

Title

Change in the dominance structure of two marine fish assemblages over three decades
(doi: [10.1111/jfb.13868](https://doi.org/10.1111/jfb.13868))

Authors

Faye Moyes and Anne E. Magurran

Centre for Biological Diversity and Scottish Oceans Institute, School of Biology, University of St. Andrews, St. Andrews, Fife KY16 9TH, UK

Corresponding author: Faye Moyes, email: fhm1@st-andrews.ac.uk

Abstract

Marine fish are an irreplaceable resource but are currently under threat due to overfishing and climate change. To date, most of the emphasis has been on single stocks or populations of economic importance. However, commercially valuable species are embedded in assemblages of many species and there is only limited understanding of the extent to which the structure of whole communities has altered in recent years. Most assemblages are dominated by one or a few species, with these highly abundant species underpinning ecosystem services and harvesting decisions.

This paper shows that there have been marked temporal changes in the dominance structure of Scottish marine assemblages over the last three decades, where dominance is measured as the proportional numerical abundance of the most dominant species. We report contrasting patterns in both the identity of the dominant species, and shifts in the relative abundance of the dominant in assemblages to the east and west of Scotland. This result highlights the importance of multi-species analyses of harvested stocks and has implications not only for fisheries management but also for consumer choices.

Key words: fish diversity, dominance, biodiversity, climate change, Scottish fisheries

Significance statement

Currently marine biodiversity is facing multiple threats from factors such as over exploitation and climate change. This paper investigates patterns in the dominance structure of two geographically close, yet distinct coastal ecosystems and highlights the importance of examining fish communities as a whole rather than by population.

Introduction

The ongoing biodiversity crisis is the consequence of a combination of anthropogenic impacts including over exploitation and climate change (Jackson, 2008; García Molinos *et al.*, 2016; Cheung, 2018). To date, many of the evaluations of marine fish assemblages, particularly in the context of stock assessment, have focussed on trends in individual species (Pershing *et al.*, 2015; Boyd *et al.*, 2018). Many of these (Baudron *et al.*, 2011; Engelhard *et al.*, 2014; Dutz *et al.*, 2016) report marked changes over the last few years. Recently, however, attention has turned to the dynamics of entire marine assemblages (Greenwood and Maitland, 2009), with investigators, e.g. (Jung and Houde, 2003; Magurran *et al.*, 2015; Morley *et al.*, 2017; Iacarella *et al.*, 2018), increasingly recognising the need to quantify spatial and temporal change in biodiversity. Shifts in species richness (Daan, 2006; Hiddink

and Ter Hofstede, 2008; ter Hofstede *et al.*, 2010) and size (Bell *et al.*, 2018) have been reported, but as biodiversity is a multifaceted concept (Magurran, 2013) there is still much to be learnt about the nature of biodiversity change in assemblages of wild fish.

One frequently used measure of biodiversity is relative species abundance; this quantifies the commonness or rarity of species in comparison to the overall abundance of the assemblage. Species abundance distributions (SADs), which describe the pattern of relative abundance within an assemblage, generally follow the shape of a ‘hollow curve’ with a few abundant species and many rare ones. The most dominant species typically account for a large fraction of the overall abundance, and play an important role in ecosystem function (Davies *et al.*, 2011; Ellingsen *et al.*, 2015; Wohlgemuth *et al.*, 2016; Jones and Magurran, 2018). For this reason the relative dominance of the most numerically abundant species in an assemblage is an informative measure of community structure and can potentially reveal changes that would otherwise be unseen using metrics such as species richness or total abundance (see Supplementary Figure 1).

Here we draw on time-series data of fish assemblages to the east and west of Scotland to ask how the dominance structure of these commercially important regions has changed over three decades. This time scale represents the period over which high quality assemblage data are available (ICES, 2014). The study areas being compared in the analysis are geographically close, yet are exposed to different climatic conditions and exploitation practices; as such they provide an insight into the extent of recent change in assemblage dominance structure in heavily fished regions of the North East Atlantic.

We know that fish assemblages to the west of Scotland are experiencing considerable reorganisation as a result of biotic homogenization (Magurran *et al.*, 2015), and that biotic homogenization and homogenization of water temperatures are correlated in the west coast assemblages. In contrast, the North Sea to the east of Scotland has exhibited a smaller overall increase in water temperature during the same period (ter Hofstede *et al.*, 2010). Thus, we expect to detect a shift in dominance structure in west coast fishes over the time frame of interest, with latitudinal heterogeneity in the response. No a priori predictions are made for east coast assemblages, which are included to extend the scope of the analysis and provide a comparison with west coast changes.

Materials and Methods

Materials and Data

The Scottish West Coast Groundfish survey (DATRAS, 2013) takes place annually in January, February and March whilst the North Sea International Bottom Trawl survey (DATRAS, 2015) is carried out biannually in the first and third quarters (where the first quarter is January, February and March and the third quarter is July, August and September). We used the filter ‘All Species’ when selecting the scientific trawl data; this meant that both non-commercial and commercial species were included in the analysis. CPUE (catch per unit effort) per length per haul per thirty minutes was chosen as the measure of abundance as it provided the most comprehensive dataset for both systems. Quarter 1 contains the most consistently sampled areas from both systems and is also the only quarter where all years were sampled. To maintain a fair comparison between the areas only Quarter 1 data are used here with 1985 as the starting point in both cases. Both surveys use an ICES statistical

rectangle (rectangles represent a 30' latitude by 1° longitude grid cell) based sampling strategy which is consistent through time.

The Grande Overture Verticale (GOV) trawl method is the recommended gear for all bottom trawl surveys carried out by ICES. A full description and figures detailing the gear can be found in the ICES Manual for the International Bottom Trawl Surveys (ICES, 2015). A comparative study carried out in 2012 (Reid *et al.*, 2012) showed that the results of trawling using this gear performed similarly to that using a standard commercial trawl. In order to ensure consistency between systems our study only uses the data sampled using the GOV gear.

Species and temperature data were sourced from the International Council for the Exploration of the Sea (ICES) data portal (ICES, 2014). The species data are taken from two standardised surveys incorporating the ICES regions VIa (West coast), IVa and IVb (North Sea). The trawl survey gear provides an adequate sample of a wide range of species and sizes; the complete list of fish included in the recorded catch data (“BTSSurveySpecies.xlsx” – worksheet tab allSpecies) and the subset of those featured in the study set (worksheet tab - studySpecies) are included in the supplementary materials. Surveys adhere to strict protocols (ICES, 2015) with all species within a haul identified to the lowest taxonomic level possible. Additional information is also recorded, where possible, for length, age, sex and maturity, though these data are not used in our analysis.

Electronic equipment is used to monitor net geometry during all trawls; this allows for the appropriate adjustment of sweep length according to water depth (ICES, 2015). The depths where hauls are recorded range from 10m to 250m.

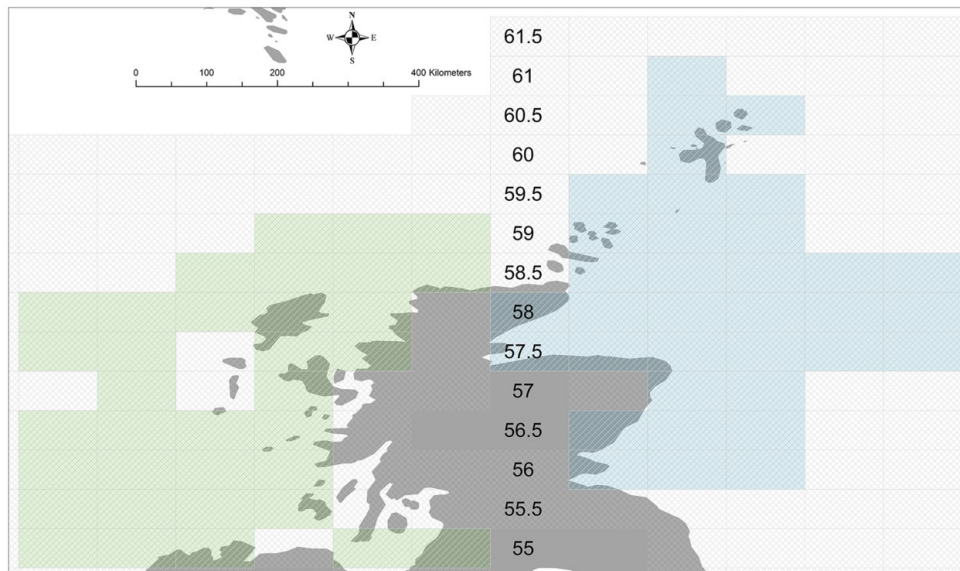


Figure 1: Study Area

The green shaded areas show the 35 ICES statistical rectangles used in the West Coast survey, whilst the blue shaded rectangles represent the 35 used in the North Sea survey. The underlying hatched area represents the ICES rectangles from the wider area and the central column of figures corresponds to the latitudinal bands used in analysis.

We selected the 35 ICES west coast rectangles (see Figure 1), as these were the ones which had been most consistently sampled (Magurran *et al.*, 2015), and chose 35 correspondingly well sampled, similarly positioned east coast rectangles for comparison. Each rectangle was assigned to its respective latitudinal band (0.5 degrees wide). The spatial coverage on the west coast extends from 55.5 degrees to 59.5 degrees north and includes 134 species (128 finfish). The corresponding 35 ICES rectangles (see Figure 1) on the east coast extend from 56.5 degrees to 61.5 degrees and include 138 species (129 finfish). For the purposes of this analysis the focus was on finfish but the numerical abundance of the dominant species was computed in relation to the entire assemblage - which also includes a few macroinvertebrates such as the European common squid *Alloteuthis subulata* (Lamarck 1798) - as these are the species amongst which resources are partitioned.

Sea surface ($\leq 10\text{m}$) temperature data ($^{\circ}\text{C}$) are collected as part of monitoring and were assigned to the relevant latitudinal band for this analysis (see Figure 1).

Methods

The study data comprises nine latitudinal bands on the west coast and eleven on the east. Community time series were compiled for each latitudinal band following sample based rarefaction (Dornelas *et al.*, 2014) (see Supporting Information – Code). Because species richness and other diversity metrics are sensitive to sample size, raw (unrarefied) data can lead to bias. Rarefaction (Gotelli and Colwell, 2011) is a statistical resampling methodology that reduces this bias. Here the minimum number of samples per year, per latitudinal band, was resampled to generate a constant number of samples to be used in the analyses. Sample-based rarefaction was used in this study as – in contrast to individual based rarefaction- it retains species identity.

The most numerically abundant species in each latitudinal band, and each year, was defined as the dominant species. In the case of a tie (where two or more species were jointly most abundant) the species occurring first in the list of species was chosen. Relative dominance was then calculated as a proportion of the total abundance of species contained within each assemblage. (R code for this function and others can be found in the supplementary R markdown document (see Supporting Information – Code)).

We first quantified the overall annual trend in relative dominance, on each coast, using ordinary least squares (OLS). Next, we computed overall annual change in the composition of the assemblage, in each latitudinal band and on each coast, relative to the first year in the time series (1985), using the Morisita-Horn dissimilarity index (vegdist function in the vegan package (Oksanen *et al.*, 2017)), and described the trend using an OLS regression. East and west coast trends in mean overall temperature data were treated in the same way. Morisita-Horn was chosen to quantify overall compositional change as it is sensitive to the abundances of the most abundant species (Magurran, 2013).

Finally we used two-way analysis of variance (ANOVA), with an interaction term, to test for differences in dominance between coasts.

```
model<-aov(relative_dominance~year*coast)
```

All analyses used R statistical software (RCoreTeam, 2018). Mapping functions were carried out using the ESRI GIS software ArcGIS (ESRI, 2015).

Results

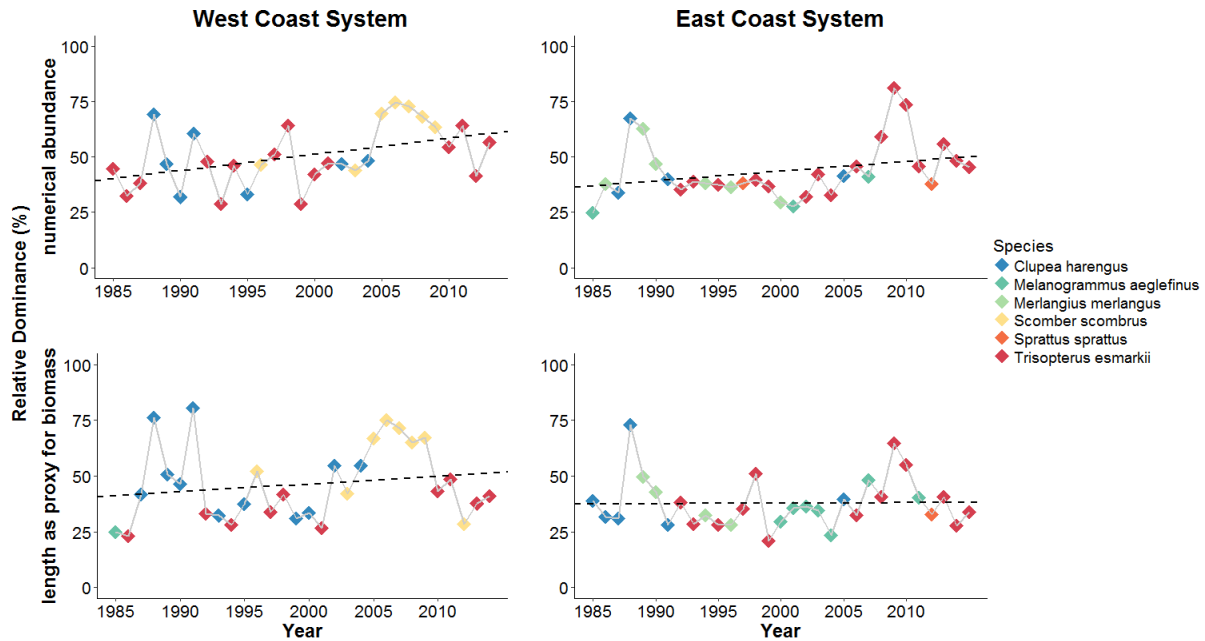


Figure 2: Upper panel of the plot shows the relative dominance (as a percentage) for the numerical abundance on each coast. This plot is the same as Figure 2 within the main text but has yearly points coloured by the changing identities of the dominant species. The dotted lines in both panels represent Ordinary Least Squares (OLS) regression trend lines. The dominant species identities are similar in both calculation methods (numerical abundance and length as a proxy for biomass). In addition the trends follow similar patterns although when using biomass the inclines are flatter in both ecosystems. West coast system - numerical abundance, slope=0.007, p-value=0.012; biomass, slope=0.003, p-value=0.33. East coast system - numerical abundance, slope=0.004, p-value=0.1; biomass, slope=0.0001, p-value=0.93.

As Figure 2 clearly demonstrates, the dominance structure of these marine assemblages changed over the thirty year duration of the study (see Figure 2). However, although dominance increased in both systems, this increase was significant only for the west coast (OLS regression: west coast p-value=0.012, east coast p-value=0.102). This result is supported by a two-way ANOVA which revealed significant differences in dominance between years ($F_{1, 56}=8.493$ p=0.005) and between coasts $F_{1, 56}=5.175$ p=0.03), (see Supplementary Table 2) but no significant interaction for year x coast [$F_{1, 56}=0.633$, p=0.43] (for full ANOVA results see Supplementary Table 1).

Both systems became increasingly dissimilar (see Figure 3) in composition over time (relative to the first year in the time series), with a significant rise in dissimilarity in the west coast, (OLS regression: p-value=0.001), but not the east coast (OLS regression: p-value=0.3). Mean sea surface temperatures from the same locations during Quarter 1 also increased in

both systems, by 1.3° C on the west coast and 0.7° C on the east coast. Once again, the trend was significant only for the west coast (OLS regression: west coast p-value=0.013, east coast p-value=0.423).

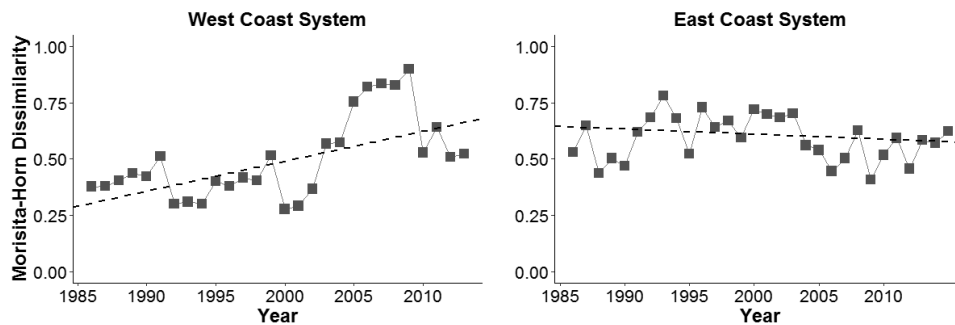


Figure 3: Trend in dissimilarity by year Morisita-Horn dissimilarity (using Year 1 – 1985 as a baseline) with an OLS regression trend line added. The trend is increasing in both systems but only significantly on the west coast (p-value=0.001).

Overall differences between the two ecosystems were underlain by within-system differences in relative dominance (see Figure 4, Supplementary Table 2 and Supplementary Figure 3). Overall dominance varied significantly over time ($F_{1, 256}=10.65$, $p=0.001$), on the west coast, but there was no effect of latitude, ($F_{1, 256}=0.1$, $p=0.75$), and no interaction between latitude and time ($F_{1, 256}=0.6$, $p=0.44$). In contrast, on the east coast there was a significant interaction between latitude and time, [$F_{1, 306}=4.84$, $p=0.03$], and a significant effect of latitude ($F_{1, 306}=21.05$, $p<0.0001$) but not of time ($F_{1, 306}=0.04$, $p=0.84$) (see Supplementary Table 1 for further details).

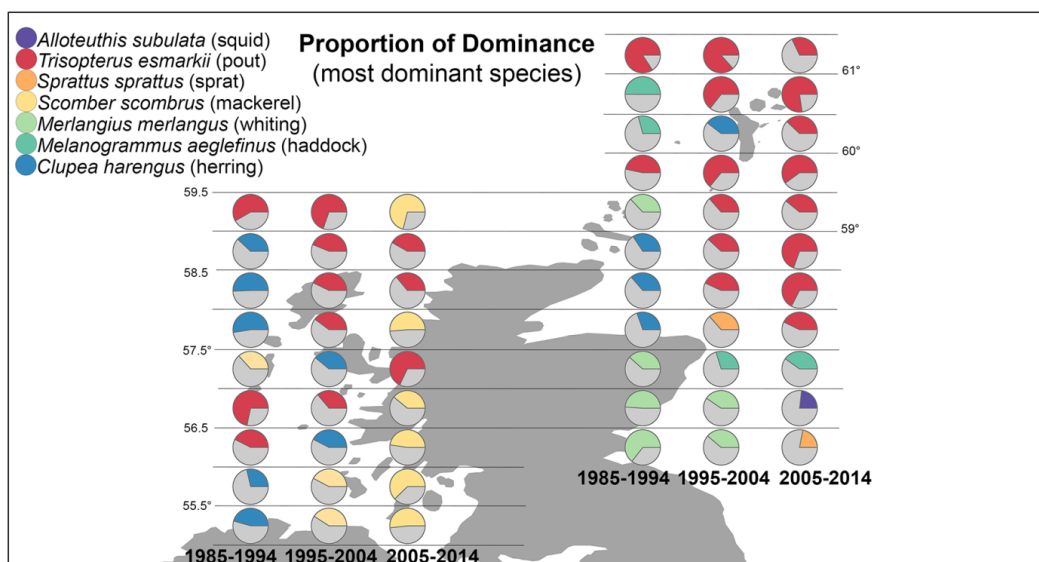


Figure 4: Map showing spatio-temporal changes in dominants (identity and amount) The map illustrates changes in the dominance of the most dominant species by latitudinal band. Each pie summarises a 10 year period and is colour coded to show the relative dominance of the most dominant species.

Discussion

The focus here on marine fish assemblages, rather than fish populations, reveals community wide changes that can be obscured in single species studies. A spatio-temporal approach (Henderson, 2017) in combination with examination of key attributes of community structure, such as the changes in dominance, is an important starting point for understanding the consequences of the melting pot of pressures these systems are currently under (Majewski *et al.*, 2017).

The two coastal systems show distinct differences not only in the proportion of dominance but also in the identity of the most dominant species. Interestingly, it was in the west coast assemblages that we detected the greatest change. Previous work (Magurran *et al.*, 2015) highlighted an increase in biotic homogenization over the same period and hypothesized that changes in water temperature may have contributed to this pattern. Another recent study (Hansen *et al.*, 2017) found that there were shifts in species dominance expected in freshwater lake systems as a result of warming waters. The observed differences in dominance found between the east and west coasts are therefore potentially linked to the different patterns of change in sea surface temperatures (Simpson *et al.*, 2011; Stuart-Smith *et al.*, 2017; Townhill *et al.*, 2017) since water temperature is a key driver of distribution patterns in marine fishes (Perry *et al.*, 2005). Indeed, the impact of climate change on North Sea circulation and its fish stocks has been discussed elsewhere (Turrell, 1992; Baudron *et al.*, 2013; Hiddink *et al.*, 2014). However, temporal variation in sea surface temperatures (Genner *et al.*, 2004; Henderson *et al.*, 2011; Miller *et al.*, 2011) is unlikely to be the only driver influencing the trends since fishing pressure also leads to marked changes in the structure of marine assemblages (Jackson *et al.*, 2001).

The contrasting outcomes in these two geographic localities illustrate why it is difficult to predict how different systems will respond to environmental and anthropogenic drivers (Poloczanska *et al.*, 2016). Such spatial heterogeneity may be a widespread phenomenon. Contrasting patterns of biodiversity change were also evident in two zones of a bay in Brazil, monitored over three decades, (Araújo *et al.*, 2016).

On the east coast - which exhibits less temporal variation in identity of the most dominant species - the Norway pout *Trisopterus esmarkii* (Nilsson, 1855) is the overall dominant for around two thirds of the time series with the exception of the initial decade where haddock *Melanogrammus aeglefinus* L. features more prominently. In contrast, on the west coast the identities change from Atlantic herring *Clupea harengus* L. in the first decade, to *T. esmarkii* in the second and finally Atlantic mackerel *Scomber scombrus* L. in the third. These species make different contributions to ecosystem function and have different economic values. For example, *S. scombrus* is thought to be a predator of juvenile *T. esmarkii* (ICES, 2005), and while *S. scombrus* catches have high commercial value, *T. esmarkii* is considered useful only as food in the aquaculture industry (ICES, 2005).

Historically, Scotland's economy has enjoyed a significant contribution from the fishing sector and it is important that this tradition be maintained, but only if it can be done in a sustainable manner. A better understanding of fish communities can lead to more efficient management strategies (Cheung *et al.*, 2018; Moriarty *et al.*, 2018). Currently there are new opportunities for the development of broader, constructive approaches to fisheries

management (Jacobs *et al.*, 2018) where fish biology plays an important role in informing wild fisheries and their continued sustainability.

Science has a vital part to play in the conservation and management of fish resources (Obregón *et al.*, 2018) but, as this study has demonstrated, greater understanding of how fish assemblages respond to change can be gained if fisheries managers take advantages of the rich toolkit of biodiversity metrics. Even simple measures, such as the dominance index used here, reveal patterns that have hitherto been masked in population based analyses (Perry *et al.*, 2010). As such they have the potential to shed new light on the causes and consequences of ecosystem restructuring.

Acknowledgements

FM and AEM are grateful to the European Research Council (ERCAdG BioTIME 250189 and ERCPoC BioCHANGE 727440) for their funding. We are also grateful to the two anonymous reviewers whose comments have strengthened our paper considerably.

Contributions

FM and AEM conceived the project; FM undertook the analyses and both authors contributed to the manuscript.

References

- Araújo, F. G., de Azevedo, M. C. C. & Guedes, A. P. P. (2016). Inter-decadal changes in fish communities of a tropical bay in southeastern Brazil. *Regional Studies in Marine Science* **3**, 107-118.
- Baudron, A. R., Needle, C. L., Rijnsdorp, A., D. & Marshall, C., Tara (2013). Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Global Change Biology* **20**, 1023-1031.
- Baudron, A. R., Needle, C. L. & Marshall, C. T. (2011). Implications of a warming North Sea for the growth of haddock *Melanogrammus aeglefinus*. *Journal of Fish Biology* **78**, 1874-1889.
- Bell, R. J., Collie, J. S., Branch, T. A., Fogarty, M. J., Minto, C., Ricard, D. & Handling editor: Ken, A. (2018). Changes in the size structure of marine fish communities. *ICES Journal of Marine Science* **75**, 102-112.
- Boyd, R., Roy, S., Sibly, R., Thorpe, R. & Hyder, K. (2018). A general approach to incorporating spatial and temporal variation in individual-based models of fish populations with application to Atlantic mackerel. *Ecological Modelling* **382**, 9-17.
- Cheung, W. W. L. (2018). The future of fishes and fisheries in the changing oceans. *Journal of Fish Biology* **92**, 790-803.
- Cheung, W. W. L., Jones, M. C., Reygondeau, G. & Frölicher, T. L. (2018). Opportunities for climate-risk reduction through effective fisheries management. *Global Change Biology* **0**.
- Daan, N. (2006). Spatial and temporal trends in species richness and abundance for southerly and northerly components of the North Sea fish community separately, based on IBTS data 197702005.

- DATRAS (2013). ICES Scottish West Coast Survey For Commercial Fish Species 1985-2013. Available at <https://datras.ices.dk>, accessed 2014.
- DATRAS (2015). ICES North Sea International Bottom Trawl Survey For Commercial Fish Species 1985-2014. (DATRAS, ed.): <https://datras.ices.dk>.
- Davies, T. W., Jenkins, S. R., Kingham, R., Kenworthy, J., Hawkins, S. J. & Hiddink, J. G. (2011). Dominance, Biomass and Extinction Resistance Determine the Consequences of Biodiversity Loss for Multiple Coastal Ecosystem Processes. *PLOS ONE* **6**, e28362.
- Dornelas, M., Gotelli, N. J., McGill, B. J., Shimadzu, H., Moyes, F., Sievers, C. & Magurran, A. E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science* **344**, 296-299.
- Dutz, J., Støttrup, J. G., Stenberg, C. & Munk, P. (2016). Recent trends in the abundance of plaice *Pleuronectes platessa* and cod *Gadus morhua* in shallow coastal waters of the Northeastern Atlantic continental shelf – a review. *Marine Biology Research* **12**, 785-796.
- Ellingsen, K. E., Anderson, M. J., Shackell, N. L., Tveraa, T., Yoccoz, N. G. & Frank, K. T. (2015). The role of a dominant predator in shaping biodiversity over space and time in a marine ecosystem. *Journal of Animal Ecology* **84**, 1242-1252.
- Engelhard, G. H., Righton, D. A. & Pinnegar, J. K. (2014). Climate change and fishing: a century of shifting distribution in North Sea cod. *Global Change Biology* **20**, 2473-2483.
- ESRI (2015). ArcGIS Desktop: Release 10.1 Redlands, CA: Environmental Systems Research Institute.
- García Molinos, J., Halpern, B. S., Schoeman, D. S., Brown, C. J., Kiessling, W., Moore, P. J., Pandolfi, J. M., Poloczanska, E. S., Richardson, A. J. & Burrows, M. T. (2016). Climate velocity and the future global redistribution of marine biodiversity. *Nature Clim. Change* **6**, 83-88.
- Genner, M. J., Sims, D. W., Wearmouth, V. J., Southall, E. J., Southward, A. J., Henderson, P. A. & Hawkins, S. J. (2004). Regional climatic warming drives long-term community changes of British marine fish. *Proceedings of the Royal Society of London B: Biological Sciences* **271**, 655-661.
- Gotelli, N. J. & Colwell, R. K. (2011). Estimating species richness. *Biological diversity: frontiers in measurement and assessment* **12**, 39-54.
- Greenwood, M. F. D. & Maitland, P. S. (2009). Long-term changes in fish-assemblage composition from cooling-water intake screens in the Forth Estuary, Scotland, UK. *Marine Biodiversity Records* **2**, e8.
- Hansen, G. J. A., Read, J. S., Hansen, J. F. & Winslow, L. A. (2017). Projected shifts in fish species dominance in Wisconsin lakes under climate change. *Global Change Biology* **23**, 1463-1476.
- Henderson, P. A. (2017). Long-term temporal and spatial changes in the richness and relative abundance of the inshore fish community of the British North Sea Coast. *Journal of Sea Research* **127**, 212-226.
- Henderson, P. A., Seaby, R. M. H. & Some, J. R. (2011). Community level response to climate change: the long-term study of the fish and crustacean community of the Bristol Channel. *Journal of Experimental Marine Biology and Ecology* **400**, 78-89.
- Hiddink, J. G., Burrows, M. T. & García Molinos, J. (2014). Temperature tracking by North Sea benthic invertebrates in response to climate change. *Global Change Biology* **21**, 117-129.

- Hiddink, J. G. & Ter Hofstede, R. (2008). Climate induced increases in species richness of marine fishes. *Global Change Biology* **14**, 453-460.
- Iacarella, J. C., Adamczyk, E., Bowen, D., Chalifour, L., Eger, A., Heath, W., Helms, S., Hessian-Lewis, M., Hunt, B. P. V., MacInnis, A., O'Connor, M. I., Robinson, C. L. K., Yakimishyn, J. & Baum, J. K. (2018). Anthropogenic disturbance homogenizes seagrass fish communities. *Global Change Biology* **24**, 1904-1918.
- ICES (2005). ICES-FishMap is an atlas of North Sea fish, including fact sheets of key species and distribution maps. Available at <http://www.ices.dk/marine-data/maps/Pages/ICES-FishMap.aspx>.
- ICES (2014). International Council for the Exploration of the Sea (ICES) Data Collections. Available at <http://ecosystemdata.ices.dk/>.
- ICES (2015). Manual for the International Bottom Trawl Surveys. . *Series of ICES Survey Protocols* 86 pp.
- Jackson, J. B. C. (2008). Ecological extinction and evolution in the brave new ocean. *Proceedings of the National Academy of Sciences* **105**, 11458-11465.
- Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J. & Warner, R. R. (2001). Historical Overfishing and the Recent Collapse of Coastal Ecosystems. *Science* **293**, 629-637.
- Jacobs, A., Doran, C., Murray, D. S., Telsnig, J. D., Laskowski, K. L., Jones, N. A. R., Auer, S. K. & Præbel, K. (2018). On the challenges and opportunities facing fish biology: a discussion of five key knowledge gaps. *Journal of Fish Biology* **92**, 690-698.
- Jones, F. A. M. & Magurran, A. E. (2018). Dominance structure of assemblages is regulated over a period of rapid environmental change. *Biology Letters* **14**.
- Jung, S. & Houde, E. D. (2003). Spatial and temporal variabilities of pelagic fish community structure and distribution in Chesapeake Bay, USA. *Estuarine, Coastal and Shelf Science* **58**, 335-351.
- Magurran, A. E. (2013). *Measuring biological diversity*: John Wiley & Sons.
- Magurran, A. E., Dornelas, M., Moyes, F., Gotelli, N. J. & McGill, B. (2015). Rapid biotic homogenization of marine fish assemblages. *Nature Communications* **6**, 8405.
- Majewski, A. R., Atchison, S., MacPhee, S., Eert, J., Niemi, A., Michel, C. & Reist, J. D. (2017). Marine fish community structure and habitat associations on the Canadian Beaufort shelf and slope. *Deep Sea Research Part I: Oceanographic Research Papers* **121**, 169-182.
- Miller, E. F., Pondella, I. I. D. J., Beck, D. S. & Herbinson, K. T. (2011). Decadal-scale changes in southern California sciaenids under different levels of harvesting pressure. *ICES Journal of Marine Science* **68**, 2123-2133.
- Moriarty, M., Sell, A. F., Trenkel, V. M., Lynam, C. P., Burns, F., Clarke, E. D., Greenstreet, S. P. R., McGonigle, C. & Handling editor: Michel, K. (2018). Resolution of biodiversity and assemblage structure in demersal fisheries surveys: the role of tow duration. *ICES Journal of Marine Science* **75**, 1672-1681.
- Morley, J. W., Batt, R. D. & Pinsky, M. L. (2017). Marine assemblages respond rapidly to winter climate variability. *Global Change Biology* **23**, 2590-2601.

- Obregón, C., Lyndon, A. R., Barker, J., Christiansen, H., Godley, B. J., Kurland, S., Piccolo, J. J., Potts, R., Short, R., Tebb, A. & Mariani, S. (2018). Valuing and understanding fish populations in the Anthropocene: key questions to address. *Journal of Fish Biology* **92**, 828-845.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. J., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., Szoecs, E. & Wagner, H. (2017). vegan: Community Ecology Package. R package version 2.4-3. <https://CRAN.R-project.org/package=vegan>.
- Perry, A. L., Low, P. J., Ellis, J. R. & Reynolds, J. D. (2005). Climate Change and Distribution Shifts in Marine Fishes. *Science* **308**, 1912-1915.
- Perry, R. I., Cury, P., Brander, K., Jennings, S., Möllmann, C. & Planque, B. (2010). Sensitivity of marine systems to climate and fishing: Concepts, issues and management responses. *Journal of Marine Systems* **79**, 427-435.
- Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Le Bris, A., Mills, K. E., Nye, J. A., Record, N. R., Scannell, H. A., Scott, J. D., Sherwood, G. D. & Thomas, A. C. (2015). Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* **350**, 809-812.
- Poloczanska, E. S., Burrows, M. T., Brown, C. J., Garcia Molinos, J., Halpern, B. S., Hoegh-Guldberg, O., Kappel, C. V., Moore, P. J., Richardson, A. J., Schoeman, D. S. & Sydeman, W. J. (2016). Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science* **3**.
- RCoreTeam (2018). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing, <http://www.R-project.org/>.
- Reid, D. G., Kynoch, R. J., Penny, I., Summerbell, K., Edridge, A. & O'Neill, F. G. (2012). A comparison of the GOV survey trawl with a commercial whitefish trawl. *Fisheries Research* **121-122**, 136-143.
- Simpson, Stephen D., Jennings, S., Johnson, Mark P., Blanchard, Julia L., Schön, P.-J., Sims, David W. & Genner, Martin J. (2011). Continental Shelf-Wide Response of a Fish Assemblage to Rapid Warming of the Sea. *Current Biology* **21**, 1565-1570.
- Stuart-Smith, R. D., Edgar, G. J. & Bates, A. E. (2017). Thermal limits to the geographic distributions of shallow-water marine species. *Nature Ecology & Evolution* **1**, 1846-1852.
- ter Hofstede, R., Hiddink, J. G. & Rijnsdorp, A. D. (2010). Regional warming changes fish species richness in the eastern North Atlantic Ocean. *Marine Ecology Progress Series*.
- Townhill, B., Pinnegar, J., Tinker, J., Jones, M., Simpson, S., Stebbing, P. & Dye, S. (2017). Non-native marine species in north-west Europe: Developing an approach to assess future spread using regional downscaled climate projections. *Aquatic Conservation: Marine and Freshwater Ecosystems* **27**, 1035-1050.
- Turrell, W. R. (1992). New hypotheses concerning the circulation of the northern North Sea and its relation to North Sea fish stock recruitment. *ICES Journal of Marine Science: Journal du Conseil* **49**, 107-123.
- Wohlgemuth, D., Solan, M. & Godbold, J. A. (2016). Specific arrangements of species dominance can be more influential than evenness in maintaining ecosystem process and function. *Scientific Reports* **6**, 39325.

