exploited fish stock. Journal of Applied Ecology 52(4):969-979.

CPC (Coral Point Count). Tools and resources. Available at: http://cnso.nova.edu/cpce/ (accessed 08 October 2013).

Costanza, R. 1999. The ecological, economic, and social importance of the oceans. Ecological Economics 31:199-213.

Costanza, R., R. D'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V O'Neill, J. Paruelo, R. G. Raskin, P. Sutton, and M. van den Belt. 1997. The value of the world's ecosystem services and natural capital. Nature 387:253-260.

Costanza, R., R. de Groot, P. Sutton, S. van der Ploeg, S. J. Anderson, I. Kubiszewski, S. Farber, and R. K. Turner. 2014. Changes in the global value of ecosystem services. Global Environmental Change 26:52-158.

Costello, M. J., M. McCrea, A. Freiwald, T. Lundalv, L. Jonsson, B. J. Bett, T. C. E. van Weering, H. de Hass, M. J. Roberts, and D. Allen. 2005. Role of cold-water Lophelia pertusa coral reefs as fish habitat in the NE Atlantic. Cold-water Corals and Ecosystems: 771-805.

Cote, D., S. Moulton, D. A. Scruton, and R. S. McKinley. 2001. Microhabitat Use of Juvenile Atlantic Cod in a Coastal Area of Bonavista Bay, Newfoundland. Transactions of the American Fisheries Society 130:1217-1223.

Cote, D., S. Moulton, P. Frampton, D. Scruton, and R. McKinley. 2004. Habitat use and early winter movements by juvenile Atlantic cod in a coastal area of Newfoundland. Journal of Fish Biology 64:665-679.

Cote, D., L. Ollerhead, D. Scruton, and R. McKinley. 2003. Microhabitat use of juvenile Atlantic cod in a coastal area of Newfoundland determined by 2D telemetry. Marine Ecology Progress Series 265:227-234.

Crain, C. M., B. S. Halpern, M. W. Beck, and C. V Kappel. 2009. Understanding and managing human threats to the coastal marine environment. Annals of the New York Academy of Sciences 1162:39-62.

Crawley, M. J. 2012. The R book. John Wiley and Sons, west sussex, England.

Cribari-Neto, F., and A. Zeileis. 2010. Beta Regression in R. Journal of Statistical Software 34(2): 1-24. Available at: http://www.jstatsoft.org/v34/i02/ (accessed 15 October 2015).

Curtin, R., and R. Prellezo. 2010. Understanding marine ecosystem based management: a literature review. Marine Policy 34:821-830.

Cullmann, A. D. 2015. HandTill2001: Multiple Class Area under ROC Curve. R package version 0.2-10. Available at: http://CRAN.R-project.org/package=HandTill2001 (accessed 01 August 2015).

Dalley, E., and J. Anderson. 1997. Age-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in inshore/offshore northeast Newfoundland. Canadian Journal of Fisheries and Aquatic Science 54:168-176.

Darwin, C. 1872. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. London: John Murray, 6th edition.

DATRAS. 2015. DAtabase of TRAwl Surveys. Available at: www.datras.com (accessed 06 December 2015).

Dauvin, J. C., G. Bellan, and D. Bellan-Santini. 2008a. The need for clear and comparable terminology in benthic ecology. Part I. Ecological concepts. Aquatic Conservation: Marine and Freshwater Ecosystems 18:432-445.

Dauvin, J. C., G. Bellan, and D. Bellan-Santini. 2008b. The need for clear and comparable terminology in benthic ecology. Part II. Application of the European Directives. Aquatic Conservation: Marine and Freshwater Ecosystems 18:446-456.

Degnbol, P., H. Gislason, S. Hanna, S. Jentoft, J. R. Nielsen, S. Sverdrup-Jensen, and D. C. Wilson. 2006. Painting the floor with a hammer: technical fixes in fisheries management. Marine Policy 30:534–543.

Demain, D. K., A. Gallego, A. Jaworski, I. G. Priede, and E. G. Jones. 2011. Diet and feeding niches of juvenile *Gadus morhua*, *Melanogrammus aeglefinus* and *Merlangius merlangus* during the settlement transition in the northern North Sea. Journal of Fish Biology 79:89–111.

Deter, J., P. Descamp, P. Boissery, L. Ballesta, and F. Holon. 2012. A rapid photographic method detects depth gradient in coralligenous assemblages. Journal of Experimental Marine Biology and Ecology 418-419:75–82.

Diaz, R. J., M. Solan, and Valente, R. M. 2004. A review of approaches for classifying benthic habitats and evaluating habitat quality. Journal of Environmental Management 73:165–181.

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

Dobson, A. P., A. D. Bradshaw, and M. Baker. 1997. Hopes for the Future: Restoration Ecology and Conservation Biology. Science 277:515–522.

Drinkwater, K. 2005. The response of Atlantic cod (*Gadus morhua*) to future climate change. ICES Journal of Marine Science 62:1327–1337.

Du Preez, C. 2015. A new arc–chord ratio (ACR) rugosity index for quantifying three-dimensional landscape structural complexity. Landscape Ecology 30:181–192.

Dulvy, N. K., Y. Sadovy, and J. D. Reynolds. 2003. Extinction vulnerability in marine populations. Fish and Fisheries 4:25-64.

Dunlop, E. S., K. Enberg, C. Jørgensen, and M. Heino. 2009. Toward Darwinian fisheries management. Evolutionary Applications 2:245–259.

Dunlop, K. M., G. D. Ruxton, E. M. Scott, and D. M. Bailey. 2015. Absolute abundance estimates from shallow water baited underwater camera surveys; a stochastic modelling approach tested against field data. Journal of Experimental Marine Biology and Ecology 472:126-134.

Dunlop, K. M, M. Scott, D. Parsons, and D. Bailey. 2014. Do agonistic behaviours bias baited remote underwater video surveys of fish? Marine Ecology 36:810-818.

Dutilleul, P. 1993. Spatial heterogeneity and the design of ecological field experiments. Ecology 74:1646–1658.

Easton, R. R., S. S. Heppell, and R. W. Hannah. 2015. Quantification of Habitat and Community Relationships among Nearshore Temperate Fishes through Analysis of Drop Camera Video. Marine and Coastal Fisheries 7:87–102.

EC (European Commission). 2009. Green Paper. Reform of the Common Fisheries Policy. Brussels, 22.4.2009,COM(2009) 163 final. Available at: http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=COM:2009:0163:FIN:EN:PDF (accessed 08 February 2016).

EDINA Geology Digimap Service 1:250 000 Offshore Geology [SHAPE geospatial data], Scale 1:250000, Tiles: GB, Updated: 1 June 2007, BGS. 2007. Lexicon of Named Rock Units. [XLS geosp11111111atial data], Scale 1:50000, Tiles: GB. 2011, BGS, Using: EDINA Geology Digimap Service. Available at: http://digimap.edina.ac.uk (accessed 28 May 2015).

Edwards, A. 1980. Ecological studies of the kelp, *Laminaria hyperborea* , and its associated fauna in South-West Ireland. Ophelia 19:47–60.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. a. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. C. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129-151.

Elith, J., and J. R. Leathwick. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology, Evolution, and Systematics 40:677–697.

Elliott, M., and D. S. McLusky. 2002. The need for definitions in understanding estuaries. Estuarine, Coastal and Shelf Science 55:815–827.

Ellis, T., and R. Gibson. 1995. Size-selective predation of 0-group flatfishes on a Scottish coastal nursery ground. Marine Ecology Progress Series 127:27–37.

Enberg, K., C. Jørgensen, E. S. Dunlop, M. Heino, and U. Dieckmann. 2009. Implications of fisheries-induced evolution for stock rebuilding and recovery. Evolutionary Applications 2:394–414.

Eschmeyer, W. N., R. Fricke, J. D. Fong, and D. Polack. 2010. Marine fish diversity: history of knowledge and discovery (Pisces). Zootaxa 2525:19–50.

EEA (European Environment Agency). 2011. Status of marine fish stocks. AC09375827, Anonymous, ed. Review of the state of world marine fishery resources. Available at: http://www.eea.europa.eu/data-and-maps/indicators/status-of-marine-fish-stocks/status-of-marine-fish-stocks-8 (accessed 21 January 2016).

EU (European Union). 2008. Directive 2008/56/EC of the European Parliament and of the Council 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, L 164, 25/06/2008, 19-40. Available at: http://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32008L0056&from=EN (accessed 27 November 2014).

EU. 2014. DIRECTIVE 2014/89/EU OF THE EUROPEAN PARLIAMENT AND OF THE COUNCIL of 23 July 2014 establishing a framework for maritime spatial planning. Available at: http://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32014L0089&from=EN (accessed 23 December 2015).

Evans, J. L., F. Peckett, and K. L. Howell. 2015. Combined application of biophysical habitat mapping and systematic conservation planning to assess efficiency and representativeness of the existing High Seas MPA network in the Northeast Atlantic. ICES Journal of Marine Science 72:1483–1497.

FAO (Food and Agriculture Organization of the United Nations). 2009. International guidelines for the management of deep-sea fisheries in the high seas. Rome: FAO. Available at: http://www.fao.org/docrep/011/i0816t/i0816t00.htm (accessed 20 July 2014).

FAO (Food and Agriculture Organization) of the United Nations. 2011. Review of the state of world marine fishery resources. FAO and fisheries aquaculture technical paper 569. Rome. Available at: http://www.fao.org/docrep/015/i2389e/i2389e.pdf (accessed 21 January 2016).

FAO (Food and Agricultural Organisation). 2014. The State of World Fisheries and Aquaculture, opportunities and challenges, Rome. Available at: http://www.fao.org/3/a-i3720e.pdf (accessed 11 February 2015).

Faraway, J. J. 2005. Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. CRC press.

Fernandes, P. G., and R. M. Cook. 2013. Reversal of Fish Stock Decline in the Northeast Atlantic. Current Biology 23:1432–1437.

Fernández-Chacón, A., E. Moland, S. H. Espeland, and E. M. Olsen. 2015. Demographic effects of full vs. partial protection from harvesting: inference from an empirical before-after control-impact study on Atlantic cod. Journal of Applied Ecology 52:1206–1215.

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

Fitzpatrick, B., E. Harvey, A. Heyward, E. Twiggs, and J. Colquhoun. 2012. Habitat specialization in tropical continental shelf demersal fish assemblages. PloS one 7:e39634.

Fletcher, K.M., and S. E. O'Shea. 2000. Essential fish habitat: Does calling it essential make it so? Environmental Law 30:51–98.

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

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, and J. H. Helkowski. 2005. Global Consequences of Land Use. Science 309:570–574.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual review of ecology and systematics 35:557–581.

Francis, R.C., M. A. Hixon, M. E. Clarke, S. A. Murawski, and S. Ralston. 2007. Ten commandments for ecosystem-based fisheries scientists. Fisheries 32:217–233.

Fraschetti, S., A. Terlizzi, and F. Boero, F. 2008. How many habitats are there in the sea (and where)? Journal of Experimental Marine Biology and Ecology 366:109–115.

Freemark, K. E., and H. G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biological Conservation 36:115–141.

Freese, L., P. J. Auster, J. Heifetz, and B. L. Wing. 1999. Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. Marine Ecology Progress Series 182:119–126.

Friedlander, A.M., and J. D. Parrish. 1998a. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. Journal of Experimental Marine Biology and Ecology 224:1–30.

Friedlander, A.M., and J. D. Parrish. 1998b. Temporal dynamics of fish communities on an exposed shoreline in Hawaii. Environmental Biology of Fishes 53:1–18.

Friedman, A., O. Pizarro, S. B. Williams, and M. Johnson-Roberson. 2012. Multi-scale measures of rugosity, slope and aspect from benthic stereo image reconstructions. PloS one 7:e50440.

Fitzpatrick, B., E. Harvey, A. Heyward, E. Twiggs, and J. Colquhoun. 2012. Habitat specialization in tropical continental shelf demersal fish assemblages. PloS one 7:e39634.

Fromentin, J. M., N. C. Stenseth, J. Gjøsæter, O. N. Bjørnstad, W. Falck, and T. Johannessen. 1997. Spatial patterns of the temporal dynamics of three gadoid species along the Norwegian Skagerrak coast. Marine Ecology Progress Series 155:209–222.

Gaillard, J. M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 365:2255–65.

Galley, E., P. Wright, and F. Gibb. 2006. Combined methods of otolith shape analysis improve identification of spawning areas of Atlantic cod. ICES Journal of Marine Science 63:1710–1717.

Galparsoro, I., D. W. Connor, Á. Borja, A. Aish, P. Amorim, T. Bajjouk, C. Chambers, R. Coggan, G. Dirberg, H. Ellwood, D. Evans, K. L. Goodin, A. Grehan, J. Haldin, K. Howell, C. Jenkins, N. Michez, G. Mo, P. Buhl-Mortensen, B. Pearce, J. Populus, M. Salomidi, F. Sánchez, A. Serrano, E. Shumchenia, F. Tempera, and M. Vasquez. 2012. Using EUNIS habitat classification for benthic mapping in European seas: Present concerns and future needs. Marine Pollution Bulletin 64:2630–2638.

Gamfeldt, L., H. Hillebrand, and P. R. Jonsson. 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. Ecology 89:1223–1231.

Gavaris, S. 2009. Fisheries management planning and support for strategic and tactical decisions in an ecosystem approach context. Fisheries Research 100:6–14.

GEBCO (General Bathymetric Chart of the Oceans). 2014. Gridded bathymetry data. Available at: https://www.bodc.ac.uk/data/online_delivery/gebco/ (accessed 23 June 2014).

Gibb, F. M., I. M. Gibb, and P. J. Wright. 2007. Isolation of Atlantic cod (*Gadus morhua*) nursery areas. Marine Biology 151:1185–1194.

Gibb, F. M., P. J. Wright, I. M. Gibb, and M. O. Sullivan. 2004. Fisheries Research Services Internal Report 11 / 04 Haddock and Whiting spawning areas. Marine Scotland Science.

Gibson, R. N. 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. Netherlands Journal of Sea Research 32:191–206.

Gibson, R. N., L. Robb, M. T. Burrows, and A. D. Ansell. 1996. Tidal, diel and longer term changes in the distribution of fishes on a Scottish sandy beach. Marine Ecology Progress Series 130:1–17.

Girdhar, Y., and D. Gregory. 2014. Exploring underwater environments with curiosity. Computer and Robot Vision (CRV). Canadian Conference on. IEEE. Montreal, QC. 104-110.

Goetze, J. S., S. D. Jupiter, T. J. Langlois, S. K. Wilson, E. S. Harvey, T. Bond, and W. Naisilisili. 2015. Diver operated video most accurately detects the impacts of fishing within periodically harvested closures. Journal of Experimental Marine Biology and Ecology 462:74–82.

GIMP (GNU Image Manipulation Program). The Free and Open Source Image Editor. Available at: https://www.gimp.org/ (accessed 22 June 2013).

Gorman, A. M., R. S. Gregory, and D. C. Schneider. 2009. Eelgrass patch size and proximity to the patch edge affect predation risk of recently settled age 0 cod (*Gadus*). Journal of Experimental Marine Biology and Ecology 371:1–9.

Gotceitas, V., and J. A. Brown. 1993. Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. Oecologia 93:31–37.

Grant, S. M., and J. A. Brown. 1998. Nearshore settlement and localized populations of age 0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland. Canadian journal of fisheries and aquatic sciences 55:1317–1327.

Gratwicke, B., and M. R Speight. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. Journal of Fish Biology 66:650–667.

Gregory, R., and J. Anderson. 1997. Substrate selection and use of protective cover by juvenile Atlantic cod *Gadus morhua* in inshore waters of Newfoundland. Marine Ecology Progress Series 146:9–20.

Grol, M., A. Rypel, and I. Nagelkerken. 2014. Growth potential and predation risk drive ontogenetic shifts among nursery habitats in a coral reef fish. Marine Ecology Progress Series 502:229–244.

Guarinello, M.L., E. J. Shumchenia, and J. W. King. 2010. Marine habitat classification for ecosystem-based management: a proposed hierarchical framework. Environmental Management 45:793–806.

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

Hall, S. J., D. Raffaelli, D. J. Basford, M. R. Robertson, and R. Fryer. 1990. The feeding relationships of the larger fish species in a Scottish sea loch. Journal of Fish Biology 37:775–791.

Hall, L.S., P. R. Krausman, and M. L. Morrison. 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin 25:173–182.

Hall-Spencer, J. M., J. Grall, P. G. Moore, and R. J. Atkinson. 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., K. A Selkoe, F. Micheli, and C. V Kappel. 2007. Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. Conservation biology: The Journal of the Society for Conservation Biology 21:1301–15.

Halpern, B. S., S. E. Lester, and K. L. McLeod. 2010. Placing marine protected areas onto the ecosystem-based management seascape. Proceedings of the National Academy of Sciences of the United States of America 107:18312–18317.

Halpern, B. S., S. Walbridge, K. A. Selkoe, C. V. Kappel, F. Micheli, C. D'Agrosa, J. F. Bruno, K. S. Casey, C. Ebert, H. E. Fox, R. Fujita, D. Heinemann, H. S. Lenihan, E. M. P. Madin, M. T. Perry, E. R. Selig, M. Spalding, R. Steneck, and R. Watson. 2008. A Global Map of Human Impact on Marine Ecosystems. Science 319:948–952.

Hammer, M., A. M. Jansson, and B. O. Jansson. 1993. Diversity Change and Sustainability and Implications for fisheries. Ambio 22:97–105.

Hand, D. J., and R. J. Till. 2001. A Simple Generalisation of the Area Under the ROC Curve for Multiple Class Classification Problems. Machine Learning 45:171–186.

Harvey, E. S., D. Fletcher, and M. Shortis. 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., J. Goetze, B. McLaren, T. Langlois, and M. R. Shortis. 2010. Influence of Range, Angle of View, Image Resolution and Image Compression on Underwater Stereo-Video Measurements: High-Definition and Broadcast-Resolution Video Cameras Compared. Marine Technology Society Journal 44:75–85.

Harvey, E. S., M. Cappo, and J. Butler. 2007. Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. Marine Ecology Progress Series 350:245–254.

Harvey, E.S., and M. R. Shortis. 1995. A System for Stereo-Video Measurement of Sub-Tidal Organisms. Marine Technology Society Journal 29:10–22.

Harvey, E. S., and M. R. Shortis. 1998. Calibration Stability of an Underwater Stereo Video System : Implications for Measurement Accuracy and Precision. Marine Technology Society Journal 32:3-17.

Harvey, R., and R. Batty. 2002. Cutaneous taste buds in gadoid fishes. Journal of fish biology 60:583–592.

Heath, M. R., and A. Gallego. 1997. From the biology of the individual to the dynamics of the population: bridging the gap in fish early life studies. Journal of Fish Biology 51:1–29.

Heath, M. R., and A. Gallego. 1998. Bio-physical modelling of the early life stages of haddock, *Melanogrammus aeglefinus* , in the North Sea. Fisheries Oceanography 7:110–125.

Heath, M. R., and D. C. Speirs. 2012. Changes in species diversity and size composition in the Firth of Clyde demersal fish community (1927-2009). Proceedings of the Royal Society 279:543–52.

Heath, M. R., P. A. Kunzlik, A. Gallego, S. J. Holmes, and P. J. Wright. 2008. A model of meta-population dynamics for North Sea and West of Scotland cod—The dynamic consequences of natal fidelity. Fisheries Research 93:92–116.

Heath, M. R., and R. G. Lough. 2007. A synthesis of large-scale patterns in the planktonic prey of larval and juvenile cod (*Gadus morhua*). Fisheries Oceanography 16:169–185.

Heath, M. R., F. C. Neat, J. K. Pinnegar, D. G. Reid, D. W. Sims, and P. J. Wright. 2012. Review of climate change impacts on marine fish and shellfish around the UK and Ireland. Aquatic Conservation: Marine and Freshwater Ecosystems 22:337–367.

Heino, M., and O. R. Godø. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Bulletin of Marine Science 70:639-656

Hermansen, Ø., J. R. Isaksen, and B. Dreyer. 2012. Challenging spatial and seasonal distribution of fish landings—Experiences from vertically integrated trawlers and delivery obligations in Norway. Marine Policy 36:206–213.

Hiddink, J. G., S. Jennings, M. J. Kaiser, A. M. Queirós, D. E. Duplisea, and G. J. Piet. 2006. Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. Canadian Journal of Fisheries and Aquatic Sciences 63:721–736.

Hilborn, R. 2007. Moving to sustainability by learning from successful fisheries. Ambio 36:296–303.

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

Hilborn, R., A. E. Punt, and J. Orensanz. 2004a. Beyond band-aids in fisheries management: fixing world fisheries. Bulletin of Marine Science 74:493-507.

Hilborn, R., K. Stokes, J. J. Maguire, T. Smith, L. W. Botsford, M. Mangel, J. Orensanz, A. Parma, J. Rice, J. Bell, K. L. Cochrane, S. Garcia, S. J. Hall, G. P. Kirkwood, K. Sainsbury, G. Stefansson, and C. Walters. 2004b. When can marine reserves improve fisheries management? Ocean and Coastal Management 47:197–205.

Hill, M. O. 1973. Diversity and Evenness: A Unifying Notation and Its Consequences. Ecology 54:427-432.

Hiscock, K., A. Southward, I. A. N. Tittley, and S. Hawkins. 2004. Effects of changing temperature on benthic marine life in Britain and Ireland. Aquatic Conservation: Marine and Freshwater Ecosystems 14:333-362.

Hislop, J. R. G. 1975. The breeding and growth of whiting, *Merlangius merlangus* in captivity. ICES Journal of Marine Science 36:119–127.

Hislop, J. R. G. 1996. Changes in North Sea gadoid stocks. ICES Journal of Marine Science 53:1146–1156.

Holmes, K. W., K. P. Van Niel, B. Radford, G. A. Kendrick, and S. L. Grove. 2008. Modelling distribution of marine benthos from hydroacoustics and underwater video. Continental Shelf Research 28:1800–1810.

Holmes, S. J., C. P. Millar, R. J. Fryer, and P. J. Wright. 2014. Gadoid dynamics: differing perceptions when contrasting stock vs. population trends and its implications to management. ICES Journal of Marine Science 71:1-10.

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

Hosmer J. R., D. W. Lemeshow, S. and R. X. Sturdivant. 2013. Logistic Regression Models for Multinomial and Ordinal Outcomes. Applied Logistic Regression, Third Edition, 269-311. Available at: http://onlinelibrary.wiley.com.ezproxy.lib.gla.ac.uk/doi/10.1002/9781118548387.ch5/pdf (accessed 15 August 2015).

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous Inference in General Parametric Models. Biometrical Journal 50(3):346–363.

Howarth, L. M., S. E. Pickup, L. E. Evans, T. J. Cross, J. P. Hawkins, C. M. Roberts, and B. D. Stewart. 2015. Sessile and mobile components of a benthic ecosystem display mixed trends within a temperate marine reserve. Marine Environmental Research 107:8–23.

Howell, K. L., R. Holt, I. P. Endrino, and H. Stewart. 2011. When the species is also a habitat: Comparing the predictively modelled distributions of *Lophelia pertusa* and the reef habitat it forms. Biological Conservation 144:2656-2665.

Hsu, S. L., and J. E. Wilen. 1997. Ecosystem management and the 1996 Sustainable Fisheries Act. Ecology Law Quarterly 24:799-812.

Hunter, W. R., and M. D. J. Sayer. 2009. The comparative effects of habitat complexity on faunal assemblages of northern temperate artificial and natural reefs. ICES Journal of Marine Science 66:691–698.

Hutchings, J. A., and J. D. Reynolds. 2004. Marine Fish Population Collapses: Consequences for Recovery and Extinction Risk. BioScience 54:297-309.

Huwer, B., H. Hinrichsen, U. Böttcher, R. Voss, and F. Köster. 2014. Characteristics of juvenile survivors reveal spatio-temporal differences in early life stage survival of Baltic cod. Marine Ecology Progress Series 511:165–180.

ICES. 2007. Collection of acoustic data from fishing vessels. ICES Cooperative Research Report No. 287. 83 pp.

ICES. 2014. Report of the Working Group on Celtic Seas Ecoregion (WGCSE), 13-22. May, Copenhagen, Denmark. ICES CM 2014/ACOM:12. Available at: http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2014/WGCSE/01_02_Introduction_ExSumm_DataMethods_2014.pdf (accessed 12 December 2015).

ICES. 2015a. Cod (*Gadus morhua*) in division Via (West of Scotland). Available at: http://www.ices.dk/sites/pub/Publication%20Reports/Advice/2015/2015/cod-scow.pdf (accessed 08 February 2015).

ICES. 2015b. Haddock (*Melanogrammus aeglefinus*) in Subarea IV and Divisions VIa and IIIa West (North Sea, West of Scotland, Skagerrak). Available at: http://www.ices.dk/sites/pub/Publication%20Reports/Advice/2015/2015/had-346a.pdf (accessed 08 February 2015).

ICES. 2015c. Whiting (*Merlangius merlangus*) in Division VIa (West of Scotland). Available at: http://www.ices.dk/sites/pub/Publication%20Reports/Advice/2015/2015/whg-scow.pdf (accessed 08 February 2015).

ICES. 2015d. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK), 28 April-7 May, ICES HQ, Copenhagen, Denmark. ICES CM 2015/ACOM:13. 1031. Available at: http://ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2015/WGNSSK/02%20WGNSSK%20report%20-%20Executive%20Summary.pdf (accessed 12 December 2015).

Ings, D. W., R. S. Gregory, and D. C. Schneider. 2008. Episodic downwelling predicts recruitment of Atlantic cod, Greenland cod and white hake to Newfoundland coastal waters. Journal of Marine Research 66:529-561.

Isaacs, J. D., and R. A. Schwartzlose. 1975. Active Animals of the Deep-Sea Floor. Scientific American 233:84–91.

IUCN. 2015. The IUCN Red List of Threatened species. *Gadus morhua*. Available at: http://www.iucnredlist.org/details/8784/0 (accessed 24 December 2015).

Jackson, E., A. Rowden, A. Atrill, S. Bossey, and M. Jones. 2001. The importance of seagrass beds as a habitat for fishery species. Oceanography and Marine Biology Annual Review 39:269–304.

Jackson, J., M. Kirby, W. Berger, K. Bjorndal, L. Botsford, B. Bourque, R. Bradbury, R. Cooke, J. Erlandson, J. a Estes, T. P. Hughes, S. Kidwell, C. Lange, H. Lenihan, J. Pandolfi, C. Peterson, R. Steneck, M. Tegner, and R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-37.

Jaworski, A., and Penny, I. 2009. West of four - effectiveness of windsock area closure. Scottish Industry / Science Partnership (SISP). Report No 02/09. Marine Scotland Science. Available at: http://www.gov.scot/Uploads/Documents/SISP0209.pdf (accessed 11 February 2016).

Jennings, S., and M. J. Kaiser. 1998. The Effects of Fishing on Marine Ecosystems. Advances in Marine Biology 34:201–352

JNCC (Joint Nature Conservation Committee). 2016. Habitat Mapping. Available at: http://jncc.defra.gov.uk/page-1586 (accessed 10 January 2016).

Johnson, A. F. 2012. Determining the habitat requirements of demersal fish for the design of marine protected areas design of marine protected areas. University of Bangor. PhD thesis.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, P. C. D., S. E. Barry, H. M. Ferguson, and P. Müller. 2015. Power analysis for generalized linear mixed models in ecology and evolution. Method in Ecology and Evolution 6:133-142.

Jost, L. 2006. Entropy and diversity. Oikos 113:363–375.

Jost. L. 2015. The new synthesis of diversity indices and similarity measures. Available at: http://www.loujost.com/Statistics%20and%20Physics/Diversity%20and%20Similarity/EffectiveNumberOfSpecies.htm (accessed 15 August 205).

Juanes, F. 2007. Role of habitat in mediating mortality during the post-settlement transition phase of temperate marine fishes. Journal of Fish Biology 70:661–677.

Kaiser, H. F. 1960. The application of electronic computers to factor analysis. Educational and Psychological Measurement 20:141-151.

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

Kaiser, M. J., S. J. Rogers, and J. R. Ellis. 1999. Importance of benthic habitat complexity for demersal fish assemblages. American Fisheries Society Symposium 22:212–223.

Kamenos, N. A. 2004. Small-scale distribution of juvenile gadoids in shallow inshore waters; what role does maerl play? ICES Journal of Marine Science 61:422–429.

Kamenos, N. A., P. G. Moore, and J. M. Hall-Spencer. 2003. Substratum heterogeneity of dredged vs un-dredged maerl grounds. Journal of the Marine Biological Association of the UK 83:411-413.

Keats, D. W., and D. H. Steele. 1992. Diurnal feeding of juvenile cod (*Gadus morhua*) which migrate into shallow water at night in eastern Newfoundland. Journal of Northwest Atlantic Fishery Science 13:7–14.

Kenny, A. J., I. Cato, M. Desprez, G. Fader, R. T. E. Schüttenhelm, and J. Side. 2003. An overview of seabed-mapping technologies in the context of marine habitat classification. ICES Journal of Marine Science 60:411–418.

Kimmel, J. J. 1985. A new species-time method for visual assessment of fishes and its comparison with established methods. Environmental Biology of Fishes 12:23–32.

Kohler, K. E., and S. M. Gill. 2006. Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Computers and Geosciences 32:1259–1269.

Kovalenko, K.E., S. M. Thomaz, and D. M. Warfe. 2012. Habitat complexity: Approaches and future directions. Hydrobiologia 685:1–17.

Kraak, S. B. M., N. Bailey, M. Cardinale, C. Darby, J. A. A. De Oliveira, M. Eero, N. Graham, S. Holmes, T. Jakobsen, A. Kempf, E. Kirkegaard, J. Powell, R. D. Scott, E. J. Simmonds, C. Ulrich, W. Vanhee, and M. Vinther. 2013. Lessons for fisheries management from the EU cod recovery plan. Marine Policy 37:200–213.

Kramer, D. L., R. W. Rangeley, and L. J. Chapman. 1997. Habitat selection: patterns of spatial distributions from behavioural decisions. In Behavioural Ecology of Teleost Fishes, J.J. Godin (ed.). New York: Oxford University Press, 37-80.

Krausman, P.R. 1999. Some basic principles of habitat use. In Grazing Behavior of Livestock and Wildlife, K.L. Launchbaugh et al. (eds). Station Bulletin 70, Moscow, Idaho: Idaho Forest, Wildlife and Range Experiment Station, University of Idaho, 85-90. Available at: http://www.webpages.uidaho.edu/range456/readings/krausman.pdf (Accessed 25 January 2016).

Kutti, T., J. H. Fosså, and O. A. Bergstad. 2015. Influence of structurally complex benthic habitats on fish distribution. Marine Ecology Progress Series 520:175–190.

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

Langton, R., R. Steneck, V. Gotceitas, F. Juanes, and P. Lawton. 1996. The Interface between Fisheries Research and Habitat Management. North American Journal of Fisheries Management 16:1–7.

Laurel, B., A. Stoner, C. Ryer, T. Hurst, and A. Abookire. 2007. Comparative habitat associations in juvenile Pacific cod and other gadids using seines, baited cameras and laboratory techniques. Journal of Experimental Marine Biology and Ecology 351:42–55.

Laurel, B., C. H. Ryer, B. Knoth, and A. W. Stoner. 2009. Temporal and ontogenetic shifts in habitat use of juvenile Pacific cod (*Gadus macrocephalus*). Journal of Experimental Marine Biology and Ecology 377:28–35.

Laurel, B., R. Gregory, and J. Brown. 2003a. Predator distribution and habitat patch area determine predation rates on Age-0 juvenile cod *Gadus* spp. Marine Ecology Progress Series 251:245–254.

Laurel, B., R. Gregory, and J. Brown. 2003b. Settlement and distribution of Age-0 juvenile cod , *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation. Marine Ecology Progress Series 262:241–252.

Laurel, B., R. Gregory, J. Brown, J. Hancock, and D. Schneider. 2004. Behavioural consequences of density-dependent habitat use in juvenile cod *Gadus morhua* and *G. ogac*: the role of movement and aggregation. Marine Ecology Progress Series 272:257–270.

Leathwick, J. R., J. Elith, and T. Hastie. 2006. Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. Ecological Modelling 199:188–196.

Lekve, K., K. Enersen, S. Enersen, J. Gjosaeter, and N. Stenseth. 2006. Interannual variability in abundance and length of young coastal cod in the subtidal zone. Journal of Fish Biology 68:734–746.

Levin, S. 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967.

Lilley, R. J., and R. K. F. Unsworth. 2014. Atlantic Cod (*Gadus morhua*) benefits from the availability of seagrass (*Zostera marina*) nursery habitat. Global Ecology and Conservation 2:367–377.

Lilly, G. R., K. Wieland, B. J. Rothschild, S. Sundby, K. F. Drinkwater, K. M. Brander, G. Ottersen, J. E. Carscadden, G. B. Stenson, G. A. Chouinard, D. A. Swain, N. Daan, K. Enberg, M. O. Hammill, A. Rosing-Asvid, H. Svedäng, and A. Vázquez. 2008. Decline and recovery of Atlantic cod (*Gadus morhua*) stocks throughout the North Atlantic. Resiliency of gadid stocks to fishing and climate change 39:39-66.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Lindholm, J. B., P. J. Auster, M. Ruth, and L. Kaufman. 2001. Modeling the Effects of Fishing and Implications for the Design of Marine Protected Areas: Juvenile Fish Responses to Variations in Seafloor Habitat. Conservation Biology 15:424–437.

Linehan, J. E., R. S. Gregory, and D. C. Schneider. 2001. Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. Journal of Experimental Marine Biology and Ecology 263:25–44.

Liquete, C., N. Cid, D. Lanzanova, B. Grizzetti, and A. Reynaud. 2016. Perspectives on the link between ecosystem services and biodiversity: The assessment of the nursery function. Ecological Indicators 63:249–257.

Løkkeborg, S. 1998. Feeding behaviour of cod, *Gadus morhua*: activity rhythm and chemically mediated food search. Animal behaviour 56:371–378.

Løkkeborg, S., A. Fernö, and T. Jørgensen. 2002. Effect of position-fixing interval on estimated swimming speed and movement pattern of fish tracked with a stationary positioning system. Hydrobiologia 483:259–264.

Lotze, H. K. 2006. Depletion, Degradation, and Recovery Potential of Estuaries and Coastal Seas. Science 312:1806–1809.

Lough, R. G. 2010. Juvenile cod (*Gadus morhua*) mortality and the importance of bottom sediment type to recruitment on Georges Bank. Fisheries Oceanography 19:159–181.

Lough, R.G., P.C. Valentine, and D.C. Potter. 1989. Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. Marine Ecology Progress Series 56:1–12.

Lowry, M., H. Folpp, M. Gregson, and I. Suthers. 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.

Lucas, M. C., and E. Baras. 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. Fish and Fisheries 1:283-316.

Magill, S. H., and M. D. J. Sayer. 2004. Abundance of juvenile Atlantic cod (*Gadus morhua*) in the shallow rocky subtidal and the relationship to winter seawater temperature. Journal of the Marine Biological Association of the UK 84:439–442.

Magurran, A. E. 2004. Measuring Biological Diversity. John Wiley & Sons.

Mallet D, Pelletier D (2014) Underwater video techniques for observing coastal marine biodiversity: A review of sixty years of publications (1952–2012). Fisheries Research 154:44–62.

Mangel, M., P. Levin, and A. Patil. 2006. Using Life History and Persistence Criteria to Prioritize Habitats for Management and Conservation. Ecological applications 16:797–806.

Marasco, R. J., D. Goodman, C. B. Grimes, P. W. Lawson, A. E. Punt, and T. J. Quinn. 2007. Ecosystem-based fisheries management: some practical suggestions. Canadian Journal of Fisheries and Aquatic Sciences 64:928–939.

Marty, L., M. Rochet, and B. Ernande. 2014. Temporal trends in age and size at maturation of four North Sea gadid species: cod, haddock, whiting and Norway pout. Marine Ecology Progress Series 497:179–197.

Matthiopoulos, J., J. Fieberg, G. Aarts, J. L. Beyer, J. M. Morales, and D. T. Haydon. 2015. Establishing the link between habitat-selection and animal population dynamics. Ecological Monographs 85:413–436.

McCloskey, R. M., and R. K. F. Unsworth. 2015. Decreasing seagrass density negatively influences associated fauna. PeerJ 3:e1053.

McCormick, M. I. 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. Marine Ecology Progress Series 112:87–96.

McCoy, E. D., and S. S. Bell. 1991. Habitat structure: the evolution and diversification of a complex topic. In Habitat Structure: The Physical Arrangement of Objects in Space, S.S. Bell et al. (eds). London: Chapman and Hall, 4-27.

McEvoy, L. A., and J. McEvoy. 1992. Multiple spawning in several commercial fish species and its consequences for fisheries management, cultivation and experimentation. Journal of Fish Biology 41:125–136.

McIntyre, F., P. Fernandes, and W. R. Turrell. 2012. Scottish Marine and Freshwater Science Report Volume 3 Number 3: Clyde Ecosystem Review. Scottish Marine and Freshwater Science Report. Marine Scotland Science, 1-123. Available at http://www.gov.scot/Publications/2012/06/7562 (Accessed 03 March 2014).

McQuatters-Gollop, A. 2012. Challenges for implementing the Marine Strategy Framework Directive in a climate of macroecological change. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 370:5636–5655.

Misa, W. F. X. E., J. C. Drazen, C. D. Kelley, and V. N. Moriwake. 2013. Establishing species-habitat associations for 4 eteline snappers with the use of a baited stereo-video camera system. Fishery Bulletin 111:293-308.

MMO (Marine Management Organisation). 2015. UK Fisheries Statistics 2014. UK Sea Fisheries Annual Statistics: Available at: https://www.gov.uk/government/collections/uk-sea-fisheries-annual-statistics (accessed 12 December 2015).

Moland, E., E. M. Olsen, H. Knutsen, P. Garrigou, S. H. Espeland, A. R. Kleiven, C. Andre, and J. A. Knutsen. 2013. Lobster and cod benefit from small-scale northern marine protected areas: inference from an empirical before-after control-impact study. Proceedings of the Royal Society B: Biological Sciences 280:1-10.

Moore, C. H., E. S. Harvey, and K. Niel. 2010. The application of predicted habitat models to investigate the spatial ecology of demersal fish assemblages. Marine Biology 157:2717–2729.

Moore, C. H., J. C. Drazen, B. T. Radford, C. Kelley, and S. J. Newman. 2016. Improving essential fish habitat designation to support sustainable ecosystem-based fisheries management. Marine Policy 69:32–41.

Moore, C. H., K. Van Niel, and E. S. Harvey. 2011. The effect of landscape composition and configuration on the spatial distribution of temperate demersal fish. Ecography 34:425-435.

Morris, D. W. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1–13.

Morris, K. J., B. J. Bett, J. M. Durden, V. A. I. Huvenne, R. Milligan, D. O. B. Jones, S. McPhail, K. Robert, D. M. Bailey, and H. A. Ruhl. 2014. A new method for ecological surveying of the abyss using autonomous underwater vehicle photography. Limnology and Oceanography: Methods 12:795–809.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. Wildlife-Habitat Relationships: Concepts and Applications. Madison, Wisconsin: University of Wisconsin Press.

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

Murphy, D.D., and B. D. Noon. 1991. Coping with uncertainty in wildlife biology. The Journal of Wildlife Management 55:773–782.

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

Myers, R. A., J. A. Hutchings, and N. J. Barrowman. 1996. Hypotheses for the decline of cod in the North Atlantic. Marine Ecology Progress Series 138:293–308.

Myers, R. A., and N. G. Cadigan. 1993. Density-Dependent Juvenile Mortality in Marine Demersal Fish. Canadian Journal of Fisheries and Aquatic Sciences 50:1576–1590.

Nagelkerken, I., M. Sheaves, R. Baker, and R. M. Connolly. 2013. The seascape nursery: A novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish and Fisheries 16(2):362-371.

Nickell, L. A., and M. D. J. Sayer. 2009. Occurrence and activity of mobile macrofauna on a sublittoral reef: diel and seasonal variation. Journal of the Marine Biological Association of the United Kingdom 78:1061–1082.

O'Boyle, R., and M. Sinclair. 2012. Seal-cod interactions on the Eastern Scotian Shelf: Reconsideration of modelling assumptions. Fisheries Research 115-116:1–13.

Olenin, S., and J. P. Ducrotoy. 2006. The concept of biotope in marine ecology and coastal management. Marine Pollution Bulletin 53:20–29.

Olsen, E. M., and E. Moland. 2010. Fitness landscape of Atlantic cod shaped by harvest selection and natural selection. Evolutionary Ecology 25:695–710.

Olsen, E. M., J. Gjosaeter, and N. C. Stenseth. 2004. Evaluation of the Use of Visible Implant Tags in Age-0 Atlantic Cod. North American Journal of Fisheries Management 24:282–286.

Olsen, E. M., S. Aanes, S. Mehl, J. C. Holst, A. Aglen, and H. Gjøsæter. 2010. Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: A review of the biological value of the area. ICES Journal of Marine Science 67:87–101.

Onsrud, M. S. R., S. Kaartvedt, and M. T. Breien. 2005. In situ swimming speed and swimming behaviour of fish feeding on the krill *Meganyctiphanes norvegica*. Canadian Journal of Fisheries and Aquatic Sciences 62:1822-1832.

OSPAR. 2014. Intersessional Correspondence Group on the Coordination of Biodiversity Assessment and Monitoring. Available at: http://www.ospar.org/meetings/archive/intersessional-correspondence-group-on-the-coordination-of-biodiversity-assessment-and-monitoring-2 (accessed 16 January 2016).

Ottersen, G., D. O. Hjermann, and N. C. Stenseth. 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. Fisheries Oceanography 15:230-243.

Parma, A.M., R. Hilborn, and J. M. Orensanz. 2006. The good, the bad, and the ugly: learning from experience to achieve sustainable fisheries. Bulletin of Marine Science 78:411–427.

Paulo, J., P. J. Ribeiro, and P. J. Diggle. 2015. geoR: Analysis of Geostatistical Data. R package version 1.7-5.1. Available at: http://CRAN.R-project.org/package=geoR (accessed 12 October 2015).

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology & Evolution 10:430.

Pauly, D., and D. Zeller. 2016. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. Nature Communications 7:1–9.

Perry, R. I., P. Cury, K. Brander, S. Jennings, C. Möllmann, and B. Planque. 2010. Sensitivity of marine systems to climate and fishing: Concepts, issues and management responses. Journal of Marine Systems 79:427–435.

Perry, R. I., and S. Smith. 1994. Identifying habitat associations of marine fishes using survey data: an application to the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Science 51:589–602.

Persson, A., P. Ljungberg, M. Andersson, E. Götzman, and P. A. Nilsson. 2012. Foraging performance of juvenile Atlantic cod *Gadus morhua* and profitability of coastal habitats. Marine Ecology Progress Series 456:245–253.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190:231–259.

Pikitch, E. K., C. Santora, E. A. Babcock, A. Bakun, R. Bonfil, D. O. Conover, P. A. O. Dayton, P. Doukakis, D. Fluharty, B. Heneman, E. D. Houde, J. Link, P. A. Livingston, M. Mangel, M. K. McAllister, J. Pope, and K. J. Sainsbury. 2004. Ecosystem-Based Fishery Management. Science 305:346–347.

Pineda, J. 1994. Internal tidal bores in the nearshore: Warm-water fronts, seaward gravity currents and the onshore transport of neustonic larvae. Journal of Marine Research 52:427–458.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2014. Linear and nonlinear mixed effects models. R package version 3.1-118 Available at: http://CRAN.R-project.org/package=nlme (accessed 12 October 2015).

Pinnegar, J. K., W. L. Cheung, and M. Heath. 2010. MCCIP ARC Science Review 2010-11 Fisheries:1–19. Available at: www.mccip.org.uk/arc (accessed 12 December 2014).

Planque, B., and C. Fox. 1998. Interannual variability in temperature and the recruitment of Irish Sea cod. Marine Ecology Progress Series 172:101–105.

Planque, B., and T. Frédou. 1999. Temperature and the recruitment of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 56:2069–2077.

Potts, T., T. O'Higgins, and E. Hastings. 2012. Oceans of opportunity or rough seas? What does the future hold for developments in European marine policy? Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 370:5682–5700.

Priede, I. G., and N. Merrett. 1996. Estimation of abundance of abyssal demersal fishes; a comparison of data from trawls and baited cameras. Journal of Fish Biology 49:207–216.

Priede, I. G., P. M. Bagley, A. Smith, S. Creasey, and N. R. Merrett. 1994. Scavenging deep demersal fishes of the Porcupine Seabight, north-east

Atlantic: observations by baited camera, trap and trawl. Journal of the Marine Biological Association of the United Kingdom 74:481-498.

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

Probst, W. N., V. Stelzenmüller, and G. Kraus. 2013. A simulation-approach to assess the size structure of commercially exploited fish populations within the European Marine Strategy Framework Directive. Ecological indicators 24:621-632.

Reiss, H., S. Birchenough, A. Borja, L. Buhl-Mortensen, J. Craeymeersch, J. Dannheim, A. Darr, I. Galparsoro, M. Gogina, H. Neumann, J. Populus, A. M. Rengstorf, M. Valle, G. van Hoey, M. L. Zettler, and S. Degraer. 2015. Benthos distribution modelling and its relevance for marine ecosystem management. ICES Journal of Marine Science 72:297–315.

Reiss, H., S. Cunze, K. König, H. Neumann, and I. Kröncke. 2011. Species distribution modelling of marine benthos: a North Sea case study. Marine Ecology Progress Series 442:71–86.

Renkawitz, M. D., R. S. Gregory, and D. C. Schneider. 2011. Habitat dependant growth of three species of bottom settling fish in a coastal fjord. Journal of Experimental Marine Biology and Ecology 409:79-88.

Ribeiro, P. J and P. J. Diggle. 2015 geoR: Analysis of Geostatistical Data. R package version 1.7-5.1. Available at: http://CRAN.R-project.org/package=geoR (accessed 20 August 2015).

Rice, J. C. 2005. Understanding fish habitat ecology to achieve conservation. Journal of Fish Biology 67:1–22.

Rijnsdorp, A.D., G. J. Piet, and J. J. Poos. 2001. Effort allocation of the Dutch beam trawl fleet in response to a temporarily closed area in the North Sea. ICES Conference and Meeting (CM) Document 2001/N: 01, Copenhagen, Denmark: International Council for the Exploration of the Sea, 1–17. Available at: http://www.ices.dk/sites/pub/CM%20Doccuments/2001/N/N0101.pdf (accessed 21 September 2015).

Roberts, C. M., J. P. Hawkins, and F. R. Gell. 2005. The role of marine reserves in achieving sustainable fisheries. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 360:123–132.

Robin, X., N. Turck, A. Hainard, N. Tiberti, F. Lisacek, J. Sanchez, and F. Müller. 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinformatics, 12, 77. Available at: http://www.biomedcentral.com/1471-2105/12/77/ (accessed 11 June 2015).

Rogers, L., E. Olsen, H. Knutsen, and N. Stenseth. 2014. Habitat effects on population connectivity in a coastal seascape. Marine Ecology Progress Series 511:153–163.

Ronnegard, L., X. Shen, and M. Alam. 2010. hglm: A Package for Fitting Hierarchical Generalized Linear Models. The R Journal, 2(2): 20-28. Available at: http://journal.r-project.org/archive/2010-2/RJournal_2010-2_Roennegaard~et~al.pdf (accessed 12 October 2015).

Ross, D., K. Thompson, and J. E. Donnelly. 2009. State of the Clyde: Environment Baseline Report 110. SSMEI Clyde Pilot Project, Scottish Sustainable Marine Environment Initiative. Available at: http://www.gov.scot/seag/seagDocs/SEA-00236/8087.pdf (accessed 13 July 2013).

Ross, R. E., and K. L. Howell. 2013. Use of predictive habitat modelling to assess the distribution and extent of the current protection of 'listed' deep-sea habitats. Diversity and Distributions 19:433–445.

Rubec, P. J., J. C. Bexley, H. Norris, M. S. Coyne, M. E. Monaco, S. G. Smith and J. S. Ault. 1999. Suitability modeling to delineate habitat essential to sustainable fisheries. In Fish Habitat: Essential Fish Habitat and Habitat Rehabilitation, L.R. Beneka (ed.). American Fisheries Society Symposium 22:108–133.

Ryan, M. R., and D. M. Bailey. 2012. Trawling and Dredging in the Clyde Sea Area: History , Impacts and Prospects for Recovery. A report to the Sustainable Inshore Fisheries Trust. University of Glasgow. Available at: http://www.sift-uk.org/media/file/RRyan%20&%20Bailey%20(2012),%20Trawling%20and%20Dredging%20in%20the%20Clyde%20Sea%20Area,pdf.pdf (accessed 03 December 2012).

Ryan, M. R., S. Killen, R. Gregory, and P. Snelgrove. 2012. Predators and distance between habitat patches modify gap crossing behaviour of juvenile Atlantic cod (*Gadus morhua*, L. 1758). Journal of Experimental Marine Biology and Ecology 422-423:81–87.

Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecological Applications 9:135–151.

Sabatino, A. D., R. B. Murray, D. C. Speirs, and M. R. Heath. In Review. Modelling surges in the Clyde Sea. Natural Hazards.

Sale, P. F. 1991. Habitat structure and recruitment in coral reef fishes. In Habitat Structure: The Physical Arrangement of Objects in Space, S.S. Bell et al. (eds). London: Chapman and Hall, 197–210.

Sale, P. F., R. K. Cowen, B. S. Danilowicz, G. P. Jones, J. P. Kritzer, K. C. Lindeman, S. Planes, N. V. C. Polunin, G. R. Russ, Y. J. Sadovy, and R. S. Steneck. 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution 20:74–80.

SAMS (Scottish Association for Marine Science). 2013. Burrows Wave fetch model description. Available at: http://www.sams.ac.uk/michael-burrows/wave-fetch-model-description (accessed 26 January 2014).

Sanderson, E. W., M. Jaiteh, M. A. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002. The Human Footprint and the Last of the Wild. BioScience 52:891-904.

Santos, M.N., M. T. Oliveira, and J. Cúrdia. 2012. A comparison of the fish assemblages on natural and artificial reefs off Sal Island (Cape Verde). Journal of the Marine Biological Association of the United Kingdom 93:437–452.

Sarthou, C.M. 1999. An environmentalist's perspective on essential fish habitat. In Fish Habitat: Essential Fish Habitat and Habitat Rehabilitation, L.R. Beneka (ed.). American Fisheries Society Symposium 22:11–22.

Sayer, M. D. J, and C. Poonian. 2007. The influences of census technique on estimating indices of macrofaunal population density in the temperate rocky subtidal zone. Underwater Technology: The International Journal of the Society for Underwater 27:119–139.

Schmitten, R. 1999. Essential fish habitat: opportunities and challenges for the next millennium. In Fish Habitat: Essential Fish Habitat and Habitat Rehabilitation, L.R. Beneka (ed.). American Fisheries Society Symposium 22:3-10.

Schneider, D. C., M. J. Norris, and R. S. Gregory. 2008. Predictive analysis of scale-dependent habitat association: Juvenile cod (*Gadus* spp.) in eastern Newfoundland. Estuarine, Coastal and Shelf Science 79:71–78.

Schubert, P., W. Hukriede, R. Karez, and T. Reusch. 2015. Mapping and modeling eelgrass *Zostera marina* distribution in the western Baltic Sea. Marine Ecology Progress Series 522:79-95.

Scott, B., G. Marteinsdottir, and P. Wright. 1999. Potential effects of maternal factors on spawning stock-recruitment relationships under varying fishing pressure. Canadian Journal of Fisheries and Aquatic Sciences 56:1882–1890.

Scottish Government. 2015. South Arran Marine Conservation Order. Available at: http://www.gov.scot/Topics/marine/marine-environment/mpanetwork/MPAMGT/protectedareasmgt (accessed 22 December 2015).

SeaGIS (2013). EventMeasure user guide. Version 3.42. SeaGIS Pty Ltd. Available at: http://www.seagis.com.au/event.html (accessed 25 June 2013).

SeaZone. 2014. By Product. Available at: http://www.seazone.com/marine-maps/products (accessed 25 June 2014).

Sebens, K.P. 1991. Habitat structure and community dynamics in marine benthic systems. In Habitat Structure: The Physical Arrangement of Objects in Space, S.S. Bell et al. (eds). London: Chapman and Hall, 211-234.

Seitz, R. D., H. Wennhage, U. Bergström, R. N. Lipcius, and T. Ysebaert. 2014. Ecological value of coastal habitats for commercially and ecologically important species. ICES Journal of Marine Science 71:648–665.

Sherwood, G. D., and J. H. Grabowski. 2016. A comparison of cod life-history parameters inside and outside of four year-round groundfish closed areas in New England, USA. ICES Journal of Marine Science 73: 316-328.

Shortis, M. 2015. Calibration Techniques for Accurate Measurements by Underwater Camera Systems. Sensors 15:30810–30826.

Shortis, M., E. Harvey, and D. Abdo. 2009. A review of underwater stereo-image measurement for marine biology and ecology applications. Oceanography and Marine Biology: An Annual Review. 47:257-292Simpson, E. H. 1949. Measurement of Diversity. Nature 163:688-688.

Sinclair, M., R. Arnason, J. Csirke, Z. Karnicki, J. Sigurjonsson, H. Rune Skjoldal, and G. Valdimarsson. 2002. Responsible fisheries in the marine ecosystem. Fisheries Research 58:255–265.

Sing, T., O. Sander, N. Beerenwinkel, and T. Lengauer. 2005. ROCR: visualizing classifier performance in R. Bioinformatics, 21(20):7881. Available at: http://rocr.bioinf.mpi-sb.mpg.de (accessed 11 June 2015).

Skaug, H., D. Fournier, A. Nielsen, A. Magnusson, and B. Bolker. 2012. Generalized linear mixed models using AD Model Builder. R package version 0.7. 2.12. Available at: http://glmmadmb.r-forge.r-project.org/ (accessed 05 February 2015).

Smale, M. J., B. A. Roel, A. Badenhorst, A. and J. G. Field. 1993. Analysis of the demersal community of fish and cephalopods on the Agulhas Bank, South Africa. Journal of Fish Biology 43:169–191.

Smout, S., A. Rindorf, P. S. Hammond, J. Harwood, and J. Matthiopoulos. 2014. Modelling prey consumption and switching by UK grey seals. ICES Journal of Marine Science 71:81–89.

SNH (Scottish Natural Heritage). 2010. Priority Marine Features in Scottish territorial waters External peer review feedback. Available at: http://www.snh.gov.uk/docs/B1150960.pdf (accessed 11 February 2016).

SNH (Scottish Natural Heritage). 2014. South Arran Protected Area. Available at: http://www.snh.gov.uk/protecting-scotlands-nature/protected-areas/national-designations/mpas/mpa-arr/ (accessed 15 April 2015).

Sodhi, N. S., L. H. Liow, and F. A. Bazzaz. 2004. From Tropical and Avian Extinctions Forests. Annual Review of Ecology, Evolution, and Systematics 35:323-345.

Soetaert, K., and C. Heip. 1990. Sample-size dependence of diversity indices and the determination of sufficient sample size in a high-diversity deep-sea environment. Marine Ecology Progress Series 59:305-307.

Spatial ecology. 2013. Geospatial Modelling Environment. Available at: http://spatialecology.com/ (accessed 21 May 2013)

Spencer, M. L., A. W. Stoner, C. H. Ryer, and J. E. Munk. 2005. A towed camera sled for estimating abundance of juvenile flatfishes and habitat characteristics: Comparison with beam trawls and divers. Estuarine, Coastal and Shelf Science 64:497-503.

Staaterman, E., and C. B. Paris. 2014. Modelling larval fish navigation: The way forward. ICES Journal of Marine Science 71:918-924.

Stoner, A. W., B. J. Laurel, and T. P. Hurst. 2008. Using a baited camera to assess relative abundance of juvenile Pacific cod: Field and laboratory trials. Journal of Experimental Marine Biology and Ecology 354:202-211.

Sundblad, G., U. Bergstrom, A. Sandstrom, and P. Eklov. 2014. Nursery habitat availability limits adult stock sizes of predatory coastal fish. ICES Journal of Marine Science 71:672-680.

Svåsand, T., T. Kristiansen, T. Pedersen, A. V Salvanes, R. Engelsen, G. Naevdal, and M. Nødtvedt. 2000. The enhancement of cod stocks. Fish and Fisheries 1:173-205.

Takashina, N., and A. Mougi. 2014. Effects of marine protected areas on overfished fishing stocks with multiple stable states. Journal of Theoretical Biology 341:64-70.

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

Tews, J., U. Brose, and V. Grimm. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31:79-92.

Thrush, S. F., and P. K. Dayton. 2002. Disturbance to Marine Benthic Habitats by Trawling and Dredging: Implications for Marine Biodiversity. Annual Review of Ecology and Systematics 33:449-473.

Thrush, S. F., K. E. Ellingsen, and K. Davis. 2016. Implications of fisheries impacts to seabed biodiversity and ecosystem-based management. ICES Journal of Marine Science 73:i44-i50.

Thurstan, R. H., and C. M. Roberts. 2010. Ecological meltdown in the Firth of Clyde, Scotland: two centuries of change in a coastal marine ecosystem. PloS one 5:e11767.

Tupper, M., and R. Boutilier. 1995a. Effects of habitat on settlement , growth , and postsettlement survival of Atlantic cod *Gadus morhua*. Canadian Journal of Fisheries and aquatic science 52:1834-1841.

Tupper, M., and R. Boutilier. 1995b. Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. Marine Ecology Progress Series 118:295-300.

Turner, I. M. 1996. Species Loss in Fragments of Tropical Rain Forest: A Review of the Evidence. The Journal of Applied Ecology 33:200-209.

Tyler-Walters, H., B. James (eds.), C. Wilding, O. Durkin, C. Lacey, E. Philpott, L. Adams, P. D. Chaniotis, P. T. V. Wilkes, R. Seeley, M. Neilly, J. Dargie, and O. T. Crawford-Avis. 2012. Descriptions of Marine Protected Area (MPA) search features. A report produced by MarLIN (Marine Life Information Network), SMRU Ltd., Scottish Natural Heritage and the Joint Nature Conservation Committee, for the Scottish Marine Protected Areas Project. Available at: http://www.gov.scot/Topics/marine/marine-environment/mpanetwork/engagement/140312/searchfeature (accessed 11 February 2016).

Unsworth, R. K. F., J. R. Peters, R. M. McCloskey, and S. L. Hinder. 2014. Optimising stereo baited underwater video for sampling fish and invertebrates in temperate coastal habitats. Estuarine, Coastal and Shelf Science 150:281–287.

USDOC (US Department of Commerce). 1996. Magnuson-Stevens Fishery Conservation and Management Act as amended through October 11, 1996. National Oceanic and Atmospheric Administration Technical Memorandum NMFS-F/SPO-23. Silver Spring, Maryland: National Oceanic and Atmospheric Administration National Marine Fisheries Service. Available at: http://www.nmfs.noaa.gov/sfa/magact/ (accessed 15 June 2014).

Uzars, D. 2000. Cod (*Gadus morhua* L.) cannibalism in the Central Baltic: interannual variability and influence of recruit abundance and distribution. ICES Journal of Marine Science 57:324-329.

Vasconcelos, R. P., D. B. Eggleston, O. Le Pape, and I. Tulp. 2014. Patterns and processes of habitat-specific demographic variability in exploited marine species. ICES Journal of Marine Science 71:638–647.

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

Walkinshaw, H. J. 2014. An investigation of the most effective sampling method for marine benthos which balances sensitivity and efficiency using Coral Point Count . University of Glasgow, BSc dissertation.

Ware, S. J. 2009. The importance of inshore areas on the west coast of Scotland as nursery grounds for commercially important fish species. University of London. PhD thesis.

Warren, M. A., R. S. Gregory, B. J. Laurel, and P. V. R. Snelgrove. 2010. Increasing density of juvenile Atlantic (*Gadus morhua*) and Greenland cod (*G. ogac*) in association with spatial expansion and recovery of eelgrass (*Zostera marina*) in a coastal nursery habitat. Journal of Experimental Marine Biology and Ecology 394:154–160.

Warton, D. I., and F. K. C. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3-10.

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

Wentworth, C. 1922. A scale of grade and class terms for clastic sediments. The Journal of Geology 30:377–392.

Werner, E., and J. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15:393–425.

White, C., B. S. Halpern, and C. V Kappel. 2012. Ecosystem service trade off analysis reveals the value of marine spatial planning for multiple ocean uses. Proceedings of the National Academy of Sciences 109:4696–4701.

Wilding, T. A. C. A. Rose, and M. J. Downie. 2007. A novel approach to measuring subtidal habitat complexity. Journal of Experimental Marine Biology and Ecology 353:279-286.

Wilding, T. A., and M. D. J. Sayer. 2002. Evaluating artificial reef performance: approaches to pre- and post-deployment research. ICES Journal of Marine Science 59 (suppl.), S222-S230.

Wilson, S. K., N. A. J. Graham, and N. V. C. Polunin. 2006. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Marine Biology 151:1069–1076.

Worldometers. 2015. Current World Population. Available at: http://www.worldometers.info/world-population/ (accessed 30 January 2016).

Worm, B., E. Barbier, N. Beaumont, J. Duffy, C. Folke, B. Halpern, J. Jackson, H. Lotze, F. Micheli, S. R. Palumbi, E. Sala, K. Selkoe, J. Stachowicz, and R. Watson. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314:787–90.

Worm, B., R., J. Hilborn, T. Baum, J. Branch, C. Collie, M. J. Costello, E. Fogarty, J. Fulton, S. Hutchings, O. Jennings, H. Jensen, P. Lotze, T. Mace, C. McClanahan, S. Minto, A. Palumbi, D. Parma, A. Ricard, R. Rosenberg, R. Watson, and D. Zeller. 2009. Rebuilding global fisheries. Science 325:578–85.

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

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

Wright, P. J., and E. A. Trippel. 2009. Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. Fish and Fisheries 10(3):283-304.

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

Zajac, R. N. 1999. Understanding the sea floor landscape in relation to impact assessment and environmental management in coastal marine sediments. In Biogeochemical Cycling and Sediment Ecology, J.S. Gray et al. (eds). NATO ASI Series vol. 59. Dordrecht, Netherlands: Kluwer Academic Publishing, 211–227.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Gail et al. (eds.). Springer.