Monograph:
Law, Richard, Heath, Michael and Searle, Kate (2017) Scoping the background information for an ecosystem approach to fisheries in Scottish waters: Review of predator-prey interactions with fisheries, and balanced harvesting: A Report Commissioned by Fisheries Innovation Scotland (FIS) http://www.fiscot.org/. Research Report. Fisheries Innovation Scotland (FIS)

Fisheries
Innovation
Scotland

FIS013 – Scoping the background information for an ecosystem approach to fisheries in Scottish waters: Review of predator-prey interactions with fisheries, and balanced harvesting

A REPORT COMMISSIONED BY FIS
AND PREPARED BY

Michael Heath – University of Strathclyde

Published by: Fisheries Innovation Scotland (FIS)

This report is available at: http://www.fiscot.org.

Suggested Citation:

Heath, M., Law. R. and Searle. K. 2017. Scoping the background information for an ecosystem approach to fisheries in Scottish waters: Review of predator-prey interactions with fisheries, and balanced harvesting. A study commissioned by Fisheries Innovation Scotland (FIS) http://www.fiscot.org/

Title: FIS013 – Scoping the background information for an ecosystem approach to fisheries in Scottish waters: Review of predator-prey interactions with fisheries, and balanced harvesting

ISBN: 978-1-911123-10-1

First published: 2017

Fisheries Innovation Scotland: contract FIS013

Scoping the background information for an ecosystem approach to fisheries in Scottish waters: Review of predator-prey interactions with fisheries, and balanced harvesting

Project leader: Michael Heath (University of Strathclyde)
Workshop leaders: Richard Law (University of York), Kate Searle (Centre for Ecology and Hydrology)

Project partners:

University of Strathclyde	Robin Cook, Michael Heath, Douglas Speirs
Centre for Ecology and Hydrology, Edinburgh	Francis Daunt, Kate Searle, Sarah Wanless
Centre for Environment Fisheries and Aquaculture Science, Lowestoft	Kieran Hyder, John Pinnegar, Robert Thorpe
Edinburgh Napier University	Karen Diele
Marine Scotland Science	Neil Campbell, Peter Wright, James Thorburn
MRAG Ltd, London	Robert Arthur
North Atlantic Fisheries College	Paul Macdonald, Beth Mouat
Scottish Association for Marine Science	Clive Fox, Sheila Heymans
Scottish Fishermen's Federation	Ken Coull
Seawatch Foundation, Anglesey	Peter Evans
University of Aberdeen	Paul Fernandes
University of St Andrews	Phil Hammond, Sophie Smout
University of York	Richard Law

Invited experts

University of Bergen	Jeppe Kolding
Institute of Marine Research, Galway	David Reid

Lead author contact details:
Michael Heath: m.heath@strath.ac.uk
Richard Law: richard.law@york.ac.uk
Kate Searle: katrle@ceh.ac.uk

Co-support
The project was conceived though discussions in the **Marine Science and Technology Scotland (MASTS) Fisheries Forum**. Input to the project was also provided from the **NERC Marine Ecosystems Research Programme (MERP)** through the Centre for Ecology and Hydrology, Centre for Environment Fisheries and Aquaculture Science, Scottish Association for Marine Science, Seawatch Foundation, and University of Strathclyde.

Summary

The generic process of putting into practice an Ecosystem Approach to Fisheries has been set out in a series of FAO, IUCN and EU Working Group reports. Of foremost importance is the identification of key predator-prey relationships that are affected by fisheries. The first objective of this project was therefore to scope the background information on predator-prey interactions with fisheries to inform the implementation of an Ecosystem Approach in Scottish waters, and to identify key areas requiring further research.

Related to the principle of taking a more eco-friendly approach to fisheries is the concept of 'balanced harvesting'. This requires setting harvesting rate (fishing mortalities) to be proportional to production rates of size classes or species (or both), to keep the impact on the ecosystems small while allowing sustainable exploitation of the living resources they contain. The majority of highly managed fisheries are thought to be far from balanced. Hence the second objective of this project was to review the social, economic and technical practicalities of implementing a balanced harvesting scheme in Scottish fisheries.

The project achieved these goals by hosting two workshops attended by scientific experts and representative FIS Board members. The main deliverables were a) increased understanding of the issues that would be faced in implementing an Ecosystem Approach to fisheries in Scotland, and b) a prioritised catalogue of knowledge gaps and researchable constraints that can be used by FIS and other funding bodies as the basis for directing future research-spend.

Predator-prey interactions

The report identifies a) for each of the key fish stocks for Scotland, which are the main predators and prey; and b) for each of the main predators, how they are directly and indirectly affected by fisheries in Scotland. The headline conclusions are that, at current population levels, top-predators are in general unlikely to be capable of depleting fishery resources. An exception here is the case of grey seals on the west coast of Scotland, which appear to be having a significant impact on the recovery of cod stocks. In terms of the impact of fisheries on predators there is more scope for concern. Among the seabird species, black-legged kittiwake in particular are judged to be vulnerable to depletion of their food sources by fisheries. However, there remain uncertainties regarding the relative vulnerability of less well-studied seabird species (e.g., terns), seal and cetacean species to both direct (by-catch) and indirect (food depletion) effects from fisheries. This emerges as the key conclusion from the workshop.

The report identifies **ten research priorities**, illustrated by three case studies. The central point of these priorities is the need for much better information on where and when the key food concentrations for top predators occur, and how these can be protected from the effects of fishing so that Scotland's natural capital of birds, seals, cetaceans and elasmobranchs can co-exist with productive fisheries.

1. **Diet**: what are the diets of forage fish, predatory fish and top predators? How selective are they? How much do diets vary regionally and seasonally? How have diets varied over time? How does diet vary with age or size? How does competition between predators, or between predators and fisheries, affect the dietary niche width of marine top predators and their trophic interactions? How does diet vary over a spatial range in migratory predators?

2. **Marine Ecosystem Models**: what is the current scope, biological scale (e.g., trophic levels, guilds, species) and spatial extent (e.g., geographic area) of marine ecosystem models? What models have been developed for Scottish or UK waters? How can ensemble modelling be used to improve simulations of the marine environment, particularly in terms of characterising risk, thereby improving the quality of decision-making?

3. **Population Structure**: what is the population structure of important prey species? How much movement/overlap is there between regionally distinct populations? What tools are available to assess population structure and movement patterns of key prey species? How can we assess the

likelihood that fishing activity will result in local depletion or extinction of important prey species populations? Can we match the spatial scale of exploitation to the spatial scale of population structures in different species, and what are the potential benefits of doing so? Finally, what is the population structure of important top predator species and how does this interact with and affect the population dynamics of their prey?

4. **Prey Catchability and Predator Activity**: does fishing activity affect spatial aggregation of prey? Does fishing activity affect the availability of prey to predators by altering their distribution, seasonal dynamics or behaviour? Equally, does the activity of predators affect the catchability of prey for fishing?

5. **Seasonal and Regional Variations in Predator Distributions**: how do top predator distribution and abundance vary seasonally? Are there strong regional differences in top predator community composition that are likely to affect the interaction with fishing? Does prey location affect predator migrations?

6. **Effect of Management**: how do spatial management measures affect predator-prey interactions and dietary niche widths? How can predator-prey interactions affect the probability of success of different management strategies (e.g., should the scale of the management intervention be matched to the scale of the predator-prey interaction)?

7. **Knowledge Exchange**: how can we improve knowledge exchange between scientists, fishers and policy makers? Can we map conflict between fishers and predators to identify common elements of the ecology-fishing interaction that tend to drive conflicts? Can we exploit existing observer schemes on board vessels to promote knowledge exchange between fishers and scientists and increase the acceptance of predator-related science?

8. **Key Environmental Drivers and Spatio-temporal Mismatches**: what are the key environmental drivers affecting predator-prey relationships? Can we identify and predict spatial and temporal mismatches between predators and their prey that are likely to result in significant changes in community structure?

9. **Historic background and Threshold Indicators**: can we quantify the historic background variability in predator and prey abundances? What can this tell us about system thresholds that are likely to result in significant changes to predator-prey interactions?

10. **Disease, Parasites and Pathogens**: how important is the role of disease, parasites and pathogens in affecting predator-prey interactions? What are the key hosts and vectors involved in these relationships? What conditions promote or ameliorate disease risk?

Balanced harvesting

Balanced harvesting (BH) is an ecosystem-based approach to fisheries management intended to bring fishing mortality, set at moderate levels, in line with the productivity of components of aquatic ecosystems. Work on BH is in its early stages, and BH is not yet accepted as a legitimate basis for exploiting living aquatic resources.

The literature does not provide a single clear measure of productivity against which BH can set fishing mortality. We suggest that production rate (dimensions: mass area^{-1} time^{-1}) is an appropriate measure. If fishing mortality rate is set in proportion to the production rates of ecosystem components, this protects components that are rare, and allows more exploitation of those that are abundant.

We find that little empirical information is currently available to examine the balance of exploitation to production of fish of different species and body sizes in the seas around Scotland. An Ecopath analysis of the west of Scotland shelf ecosystem in 1985 showed no relationship between fishing mortality rate and production rate of species and broader groups. This implies a major imbalance across species, because BH requires fishing mortality rate to be proportional to the production rate. In addition, production rate was seen to fall as fish become large for their species, whereas fishing mortality rate does not; fishing is therefore also unbalanced with respect to body size within species.

There are many assumptions built into this analysis, and it should be treated with caution.
Moving towards BH is likely to require a reduction in fishing on species that grow to large sizes, as these tend to have low production rates at present, and tend to be heavily exploited. However, some compensation for this is possible by increased fishing on small species with high production rates. This may include taxa further down the food chain that are exploited little, if at all, at the present time.

A move towards BH raises the social questions about the acceptability of reducing the catch of large fish that consumers are accustomed to, and of increasing that of small fish, some of which may be new to consumers. It also raises an issue of the impact of exploitation of forage fish, as these provide food for larger fish, seabirds and sea mammals. A broad societal discussion would be needed about the consequences for the fishing sector, the supply chain, the consumer, the ecosystem, local economies, and national economies.

Two marketing challenges would need to be addressed in a shift towards BH. First, an existing low market price for certain species/sizes could make harvesting uneconomic. Second a market may not exist for species/sizes that are not currently exploited. The use of all the new species and sizes being caught and probably landed would need to be addressed – human consumption, animal feed, or other uses. The same issues occur with the EU landing obligation.

BH would need to be reconciled with current regulations and management objectives. For instance, in the context of landing obligation in EU waters, landing fish that would previously have been discarded is not necessarily detrimental from the perspective of BH: the aim would be to land, and sell, all fish that are caught. Before embarking on a path towards BH, we should be clear on the biological, ecosystem, economic and social objectives, and their relative priorities. This should be done regardless of whether a move towards BH is proposed, but would be essential for such a new departure.

Given that a major imbalance exists between fishing mortalities and production rates, the management target would be to move fishing mortalities gradually in directions that would improve the balance. This target itself is expected to shift over time, because production rate changes directly through fishing and indirectly through biological processes. Management that can respond and adapt to such changes would be required.

In terms of **data and research priorities**, management to implement a shift towards BH in a Scottish context would need to adopt new methods. Broad-brush, métier-based management is suggested as a possible approach, with a strong industry involvement, or even responsibility, much greater flexibility from managers and fishers, and a results-based, multi-year approach to targets and objectives.

The immediate **data requirement** for developing BH in Scottish waters is an inventory of the present relationship between fishing mortality and production rates of the assessed stocks. In due course this would need to be extended to incorporate other components of the ecosystems that are not currently assessed, especially those that might be chosen for increased exploitation.

A **priority for research** to support a move towards BH is to develop multispecies models that account properly for the flow of biomass through marine ecosystems, parameterised to match the important features of Scottish waters. Such models are needed to examine the consequences of different multispecies fishing scenarios on structure and function of marine ecosystems. They are also needed to find safe, efficient and potentially profitable paths towards BH, to check effects of different overall fishing pressures, and to link exploited fish stocks to other components of marine ecosystems such as seabirds and mammals.

General Introduction

Marine ecosystems are inevitably affected by fishing because this involves the removal of a portion of the natural production to meet the human need for food. Through most of the 20th century, fisheries management has focussed on regulating harvesting to secure the long-term sustainability of targeted fish stocks, but has assumed that these exist in isolation from the rest of the ecosystem. In reality, fishing practices have, through a variety of processes, affected the functioning of the ecosystem as a whole by impacting on a wide range of non-target species. In many cases this has undermined the productivity of targeted fish stocks and compromised other qualities and services provided by the ecosystem that human societies also value. Recognition of these impacts has led to calls for urgent corrective action (Anon 2010, Dickey-Colas 2014, FAO 2003, 2005, 2006, Garcia *et al*. 2003, Garcia and Cochrane 2005, ICES 2005, Pikitch *et al*. 2004).

Several key international agreements adopted since the 1990's, such as the 1995 FAO Code of Conduct for Responsible Fisheries, and the Convention on Biological Diversity (CBD), stress the need for the adoption of ecosystem approaches to fisheries (EAF). In 2001, 57 countries issued the Reykjavik Declaration on Responsible Fisheries in the Marine Ecosystem, which included a declaration of their intention to work on incorporating ecosystem considerations into fisheries management. The 2002 Plan of Implementation of the World Summit on Sustainable Development called for, amongst other things, the application of the Reykjavik Declaration by 2010 as one of the steps essential for ensuring the sustainable development of the oceans. Despite these good intentions and some progress in implementation in many parts of the world, in most if not all countries more progress in ecosystem research and institutional development is still needed before the implications of the approach are fully understood and credible management strategies are adopted and effectively implemented. In addition to governmental initiatives, environmental NGOs have been particularly active in raising awareness of governments and society and have proposed a number of basic principles for ecosystem conservation.

The overarching principles of an ecosystem approach for fisheries are an extension of the conventional principles for sustainable fisheries development, designed to encompass the processes and integrity of the ecosystem as a whole. They aim to ensure that, despite variability, uncertainty and likely natural changes in the ecosystem, the capacity of the aquatic ecosystems to produce food for human consumption, revenues, employment and, more generally, other essential services and livelihood, is maintained indefinitely for the benefit of the present and future generations. The FAO Technical Guidelines on the ecosystem approach to fisheries (FAO 2003) define EAF as follows:

"An ecosystem approach to fisheries strives to balance diverse societal objectives, by taking into account the knowledge and uncertainties about biotic, abiotic and human components of ecosystems and their interactions and applying an integrated approach to fisheries within ecologically meaningful boundaries."

A primary implication is the need to cater both for human as well as ecosystem wellbeing. This implies conservation of the wide range of non-target species, which make up the food web and ecosystem structures, through adaptation of fisheries to ensure sustainable use. Inevitably this will require the consideration of a range of frequently conflicting objectives where the needed consensus may not be readily attained without equitable distribution of benefits. In general, the tools and techniques of EAF will remain the same as those used in traditional fisheries management, but they will need to be applied in a manner that addresses the wider interactions between fisheries and the whole ecosystem. For example, catch and effort quotas, or gear design and restrictions, will be based not just on sustainable use of the target resources, but on their impacts on other predator and prey species and implications for the whole ecosystem.

The generic process of putting into practice an Ecosystem Approach has been set out in varying degrees of detail by a series of FAO, EU, IUCN and ICES Working Group reports (Anon 2010, Dickey-Colas 2014, FAO 2003, 2005, 2006, Garcia *et al*. 2003, Garcia and Cochrane 2005, ICES 2005, Pikitch *et al*. 2004), and is currently being summarised again by the EU-MAREFRAME project (MAREFRAME 2016). However, progress in implementing an EAF in Scotland, and in the UK in general, has been relatively limited. The process has become entwined with conservation legislation and marine spatial planning. Hence a major tool for meeting the ecosystem objective has been the establishment of Marine Protected Areas (MPAs). However, this falls well short of the wider goals of EAF as defined by FAO and international agreements, which demand a more fundamental review of the wider strategy for harvesting living resources from each marine ecosystem. It is not axiomatically the case that by protecting a proportion of representative seabed habitats and sensitive species from the physically damaging impacts of certain fishing gears, that the ecosystem will be harvested in a more balanced way and that the underlying productivity and functions will be protected.

The concept of balanced harvesting (BH) has been widely discussed in the scientific literature (Froese et al. 2015, Garcia et al. 2012, 2015, Jacopsen et al. 2014, Kolding and van Zwieten 2014, Kolding *et al.* 2015a,b, Law *et al.* 2012, 2015) as a vehicle for implementing an Ecosystem Approach. The strategy aims to "distribute a moderate mortality from fishing across the widest possible range of species, stocks, and sizes in an ecosystem, in proportion to their natural production, so that the relative size and species composition is maintained" [12]. However, there is speculation as to whether the concept has any practical applicability beyond African lakes where it has been empirically demonstrated (Kolding and van Zwieten 2014, Kolding *et al*. 2015b, Misund et al. 2002, Jul-Larsen *et al.* 2003.

FAO documentation lists a range of likely impediments to implementation of an EAF in any given region (FAO 2003, 2005, 2006). Among these, insufficient knowledge of fishing and ecosystem interactions and of the response of different ecosystem components to specific management actions are listed as key concerns. Among key research areas are listed the collection of better information on ecosystem function and assessment of the impact of fishing on non-target species through by-catch and discarding, and improved knowledge of how ecological support systems (food webs, physical-biological coupling, etc.) are linked to the provision of goods and services that benefit, and are utilised by humans. In relation to balanced harvesting, Reid *et al.* (2015) examined what implementation would be required in practical terms for developed and managed fisheries with price-structured markets. Their conclusion was that "BH would be possible to implement in intensively managed fisheries such as in the EU and North America, but would likely require such a degree of micromanagement as to make it operationally impractical."

The purposes of this project were to add detail to the FAO guidance for Scottish fisheries with respect to a) background information on predator-prey interactions that are affected by fisheries and, b) the practicalities of implementing a balanced harvesting scheme in Scottish fisheries as a more eco-friendly alternative to current harvesting patterns.

References for the General Introduction

Anon (2010). Science dimensions of an Ecosystem Approach to Management of Biotic Ocean Resources (SEAMBOR). Marine Board-ESF Position Paper 14, April 2010. 92..

Dickey-Collas, M. (2014). Why the complex nature of integrated ecosystem assessments requires a flexible and adaptive approach. *ICES Journal of Marine Science* 71, 1174–1182. (doi:10.1093/icesjms/fsu027)

FAO. (2005). Putting into practice the ecosystem approach to fisheries. Rome, FAO. 76 pp.

FAO Fisheries Department. (2003). The ecosystem approach to fisheries. *FAO Technical Guidelines for Responsible Fisheries*. No. 4, Suppl. 2. Rome, FAO. 112 pp.

FAO. (2006). Report of the Expert Consultation on the Economic, Social and Institutional Considerations of Applying the Ecosystem Approach to Fisheries Management. Rome, 6–9 June 2006. *FAO Fisheries Report*. No. 799. Rome, FAO. 2006. 15pp.

Froese, R., Walters, C., Pauly, D., Winker, H., Weyl, O.L.F., Demirel, N., Tsikliras, A.C. and Holt, S.J. (2015). Food for Thought. A critique of the balanced harvesting approach to fishing. *ICES Journal of Marine Science* 73, 1640-1650. doi:10.1093/icesjms/fsv122 (2015)

Garcia, S.M., Zerbi, A., Aliaume, C., Do Chi, T., Lasserre, G. (2003).The ecosystem approach to fisheries. Issues, terminology, principles, institutional foundations, implementation and outlook. *FAO Fisheries Technical Paper*. No. 443. Rome, FAO. 71 pp.

Garcia, S.M. and Cochrane, K.L. (2005). Ecosystem approach to fisheries: a review of implementation guidelines. *ICES Journal of Marine Science* 62, 311-318. (doi:10.1016/j.icesjms.2004.12.003).

Garcia, S., Kolding, J., Rice, J., Rochet, M-J., Zhou, S., Arimoto, T., Beyer, J. E., *et al.* (2012). Reconsidering the consequences of selective fisheries. *Science* 335, 1045–1047.

Garcia, S. M., Bianchi, G., Charles, A., Kolding, J., Rice, J., Rochet, M-J., Zhou, S., *et al.* (2015). Balanced Harvest in the Real World. Scientific, Policy and Operational Issues in an Ecosystem Approach to Fisheries. Report of an international scientific workshop of the IUCN Fisheries Expert Group (IUCN/CEM/FEG) organized in close cooperation with the Food and Agriculture Organization of the United Nations (FAO), Rome, 29/09–02/10/2014. IUCN, EBCD, FAO, Gland, Switzerland, Brussels (Belgium) and Rome (Italy). 94 pp.

ICES. (2005). Guidance on the Application of the Ecosystem Approach to Management of Human Activities in the European Marine Environment, *ICES Cooperative Research Report*, No. 273. 22 pp.

Jacobsen NS, Gislason H, Andersen KH. (2014). The consequences of balanced harvesting of fish communities. *Proceedings of the Royal Society* B, 281, 20132701. http://dx.doi.org/10.1098/rspb.2013.2701

Jul-Larsen, E., Kolding, J., Nielsen, J. R., Overa, R., and van Zwieten, P. A. M. (2003). Management, co-management or no management? Major dilemmas in southern African freshwater fisheries. 2. Case studies. *FAO Fisheries Technical Paper*. No. 426/2. FAO, Rome. 271 pp.

Kolding, J., and van Zwieten, P. A. M. (2014). Sustainable fishing of inland waters. *Journal of Limnology*, 73, 132–148.

Kolding, J., Bundy, A., van Zwieten, P. A.M., and Plank, M. J. (2015). Fisheries, the inverted food pyramid. *ICES Journal of Marine Science* 73, 1697-1713. doi: 10.1093/icesjms/fsv225.

Kolding, J., Jacobsen, N. S., Andersen, K. H., and van Zwieten, P. A. M. (2015). Maximizing fisheries yields while maintaining community structure. Canadian *Journal of Fisheries and Aquatic Sciences* 73, 644-655. doi:10.1139/cjfas-2015-0098.

Law, R., Plank, M.J., and Kolding, J. (2012). On balanced exploitation of marine ecosystems: results from dynamic size spectra. *ICES Journal of Marine Science* 69, 602–614. (doi:10.1093/icesjms/fss031)

Law, R., Kolding, J., Plank, M.J. (2015). Squaring the circle: reconciling fishing and conservation of aquatic ecosystems. *Fish and Fisheries* 16, 160–174. (doi: 10.1111/ faf.12056)

MAREFRAME (2016). Co-creating Ecosystem-based Fisheries Management Solutions. http://mareframe-fp7.org/

Misund, O. A., Kolding, J., and Fréon, P. (2002). Fish capture devices in industrial and artisanal fisheries and their influence on management. In Handbook of Fish Biology and Fisheries, vol. 2, Fisheries, pp. 13–36. Ed. by P. J. B. Hart, and J. D. Reynolds. Blackwell Publishing, Oxford, UK. 410 pp.

Pikitch E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P. *et al.* (2004). Ecosystem-based fishery management. *Science* 305, 346–347. (doi:10.1126/science.1098222)

Reid, D. G., Graham, N., Suuronen, P., He, P., and Pol, M. (2015). Implementing balanced harvesting: practical challenges and other implications. *ICES Journal of Marine Science* 73, 1690-1696. doi: 10.1093/icesjms/fsv253.

Workshop Report: Predator-prey interactions in the context of Scottish fisheries

University of St Andrews, 24-25 August 2016

Chair and lead author: Kate R. Searle, NERC Centre for Ecology and Hydrology, Edinburgh

Participants:

- Robin M. Cook, Department of Mathematics and Statistics, University of Strathclyde
- Francis Daunt, NERC Centre for Ecology and Hydrology, Edinburgh
- Karen Diele, Edinburgh Napier
- David Donnan, Scottish Natural Heritage
- Peter G. H. Evans, Sea Watch Foundation & Bangor University
- Paul G. Fernandes, University of Aberdeen
- Allan Gibb, Marine Scotland
- John Goodlad, Fisheries Innovation Scotland
- Philip S. Hammond, Sea Mammal Research Unit, University of St Andrews
- Michael Heath, Department of Mathematics and Statistics, University of Strathclyde
- Sheila J. J. Heymans, Scottish Association for Marine Science
- Beth Mouat, North Atlantic Fisheries College, Scalloway, Shetland
- Richard Slaski, Fisheries Innovation Scotland
- Sophie C. Smout, Centre for Research into Ecological & Environmental Modelling, University of St Andrews
- James Thorburn, Marine Scotland Science, Marine Laboratory Aberdeen (by correspondence)
- Robert B. Thorpe, Centre for Environment, Fisheries and Aquaculture Science (Cefas)
- Sarah Wanless, NERC Centre for Ecology and Hydrology, Edinburgh
- Peter J. Wright, Marine Scotland Science, Marine Laboratory Aberdeen

Introduction

The animals and plants in the sea form a network in which all species are interconnected either directly or indirectly, however distant, through predator-prey connections. A disturbance that directly affects a given species will eventually propagate through the system to affect all other species to some degree. This propagation through the network is often referred to as a 'trophic cascade'. The strength of the trophic cascade – whether it is attenuated or amplified as it progresses – depends on the predator-prey connections linking components of the ecosystem. Hence, an important prelude to advising on the ecosystem consequences of fisheries is to document the predator-prey connections that are directly related to the target and by-catch species of fisheries.

Project outline

The main objective in this project is to raise awareness and understanding in the FIS Board of the issues relating to predator-prey interactions with fisheries. This will enable the FIS Board to make objective decisions in the future as to priorities for funding of research projects in this area.

To this aim, we ran a workshop with the active participation of FIS Board members, scientists and other stakeholders to discuss and identify key predator-prey relationships affecting Scottish fisheries, and the research needs underpinning an implementation of this understanding within an ecosystem approach to fisheries management.

This report documents the discussions and findings of the workshop, presenting the following key outcomes:

Outcome 1: Identification of the predators and prey linked with internationally and nationally important fisheries stocks in Scottish waters

Outcome 2: Identification of the key linkages between important predator species (seabirds, cetaceans, pinnipeds) and their interactions with Scottish fisheries

Outcome 3: A list of research priorities critical to facilitate the implementation of an ecosystem approach to fisheries management in Scotland and to support future management

Outcome 4: Exemplar case studies outlining how research priorities could be addressed

Outcome 5: Final recommendations for successful implementation of an ecosystem fisheries approach in Scotland

Outcomes 1 & 2: Identification of marine predator-prey relationships in Scottish waters that have significant direct and indirect interactions with fisheries

A major output of the FIS013 workshop on predator-prey interactions, designed to address Objectives 1 and 2, was an inventory of the evidence for identifying species that are predators on, or are prey for fish and shellfish, which are currently exploited by Scottish fisheries. This summary is given in Table 1. As our basis for identifying the fish and shellfish stocks of importance to Scotland, we relied on the report *FIS001 - A Review of Scotland's Marine Fisheries: Stock Status, Knowledge Gaps, Research Requirements and Stakeholder Engagement Report*. http://www.fiscot.org/media/1283/fis001-2.pdf. We then identified the key predator species interacting with these fish stocks, and for each of these assessed the evidence for a) the predator being affected by by-catch, b) the predator being capable of depleting the fish stock, c) the predator being likely to be adversely affected by fishery activities leading to prey depletion, and d) the predator being likely to be affected by discarding from the fishery (Table 2).

Current evidence suggests that, at present, population levels of top predators (including large migratory fish) are unlikely to be capable of depleting fishery resources, with the exception of grey seals on the west coast of Scotland which appear to be having a significant impact on the west of Scotland cod stock. This impact, however, appears not to be the cause of stock decline in cod but rather to impair recovery. The potential for significant impact upon whiting and sandeel stocks by pinnipeds was also highlighted due to the strong predator-prey interaction between these species (Tables 1 & 2). Northern gannets were identified as having the potential to deplete stocks of sandeels, and to potentially alter the behaviour of mackerel stocks, although the potential spatial and temporal extent of this alteration is currently unknown (Table 2). Finally, common eider were identified as having the ability to locally deplete mussel stocks. However, in all these cases, it was considered that currently available evidence is insufficient to robustly determine the strength and extent of these effects. Whilst we are aware of no current evidence demonstrating effects of other top predator species on prey contributing to Scottish fisheries, there are likely to be significant, and potentially strong interactions involving a range of species. For instance, we anticipate that harbour seal, harbour porpoise, minke whale and auks will be interacting strongly with sandeel, sprat, and whiting; and that in offshore waters, killer whales will interact strongly with herring and mackerel. Locally, there is also potential for baleen whales such as the humpback whale, to have an impact on smaller forage fish such as sprat. Several elasmobranch species also have the potential to impact stocks at both a local and at a wider regional context. Spurdog form large aggregations that have the potential to impact shoaling species such as mackerel and herring. Highly migratory, shoaling species such as tope will have localised impact at feeding areas along their migration routes. Due to many elasmobranchs opportunistic diets and poor understanding of variation in regional diet compositions and predator-prey interactions, the impacts of elasmobranchs on commercial species are poorly understood. Finally, several marine mammal species potentially alter the behaviour of fish by corralling them. Examples include killer whales and herring; common dolphins and a number of species (e.g., herring, whiting, sardine, anchovy); white-beaked dolphins and whiting, mackerel, and sprat; minke and humpback whales and sprat, sandeel, herring and mackerel. Whilst much anecdotal evidence for these types of interactions and behaviours exist, research has not yet assessed their effects on stock sizes.

Several seabird species were identified as a potential cause for concern in relation to negative impacts caused by fisheries activities (Table 2). In particular, black-legged kittiwake were identified as being at risk from negative effects of prey depletion caused by fishing activities on forage fish stocks such as sprat and sandeel, and other seabirds, pinnipeds and cetaceans could potentially also be affected. In addition, the majority of predator species were identified as being at some risk of by-catch from a range of fishing activities, highlighting the need for more research and assessment of these effects. In Scottish waters, minke whales and humpbacks are particularly susceptible to entanglement in creel lines and ghost netting (Northridge et al., 2010; Ryan et al., 2016); and harbour porpoises to bottom set gillnets and tangle nets. Grey seals also suffer bycatch from entanglement in creel lines and ghost netting. Furthermore, a number of seabirds forage on discards and implementation of the EC Landing Obligation will lead to an eventual halt to discarding fish from vessels and remove an important food source for these species. Finally, whilst the direct negative effect of single fishing activities on predators may be relatively minimal in most cases, when combined with other environmental and anthropogenic changes in the marine environment, the cumulative consequences for top predator species may become significant. This potential for an additive effect of multiple drivers emphasizes the need for a more holistic approach to marine management in Scottish waters.

Table 1. *International and National fish stocks and their key interactions with predators and prey by taxonomic group. Stocks are identified from the FIS001 - A Review of Scotland's Marine Fisheries: Stock Status, Knowledge Gaps, Research Requirements and Stakeholder Engagement Report.* *http://www.fiscot.org/media/1283/fis001-2.pdf*. ***Yellow indicates potential for very strong effect of predator on prey; green indicates prey that would influence sustainability of targeted stock.***

A. International Stocks:

	Predators of stock						Prey of stock			
Stock	**Fish predators**	**Pinniped predators**	**Small cetaceans**	**Large cetaceans**	**seabirds**	**elasmobranchs**	**inverts**	**fish**	**benthic inverts**	**zooplankton**	**phytoplankton**
Mackerel in the northeast Atlantic (combined Southern, Western, and North Sea spawning components)	Cod, tuna, anglerfish, whiting	harbour seal	white-beaked dolphin	killer whale, minke whale, fin whale, humpback whale	gannet	porbeagle, thresher spurdog lesser spotted dogfish nursehound tope blue shark	Squid (small fish only)	sprat, sandeels, hake,herring, juvenile fish, and other pelagic invertebrates	x	krill, copepods, amphipods, mysid shrimps, pelagic molluscs euphaussid, pandalid and crangoid shrimp, chaetognaths, pelagic polychaetes, crab larvae, squid (Loligo),	x
Horse mackerel (Trachurus trachurus) in Divisions IIa, IVa, Vb, VIa, VIIa–c, e–k, and VIIIa–e (Western stock)	pollock, whiting, blue whiting, mackerel, squid	harbour seal	common dolphin, white-beaked dolphin, Atlantic white-sided dolphin		x	Porbeagle, tope spurdog	cephalopods	juvenile haddock, juv whiting, herring, Norway pout	crustaceans	large and small zooplankton	
Cod in Division VIa (West of Scotland) Cod in Subarea IV (North Sea) and Divisions VIId (Eastern Channel) and IIIa West (Skagerrak)	cod, whiting, haddock, hake, anglerfish	harbour seal, grey seal (strong in west of Scotland)	harbour porpoise, bottlenose dolphin, white-beaked dolphin	minke whale, killer whale, long-finned pilot whale	guillemot, shag (West of Scotland)	porbeagle, thresher spurdog lesser spotted dogfish tope Greenland shark		many fish	nephrops + many others (strong in west of Scotland)	many	

Nephrops in Division VIa Nephrops in Subarea IV (North Sea) Nephrops in Subarea VII	cod, flatfish, lesser spotted dogfish,				x	lesser spotted dogfish, nursehound Smoothhound Spurdog Tope Common skate Small skates and rays	cephalopods		epifauna, infauna, crustaceans, edible crabs, velvet crabs, molluscs, polychaetes, echinoderms	large and small zooplankton, ostracods, amphipods	
Haddock in Subarea IV and Divisions IIIa West and VIa (North Sea, Skagerrak, and West of Scotland) Haddock in Divisions VIIb–k	pollock, cod, anglerfish	harbour seal, grey seal	white-beaked dolphin, bottlenose dolphin,	minke whale	x	Porbeagle tope Greenland shark					
Anglerfish (Lophius piscatorius and L. budegassa) in Division IIIa and Subareas IV and VI	cod				x	Greenland shark Common skate		sandeel, herring, Norway pout, mackerel, cod, whiting, flatfish, gurnards, pollock, haddock	cephalopods (not really benthic invert but nowhere else to put it)		
Herring in Subarea IV and Divisions IIIa and VIId (North Sea autumn spawners) Herring in Division VIa (North) Herring in Subareas I, II, and V, and in Divisions IVa and XIVa (Norwegian spring-spawning herring)	mackerel, pollock, cod, haddock, whiting, gurnards, anglerfish	harbour seal, grey seal	x	x	x	Porbeagle Blue shark Greenland shark tope spurdog lesser spotted dogfish	cephalopods	sandeel, sprat	crustaceans	large zooplankton	x
Hake in Division IIIa, Subareas IV, VI, and VII, and Divisions VIIIa,b,d (Northern stock)		harbour seal, grey seal			x	Porbeagle Blueshark Tope					
Whiting in Subarea IV (North Sea) and Division VIId (Eastern Channel) Whiting in Division VIIa (Irish Sea) Whiting in Division VIa (West of Scotland)	pollock, cod, anglerfish	harbour seal, grey seal (strong interaction in west of Scotland)	harbour porpoise, bottlenose dolphin, white-beaked dolphin, common dolphin	minke whale	x	Porbeagle Tope Blue shark Spurdog Nursehound Lesser spotted dogfish Common skate		herring, mackerel, sprat, sandeel, juvenile whiting, juvenile cod, juvenile haddock, poorcod, Norway pout,	epifauna, cephalopods, edible crab, scallops, lobster, velvet crabs, other crustaceans,	large zoopl	

								horse mackerel, flatfish, pollock			
Blue whiting in Subareas I–IX, XII, and XIV		harbour seal	Atlantic white-sided dolphin, common dolphin	fin whale	x						
Saithe in Subarea IV (North Sea), Division IIIa (Skagerrak), and Subarea VI (West of Scotland and Rockall)	anglerfish, flatfish	harbour seal, grey seal	harbour porpoise, bottlenose dolphin	minke whale	x	Porbeagle Blue shark Greenland shark Tope Spurdog Nursehound Common skate		herring, Norway pout, sprat, sandeel, blue whiting, other plagics, horse mackerel, juv. cod, juvenile, haddock, juvenile whiting, flatfish	crustaceans	large zoopl	
Megrim (Lepidorhombus spp.) in Divisions IVa and Via (Northern North Sea, West of Scotland)		grey seal			x						
Megrim (Lepidorhombus whiffiagonis) in Divisions VIIb–k and VIIIa, b, d (L. whiffiagonis and L. boscii)					x						
Ling (Molva molva) in Divisions IIIa and IVa, and in Subareas VI, VII, VIII, IX, XII, and XIV (other areas)		harbour seal, grey seal			x						
Blue ling (Molva dypterygia) in Division Vb and Subareas VI and VII					x						
Plaice in Subarea IV (North Sea)		harbour seal, grey seal	bottlenose dolphin		x						

Lemon sole in Subarea IV (North Sea) and Divisions IIIa (Skagerrak–Kattegat) and VIId (Eastern Channel)		harbour seal, grey seal			x	Tope Skate and rays					
Sole in Subarea IV (North Sea)		harbour seal, grey seal	bottlenose dolphin, white-beaked dolphin		x	Tope Skate and rays					
Turbot in Subarea IV (North Sea)					x						
Pollack in Subarea IV (North Sea) and Division IIIa (Skagerrak–Kattegat)				long-finned pilot whale	x	Tope, spurdog, porbeagle					
Boarfish in the northeast Atlantic					x						
Witch in Subarea IV (North Sea) and Divisions IIIa (Skagerrak–Kattegat) and VIId (Eastern Channel)					x						
Sandeel in Subarea IV	haddock, mackerel, whiting, grey gurnard, horse mackerel, cod, saithe	harbour seal, grey seal	harbour porpoise, bottlenose dolphin, white-beaked dolphin	minke whale, humpback whale	kittiwake, Arctic tern, guillemot, razorbill, shag, gannet, puffin	Vulnerable to most shark, skate and ray species.		Fish eggs, fish larvae including sandeel		Copepods, Larvacea, Mysids, Euphausids	
Atlantic halibut in Subarea IV				killer whale	x	Greenland shark					
Greenland halibut in Subarea IV Greenland halibut in Subareas V, VI, XII, and XIV Greenland halibut in Subareas I and II					x	Greenland shark					
Albacore tuna in Subarea VII					x						
Albacore tuna in Subarea X					x						
Golden redfish (Sebastes norvegicus) in Subareas I and II and Beaked redfish (Sebastes mentella) in Subareas I and II					x						
Redfish in Subarea IV (North Sea)					x						

Greater forkbeard (Phycis blennoides) in the Northeast Atlantic					x						
Sprat in Subarea VI and Divisions VIIa–c and f–k (Celtic Sea and West of Scotland)	haddock, pollack, blue whiting, whiting, poor cod, cod, gurnars, herring, mackerel		harbour porpoise, bottlenose dolphin, common dolphin, white-beaked dolphin,	minke whale, humpback whale	x	Vulnerable to most shark, skate and ray species.	cephalopods		crustaceans	large and small zoopl	

B. National stocks:

	Predators of stock							**Prey of stock**			
Stock	**Fish predators**	**Pinniped predators**	**Small cetaceans**	**Large cetaceans**	**seabirds**	**elasmobranchs**	**invertebrates**	**fish**	**benthic inverts**	**zooplankton**	**phytoplankton**
Great Atlantic scallop	Whiting				x	Nursehound Lesser spotted dogfish Common skate Small skates and rays	Starfish (e.g. Asterias rubens), crabs (e.g. Cancer pagurus), cephalopods				Seston including phytoplankton, especially single celled algae,
Queen scallop	Whiting, Dragonet (Callyonimus lyra)				x	Nursehound Lesser spotted dogfish Common skate Small skates and rays	Starfish (e.g. Asterias rubens), crabs (e.g. Cancer pagurus, Pagurus spp., cephalopods			halacarid mites, calanoid copepods, halacarid fragments, copepod fragments, crustacean nauplii, barnacle cyprids, and cladocerans.	Yes
European lobster	Larvae: Herring, cod, Whiting				x	Larvae: Basking shark	Octopus	occasionally	Main diet. Crabs, molluscs, sea urchins, polychaetes, starfish		
Palinurid spiny lobsters	Conger eel				x		Octopus		Polychaetes, crabs, sponges, echinoderms, molluscs, carrion		
Edible crab	cod, wolf fish,	Grey seal	Bottlenose		large gulls	Nursehound	Octopus		Crabs (e.g.		

	whiting		dolphin			Lesser spotted dogfish tope Starry Smoothhound Common skate Small skates and rays			Carcinus maenas, Pilumnus hirtellus, Porcellana platycheles, Nephrops Pisidia longicornis), squat lobster, molluscs (e.g. Nucella lapillus, Littorina littorea, Ensis, Mytilus edulis, Cerastoma edule, Ostrea edulis, Lutraria lutraria		
Velvet swimming crab	Whiting				large gulls	Nursehound Lesser spotted dogfish Starry Smoothhound Spurdog Tope Common skate Small skates and rays	x		Crustacea (e.g. Nephrops), mollusca		Laminaria (not planktonic)
Green crab	yes				large gulls, cormorants, eider ducks	Nursehound Lesser spotted dogfish Starry Smoothhound Spurdog Tope Common skate Small skates and rays	Octopus		Mollusca (e.g. dogwhelk, Littorina, oysters, mussels), Crustacea (e.g. other crabs, barnacles), Annelida, carrion		Benthic algae
Solen razor clams					Gulls, other shorebirds (e.g. oyster catcher)		Green crab			Yes - filterfeeder	Yes - filterfeeder
Blue mussel					Eider duck, oystercatcher		Green crab, dog-whelk, starfish			yes	yes
Whelk					x		sea urchins, starfish, lobster (?)			Polychaetes, oysters, scallops, other molluscs,	

										urchins, carrion	
Periwinkles					shorebirds (occasionally)		Green crab, edible crab, lobster			Invertebrate larvae (e.g. barnacles)	Grazing on diatoms and small macroalgae
Cockles	yes				Wading birds		Green crab			yes	yes
Common squids		harbour seal, grey seal	Risso's dolphin		x	Blueshark Nursehound Lesser spotted dogfish Smoothhound Spurdog Tope Common skate Small skates and rays					
Cuttlefish, bobtail squids			Risso's dolphin		x	Spurdog Tope					
Wolffishes					x						
European seabass			bottlenose dolphin		x						
John dory					x	Porbeagle					
Sand gaper					x						
Gurnards			bottlenose dolphin		x						

Table 2. *Key predator species interacting with National fisheries stocks. For each predator species, the affected fishery and region is identified, the potential for bycatch of the predator as a result of fisheries activity, whether the predator is likely to deplete the fisheries stock, whether the predator is likely to be affected by the fishery in terms of suffering prey depletion, and finally whether the predator is affected by discards from the fishery.* ***Yellow indicates a potentially strong effect of the predator on the fishery.***

Predator Species	Affected fishery and region	Potential for bycatch of predator	Predator likely to deplete stock	Predator likely to be affected by fishery	Predator affected by discards
black-legged kittiwake	sandeel	none		yes (fishery affects predator)	yes - will take discards
common guillemot	sandeel	none		perhaps (fishery may affect predator)	no
	cod, herring, sprat (particularly W coast)	some	no	no	no
razorbill	sandeel	none		perhaps (fishery may affect predator)	no
	herring, sprat, hake	none	no	no	no
European shag	sandeel	some (set longlines - hake, bream, cod, haddock, ling, tusk; trammelnet)	unlikely, very little interaction	unlikely, very little interaction	no
	cod, saithe, poor cod, rockling, pollack	none	no	no	no
northern gannet	sandeel	some (pelagic trawl - sea bass, pelagic fish; set longlines - hake, bream, cod, haddock, ling, tusk; trammelnet)	potential for depletion of stock		yes - will take discards
	mackerel	some (pelagic trawl - sea bass, pelagic fish; set longlines - hake, bream, cod, haddock, ling, tusk; trammelnet)	potential for altering behaviour of prey	potential for altering behaviour of prey	yes - will take discards
	haddock, whiting, cod, sprat, poor cod, saithe, anchovy, sardine	some (pelagic trawl - sea bass, pelagic fish; set longlines - hake, bream, cod, haddock, ling, tusk; trammelnet)	no	no	yes - will take discards
northern fulmar	haddock, whiting, gadoid	some (set longlines - hake, bream, cod, haddock, ling, tusk)	no	no	yes - will take discards
Atlantic puffin	sandeel, sprat, herring, rockling	none		perhaps (fishery may affect predator)	no
great black-backed gull	haddock, whiting, gadoid	some (set longlines - hake, bream, cod, haddock, ling, tusk)	no	no	yes - will take discards
lesser black-backed gull	haddock, whiting, gadoid	some (set longlines - hake, bream, cod, haddock, ling, tusk)	no	no	yes - will take discards
Manx shearwater	sardine, anchovy, herring, sprat, sandeel	trammelnet? (ICES bycatch report for 'shearwaters'); longlines			

common eider	mussels	trammelnet? (ICES bycatch report for 'diving ducks')	yes (predator can deplete stock)		no
herring gull	haddock, whiting, gadoid	some (set longlines - hake, bream, cod, haddock, ling, tusk)	no	no	yes - will take discards
harbour seal	sandeel, gadoid, herring, mackerel	gillnets, tanglenets, trawls	Perhaps (cod on West coast Scotland)	perhaps - fisheries may affect predator	on occasion
grey seal	sandeel, gadoid	gillnets, tanglenets, trawls	probably (gadoids on West coast Scotland)	perhaps - fisheries may affect predator	on occasion
fin whale	herring, mackerel, sandeel, sprat, blue whiting, euphausiids	creel lines, ghost nets		perhaps - fisheries may affect predator	no
minke whale	sandeel, sprat, herring, cod, mackerel	creel lines, ghost nets		perhaps - fisheries may affect predator	no
humpback whale	sandeel, sprat, herring	creel lines, ghost nets		perhaps - fisheries may affect predator	no
sperm whale	mainly mesopelagic squid	drift nets	probably not	probably not	no
killer whale	herring, mackerel, cod, halibut, marine mammals	rarely in creel lines		perhaps - fisheries may affect predator	yes - will take discards
harbour porpoise	sandeel, whiting, cod, herring, pouts, hake, haddock	bottom set gillnets, tanglenets, trawls	perhaps (North Sea gadoids) but very little supporting evidence	perhaps - fisheries may affect predator	possibly (may follow vessels during hauls)
bottlenose dolphin	seabass, salmon, whiting, cod, herring, sandeel, sprat, saithe, haddock, pouts	sometimes in trawls		perhaps - fisheries may affect predator	no
Risso's dolphin	mainly small squid, octopus, cuttlefish	sometimes in longlines		squid fisheries might affect predator	no
common dolphin	sardine, anchovy, pouts, blue whiting, sprat, sandeel, cod, whiting	pelagic trawls		perhaps - fisheries may affect predator	no
white-beaked dolphin	whiting, cod, herring, mackerel, hake, scad	sometimes in trawls		perhaps - fisheries may affect predator	no
Atlantic white-sided dolphin	blue whiting, herring, mackerel, horse mackerel, pouts, scad	pelagic trawls		perhaps - fisheries may affect predator	no
Blue Shark	Squid, pelagic fish	Longlines		perhaps - fisheries may affect predator	
Porbeagle	Cod, hake, haddock, whiting, mackerel, herring, john dory, squid	Longlines, bottom trawls, hand lines, gillnets	no	perhaps - fisheries may affect predator	Yes, will take discards

Tope	Cod, haddock, hake, saithe, whiting, mackerel, sandeel, herring, sole, halibut, squid, crab sp.	Long lines, sometimes in trawls		perhaps - fisheries may affect predator	possibly
Spurdog	Herring, whiting, saithe, mackerel, sandeel, squid, green crab, velvet crab, nephrops	Longlines, trawls		perhaps - fisheries may affect predator	Yes, will take discards
Greenland shark	Herring, salmon, char, cod, link, saithe, haddock, halibut, benthic crustacea	Occasional bycatch	no	perhaps - fisheries may affect predator	Yes, will take discards
Smoothhound	Mostly Crab sp. And benthic crustacea	Longlines, bottom trawls, gillnets		perhaps - fisheries may affect predator	possibly
Nursehound	Mostly Crab sp. And benthic crustacea, squid, mackerel, herring, juvenile bentho-pelagic teleosts	Longlines, bottom and occasional pelagic trawls, gillnets, creels		perhaps - fisheries may affect predator	Yes, will take discards
Lesser spotted dogfish	Benthic crustacea and molluscs	Longlines, bottom trawls, gillnets, creels		no	Yes, will take discards
Common skate	Angler fish, gurnards, herring, benthic crustacea, mollusc, cephalopods	Bottom trawls		no	Yes, will take discards
Small skates and rays	Mostly benthic crustacea and molluscs with some groundfish and pelagic fish	Bottom trawls, creel		perhaps - fisheries may affect predator	Yes, will take discards

Outcome 3: A list of research priorities critical to facilitate the implementation of an ecosystem approach to fisheries management in Scotland and to support future management

Implementing a whole ecosystem approach to fisheries management in Scotland requires leveraging existing data and research, as well as targeted new research, to address fundamental research questions in the marine environment. Over the course of the workshop and subsequent communications within this project, we have identified what we consider to be the ten most important research priorities most likely to result in significant advances towards implementing a whole ecosystem approach to managing Scottish fisheries (note although numbered, the list below does not imply a ranking).

Research priorities

1. **Diet**: what are the diets of forage fish, predatory fish and top predators? How selective are they? How much do diets vary regionally and seasonally? How have diets varied over time? How does diet vary with age or size? How does competition between predators, or between predators and fisheries, affect the dietary niche width of marine top predators and their trophic interactions? How does diet change over a spatial range in migratory predators?

2. **Marine Ecosystem Models**: what is the current scope, biological scale (e.g., trophic levels, guilds, species) and spatial extent (e.g., geographic area) of marine ecosystem models? What models have been developed for Scottish or UK waters? How can ensemble modelling be used to improve simulations of the marine environment, particularly in terms of characterising risk, thereby improving the quality of decision-making?

3. **Population Structure**: what is the population structure of important prey species? How much movement/overlap is there between regionally distinct populations? What tools are available to assess population structure and movement patterns of key prey species? How can we assess the likelihood that fishing activity will result in local depletion or extinction of important prey species populations? Can we match the spatial scale of exploitation to the spatial scale of population structures in different species, and what are the potential benefits of doing so? Finally, what is the population structure of important top predator species and how does this interact with and affect the population dynamics of their prey?

4. **Prey Catchability and Predator Activity**: does fishing activity affect spatial aggregation of prey? Does fishing activity affect the availability of prey to predators by altering their distribution, seasonal dynamics or behaviour? Equally, does the activity of predators affect the catchability of prey for fishing?

5. **Seasonal and Regional Variations in Predator Distributions**: how do top predator distribution and abundance vary seasonally? Are there strong regional differences in top predator community composition that are likely to affect the interaction with fishing? Does prey location affect predator migrations?

6. **Effect of Management**: how do spatial management measures affect predator-prey interactions and dietary niche widths? How can predator-prey interactions affect the probability of success of different management strategies (e.g., should the scale of the management intervention be matched to the scale of the predator-prey interaction)?

7. **Knowledge Exchange**: how can we improve knowledge exchange between scientists, fishers and policy makers? Can we map conflict between fishers and predators to identify common elements of the ecology-fishing interaction that tend to drive conflicts? Can we exploit existing observer schemes on board vessels to promote knowledge exchange between fishers and scientists and increase the acceptance of predator-related science?

8. **Key Environmental Drivers and Spatio-temporal Mismatches**: what are the key environmental drivers affecting predator-prey relationships? Can we identify and predict spatial and temporal mismatches between predators and their prey that are likely to result in significant changes in community structure?

9. **Historic background and Threshold Indicators**: can we quantify the historic background variability in predator and prey abundances? What can this tell us about system thresholds that are likely to result in significant changes to predator-prey interactions?

10. **Disease, Parasites and Pathogens**: how important is the role of disease, parasites and pathogens in affecting predator-prey interactions? What are the key hosts and vectors involved in these relationships? What conditions promote or ameliorate disease risk?

Outcome 4: Exemplar case studies outlining how research priorities could be addressed

To provide tangible examples of how these research priorities have been addressed, or could be addressed in future research, we have identified three illustrative case studies in Scottish waters.

1. Grey seal predation on West of Scotland roundfish

Diet studies by the Sea Mammal Research Unit in 1985 and 2002 provide estimates of quantities of fish consumed annually by the grey seal population foraging in the West of Scotland area. For the three main roundfish species targeted by the Scottish demersal fleet (cod, haddock and whiting), the total biomass consumed by seals is of a similar order of magnitude to the commercial catch and may therefore have appreciable impact on the performance of the fishery.

The SMRU also provide estimates of the size composition of the prey consumed and this can be used in a conventional stock assessment model to calculate mortality rates due both to fishing and seal predation. Cook et al (2015) and Cook and Trijoulet (2016) estimated grey seal predation mortality on cod for West of Scotland cod using the SMRU data, which suggested that the mortality was large and increasing. Accounting for seal predation in the assessment resulted in lower estimates of fishing mortality in recent years, which is more consistent with recorded fishing effort reductions than is apparent in the ICES assessment. The analysis also suggested that the level of catch misreporting estimated in the assessment with seals was consistent with records from the enforcement authorities. Overall, the assessment with seals appears to be an improvement over the conventional ICES assessment.

A bioeconomic analysis by Trijoulet (2016) that considered seal predation on all three roundfish species showed that predation on cod had by far the most important effect on fleet revenues. Typically, the seal predation mortality on haddock and whiting was much lower than that for cod. However, the sensitivity to predation on cod was restricted mainly to trawlers over 24m. This sector represents a small number of vessels but which take a high proportion of the total catch.

The assessment models that include seal predation make simplistic assumptions about the foraging behaviour of seals that may be unrealistic. There were indications that a type II functional response described foraging by cod (where intake rate increases asymptotically with prey density, being ultimately limited by handling time of prey items). However, the lack of a time series of seal diet data make it problematic to include a parameter rich predation sub-model such as a type III functional response (where intake rate increases as an S-shaped function of prey density, capturing more complex behavioural processes such as ‘search images’ and increased predator efficiency). This limitation is of particular importance in making forward projections where model misspecification is likely to lead to cumulative errors that may be substantial.

The analyses by Cook et al. (2015) and Cook and Trijoulet (2016) assume that the fish stocks are well mixed and all individuals are equally available to the seal population. Area separation between the fishing fleets and the seal foraging areas may violate this assumption if the cod population is spatially structured (Matthiopoulos et al., 2004). This remains an important area of uncertainty.

Research that would improve assessments include:

- More years of seal diet and consumption data including access to the 2010/2011 SMRU data would be a major step forward in reducing uncertainty in assessments **(Research Priorities 1 & 4)**.
- A more realistic seal foraging sub-model is needed for the assessments, which can only be effectively achieved with more years of data. It would also be desirable to include harbour seal predation where this is thought to be important **(Research Priorities 3, 4 & 5)**.
- The extent to which seals and the fisheries exploit the same/separate populations needs to be established **(Research Priorities 3, 5 & 8)**.

2. Changes in the fish community composition in the Firth of Clyde

Between 1889 and 1962 the entire Firth of Clyde was closed to trawlers larger than 8 tons in order to protect herring fishing grounds and areas used by small inshore fishers. In 1962 the closure was repealed for waters beyond 3 miles of the coast and, with the resumption of trawling, demersal fish landings increased to a peak in 1973 before starting to decline. Then, in 1984 the waters within 3 miles were also opened to trawling in an attempt to maintain catch levels and exploit inshore Norway lobster (*Nephrops norvegicus*) stocks. However, fish landings continued to decline. In 2001 and each year thereafter, a seasonal prohibition on demersal fish trawling has been implemented in parts of the Clyde to protect spawning cod, but the targeted demersal fishery ceased in about 2005. By the late 2000's, the only demersal fish landed from the Clyde were by-catch from the trawl fishery for Norway lobster.

It has been asserted that the record of demersal fish landings demonstrates that the Clyde is an ``ecosystem nearing the endpoint of overfishing, a time when no species remain that are capable of sustaining commercial catches'' (Thurstan & Roberts, 2010). However, landings data alone are insufficient to diagnose exactly what has happened. The relationship between species landings and abundance in the sea, is affected by a range of socio-economic factors in addition to management regulation of fishing effort and opportunities. Analyses of research vessel trawl survey data can provide a different perspective. Scottish demersal trawl survey records between 1927 and 2015 include a small number of sampling sites in the Firth of Clyde every year, usually in the spring. Estimates of species biomass density, species diversity, and length structure of the demersal fish community showed that in fact the community biomass since the loss of the demersal fishery has been as high as during the 1930's-1950's (Figure PP1; Heath & Speirs, 2012). However, the community composition was dramatically different. Even though the species richness (number of species recorded) remained constant through the 88- year period, the species evenness had drastically reduced. Up until 1960, nine species contributed 85% of the demersal fish biomass, but by the late 1990's this had reduced to only one species (whiting) (Figure PP2). In addition, post-1980, the community contained very few fish of any species, which were larger than the minimum landing sizes. Hence, the fishery ceased because of a large change in the size composition of fish, not because of a change in biomass. Since 2000, the species evenness has recovered slightly, with three species (whiting, haddock and Norway pout) comprising 85% of the biomass today (whiting, haddock and Norway pout). However, large fish remain scarce and confined to the deeper parts of the sea lochs.

Analysis of the Scottish trawl survey data shows a similar pattern of declining species evenness and diminishing size of fish throughout the inshore waters of the west of Scotland, but the trend is particularly steep in the Firth of Clyde. Detailed analysis of the individual length, age and maturity data of the main demersal fish species collected during the surveys showed that a) there has been a decline in the size at maturation of cod, haddock and whiting, so that fish undergo maturation at up to 10cm smaller sizes in 2015 than in 1980 (Hunter et al., 2015). In addition, growth rates of haddock and whiting (but not cod) in the Clyde have declined, so that a 3-year old whiting in 2015 was 10cm smaller than in 1980 (Hunter et al., 2016).

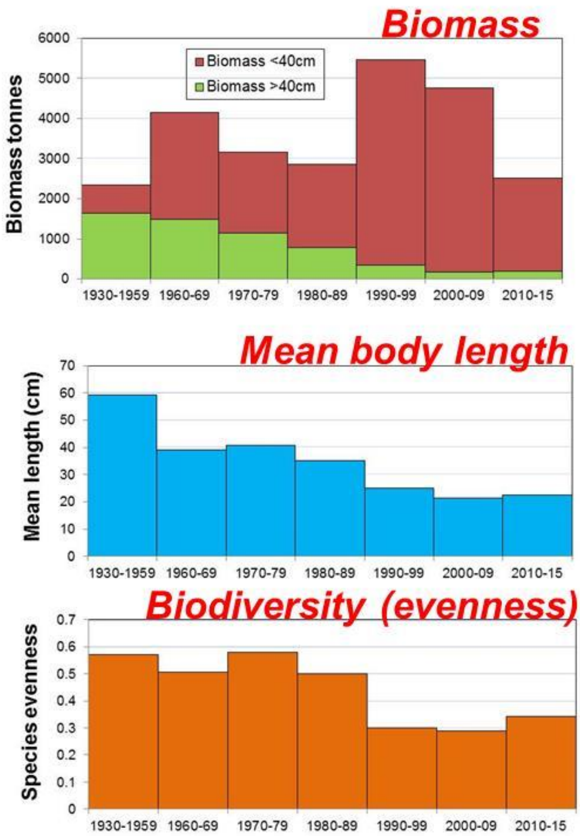

Figure PP1. *Changes in demersal fish community biomass in two size classes (upper panel), community mean body length (middle panel), and species evenness (lower panel), in the Firth of Clyde, 1930-2015, derived from research vessel trawl survey data (redrawn and extended from Heath & Speirs, 2012).*

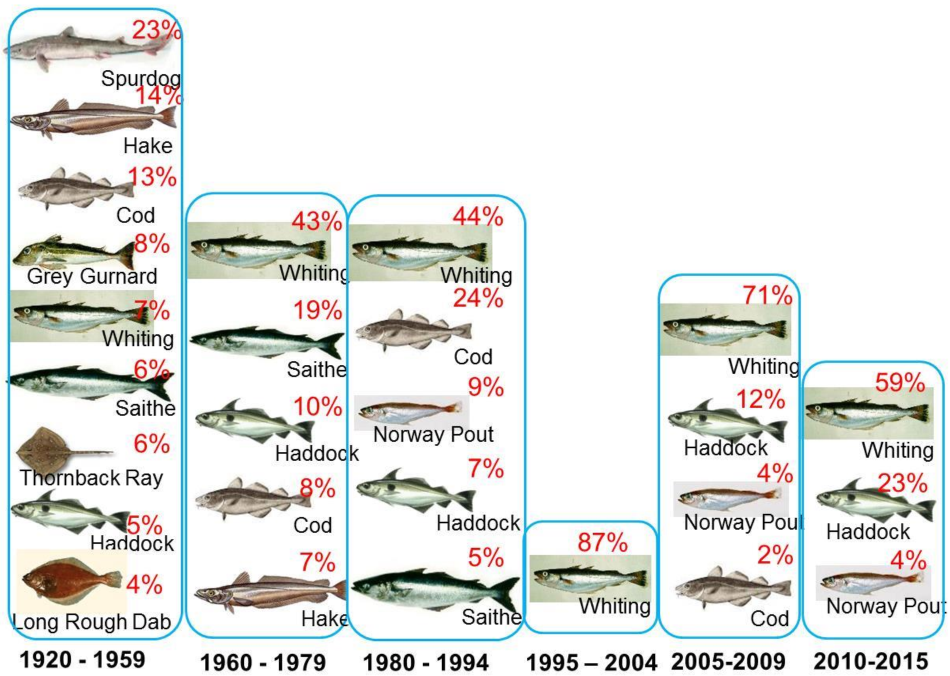

Figure PP2. *Changes in the number and composition of species making up 85% of the demersal fish community biomass over the period 1920-2015, derived from analysis of Scottish trawl survey data (redrawn and extended from Heath & Speirs, 2012).*

The changes in growth and maturation of whiting and haddock, and maturation of cod, could have contributed to the decline in the mean size of fish in the community as a whole (since whiting and haddock made up a large fraction of the community biomass). However, there are other possible factors that may have been involved. In particular, research on migration patterns of whiting (Neil Burns, University of Glasgow) has shown that fish progressively move out of the Clyde with age, so that we would expect to see a disproportionately small number of old fish within the Clyde. However, we do not know whether this migration pattern has become more predominant since the 1980's.

Obviously, the management aspiration is to take actions that will promote the recovery of the Clyde demersal stocks as a harvestable resource. So, the research question is, are there any interventions that would promote a change in the state of the Clyde to one in which large fish are once more abundant? Issues that have been proposed for consideration include:

- *Benefits of a 3-mile limit trawling ban?*
- *Are by-catch rates of demersal fish in the Nephrops trawl fishery inhibiting recovery?*
- *Benefits of Marine Protected Areas?*
- *Segregation of towed and static gears?*

From a research perspective, there is also a question as to whether it is realistic to expect to recover the past state of the ecosystem, given that:

- *Nutrient loads have changed*
- *Temperature is rising*
- *Fish growth and maturation changes may be genetic (evolutionary) rather than adaptive*
- *Other key predator-prey interactions may be dictating the state of the Clyde.*

Predator-prey issues that may be important include:

- If the lack of large demersal fish can be explained by predation, what are the predators?
- How might predator-prey relationships be affected by the changes in growth rate of demersal fish?
- What is the role of harbour seals in preventing demersal fish recovery (given the impact of grey seals on cod in the wider west of Scotland region)?
- Why are herring in the Clyde at a low state – is this predation, or competition from sprat? What are the predators? - harbour porpoise, minke whale and gannet are potential candidates. Is the decline of herring linked to the reducing growth rates of demersal fish, given that juvenile herring are potentially an important prey species for whiting and cod?
- What is the role of sprats as prey species in the Clyde?
- If we recover demersal fish in the Clyde, will the *Nephrops* stocks suffer as a result of increased predation?
- Do starfish numbers pose a predation threat to scallop stocks?

Research priorities regarding predator-prey interactions in the Clyde should include:

- Publication of the inventory of acoustic survey results from the Clyde to show the changes in herring, sprat, and krill abundances and distributions, as well as new surveys to assess abundance and distribution of porpoises **(Research Priorities 3, 5 & 9)**.
- Analysis of trends in the diet composition of piscivorous birds to determine whether these reflect the changes in the ecosystem **(Research Priorities 1 & 9)**.
- Detailed study on the diet and feeding rate of harbour seals and porpoises in the Clyde **(Research Priorities 1 & 4).**
- Analysis of trends in the abundance and production of benthos in the Clyde and the proportion of benthos in the diet of demersal fish **(Research Priorities 1, 3 & 8)**.
- Survey and assessment of scallop populations in the Clyde and the incidence of starfish predators **(Research Priorities 3 & 8)**.

3. North Sea and sandeels – the North East UK Closure

During the latter half of the twentieth century, the lesser sandeel (*Ammodytes marinus*) was one of the commonest fish species in the North Sea and an important prey for many marine mammals, birds and fish (Daan et al. 1990; Furness and Tasker 2000; Englehard et al. 2014). Sandeels were also the target of the largest single species fishery in the area (Gislasson and Kirkegard 1998). The magnitude of the fishery and the importance of sandeels for marine predators led to increasing concern over the potential impact of sandeel catches on the North Sea ecosystem (Monaghan 1992). One of the areas of greatest interest was ICES sub-area IV, off the Firth of Forth in the northwestern North Sea where a sandeel fishery developed on the Wee Bankie, Marr Bank and Scalp Bank in the early 1990s. The landings from this fishery peaked at over 100,000 t in 1993 and then subsequently declined (Rindorf et al. 2000). The Firth of Forth area is noted for its breeding seabirds, seals and gadoid fish, and the removal of such large quantities of sandeels became a major conservation issue. Initial analyses of seabird breeding success and diet, principally from long-term studies on the Isle of May, a major breeding colony in the area, suggested that declines in breeding success of black-legged kittiwakes (*Rissa tridactyla*, hereafter kittiwake), which occurred after the start of the fishery, were associated with changes in sandeel availability (Harris and Wanless 1997). In 1999, the UK government called for a moratorium on sandeel fishing adjacent to seabird colonies along the UK coast, including the Wee Bankie area (Figure PP3). A condition of a three-year closure coming into force in 2000, was the establishment of an ICES Study Group to 1) assess whether the removal of sandeels by fisheries had a measurable effect on sandeel predators such as seabirds, marine mammals, and other fish species, 2) assess if the establishment of closed areas and/or seasons for sandeel fisheries could ameliorate any deleterious effects, and 3) identify possible closed seasons/areas as specifically as possible.

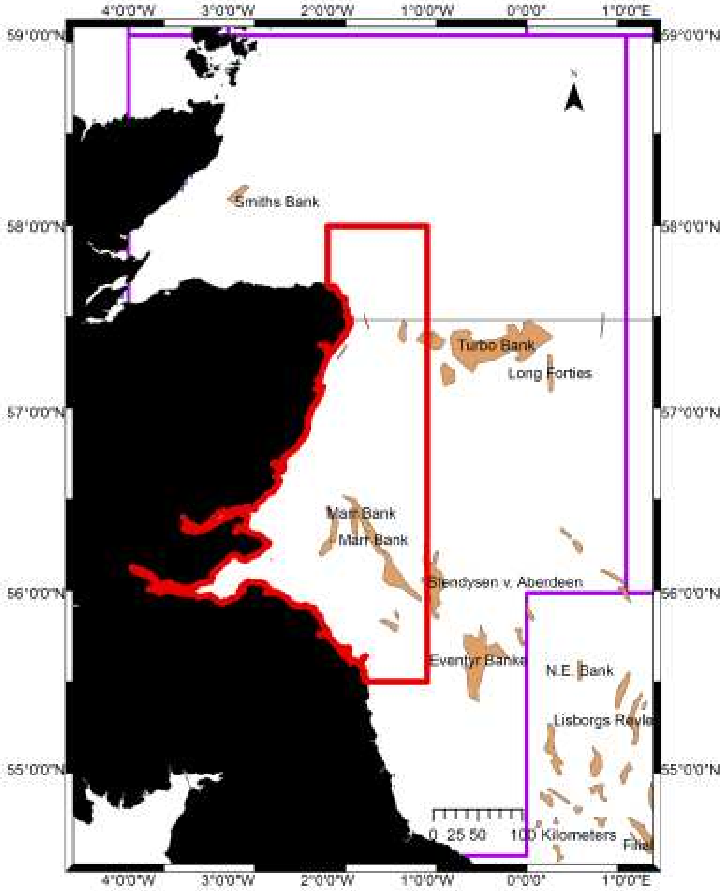

Figure PP3. *Map showing the North East closed area (red polygon) and ICES Sandeel assessment area 4 (purple polygon).*

Research on the Isle of May indicated that breeding success and adult survival of kittiwakes were lower when the sandeel fishery was operating, and both were also negatively correlated with winter sea surface temperature (wSST), a proposed proxy for sandeel availability (Frederiksen et al. 2004;

Figure PP4). Applying this model to breeding success data for six other regularly monitored kittiwake colonies in east Scotland and northeast England indicated very similar relationships across the region (Frederiksen et al. 2007). Further confirmation that the presence of the sandeel fishery had led to reductions in demographic performance of kittiwakes, was obtained using a BACI (Before-After-Control-Impact) design to compare breeding success in colonies in the closure zone where the sandeel fishery was active in the 1990s but was closed in 2000, with a control zone where sandeel fishing occurred before, during and after the 1990s (Frederiksen et al. 2008). The BACI analysis showed that 1) breeding success in the closure zone was depressed during the fishery period relative to the control zone and 2) breeding success was negatively correlated with fishery effort in the closure zone but not in the control zone. In addition, Daunt et al. (2008) demonstrated that estimated sandeel consumption and breeding success of kittiwakes in the closure zone were positively correlated with local sandeel abundance during and after the fishery. However, whilst there was compelling evidence that kittiwakes, which are surface feeders, were negatively affected by the sandeel fishery, no detectable effect was apparent in pursuit-diving seabirds e.g., common guillemots (*Uria aalge*), Atlantic puffins (*Fratercula arctica*) and European shags (*Phalacrocorax aristotelis*) (Daunt et al. 2008; Frederiksen et al. 2008). This implied that the reduction in sandeel abundance caused by the fishery was insufficient to impact diving species that can potentially access the entire water column and/or that fishing activity caused a vertical redistribution of sandeels such that the proportion available to surface feeders such as kittiwakes, was reduced.

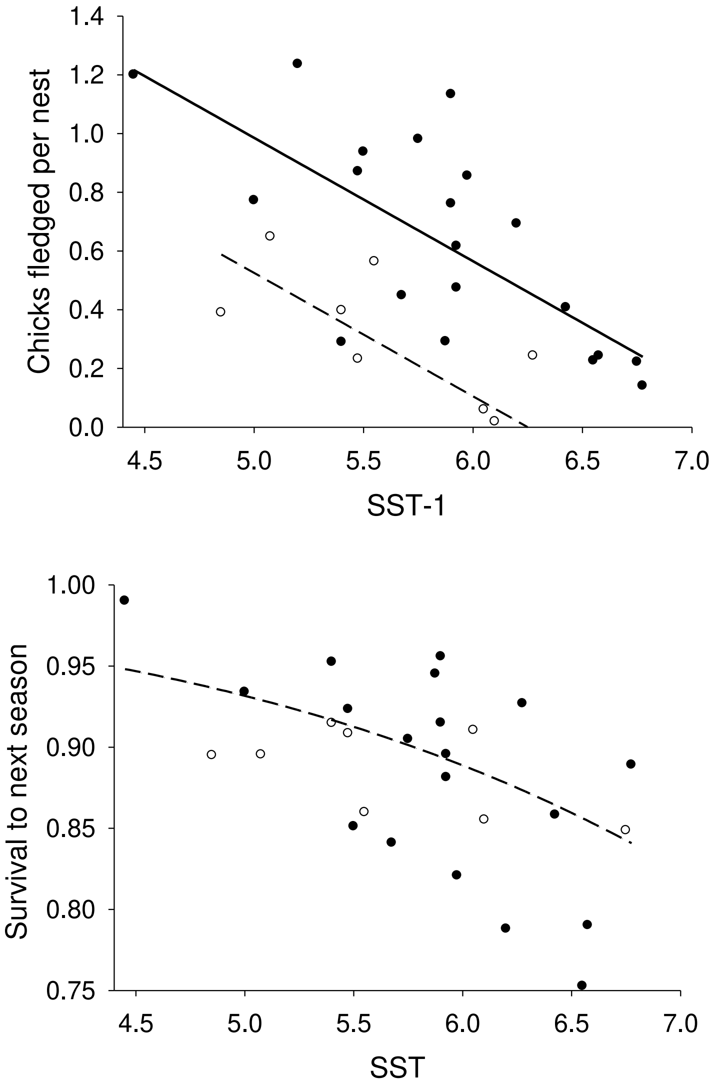

***Figure PP4**. Relationships between sea surface temperature and breeding success and adult survival of kittiwakes on the Isle of May. Filled symbols indicate non-fishery years and open symbols years when the fishery was operating. Updated from Frederiksen et al. (2004), redrawn from Frederiksen (2014).*

The rationale behind the sandeel closure was that it would segregate the inshore areas used by the predators from the offshore areas where commercial sandeel fishing was still allowed. A bioenergetics model of the Firth of Forth seabird community indicated that spatial segregation had been achieved (Daunt et al. 2008). However, when the boundary of the closed area was set, few empirical data on where individual breeding birds foraged were available. Since then there have been major advances in tracking techniques, and recent studies indicate that shags, guillemots, razorbills, puffins and kittiwakes at colonies in eastern Scotland feed almost exclusively in the closed area but that northern gannets (Morus bassanus) from the Bass Rock have a substantially longer foraging range, meaning that they potentially overlap with the commercially exploited area (Bogdanova et al. 2014; Daunt et al. 2011a, b; Hamer et al. 2009; Harris et al. 2012).

The North East UK closure remains one of the very few cases worldwide where a no-take zone for a particular species has been established, largely with the aim of protecting top predators, and where research has documented both negative impacts of the fishery and beneficial effects of the closure. Since 2000 there have been several scientific reviews of this closure. Concerns over local impacts of sandeel fisheries on top predators have not fundamentally changed and the ban has remained in place up until the 2016 season. Studies by fishery biologists have shown that sandeels in the Wee Bankie region are reproductively isolated from other fished aggregations in the North Sea (Boulcott and Wright 2011). In addition, life history characteristics of sandeels in the Wee Bankie aggregation, notably growth rate and length-at-age, differ markedly from other North Sea stocks making the Wee Bankie aggregation particularly vulnerable to recruitment overfishing (Wanless et al. 2004; Rindorf et al. 2016). Evaluating changes in sandeel abundance in the Wee Bankie stock have been hampered by the lack of a robust stock assessment method, but acoustic, trawl and dredge surveys and commercial abundance indices suggest an initial increase in sandeel abundance during the period of the closure (Greenstreet et al. 2006). In 2016 the first assessment of ICES area IV using available commercial catch data and winter dredge surveys was carried out by Marine Scotland. Results provide further support that this is a relatively unproductive stock and suggest that the TAC is at a level that can be met outside the closed area, thus reducing pressure for its re-opening.
It is, however, possible that the fishing ban could be lifted at some point in the future. Resumption of sandeel fishing would create further opportunities for research on the interactions between predators, sandeels and fisheries to provide management advice on options to minimise adverse impacts of commercial fishing for sandeels on top predators. Research priorities should include:

- **Updating the analyses of kittiwake breeding success and survival on the Isle of May in relation to wSST and fishing activity (Research Priorities 4, 5 & 8).** An interim analysis using data up to 2013 showed that the relationship with breeding success was largely unchanged with both wSST and the fishery effect still highly significant (Frederiksen 2014). However, the situation for survival had changed such that the fishery effect was no longer significant whereas the wSST effect had become stronger.

- **Elucidating the factors underpinning spatio-temporal variation of North Sea food web dynamics on kittiwake performance (Research Priorities 5 & 8).** Results from the Isle of May have previously indicated that breeding success of kittiwakes and other seabird species is mediated through bottom-up changes in conditions for sandeels (Frederiksen et al. 2006). However, the precise mechanism remains unclear and poor seabird productivity is not always associated with low sandeel availability (Frederiksen et al. 2006). Recent studies have also highlighted that environmental covariates such as stratification strength or timing correlate better with kittiwake breeding success than wSST at several colonies in eastern Britain (Carroll et al. 2015), and that at Fowlsheugh, 90 km north of the Isle of May, although kittiwake breeding success showed some sensitivity to local sandeel abundance, it is not a reliable indicator of climate-driven changes in the local food web (Eerkes-Medrano et al. 2017).

- **Deriving species-specific predator-prey relationships to identify critical thresholds in prey abundance for the east coast region (Research Priorities 5, 8 & 9).**

- **Targeted work to investigate if the fishery alters the behaviour of sandeels making them less available to surface feeders like kittiwakes (Research Priority 4).**

- **Determining and understanding the spatial and temporal distribution of sandeel, and their predators in the North Sea (Research Priorities 3, 5 & 8).**

Central to carrying out this research would be:

- Maintaining collection of data on seabird breeding performance at east coast colonies.

- Increasing the number of colonies where diet data are collected during the breeding season to assess the importance of sandeels as prey for seabirds throughout the region.

- Increasing the number of sites where long term time-series data on sandeels and other forage fish, zooplankton and phytoplankton abundance and phenology are collected.

Outcome 5: Final recommendations for successful implementation of an ecosystem fisheries approach in Scotland

Research priorities and data gaps

The research priorities we have identified highlight significant knowledge gaps currently hindering a proper understanding of the interactions between fisheries stocks and activities, and the ways in which they are affected by different predator-prey relationships. However, in some cases there are existing data that could be collated and analysed in new ways or combined with new data to reduce these impediments.

Sufficient data and expertise currently exists, for instance, to develop broad qualitative maps for how different fish species, elasmobranch species, seabird species and cetacean species migrate in and out of important fishing areas such as the North Sea or the West Coast. Distribution maps would help to detect resident and migratory populations for important predator and prey species, and to identify key closed populations within fishing regions. They would thereby identify which species and populations are most likely to interact strongly with, and affect or be affected by commercial fishing activities, and in which season this interaction will be at its most influential. On the west coast, existing data on seasonal distributions of key fish species (herring, sprat, Norway pout) could be combined with new data collected on the diet of top predators (seabirds, elasmobranchs, cetaceans, pinnipeds) to better understand which predator species are mostly likely to affect the seasonal abundance and distribution of important commercial fish species.

Similarly, tracking data for animals is increasingly available as technology advances. Existing tagging data could be mined to address new questions, such as within the Firth of Clyde where tagging data on seals could be re-analysed with data on cod distribution and movement to advance spatially explicit models of both seals and cod and their seasonal interactions. The tagging of seabirds could be paired with on-going acoustic surveys for fish, particularly in the seabird non-breeding season where there is a particular data deficit. There is tagging data available on several elasmobranch species. For the areas in question, this tends to be mark and recapture (MR) data focusing historically on offshore regions through fisheries research, and more recently on coastal regions through angler-led MR projects. This could be re-analysed to address contemporary questions and to aid in setting a base line for future comparisons. However, spatial data on many Scottish elasmobranchs is non-existent, even in MR form and only four species (tope, spurdog, porbeagle and common skate) have been the focus of research involving electronic tagging. Tagging of elasmobranch species identified as stock predators could be done in conjunction with tagging of prey species in areas where interactions take place to better inform interactions and the spatial impact of these predators. Any data on the movements of elasmobranchs, identifying behaviours such as residency or site fidelity would help inform impact on commercial stocks, especially in conjunction with localised diet analysis. Expert solicitation could identify particular fishing regions that should be targeted based on knowledge of the strength of interactions between seabirds and fish prey (e.g., northern gannets and sandeel and mackerel fisheries, and common eiders and mussel habitats; Table 2). These types of data could start to address the fundamental question as to the extent to which marine top predators are exploiting the same prey populations as fisheries.

In the Firth of Clyde, at-sea surveys of seabirds and cetaceans (minke whales) could be matched to on-going surveys for fisheries (herring, sprat, krill) and smaller cetaceans (porpoises and seals), which typically occur in October. The use of fixed cameras on fishing vessels could also provide an additional source of time-stamped distribution data for seabirds and some marine mammals. The involvement of fishers in data collection via on-vessel survey methods, particularly for marine top predators, would also help to build trust amongst fishers in relation to the quality and accuracy of scientific evidence, for instance in relation to the size of seal populations in cod fisheries off the west coast of Scotland.

The expansion of offshore renewable energy developments presents an opportunity to collate data from multiple sites to develop better models and mapping of fish habitat such as sandeel grounds where existing echo sounding data can be used to resolve habitat types. More could be done to incentivise private companies to share these data upon request with scientists and other stakeholders, for instance by facilitating open access to data within the licensing process.

Current marine ecosystem models exist for both the West Coast (Alexander et al., 2015) and the North Sea (Heath 2012; Romagnoni et al., 2015). However, these models need to incorporate new data on key biological components and processes at appropriate spatial scales to quantify interactions between predators and prey. Other possible research avenues might include modelling mixed fisheries and multispecies effects together in the same framework, and developing an individual-based modelling approach to understand the response of fishermen to regulation. Marine ecosystem models can give more robust results if an ensemble modelling approach was to be used to improve simulations of the marine environment and gain a better understanding of the key drivers of conflict between fishers and predators. Ensemble modelling allows for the exploration of uncertainty, and translates naturally into the language of risk and decision-making. For instance, ensembles can identify the sources of greatest uncertainty and hence the priorities for data-collection and improvement of process understanding (e.g., Thorpe et al., 2015). These approaches would greatly facilitate the development of coherent storylines for possible futures (i.e., a marine version of the IPCC process), critical for long-term strategic management.

Recommendations

Using the ten research priorities outlined above (Outcome 3), we recommend that FIS develop a programme of research and networking activities to identify sub-projects within each research priority capable of attracting additional funding in their own right. The development and promotion of an overarching research programme would help to identify other activities and research occurring in analogous situations in other countries encouraging exchange and engagement with overseas scientists and the development of industry funding and partnerships.

References for Predator-Prey Workshop report

Alexander, K. A., J. J. Heymans, S. MaGill, M. Tomczak, S. Holmes, and T. A. Wilding. (2015). Investigating the recent decline in gadoid stocks in the west of Scotland shelf ecosystem using a food-web model. *ICES Journal of Marine Science* 72,436-449.

Bogdanova, M.I., Wanless, S., Harris, M.P., Linström, J., Butler, A., Newell, M.A., Sato, K., Watanuki, Y., Parsons, M. and Daunt, F. (2014). Among-year and within-population variation in foraging distribution of European shags *Phalacrocorax aristotelis* over two decades: implications for marine spatial planning. *Biological Conservation* 170, 292-299.

Boulcott, P. and Wright, P.J. (2011). Variation in fecundity in the lesser sandeel: implications for regional management. Journal of the Marine Biological Association of the UK 91, 1273-1280.

Carroll, M. J., Butler, A., Owen, E., Ewing, S. R., Cole, T., Green, J. A., Soanes, L. M., Arnould, J. P. Y., Newton, S. F., Baer, J., Daunt, F., Wanless, S., Newell, M. A., Robertson, G. S., Mavor, R. A. & Bolton, M. (2015) Effects of sea temperature and stratification changes on seabird breeding success*. Climate Research* 66, 75-89.

Compagno, Leonard JV. 1984. An Annotated and Illustrated Catalogue of Shark Species Known to Date. Part 2: Carcharhiniformes. Vol. 4.

Cook, R.M. and Trijoulet, V. (2016). The effects of grey seal predation and commercial fishing on the recovery of a depleted cod stock. *Canadian Journal of Fisheries and Aquatic Science*. 73, 1319–1329 (2016) dx.doi.org/10.1139/cjfas-2015-0423

Cook, R.M., Holmes, S. and Fryer, R. J.(2015). Grey seal predation impairs recovery of an over-exploited fish stock. *Journal of Applied Ecology* 52, 969–979, DOI: 10.1111/1365-2664.12439

Daan, N., Bromley, P.J., Hislop, J.R.G. and Nielsen, N.A. (1990). Ecology of North Sea fish. *Netherlands Journal of Sea Research* 26, 343-386.

Daunt, F., Bogdanova, M.I., Newell, M., Harris, M.P. & Wanless, S. (2011a). GPS tracking of common guillemot, razorbill and black-legged kittiwake on the Isle of May, summer 2010. Report to Forth & Tay Offshore Wind Developers Group (FTOWDG).

Daunt, F., Bogdanova, M.I., Redman, P., Russell, S. & Wanless, S. (2011b). GPS tracking of black-legged kittiwake and observations of trip durations and flight directions of common guillemot at Fowlsheugh and St Abb's Head, summer 2011. Report to Forth & Tay Offshore Wind Developers Group (FTOWDG).

Daunt, F., Wanless, S., Greenstreet, S.P.R., Jensen, H., Hamer, K.C. and Harris, M.P. (2008). The impact of the sandeel fishery closure on seabird food consumption, distribution, and productivity in the northwestern North Sea. *Canadian Journal of Fisheries and Aquatic Sciences* 65, 362-381.

Eerkes-Medrano, D., Fryer, R.J., Cook, K.B. and Wright, P.J. (2017). Are simple environmental indicators of food web dynamics reliable: Exploring the kittiwake-temperature relationship. *Ecological Indicators* 75, 36-47.

Ellis J., Pawson M., Shackley S. 1996. The Comparative Feeding Ecology of Six Species of Shark and Four Species of Ray (Elasmobranchii) In The North-East Atlantic. Journal of the Marine Biological Association of the United Kingdom 76:1. 89-106.

Engelhard, G.H., Peck, M.A., Rindorf, A., Smout, S.C., van Deurs, M., Raab, K., Andersen, K.H., Garthe, S., Lauerburg, R., Scott, F., Brunel, T., Aarts, G., van Kooten, T. and Dickey-Collas, M. (2014). Forage fish, their fisheries, and their predators: who drives whom? *ICES Journal of Marine Science* 71, 90-104.

Furness, R.W. and Tasker, M.L. (2000). Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series* 202, 253-264.

Frederiksen, M. (2014). Environmental demography – Exploring the links between vital rates and a fluctuating environment. Doctor's dissertation. Aahus University. Department of Biosciences. Denmark 80 pp.

Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C. and S. Wanless. (2006). From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology* 75:1259-1268.

Frederiksen, M., Mavor, R.A. and Wanless, S. (2007). Seabirds as environmental indicators: the advantage of combining data sets. *Marine Ecology Progress Series* 352, 201-211.

Frederiksen, M., Jensen, H., Daunt, F., Mavor, R.A. and Wanless. S. (2008). Differential effects of a local industrial sand lance fishery on seabird breeding performance. *Ecological Applications* 18, 701–710.

Frederiksen, M., Wanless, S., Harris, M.P., Rothery, P. and Wilson, L.J. (2004). The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *Journal of Applied Ecology* 41, 1129-1139.

Gislasson, H. and Kirkegaard, E. (1998). Is the industrial fishery in the North Sea sustainable? In: Symes, D. (ed) Northern waters: management issues and practice. Fishing News Books, Blackwells, Oxford, p 195–207.

Greenstreet, S.P.R., Armstrong, E., Mosegaard, H., Jensen, H., Gibb, I.M., Fraser, H.M., Scott, B.E., Holland, G.J. and Sharples, J. (2006). Variation in the abundance of sandeels *Ammodytes marinus* off southeast Scotland: an evaluation of area closure fisheries management and stock abundance assessment methods. *ICES Journal of Marine Science* 63, 1530-1550.

Hamer, K.C., Humphreys, E.M., Magalhaes, M.C., Garthe, S., Hennicke, J., Peters, G., Gremillet, D., Skov, H. and Wanless, S. (2009). Fine-scale foraging behaviour of a medium-ranging marine predator. *Journal of Animal Ecology* 78, 880–889.

Harris, M.P. and Wanless, S. (1997). Breeding success, diet and brood neglect in the kittiwake (*Rissa tridactyla*) over an 11-year period. *ICES Journal of Marine Science* 54, 615-623.

Harris, M.P., Bogdanova, M.I., Daunt, F. and Wanless, S. (2012). Using GPS technology to assess feeding areas of Atlantic puffins *Fratercula arctica*. *Ringing & Migration* 27, 43-49.

Heath, M. R. (2012). Ecosystem limits to food web fluxes and fisheries yields in the North Sea

simulated with an end-to-end food web model. *Progress in Oceanography* 102:42-66.
Heath, M.R. and Speirs, D.C.(2012). Changes in species diversity and size composition in the Firth of Clyde demersal fish community, 1927-2009. *Proceedings of the Royal Society* B. 279, 543–552. Published online 6 July 2011, doi: 10.1098/rspb.2011.1015
Hunter, A., Speirs, D.C. and Heath, M.R.. (2015). Fishery-induced changes to age and length dependent maturation schedules of three demersal fish species in the Firth of Clyde. *Fisheries Research*, 170, 14-23.
Hunter, A., Speirs, D.C. and Heath, M.R.. (2016). Investigating the growth parameters of five demersal species in the Firth of Clyde. *Fisheries Research* 117, 71-81.
Matthiopoulos, J., McConnell, B., Duck, C. and Fedak, M. (2004). Using satellite telemetry and aerial counts to estimate space use by grey seals around the British Isles. *Journal of Applied Ecology* 41, 476–491. doi: 10.1111/j.0021-8901.2004.00911.x
Mavor, R. and Bolton, M. (2015). Effects of sea temperature and stratification changes on seabird breeding success. *Climate Research* 66, 75-89.
Monaghan, P. (1992). Seabirds and sandeels: the conflict between exploitation and conservation in the northern North Sea. *Biodiversity and Conservation* 1, 98–111.
Northridge, S., Cargill, A., Coran, A., Mandleberg, L., Calderan, S., and Reid, R.J. (2010). Entanglement of minke whales in Scottih waters: an investigation into occurrence, causes and mitigation. Sea Mammal Research Unit, Final Report to Scottish Government CR/2007/49. 57pp.
Rindorf, A., Wanless, S. and Harris, M.P. (2000). Effects of changes in sandeel availability on the reproductive output of seabirds. *Marine Ecology Progress Series* 202, 241-252.
Rindorf, A., Wright, P.J., Jensen, H. and Maar, M. (2016). Spatial differences in growth of lesser sandeel in the North Sea. *Journal of Experimental Marine Biology and Ecology* 479, 9-19.
Romagnoni, G., S. Mackinson, J. Hong, and A. M. Eikeset. (2015). The Ecospace model applied to the North Sea: Evaluating spatial predictions with fish biomass and fishing effort data. *Ecological Modelling* 300, 50-60.
Ryan, R., Leaper, R., Evans, P.G.H., Dyke, K., Robinson, K.P., Haskins, G.N., Calderan, S., van Geel, N., Harries, O., Froud, K., Brownlow, A., and Jack, A. (2016). Entanglement: an emerging threat to humpback whales in Scottish waters. IWC SC/66b/HIM/01. 12pp.
Thorpe, R.B., Le Quesne, W.J.F., Luxford, F., Collie, J.S. & Jennings, S. (2015). Evaluation and management implications of uncertainty in a multispecies size-structured model of population and community responses to fishing, *Journal of Methods in Ecology and Evolution* 6, 49-58.
Thurstan, R.H. & Roberts, C.M. (2010). Ecological Meltdown in the Firth of Clyde, Scotland: Two Centuries of Change in a Coastal Marine Ecosystem. *PLoS ONE* 5(7):e11767. (doi:10.1371/journal.pone.0011767)
Trijoulet, V. (2016). Bioeconomic modelling of seal impacts on West of Scotland fisheries. PhD thesis, University of Strathclyde.
Wanless, S., Wright, P.J., Harris, M.P. and Elston, D. A. (2004). Evidence for decrease in size of lesser sandeels *Ammodytes marinus* in a North Sea aggregation over a 30-yr period. *Marine Ecology Progress Series* 279, 237-246.

Workshop Report: Balanced harvesting in the context of Scottish Fisheries

University of Strathclyde Ross Priory Conference Centre, 24-16 October 2016

Chair and lead author: Richard Law, York Centre for Complex Systems Analysis, University of York.

Participants

- Robert I. Arthur, MRAG Ltd, London
- Neil Campbell, Marine Scotland Science, Marine Laboratory Aberdeen
- Robin M. Cook, Department of Mathematics and Statistics, University of Strathclyde
- Clive Fox, Scottish Association for Marine Science, Oban
- Michael R. Heath, Department of Mathematics and Statistics, University of Strathclyde
- Jeppe Kolding, Department of Biology, University of Bergen
- Paul MacDonald, NAFC Marine Centre, Scalloway
- David G. Reid, Institute of Marine Research, Galway
- Richard Slaski, Fisheries Innovation Scotland
- Douglas C. Speirs, Department of Mathematics and Statistics, University of Strathclyde

Acknowledgments

The theoretical results described here were developed independently of this report in collaboration with Michael J Plank, University of Canterbury, Christchurch, New Zealand.

Summary

1. Balanced harvesting (BH) is an ecosystem-based approach to fisheries management intended to bring fishing mortality, set at moderate levels, in line with the productivity of components of aquatic ecosystems. Work on BH is in its early stages, and BH is not yet accepted as a legitimate basis for exploiting living aquatic resources.
2. The literature does not provide a single clear measure of productivity against which BH can set fishing mortality. We suggest here production rate (dimensions: mass area^{-1} time^{-1}) as an appropriate measure. If fishing mortality rate is set in proportion to the production rates of ecosystem components, this protects components that are rare, and allows more exploitation of those that are abundant.
3. Little empirical information is currently available to examine the balance of exploitation to production of fish of different species and body sizes in the seas around Scotland. An Ecopath analysis of the west of Scotland shelf ecosystem in 1985 showed no relationship between fishing mortality rate and production rate of species and broader groups. This implies a major imbalance across species, because BH requires fishing mortality rate to be proportional to the production rate. In addition, production rate was seen to fall as fish become large for their species, whereas fishing mortality rate does not; fishing is therefore also unbalanced with respect to body size within species. There are many assumptions built into this analysis, and it should be treated with caution.
4. We suggest a multispecies plot of the logarithm of yield versus logarithm of production rate as a way to get a straightforward overview on the balance between yields and production rates of exploited species in a marine ecosystem. This also shows the directions in which fishing would need to change to improve the balance among species. In general, balance is not achieved by working to a fixed exploitation ratio. Evidence suggests that the exploitation ratio should usually be smaller in species with low production rates, and bigger those with high production rates.
5. Moving towards BH is likely to require a reduction in fishing on species that grow to large sizes, as these tend to have low production rates at present, and tend to be heavily exploited. However, some compensation for this is possible by increased fishing on small species with high production rates. This may include taxa further down the food chain that are exploited little, if at all, at the present time.
6. A move towards BH raises the social questions about the acceptability of reducing the catch of large fish that consumers are accustomed to, and of increasing that of small fish, some of which may be new to consumers. It also raises an issue of the impact of exploitation of forage fish, as these provide food for larger fish, seabirds and sea mammals. A broad societal discussion would be needed about the consequences for the fishing sector, the supply chain, the consumer, the ecosystem, local economies, and national economies.
7. Two marketing challenges would need to be addressed in a shift towards BH. First, an existing low market price for certain species/sizes could make harvesting uneconomic. Second a market may not exist for species/sizes that are not currently exploited. The use of all the new species and sizes being caught and probably landed would need to be addressed – human consumption, animal feed, or other uses. The same issues occur with the EU landing obligation.
8. BH would need to be reconciled with current regulations and management objectives. For instance, in the context of landing obligation in EU waters, landing fish that would previously have been discarded is not necessarily detrimental from the perspective of BH: the aim would be to land, and sell, all fish that are caught. Before embarking on a path towards BH, we should be clear on the biological, ecosystem, economic and social objectives, and their relative priorities. This should be done regardless of whether a move towards BH is proposed, but would be essential for such a new departure.
9. Given that a major imbalance exists between fishing mortalities and production rates, the management target would be to move fishing mortalities gradually in directions that would improve the balance. This target itself is expected to shift over time, because production rate changes directly through fishing and indirectly through biological processes. Management that can respond and adapt to such changes would be required.
10. Management to implement a shift towards BH in a Scottish context would need to adopt new methods. Broad-brush, métier-based management is suggested as a possible approach, with a strong industry involvement, or even responsibility, much greater flexibility from managers and fishers, and a results-based, multi-year approach to targets and objectives.
11. The immediate data requirement for developing BH in Scottish waters is an inventory of the present relationship between fishing mortality and production rates of the assessed stocks. In

due course this would need to be extended to incorporate other components of the ecosystems that are not currently assessed, especially those that might be chosen for increased exploitation.

12. A priority for research to support a move towards BH is to develop multispecies models that account properly for the flow of biomass through marine ecosystems, parameterised to match the important features of Scottish waters. Such models are needed to examine the consequences of different multispecies fishing scenarios on structure and function of marine ecosystems. They are also needed to find safe, efficient and potentially profitable paths towards BH, to check effects of different overall fishing pressures, and to link exploited fish stocks to other components of marine ecosystems such as seabirds and mammals.

Introduction

Scottish fisheries take place within the framework of the Law of the Sea Convention and the Fish Stock Agreement of the United Nations, agreements that are built largely on a foundation of a single-species maximum sustainable yield (MSY). In addition to this, the United Kingdom, like most other countries, is a Party to the Convention on Biological Diversity (CBD). This includes the Malawi Principles, of which Principle 5 states that "conservation of ecosystem structure and functioning, in order to maintain ecosystem services, should be a priority target of the ecosystem approach". It is this ecosystem approach that, when applied to fisheries: (1) raises the need to take account of the dynamic coupling among marine species and with the abiotic environment these species live in, and (2) recognizes our incomplete knowledge of how the coupling works (Garcia et al. 2016a). A consequence of this is that the EU Common Fisheries Policy (CFP) explicitly acknowledges our limited understanding of marine ecosystems, and "adopts a cautious approach which recognizes the impact of human activity on all components of the ecosystem". Scottish fisheries, currently operating within the CFP, therefore need to be managed with their impacts on marine ecosystems in mind.

Balanced harvesting (BH) can be thought of as a systematic attempt to take fisheries management to the ecosystem level – the ecosystem-based approach to fisheries management (EBFM). Ideas about BH have been developing over many years (Caddy and Sharp 1986, Misund et al. 2002, Jul-Larsen et al. 2003, Bundy et al. 2005, Zhou et al. 2010). A working definition has recently been suggested as fishing that "*distributes a moderate mortality from fishing across the widest possible range of species, stocks, and sizes in an ecosystem, in proportion to their natural productivity, so that the relative size and species composition is maintained*" (Garcia et al. 2012). The motivation here of exploiting marine ecosystems in a way that keeps them close to a natural state is clear. Moreover, it is in keeping with the intuition that less productive components of ecosystems are able to support less exploitation than productive components. Various definitions of 'productivity' are in the literature; this report recommends the use of 'production rate' in the section: 'A measure for balancing fishing mortality rate'.

BH goes beyond the current focus on catching large fish that often have low production rates, with the aim of bringing fishing more in line with production rates of components of marine ecosystems. The current approach is illustrated in Fig. BA1a, where, for simplicity, a multispecies fish assemblage has been aggregated to show just the body-size dependence of production rate (which falls here with increasing body size). As of now, large fish tend to be the focus of fishing, as shown diagrammatically in Fig. BA1a. A step in the direction of BH (Fig. BA1b), would be to reduce fishing mortality on large fish, and to increase it on smaller fish in line with their greater production rates. The motivation is to reduce the damage to the structure and functioning of marine ecosystems being caused by fishing, and to open up new opportunities for less disruptive fishing activities.

BH has necessarily to move on from the current focus of fisheries management on single-species MSY (Voss et al. 2014, Skern-Mauritzen et al. 2016), because species in marine ecosystems are coupled through predator-prey interactions. This is essentially the price to be paid for moving from single species to ecosystem-based management. One way to tackle the coupling is to pick out predator-prey interactions recognized to be of particular importance. BH complements this approach at a broader ecosystem level by considering the rate of flow of biomass among the components of marine ecosystems, and how harvesting could be organized in relation to this flow.

To gain knowledge of how mass flows through marine ecosystems, a formal mathematical framework, based on dynamics of size spectra is available, and is itself the subject of continuing research (Silvert and Platt 1978, 1980, Benoît and Rochet 2004, Andersen and Beyer 2006, Capitàn and Delius 2010, Datta et al. 2010, 2011, Hartvig et al. 2011, Guiet et al. 2016, Blanchard et al. 2017). These size-spectrum models deal explicitly with the transfer of mass from prey to predator governed primarily by size-dependent predation, on the basis that most marine organisms grow in mass by eating smaller organisms, and die mostly because they are eaten by larger organisms. Internalizing growth and death ensures that components of an ecosystem are coupled, and does the bookkeeping of biomass as it flows through the ecosystem. The models have been used as a basis to develop ideas about BH (Law et al. 2012, 2015, 2016, Jacobsen et al. 2014).

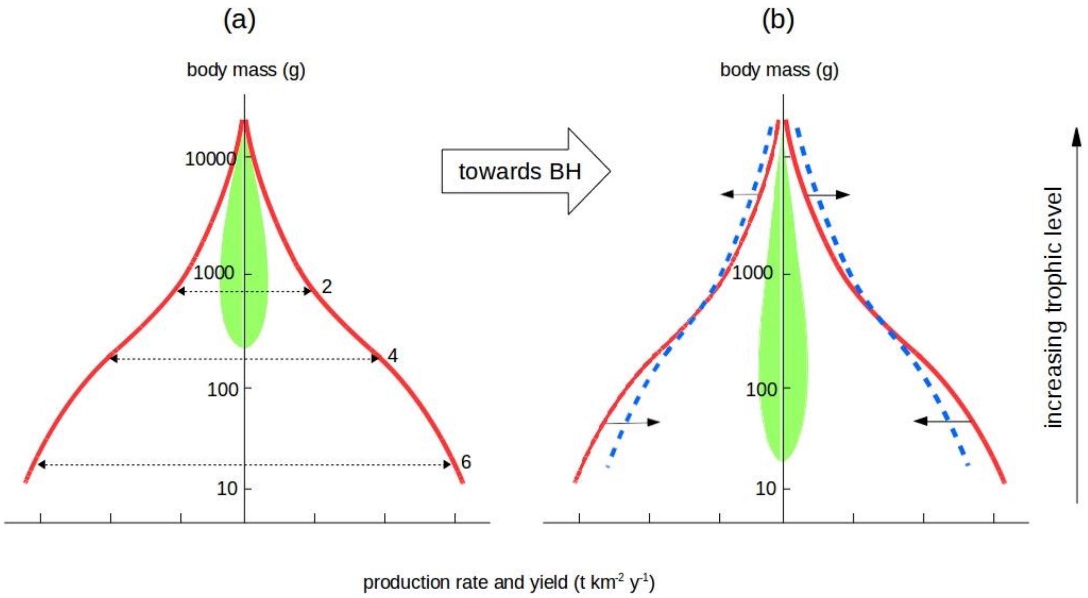

Figure BA1. *A step towards BH of a fish community. The continuous red line is production rate as a function of body mass after aggregating over an assemblage of fish species. (a) Current state with fishing concentrated at large body sizes; the yield is shown by the green shaded area. (b) A step in the direction of BH; this reduces fishing mortality on large fish where production rates are low; BH also allows some fishing mortality on smaller fish, if the production rates at these smaller sizes are large, as in this diagram. The effect is to increase production rates of larger fish and to reduce production rates of smaller fish (blue dashed line). The vertical axis here can also be thought of as trophic level, and the diagrams as depicting trophic pyramids of production rates.*

Neither the size-spectrum methodology, nor the possible benefits of BH are yet accepted in fisheries science (Andersen et al. 2016, Burgess et al. 2016, Froese et al. 2016a, 2016b, Pauly et al. 2016). Work on BH is in its early stages, and it is important to be aware of its limitations. For clarity, we list of some things that BH is not:

- It is not a solution to overfishing. It deals primarily with how fishing mortality could be distributed across components of the ecosystem. It does however call for fishing mortality to be 'moderate' (a term left undefined). Ideas about BH stem from African lakes where much of the fishing is small-scale, using simple and inefficient gears. It is essential to understand that an automatic, unconsidered application of BH to the efficient, industrial fisheries in the developed world would most likely lead to their rapid collapse.

- It is not a call for an unselective, free-for-all in the fishing industry. In fact it has been argued that the degree of selectivity on fishing mortality needed to match the detailed productivity of ecosystem components could make exact balancing unachievable in practice (Breen et al. 2016, Reid et al. 2016, He et al. 2016).

- It is not an argument that exploitation has to span a range from microorganisms to large marine mammals. BH has to operate within a societal context, and society will ultimately judge the range of marine organisms on which exploitation is sensible and acceptable.

- It is not an unqualified call to go out and catch small fish. Bringing fishing mortality more in line with production rates, may or may not involve small fish, depending on where productivity is concentrated. However, production rates are typically low for fish that are big for their species, and BH does call for correspondingly low fishing mortality of these big fish.

- It is not necessarily invalid, even if the best balancing that can be achieved is less than perfect. For instance, some fisheries scientists argue that balancing to the overall production rate of species would be a useful step forward, without balancing to production rates by body size.

Science of balanced harvesting

Background

Ideas about BH have grown out of studying small-scale artisanal fisheries in African lakes where fisheries regulations are weak (Jul-Larsen et al. 2003, Kolding and van Zwieten 2011, 2014). These fisheries catch a wide variety of fish species and sizes, including small fish. There is evidence that these fisheries can generate more biomass yield than fisheries managed by conventional methods based on minimum-size regulations, and that they do so without major disruption to the species composition of the fish communities. These features have also emerged in recent numerical modelling of Lake Kariba fisheries (Kolding et al. 2016a). An interpretation is that this pattern of small-scale fishing, arising from using a wide variety of gears, distributes fishing effort closer to the production rate of components of the ecosystem than the standard fishing methods focused on single-species and net-mesh regulations (Kolding et al. 2016b).

Natural state

Below the surface of BH and more generally CBD Principle 5, there is an issue about what the 'natural' state of marine ecosystems would be if human impact was small. Given the ubiquitous, heavily-exploited and unbalanced state of our marine ecosystems, this seems impossible to answer objectively, and may mean that the 'desired' state of a marine ecosystem has to be agreed on the basis of cultural or social values. There is however an organizing principle in the empirical finding by Sheldon et al. (1972) that the biomass spectrum of assemblages of pelagic organisms is relatively flat over many orders of magnitude when logarithmically scaled to body mass; see Guiet et al. (2016) and Sprules and Barth (2016) for recent reviews. Writing the logarithm of body mass $x = \log(w/w_0)$, where w_0 is an arbitrary reference mass, the observation is that biomass $B(x)$ in a given volume or surface area of the sea has the following property as x changes:

$$B(x) \approx constant.$$

(The convention of working with log body mass x is adopted throughout this report.) To put the observation another way, at the level of the whole assemblage (ignoring species identity), there is roughly the same amount of biomass per unit area in organisms of body mass 1 to 2 g, as in those between 2 to 4 g, 4 to 8 g, and so on. This property was first observed in plankton assemblages outside the size range directly affected by human exploitation, and it could therefore give some clues about the natural state of such systems. We do not know of any studies of marine assemblages in the exploited size range of fish which have demonstrated this property, but this may itself be a result of the long history of exploitation of fish.

There are many caveats to Sheldon's rule. The pattern is not exact – no ecological patterns ever are.

It is best seen as an average property of pelagic ecosystems, and becomes more evident as the spatial region and time period are increased (this is because the spectrum becomes averaged over larger areas and time periods smoothing out local variability). Sheldon's rule also does not deal with the species composition within the assemblage: different compositions can lead to a similar size structure at the level of the assemblage. The assemblage of pelagic organisms is often part of a larger ecosystem that encompasses benthic detritivores structured in other ways (Blanchard et al. 2011), as well as other groups such as seabirds and marine mammals. However, the repeatability of Sheldon's observation does suggest a rather basic structural feature of marine ecosystems, probably tied to the way in which biomass (energy) flows through the system, which can be seriously disrupted by fishing.

In the context of this disruption, Blanchard et al. (2005) noted a significant steepening of the slope of multispecies size spectra in the Celtic Sea over the period 1987 to 2003, with fishing having a stronger effect than climate. Associated with this change was an increase in abundance of small fish in the size range 4–25 g and a decrease in the abundance of large fish in the size range 100–121 and 144–169 g. A similar steepening of the slope and increase in intercept of multispecies size spectra was documented in the North Sea between 1977 and 1993 (Rice and Gislason 1996). Guénette and Gascuel (2012) also observed a major truncation in length and age distributions in the Celtic Sea and Bay of Biscay over the period 1950 to 2008.

Productivity and production rate

Ecologists typically use the term productivity and production rate interchangeably (Odum 1959, p. 69) to mean the amount of new living material produced by some set of organisms in a given region per unit time (dimensions: mass area^{-1} time^{-1}). This usage was in place by the time of Lindeman's (1942) founding paper on trophic dynamics, and these ideas were adopted in fisheries science. For instance Allen (1971), writing on the relation between production rate and biomass, called P/B the production-biomass ratio, and Christensen and Pauly (1993, page 340) called P/B the “ratio of system productivity over biomass”.

However productivity in fisheries science has more recently taken on a new meaning, that of P/B (dimensions time^{-1}), so the terms 'productivity' and 'production' as currently used in fisheries science are entirely different. The latter is called 'production rate' rather than production here, as is usual in ecology for quantities containing a dimension time^{-1}.

Production rate $p_i(x)$ is the total rate at which biomass is appearing in species i at log body mass x in some area. (The index i could refer to some other grouping of organisms; we take it to refer to species in this report, unless otherwise stated.) In other words, it is the product of biomass density $b_i(x)$ and the growth rate $g_i(x)$ per unit mass, i.e. the mass-specific growth rate (dimensions: time^{-1})

$$p_i(x) = g_i(x)b_i(x). \qquad \text{(mass area}^{-1}\text{ time}^{-1}\text{)} \qquad (1)$$

The biomass density is given by

$$b_i(x) = w_0 e^x u_i(x), \qquad \text{(mass area}^{-1}\text{)} \qquad (2)$$

where $u_i(x)$ is the density of i (dimensions: area^{-1}), and w_0e^x is the mass of an individual (dimensions: mass), both at size x.

Productivity, in its current fisheries usage, is the mass-specific rate of production

$$g_i(x) \quad . \qquad \text{(time}^{-1}\text{)} \qquad (3)$$

In terms more familiar in fisheries science, the total production rate P_i and total biomass B_i can be thought of as integrals over body mass, given for species i as:

$$P_i = \int g_i(x)b_i(x)dx \qquad \text{(mass area}^{-1}\text{ time}^{-1}\text{)} \qquad (4)$$

$$B_i = \int w_0 e^x u_i(x)dx. \qquad \text{(mass area}^{-1}\text{)} \qquad (5)$$

The productivity, i.e. the mass-specific rate, is then given by P_i/B_i, when body-size is ignored. All these measures apply at a single point in time, and can be expected to change over time unless the ecosystem is at steady state.

The distinction between production rate and productivity becomes important in discussions about BH, because fishing mortality is intended to be proportional to some measure of production, and the choice of measure has fundamental effects on the outcome as described in the measure for balancing fishing mortality rate below.

Natural production rate

Assuming the aggregated biomass spectrum remains near to constant (Sheldon's rule) as log body mass increases, the natural production rate should scale with body mass in the same way as mass-specific body growth rate aggregated over species. This is because the production rate is the product of biomass and mass-specific growth rate, and the changes in biomass with log body mass are small. A scaling exponent of mass-specific growth rate with respect to body mass in the region of -0.2 have been suggested (Andersen and Beyer 2006, Law et al. 2015). In this case, production rates are lower in larger organisms than in smaller ones. There is no surprise in this: nearly all biomass in the organisms in marine ecosystems comes from the solar energy captured by phytoplankton which are among the smallest organisms in pelagic assemblages, and the transfer of energy from one trophic level to the next is inefficient. (A widely accepted approximate energy transfer efficiency between trophic levels is 10%, meaning that 90% of the energy consumed by the organisms within a trophic level is lost to metabolic costs, excretion or non-predation related mortality.)

In terrestrial ecosystems it is rather obvious that the inefficient transfer of biomass from one trophic level to the next makes production rates lower further up the food chain: for instance, production rates of lions are lower than those of their antelope prey, which in turn are lower than those of the plants on which the herbivores feed. Teleost fish in marine ecosystems, however, have the feature of moving through several trophic levels as they grow from microscopic planktonic eggs to maturity. This makes it harder to assign a meaningful trophic level to many marine species, although the transfer of biomass still remains inefficient as it passes from prey to predator. Body size is arguably a better starting point for trophic dynamics in the marine world than species identity, and evidence from stable isotope research gives some support to this (Jennings et al. 2001). However, body size is no more than a starting point, because some fish species also have adaptations for particular kinds of feeding, such as gill rakers that enable planktivory (Canales et al. 2016).

Note that Sheldon's rule refers to the aggregated assemblage of species. This is not to say that the production rate within individual species has to scale in the same way with body mass. It is quite possible for production rates within species to be different from that of the whole assemblage, and yet for a near-to-constant biomass spectrum to emerge after aggregation over species.

A measure for balancing fishing mortality rate

There has not been a consensus about the measure against which fishing mortality should be balanced in BH, and this has generated some confusion. Two natural candidates are production rate and productivity (in its current sense in fisheries science). In describing these below, all variables are disaggregated to log body mass x within species i.

Balance to production rate (BH1): Here fishing mortality rate $f_i(x)$ of species i is set in proportion to its production rate $p_i(x) = g_i(x)\, b_i(x)$ as in eq. (1)

$$f_i(x) \;=\; c_1 p_i(x) \;=\; c_1 g_i(x) b_i(x), \tag{6}$$

with a corresponding yield to the fishery $y_i(x)$

$$y_i(x) \;=\; f_i(x) b_i(x) = \; c_1 g_i(x)[b_i(x)]^2, \tag{7}$$

where c_1 is a constant of proportionality (dimensions: area mass^{-1}) that determines the intensity of exploitation.

Balance to productivity (BH2): Here fishing mortality is in proportion to the mass-specific production rate (productivity) as in eq. (3)

$$f_i(x) \quad = \quad c_2 p_i(x)/b_i(x) \quad = \quad c_2 g_i(x), \tag{8}$$

with a corresponding yield to the fishery $y_i(x)$

$$y_i(x) \quad = \quad f_i(x) b_i(x) \quad = \quad c_2 g_i(x) b_i(x). \tag{9}$$

The constant of proportionality c_2 here is dimensionless, and determines the intensity of exploitation (the so-called exploitation ratio).

The key difference between BH1 and BH2 is that the fishing mortality rate in BH1 is sensitive to the biomass of species *i* (eq. 6), and tends to zero as $b_i(x)$ gets small. In other words, it protects components with low biomass from exploitation, and allows those with high production to be harvested more. By contrast, fishing mortality in BH2 has no direct dependence on biomass (eq. 8), and could in principle allow a species to be exploited to extinction. In effect, the distinction between BH1 and BH2 is between fishing mortality being density-dependent (BH1) and density-independent (BH2). As a biomass spectrum flattens towards a Sheldon shape, fishing mortalities in BH1 and BH2 converge, because in this special case, productivity and production rate are proportional to one another. But this does not alter the basic difference between density-dependent (BH1) and density-independent (BH2) fishing mortalities.

Which measure, BH1 or BH2, should be adopted? BH is an ecosystem approach to fishing with an explicit aim of maintaining the species richness of marine ecosystems. The density-dependent fishing mortality in BH1 achieves this, and the density-independent mortality in BH2 does not. To avoid any further confusion, we therefore argue that BH should be defined as bringing fishing mortality into line with the production rates of components of the ecosystem (BH1), not with productivity in its current fisheries usage (BH2). We therefore propose the definition of BH should read as distributing:

> *"a moderate mortality from fishing across the widest possible range of species, stocks, and sizes in an ecosystem, in proportion to their natural production rates, so that the relative size and species composition is maintained"*

(cf. Garcia et al. 2012). This definition has been used by Plank (2016), and we adopt it for the remainder of this report.

The exploitation ratio *Y/P*

Note that a yardstick of fisheries science, that harvesting should work towards a fixed exploitation ratio, does not in general apply under BH (i.e. BH1). The exploitation ratio is defined as Y/P, the ratio of total yield to total production, and is taken to be about 0.5, or more cautiously near 0.4 (Patterson 1992).

To understand the problem, consider the following size-aggregated measures for species *i*: fishing mortality F_i, yield Y_i, production P_i (eq. 4), and biomass B_i (eq. 5), where $F_i = Y_i/B_i$ and $Y_i = \int f_i(x) b_i(x) dx$. BH calls for F_i to be proportional to P_i, or equivalently for $Y_i = F_i B_i$ to be proportional to $P_i B_i$. Current evidence from exploited marine ecosystems suggests a power-law relationship between P_i with B_i, i.e. a scaling of P_i with B_i of the form P_i^{α}, where α is positive (Fig. BA2). This gives a relationship $\log(Y_i/P_i) = c + \alpha \log P_i$ with an intercept *c*. In other words, BH requires the ratio Y_i/P_i to be smaller in species with low production rates than in species with high production rates. At the present time, it is usually the species that grow to large sizes that have the low production rates. In these circumstances, fishing to achieve a constant exploitation ratio Y/P is unbalanced because it either takes either too little biomass of the small-bodied species, or too much biomass of the large-bodies species (or both) relative to the production rates of the species.

Only if $\alpha = 0$, i.e. if total biomass does not scale with body mass, is a constant exploitation ratio Y/P consistent with BH. Although assemblages might eventually approach this state under BH, currently our heavily exploited marine ecosystems have biomasses strongly tilted in favour of small species, with α's away from zero. (The exploitation ratio is developed further in the case of the west of Scotland shelf below.)

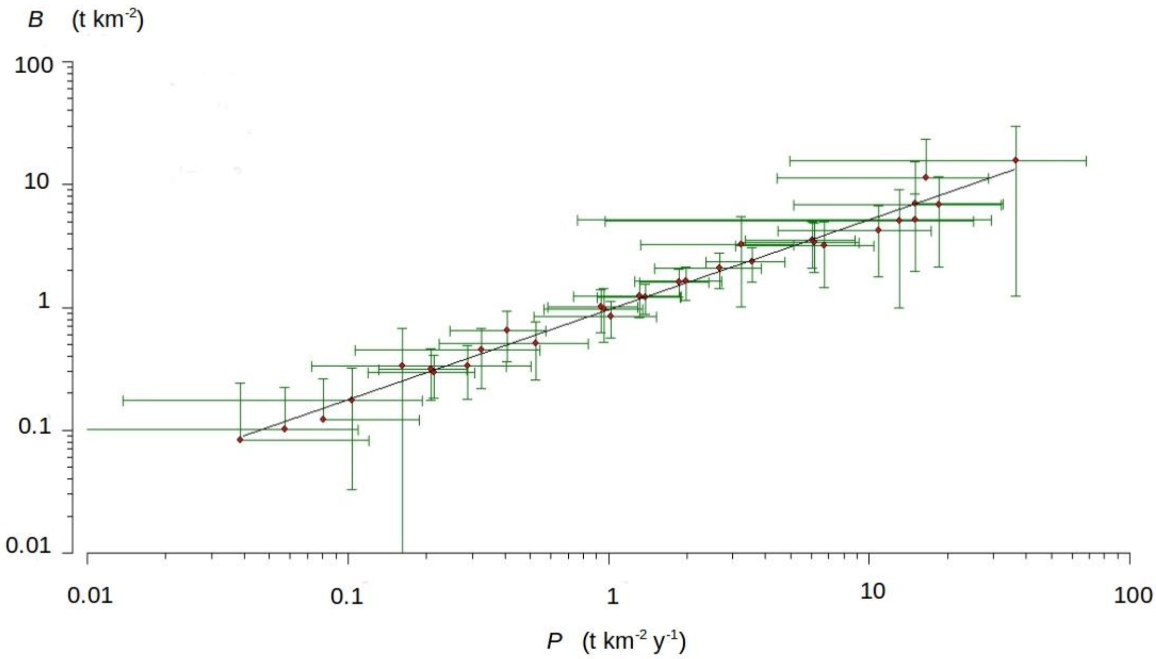

Figure BA2. *Relationship between production rate P and biomass B from 110 Ecopath models chosen as in Kolding et al. (2016c). Each point refers to a trophic level, taken in increments of 0.1, from which mean P and B of all teleost and elasmobranch groups were computed. Bars are 95% confidence intervals. Plants, invertebrates, birds and mammals were excluded.*

How balanced is exploitation of Scottish marine ecosystems?

We take the west coast of Scotland shelf as a case study in which to examine the balance between fishing and production rate. This region corresponds to the part of ICES area VIa that is shallower than 200 m.

Our results are based on data from an Ecopath model (Alexander et al. 2015) parameterised and balanced for the year 1985, which provided a starting baseline for a subsequent Ecosim model. This is an equilibrium model, i.e. each component of production within the year is balanced by loss; this contrasts with the full Ecosim implementation where biomass accumulation and loss over time is allowed (although overall the total amount of energy put into the system must balance that accumulated and removed). Clearly, the Ecopath model does not represent the current state of the ecosystem, and we use this study because it was the only multispecies model available to us giving ecosystem-level information on the shelf. (The Ecosim model which extends the Ecopath model to more recent years is currently being updated and was not available at the time of the workshop.) The Ecopath analysis gives estimates of biomass density B_i (t km^{-2}), yield Y_i (t km^{-2} y^{-1}), and total mortality rate (natural plus fishing mortality) Z_i (y^{-1}) (Alexander et al. 2015 ,Table 2). Biomasses of some of these groups were estimated from research surveys and were inputs into Ecopath, and biomasses of other groups were estimated by Ecopath. The aggregated B_i, Y_i and Z_i values were used to obtain production rate $P_i = B_i Z_i$ and fishing mortality rate $F_i = Y_i/B_i$ for each group.

The broad relationship between F_i and P_i across the groups shows there was a major imbalance between fishing and production rates. In fact, we found no evidence of any relationship between F_i and P_i in the data in Fig. BA3a (a test for a non-zero slope of the linear regression line has p = 0.11). This is in contrast to BH which requires a positive linear relationship between $\log F_i$ and $\log P_i$ with slope = 1, shown as the line in Fig. BA3a.

In keeping with Fig. BA2, there was however a strong positive relationship between P_i and B_i (Fig. BA3b), production rates being greater in the groups with greater biomass, the slope of the $\log B_i$ $\log P_i$ plot being α = 0.84. Thus, to move fishing mortality F_i towards a balance with production rate P_i, a lower ratio Y_i/P_i would be needed in groups with lower production rate (see Section: 'The exploitation ratio'). The slope of the relationship between $\log Y_i$ and $\log P_i$ that would be consistent with BH is the line 1+ α = 1.84 in Fig. BA3c. The data themselves show no evidence of a relationship between $\log Y_i$ and $\log P_i$ (a test for a non-zero slope of the linear regression line has p = 0.28).

These results suggest that, for the baseline year of 1985, a shift in the direction of BH would have called for relatively less exploitation of groups with low production rates (such as cod), but that this could have been accompanied by relatively more exploitation of those with high production rates. Where to set the line is an important issue, as there is no single exploitation ratio Y/P to aim for. We return to this below, in the context of implementation (see Section: 'Implementation of BH'). It is important to understand that both biomass and production rates change in response to fishing, so moving fishing in the direction of BH is an iterative and adaptive process that keeps track of P_i and B_i, as well as F_i and Y_i.

In addition to these results on the aggregated quantities, we disaggregated B_i down to log body mass $b_i(x)$, to build up a biomass spectrum of the fish assemblage, and to examine the relationship between body size and production rate $p_i(x)$. To do this, we worked from a technique suggested by Pauly and Christensen (2002:221), carrying out the disaggregation using a growth equation (Appendix A). Parameter estimates for the von Bertalanffy growth equation were taken from Kienzle (2005) and Gislason et al. (2008), converted to mass using allometric parameters in Robinson et al. (2010). We took a subset of thirteen teleost fish groups used in the Ecopath study (Alexander et al. 2015) for this work. Ranked by decreasing biomass these were: herring, horse mackerel, mackerel, flatfish, sprat, blue whiting, sandeel, Norway pout, haddock, pollock, monkfish, whiting and cod. Mass-specific growth rates $g_i(x)$ were also obtained from the growth equations, so that production rates by body size could be estimated as $p_i(x) = g_i(x)b_i(x)$. For the group 'flatfish' the average of the values of the four most important species (common dab, flounder, place and sole) were used. Also, for simplicity, immature and mature haddock were taken as a single category, summing the biomasses and taking the average of total mortalities; the same procedure was adopted for whiting and cod.

Biomass, when disaggregated to body size by the von Bertalanffy equation, has a characteristic shape within species, rising to a maximum fairly late in life, generated by the structure of the equation (Fig. BA4a). From this information, we constructed the biomass spectrum of the assemblage as a whole; the result was a long way from the flat structure of Sheldon's rule. However, the assemblage here is just a subset of the species which are actually present in the west of Scotland shelf ecosystem. For instance, our results do not contain zooplankton, crustaceans and molluscs that would form a major part of the biomass at the left-hand end. Also rays, sharks, 'large demersals', marine mammals and seabirds are missing towards the right-hand end.

In keeping with the aggregated results (Fig. BA3), production rates at the time of the Ecopath study tended to be greater in the species with smaller body sizes. In addition, production rates rose to a maximum with respect to body size in all of the species, beyond which they declined as growth slowed down and biomass fell (Fig. BA4b); this follows from the fact that production rate is proportional to cohort biomass, and is distinct from assumptions in the Ecopath model (Appendix A). Balanced harvesting therefore requires fishing mortality to fall as fish get larger and older, in line with calls by EBFM to protect BOFFFFs (big old fat fecund female fish) as a means of minimising the risk of recruitment failures (Hixon et al. 2014). Unfortunately such selectivity is hard to achieve with mobile fishing gears, such as trawls and seines that preferentially retain the larger fish, and as a result fishing mortality rates become increasingly out of kilter with production rates at large body sizes. The low density of large fish that follows from this is one of the most obvious and frequently cited effects of contemporary patterns of fishing on the structure of marine ecosystems, and has led to the development of the large fish indicator as a measure of ecological quality of marine fish assemblages (Greenstreet et al. 2011, Modica et al. 2014, Engelhard et al. 2015). With knowledge of the relationship between production rate and body size, the relative levels fishing mortality over body size needed to achieve BH become clear.

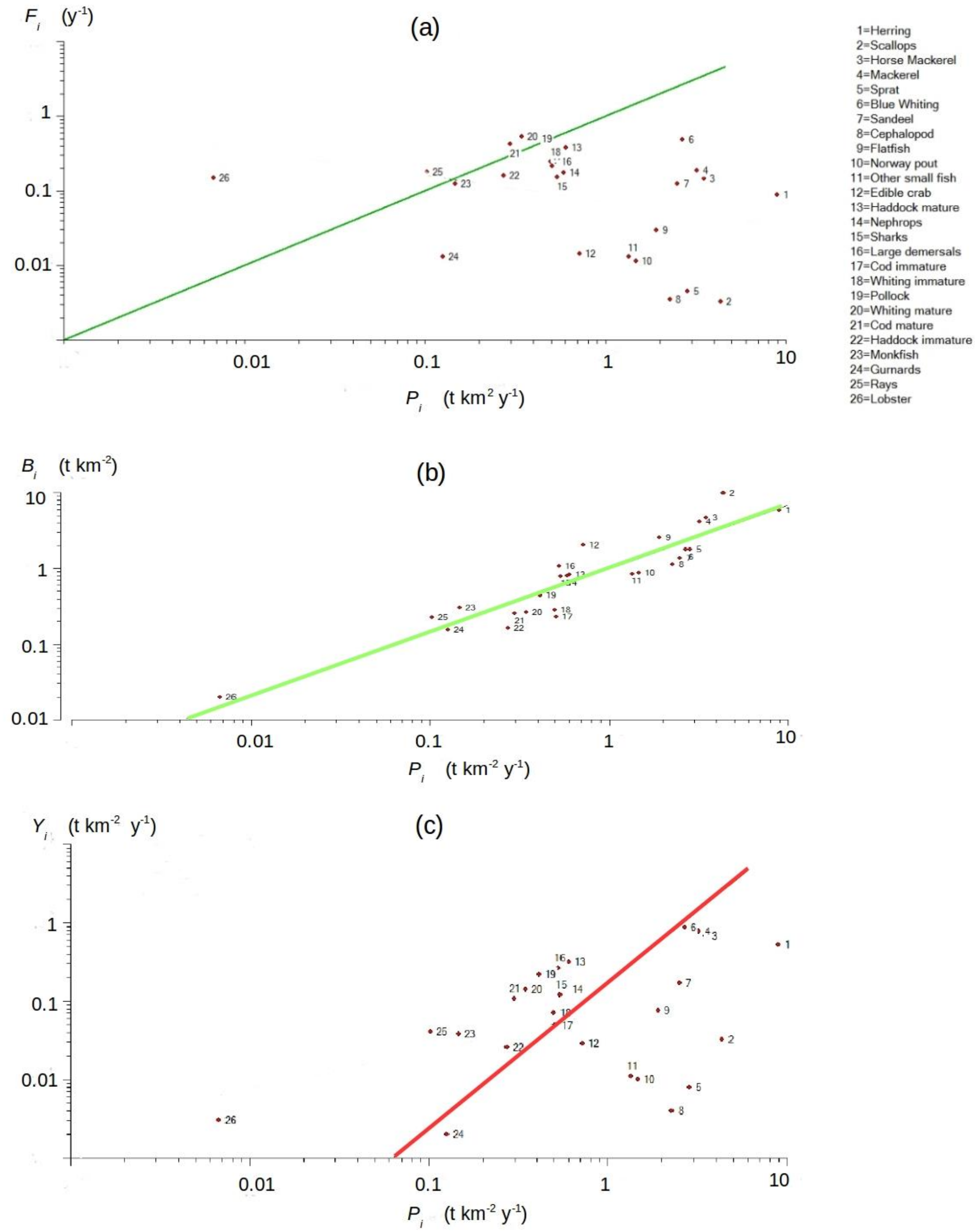

Figure BA3. *An Ecopath analysis on the west of Scotland shelf ecosystem in 1985. (a) No clear relationship between F_i and P_i; BH would have slope $logF_i$ vs $logP_i$ = 1 (green line). (b) An approximate power-law relationship between B_i and P_i, with a slope of $logB_i$ vs $logP_i$ α = 0.84 (green line). (c) No clear relationship between Y_i and P_i; BH would have slope of $logY_i$ vs $logP_i$ 1+ α = 1.84 (red line).*

There are various caveats about the Ecopath analysis. First are those inherent in the equilibrium Ecopath model itself. Secondly, to disaggregate to body size, we used an equivalence between production rate and cohort biomass from a steady-state solution of the McKendrick von Foerster equation (Law et al. 2016, Appendix E). Thirdly, the von Bertalanffy equation is assumed to be a good representation of growth from an initial body size of 1 g. This equation is not a good model for the early life stages (egg to young adult), but was used here as parameter values for the species were available. Fourthly, mortality rate was taken to be constant over age; this is not a good assumption because fishing mortality changes as fish get larger as does natural mortality (other assumptions about natural mortality would be possible). With all these caveats in mind, the results from this Ecopath study should be taken as a demonstration of the principle, rather than a source of accurate results about production rates.

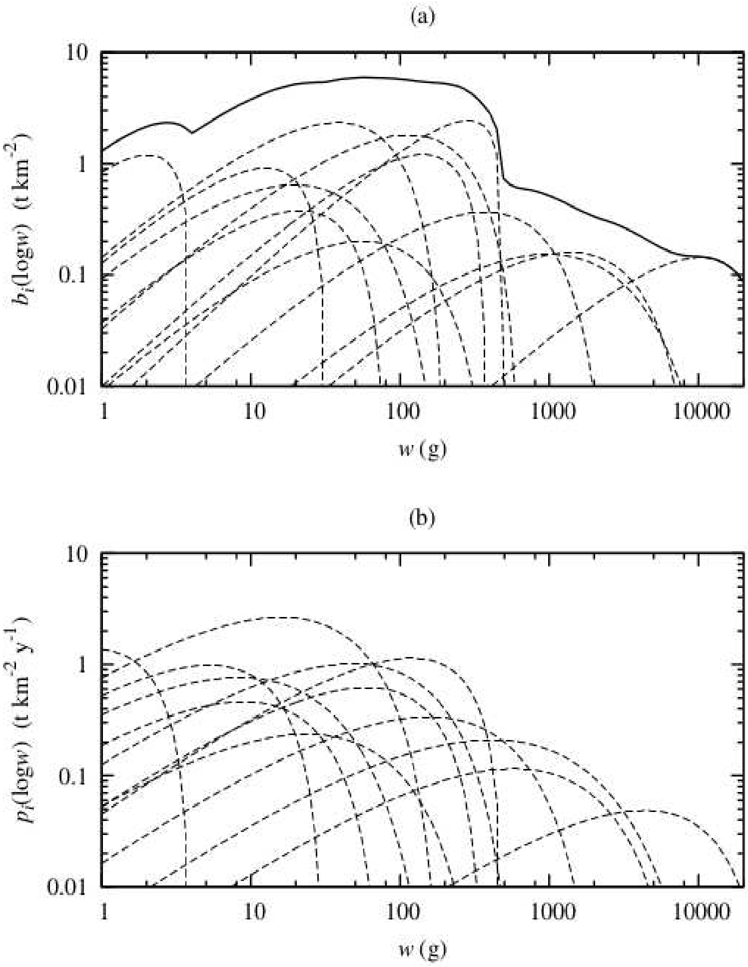

Figure BA4*. Spectra of 13 fish groups (dashed lines) constructed from an Ecopath study of the west of Scotland Shelf Ecosystem. (a) Biomass spectra; the continuous line is the biomass spectrum for the whole assemblage of fish groups. (b) Spectra of production rates; balanced harvesting would set fishing mortality rates in proportion to the these values.*

Work in progress (Speirs, personal communication), suggests that the balance of fishing mortality to production rates of species has not improved in the west of Scotland shelf ecosystem in recent years. Speirs used the International Bottom Trawl Survey of the Scottish West Coast, to get the Quarter-1, number-at-length data for 1985 and 2014, for the groups in Fig. BA3. Since the survey catchability of different taxa is unknown, but likely to vary between groups, the biomass of fish sampled by the survey for each group was scaled to give the same total regional biomass as that in the 1985 Ecopath analysis (Alexander et al 2015), and the same scalings were used for 2014. These number-at-length data were then multiplied by the growth rate in each length class, and summed over length classes to get estimates of total production rates by the taxonomic groups in 2014. Growth rates were obtained from length-based von Bertalanffy growth curves and length-weight relationships. As there are no published estimates of F for all the taxa in 2014, the ratio of reported ICES VIa landings to biomass (the harvest ratio) was used to provide an index of fishing mortality.

The results for 2014 give no better evidence of a relationship between fishing mortality and production rate than the earlier 1985 results (Fig. BA3) from the Ecopath study. The harvest ratio is lower than F because of discarding rates (which are unknown for most of the taxa, but potentially high). However, some signal of a positive relationship between harvest ratio and production rate would be expected, if fishing mortality and production rate were in balance. Clearly there is a need for more knowledge of the imbalance between fishing mortality and production rates in Scottish waters (see Section 'Data and research requirements', point 2).

Implementation of BH

Research on BH is in its early stages, and it is fair to ask whether it is premature to be thinking about how it could be implemented. However, there would be no point in doing the research if the basic approach of BH cannot be put into practice, as has been suggested by some researchers (Froese et al. 2016a). While recognising that there is still much to learn about BH, this section considers a number of the issues (socio-economic, regulatory and technical) that would need to be addressed if Scottish fisheries were to be brought closer in line with the production rates in the marine ecosystems they exploit.

General approach

As a starting point, Fig. BA5 is a simple graphical portrait of an ecosystem that shows how to shift an assemblage of exploited fish species towards an improved balance with production rates. We use the 1985 Ecopath results on the west of Scotland ecosystem for the purpose of illustration, these being the only data we have. Since there are caveats about the data, and they are historical rather than current, the purpose of the figure is just to show the principle: the graph is not intended as a basis for practical implementation.

The main band in Fig. BA5 spans a broad region, covering, for the sake of argument, a tenfold range of yield for a given production rate, within which the yields might be regarded as acceptable. This band has a slope of $1+\alpha$, consistent with BH (see Section: 'The exploitation ratio'). Exactly where to place the band is a matter for expert knowledge; concern about the gadoid stocks (Alexander 2015) suggests that point 17 (immature cod) would be close to the upper boundary. Above the band, there is a limiting line with slope = 1, on which Y/P = 0.5, corresponding to an exploitation ratio 0.5, that fishing should not transgress in any event. This leaves a cluster of points above the band as candidates for reduced exploitation that would draw them towards the band. It also leaves some points below the band on which exploitation could potentially be increased. There could also be species and groups that do not appear on the plot because exploitation on them is very low or zero; these would present opportunities for new fisheries. In this way, exploitation of the categories in the graph is put on a path towards BH.

Note that the path towards BH needs to be seen as iterative because fishing alters B_i and P_i, both directly through removal of biomass, and also indirectly through changing the predator-prey interactions in the ecosystem. B_i and P_i therefore need to be monitored over time, with adjustments to the slope of the band as changes take place. Also the changes caused by fishing are bound to be happening in a changing environment that leaves its own imprint on B_i and P_i. Indeed, fishing and environmental impacts may interact; for instance, fluctuations in recruitment may be amplified in depleted stocks. An iterative updating of fishing should be adaptive and responsive to changes in B_i and P_i caused by fishing and the environment.

Note also that changing the balance of aggregated measures Y_i, B_i and P_i across species and broader taxonomic groups is part, but not all, of BH because production rates depend on body size within species as well as species as a whole. There is also much that can be done to bring fishing more line with production rates at different sizes within species. An obvious change that BH calls for is lower fishing mortality on the large, slow growing fish that have inherently low production rates.

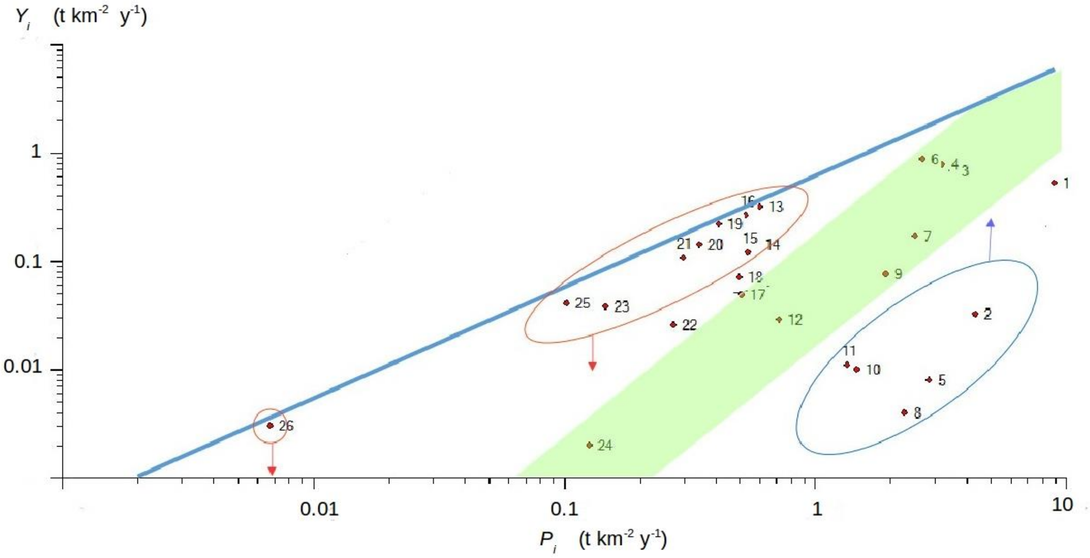

Figure BA5. *Changes needed to move exploitation in the direction of BH according to an Ecopath analysis on the west of Scotland shelf ecosystem in 1985. The green band has a slope 1+ α = 1.84, corresponding to BH; here α is the slope of the logB vs logP relationship in Fig. BA3b. The band is limited by an exploitation ratio Y/P = 0.5, shown as the blue line. Species groups are labelled as in Fig. BA3. With the band as located, the balance between yield and production rate would be improved by reducing fishing mortality on species above the band, and by increasing fishing on those below the band. Note however, that the location of the band needs to be set on the basis of expert knowledge of the ecosystem. Note also that the data are not of a quality to provide a basis for practical implementation*.

As previously mentioned, the detailed structure of Fig. BA5 should not be trusted as a basis for implementation. But it does draw attention to three general ways in which fishing would probably need to change to move in the direction of BH: (1) reduction of fishing mortality on species that grow to large sizes and that are currently heavily exploited; (2) a possible increase in fishing on smaller species with high production rates; (3) exploitation of taxa further down the food chain that are currently fished little, if at all. Below, we therefore highlight some of the issues that stem from altering the size-based and species-specific mortalities associated with fishing and changes in the nature of landings. Whether harvesting is balanced across species currently exploited, (including increasing the exploitation of those species caught that have little commercial value), or balanced across trophic levels, we expect a move towards BH to lead towards a broader range of species being caught and a larger range of sizes within species being landed. Change in the behaviour of the fishing fleets is to be expected, to accommodate this.

Issues of social acceptability

Social acceptance of a more balanced approach to harvesting would need to be addressed. BH has the benefit of being intuitively appealing and appears at a time when fisheries have been identified as problematic in a number of ways (e.g. Pauly 2011). Similarly, there has been public support for a landing obligation within the EU that is likely to increase landings of species that might otherwise be discarded (Borges et al. 2016). These factors could possibly enhance the acceptability of BH. However, some of the implications of implementing the approach are likely to be less acceptable. This includes reductions in landings of species and sizes that are popular with consumers. Also the increased targeting of small or lower trophic species could prove to be controversial (e.g. Smith et al. 2011, Burgess et al. 2016).

Decreases in availability of fish that consumers prefer may be compensated through increased imports with a consequent impact on the balance of trade in fisheries products. Already the majority of cod consumed in the UK is caught elsewhere, although that may change if the North Sea stocks continue to rebuild. Also, some small, lower trophic level species (e.g. sprat and sandeel) are already subject to fishing pressure (e.g. Engelhard et al. 2014) and are caught in fisheries for human consumption and industrial use (sandeel).

Fish feeding at low trophic levels include both the early life stages of species that grow to large sizes and also forage fish that mature while still small. The latter have been highlighted as providing the primary means for the transfer of production through the food chain (Smith et al. 2011). Small pelagic fish comprise around 12.5% of the overall food consumed by the world's seabirds, and up 20% of the diet of any marine mammal species (Alder et al. 2008). From a global analysis of the diet data in 72 Ecopath models, Pikitch et al. (2014) found 30 fish species, 9 bird species and 12 mammal species in which forage fish made up at least 75% of the diet. Alterations to the abundance of forage fish can clearly have an important impact on species that eat them, and this includes seabirds and marine mammals (Cury et al. 2011, Smith et al. 2011, Pikitch et al. 2014).

Importantly, BH is as much about reducing fishing on large fish with low production rates as it is about increasing fishing on small pelagic species. BH would have the effect of enhancing spawning stock biomasses of species that grow to large body sizes, potentially increasing their contribution they make to the abundance of small fish. It needs to be shown how BH rebuilds the multispecies size distribution of fish in marine ecosystems, and the effect this has on food for large fish, seabirds and mammals. Clearly, a severe scarcity of prey would result in the reduction of long-term breeding success of seabirds and therefore threaten their populations (Cury et al. 2011).

A social perception, by itself, that harvesting small fish could impact on seabirds and mammals would be a matter of concern that would need to be addressed. At the other end of the spectrum, there already is serious concern over the culling of large marine animals, such as sharks and mammals. Whether there would be a call for some control on large animals in moving towards balancing would depend on their feeding and production rates, which might well be low. However, society would ultimately make a judgement about the acceptability of such culling, were it to be proposed.

Issues of marketing

Adopting a more balanced approach to harvesting needs landings of some species/sizes which are currently exploited too heavily (in BH terms) to be reduced. Overall, it is possible (though by no means certain) that a greater overall biomass could be landed as a result of fishing lower in the food chain (e.g. Garcia et al. 2012). Furthermore, it is not clear what the effect would be on aggregate revenues, harvesting, and processing costs (Charles et al. 2016, Howell et al. 2016). Fish from lower trophic levels often attract lower prices and may present a marketing challenge. As a result, any increases in biomass yield may not increase revenue or profits or increase the value of the catch (Jacobsen et al. 2014, Burgess et al. 2016, Charles et al. 2016). There are clearly large differences between African-lake fisheries, where catches provide vital sources of nutrition for the local populations, and European countries, where alternative sources of protein are available.

There are two particular challenges for catching and marketing living marine resources in a more balanced way. Firstly, the existing low market price of some species/sizes may make exploitation uneconomic. Secondly, there may not be a market at present for some of the species and/or sizes that currently either are not targeted, or are not exploited (Charles et al. 2016). The latter would become an issue if BH were to include ecosystem components that are currently unexploited, such as zooplankton and phytoplankton that might also be harvested in large quantities. Successful implementation of BH depends on the components caught and the existence, or creation, of markets for all new species and sizes landed, particularly if BH is to be combined with the landings obligation (Garcia et al. 2012, Kolding et al. 2016d).

Low existing market prices can be addressed in a number of ways. Firstly it may be possible to increase the market price by increasing demand, for example developing new products and shifting consumer preferences. The Cornish sardine provides an example of a product that has overcome a lack of demand[1]. The fish, (*Sardina pilchardus*) is known as sardine when small and pilchard when over 15 cm (as caught in Cornwall). Although abundant enough to fish on, by the mid-1990s the landing of pilchards were less than 10 tonnes a year. Market research undertaken by The Pilchard Works indicated that, while there were negative associations with ‘pilchard’, people were more accepting of ‘sardine’. Rebranding of the fish as ‘Cornish sardine’ and working closely with retailers has increased the appeal and sales of the fish. Landings have increased to around 2,000 tonnes, and the fishery has been awarded both Marine Stewardship Council (MSC) certification and protected geographical indication (PGI) status. Another example is the transformation in the 1970s of *Nephrops* from a “rubbish” fish to “scampi”, where it attracted a premium. Subsequently, as *Nephrops* fisheries came under pressure, this species was sometimes replaced by monkfish, then another “rubbish” fish, and now a premium product.

A second approach is to identify new markets. For example, there is a tradition of eating smaller fish in Mediterranean countries and there may be demand for small fish and species that are not consumed to the same extent in Scotland. Markets outside Scotland are important for the Scottish fishing industry – 36% of all landings by Scottish vessels were abroad in 2014, of which 95% were pelagic (Marine Scotland 2015). Changes to exploitation patterns could affect and be affected by markets in other countries.

Thirdly, there may be market options to explore other than for human consumption, such as for pet food or fish meal, e.g. for the aquaculture industry. Markets for derivative products such as essential oils, and food supplements etc. are also growing. Adding value to fisheries products is currently an area supported under the European Maritime and Fisheries Fund (EMFF).

Where it is not possible to increase demand or to identify products that would allow fishing to be economically viable, there would need to be either a compromise on the extent of balancing, or provision of subsidies for otherwise uneconomic fishing operations (Charles et al. 2016).

Potential interaction with existing regulation/institutional structures

In recent years the challenges facing both fishers and resource managers within Europe have increased with commitments to implement spatial planning, ecosystem-based management, landings obligation and the uncertainties of change related to Brexit. At the same time there are international obligations, for example relating to the World Summit on Sustainable Development (WSSD) and the Code of Conduct for Responsible Fisheries. It has been suggested that BH is not compatible with existing regional and international policy (Pauly et al. 2016). A key challenge therefore is to establish the extent (or otherwise) that BH would be consistent with current targets and regulations.

We stress that BH is not about allowing individual vessels to fish unselectively. Its purpose is to bring the overall fishing pressure on species and body sizes more in line with production rates (e.g. Garcia et al. 2016b). This calls for ideas about management that scale up from gear selectivity of individual vessels to the level of métiers and fishing fleets. However, this will require changes to selectivity patterns and effort that are likely to conflict with current management regulations. Charles et al. (2016) suggest therefore that a possible starting point for regulatory reform is to review existing regulations to understand the purpose and objective of the regulation (environmental, social or economic). This assessment will highlight where there might be inconsistencies with the objectives of a BH approach and where there might be a trade-off with other objectives. It can be argued that this should be done whether BH is adopted or not.

Within the EU, the landings obligation is currently a key issue. Borges et al. (2016) consider whether discard bans such as the landings obligation support or contradict BH. They point out that the discard bans and BH have quite different starting points. While BH is a strategy that attempts to plan what is caught in advance, the landings obligation is a strategy for dealing with what has actually been caught. When policies such as the landings obligation are fully implemented, fishing operations are expected to become more selective on the main commercial species. The driver for such a change is

1 Information drawn from http://www.cornishsardines.org.uk/historical-background.html

that there will be additional costs to fishers of landing unwanted bycatch. These costs can be indirect because, for example, the bycatch takes up hold space on fishing vessels which would otherwise be occupied by more valuable catch, or direct because, for example, fishers may be asked to contribute to the disposal costs of un-marketable catch components landed. From this perspective, by generating a market for the unwanted catch, BH may work against the actual aim of discard bans. On the other hand, setting the goals of the landings obligation differently and in line with BH objectives of balancing fishing pressures, the landings obligation may provide a management tool that contributes both to BH and also to reduced discarding. A landings obligation does not necessarily conflict with BH. After all, it is a strategy to realise a policy goal. The implications and interactions of these policies could be assessed through modelling of catches based on current landings.

Identifying targets and appropriate levels of fishing mortality

Among the key practical challenges involved in implementing BH is assessing the state of the ecosystem and evaluating the harvesting strategy (e.g. Garcia et al. 2016b). The general approach of bringing fishing mortality rates more in line with production rates, as suggested by the example in Fig. BA5, is to set directions in which to change fishing mortalities to bring them closer to a balanced state at the level of species within the ecosystem. Also Fig. BA4 makes it clear that, within species, fishing mortality on fish that are large for their species would need to decrease in line with their declining production rates, as they get large. Setting the correct directions of change in fishing mortality across species and body sizes in the ecosystem is the first target.

The limited results we have been able to obtain (Section: 'How balanced is exploitation of Scottish marine ecosystems?'), suggest the existence of a substantial imbalance between fishing mortality rates and production rates. If further data analysis supports this (Section: 'Data and research requirements', point 2), moving Scottish fisheries towards BH would not be a matter of fine tuning: simple and heuristic approaches to the estimation of the most important parameters would be enough to get started. The measures are biomass, production rate, and fishing mortality rate by species and body size (eqs 1, 2, 4, 5). We could then evaluate how well these measures function in the assessment/management advice framework, possibly using some of the many established Management Strategy Evaluation methods. The key point here is to identify what we NEED to know to move towards a more balanced regime, rather than what we might LIKE to know to obtain an exact balance in a perfect world.

To go further than this, will require ecosystem models considerably more complex than the single-species models used at present in fisheries management. In part, this is a generic consequence of moving from single species towards EBFM (as opposed to a special issue caused by BH). The reason is that EBFM has to deal with the coupling of species through predator-prey interactions. This necessarily requires knowledge of the predator-prey interactions. This knowledge has then to be built into the models, and the parameters associated with the interactions estimated. Such matters do not arise in single-species models that assume species can be treated as though living in isolation.

However, BH does raise some specific issues beyond those generic to EBFM. Increasing the scope of what is targeted, makes the requirements for monitoring greater. There becomes a need to identify changes in production rate and vulnerability to the fishery, and to track responses to fishing effort and selectivity. This is a particular challenge for data-poor stocks. Going beyond stock biomass to monitor and assess production rates by body size, requires knowledge of mass-specific growth rates, species by species. Growth and mortality are also affected by environmental factors, and this can be particularly important both for short-lived species and also for the early life stages. Such changes cause interannual variability in recruitment, but more importantly can lead to overall longer-lasting changes in stock production rates. Changes of this kind are expected to become more common due to climate change. In species with volatile recruitment, like haddock that are important to Scottish fisheries, management advice might need to be taken down to year class, to avoid overexploitation of classes with low production rates. Management advice is especially challenging for early stages of year classes, given the uncertainty associated with stock-recruitment relationships. Increasing the number of species targeted increases the scale of the challenge, particularly for data-poor stocks.

The dynamic nature of marine ecosystems creates uncertainty that makes identifying relationships challenging. At the same time, shifts and changes in the nature of the system (e.g. due to changing climate or patterns of exploitation resulting from implementing BH) mean that the targets set to move towards a better balance are shifting over time. Monitoring the stocks, and setting the management advice needs to be iterative, responding adaptively to changing ecosystem states.

Managing and fine-tuning fishing mortalities in practice

Given the requirement for additional data, potentially more frequent updates, and fine tuning of selectivity across fleets to ensure balancing of harvests, it is likely that BH would require greater industry authority and responsibility. From a positive perspective, in terms of EBFM, BH provides a potential entry point for different groups of people (within the fisheries and other sectors and across disciplines) to agree on a common concern and begin to work together to address it. However, given vested interests, it should not be assumed that consensus will be readily achieved. For example, there is a long history of exploitation of marine fisheries, e.g. in the North Sea and Firth of Clyde with changes in abundance and possibility of alternative equilibrium states (e.g. Heath and Speirs 2011) such that establishing agreement as to what constitutes the 'natural' state and appropriate extent of balancing is likely to be challenging. This is likely to be particularly so if it means creating additional catching and marketing burdens on fishers (see above and below).

Coordination across fisheries becomes more important with a BH approach. For example, sandeel are a small part of Scottish landings but are targeted at significant levels by other countries. Concurrently, most of the demersal landings by the Scottish fleet are from the North Sea (70% in 2014: Marine Scotland 2015). Balancing harvesting across this fishery is likely to require increased coordination between countries and across fleets and may require innovations such as métier/quota pooling.

Reid et al. (2016) considered and rejected several ways in which BH might be implemented. At one end of the spectrum, a simple "laissez-faire" approach of unregulated fishing practiced in some African lakes is not an option for Scottish fisheries. European fisheries are strongly regulated, with annual quotas, restrictions on minimum landing size, effort and license restrictions, and so on. They have specific management targets for each stock, and a commitment to fishing at levels consistent with MSY theory as well as the inclusion of ecosystem objectives such as those in the marine strategy framework directive (MSFD). At the other end of the spectrum, micro-management of TACs to bring species and body sizes in line with their production rates would probably be prohibitively complex. An intermediate approach of focusing on body size or trophic level, ignoring species, would miss the effects of fishing on biodiversity, and would be inappropriate for the purpose of conservation.

Reid et al. (2016) suggested an alternative that comes closer to the situation in African lakes: to utilise the many métiers employed by fishers. Kolding and van Zweiten (2014) suggest that the BH aim of distributing a moderate fishing mortality across the widest possible range of species, stocks, and sizes in an ecosystem "*can only be achieved by a range of different gears that are flexibly used in time and space over available habitats*". They go on to suggest that "*Such a fishing pattern can only be obtained by fishing with a varied balanced multitude of different fishing methods, adaptable to the specific hydrodynamic regime of an ecosystem*". This suggestion is broadly analogous to the concept of fishing métiers (ICES 2003) where a métier is defined as a combination of the vessel/gear configuration and the species mixture captured. Davie and Lordan (2011) identified 33 métiers in the Irish otter trawl fleet alone, based on fishing gear, mesh size, vessel length, species composition, area, and month, and there are other métiers in the Irish fleet based on beam trawls, dredges, seines, and a range of passive gears. The same complexity is also likely to be found in the Scottish fleet.

Different métiers have different size and species selectivity patterns (Punt et al. 2013, Sampson 2014). Métiers using passive gears such as gillnets tend to have dome-shaped selectivity (Madsen et al. 1999). Most mobile-gear métiers exhibit a form of sigmoid selectivity, although the addition of a large-fish escape panel can also result in a dome-shaped selectivity (Sampson and Scott 2012). Some métiers tend to select more for one species than another (Huse et al. 2000). Management under BH for all species could encourage one métier and discourage another, depending on their known selectivity profiles, and progress towards BH targets. Essentially, we could see this as having effort quota for each métier that would allow all to reach BH targets at the end of the year. If the catch rate turned out, through a given year, to be too high for a given species, then we could manage to reduce effort by those métiers that preferentially caught that species. Fishing vessels could also consider working in a number of métiers, allowing them to switch in such a case.

This approach may also be easier to implement if a degree of tolerance around BH targets is allowed, as implied by the band in Fig. BA5. Tolerance levels allowing a “partial implementation” of BH could be determined through Management Strategy Evaluations, and from experience. We could also consider using a management approach aiming for BH targets over several years, rather than the current single year management cycle used in many regions, and adjust effort strategically within that period. This approach could be considered as results-based management. It would help considerably if the fishing fleets were able to shift métiers relatively easily. That is, if a particular métier, or even one species in a métier was overexploited, the fleet could switch to a different métier. This shifting would probably also entail vessels having access to fishing in a number of different management areas, so that a métier switch could entail a change of management unit rather than a change in fishing pattern. This approach could be dubbed métier management, where national or international management agencies would intervene only when necessary, and regionally based industry groups could manage the effort by métier. This scheme could also be made easier by more cooperative industry approaches, where, say, some vessels could focus on a particular métier and take up effort quota as the representatives of a larger group. However, it needs to be acknowledged that a broad-brush approach such as this would require a very substantial change in both the philosophy and practice of the fishery management approach, and in the way fishing vessels would operate within that.

We are not proposing métier management as the best or only way forward to deal with ecosystem level issues of fisheries management, but we think it is worth considering. A key issue for management would be to monitor potential “technological creep”: as gear or practice improve, the performance of a unit of effort in a given métier may result in a different catch profile. At the level of species, a warning signal could be obtained from the time trajectories of $\log Y_i$ versus $\log P_i$ (Fig. BA5), showing a tendency for Y_i to increase while P_i remains constant or decreases.

Data and research requirements

The key idea behind BH is that categories of biomass should be harvested from marine ecosystems in proportion to their production rates. The rate of flow of biomass, from primary producers onwards to zooplankton, to fish and to other consumers, is fundamental in the functioning of marine ecosystems, and body size is the major axis of variation that determines this flow. The priorities for data and research listed below are motivated by the need to increase knowledge of these flows of biomass in Scottish waters, and to understand the effects of moving towards BH on the fisheries and marine ecosystems.

Data

1. Production rates. There are few analyses of marine ecosystems in which production rates are disaggregated to species and body-size categories. Better knowledge of how biomass flows through Scottish marine ecosystems should be a priority, whether or not a move towards BH is considered to be beneficial. Getting this information is feasible for fish species that are currently assessed. For biomasses, data on abundances are already available, in the form of assessment survey data, although care is needed in their analysis because catchability is poorly estimated in some species and it changes with fish size. With appropriate analysis and processing, these survey data provide estimates of numbers of individuals and biomasses of fish in a region categorised by species and body size classes. To obtain mass-specific growth rates, parameterised models of fish growth are available, also categorised by species and body size. Taken together, the biomasses and growth rates give estimates of the production rates.

Harder to deal with, but just as important, are the majority of species that are not currently assessed, some of which are rare. If new markets are being considered for species little exploited at present, it is especially important to have knowledge of their production rates.

2. Fishing mortality relative to production rate. To assess the match between fishing mortality and production rates of fish stocks requires information on the full range of catch (landings plus discards, by species and body size). In principle, this information is available region by region, broken down by species and body size, though in practice this is hard to assemble from existing easily accessible market sampling and observer data. We suggest building an inventory of the present relationship between fishing mortality and production rates by species and body size of the Scottish stocks that are currently assessed, as a baseline for future reference.

3. Life-history data on unassessed species. The main data gap for assessing BH at the ecosystem level is the limited information on life-history parameters of species not included in routine annual assessments. Parameters of growth rates, length vs weight relationships, recruitment and maturity are readily available for most of the major commercially targeted species, but not for the majority of non-target species. Assembling a robust, region-specific database of these parameters for the species which are regularly encountered in surveys and fisheries would be a significant task, but important for EBFM, and for pursuing an assessment of BH.

4. Catch profiles by métier. If implementation of BH were to be based on métier management, as defined in Section: 'Managing and fine-tuning fishing mortalities in practice', detailed knowledge of the catch profiles of these métiers would be needed. Métiers have been defined to date in terms of commercial species, but the 80-90% of species that are not routinely landed also matter in the ecosystem context. This could be a process where industry provides considerable support, collecting samples of the non-target discard for all the métiers, and ideally quantifying these samples to species and size with the help of fisheries scientists. While this analysis would be invaluable for implementing BH, it would also be of great use in evaluating the impact of fishing on all the species that the fishery encounters beyond the context of BH.

Research

5. Biomass flow in fishery models. It has recently been claimed that no ecosystem model commonly used in fisheries is dealing properly with the energy budget (Persson et al. 2014). Size-spectrum models provide a formal mathematical framework specifically for the purpose, because they do the bookkeeping of biomass in marine ecosystems, as it moves from primary production of unicellular phytoplankton, through successive predation events, up to large vertebrates (Law et al. 2016). However, the formal theory is at an early stage of development and needs a lot more work. To be fit for the purpose of describing Scottish marine ecosystems entails moving on from current simple model fish assemblages to multispecies settings; it also requires size-spectrum models to be coupled to the dynamics of plankton, detritivores, birds, and sea mammals.

6. Robustness of size-spectrum models. Research is also required to establish whether size spectrum models are sufficiently robust to provide ecosystem based fishery management reference points, and if so what level of complexity in these models is required. Two kinds of question have been raised about their value as management tools. First is their performance in the presence of uncertainty or error in parameters (e.g. Thorpe et al. 2016) and the effect of high levels of variability (e.g. in recruitment of small fish). Assessment of the structural uncertainty in the performance of the model itself is also needed. Second are the cost implications of using more complex models for managing fisheries, for example the costs of parameterising the models, monitoring fishing mortalities and assessing performance of the harvesting strategy.

7. Models of intermediate complexity. In addition to size-spectrum models, it would be useful to develop an operating model for a Scottish fishery/ecosystem of intermediate complexity that provided an experimental tool with which some of the key ideas emerging from BH could be investigated. This could include (a) To what extent can the concept be applied to fin-fish fisheries alone without the inclusion of top predators (birds, mammals etc) or micro-organisms? (b) How close are current fisheries to BH? (c) To what extent are the theories of MSY and BH in conflict or in concordance? (d) What are the key changes to the fishery that would be required to move closer to BH?

8. Managing transitions towards BH. If Scottish marine ecosystems are a long way from being balanced, what would be safe and efficient paths to move them towards a more balanced state? Managing the transition is important, calling both for reductions in fishing pressure on heavily exploited species, and also for identifying opportunities to catch under-exploited species. Caution is needed in making such changes, with gradual shifts in fishing mortality. It is usually the species that grow to large body sizes and have long generation times that are over-exploited, and the change in size structure of such species is relatively slow (e.g. Fung et al. 2013). Modelling could provide some insights into the likely short-term and long-term costs and benefits and their distribution across existing fleets and value-chain actors, as well as identifying efficient and profitable long term harvesting levels.

9. Changes in catch composition. Moving Scottish fisheries towards BH entails changes in the size and species composition of the catches. Some of these species and size classes are likely to have little or no market value at present. Research is needed to examine the extent of this challenge, and to identify opportunities to develop new markets and change in consumer attitudes. New markets could be for human consumption, but also, say, for aquaculture feed. If métier management were adopted, the weights required for different métiers to achieve an appropriate aggregate pattern of fishing would need to be worked out. Increasing the number of exploited species will lead to inclusion of data-poor ones. From a practical perspective it would be useful to have studies on the effect on balancing and ecosystem integrity of excluding from the fishery, or more conservatively exploiting, the smallest year classes and data-poor stocks.

10. Ending discards. Some of the interest in BH has been generated by the intention to eliminate discards in EU waters, to be achieved by increasing the selectivity of fishing operations. The motivation for the ban is the belief that discarding of (usually small) fish undermines sustainability objectives derived from classical fishery models. From a BH perspective, landing fish that would previously have been discarded, may not, *per se*, be detrimental to the ecosystem: it is their disposal as sea which may be regarded as wasteful. The aim would ideally be to land, and sell, all the fish that are caught. This would change the fish handling needs on the vessel and indeed at landing, and would call for new markets. An analysis that set out clearly the consequences of discarding within a BH framework would be useful.

11. Fishing intensity. Much of the theory of BH relates to the issue of selectivity both by size and species in order to exploit the range of production in the ecosystem. How heavily the system should be exploited remains a crucial unanswered question. The answer is likely to differ from one ecosystem to another, depending on the rate at which energy enters the system through the primary producers. Research is required on how heavily to exploit ecosystems under BH to deliver sustainability.

12. Little-exploited taxa. Some components of marine ecosystems would most likely still remain largely or completely free from exploitation under BH. These include planktonic taxa that are small in size and for which a market would not be realistic, large charismatic species on which exploitation would be socially unacceptable, and no doubt some taxa of intermediate size that would still have relatively low fishing mortality through low catchability. Balancing would thus never be complete, and it is important to understand the consequences this has on the structure and functioning of exploited ecosystems. Could there be unintended consequences such as regime shifts moving marine ecosystems into alternative unwanted states? Or are there feedbacks that could hold this in check?

13. Mortality on large fish. Quite apart from balancing across species, it is clear that fish that are large in size for their species have relatively low production rates (Fig. BA4). This is because, compared with smaller, younger fish, (a) they grow slowly, and (b) they have low biomass per unit area, a property exacerbated by historical patterns of exploitation. These big fish are thought to be crucial to protect stocks and to ensure recruitment in the future (Hixon et al. 2014). The mobile gears often used to catch these fish do not readily allow fishing mortality to fall as fish get large. Fishing has therefore led to a major distortion of the natural size distributions of marine fish species through the loss of big fish. Research is needed on how to protect big fish better by gear with more dome-like selectivity, and by marine protected areas.

It would also help to clarify the approximate body size at which production rate peaks. On one hand, standard fishery models on cohort biomass find this happens near the size of maturation, where somatic growth starts to fall. On the other hand, some size-spectrum models, that couple body growth to predation mortality, find the peak can occur when fish are a good deal smaller than this.

References for Balanced Harvesting Workshop Report

Alder, J., Campbell, B., Karpouzi V., Kaschner K. and Pauly D. (2008) Forage Fish: From Ecosystems to Markets https://www.rspb.org.uk/Images/foragefish_tcm9-246786.pdf. Accessed January 4, 2017.

Alexander, K.A., Heymans, J.J., Magill, S., Tomczak, M.T., Holmes, S.J. and Wilding, T.A. (2015) Investigating the recent decline in gadoid stocks in the west of Scotland shelf ecosystem using a foodweb model. *ICES Journal of Marine Science* 72, 436-449.

Allen, K.R. (1971) Relation between production and biomass. *Journal of the Fisheries Research Board Canada* 28, 1573-1581.

Andersen, K.H. and Beyer, J.E. (2006) Asymptotic size determines species abundance in the marine size spectrum. *American Naturalist* 168, 54-61.

Andersen, K.H., Blanchard, J.L., Fulton, E.A., Gislason, H., Jacobsen, N.S. and van Kooten, T. (2016) Assumptions behind size-based ecosystem models are realistic. *ICES Journal of Marine Science 73, 1651-1655.*

Benoît, E. and Rochet, M.-J. (2004) A continuous model of biomass size spectra governed by predation and the effects of fishing on them. *Journal of Theoretical Biology* 226, 9-21.

Blanchard, J.L., Dulvy, N.K., Jennings, S., Ellis, J.R., Pinnegar, J.K., Tidd, A. and Kell, L.T. (2005) Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? *ICES Journal of Marine Science* 62, 405-411.

Blanchard, J.L., Heneghan, R.F., Everett, J.D., Trebilco, R. and Richardson, A.J. (2017) From bacteria to whales: using functional size spectra to model marine ecosystems. *Trends in Ecology & Evolution* in press.

Borges, L., Cocas, L. and Nielsen, K.N. (2016) Discard ban and balanced harvest: a contradiction? *ICES Journal of marine Science 73, 1632-1639.*

Blanchard, J.L., Law, R., Castle, M.D. and Jennings, S. (2011) Coupled energy pathways and the resilience of size-structured food webs. *Theoretical Ecology* 4, 289-300.

Breen, M., Graham, N., Pol, M., He, P., Reid, D. and Suuronen, P. (2016) Selective fishing and balanced harvesting. *Fisheries Research* 184, 2–8.

Bundy, A., Fanning, P. and Zwanenburg, K.C.T. (2005) Balancing exploitation and conservation of the eastern Scotian Shelf ecosystem: application of a 4D ecosystem exploitation index. *ICES Journal of Marine Science* 62, 503-510.

Burgess, M.G., Diekert, F.K., Jacobsen, N.S., Andersen, K.H. and Gaines, S.D. (2016) Remaining questions in the case for balanced harvesting. *Fish and Fisheries* 17, 1216-1226.

Caddy, J.F. and Sharp, G.D. (1986) An ecological framework for marine fishery investigations. Rome: FAO Technical Paper 283.

Canales, T.M., Law, R. and Blanchard, J.L (2016) Shifts in plankton size spectra modulate growth and coexistence of anchovy and sardine in upwelling systems. *Canadian Journal of Fisheries and Aquatic Sciences* 73, 611-621.

Capitàn, J.A. and Delius, G.W. (2010) Scale-invariant model of marine population dynamics. *Physical Review E* 81, 061901.

Christensen, V. and Pauly, D. (eds.) (1993) *Trophic Models of Aquatic Ecosystems*. ICLARM Conference Proceedings No. 26.

Charles, A., Garcia, S.M. and Rice, J. (2016) Balanced harvesting in fisheries: economic considerations. *ICES Journal of Marine Science* 73, 1679-1689.

Cury, P.M., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J.M., Furness, R.W., Mills, J.A., et al. (2011) Global Seabird Response to Forage Fish Depletion—One-Third for the Birds. http://archimer.ifremer.fr/doc/00056/16770/14307.pdf. Accessed January 4, 2017.

Datta, S., Delius, G.W. and Law, R. (2010) A jump-growth model for predator–prey dynamics: derivation and application to marine ecosystems. B*ulletin of Mathematical Biology* 72, 1361-1382.

Datta, S., Delius, G.W., Law, R. and Plank, M.J. (2011) A stability analysis of the power-law steady state of marine size spectra. *Journal of Mathematical Biology* 63, 779-799.

Davie, S., and Lordan, C. (2011) Definition, dynamics and stability of métiers in the Irish otter trawl fleet. *Fisheries Research* 111, 145-158.

Engelhard, G. H., Peck, M. A., Rindorf, A., Smout, S. C., van Deurs, M., Raab, K., Andersen, K. H., Garthe, S., Lauerburg, R. A. M., Scott, F., Brunel, T., Aarts, G., van Kooten, T., and Dickey-Collas, M. (2014) Forage fish, their fisheries, and their predators: who drives whom? – *ICES Journal of Marine Science*, 71, 90-104.

Engelhard, G.H., Lynam, C.P., García-Carreras, B., Dolder, P.J. and Mackinson, S. (2015) Effort

reduction and the large fish indicator: spatial trends reveal positive impacts of recent European fleet reduction schemes. *Environmental Conservation* 42, DOI: 10.1017/S0376892915000077.
Froese, R., Walters, C., Pauly, D., Winker, H., Weyl, O.L.F., Demirel, N., Tsikliras, A.C. and Holt, S.J. (2016a) A critique of the balanced harvesting approach to fishing. *ICES Journal of Marine Science* 73, 1640-1650.
Froese, R., Walters, C., Pauly, D., Winker, H., Weyl, O.L.F., Demirel, N., Tsikliras, A.C. and Holt, S.J. (2016b) Reply to Andersen *et al.* (2016) "Assumptions behind size-based ecosystem models are realistic" *ICES Journal of Marine Science* 73, 1656-1658.
Fung, T., Farnsworth, K.D., Shephard, S., Reid, D.G. and Rossberg, A.G. (2013) Why the size structure of marine communities can require decades to recover from fishing. *Marine Ecology Progress Series* 484, 155-171.
Garcia S. M., Kolding J., Rice J., Rochet M.-J., Zhou S., Arimoto T., Beyer J. E., Borges, L., Bundy, A., Dunn, D., Fulton, E.A., Hall, M., Heino, M., Law, R., Makino, M., Rijnsdorp, A.D., Simard, F. and Smith, A.D.M. (2012) Reconsidering the consequences of selective fisheries. *Science*, 335, 1045–1047.
Garcia, S.M., Rice, J. and Charles, A. (2016a) Bridging fisheries management and biodiversity conservation norms: potential and challenges of balancing harvest in ecosystem- based frameworks. *ICES Journal of Marine Science* 73, 1659-1667.
*Garcia, S.M., Rice, J. and Charles, A. (*2016b) Balanced harvesting in fisheries: a preliminary analysis of management implications. *ICES Journal of Marine Science 73, 1668-1678.*
Gislason, H., Pope, J. G., Rice, J. C. and Daan, N. (2008) Coexistence in North Sea fish communities: implications for growth and natural mortality. *ICES Journal of Marine Science* 65, 514-530.
Greenstreet, S.P.R., Rogers, S.I., Rice, J.C., Piet, G.J., Guirey, E. J., Fraser, H.M. and Fryer, R.J. (2011) Development of the EcoQO for the North Sea fish community. *ICES Journal of Marine Science* 68, 1-11.
Guénette, S. and Gascuel, D. (2012) Shifting baselines in European fisheries: The case of the Celtic Sea and Bay of Biscay. *Ocean & Coastal Management* 70, 10-21.
Guiet, J., Poggiale, J.-C. and Maury, O. (2016) Modelling the community size-spectrum: recent developments and new directions. *Ecological Modelling* 337, 4-14.
Hartvig, M., Andersen, K.H. and Beyer, J.E. (2011) Food web framework for size-structured populations. *Journal of Theoretical Biology* 272, 113-122.
He, P., Pol, M. and Suuronen, P. (2016) Selective fishing and balanced harvest: Means, methods and implications. *Fisheries Research* http://dx.doi.org/10.1016/j.fishres.2016.08.015 Accessed January 17, 2017
Heath, M.R. and Speirs, D.C. (2011) Changes in species diversity and size composition in the Firth of Clyde demersal fish community (1927-2009). *Proceedings of the Royal Society B* 279, 543-552.
Hixon, M.A., Johnson, D.W. and Sogard, S.M. (2014) BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science* 71, 2171-2185.
Howell, D., Hansen, C., Bogstad, B. and Skern-Mauritzen, M. (2016) Balanced harvesting in a variable and uncertain world: a case study from the Barents Sea. *ICES Journal of Marine Science* 73, 1623-1631.
Huse, I., Løkkeborg, S. and Soldal, A.V. (2000) Relative selectivity in trawl, longline and gillnet fisheries for cod and haddock. *ICES Journal of Marine Science* 57, 1271-1282.
ICES, 2003. Report of the study group on the development of fishery-based forecasts (SGDFF). ICES CM 2003/ACFM:08.
Jacobsen, N.S., Gislason, H. and Andersen, K.H. (2014) The consequences of balanced harvesting of fish communities. *Proceedings of the Royal Society B* 281, 20132701.
Jennings, S., Pinnegar, J.K., Polunin, N.V.C. and Boon, T.W. (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology* 70, 934-944.
Jul-Larsen E., Kolding J., Nielsen J. R., Overa R. and van Zwieten P. A. M. (2003) Management, co-management or no management? Major dilemmas in southern African freshwater fisheries. Fisheries Technical Report 426/1–2. FAO, Rome.
Kienzle, M. (2005) Estimation of the parameters of the von Bertalanffy growth function for the main commercial species of the North Sea. Fisheries Research Services Internal Report No 05/05, Aberdeen.
Kolding, J. and van Zwieten, P.A.M. (2011) The tragedy of our legacy: How do global management

discourses affect small scale fisheries in the south? *Forum for Development Studies* 38, 267-297.
Kolding, J. and van Zwieten, P.A.M. (2014) Sustainable fishing of inland waters. J*ournal of Limnology* 73, 132-148.
Kolding, J., Jacobsen, N.S., Andersen, K.H. and van Zwieten, P.A.M. (2016a) Maximizing fisheries yields while maintaining community structure. *Canadian Journal Fisheries and Aquatic Sciences* 73, 644-655.
Kolding, J. Law, R., Plank, M. and van Zwieten, P.A.M. (2016b) The optimal fishing pattern. In *Freshwater Fisheries Ecology,* J.F. Craig (ed.), pp 524-540,Wiley.
Kolding, J., Bundy, A.,van Zwieten, P.A.M. and Plank, M.J. (2016c) Fisheries, the inverted food pyramid. *ICES Journal of Marine Science* 73, 1697-1713.
Kolding, J., Garcia, S.M., Zhou, S. and Heino, M. (2016d) Balanced harvest: utopia, failure, or a functional strategy? *ICES Journal of Marine Science* 73, 1616-1622.
Law, R., Plank, M.J. and Kolding, J. (2012) On balanced exploitation of marine ecosystems: results from dynamic size spectra. *ICES Journal of Marine Science* 69, 602-614.
Law, R., Kolding, J. and Plank, M.J. (2015) Squaring the circle: reconciling fishing and conservation of aquatic ecosystems. *Fish and Fisheries* 16, 160-174.
Law, R., Plank, M.J. and Kolding, J. (2016) Balanced exploitation and coexistence of interacting, size-structured, fish species. *Fish and Fisheries* 17, 281-302.
Lindeman, R.L. (1942) The trophic-dynamic aspect of ecology. *Ecology* 23, 399-417.
Madsen, N., Holst, R., Wileman, D., and Moth-Poulsen, T. (1999). Size selectivity of sole gill nets fished in the North Sea. *Fisheries Research* 44, 59-73.
Marine Scotland (2015) Scottish Sea Fisheries Statistics 2014. The Scottish Government, Edinburgh
Misund, O.A., Kolding, J. and Fréon, P. (2002) Fish capture devices in industrial and artisanal fisheries and their influence on management. In *Handbook of Fish Biology and Fisheries, Vol 2 Fisheries*, P.J.B. Hart and J.D. Reynolds (eds), pp 13-36, Blackwell Science, London.
Modica, L., Velasco, F., Preciado, I., Soto, M. and Greenstreet, S.P.R. (2014) Development of the large fish indicator and associated target for a Northeast Atlantic fish community. *ICES Journal of Marine Science* 71, 2403-2415.
Odum, E.P. (1959) Fundamentals of Ecology, 2nd Edition. Saunders, Philadelphia.
Pauly, D. (2011) Beyond duplicity and ignorance in global fisheries. *Pacific Ecologist* 20: 32-36.
Pauly, D. and Christensen, V. (2002) Ecosystem models. In *Handbook of Fish Biology and Fisheries, Vol 2 Fisheries*, P.J.B. Hart and J.D. Reynolds (eds), pp 211-227, Blackwell Science, London.
Pauly, D., Froese, R. and Holt, S.J. (2016) Balanced harvesting: the institutional incompatibilities. *Marine Policy* 69, 121-123.
Patterson, K. (1992) Fisheries for small pelagic species: an empirical approach to management targets. *Reviews in Fish Biology and Fisheries* 2, 321-338.
Persson, L. Van Leeuwen, A. and De Roos, A.M. (2014) The ecological foundation for ecosystem-based management of fisheries: mechanistic linkages between the individual-, population-, and community-level dynamics. *ICES Journal of Marine Science* 71, 2268-2280.
Pikitch, E.K., Rountos, K.J., Essington, T.E., Santora, C., Pauly, D., Watson, R., Sumaila, U.R., Boersma, P.D., Boyd, I.L., Conover, D.O., Cury, P., Heppell, S.S., Houde, E.D., Mangel, M., Plagányi, E., Sainsbury, K., Steneck, R.S., Geers, T.M., Gownaris,N. and Munch, S.B. (2012) The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries* 15, 43-64.
Punt, A., Hurtado-Ferro, F. and Whitten, A.R. (2013) Model selection for selectivity in fisheries stock assessments. *Fisheries Research* 158, 124–134.
Reid, D.G., Graham, N., Suuronen, P., He, P. and Pol, M. (2016) Implementing balanced harvesting: practical challenges and other implications. *ICES Journal of Marine Science* 73, 1690-1696.
Rice, J. and Gislason, H. (1996) Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. *ICES Journal of Marine Science* 53, 1214-1225.
Robinson, L.A., Greenstreet, S.P.R., Reiss, H., Callaway, R., Craeymeersch, J., de Doois, I., Degraer, S., Ehrich, S., Fraser, H.M., Goffin, A., Kröncke, I., Jorgenson, L.L., Robertson, M.R. and Lancaster, J. (2010) Length–weight relationships of 216 North Sea benthic invertebrates and fish. *Journal of the Marine Biological Association UK* 90, 95-104.
Sampson, D. B. (2014) Fishery selection and its relevance to stock assessment and fishery management. *Fisheries Research* 158, 5-14.
Sampson, D. B. and Scott, R.D. (2012) An exploration of the shapes and stability of population–selection curves. *Fish and Fisheries* 13, 89-104.

Sheldon, R.W., Prakash, A. and Sutcliffe Jr., W.H. (1972) The size distribution of particles in the ocean. *Limnology and Oceanography* 17, 327-340.
Silvert, W. and Platt, T. (1978) Energy flux in the pelagic ecosystem: a time-dependent equation. *Limnology and Oceanography* 23, 813-816.
Silvert, W. and Platt, T. (1980) Dynamic energy-flow model of the particle size distribution in pelagic ecosystems. In: *Evolution and Ecology of Zooplankton Communities*, Kerfoot, W.C. (ed.), pp. 754-763, University Press of New England, Hanover.
Skern-Mauritzen, M., Ottersen, G., Handegard, N.O., Huse, G., Dingsør, G.E., Stenseth, N.C. and Kjesbu, O.S. (2016) Ecosystem processes are rarely included in tactical fisheries management. *Fish and Fisheries* 17, 165-175.
Smith, A.D.M., Brown, C.J., Bulman, C.M., Fulton, E.A., Johnson, P., Kaplan, I.C., Lozano-Montes, H., Mackinson, S., Marzloff, M., Shannon, L.J., Shin, Y.-J. and Tam, J. (2011) Impacts of fishing low-trophic level species on marine ecosystems. *Science* 333, 1147-1150.
Sprules, W.G. and Barth, L.E. (2016) Surfing the biomass size spectrum: some remarks on history, theory, and application. *Canadian Journal of Fisheries and Aquatic Sciences* 73, 477-495.
Thorpe, R.B., Le Quesne, W.J.F., Luxford, F., Collie, J.S. and Jennings, S. (2016) Evaluation and management implications of uncertainty in a multispecies size-structured model of population and community responses to fishing. *Methods in Ecology and Evolution* 5, 49-58.
Voss, R., Quaas, M.F.,Schmidt, J.O. and Hoffmann, J. (2014) Regional trade-offs from multi-species maximum sustainable yield (MMSY) management options. *Marine Ecology Progress Series* 498, 1-12.
Zhou, S., Smith, A.D.M., Punt, A.E., Richardson, A.J., Gibbs, M., Fulton, E.A., Pascoe, S., Bulman, C., Bayliss, P. and Sainsbury, K. (2010) Ecosystem-based fisheries management requires a change to the selective fishing philosophy. *Proceedings of the National Academy of Sciences* 107, 9485-9489.

Balanced harvesting in the context of Scottish Fisheries: Appendix A

The method comes from Pauly and Christensen (2002 p.221), who suggested Ecopath could be used for the purpose of constructing size spectra. The intention is to construct a biomass spectrum using at the Ecopath equilibrium using:

- B_i, the total biomass at equilibrium for each group i; this is a scalar quantity aggregated over body size that needs to be taken apart and expressed as a function of body size;
- Z_i, the total death rate of each group i;
- $l_i(a)$, a parameterized von Bertalanffy growth equation for length l at age a for each group i,;
- $\alpha_i l^{\beta_i}$, an allometric scaling from length to mass of group i.

Here 'group' is a general term to encompass the categories in Ecopath, which might be species or something else.

Size spectra are most conveniently expressed as a function of log body mass, so a size variable $x = \log(w/w_1)$ is used, where w is mass and w_1 is a starting mass common to all groups (notionally 1 g). Individuals grow in body mass according to a standard growth equation for group i, which sets the size they are at age a, $x = f_i(a)$. The age at which individuals are at size w_1 is denoted a_1.

The aim is to construct a biomass spectrum $b_i(x)$ consistent with Ecopath and some information on growth of individuals. To do this we use a basic equivalence between the cohort biomass $b_i^{(c)}(x)$ at size x (and age a) and the production rate $p_i(x)$ at this size and age, shown for the McKendrick von Foerster equation at steady state (Law et al 2016, Appendix E):

$$p_i(x) \propto b_i^{(c)}(x). \tag{1}$$

Since $p_i(x) = g_i(x)b_i(x)$, the biomass spectrum has the proportionality

$$b_i(x) \propto \frac{b_i^{(c)}(x)}{g_i(x)}; \tag{2}$$

note here that the biomass spectrum is not the same as the distribution of biomass along the trajectory of growth of a cohort of individuals. Writing $b_i'(x) = b_i^{(c)}(x)/g_i(x)$, the constant of proportionality is set by the total biomass B_i of group i from Ecopath:

$$b_i(x) = B_i \frac{b_i'(x)}{\int_0^\infty b_i'(x)dx}. \tag{3}$$

This still leaves the cohort biomass to be specified, which is proportional to product of the survivorship from size 0 to x, multiplied by the mass $w_1 e^x$:

$$b_i^{(c)}(x) \propto e^x \rho_i(x). \tag{4}$$

The survivorship $\rho_i(x)$ here is the same as the survivorship $\rho_i(a)$ from age a_1 to the age a corresponding to x:

$$\rho_i(x) = \rho_i(a) = \exp\left(- \int_{a_1}^{a} \mu_i(a')da' \right) \tag{5}$$

where $\mu_i(a')$ is the death rate at age a'. Ecopath only provides the total mortality rate Z_i for group i, so we assume the death rate to be constant over age, giving a survivorship from age a_1 to a:

$$\rho_i(a) = e^{-Z_i(a-a_1)}. \tag{6}$$

The von Bertalanffy growth equation, with parameters k_i, $w_{\infty,i}$ and the allometric constant β_i, gives the time it takes to get from a_1 to age a corresponding to size x:

$$a - a_1 = \frac{1}{k_i} \log\left[\frac{(w_{\infty,i})^{1/\beta_i} - 1}{(w_{\infty,i})^{1/\beta_i} - w^{1/\beta_i}} \right]. \tag{7}$$

So

$$\rho(a) = \left[\frac{(w_{\infty,i})^{1/\beta_i} - 1}{(w_{\infty,i})^{1/\beta_i} - w^{1/\beta_i}} \right]^{-Z_i/k_i} \tag{8}$$

is the required survivorship $\rho_i(x)$ for constructing the cohort biomass in expression (2). The remaining term needed is the mass-specific growth rate, which also comes from the von Bertalanffy growth equation

$$\begin{aligned} g_i(x) &= \frac{1}{w}\frac{dw}{dt} && (9) \\ &= \beta_i k_i \left[\left(\frac{w}{w_{\infty,i}} \right)^{-1/\beta_i} - 1 \right]. && (10) \end{aligned}$$

Caveats and assumptions about this method are given in Section: 'How balanced is exploitation of Scottish marine ecosystems?' of the report on Balanced Harvesting.

Scottish Charity Number SC045119

Company Number SC477579

FIS MEMBER ORGANISATIONS