

Ecosystem Tipping Points: Learning from the Past to Manage for the Future

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Ecosystem Tipping Points: Learning from the Past to Manage for the Future

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Prepared for the Environmental Protection Agency

by

Galway Mayo Institute of Technology

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Executive Summary

Context

Marine ecosystems are undergoing unprecedented change, with natural capital declining to the point that benefits accrued by humans are at risk. In parallel, demands for natural resources and ecosystem services are increasing. Ecosystem change can occur abruptly in a non-linear fashion until a tipping point is reached and the ecosystem shifts to an alternative state. After a regime shift, the ecosystem may not return to its previous state, even when an external pressure is removed or reduced. This makes it difficult to predict ecosystem responses to human impacts and to identify appropriate indicators and targets for ecosystem-based management, as is required under environmental legal instruments such as the Marine Strategy Framework Directive.

The analysis of long-term environmental and biological datasets provides a historical context for ecosystem change, allowing natural short-term variability to be separated from long-term trends; regime shifts to be detected; and links between ecosystem components to be identified. Ultimately, these data can provide early warning indicators to signal an approaching threshold before it is reached, allowing management to respond to avert a regime shift.

Objectives

This project aimed to collate and integrate datasets describing the Celtic Sea ecosystem (as defined by the geographic area of the Celtic Sea), to use these data to quantify how physical and biological ecosystem components have changed in recent decades and to establish relationships between ecosystem responses and external pressures. A primary objective was to develop analytical tools for detecting step changes and to use these tools to determine if ecological tipping points have occurred in the Celtic Sea ecosystem.

Progress Made

The project database provides a valuable resource for exploring ecological change, adding value to previously collected data and integrating data

generated within the project. These data describe the physical environment of the Celtic Sea from 1900 to 2018 (wind conditions, sea surface temperature, ocean salinity and climatic indices) and capture change across multiple trophic levels (phytoplankton, zooplankton, 14 fish species, seabirds and turtles) from the 1950s to the present. Some data originated from ocean monitoring infrastructure and scientific surveys; others were obtained from opportunistic records and citizen science initiatives. Data generated for scientific assessment of commercial fisheries provided population-level estimates of abundance, growth and fishing mortality. Measurements of growth marks in fish otoliths (ear stones) were used to examine multidecadal changes in growth across several species.

The project has developed national capacity in the statistical analysis of ecological time series. Methods were applied and developed within the project to identify common trends across multiple time series, to model complex relationships between drivers and an ecological response, to detect change in highly variable time series, and to isolate a response to an external driver from other sources of variability. Statistical tools were used to account for sources of error and bias inherent in data collected by human observers as part of citizen science initiatives. Significant progress was made in the early detection of ecosystem change points using the Bayesian online change-point detection (BOCPD) algorithm.

Key Findings

Analysis of the time series showed that there have been considerable changes in the physical environment and across multiple trophic levels in the Celtic Sea over the last 50 years, many of which are associated with ocean warming.

The abundance of jellyfish and their predators has increased

As the Celtic Sea environment changes some species are increasing in abundance; Continuous Plankton

Recorder (CPR) data showed a pronounced increase in the abundance of gelatinous zooplankton (jellyfish). Increasing jellyfish numbers are thought to indicate an ecosystem shift that may be triggered by climate change, overfishing, eutrophication, translocation and habitat modification.¹ Field survey results reveal the importance of oceanographic features in the Celtic Sea for structuring gelatinous zooplankton communities and provide estimates of the relative biomass of different taxa within this group; at times, siphonophores contribute up to 42% of the total zooplankton biomass (mg C m^{-3}). The warm water gelatinous community of the Celtic Sea typically had a ~40% greater gelatinous biomass than the cold water gelatinous community and therefore jellyfish in warm water communities may have a greater predatory impact on commercial fish species. These baseline data are important for evaluating potential impacts of increasing jellyfish abundance. The change-point analysis showed that there was a significant step change in the jellyfish time series in the late 1990s. This coincided with an increase in the occurrence of sunfish, which are predators of jellyfish; however, the analysis suggests that the increase in occurrence of sunfish is linked to warming rather than increased food supply.

Changes in wind-driven circulation patterns reduce the delivery of herring to known nursery areas

Wind patterns in the Celtic Sea have changed since the 1960s, with the prevailing south-west winds becoming more frequent and with evidence of a change point around 1990. Simulation of the dispersal of herring larvae from a spawning ground in the Celtic Sea using oceanographic modelling shows that, as the strength and frequency of prevailing winds increase, more larvae are dispersed away from Celtic Sea retention areas and areas that are known to support juvenile growth and survival. Changes in wind patterns are therefore likely to impact on the delivery of herring larvae to nursery areas, with potential consequences for early life survival and recruitment to adult fisheries. Other dispersing organisms could also potentially be affected.

Fish growth rates are changing, with some species showing declines

In recent decades several commercial fish species have shown changes in growth that have consequences for stock productivity and may indicate a change in ecosystem structure and functioning. These changes are reflected in individual fish length and otolith measurements, and in population mean weights at age. Most notably, there was a sharp reduction in size at age of Celtic Sea herring from the mid-1970s to the 2000s, which was most strongly and non-linearly associated with temperature; the length of three-winter-ring (4-year-old) herring decreases sharply above a threshold temperature of 14.1°C. There was also evidence of density dependence (size at age was negatively correlated with population size) and a positive relationship with food availability. Weight-at-age trends varied between species but overall there was a reduction in fish size in the Celtic Sea that was associated with increases in sea surface temperature. Archived otolith collections proved valuable for describing temporal trends in growth of Celtic Sea fish species over extended time periods and for investigating associations with environmental, population and fishing-related variables. After accounting for individual and age-related effects, annual growth signals were significantly correlated across species (herring, plaice and haddock), which may indicate a common response to environmental change.

Change points are detected across multiple taxa and trophic levels, but no simultaneous regime shift

The BOCPD algorithm provided quantified evidence for the occurrence of change points across the Celtic Sea ecosystem. The BOCPD algorithm is appropriate for ecosystem monitoring because it estimates the probability that a change point has occurred at each year in a time series. Abrupt changes are detected quickly, providing a means for early detection. The model identified periods of coherent environmental change during the late 1980s and mid-1990s (temperature, salinity, wind patterns, climatic indices). For other ecosystem components, important changes occurred but were not tightly coupled or apparently

1 Richardson, A.J., *et al.*, 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology & Evolution* 24: 312–322. <https://doi.org/10.1016/j.tree.2009.01.010>

cascading across series; instead, the timing of step changes varied across the time series. Although a simultaneous regime shift across the ecosystem was not detected, there was strong evidence that change occurred across multiple taxa and trophic levels in the Celtic Sea ecosystem over the last 50 years, which has important consequences for management.

Summary Recommendations

- *Sustain long-term datasets.* A balanced and integrated ocean-observing system is needed to support ecosystem management.² At a national level, long-term support should be provided to maintain extended ecological time series and to integrate them with data resources from national monitoring programmes.
- *Implement statistical methods for handling observer time series.* Citizen science initiatives enhance observation capacity while also increasing public engagement with science. To maximise value from national observer datasets, appropriate statistical methods should be used to account for inherent sources of imprecision and bias and effectively detect the underlying long-term trends. This can be achieved by involving statisticians in the design of citizen science initiatives and the subsequent analysis of time series.
- *Preserve biochronological material from national fisheries monitoring programmes.* Fish otoliths and scales contain detailed individual growth histories that can be statistically analysed to detect changes in demographic properties and identify their causes. Otoliths and scales are collected annually as part of national fisheries monitoring programmes to derive individual age estimates, which are subsequently aggregated to produce population-level estimates of size and abundance at age; the rich individual-level data that they contain are under-utilised and systems for curating the material are lacking. It is recommended that the preservation of these valuable archives is prioritised to make them available for research into climate- and fishing-related influences on fish demographics.
- *Monitor changes in wind-driven circulation and larval dispersal.* The Climate Change Sectoral Adaptation plan for the seafood sector states that “continued monitoring of the spatial distributions of commercially exploited fish stocks is essential to support future management”. This study demonstrates how changes in wind-driven circulation can influence dispersal to nursery grounds, with consequences for the distribution of adult stocks. Oceanographic simulations coupled with field studies of larval distribution can provide an early warning of potential changes to the distribution of adult fish stocks and should be incorporated into fisheries monitoring programmes.
- *Monitor changes in jellyfish abundance and associated food web effects.* The pronounced increase in the abundance of some jellyfish groups in the Celtic Sea since the late 1990s has consequences for the food web structure and ecosystem service provisioning, particularly as these groups can make a substantial contribution to zooplankton biomass in the Celtic Sea. It is recommended that some measure of the contribution of jellyfish to zooplankton be incorporated into food web indicators as these are developed. This could be provided by CPR time series in combination with dedicated programmes for monitoring larger species of jellyfish.
- *Incorporate change-point detection into ecosystem monitoring.* The BOCPD framework presented here provides a means to condense high volumes of complex ecosystem data into a single coherent analysis of ecosystem change points, allowing shifts to be rapidly identified and effectively communicated at various levels of aggregation. Incorporation into ongoing monitoring programmes would ensure that data are continually updated and results reported. This approach can be applied to ecosystem indicators that have already been prioritised for monitoring and could be used to identify variables that display significant shifts with societal consequences and might warrant inclusion within a Framework for Ocean Observing.³

2 Benedetti-Cecchi, L., et al. (eds), *Future Science Brief 3 of the European Marine Board*. European Marine Board, Ostend, Belgium.

3 Lindstrom, E., et al., 2012. *A Framework for Ocean Observing*. By the Task Team for an Integrated Framework for Sustained Ocean Observing, UNESCO 2012 (revised in 2017), IOC/INF-1284 rev.2. Available online: <https://unesdoc.unesco.org/ark:/48223/pf0000211260> (accessed 16 April 2020).

1 Introduction

1.1 Ecosystem Change, Thresholds and Tipping Points

“Ecosystem services” are the direct and indirect benefits that humans derive from natural capital and ecosystem functions, including food, materials, nutrient cycling, climate regulation, and recreational and cultural benefits. Although critical to human welfare and of immense economic importance (Costanza *et al.*, 1997), continued provision of these services is threatened by human impacts on natural systems, resulting in alterations to ecosystem functioning that may be accelerating, abrupt and irreversible (UNEP, 2006). There is mounting evidence that natural capital is declining to the point that the benefits accrued by humans are at risk (Mace *et al.*, 2015). Therefore, effective management of natural capital urgently requires an improved understanding of how ecosystems change in response to pressures, as well as development of monitoring tools to detect and predict change (Hughes *et al.*, 2005).

Ecosystems are characteristically dynamic and subject to change, displaying small-scale variability overlaid on long-term trends (Stenseth *et al.*, 2003; Edwards *et al.*, 2010; McQuatters-Gollop, 2012). Often, change is non-linear and responses to external pressures can be abrupt, leading to sudden changes in ecosystem structure or function, known as ecological thresholds (Groffman *et al.*, 2006). Intrinsic properties of the system may accelerate change through positive feedback, pushing it to an alternative state; in this situation, the threshold is referred to as a tipping point (van Nes *et al.*, 2016). After a tipping point is reached, an ecosystem may undergo a regime shift: a sudden and persistent transition to an alternative stable state occurring across multiple trophic levels (Lees *et al.*, 2006).

The occurrence of regime shifts is well documented in aquatic and terrestrial systems (Folke *et al.*, 2004; Moellmann and Diekmann, 2012). Although the underlying mechanisms are not always clear, regime shifts are generally thought to occur in response to external pressures, such as climate change, intensive harvesting, eutrophication and the presence

of invasive species, or as a result of the internal properties of the system itself (Andersen *et al.*, 2009). Regime shifts impact on multiple trophic levels, often with severe consequences for ecosystem service provision (e.g. fish stock collapse, desertification, loss of water quality) and thus for human economies and society (Biggs *et al.*, 2009; Eason *et al.*, 2014). When an ecosystem reaches an ecological threshold, small changes in an external pressure can produce a large response in the ecosystem (Groffman *et al.*, 2006). Critically for management, reversing a regime shift may require that the pressure is reduced well below the levels that existed prior to the system reaching the tipping point (“hysteresis”) (Scheffer *et al.*, 2001; Suding *et al.*, 2004; Layer *et al.*, 2011).

1.2 Ecosystem-based Management in the Context of Change

Environmental legal instruments, such as the Marine Strategy Framework Directive (MSFD) (2008/56/EC; EU, 2008), prioritise holistic ecosystem-based management approaches. The MSFD seeks to achieve Good Environmental Status (GES) of Europe’s seas through the implementation of appropriate targets and indicators, established by individual Member States. The dynamic nature of marine ecosystems makes the determination of GES, the identification of appropriate indicators and the setting of targets particularly challenging (McQuatters-Gollop, 2012). The analysis of long-term environmental and biological datasets can support the implementation of the MSFD and other ecosystem management approaches by providing a historical context for changes in indicators, allowing natural short-term variability to be separated from long-term trends, regime shifts to be detected, and links between ecosystem components to be identified (Edwards *et al.*, 2010; McQuatters-Gollop, 2012; Boero *et al.*, 2015). The ultimate goal for researchers, managers and policymakers is to develop early warning indicators that signal an approaching threshold before it is reached, allowing management to respond to avert a regime shift (Scheffer *et al.*, 2012; Moss *et al.*, 2013; Burthe *et al.*, 2016).

1.3 Marine Ecosystem Time Series

Despite their value for supporting evidence-based decision-making, long-term datasets for the marine environment are rare relative to terrestrial systems. Data describing change across multiple trophic levels over broad spatial scales in the open ocean are particularly lacking (Edwards *et al.*, 2010). The maintenance of extended time series is threatened by irregular funding, leading to gaps in spatial and temporal coverage (Barner *et al.*, 2017). A lack of co-ordination across monitoring stations can produce variability in methodologies, sampling frequency and data quality (Boero *et al.*, 2015). Ecological data are inherently heterogeneous and complex and so even consistent reliable time series can be highly variable, can be subject to measurement error and may contain a high proportion of zero observations. Notwithstanding these challenges, advances in information technology have increased the accessibility of large datasets while developments in data management and modelling provide tools for detecting signals in complex and “noisy” data (Myers and Mertz, 1998; Zuur *et al.*, 2007; Farley *et al.*, 2018). Of particular importance are statistical modelling developments providing probabilistic algorithms capable of deciphering signal from noisy observations – methods often borrowed from and developed in the engineering field (Harvey, 1990; Clark, 2007; Aeberhard *et al.*, 2018). Increasingly, long-term datasets are directly informing marine ecosystem management, with the most notable example being the Continuous Plankton Recorder (CPR) survey, operated by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) (Brander *et al.*, 2003; Stevens *et al.*, 2006; McQuatters-Gollop, 2012). Applying advanced detection methodologies to such valuable long-term datasets represents an exciting opportunity to contribute to understanding change.

1.4 Investigating Change in the Celtic Sea Ecosystem

The Celtic Sea is a productive shelf sea ecosystem (Joint *et al.*, 2001) that has a high diversity of invertebrate and fish species and that supports many commercial fisheries (Pinnegar *et al.*, 2002; Martinez *et al.*, 2013). It is an important region for seabirds (Cox *et al.*, 2016; Lambert *et al.*, 2017; Waggitt *et al.*, 2018) and marine mammals (Berrow *et al.*, 2010;

Leeney *et al.*, 2012; Lambert *et al.*, 2017). The diverse zooplankton community of the Celtic Sea is dominated by copepods (Williams *et al.*, 1994), which have shown fluctuations in abundance and distribution over time (Beaugrand *et al.*, 2000). Fishing activity is a key anthropogenic pressure on the Celtic Sea ecosystem. Fishing efforts in the region intensified dramatically after 1970, with a peak in the 1990s and a subsequent decline (Gascuel *et al.*, 2016). The impacts of intensive harvesting are evidenced by reductions in biomass, species composition and size structure of fish populations (Pinnegar *et al.*, 2002; Guenette and Gascuel, 2012). The demand for resources and space in the Celtic Sea is increasing because of growth in offshore windfarm development, demand for sand and gravel abstraction, marine transport, tourism and leisure activity and aquaculture, and the potential expansion of oil and gas extraction (Roxburgh, 2012). Against this backdrop of competing stakeholder demands, it is imperative that policymakers and managers are equipped with knowledge of long-term changes in the Celtic Sea ecosystem and the relationships between key ecosystem components. There is a need for greater integration of available datasets describing change in the system, as well as analytical tools to identify step changes and potential regime shifts that may impact on ecosystem management targets.

In the North-East Atlantic in the mid-1990s, pronounced atmospheric and oceanographic changes coincided with increases in temperature, salinity and sea ice melting (Alheit *et al.*, 2019). This period marked the beginning of a prolonged warming period associated with anthropogenic climate change overlaid on a positive phase of the Atlantic Multi-decadal Oscillation (AMO) index (Macias *et al.*, 2013; Ting *et al.*, 2014). These changes have been associated with a regime shift in the North Sea ecosystem (Alvarez-Fernandez *et al.*, 2012; Beaugrand *et al.*, 2014), as evidenced by abrupt changes in distribution and abundance across trophic levels, from phytoplankton to top predators, in the mid-1990s (reviewed in Alheit *et al.*, 2014). Changes in other parts of the North-East Atlantic have not been as widely studied; however, there is evidence that biogeographic shifts in certain fish (Poulard and Blanchard, 2005; Coad *et al.*, 2014) and plankton (Lindley and Daykin, 2005; Valde *et al.*, 2007; Beaugrand *et al.*, 2009) species occurred during the mid-1990s across a broad area, from the Bay of

Biscay to the Celtic Sea and the area to the west of Britain and Ireland. Abrupt change across multiple trophic levels led Beaugrand and Reid (2012) and Luczak *et al.* (2011) to propose that an ecosystem regime shift occurred across the North-East Atlantic during this period. However, a finding of weak climate signals across four trophic levels (phytoplankton, zooplankton, mid-trophic-level fish and seabirds) prompted Lauria *et al.* (2012) to suggest that impacts on the Celtic Sea ecosystem are not as marked as in the North Sea, and to call for more research at regional scales.

1.5 Objectives

- Collate and integrate existing data resources for the Celtic Sea ecosystem.
- Build empirical understanding of relationships between pressures and ecosystem structure and functioning.
- Develop simulation and modelling tools to interrogate temporal trends and detect step changes or ecological tipping points.

1.6 The Study Approach

This study addressed current knowledge gaps using the following approach:

- *Data access.* Available datasets that describe the physical environment and key biological taxa across multiple trophic levels in the Celtic Sea were consolidated into a coherent database and key temporal trends were visually examined.

- *Ecosystem tools.* Analytical tools appropriate for ecological time series were developed to:
 - aggregate large complex datasets and align variables in time and space;
 - visualise broad trends across time series;
 - deal with missing data/sources of bias;
 - determine relationships with multiple interacting drivers;
 - partition endogenous and exogenous sources of variation;
 - distinguish between trends and step changes.
- *Boom/bust cycles.* Increases in jellyfish have been associated with ecosystem change and regime shifts elsewhere (Akoglu *et al.*, 2014; Hosia *et al.*, 2014). Historical time series and contemporary surveys were used to:
 - estimate biomass and evaluate the importance of key jellyfish species in the Celtic Sea;
 - examine relationships between the physical environment and jellyfish abundance/distribution;
 - investigate temporal changes in the abundance of jellyfish and their predators.
- *Ecosystem dynamics.* The statistical tools developed within the project were applied to the available data for the Celtic Sea to address specific hypotheses relating to:
 - temporal trends in growth and productivity;
 - synchronicity across species;
 - relationships with external drivers;
 - the occurrence of step changes/tipping points.

2 Consolidating Data Resources for the Celtic Sea Ecosystem

2.1 The Study Area

In the context of this study, the “Celtic Sea” generally refers to the geographic area shown by the blue box in Figure 2.1. Data from overlapping International Council for the Exploration of the Sea (ICES) management areas were included in some analyses (area 7e–7k). Widely distributed fish stocks whose distribution includes the Celtic Sea were considered. OSPAR Commission indicators for the broader “Celtic Seas ecoregion”, which includes the Celtic Sea, the Irish Sea and the Malin Shelf areas, were also included in the analyses of step changes (see Chapter 7). The same delineation was used within the MSFD to define the “Celtic Seas” area.

2.2 Data Access

Data used in the project are housed within a Microsoft Access database, linked to the R software environment (R Core Team, 2018) through the RODBC (v. 1.3-15) package (Ripley and Lapsley, 2017). Data processing and analysis were conducted using the R (R Core Team, 2018) and Python (Python Software Foundation, 2019) programming languages. Sample scripts to support the analyses presented in the report are made available through the GitHub repository (links provided within report). Data sources used within the project are detailed in Table 2.1.

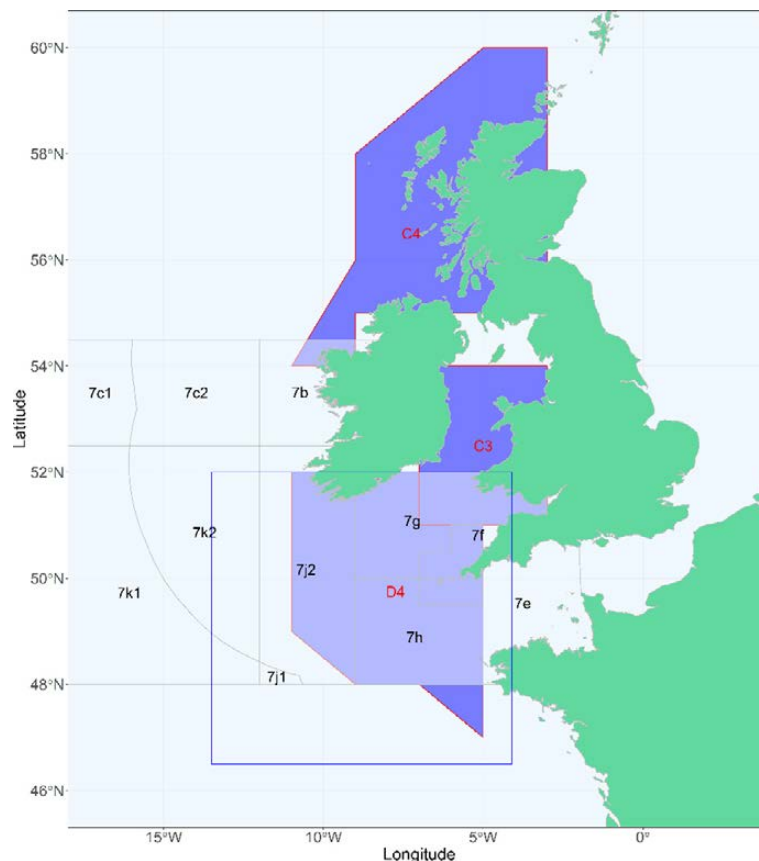


Figure 2.1. Map of the study location. The blue box indicates the area defined as the Celtic Sea for the purpose of this study. ICES fisheries management divisions are marked in grey. CPR standard areas are shaded in blue (C3, C4, D4).

Table 2.1. Details of the main data sources used within the project

Variable	Timespan	Source ^a	Citation
Mean monthly sea surface temperature (SST)	1900–2017	NOAA Extended Reconstructed Sea Surface Temperature (SST), version 5 (https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.ersst.v5.html)	Huang <i>et al.</i> (2017)
Mean monthly temperature at 39 depth intervals (5–4443 m)	1900–2018	MET Office Hadley Centre, EN4: quality controlled ocean data version: EN.4.2.1 (https://www.metoffice.gov.uk/hadobs/en4/download-en4-2-1.html)	Good <i>et al.</i> (2013)
Mean monthly salinity at 39 depth intervals (5–4443 m)			
Mean monthly wind speed	1962–2016	Cork Airport Met Éireann synoptic station (https://www.met.ie/climate/available-data/historical-data)	
Mean monthly wind direction			
AMO index	1900–2017	Detrended time series of unsmoothed monthly means (www.esrl.noaa.gov/psd/data/timeseries/AMO/)	Enfield <i>et al.</i> (2001)
North Atlantic Oscillation index	1900–2017	www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/NAO	Jones <i>et al.</i> (1997)
Sub-Polar Gyre Index		http://dx.doi.org/10.7489/1806-1	Berx and Payne (2017)
Atlantic-Iberian Biscay Irish-Ocean Physics Reanalysis (2002–2014)	2002–2014	http://marine.copernicus.eu/services-portfolio/access-to-products/?option=com_csw&view=details&product_id=IBI_REANALYSIS_PHYS_005_002	Sotillo <i>et al.</i> (2015)
Phytoplankton Colour Index	1971–2016	CPR dataset (standard area D4), SAHFOS, Plymouth (https://www.cprsurvey.org/)	SAHFOS (2017)
Abundance of gelatinous zooplankton taxa: Cnidaria, Siphonophora, Thaliacea, Doliolidae			
Abundance of selected zooplankton taxa: total eye-count copepods, <i>Calanus finmarchicus</i> , <i>Calanus helgolandicus</i> , <i>Paracalanus</i> , <i>Pseudocalanus</i> , Hyperitidae, Euphausiacea	1958–2014	CPR dataset (standard area D4), SAHFOS, Plymouth (https://www.cprsurvey.org/)	SAHFOS (2017)
OSPAR PH2 indices of total copepod abundance	1958–2012	CPR data processed as part of the OSPAR Intermediate Assessment 2017	SAHFOS (2012), OSPAR (2017a)
Estimates of recruitment, spawning stock biomass and weight at age for selected commercial fish species	1958–2018 (varies by species)	ICES stock assessment reports and ICES database (http://standardgraphs.ices.dk/stockList.aspx)	ICES (2017a,b,c,d)
Individual length at age for Celtic Sea herring	1958–2012	Marine Institute dataset held by D. Brophy	
Individual otolith growth chronologies for plaice, herring and haddock	1985–2014 (varies by species)	Data generated within the project held by D. Brophy	
Sightings per minute of observation for ocean sunfish (<i>Mola mola</i>)	1971–2017	Cape Clear Bird Observatory bird migration monitoring programme. Data held by T. Doyle	
Sightings per minute of observation for leatherback turtles (<i>Dermochelys coriacea</i>)			
Sightings per minute of observation for basking sharks (<i>Cetorhinus maximus</i>)			
Estimates of abundance and breeding success for selected sites for guillemot, razorbill and kittiwake, standardised for variation between sites	1985–2018	Joint Nature Conservation Committee (JNCC) Seabird Monitoring Programme database (http://jncc.defra.gov.uk/smp/)	
OSPAR indicator B3 – marine bird breeding success or failure	1986–2015	OSPAR Intermediate Assessment 2017	OSPAR (2017b)
OSPAR indicator B1 – marine bird abundance	1991–2015	OSPAR Intermediate Assessment 2017	OSPAR (2017c)

^aAll URLs accessed 16 April 2020.

2.3 Broad Temporal Trends in the Celtic Sea Ecosystem

2.3.1 *The physical environment*

Broad temporal trends in the physical environment are visualised in Figure 2.2 and briefly described below:

- **Temperature.** Sea surface temperature (SST) in the Celtic Sea shows an increasing trend since 1900, with a sharp rise in the rate of increase after about 1990. Water column temperatures and the mean annual latitude of the 13°C isotherm reflect this warming trend.
- **Salinity.** There was a slight increase in salinities after 1990, which was most pronounced at depth, suggesting changes in the movement of open water masses. Salinity at a depth of 200m showed a sharp decline after 2012, which was not evident at shallower depths.
- **Wind.** Wind conditions fluctuated across the period examined. The strength of the prevailing south-west winds appeared to cycle, increasing from the 1960s to the mid-1980s, then decreasing until 2000 and increasing towards the end of the time series. Across the period examined there was a decrease in the variability of the wind direction: the prevailing south-west winds became more frequent. An extreme value in the time series of south-west winds (total count in hours) reflected a period of storminess in February 1990.
- **Climatic indices.** Three broadscale climatic indices, reflecting conditions across the Atlantic, were included in the analyses: the AMO, the North Atlantic Oscillation (NAO) and the Sub-Polar Gyre (SPG) Index.

The AMO is the 10-year running mean of North Atlantic SST anomalies, detrended to remove the effect of anthropogenic warming (Enfield *et al.*, 2001). The AMO moved from a negative to a positive phase in the mid-1920s, returning to a negative phase in the 1960s and subsequently increasing. AMO conditions have been positive since the late 1990s. As well as reflecting temperature conditions, oscillations between warm and cold phases of the AMO are associated with changes in ocean circulation patterns and advection of water masses (Alheit *et al.*, 2014).

The NAO (the difference in the atmospheric pressure anomalies between the Azores and Iceland; Jones *et al.*, 1997) was in a negative phase in the 1930s, 1960s and 2000s. An extreme low in 2010 reflected unusually cold conditions in Europe in the winter of 2009/2010. The index increased subsequently and is currently in a positive phase. A positive NAO is linked to higher temperatures and strong winter storms in the North-East Atlantic, whereas colder, calmer conditions are observed during negative phases (Hurrell, 1995).

The SPG is a cyclonic gyre encompassing the North Atlantic, East Greenland and Labrador Currents. Changes in the extent and strength of the SPG have been linked to changes in circulation and marine ecosystem productivity. Since the mid-1990s, the SPG has declined steeply, reflecting a contraction and weakening of the gyre.

2.3.2 *Plankton communities*

Indices of abundance for phytoplankton and various zooplankton groups were obtained from the CPR database maintained by SAHFOS (see details in Table 2.1). Broad temporal trends are displayed in Figure 2.3 and described briefly below:

- **Phytoplankton.** The Phytoplankton Colour Index (PCI) provides a semi-quantitative index of phytoplankton abundance, based on the greenness of the silk mesh on which the sample is collected. The four PCI categories (no green, NG; very pale green, VPG; pale green, PG; and green, G) have been assigned numerical values on a ratio scale corresponding to relative chlorophyll a concentrations in acetone extracts from the silk mesh (NG=0, VPG=1, PG=2 and G=6.5) (Colebrook, 1979). These categories correspond to mean chlorophyll a concentrations in each sample (10 nautical miles of tow) of 0.16 µg for NG, 5.05 µg for VPG, 11.94 µg for PG and 23.16 µg for G (Raitsos *et al.*, 2013). Analysis of PCI values of samples from CPR area D4 (Celtic Sea) show an increase in estimated chlorophyll a concentration after 1978, with the proportion of samples in category 1 (VPG) increasing relative to the proportion of samples in category 0 (NG). This suggests an overall increase in phytoplankton abundance over that period.

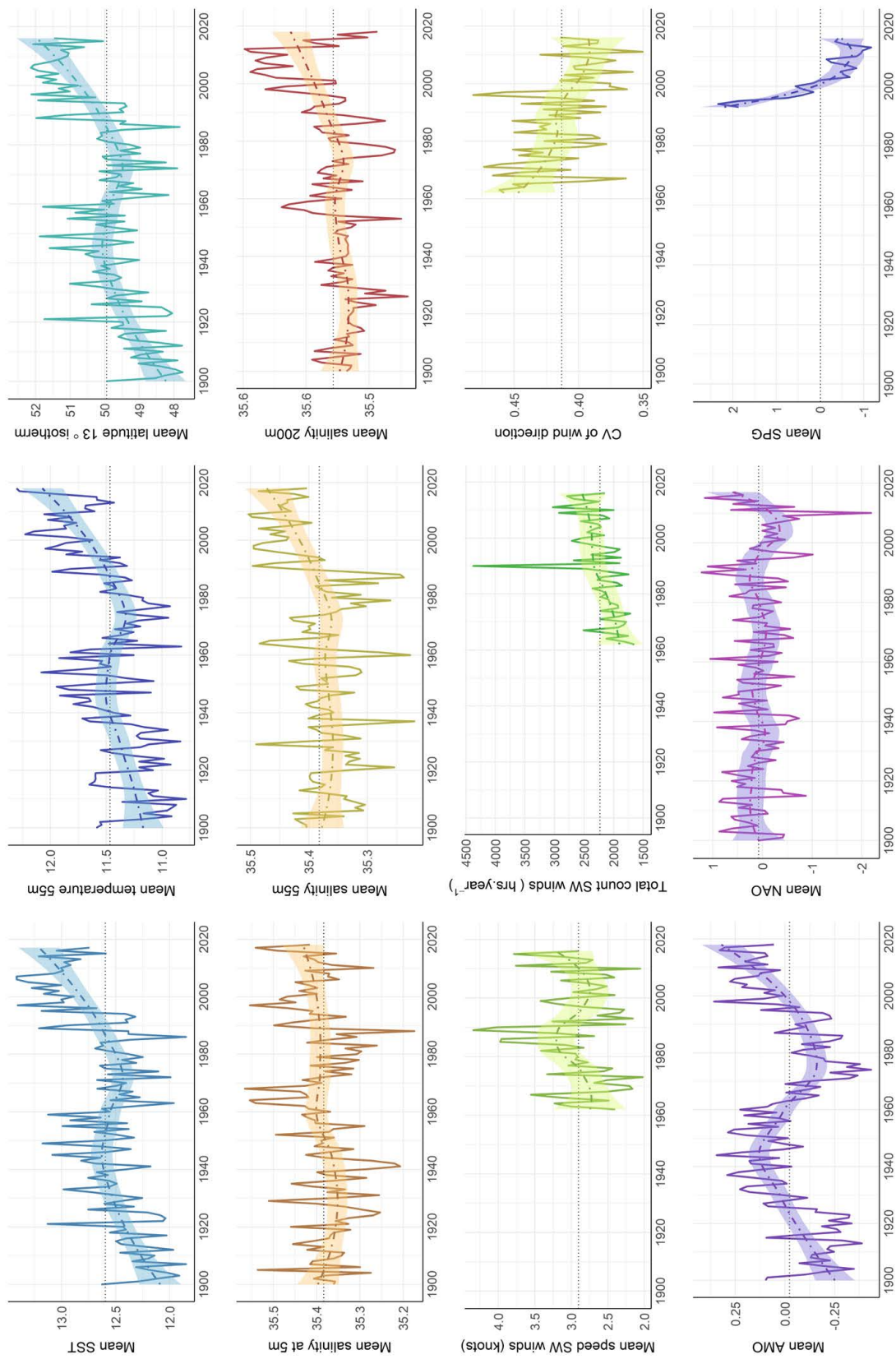


Figure 2.2. Time series describing the physical environment in the Celtic Sea, 1900–2018. Units: temperature, °C; salinity, PSU (practical salinity unit); latitude, °. The dotted horizontal line indicates the mean of each time series. The filled coloured lines show the observed trends. A less smoother (dashed coloured lines with shaded area to represent the 95% confidence limits) is fit to each time series to aid visualisation of broad trends. CV, coefficient of variation. Data sources are detailed in Table 2.1.

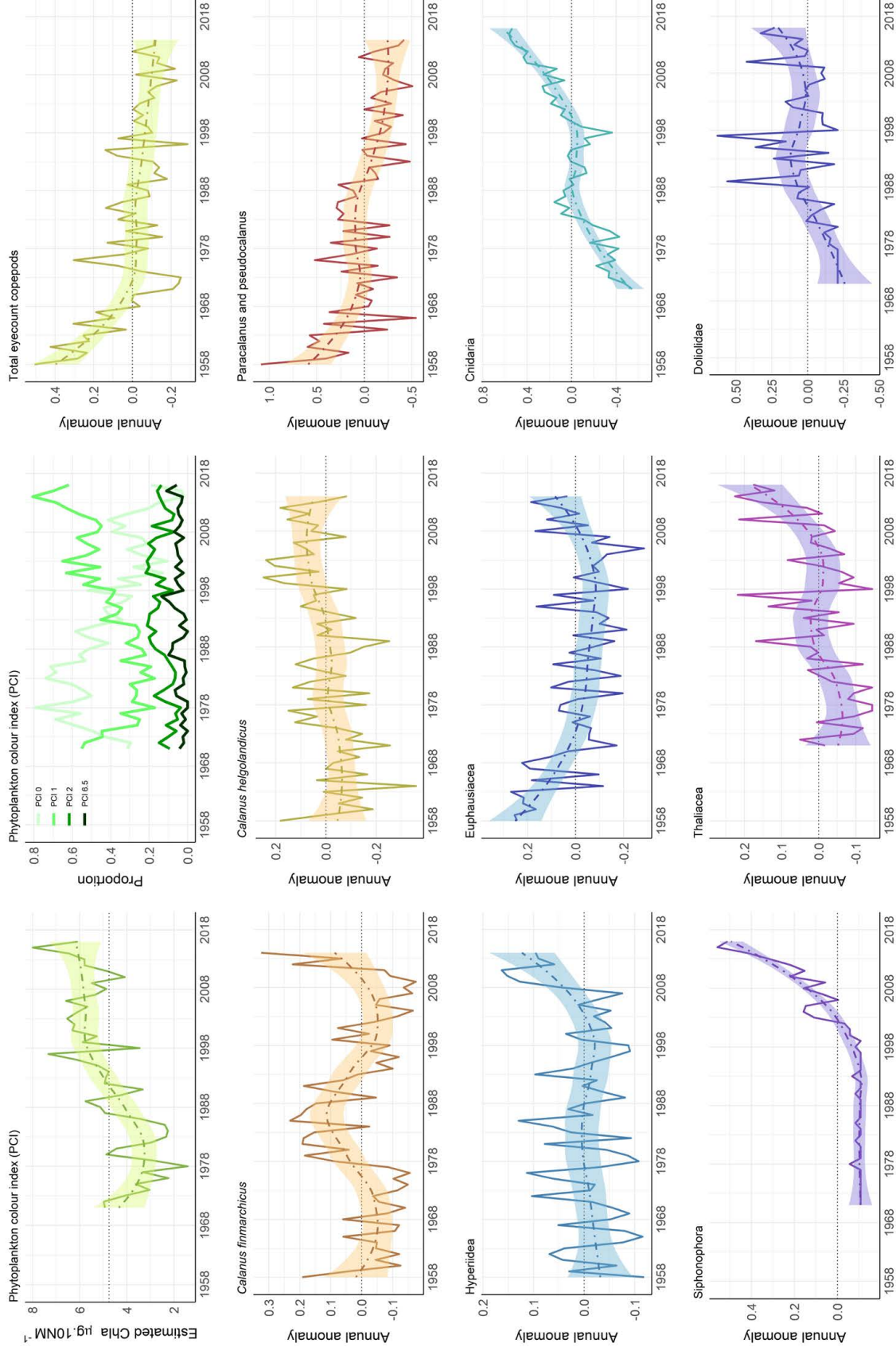


Figure 2.3. Time series describing planktonic communities in the Celtic Sea, 1958–2016. The dotted horizontal line indicates the mean of each time series. The filled coloured lines show the observed trends. A loess smoother (dashed coloured lines with shaded area to represent the 95% confidence limits) is fit to each time series to aid visualisation of broad trends. Data sources are detailed in Table 2.1.

- **Zooplankton.** Monthly mean abundance estimates (numbers per sample) were seasonally detrended and annual abundance anomalies were calculated across selected zooplankton groups:
 - Copepods. The abundance of copepods of >2 mm (total eye-count copepods) showed a sharp decrease during the 1960s and declined further after 1990. This group includes the cold water species *Calanus finmarchicus*, which declined in abundance from the late 1980s before increasing again after 2008. The warm water species *C. helgolandicus* is also included, which has shown a slight increase in abundance since 1990. The abundance of *Paracalanus* and *Pseudocalanus* species declined from the late 1980s.
 - Malacostraca. Trends were examined across two groups: the Hyperiidea (a suborder of the order Amphipoda) and Euphausiacea (krill). The abundance of Hyperiidea showed an increase in the last 3 years of the time series (2011–2014) but otherwise fluctuated around the time series mean. The abundance of Euphausiacea declined during the 1960s, with a slight increase towards the end of the time series.
 - Gelatinous zooplankton. Abundance anomalies across several groups of gelatinous zooplankton showed pronounced increases across the time period examined. The abundance of Cnidaria increased during the 1970s and 1980s and from 1998 to 2016. The Siphonophora (an order within the phylum Cnidaria) were present in very low abundance before 2000 and showed a marked increase after that. The abundance of organisms in the class Thaliacea increased during the 2000s. The Doliolidae (a family of tunicates within the order Doliolida and class Thaliacea) showed increases in abundance in the 1980s and in the period 2008–2016. Increases were also observed in the Salpidae family during the 1980s and from 2000 to 2016 (not shown here but included in the analysis in Chapter 7).

2.3.3 Fisheries

Data describing trends across 17 commercial fish stocks (14 species) were obtained from the ICES stock assessment database and working group

reports (Table 2.2). These data included estimates of abundance (spawning stock biomass, SSB; total stock biomass, TSB; number of recruits), growth (weight at age, length at age) and fishing mortality (F). Broad temporal trends for four species are shown in Figure 2.4.

- **Herring.** SSB and recruitment trends show the dramatic decline in the Celtic Sea herring population that occurred in the 1970s and led to the collapse of the fishery. Abundance subsequently fluctuated, returning to low levels in the early 2000s, with some recovery in the following decade. Growth rates increased during the 1960s and 1970s and then declined markedly during the 1980s, without recovering; this is apparent in the mean weight at age 3 trend.
- **Cod.** Recruitment, SSB and growth rates have been declining since the 1990s.
- **Haddock.** This stock shows strong fluctuations in recruitment and stock size, with a large recruitment pulse in 2009. Growth rates show a decline during the late 1990s and early 2000s followed by an increase in more recent years.
- **Plaice (7j–k).** There was a marked decline in SSB and recruitment during the mid-1990s. The trend in mean weight at age 5 indicates some decline in growth during the same period.

2.3.4 Seabirds

Colony count data and estimates of breeding success were obtained from the Seabird Monitoring Programme database co-ordinated by the Joint Nature Conservation Committee (JNCC). Trends for three species (common guillemot, kittiwake and razorbill) are shown in Figure 2.5. Count data (individuals on land for guillemot and razorbill; occupied nests for kittiwake) were obtained from six coastal sites in the Dyfed region of south-west Wales (Caldey Island, St Margaret's Island, Skomer Island, Skokholm Island, Ramsey Island, Saddle Point). Counts were standardised for variation between sites using a negative binomial generalised linear model. Estimates of breeding success (fledglings per nest/pair) were obtained from all available coastal sites in Cornwall, Devon and Dyfed. To account for possible effects of density dependence, breeding success estimates were standardised using a generalised linear model. Trends in abundance and breeding success are shown in Figure 2.5.

Table 2.2. Fish stocks included in the project database and analysis

	ICES stock code	Species	ICES subarea/division	ICES working group
Stocks in ICES subareas overlapping with the Celtic Sea	her_27_irls	Herring (<i>Clupea harengus</i>)	7g–h and 7j–k	Herring Assessment Working Group (HAWG)
	cod.27.7e-k	Cod (<i>Gadus morhua</i>)	7e–k	Working Group for the Celtic Seas Ecoregion (WGCSE)
	had_27_7b-k	Haddock (<i>Melanogrammus aeglefinus</i>)	7b–k	WGCSE
	ple.27.7e	Plaice (<i>Pleuronectes platessa</i>)	7e	WGCSE
	ple.27.7fg		7f–g	WGCSE
	ple.27.7h-k		7h–k	WGCSE
	sol.27.7fg	Sole (<i>Solea solea</i>)	7f–g	WGCSE
	sol.27.7e		7e	WGCSE
	whg_27_7b-ce-k	Whiting (<i>Merlangius merlangus</i>)	7b–c and 7e–k	WGCSE
	meg_27_7b-k8abd	Megrim (<i>Lepidorhombus whiffiagonis</i>)	7b–k, 8a–b and 8d	Working Group for the Bay of Biscay and the Iberian Waters Ecoregion (WGBIE)
mon.27.78abd	White anglerfish (<i>Lophius piscatorius</i>)	7, 8a–b, 8d	WGBIE	
Widely distributed stocks occurring in the Celtic Sea	hke_27_3a46–8abd_InRS	Hake (<i>Merluccius merluccius</i>)	4, 6 and 7, 3a, 8a–b, 8d	WGBIE
	bss_27_4bc7ad-h	Sea bass (<i>Dicentrarchus labrax</i>)	4b-c, 7a and 7d–h	WGCSE
	whb.27.1–91214	Blue whiting (<i>Micromesistius poutassou</i>)	1–9, 12 and 14	Working Group on Widely Distributed Stocks (WGWIDE)
	hom_27_2a4a5b6a7a-ce-k8	Horse mackerel (<i>Trachurus trachurus</i>)	8, 2a, 4a, 5b, 6a, 7a–c and 7e–k	WGWIDE
	mac_27_nea_InRS	Mackerel (<i>Scomber scombrus</i>)	1–8, 14, 9a	WGWIDE

- *Common guillemot*. Abundance showed a steady increase from 1985 to 2018. Breeding success showed some decline during the 2000s.
- *Kittiwake*. Abundance declined across the time period examined whereas breeding success declined during the 2000s.
- *Razorbill*. Abundance increased after 2008 whereas breeding success declined.

2.3.5 Large surface feeding planktivores

Sightings of sunfish, leatherback turtles and basking shark are recorded by observers at Cape Clear Bird Observatory as a part of a bird migration monitoring programme. Temporal trends in sightings are shown in Figure 2.6.

- *Basking shark*. Sightings fluctuated and were most frequent from 2008 to 2016.

- *Leatherback turtle*. Sightings were elevated during the 1990s relative to the rest of the time series.
- *Sunfish*. The incidence of sightings appeared to increase from the mid-1990s and was particularly high during the early 2000s.

2.4 Conclusion

The project database brings together a diverse set of data describing the biotic and abiotic elements of the Celtic Sea ecosystem. This is a valuable resource for exploring ecological change, bringing added value to previously collected data and integrating data generated within the project. Initial visual exploration of the data reveals that there has been considerable change in the physical environment and across multiple trophic levels in the Celtic Sea. The extent to which these changes are interconnected is explored in the subsequent chapters.

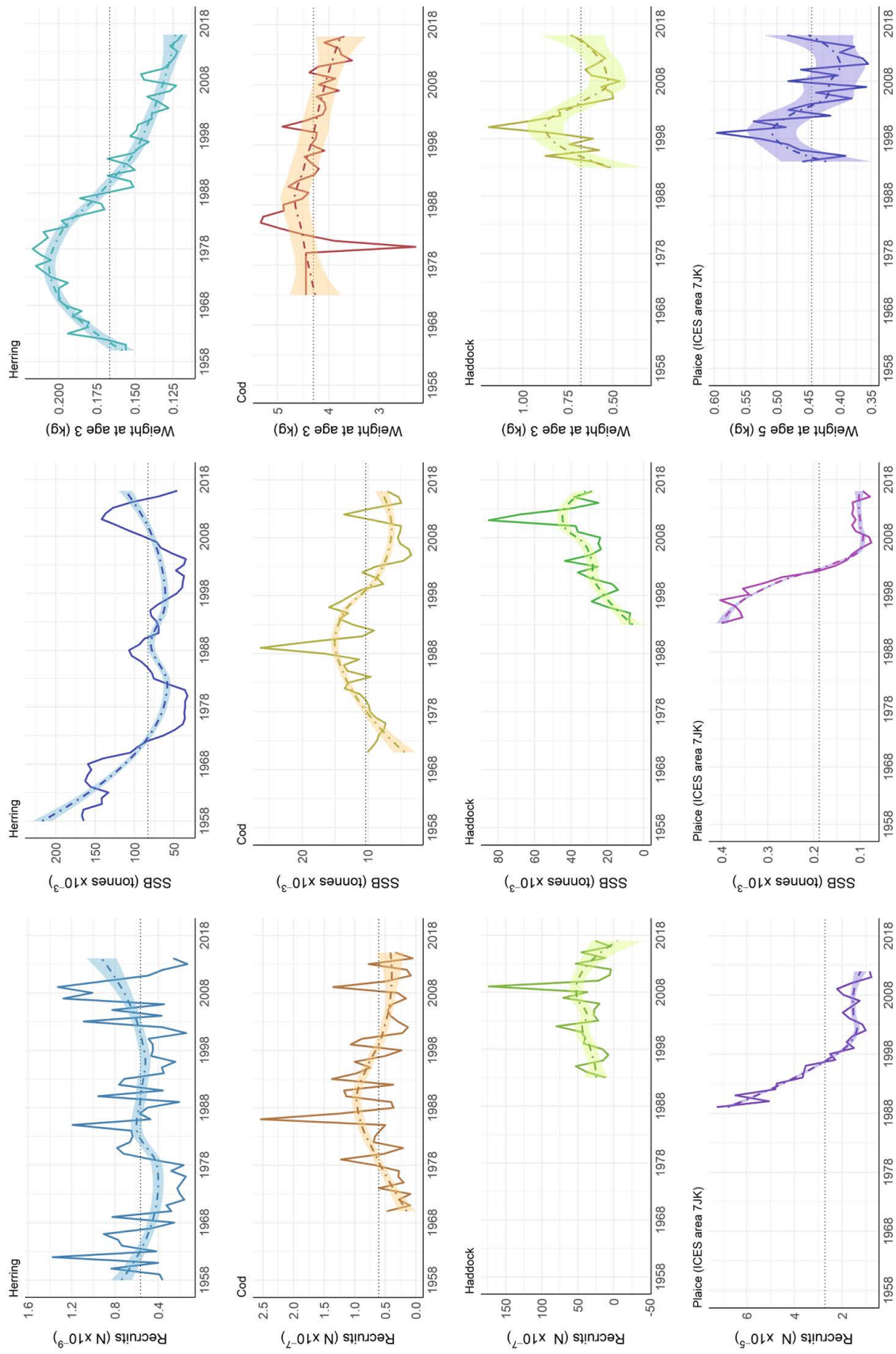


Figure 2.4. Time series describing exploited fish populations in the Celtic Sea, 1958–2016. The dotted horizontal line indicates the mean of each time series. The filled coloured lines show the observed trends. A loess smoother (dashed coloured lines with shaded area to represent the 95% confidence limits) is fit to each time series to aid visualisation of broad trends. Data sources are detailed in Table 2.1.

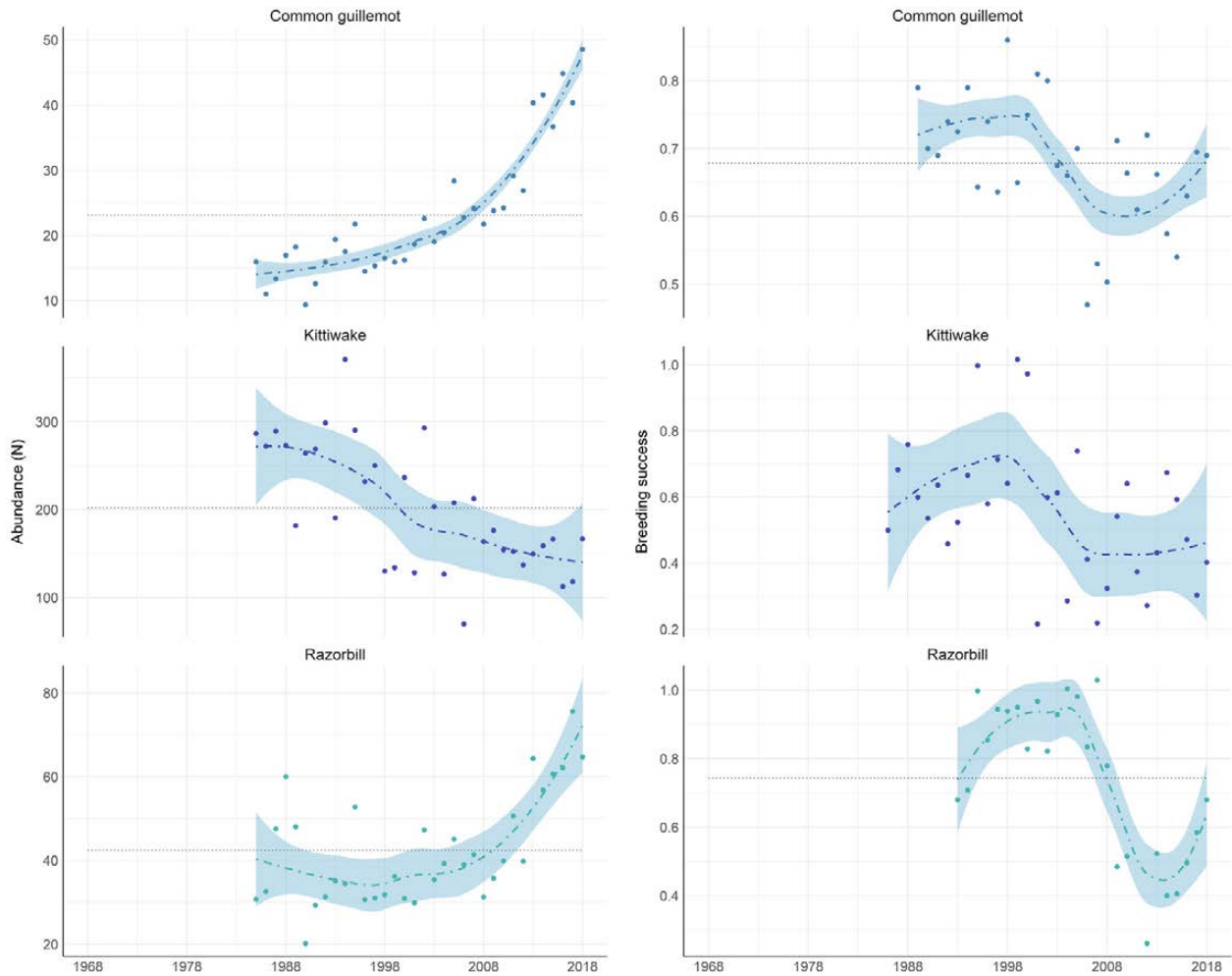


Figure 2.5. Time series describing trends in seabird populations in the Celtic Sea from the JNCC Seabird Monitoring Programme, 1968–2018. Points indicate mean values, standardised for variation between sites using a generalised linear model. Counts are of individuals on land (guillemot and razorbill) or of occupied nests (kittiwake). Breeding success is the estimated number of fledglings per breeding pair or nest. The dotted horizontal line indicates the mean of each time series. A loess smoother (dashed coloured lines with shaded area to represent the 95% confidence limits) is fit to each time series to aid visualisation of broad trends. Data sources are detailed in Table 2.1.

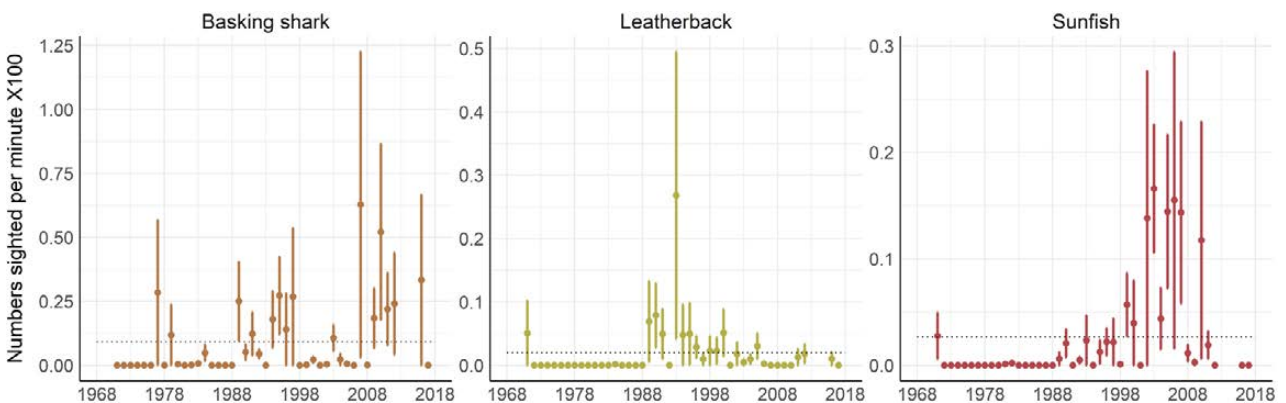


Figure 2.6. Time series of sightings of large planktivores at the water surface from Cape Clear Bird Observatory. Data sources are detailed in Table 2.1.

3 Ecosystem Tools: Statistical Approaches to Understanding Ecosystem Change

The statistical tools developed and applied in the project are outlined briefly in this chapter. The aim is not to provide a comprehensive, technical description of the methodology, but to give a conceptual overview of the benefits of each approach for dealing with ecological time series data. Relevant packages and supporting literature are identified.

3.1 Estimating Common Trends in Multiple Time Series

When investigating ecosystem change it is necessary to examine trends across multiple ecosystem components and look for commonality across those trends. Dynamic factor analysis (DFA) is a dimension reduction technique that is appropriate for the analysis of multivariate time series data (Zuur *et al.*, 2003a,b). It can be used to identify underlying common patterns between a relatively large set of time series (Harvey, 1990). These patterns can reflect common trends or seasonal cycles and they can be related to explanatory variables. DFA aims to reduce variation in a set of n observed time series using linear combinations of a set of m hidden trends, where $m \ll n$. The aim is to choose the smallest possible number of trends without losing too much information. Loading factors are estimated for each time series, which reflect the contribution of the time series to each trend. The main principle of DFA is similar to that of principle component analysis or factor analysis, with axes being restricted to be latent smoothing functions over time. Unlike other time series techniques (e.g. autoregressive integrated moving average, ARIMA), DFA can analyse short and non-stationary time series that contain missing values. This makes DFA particularly useful for ecological series that usually possess all of these properties. DFA is applied to the analysis of weight-at-age trends across multiple fish species in section 6.2 using the MARSS package in R (Holmes *et al.*, 2012, 2018). For further model specification see <https://nwfsc-timeseries.github.io/atsa-labs/sec-dfa-intro.html>.

3.2 Modelling Complex Relationships between Drivers and the Ecological Response

Ecological systems are typically influenced by multiple drivers that may combine cumulatively or interactively (Crain *et al.*, 2008) and often exert threshold or non-linear responses (Sugihara and May, 1990; Griffen *et al.*, 2016). When identifying drivers of ecological change it is necessary to look beyond correlation with individual drivers and account for additive and multiplicative effects while considering underlying mechanisms.

Parametric regression models allow for non-linear relationships but may fail to detect deep interactive effects or non-linear or abrupt changes. Ensemble methods replace a single model with a collection of simple additive regression model predictions that are averaged to give a more robust estimate of the response (Hastie *et al.*, 2009). Within ensemble methods, gradient boosting regression trees (GBRTs) form a supervised machine learning algorithm, which allows for complex non-linear interactions between environmental drivers (Friedman, 2001). Unlike parametric regression models, GBRTs do not require the data distribution to meet any assumptions. GBRTs use an algorithmic model to learn the relationship between the response variable and the covariates and to find patterns. The objective of the algorithmic model is to minimise mean squared error (MSE), by training each successive tree on the errors left over by the collection of earlier trees.

The increased availability of complex environmental datasets has stimulated interest in using machine learning techniques to explain patterns in ecological data (Olden *et al.*, 2008; Peters *et al.*, 2014). These developments are accompanied by ongoing debate about the relative merits of a hypothesis-driven compared with a data-intensive approach (Elliott *et al.*, 2016). However, when carefully applied, machine learning approaches can complement hypothesis-based research to elucidate complex non-linear

relationships in ecological systems (Muttill and Chau, 2007; Kelling *et al.*, 2009; Peters *et al.*, 2014) and can improve predictive performance relative to generalised additive models (Leathwick *et al.*, 2006). GBRTs are used here to disentangle the effects of multiple drivers on herring growth (see section 6.1). Methods developed by Elith *et al.* (2008) were modified within Python (Python Software Foundation, 2019).

3.3 Detecting Change in Highly Variable Time Series

Species that show a clumped distribution are sparse in some areas and highly abundant in others. Count data that are used to estimate abundance are therefore often highly variable (overdispersion) and may contain a high proportion of zeros (zero inflation). Overdispersed and zero-inflated data violate the assumptions of parametric models, making it difficult to detect trends in abundance and to model relationships with explanatory variables.

A hurdle model is a type of two-part model commonly used for dealing with zero-inflated and overdispersed data and is typically applied to count data. The first part of the model treats the counts as a binary response – presence or absence – with a Bernoulli probability governing the binary outcome of whether a variable has a zero or a positive realisation. The second part of the model deals with the positive observations as a continuous variable; if the realisation is positive, the hurdle is crossed and the conditional gamma distribution of the positives is governed by a truncated-at-zero model (Cragg, 1971). Hurdle models differ from other classes of zero-inflated models in that zeros and non-zeros are modelled as two separate processes. This allows them to model the zeros and non-zeros with different predictors or different roles of the same predictors (Cunningham and Lindenmayer, 2005). The hurdle model has been shown to perform well compared with other modelling approaches, such as Poisson, negative binomial, quasi-Poisson and zero-inflated Poisson approaches (Potts and Elith, 2006), when dealing with zero-inflated species abundance data. In section 4.2, a hurdle model is applied to sunfish sightings data to establish if there has been a real increase in abundance over time and to investigate relationships between the occurrence/abundance of sunfish and the environment/feeding conditions.

3.4 Isolating Responses to External Drivers from Endogenous Effects and Sources of Bias

Temporal variation in population attributes such as abundance or growth may partly reflect a response to an external driver (e.g. temperature) but can also be attributed to endogenous sources of variation (e.g. the age structure of the population) and to measurement error and bias (e.g. variation in the detectability of the species). Mixed-effects models that include both fixed and random effects are useful for partitioning variance due to these factors and for isolating an annual random effect that represents the influence of an external driver (or other unmeasured sources of variation). Random effects are conditional modes calculated as the difference between the average predicted response for a given set of fixed-effect values and the response predicted for a particular year. Once isolated, the annual signal in the random effect can be analysed as a time series to investigate relationships with environmental covariates. The mixed-effects modelling framework has many important and diverse applications in fisheries science and ecology (Thorson and Minto, 2014). Here, the approach is applied in two contexts. In section 4.2, mixed-effect models are used to standardise sunfish sightings per minute of observation for factors that cause the detectability of the organism to vary (e.g. weather conditions, number of observers). The annual signal extracted in the year random effects is then modelled as a function of the environmental covariates that are expected to be associated with abundance (e.g. temperature and abundance of prey organisms). In section 6.3, a mixed-effects modelling framework developed by Morrongiello and Thresher (2014) is modified to explore endogenous (e.g. age, sex) and exogenous (e.g. temperature, feeding conditions) sources of variation in growth rates (measured in otolith annuli). A random effect is also included to account for non-independence of repeated growth measurements from the same individuals.

3.5 Identifying Change Points in Ecological Time Series

A change point is a statistical property of a time series, characterised by a sudden or step-like increase or decrease in the level, trend or variance of the measured variable (Reeves *et al.*, 2007; Spencer

et al., 2012). When synchronous change points are observed across multiple time series that represent a broad range of ecosystem components, a regime shift may be identified – although there is no single definitive approach to determining whether or not a regime shift has occurred (Lees *et al.*, 2006). Many statistical methods are available to identify change points; these vary in their underlying assumptions, their sensitivity and the situations in which they can be applied (Reeves *et al.*, 2007). Some of the methods that are most widely used to identify ecological regime shifts do not account for issues of autocorrelation (time series measurements are not independent observations) and multiple testing (every point in the time series must be tested for the occurrence of a change point) and may have an inflated rate of false positives (detecting a step change when none has occurred) relative to more statistically robust approaches (Spencer *et al.*, 2012). Theoretical and experimental studies have demonstrated that change points in ecological time series are often preceded by increases in variance and autocorrelation, a phenomenon known as “critical slowing down”, and these properties have been proposed as potential

“early warning indicators” (EWIs) of impending regime shifts (Scheffer *et al.*, 2009; Pace *et al.*, 2013). However, this approach appears to have limited application in a “real world” ecosystem setting (Hastings and Wysham, 2010; Perretti and Munch, 2012; Krkosek and Drake, 2014); an analysis of 126 ecological time series from across 55 taxa found that EWIs were only rarely associated with change points (Burthe *et al.*, 2016).

In this study, a Bayesian online change-point detection (BOCPD) algorithm (Adams and MacKay, 2007) was applied across multiple time series describing the Celtic Sea ecosystem to identify change points in the level and standard deviation of the measured variables. The approach is fully described in Chapter 7. It has advantages over other approaches that are commonly applied to the detection of ecological regime shifts in that the Bayesian framework robustly deals with multiple testing and explicitly accounts for uncertainty. The approach can be applied online, removing the need to refit the model as new data become available and providing a means for early detection of change points.

4 Boom–Bust Cycles: Quantifying Spatial and Temporal Variability in Jellyfish and their Predators in the Celtic Sea

In this chapter a short-term contemporary field study of the gelatinous zooplankton community in the Celtic Sea is presented, alongside an analysis of extended time series describing the abundance of gelatinous zooplankton taxa and large planktivorous surface feeders (sunfish, basking sharks and leatherback turtles). This work provides insight into the trophic importance of jellyfish in the Celtic Sea and the influence of the physical environment on distribution and abundance, as well as temporal trends in the abundance of jellyfish and their predators.

4.1 Distinct Gelatinous Zooplankton Communities across a Dynamic Shelf Sea

This study is described in full in Haberlin *et al.* (2019). A synopsis of the study and the main findings in relation to gelatinous zooplankton community structure and biomass is presented below. The structure of the broader zooplankton community is also described in the full manuscript.

4.1.1 Background

Gelatinous zooplankton can exert substantial top-down pressure on prey species and, on occasion, intense blooms of particular species can cause a trophic cascade, transforming an entire ecosystem into a less desirable state, at least from a human perspective (Greve, 1994; Kideys, 2002; Kideys and Romanova, 2003). Just as important is the role of gelatinous zooplankton as competitors, whereby their rapid growth potentially allows them to outcompete planktivorous fish species (Brodeur *et al.*, 2008; Ruzicka *et al.*, 2016). Gelatinous zooplankton are consumed by a substantial number of marine predators (Hays *et al.*, 2018), including important commercial fish species (Arai, 1988; Purcell and Arai, 2001), while trophic interactions between gelatinous taxa can alter the flow of biomass through pelagic food webs (Baxter *et al.*, 2010). The structure of

gelatinous zooplankton communities is strongly influenced by local hydrography and physical forcing; understanding these relationships is important in order to predict potential ecosystem changes and be able to sustainably exploit marine ecosystems.

Although a large body of research has described how fronts, hydrographic boundaries and different water masses (e.g. mixed vs stratified) influence phytoplankton and zooplankton communities, comparatively few studies have investigated their influence on gelatinous zooplankton communities. This field study investigated the gelatinous zooplankton community in the region of the Celtic Sea front (CSF) and examined the influence of hydrography on community structure and biomass.

4.1.2 Sampling

The study site is characterised by a strong oceanic influence and profound seasonal changes. Depths range from approximately 40 m to 110 m, with the deepest region lying approximately south-west of St George's Channel, which marks the geographic boundary between the Celtic Sea and the Irish Sea (Figure 4.1a). The research cruise was undertaken aboard the *R.V. Prince Madog* between 13 and 17 July 2015, at which time the CSF had become well established (Figure 4.1b), and zooplankton sampling was carried out along five transects within the study area. In total, 49 zooplankton samples were collected, every 6 km, using a 1-m-diameter, 270- μ m-mesh plankton net with a flowmeter. At each station, the plankton net was towed vertically from a depth of 50 m to the surface at a velocity of approximately 1 m s^{-1} .

4.1.3 Results

In total 21 gelatinous taxa were identified from the 49 samples, including 17 hydromedusae, three ctenophores and one scyphozoan species. Several hydrozoans were relatively common across the survey area, with *Aglantha digitale*, *Clytia hemisphaerica*,

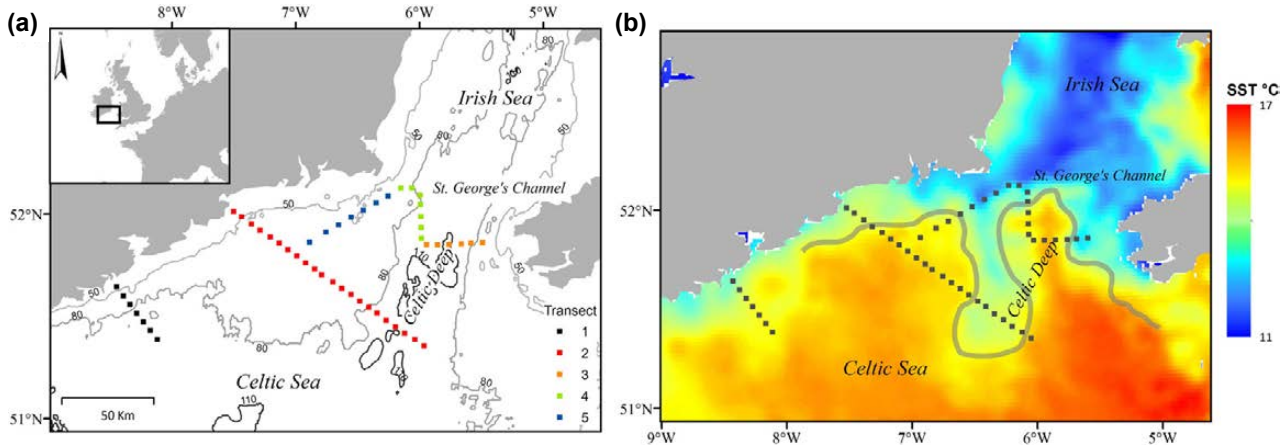


Figure 4.1. (a) Plankton survey sampling location in the north-eastern Celtic Sea with the five transects and topographic features; (b) mean SST in mid-July (8–16 July) 2015 with the CSF marked by the grey line. Source: Haberlin et al. (2019). This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

Agalma elegans, *Nanomia bijuga*, *Lizzia blondina* and *Leuckartiara octona* all recorded at >60% of stations (Figure 4.2). *A. digitale* and *L. blondina* were, by an order of magnitude, the dominant hydromedusae throughout the survey area, reaching a mean of $200 \pm 247 \text{ m}^{-3}$ and $88 \pm 159 \text{ m}^{-3}$, respectively, and being present at 80% and 75% of stations, respectively. Of the ctenophores, *Pleurobrachia pileus* was the most widespread, being present at 94% of stations, with a mean abundance of $0.25 \pm 0.23 \text{ m}^{-3}$.

Hierarchical clustering and non-metric multidimensional scaling (NMDS) ordination indicated that there were two distinct and significantly different gelatinous zooplankton communities [analysis of similarities (ANOSIM), $r=0.72$, $p<0.001$] across the survey area (Figure 4.2). The first community included stations in the warmer stratified water of the Celtic Sea lying to the west of the CSF meander. The second community included all of the stations in the cooler mixed water within the meander and contiguous with the Irish Sea, and the stations over the warm stratified Celtic Deep region (see Figure 4.1a). The total gelatinous biomass was significantly higher in the warm water gelatinous community ($2.08 \pm 1.72 \text{ mg C m}^{-3}$) than in the cold water community ($1.33 \pm 1.19 \text{ mg C m}^{-3}$). Multivariate analysis indicated that the best correlation between the environmental parameters and the community matrix was achieved with just depth and the temperature at 50-m depth included (Mantel, $r=0.53$, $p<0.001$). Including fluorescence at 50 m, the vertical temperature

difference and the vertical density difference did not substantially change the r value. There was no evidence to suggest that the gelatinous abundance of biomass was enhanced in the vicinity of the CSF.

4.1.4 Conclusions

Our results identified two distinct gelatinous communities, partially separated by the CSF, which supports previous work on other taxa, e.g. large scyphozoans (Williams *et al.*, 1994; Doyle *et al.*, 2007; McGinty *et al.*, 2014). This research suggests that the ultimate driver of these two gelatinous communities is the interaction between the underlying topography, tidal forcing and surface heating, which creates a dynamic front between two distinct water masses. Finally, this research has identified physonect siphonophores as a significant component of the gelatinous community in the warm stratified water of the Celtic Sea, which merits further attention.

4.2 Examining Temporal Changes in the Occurrence and Abundance of Sunfish

4.2.1 Background

Recent studies report surprisingly high densities of the ocean sunfish (*Mola mola*, hereafter sunfish) in the North-East Atlantic (Pálsson and Astthorsson, 2016; Breen *et al.*, 2017; Gremillet *et al.*, 2017). Incidental

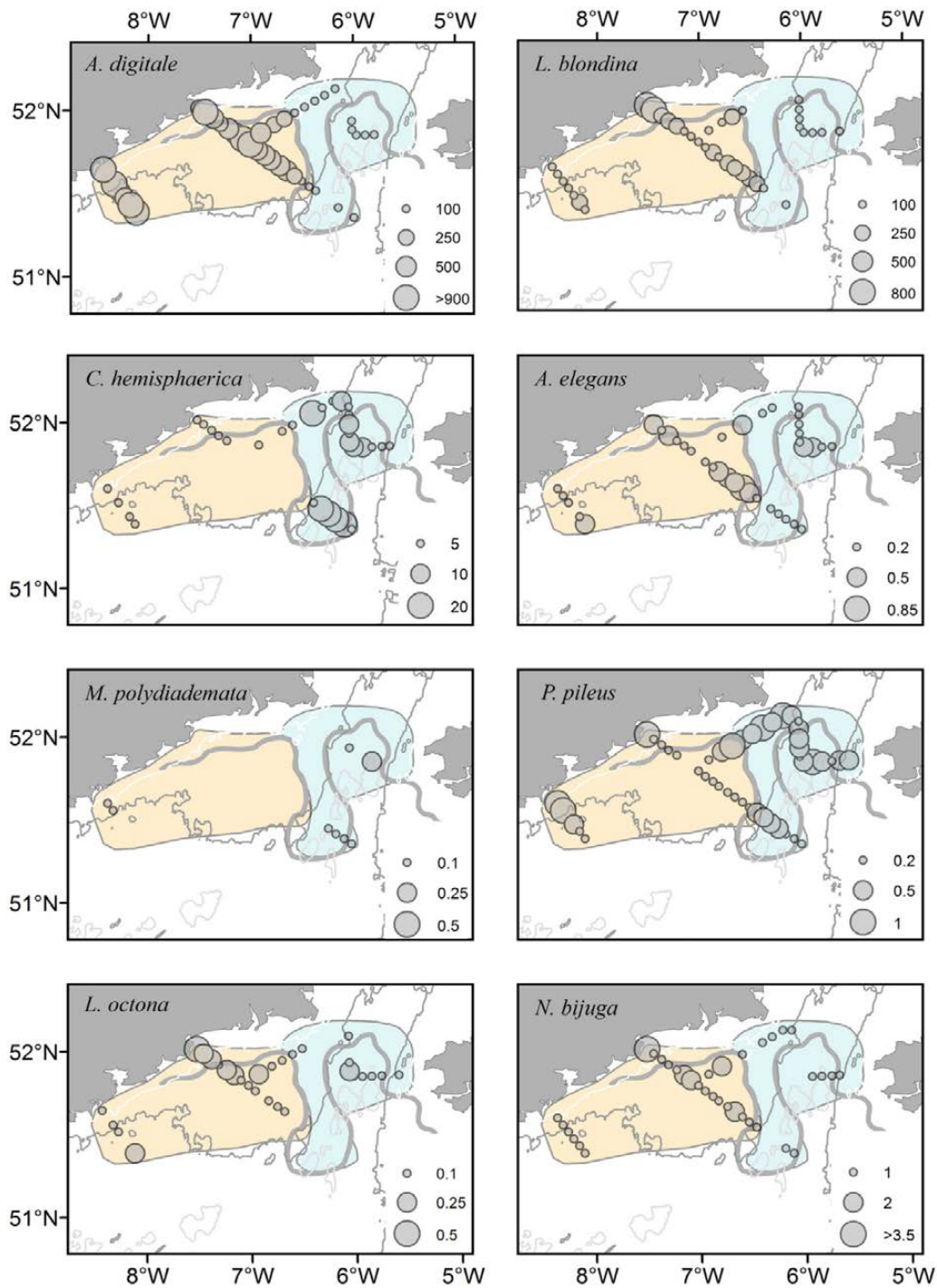


Figure 4.2. Abundance (individuals m^{-3}) and distribution of the dominant gelatinous species across the study area, which contributed to the two distinct gelatinous communities: a warm water gelatinous community (orange) and a cold water gelatinous community (blue). Note that the scale for each species is different and the shaded polygons are simply a visual aid to identify the extent of the two gelatinous communities.

sightings records indicate that the occurrence of the species at the northern end of its distribution has increased (Palsson and Astthorsson, 2016; Frafjord *et al.*, 2017). It has been proposed that the high abundance of sunfish reflects an increase

in jellyfish biomass due to ocean warming and the overexploitation of shark predators (Gremillet *et al.*, 2017). The species is not directly targeted by fisheries and, although aerial surveys have provided quantitative estimates of current densities (Breen *et*

al., 2017; Gremillet *et al.*, 2017), extended abundance time series are lacking. Therefore, very little is known about historical abundance levels and population trends, and the factors that contribute to changes in abundance and distribution have not been directly investigated.

The reconstruction of past trends in sunfish abundance relies largely on sightings records, which are collected opportunistically or as part of monitoring surveys for other species and through citizen science initiatives. Statistical tools exist to account for sources of error and bias inherent in data collected by human observers (Bird *et al.*, 2014; Isaac *et al.*, 2014). Sightings per unit time can be standardised using variables that cause detectability to vary within general linear modelling, generalised additive modelling and mixed-effects modelling frameworks, allowing the underlying long-term trend to be detected (Archibald and James, 2016; Walker and Taylor, 2017). Since the 1970s, land-based observations of sunfish have been recorded during timed watches by volunteers at the Cape Clear Bird Observatory on the south-west coast of Ireland as part of a bird migration monitoring programme co-ordinated by BirdWatch Ireland. The data include information on conditions that may affect detectability (time of year, sea state, number of observers), potentially providing a long-term index of the abundance of sunfish at this location in the Celtic Sea. The aim of this study was to use this valuable data resource to produce a standardised index of the occurrence and relative abundance of sunfish, to examine its temporal variability and to establish relationships with environmental variables.

4.2.2 Data analysis

The sightings data include 46 years of observations from April to October between 1971 and 2017, a total of 4975 records. The response variable was the number of sunfish sighted per minute of effort. For 86% of these observations no sunfish were sighted and hence these were recorded as zero. No data were available for the period 2013–2015 because of the temporary suspension of the monitoring programme. Only data that were collected during timed, shore-based watches were included in the analysis.

There were two types of explanatory variable: (1) those that are expected to influence detectability

and (2) those that might correlate with actual sunfish abundance.

The type 1 variables were the duration of the watch in minutes (watch duration), the number of observers present (observer number), month, sea state and wind direction. Local wind direction was converted from degrees to four cardinal categories: E-NE (0–68°), S-SE (68–158°), W-SW (158–248°) and N-NW (248–360°), with W-SW being the most frequently observed.

The type 2 variables described the temperature (mean latitude of the 13°C isotherm), feeding conditions for sunfish (CPR estimates of siphonophore abundance), phytoplankton abundance (PCI from the CPR) and sightings of other large plankton feeders. Details of these data sources are included in Table 2.1. All continuous variables were expressed as annual means and scaled by subtracting their mean and dividing by the standard deviation. The PCI was expressed as an annual median.

The data were analysed using a two-part gamma hurdle model to account for zero inflation. In the first (Bernoulli) part of the model the response was the binary variable: sunfish presence/absence. In the second (gamma) part the response was the continuous variable: number of sunfish sighted per minute. To isolate the effect of variables that might influence detectability and to partition out the annual signals in occurrence and abundance, the type 1 explanatory variables (watch duration, observer number, month, wind direction and sea state) were included as fixed effects in a mixed-effects model, which was applied separately to each part of the hurdle model. The factor variable “year” was included as a random effect. The year random effects (conditional modes) were extracted for each part of the hurdle model and were then included as the response variable in a series of general linear models that modelled the effect of the type 2 variables on sunfish occurrence and abundance.

4.2.3 Results

Factors affecting sunfish presence/absence

The fixed effects of watch duration, observer number, sea state and wind direction were all significant in the Bernoulli part of the hurdle model (Table 4.1),

Table 4.1. Fixed-effects summary statistics from the gamma hurdle model, showing the contribution of factors that potentially affect the detectability of sunfish

Model	Effect	Estimate	Standard error	Z-value	p-value
Bernoulli model (sunfish presence/absence)	Intercept	-2.419	0.689	-3.510	4.49 × 10 ⁻⁴ ***
	Watch duration	0.644	0.089	7.197	6.17 × 10 ⁻¹³ ***
	Month	0.042	0.072	0.580	0.562
	Observer number	0.220	0.097	2.259	0.024*
	Wind direction (N-NW)	-0.553	0.354	-1.564	0.118
	Wind direction (S-SE)	-0.016	0.382	-0.043	0.966
	Wind direction (W-SW)	-0.691	0.361	-1.913	0.056
	Sea state	-0.244	0.084	-2.896	0.004**
Gamma model (sunfish numbers)	Intercept	-2.082	0.789	-2.637	0.008**
	Watch duration	-0.579	0.061	-9.362	< 2 × 10 ⁻¹⁶ ***
	Month	-0.318	0.101	-3.138	0.001**
	Observer number	0.0579	0.095	0.609	0.542
	Wind direction (N-NW)	0.234	0.209	1.117	0.264
	Wind direction (S-SE)	-0.048	0.223	-0.217	0.828
	Wind direction (W-SW)	-0.224	0.209	-1.069	0.285
	Sea state	0.0313	0.056	0.558	0.576

*Significant at $p < 0.05$; **significant at $p < 0.01$; ***significant at $p < 0.001$.

indicating that these factors influence the detectability of sunfish. The probability of sighting a sunfish was positively associated with watch duration and observer number and negatively associated with sea state. The inclusion of year as a random effect significantly improved the model fit relative to the reduced model ($p < 1.27 \times 10^{-8}$). This showed that, after accounting for variation in detectability associated with watch duration, observer number, sea state and wind direction, there was a significant annual signal in sunfish occurrence. The mean annual probability of sighting a sunfish appears to increase after 1990, although the probability was also high at the start of the time series (1971) and low for five consecutive years towards the end of the time series (2007–2011) (Figure 4.3).

General linear models of the conditional modes of the year random effect (the annual signals described above) showed that both the PCI and the latitude of the 13°C isotherm were positively and significantly correlated with the probability of sighting a sunfish. Contrary to expectations, there was a significant negative correlation between the index of food availability (siphonophores) and the probability of detecting a sunfish (Table 4.2 and Figure 4.4).

Factors affecting the number of sunfish sighted

The gamma part of the hurdle model showed that the number of sunfish sighted was significantly negatively correlated with watch duration and observer number (see Figure 4.3). The inclusion of year as a random effect significantly improved the model fit relative to the reduced model ($p = 0.043$), showing that, after accounting for factors that influence detectability, the number of sunfish sighted varied significantly between years. The year random effect showed no clear annual trend (see Figure 4.3). The conditional modes of the year random effect from the gamma model were negatively correlated with the latitude of the 13°C isotherm and basking shark sightings per minute and positively correlated with the PCI and siphonophore abundance (Table 4.2 and Figure 4.5).

4.2.4 Conclusions

By combining a gamma hurdle model with a mixed-effects modelling framework we were able to deal with the high proportion of zero observations in the extended time series of sunfish sightings while removing potential bias resulting from variation in detectability. The approach was effective at extracting

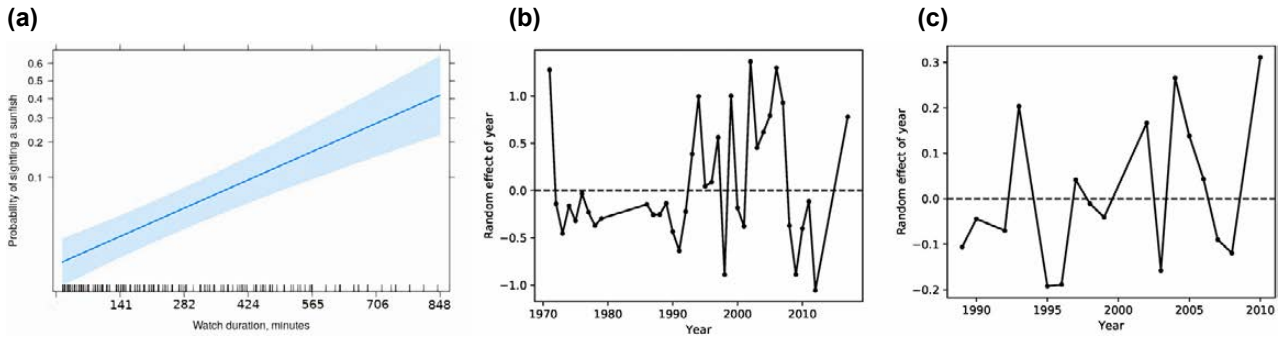


Figure 4.3. (a) Plot of the relationship between the predicted probability of detecting a sunfish and watch duration (from the Bernoulli part of the hurdle model); (b) plot of the random effect of year from the Bernoulli part of the hurdle model showing the annual signal in the relative probability of sighting a sunfish; (c) plot of the random effect of year from the gamma part of the hurdle model showing the relative number sighted after standardising for factors influencing detectability.

Table 4.2. General linear model summary statistics, showing associations of sunfish sightings with environmental covariates and sightings of other species

Model	Effect	Estimate	Standard error	t-value	p-value
Bernoulli model (sunfish presence/ absence)	Intercept	-0.336	0.030	-10.986	<2 × 10 ⁻¹⁶ ***
	Basking shark sightings minute ⁻¹	-0.005	0.011	-0.493	0.622
	Leatherback sightings minute ⁻¹	0.009	0.009	1.001	0.317
	PCI	0.395	0.033	11.886	<2 × 10 ⁻¹⁶ ***
	Siphonophore abundance	-0.143	0.014	-9.714	<2 × 10 ⁻¹⁶ ***
	13°C isotherm latitude	0.322	0.015	20.858	<2 × 10 ⁻¹⁶ ***
Gamma model (sunfish numbers)	Intercept	-0.026	0.041	-0.642	0.522
	Basking shark sightings minute ⁻¹	-0.008	0.003	-2.188	0.031*
	Leatherback sightings minute ⁻¹	-0.004	0.016	-0.243	0.808
	PCI	0.106	0.037	2.842	0.005**
	Siphonophore abundance	0.106	0.022	4.792	6.22 × 10 ⁻⁶ ***
	13°C isotherm latitude	-0.066	0.021	-3.019	0.003**

*Significant at $p < 0.05$; **significant at $p < 0.01$; ***significant at $p < 0.001$.

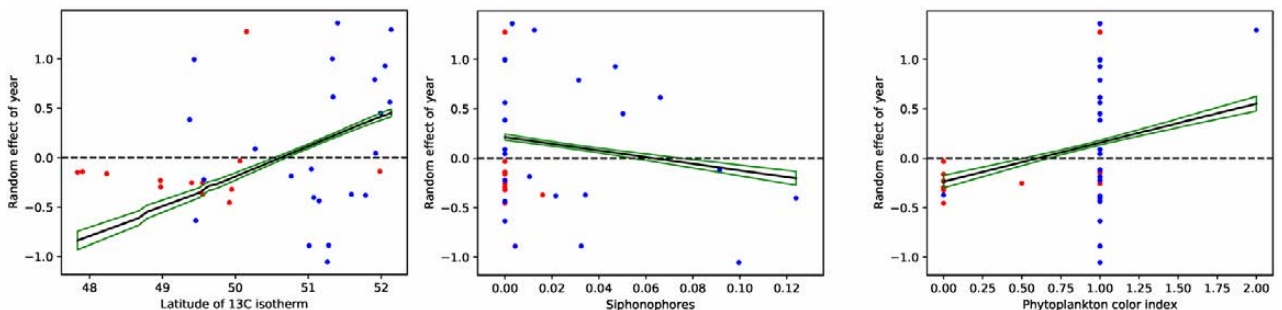


Figure 4.4. Random effect of year (from the Bernoulli part of the hurdle model) plotted against predictors. Red observations are those made before 1990; blue are those made after 1990. Superimposed lines are predicted partial slopes for a given predictor, when the other predictors were held fixed, with a 95% pointwise confidence interval for the fitted values.

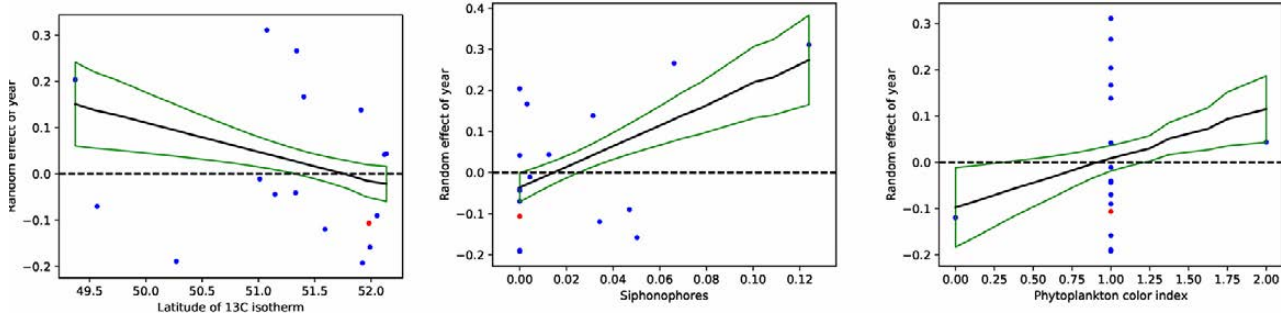


Figure 4.5. Random effect of year (from the gamma part of the hurdle model) plotted against predictors. Red observations are those made before 1990; blue are those made after 1990. Superimposed lines are predicted partial slopes for a given predictor, when the other predictors were held fixed, with a 95% pointwise confidence interval for the fitted values.

the underlying annual signals in the data. The annual trend in the presence/absence of sunfish at the Cape Clear Bird Observatory will probably provide a good indication of trends in the occurrence of sunfish in the Celtic Sea. Located 13 km offshore, the study site is well positioned for observing sunfish on-passage or feeding on offshore aggregations of jellyfish and is situated within an area of relatively high sunfish density (Breen *et al.*, 2017). The same individual filled the position of site warden for most of the time series, ensuring consistency in the collection of the data.

The results suggest that sunfish occurrence in the Celtic Sea increased markedly after the mid-1990s. This trend is associated primarily with ocean warming (the increasing latitude of the 13°C isotherm), with evidence of a weak positive association with phytoplankton abundance (PCI). Sunfish are important predators of siphonophores (Nakamura *et al.*, 2015) and have been shown to co-occur with certain species of siphonophore in the Celtic Sea (Houghton *et al.*, 2013). CPR records indicate a dramatic increase in the abundance of siphonophores in the Celtic Sea in recent decades. However, this increase appears to have occurred later than the increase in sunfish occurrence (after 2000) and persisted during the period when the sunfish sighting probability decreased (2007–2011). Consequently, the correlation between sunfish presence/absence and siphonophore abundance is negative.

Considering only the positive sightings, there is no clear increase or decrease in the numbers of sunfish sighted over the time period when most of

the positive sightings were recorded (after 1990). Contrary to what was observed with the presence/absence data, the numbers of sunfish sighted were positively associated with siphonophore abundance and negatively associated with temperature. Sightings recorded by human observers at a single location may not provide a sufficiently precise estimate of relative abundance because of spatial variability in sunfish distribution and variation between observers. Although we are confident that the increased incidence of sightings during the 1990s reflects a real change in the occurrence of sunfish in the Celtic Sea, changes in relative abundance should be interpreted with caution.

Although there is no evidence that increased siphonophore abundance led to an increase in the occurrence of sunfish in the Celtic Sea, as sunfish expand their range within the Celtic Sea they may benefit from this increase in food availability. This could explain the positive correlation with the number of sunfish sightings later in the time series. Sunfish display complex vertical migration behaviour, characterised by periods of surface basking and deep dives (Nakamura *et al.*, 2015). Both horizontal and vertical movements are influenced by temperature fronts and ocean currents (Potter *et al.*, 2011; Thys *et al.*, 2015). The influence of ocean warming on feeding, diving and aggregation behaviour of sunfish (and consequently on surface sightings) is likely to be complex. More detailed spatially resolved surveys are required to fully understand the role of the environment in shaping the distribution and abundance of this important planktivorous predator.

5 Influence of Physical Processes on Ocean Transport

A model of ocean circulation in the Celtic Sea for the period 2002–2014 was developed using the Atlantic-Iberian Biscay Irish-Ocean Physics Reanalysis product (Sotillo *et al.*, 2015). This provided a physical context for investigating change in the Celtic Sea ecosystem during that period. Using Celtic Sea herring as a case study, the potential influence of changing wind patterns on larval transport and retention was investigated. This study is described in full in Deschepper *et al.* (2019). A synopsis of the study and its main findings is presented in the following sections.

5.1 A Biophysical Model of Early Larval Transport and Retention in Atlantic Herring (*Clupea harengus* L.) in the Celtic Sea

5.1.1 Background

Larval transport processes exert a critical influence on the dynamics of fish populations. Physical oceanographic mechanisms interact with the behaviour of spawning adults and developing larvae to regulate delivery to suitable nursery habitats via dispersal or retention (Pineda *et al.*, 2007; Stephenson *et al.*, 2015; Zolck *et al.*, 2015). Inter- and intra-annual variability in hydrodynamic and meteorological conditions can contribute to temporal variation in larval distribution (Pacariz *et al.*, 2014), survival (Hinrichsen *et al.*, 2012), growth (Vikebo *et al.*, 2005) and abundance (Nielsen *et al.*, 1998), with consequences for subsequent recruitment success (Baumann *et al.*, 2006) and population exchange (Nielsen *et al.*, 1998; Huwer *et al.*, 2016).

Coupled biophysical models provide a means to reconstruct larval transport processes that are difficult to observe directly (Hinrichsen *et al.*, 2011). By reconstructing larval transport under different conditions, dispersal simulations can help to forecast the most likely impacts of changing circulation patterns on the connectivity of life history stages within the context of climate change (Rijnsdorp *et al.*, 2009; Llopiz *et al.*, 2014). This study uses an individual-based model (IBM) coupled offline to a hydrodynamic

model to reconstruct the dispersal of larval herring from a known spawning ground in the Celtic Sea.

Winter-spawned juvenile herring from the Celtic Sea are known to occupy nursery grounds in the Irish Sea, where they mix with the resident autumn-spawned population, with mixing rates showing substantial inter-annual variability (Brophy and Danilowicz, 2002; Burke *et al.*, 2009). Evidence suggests that transport happens early in the larval phase, within a month of hatching (Brophy and Danilowicz, 2002). Celtic Sea herring that disperse to the Irish Sea appear to return to the Celtic Sea as adults to spawn (Brophy *et al.*, 2006). The dispersed and retained components of the Celtic Sea herring population show differences in growth and age at maturation (Brophy and Danilowicz, 2003; Brophy *et al.*, 2006). Variability in larval dispersal is therefore likely to contribute to variation in growth, recruitment and lifetime fecundity of Celtic Sea herring.

This study investigated inter- and intra-annual variability in dispersal and retention of Celtic Sea herring and examined the influence of currents, winds and tides, as well as larval behaviour and diffusion processes, on the direction of movement. The potential influence of environmental change on larval transport processes and the consequences for fisheries were considered.

5.1.2 Methods

Study design

Hydrodynamic data were available for the period 2002–2012. From this time period, six year classes were selected for inclusion in the simulation: 2002, 2003, 2004, 2005, 2008 and 2010.

Four release dates were randomly selected in each year to coincide with the drift period of winter-spawning herring (December–February). Simulations were carried out using Ichthyop, an open-source, individual-based modelling tool (Lett *et al.*, 2008). The original Ichthyop code was modified to incorporate the behavioural parameters of herring; after 10 days of passive drift, diel vertical migration (DVM) behaviour

was incorporated into the simulations and various DVM behaviour scenarios were compared.

The release area for the simulations was the spawning ground offshore of Dunmore East on the south-east coast of Ireland (area A, Figure 5.1). On each date, 3000 particles were released in three replicate batches of 1000 particles. Particles were released at the bottom of, and at randomly selected positions within, the release area and larval transport was simulated for 30 days. On each replicate run, release position and the depth occupied at night after the onset of vertical migrations were re-randomised. The larvae were forced with vertical and horizontal currents throughout the 30-day simulation.

Ocean circulation mechanism

The three-dimensional velocity fields used to drive advection and dispersion in Ichthyop were taken from the Atlantic-Iberian Biscay Irish-Ocean Physics Reanalysis product (2002–2014) (Sotillo *et al.*, 2015). Simulations were run using two different velocity field set-ups, one based on daily mean currents, which

contained no tidal signal in the velocity fields because of daily averaging (the non-tidal simulation), and a second based on derived hourly currents, which included the tidal signal in the velocity fields (the tidal simulation). Several diffusion settings were compared in order to assess the potential impact of small-scale diffusion processes on larval transport.

Wind and tidal data

Hourly records of wind speed and direction for the period 1962–2016 were acquired from the Met Éireann synoptic weather station at Cork Airport. Hourly records were categorised based on the direction of the wind: 150–210° (SSE-SSW); 210–270° (SSW-W); 270–330° (W-NNW); 330–30° (NNW-NNE); 30–90° (NNE-E); and 90–150° (E-SSE). For each category a wind index was derived from the product of the mean monthly duration and speed of the winds in that category, producing six wind indices: ind150–210, ind210–270, ind90–150, ind270–330, ind330–30 and ind30–90. The timing of the new moon was used to derive an index of tidal state on each release date (spring tides, neap tides and moderate tides).

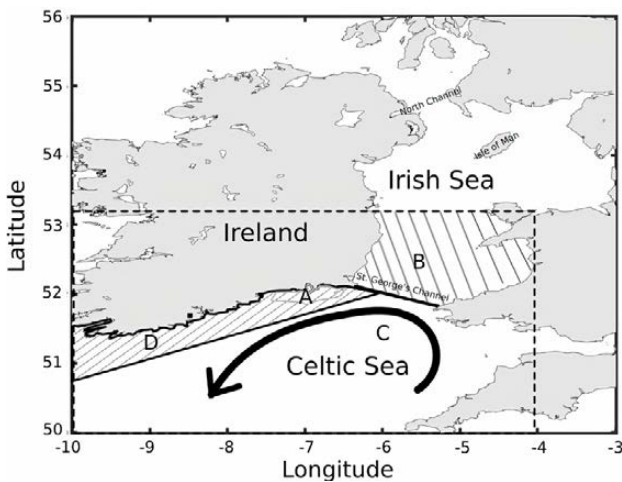


Figure 5.1. Map of the study location showing the particle release area on the Dunmore East spawning grounds (A). At the end of each simulation, particle end points were mapped and the numbers of end points in the Irish Sea (B), Celtic Sea offshore (C) and Celtic Sea inshore (D) were counted and compared between runs. The dashed box indicates the boundary of the study area used in the simulations. The position of the Met Éireann synoptic station from which wind measurements were obtained is indicated by a black square.

Statistical analysis

Particles were categorised according to their position at the end of the 30-day simulation period: transported to the Irish Sea (area B, Figure 5.1), transported offshore in the Celtic Sea (area C, Figure 5.1) or retained inshore in the Celtic Sea (areas A and D, Figure 5.1). Multinomial modelling was used to analyse variation in the end-point distributions between the non-tidal and the tidal hydrodynamic simulations, to quantify inter- and intra-annual variability in transport and retention and to investigate the influence of DVM behaviour, diffusion, wind and tidal conditions on the probability of dispersal to each area.

5.1.3 Results

Inter- and intra-annual variation in transport and retention

At the end of the 30-day simulation period, particles were distributed across all three areas (Irish Sea, offshore Celtic Sea and inshore Celtic Sea) (Figure 5.2). Across all of the release dates, the most common outcome of the simulation was retention

within the Celtic Sea (70% and 78% of particles, on average, for the non-tidal and tidal simulations, respectively), followed by dispersal offshore in the Celtic Sea (27.6% and 17.9%, on average, for the

non-tidal and tidal simulations, respectively). Dispersal to the Irish Sea was the rarest outcome (2.8% and 4.1%, on average, for the non-tidal and tidal simulations, respectively) (Figure 5.3).

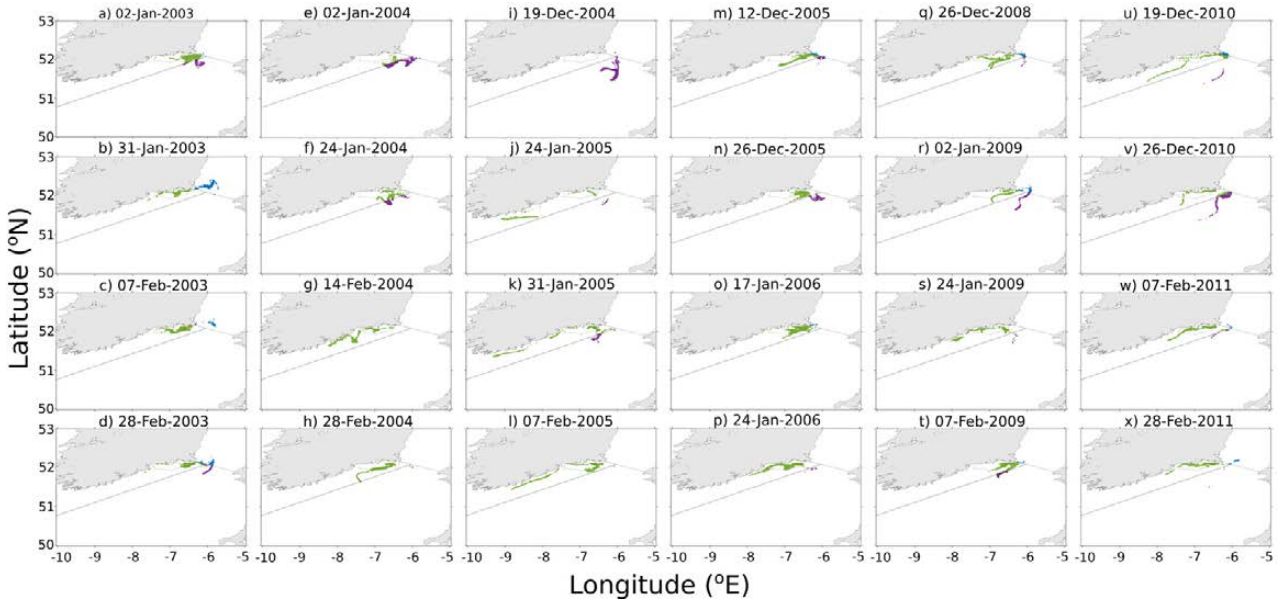


Figure 5.2. Particle distributions at the end of each 30-day simulation using the tidal simulation. Particles are colour-coded according to their position in relation to the three predefined areas indicated by the boundary lines in the maps: green, Celtic Sea; blue, Irish Sea; and purple, offshore. The first day of the simulation is indicated above each plot.

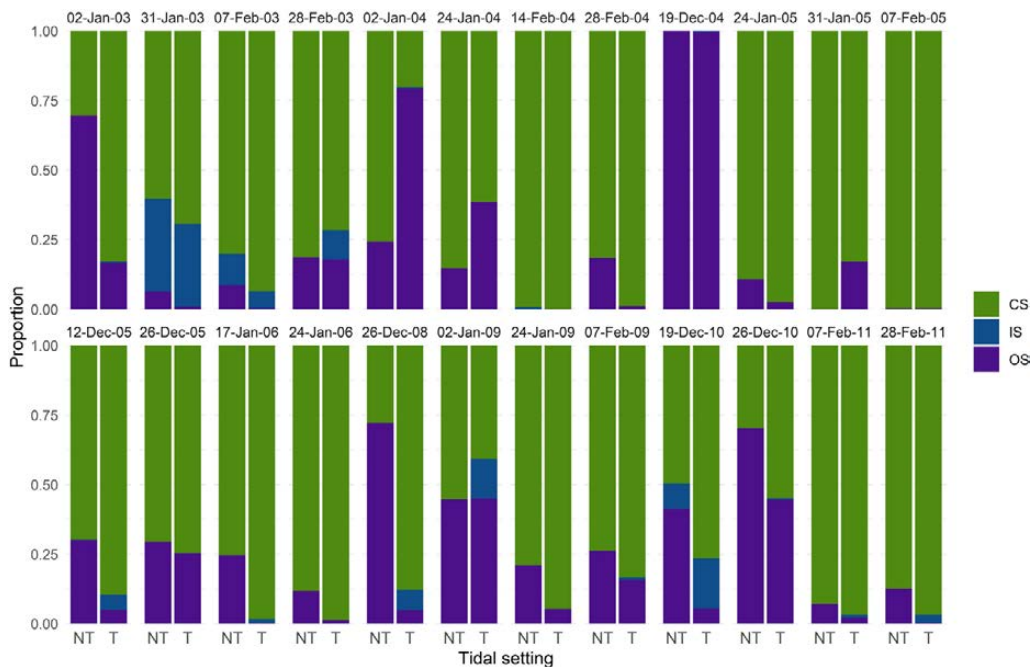


Figure 5.3. Proportion of particles in each area at the end of each 30-day simulation period using the non-tidal simulation (NT) and the tidal simulation (T). Panel borders separate the various year classes for which larval transport is simulated, e.g. the 2002 year class corresponds to the period December 2002–March 2003. The simulation start date is shown over each pair of simulations. CS, Celtic Sea; IS, Irish Sea; OS, offshore.

Relative rates of transport and retention varied substantially between release dates, with no clear annual trend (see Figure 5.3). Multinomial model outputs showed that most (65%) of the variance in end-point distributions was due to the effect of the release date, with variation between years being relatively minor (2.5%).

The influence of tides, larval behaviour and diffusion on particle transport

The probability of particles occurring in the Irish Sea at the end of the simulations was significantly higher for the tidal simulation than for the non-tidal simulation ($p < 0.001$), indicating that the tides were instrumental in delivering particles to the Irish Sea. Transport offshore was significantly less likely for the tidal simulation than for the non-tidal simulation ($p = 0.01$). Plotted particle trajectories demonstrated how tides influenced particle transport (Figure 5.4);

tidal movements appeared to push the particles across St George’s Channel and further into the Irish Sea relative to particles released from similar locations in the non-tidal simulations. Although particles moved backwards and forwards across the Channel with the ebb and flow of the tide, overall displacement was predominantly in a north-eastward direction, possibly because of asymmetry in the tidal flow.

Rates of particle delivery to each area were also influenced by DVM (chi-square = 4791; $p < 0.0001$) and horizontal diffusion (chi-square = 5153; $p < 0.0001$), highlighting the need for additional field data to validate these processes.

The influence of winds and tidal strength on larval end-point distributions

The optimal multinomial model of particle end-point probabilities included two wind indices (ind210–270 and ind90–150), as well as the tidal state index. The

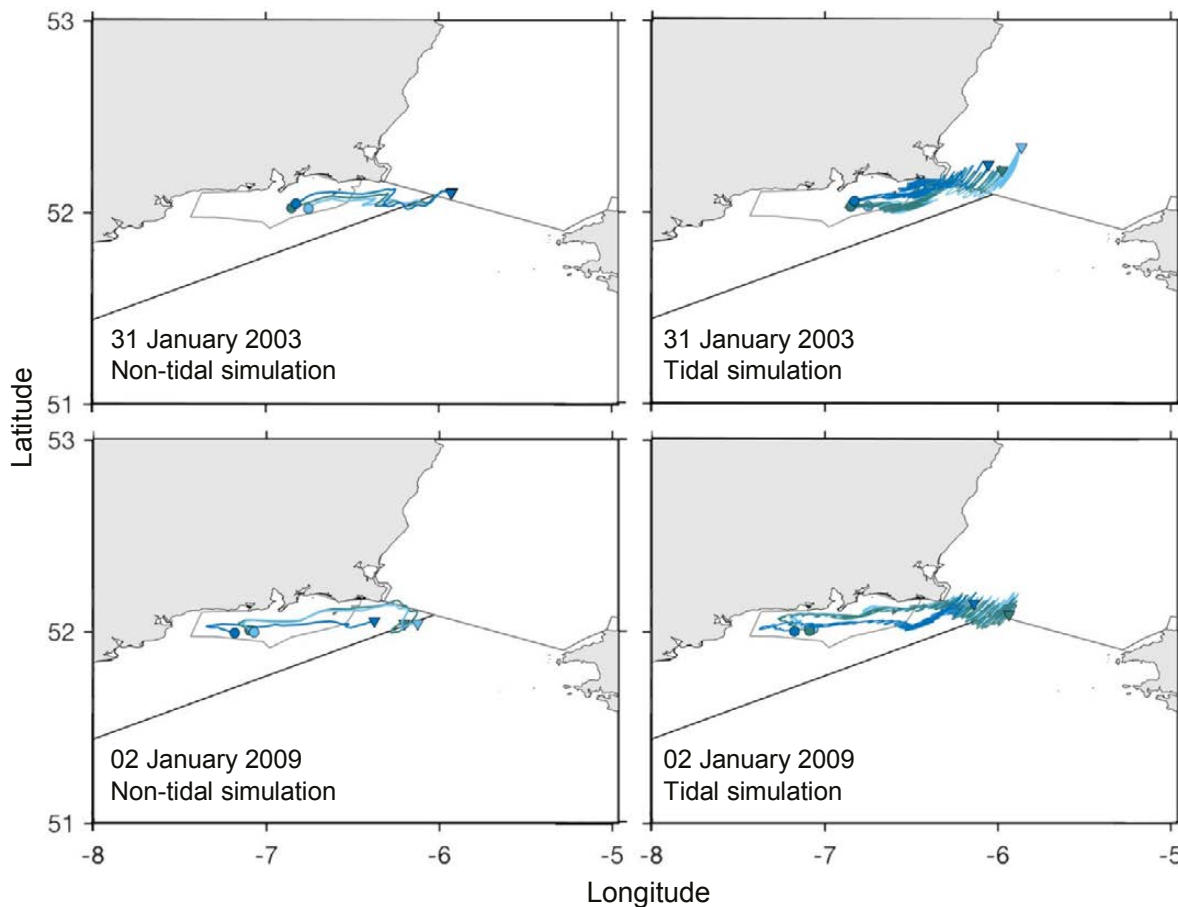


Figure 5.4. Particle trajectories for particles released from similar locations in the non-tidal (left-hand panels) and tidal (right-hand panels) simulations on two dates. Circles represent the release locations and triangles represent the positions at the end of the 30-day simulation period.

predictive power of the model was high for the Celtic Sea and offshore areas (least squares mean $R^2=0.76$ and 0.77 , respectively; $p<0.0001$). Predictions of the rarer outcome of transport to the Irish Sea were more prone to error ($R^2=0.42$; $p<0.0001$). Strong and frequent E-SSE winds (ind90–150) were associated with a higher probability of transport to the Irish Sea and retention in the Celtic Sea and a lower probability of transport offshore. Winds from the SSW-W (ind210–270) were associated with higher rates of transport to offshore areas and lower rates of retention in the Celtic Sea (Figure 5.5). The model-predicted probability of retention in the Celtic Sea was highest and the probability of transport offshore was lowest when the release date coincided with a spring tide. The probability of transport into the Irish Sea was highest on release dates that coincided with a moderate tide.

5.1.4 Conclusions

The results show that currents acting under atmospheric and tidal forcing in the Celtic Sea split the larval herring population along three trajectories. Ocean circulation patterns in the Celtic Sea during winter generally favour the retention of herring larvae in inshore areas along the south of Ireland, although transport to offshore areas in the Celtic Sea and to the Irish Sea also occurs. Strong and frequent prevailing winds from a west/south-westerly direction result in substantial transport away from the Celtic Sea retention area, into deeper offshore waters, whereas strong and frequent east to south-south-east winds increase Celtic Sea retention and transport across St George’s Channel into the Irish Sea.

Temporal trends in wind patterns from 1962 to 2016 (see Figure 2.2) show strong prevailing winds prior to 1990, followed by a period of relative calm and a more

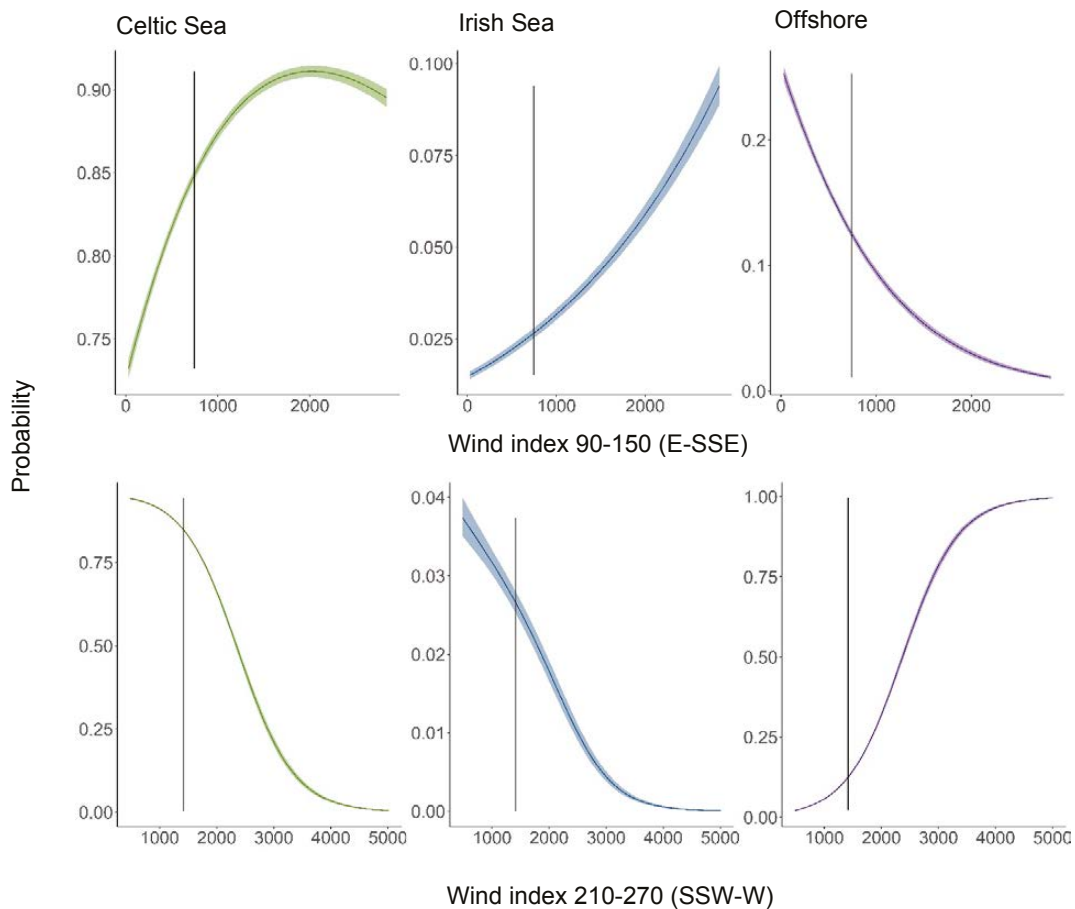


Figure 5.5. Mean predicted probabilities (plotted line) with 95% confidence limits (grey shading) of a particle occupying each of the three areas (Celtic Sea, Irish Sea, offshore) at the end of the 30-day simulation period in relation to the strength and frequency of E-SSE winds (ind90-150) and SSW-W winds (ind210-270). The vertical line indicates the mean wind index across all of the years.

recent increase. The frequency of the prevailing winds has also increased over the time series. The results of this study indicate that these changes in wind patterns could impact on the connectivity of the Celtic and Irish Seas and on the transport of herring larvae (and potentially of other dispersing organisms). This has consequences for juvenile mixing rates and the management of the associated fisheries.

Future changes in wind patterns as a result of climate change are predicted (Reyers *et al.*, 2016; La Sorte and Fink, 2017), with consequences for ocean circulation. Potential impacts of climate change on

larval dispersal are not well understood (Petitgas *et al.*, 2013). Coupling forecast climate scenarios with biophysical hydrodynamic models could help to predict the impact of future change on larval dispersal and nursery ground connectivity in the Celtic Sea (Hollowed *et al.*, 2009). The modelling framework presented here could be further developed and refined and its geographic range extended to simulate population connectivity under different climate change scenarios, providing a predictive tool to support the management of the Celtic Sea ecosystem and its fisheries.

6 Temporal Dynamics in the Growth Rates of Celtic Sea Fish Species

In fish populations, biological responses to external pressures are often manifested in changes in growth rate. Pronounced increases and decreases in growth rates of various species have been linked to ecosystem regime shifts (Ito *et al.*, 2015; Smolinski and Mirny, 2017; van der Sleen *et al.*, 2017; Matta *et al.*, 2018). Therefore, fish growth time series may provide useful indices of broader ecosystem changes.

Here, three data sources were used to describe temporal trends in growth rates of Celtic Sea fish:

- individual-based records of length, weight and age from port sampling records of herring (1958–2012);
- population mean weight-at-age estimates from ICES stock assessments for multiple species (1958–2010, varies by species);
- individual otolith growth chronologies for plaice, herring and haddock using material from Marine Institute otolith collections (1985–2014, varies by species).

Temporal growth signals were isolated from intrinsic sources of variation, and correlations with potential environmental, population or fishing-related drivers were investigated. Synchrony across species was also examined. The treatment of these data and the main findings are summarised in this chapter.

6.1 Explaining Declines in the Growth of Celtic Sea Herring

A full report of this study has been submitted to *Ecological Informatics* and is currently under revision.

6.1.1 Background

Directional changes in growth have been observed across many exploited fish populations (Neuheimer and Taggart, 2010; van Walraven *et al.*, 2010; Baudron *et al.*, 2011; Neuheimer *et al.*, 2011) and variously attributed to changes in the physical environment (typically temperature), food availability and population density and to the selective effects of fishing (Law,

2000; Conover and Munch, 2002; Swain *et al.*, 2007; Audzijonyte *et al.*, 2016). Declines in growth lead to lower overall productivity through influences on survival, recruitment, fecundity and susceptibility to stock decline (Brander, 2007). This creates an imperative to interrogate temporal change in growth, determine the combined influence of various potential contributing factors and improve understanding of the most likely future responses to the combined influence of climate and fishing (Perry *et al.*, 2010).

Growth rates of Celtic Sea herring showed a marked decline from the mid-1970s onwards (Harma *et al.*, 2012), causing concern for the state of the stock and the sustainability of the fishery. In this study, GBRTs are applied to individual length-at-age data for Celtic Sea herring to investigate potential environmental and fishery-related drivers of the decline in growth.

6.1.2 Methods

The analysis was conducted using three-winter-ringing (4-year-old) fish, as fish in this age group are fully recruited to the fishery and are therefore well represented in commercial catch samples. Age and length data were available for 35,629 individual herring from port sampling collections (1958–2012).

Correlations between length of three-ring fish and broadscale climatic indices (AMO and NAO) were investigated using general linear models, with adjusted degrees of freedom (df) to correct for temporal autocorrelation (Chelton, 1984; Pypers and Peterman, 1998).

GBRT modelling set-up

The GBRT analysis included a combination of explanatory variables describing temperature (SST), salinity and feeding conditions (CPR abundance of *C. finmarchicus*, *C. helgolandicus* and total large copepods) during the first growing season (the summer after the year of hatching). The population-related variables were year class strength (estimated recruitment) and total stock size in the year of

capture. Two measures of fishing mortality were also included: mean fishing mortality in year of capture and cumulative fishing mortality for that cohort. Month of capture was included as an explanatory variable to account for seasonal changes in size. The AMO index was highly correlated with SST and so was not included in the GBRT. Data sources are detailed in Table 2.1.

Data were split randomly into two sets: train (50%) and test (50%). Randomisation was performed using two alternative approaches: randomisation at the level of individual (RI) and randomisation at the level of year (RY). The RY approach ensured that the model was tested using previously unseen combinations of explanatory variables. The RI approach avoided the introduction of systematic biases between the test and the train datasets. An additional three-way split was performed on the RI dataset: train (50%), test (25%) and validation (25%). The model was built, tested and optimised using the train and validation sets and the model's performance was confirmed using the test set.

6.1.3 Results

Overall trends

As previously reported (Lynch, 2011; Harma *et al.*, 2012), the mean length at age of three-ring herring in the Celtic Sea showed a general increasing trend from the 1960s until the mid-1970s, followed by a decline from the 1970s through to the 2000s (Figure 6.1). The mean weight at 25 cm (the average length of a three-ring fish) remained stable across the time series, indicating that the observed decline in length at age did not coincide with a decline in condition.

Correlation with climatic indices

The mean annual AMO index in the first year of life was negatively correlated with the mean length of three-ring herring ($r = -0.65$, adjusted $df = 10$; $p < 0.001$). The decline in size of Celtic Sea herring during the late 1970s and the 1980s coincided with a steady increase in the AMO index and an eventual

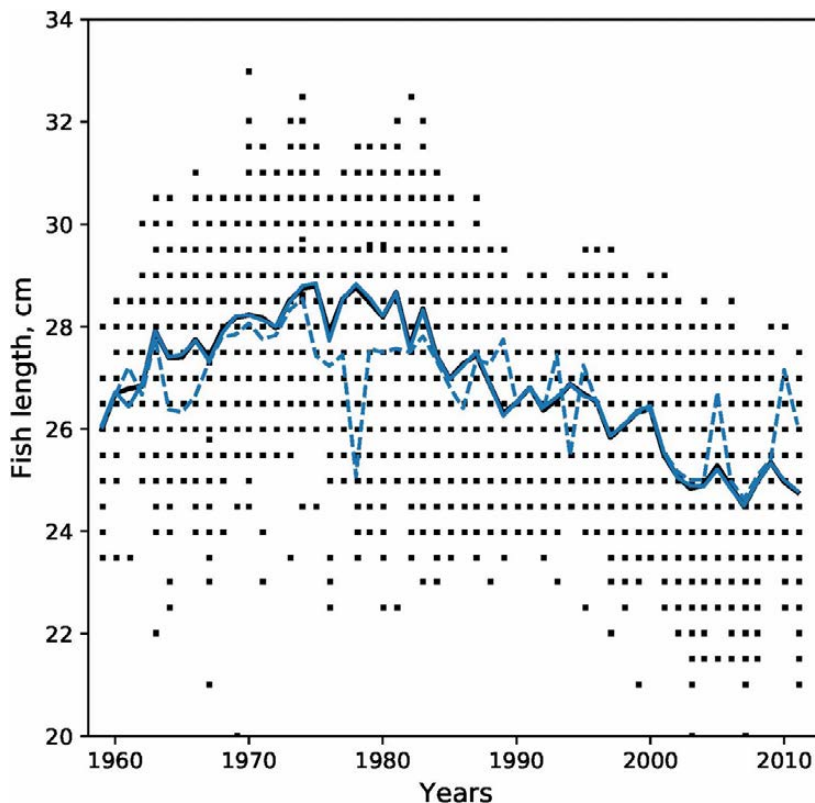


Figure 6.1. Mean length at age of three-ring Celtic Sea herring in centimetres. Measurements are rounded to the nearest 0.5 cm, except in 1967, when measurements were recorded to the nearest 0.1 cm. The solid blue line is the prediction obtained from the RI model and the dashed blue line is the prediction obtained from the RY model. Black dots represent individual observations and the black line represents the observed mean length

transition from a negative to a positive phase in the mid-1990s. Earlier increases in the size of Celtic Sea herring during the 1960s and 1970s corresponded with a negative phase of the AMO and a steady decrease until the mid-1970s (Figure 6.2). There was no significant correlation between mean length and the NAO index ($p > 0.05$).

GBRT model results

The mean length of three-ring herring predicted by the GBRT models followed similar temporal trends to the observed mean length at the three-ring stage, although the models tended to underestimate mean length at the observed peak of the time series (mid-1970s) and overestimate mean length in years when the observed mean length was at its lowest (mid-2000s) (see Figure 6.1). The relative importance of the predictors varied between the RI model and the RY model; however, some general trends were apparent (Figure 6.3). SST in the first growing season was the most important explanatory variable in both models. The high variable influence score indicates that, relative to the other variables, SST was selected most frequently for splitting and had the largest influence on predictive power. Variables describing population size (totalN) and food supply (CPR-estimated abundance of *C. finmarchicus* in area C3 – cfinC3; CPR-estimated abundance of

C. helgolandicus in area C3 – chelC3) were also included in the top four most influential predictors; however, their influence was much less marked than that of SST. Other descriptors of food availability (CPR-estimated abundance of *C. helgolandicus* in areas C3 and D4 – chelC3 and chelC4, respectively), abundance of recruits (recr), salinity (sal), fishing pressure (mean lifetime fishing pressure – cumf – and fishing pressure in year of capture – fbar) and month of capture (month) had only a minor influence on the model predictions for the Celtic Sea population.

Nature of the relationships

The partial dependence plots (Figure 6.4) display, for a selection of the more influential predictors, the marginal effects of each predictor (assuming that other covariates are held constant) on fish length at the three-ring stage. SST values above 14.1°C were associated with a decrease in size of three-ring herring in the Celtic Sea. There was some evidence of density dependence in the Celtic Sea population: both the RY model and the RI model predicted a decrease in length at higher population sizes. In terms of relationships with food availability, the strongest association was the positive correlation between the size of three-ring herring and the abundance of *C. finmarchicus* in area C3 (cfinC3).

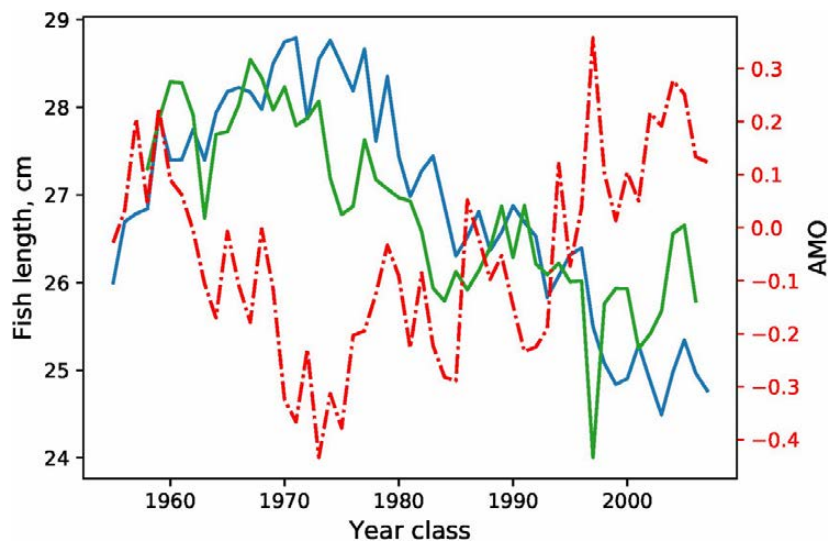


Figure 6.2. Temporal trends in the mean annual AMO index in the first year of life (red) and the mean length of three-ring herring in the Celtic Sea (blue) and the north-west of Ireland (green).

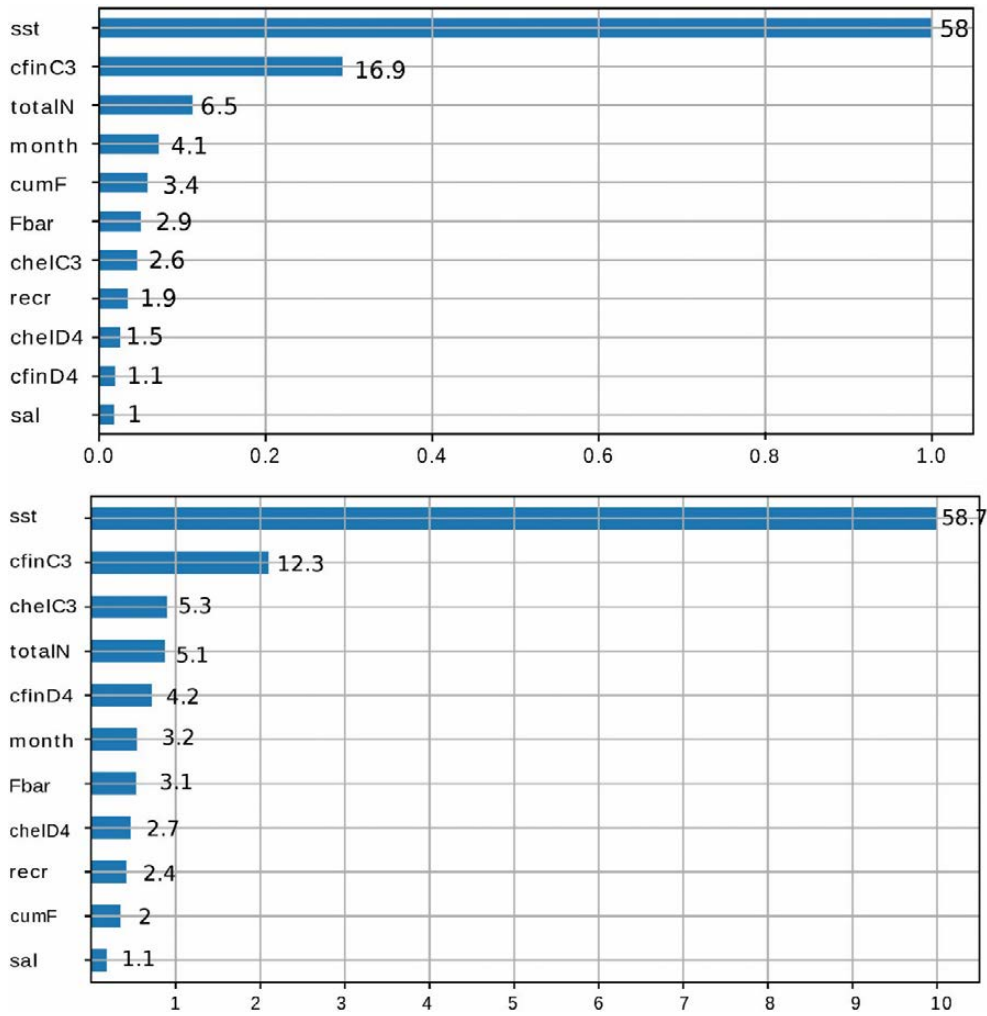


Figure 6.3. Relative importance of the variables in the GBRT models. The importance plot for the RI model (top) was produced from one GBRT model, whereas the plot for the RY model (bottom) was based on 10 GBRT models. Variable influence (VI) scores as a proportion of the maximum for each model are shown on the x-axis. The numbers beside each bar indicate the VI scores as a percentage of the total for each model.

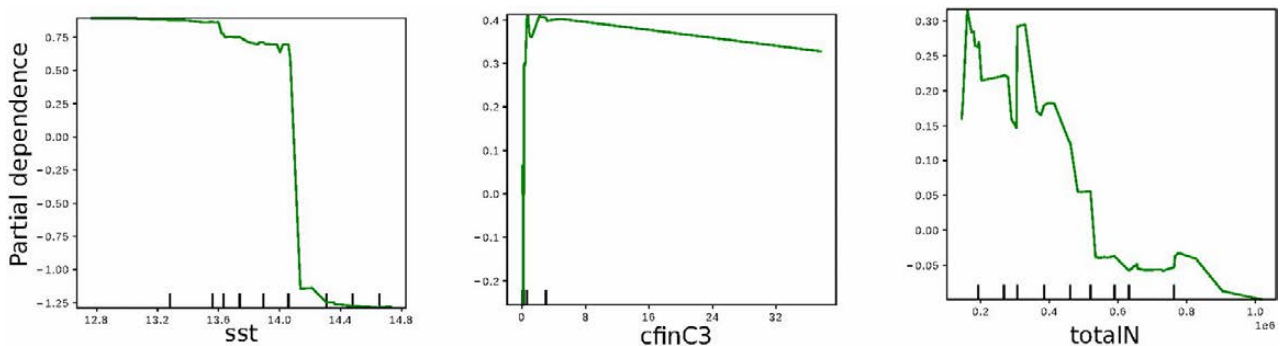


Figure 6.4. Partial dependence plots from the RI model showing relationships between length of three-ring herring and SST ($^{\circ}\text{C}$) during the first growing season, *C. finmarchicus* abundance (numbers 3m^{-3}) in area C3 (cfinC3) and total population size (numbers) (totalN).

6.1.4 Conclusions

The observed correlation between herring growth and the AMO index is consistent with previous reports of climate-driven multidecadal fluctuations in the distribution and abundance of small pelagic clupeids (Alheit *et al.*, 2014). During a previous warm period, which coincided with a positive phase of the AMO (1930s–1960s), the abundance of herring in the English Channel (at the southern limits of the species distribution) decreased and its distribution contracted (Southward *et al.*, 1988), while the abundance of the more northerly Norwegian spring-spawning herring population increased (Toresen and Ostvedt, 2000). Concurrent changes in the dynamics of other pelagic clupeids (anchovy, sardine, sardinella and sprat) and similar trends during the more recent warming period (after the mid-1990s) are indicative of climate-driven ecosystem regime shifts, which may be reflected in the AMO signal (Edwards *et al.*, 2013; Alheit *et al.*, 2014, 2019). The results of this study demonstrate that climatic fluctuations can manifest as changes in fish growth as well as abundance.

The GBRT approach proved useful for detecting non-linear relationships and step changes that would have been difficult to detect using traditional parametric approaches. In particular, a marked decrease in length above a threshold temperature (14.1°C) was detected. The metabolic optimum for herring occurs at around 15–16.1°C, with a subsequent decrease in metabolic rate occurring with further increases in temperature (Bernreuther *et al.*, 2013). During the study period, mean temperatures in the Celtic Sea from April to August ranged from 12.7°C to 14.7°C. Maximum temperatures in August remained below the thermal optimum during colder years but exceeded it in warmer years, reaching highs of above 18°C. As sea temperatures rose because of the combined effect of a positive phase of the AMO and climate change, herring in the Celtic Sea were more likely to encounter temperatures that were suboptimal for growth and metabolism. In the absence of individual temperature histories, it is not possible to determine if this exposure would be sufficiently frequent or prolonged to produce such a pronounced decline in growth. However, it is plausible that the direct effects of increasing temperature on growth and metabolism could at least partly contribute to the decline.

At northern latitudes, growth of juvenile herring tends to increase with increasing temperature (Husebo *et al.*, 2007). It has been proposed that global warming could lead to higher growth of young age classes, slower growth of older individuals and a shorter lifespan of herring (Brunel and Dickey-Collas, 2010). The results of this study suggest that predicted positive temperature–growth relationships might not apply when temperatures exceed a certain threshold. This signals caution when extrapolating climate change effects from contemporary field observations and highlights the importance of considering biological responses at distributional extremes.

6.2 Investigating Coherency in Growth Patterns across Multiple Fish Species in the Celtic Sea

6.2.1 Background

If changes in fish growth reflect ecosystem-wide change or even a regime shift, synchronous changes across multiple species are expected. This study used dynamic factor analysis to determine the extent to which weight-at-age time series display synchronous changes across multiple pelagic (herring, mackerel and blue whiting) and demersal (cod, haddock, plaice, sole and whiting) fish species that occur in the Celtic Sea.

6.2.2 Methods

Weight-at-age data were obtained from ICES stock assessment reports for three pelagic (herring in ICES sub-area 7g–h and 7j–k, mackerel in 1–8, 14 and 9a and blue whiting in 1–9, 12 and 14) and six demersal (cod in 7e–k, haddock in 7b–k, plaice in 7e, plaice in 7j–k, sole in 7e and whiting in 7b–c and 7e–k) species that occur in the Celtic Sea (detailed in Table 2.2). The analysis was conducted using a two-step approach. A series of generalised additive mixed models (GAMMs) were used to model the mean weight for each species as a function of age (modelled as a spline), with year of birth and year of capture included as random effects. Random effects and variance–covariance matrices were extracted for each year. DFA was then fitted to the year of birth and year of capture random effects, using variance–covariance as an observation error. SST was then included as a

covariate in the DFA and the model fits were assessed (with and without the covariate).

6.2.3 Results

Although herring in the Celtic Sea showed the most pronounced change in weight at age, the random effects plots showed that the growth of other species had also changed (e.g. plaice in ICES subarea 7j–k; Figure 6.5). The best-fitting DFA model included two trends, indicating some coherency in growth trends across species. The inclusion of SST as a covariate improved the model fit: both trends were negatively correlated with SST at time lag 0 ($r = -0.65$ and -0.36 for trends 1 and 2, respectively). The first trend showed an increase in growth during the 1960s followed by a steady decline from the 1970s, which became steeper around 2008 (Figure 6.6). The second trend showed a decline occurring in the 1990s. Herring made the largest contribution to the first trend and blue whiting had the strongest loading on the second trend. Both species loaded positively on the trends, indicating a decline in weight at age. Plaice in subarea 7j–k also loaded positively on trend 1. Other species had minor negative loadings on the trends (e.g. whiting on trend 1 and haddock on trend 2), indicating a tendency for increased weight at age; however, positive loadings were stronger and more common. Overall, the trends were dominated by changes in the size of herring, blue whiting and plaice in subarea 7j–k.

6.2.4 Conclusions

The GAMM models combined with DFA proved effective at extracting temporal signals from complex multivariate time series.

The results indicate that, although there is substantial variation between species, there is some coherency across the growth trends examined, with an overall tendency for reductions in fish weight in the Celtic Sea associated with increasing SST. Observed declines in growth across species are consistent with trends in the community-level indicator “typical length” used in the 2017 OSPAR intermediate assessment, which captures changes in age structure and species composition, as well as changes in size at age. Trends in typical length show a decline in the Celtic Sea from the 1990s to 2005, suggesting that fish communities are now more dominated by small-bodied fish.

6.3 Reconstructing Growth Histories across Multiple Fish Species in the Celtic Sea using Multidecadal Otolith Collections

6.3.1 Background

Sustained and detailed long-term datasets that capture individual-level variation are extremely valuable for understanding how organisms respond to population change but are rare in ecological studies. Archived otoliths (fish ear stones), collected for the purposes of age estimation and stock assessment, which are held by fisheries laboratories all over the world, hold a wealth of individual-based information collected over multidecadal timescales (Black *et al.*, 2013). Because of the chronological nature of otolith growth, visible increments can be related to specific time periods in a fish’s life. Otolith size is proportional to fish size and so otolith increment widths provide a proxy for fish growth during the corresponding period of the life history. Sclerochronological techniques allow the reconstruction of past growth histories from annual otolith increments and the investigation of temporal trends in growth at an individual and a population level (Panfili *et al.*, 2002; Black *et al.*, 2013; Rountrey *et al.*, 2014). Coupling these data with environmental and biological time series can help to elucidate drivers of observed change (van der Sleen *et al.*, 2017; Matta *et al.*, 2018). The value of otolith collections is increasingly being realised through otolith biochronology studies (Morrongiello *et al.*, 2012). Growth time series reconstructed from otoliths are proving useful as indicators of ecosystem change and regime shifts (van der Sleen *et al.*, 2017; Matta *et al.*, 2018).

In Ireland, national collections of otoliths are currently inadequately curated and their value as recorders of ecosystem change is underutilised. In this study, material from otolith collections held by the Marine Institute were used to investigate multidecadal (1980s–2010s) variability in the growth of three species from the Celtic Sea: plaice (*Pleuronectes platessa* L.), herring (*C. harengus* L.) and haddock (*Melanogrammus aeglefinus* L.). Mixed-effects modelling techniques were used to partition environmentally driven interannual growth variability and density dependence from age-related, sex-related or cohort-specific trends. The relative importance of

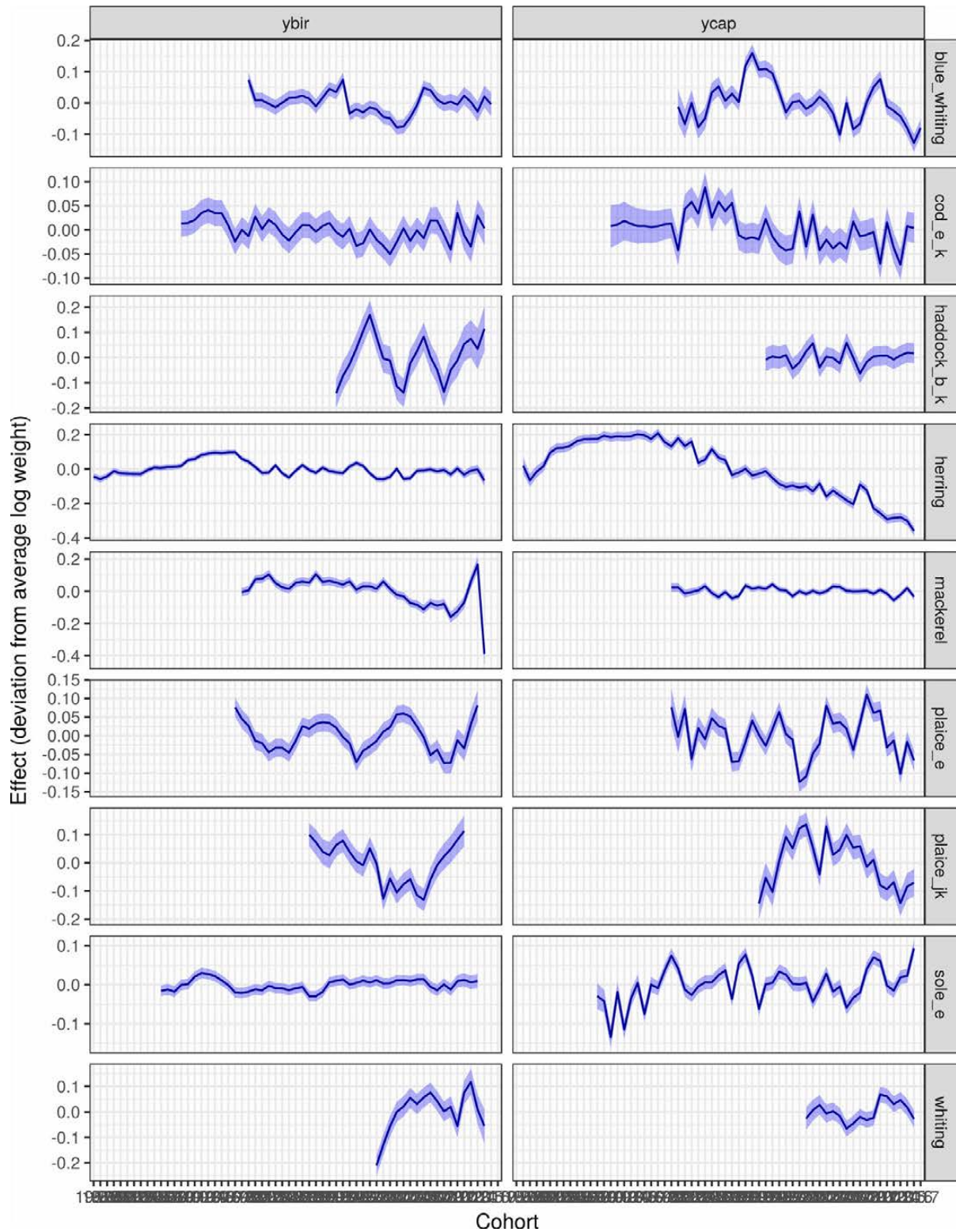


Figure 6.5. Random effects plots from GAMM models of mean population weight at age for selected fish species showing broad temporal trends in growth. The model predictions are shown by the solid line. The shaded area indicates the standard error of the model predictions. Random effects of birth year (ybir) are shown in the left panels; random effects of capture year (ycap) are shown in the right panels. Labels on the right indicate the stock names (blue_whiting: blue whiting in 1–9, 12 and 14; cod_e_k: cod in 7e–k; haddock_b_k: haddock in 7b–k; herring: herring in 7g–h and 7j–k; mackerel: mackerel in 1–8, 14 and 9a; plaice_e: plaice in 7e; plaice_jk: plaice in 7j–k; sole_e: sole in 7e; whiting: whiting in 7b–c and 7e–k).

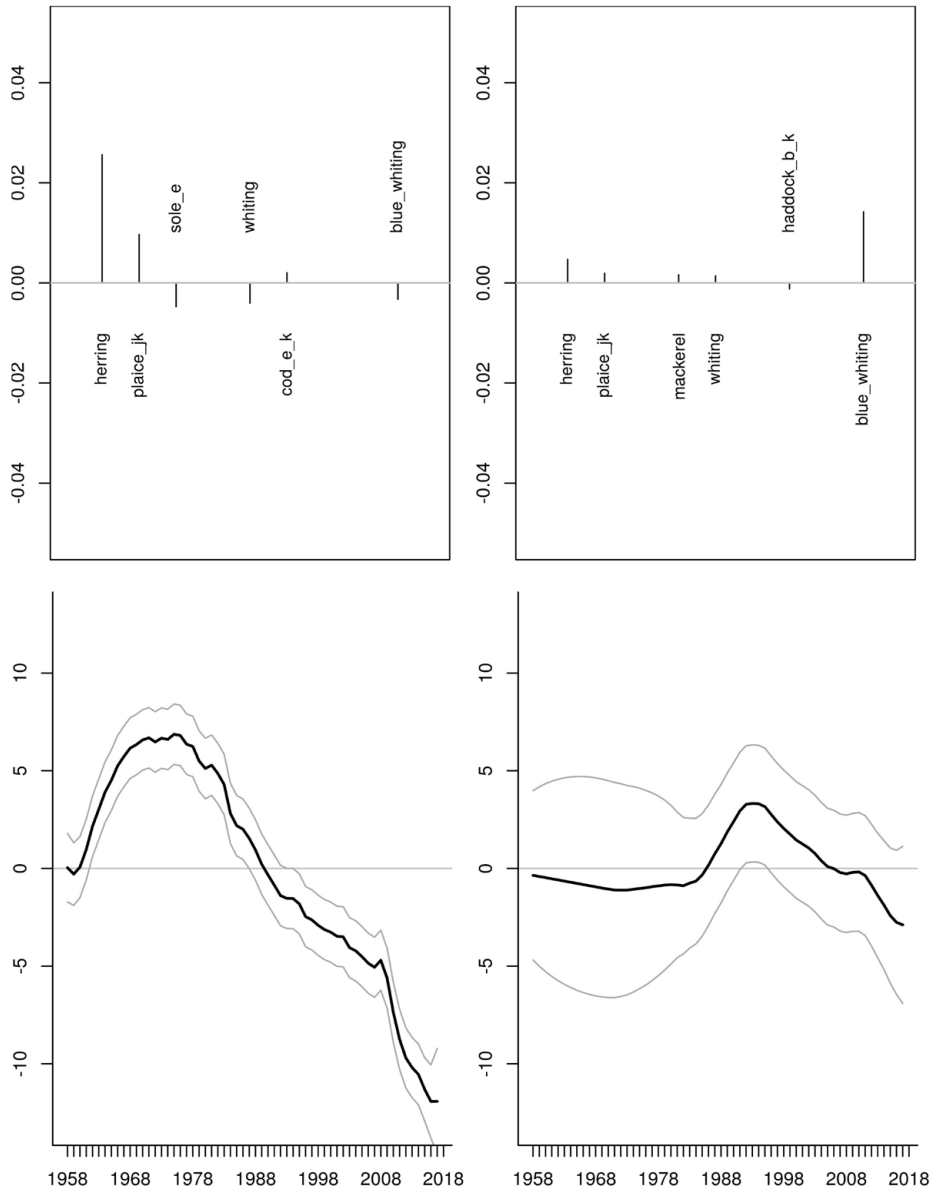


Figure 6.6. Trends (bottom panels) and factor loadings (top panel) from the DFA model with SST included as a covariate.

population-specific and broadscale ecosystem-level change in the Celtic Sea were examined.

6.3.2 Methods

Otoliths were obtained from collections held by the Marine Institute, which originated from port sampling and scientific surveys in the Celtic Sea. Sample sizes and temporal coverage for each species are summarised in Table 6.1. Otolith images

were captured using a stereomicroscope with digital camera, interfaced with a PC. Annual growth increments were measured using image analysis software, along a consistent transect, from the otolith core to the edge.

For each species, GAMMs were used to model increment width as a function of the fixed effects – age at increment formation (age), age at capture (AAC) and otolith side (side) – and the random effects – year of increment formation (year), year of hatching

(birth year) and fish ID. The inclusion of fish ID as a random effect accounted for the non-independence of repeated measurements from the same otolith. Once the optimal random- and fixed-effect structure was determined, environmental (temperature, salinity, wind patterns, zooplankton and phytoplankton abundance indices), population (stock size and recruitment) and fishing-related (estimated fishing mortality) covariates were added to each optimal model in a stepwise manner. Model selection was conducted using Akaike information criteria (AIC).

6.3.3 Results

The best-fitting GAMM for each species is shown in Table 6.2. As expected, otolith growth declined with age across all three species. Age explained most of the variability in growth in haddock and herring whereas in plaice there was a relatively high proportion of individual and unexplained variability (explained deviance estimates; see Table 6.2).

In all three species, otolith growth decreased with age at capture; the increment width at each previous age was lower in older fish (Figure 6.7). This may indicate selective mortality of faster growing fish (e.g. as a result of fishing) or may reflect the later recruitment of slower growing fish to the fishery. The influence of age at capture was greatest for plaice (3.4% explained deviance) followed by haddock (0.2% explained deviance) and herring (0.034% explained deviance) (see Table 6.2).

The year random effect showed considerable interannual variation in otolith growth across the three species (Figure 6.8). Coherency in growth across species was detected: the haddock annual growth signal was significantly correlated with the annual growth signal for plaice ($r=0.41$; $p<0.05$) and the cohort growth signal for herring ($r=0.55$; $p<0.01$). The correlation between the herring and the plaice annual growth signal was not significant ($r=0.19$; $p>0.05$).

When the year random effect was substituted for environmental, population and fishery-related covariates, some evidence of density dependence was detected: growth of herring and haddock declined at higher stock sizes. Growth of plaice declined with increasing salinity and with positive values of the AMO index (see Figure 6.7).

6.3.4 Conclusions

The study highlights the value of otolith collections for describing temporal trends in growth over extended time periods and investigating associations with environmental conditions and anthropogenic pressures. The underlying annual growth signals, after accounting for intrinsic sources of variation in growth, showed considerable interannual variability. Significant correlations in annual growth signals across species may be indicative of an ecosystem-wide response to an external signal.

Table 6.1. Sample size, age range and temporal coverage for each species

Species	Sample size	Age range (years)	Collection years	Growth time series temporal coverage
Plaice	402	1–10	1994, 1996–1998, 2005–2013	1985, 1987, 1989–1997, 1999–2012
Haddock	486	1–6	1993, 1995–2005, 2009–2014	1990–2013
Herring	529	1–9	1998–2014	1993–2013

Table 6.2. Terms included in the best-fitting GAMM of otolith increment for each species

Species	Terms in optimal model		Residual deviance
	Fixed effects (explained deviance)	Random effects	
Plaice	Age*side (38%), AAC (3.4%)	Year (2.7%), fish ID (11.7%)	44.2%
Haddock	Log(age) (88%), AAC (0.2%)	Year (0.9%), fish ID (0.8%)	10.1%
Herring	Log(age) (93%), AAC (0.034%)	Birth year (0.45), fish ID (0.2)	6.3%

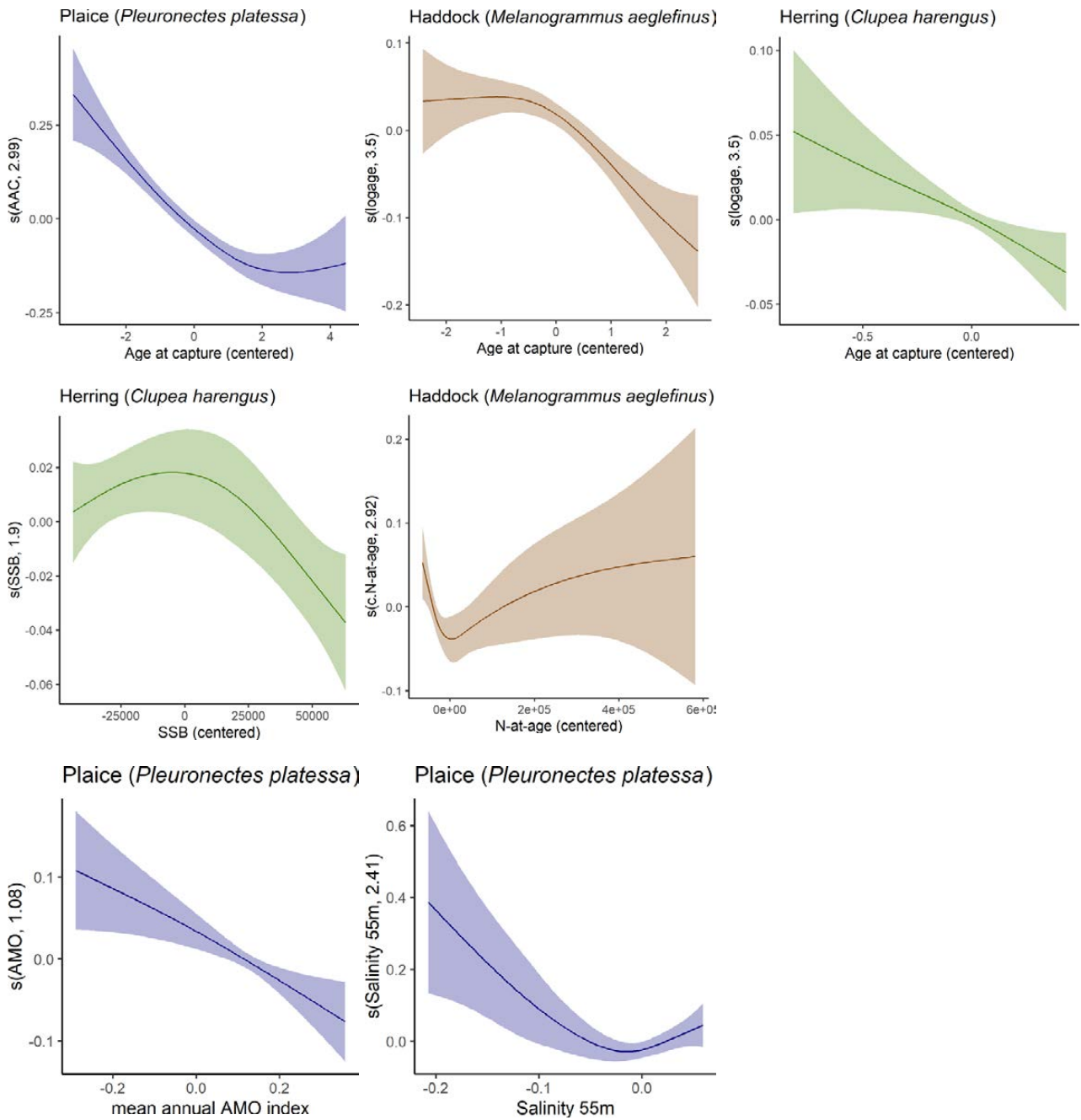


Figure 6.7. Plots showing predicted relationships between otolith growth and significant covariates from the best-fitting GAMMs.

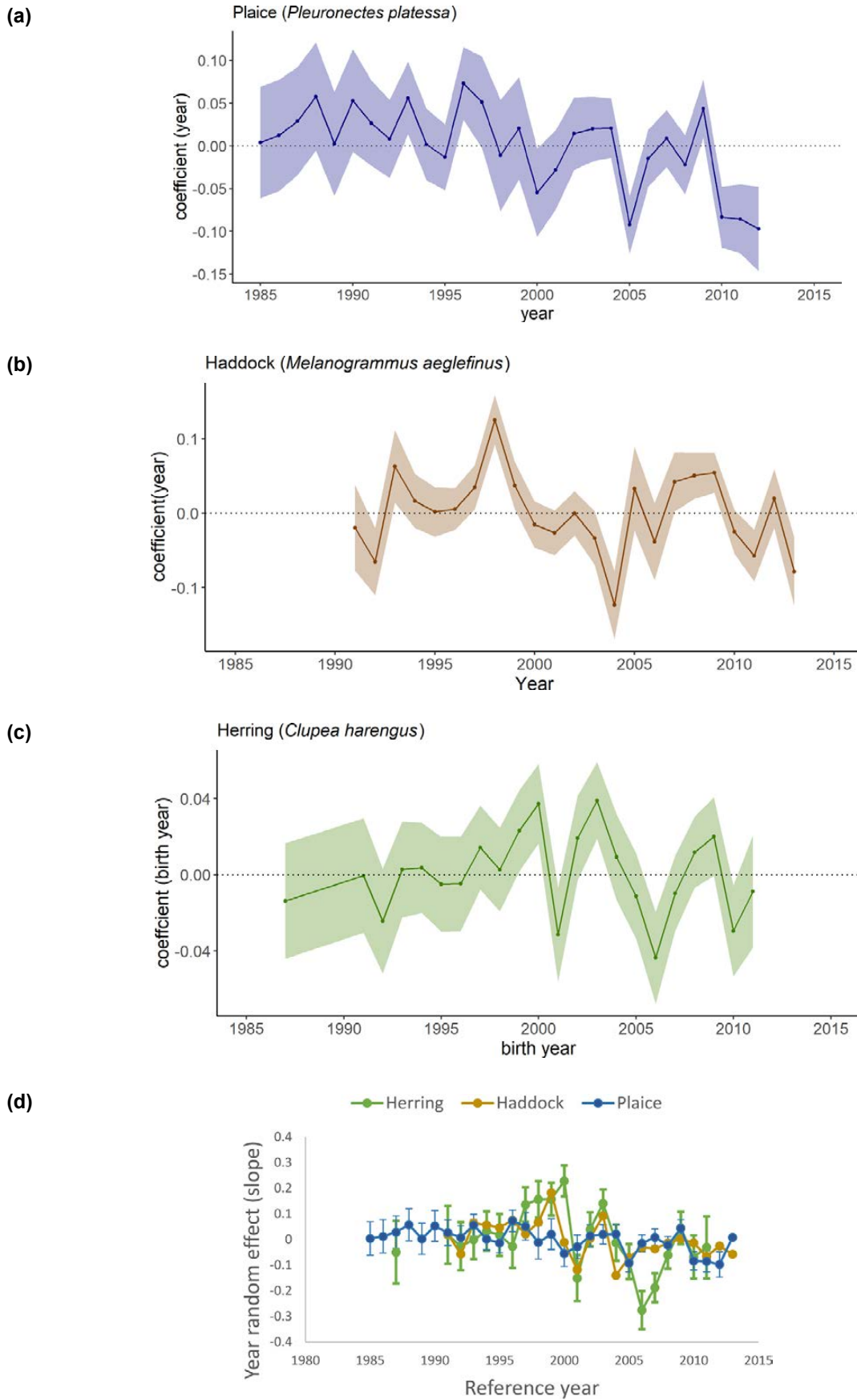


Figure 6.8. Random effects from the GAMMs plotted against year (plaice and haddock) and birth year (herring) to show annual trends in otolith growth (a–c) and interspecies cross-correlations in the annual growth signals (d).

7 Detecting Step Changes in the Celtic Sea Ecosystem using Bayesian Online Change-point Detection

7.1 Background

Technological advances are steadily enhancing our capacity to monitor the marine environment while international collaboration and online data sharing has made long time series of biological and environmental data increasingly accessible. This infrastructure can support research into marine ecosystem change, allowing us to understand change and develop appropriate management responses. To unlock that potential requires statistical methods that can effectively extract clear signals from complex and highly variable multivariate data. An important form of change is that which takes place over a short period of time (a change point) – time series may change state abruptly from one regime to another. From a management perspective it is critically important that such changes are recognised as quickly as possible so that appropriate mitigation measures can be taken. Development and application of a method for estimating such changes in a fully probabilistic framework is the focus of this chapter. The method was applied to all of the time series compiled or generated as part of the project. These data reflect temporal changes in the Celtic Sea ecosystem across multiple taxa, trophic levels and physical environmental variables.

Change-point detection is complicated by the dimensionality of the problem in that, for a series with n observations, there exists n possible change points, assuming that a change point must occur at the point of observation. Many algorithms have been developed to estimate change points in time series, including sequential t -test analysis of regime shifts (STARS) (Rodionov, 2004; Rodionov and Overland, 2005), Hamilton's Markov-switching filter (Hamilton, 1989) and online change-point detection algorithms (Page, 1955; Lorden, 1971; Desobry *et al.*, 2005). STARS focuses on changes in the mean, whereas the Hamilton filter assumes a set number of underlying states that the system switches between. In contrast, online change-point detection algorithms work with higher moments of the data (particularly the variance).

Frequentist algorithms such as those presented above rely on assumptions about repeated sampling to draw inference on the uncertainty of the system (Jaynes, 2003). Bayesian modelling draws inferences on the data using prior information and likelihood and does not rely on concepts of repeated sampling. Adams and MacKay (2007) developed a BOCPD algorithm, which has useful properties such as:

- being able to work online (no need to refit the model as new data become available);
- providing a full probabilistic description of the change-point model, including changes to the mean state and variance;
- making no assumption about the number of regimes;
- having easily interpreted run length probability distributions, affording early detection frameworks;
- having offline (smoother mode) capabilities.

As such, the BOCPD algorithm covers many of the requirements of the analytical methods of this component of the project.

Perälä and Kuparinen (2015) and Perälä *et al.* (2017) applied the BOCPD algorithm to fish breeding success (recruits per spawner and dynamic parameter estimation). Changes were detected in key rates governing the population dynamics, highlighting that fish populations are dynamic and can undergo sudden changes. To our knowledge there are no systematic applications of BOCPD to time series across multiple ecosystem components, as is the focus here.

7.2 Method

7.2.1 Model specification

A run length distribution is the main feature of the BOCPD algorithm (Adams and MacKay, 2007). For a given point in time (typically annually here), the run length distribution is the probability distribution across all possible run lengths in that year. For the next year, the current run length can either continue

or change such that a new run starts. Each possible run has parameters governing the mean and the variance (here, alternative formulations are possible) of the run starting in that year. For example, if a time series began in 1960, the parameters of the 1960 run are updated with each new observation and are effectively running means and variances from 1960 to a given time point. Runs are started at each time point although they may have a low probability of being the dominant run. The probability that each observation arises from a given run will be likely to change over time, for example, the 1960 run might not describe the 1980s observations well. As such, the probability that a given run describes the data is updated and a run may either continue or collapse in any year.

The BOCPD algorithm provides a fully probabilistic description of the data, consisting here of:

- *Underlying predictive model.* Here, assumed to be a normal likelihood with a normal-gamma prior distribution. A normal-gamma prior distribution is conjugate to a normal likelihood, resulting in a posterior distribution that is also normal-gamma. This allows for straightforward updating of the parameters without the need for Markov chain Monte Carlo sampling of the posterior distribution.
- *Priors.* Hyperparameter priors were set on the mean location, mean scale, precision shape, precision inverse scale and hazard rate parameters using the methods of Perälä and Kuparinen (2015). The hazard rate here is the prior probability of a change and can be expressed in inverse units as the expected time between change points. We set the change-point hazard rate at 1/10 (the same as Perälä and Kuparinen, 2015). Note that the priors are coupled with the data so the actual posterior frequency will be likely to be that implied by the prior, although testing sensitivity to this parameter is important.
- *Data.* The BOCPD algorithm was fit to each time series separately to avoid any a priori grouping of series. Where there were missing years, linear interpolation was used. Linear interpolation was considered more conservative here in that forward projecting methods would assume that the next time point was the same as the previous and inflate the change-point probability when the next true observation arrives. All series were fit to the entire series but presented from 1950 onwards

as, prior to this, only a relatively small number of environmental series were available.

Series were grouped according to variable type (e.g. wind, fish breeding success) within broad ecosystem component categories (e.g. environmental, plankton) to facilitate presentation and interpretation of the results.

Recursion updates were performed in the R statistical environment (R Core Team, 2018), with code developed specifically for fitting and interpreting the BOCPD algorithm.

7.2.2 *Model output*

For each series, a summary plot is presented consisting of the data, estimated run length probability distribution over time, fitted means and standard deviation (both online – filtered – and offline – smoothed – using all of the data past a given time point in contrast to the filter, which works only up to a given time point). These by-series plots are useful for querying subsequent summaries across series. Note that the run length distributions are currently presented as filtered online versions. Attempts to smooth the run lengths resulted in incorrect run lengths, although this is possible (Perälä and Kuparinen, 2015). Further work on smoothed run length distributions will improve this.

To summarise across series, we plot the probability of a change point for each series for each year. As a highly probable change point may not emerge until a number of years after the change (Perälä and Kuparinen, 2015), we use a 2-year lag but plot the run lengths at times corrected for the lag. Two versions of this summary plot are presented: a full probabilistic version with probabilities between 0 and 1, and a threshold version that displays only those change-point probabilities > 0.5.

To further summarise the data we sum the probabilities across each variable group and divide by the number of series in that group to give an average probability of a change point in a given year across all series present in that year. As the number of series present changes over time (coverage), we use the opacity of the colour to denote the coverage (proportion of series from that group present in a given year).

7.3 Results

7.3.1 By-series fits

Most series displayed at least some evidence for changes to either the mean level or the variance over their time course. Some evidence is defined as having even a low probability of change. High probabilities of change points are discussed later when threshold results are presented (see sections 7.3.3 and 7.3.4).

Selected fits illustrate features of the BOCPD algorithm applied here. Where abrupt changes occur in the distribution of the data (typically the mean although the standard deviation is also included), the model picks up on the changes quickly and with high probability (e.g. *C. finmarchicus* in Figure 7.1). This contrasts with alternative approaches such as the Kalman

filter, which take longer to adjust the mean level for a sudden change (Peterman *et al.*, 2000). Where the data display a continual trend, the model attempts to account for this by estimating multiple change points (e.g. guillemot time series in Figure 7.2) – this fit also illustrates a difficulty with priors in that the prior for the variance was too large (based on the marginal limits) and took a long time to update in the model. Highly variable data also present the model with a challenge, with many low-probability signals of changes (e.g. coefficient of variation of wind direction in Figure 7.3).

7.3.2 Across-series change points

Plotting change-point probabilities across series enables comparison of the timing of changes across all

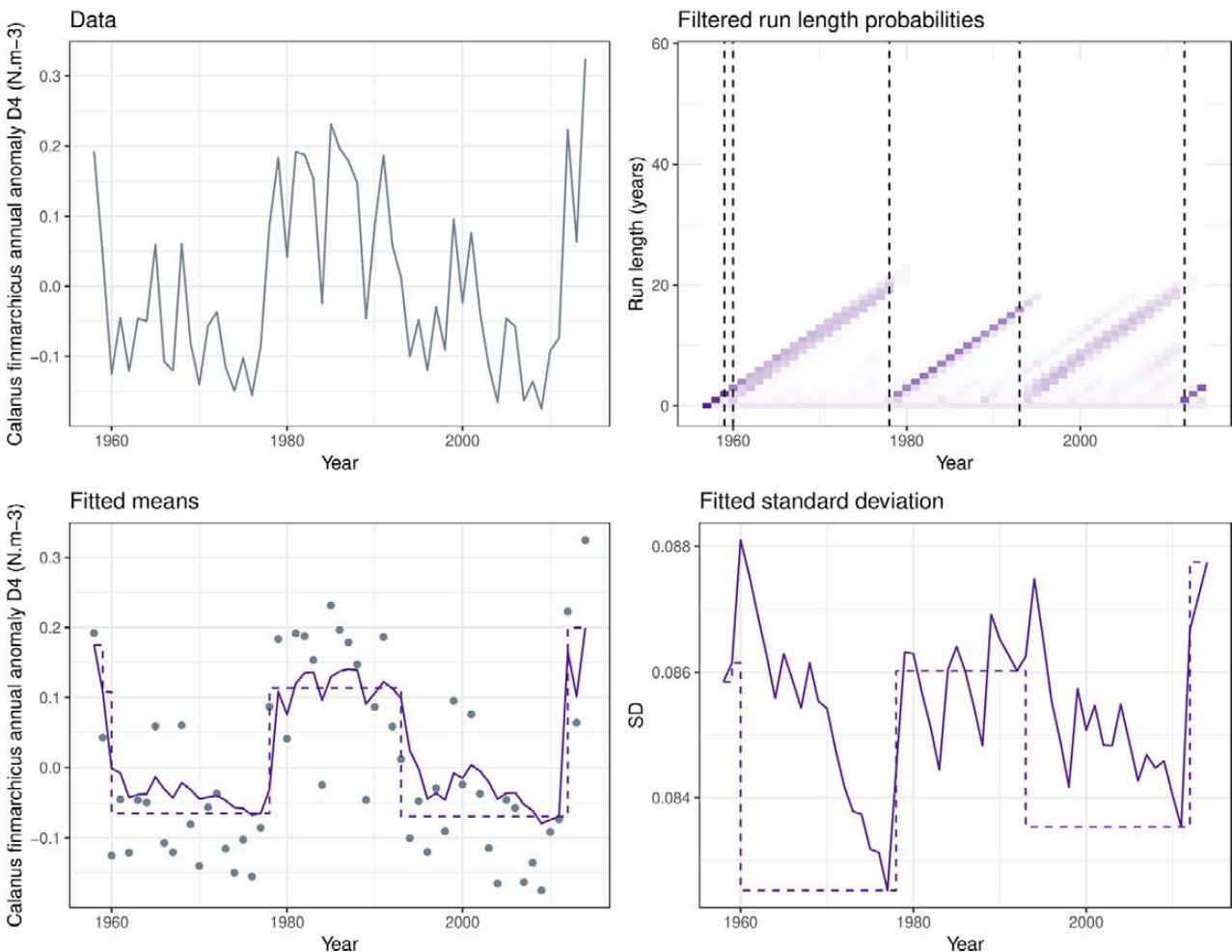


Figure 7.1. BOCPD algorithm fit to *C. finmarchicus* annual anomaly series illustrating how the model picks up on abrupt changes in the mean. The filtered run length probability plot shows the probability of each run length in purple shading and the estimated change points as dashed vertical lines. Fitted means and standard deviation plots show the filtered estimates (online) as solid lines and smoothed estimates (offline) as dashed lines.

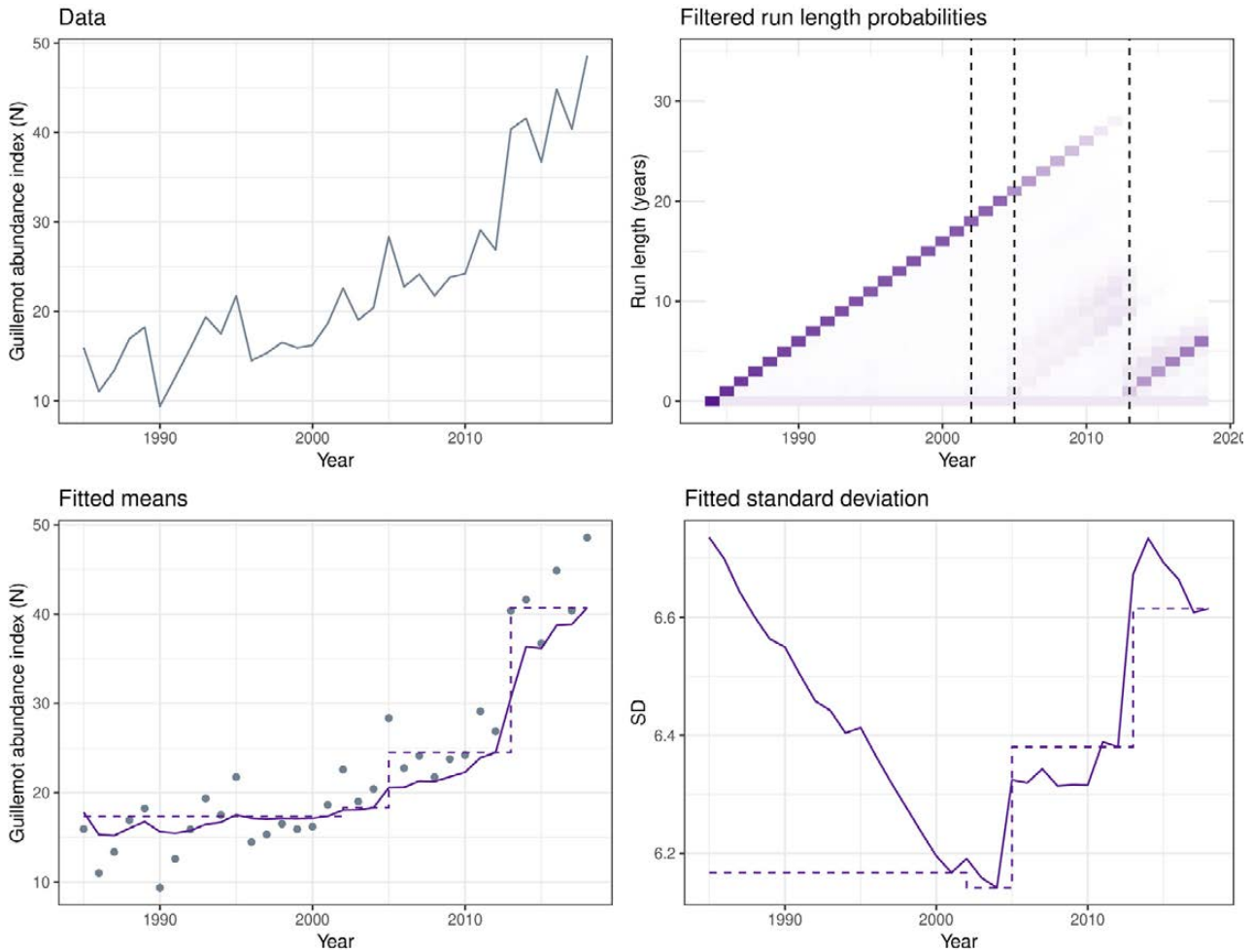


Figure 7.2. BOPD algorithm fit to the guillemot abundance series illustrating how the model attempts to account for trends by estimating multiple uncertain change points in the mid-2000s. The filtered run length probability plot shows the probability of each run length in purple shading and the estimated change points as dashed vertical lines. Fitted means and standard deviation plots show the filtered estimates (online) as solid lines and smoothed estimates (offline) as dashed lines.

series (Figures 7.4 and 7.5). The results are discussed by ecosystem component and variable group.

Environment

- Temperature: Change points occurred around 1987, with the mean latitude of the 13°C isotherm moving abruptly north and the mean annual SST increasing (note that these variables are highly correlated).
- Wind: The intensity and duration of the prevailing south-westerly wind displayed evidence for change points in 1990, with an increase in the total number of hours and a decrease in wind strength, which was elevated between 1985 and 1990.
- Salinity: Similarly, salinity at 5m and 55m displayed some evidence for a change around

1987 and 1988, with salinity increasing from a period of lower salinity during the late 1970s and early 1980s.

- Climatic indices (SPG, NAO, AMO; labelled “Index” in Figure 7.5) displayed weak evidence for change points at a later time point around 1995. These changes are weakly reflected in low but non-zero probabilities of change points in other environmental variable series at that time (wind, temperature).

Plankton

- Phytoplankton displayed some evidence for an increase in chlorophyll a concentration at a similar time to the changes in the climatic indices (around 1995).

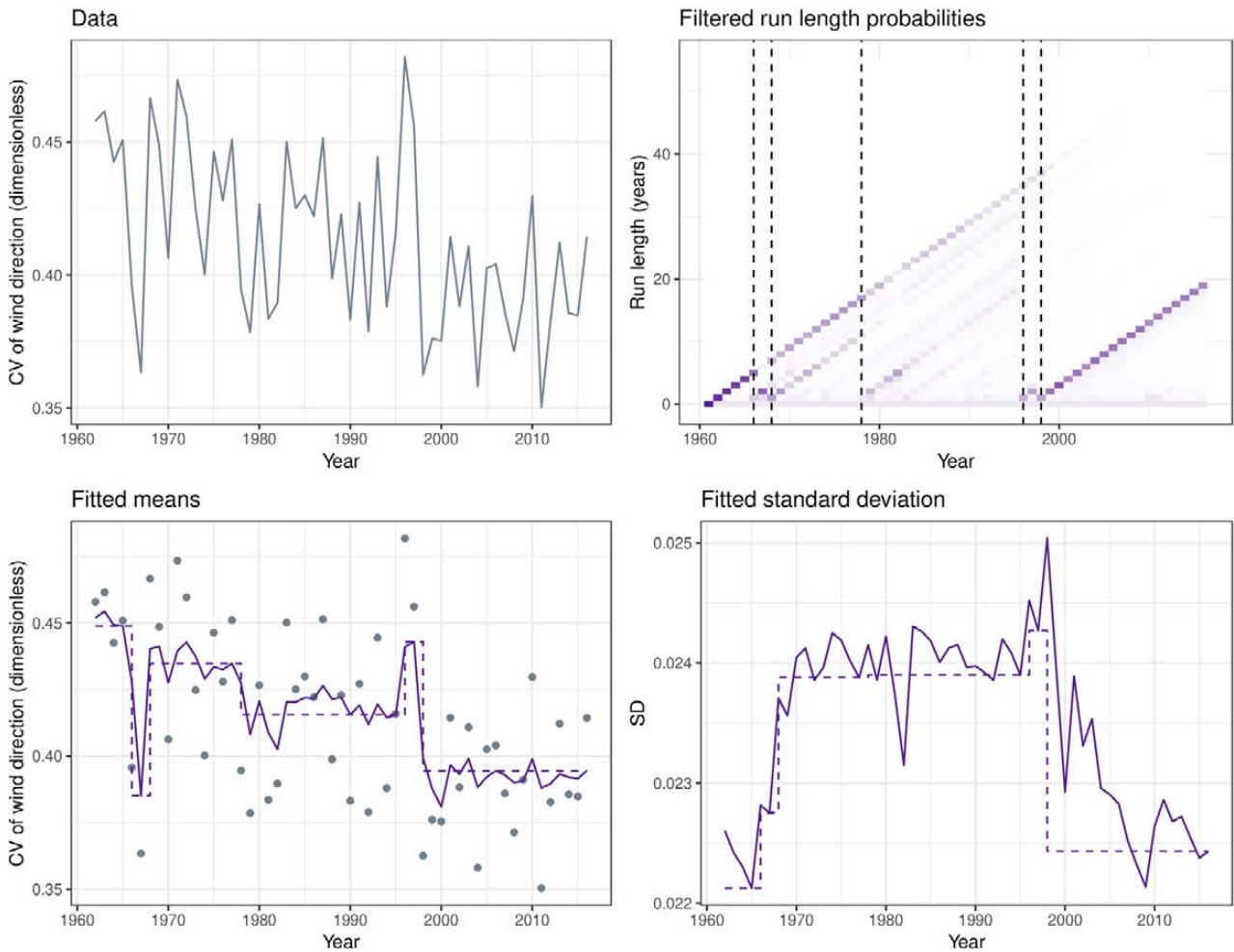


Figure 7.3. BOCPD algorithm fit to the coefficient of variation (CV) of the wind direction series illustrating how the model responds to highly variable series by estimating multiple change points.

- Zooplankton: Among the zooplankton, marked change points were observed in one of the OSPAR PH2 indices of total copepod abundance (OSPAR PH2ZOO Anomaly ECO3CS) in 2000, with a decrease and subsequent increase. *Calanus finmarchicus* Annual Anomaly D4 displayed four marked change points separated by approximately 17 or 18 years. Hyperiidea Annual Anomaly D4 displayed a marked change to higher abundance around 2009. Although many of the other series showed evidence for change points, the probabilities were typically weak and below the threshold of 0.5. This result may be masked by strong trends and directions in trends, however (see the Euphausiacea Annual Anomaly D4 or OSPAR PH2ZOO Anomaly ECO5CS fits on GitHub). The gelatinous zooplankton, Doliolidae and Thaliacea, displayed evidence for change points around 1997, with decreases in abundance following highly variable periods on a background

of a generally increasing trend. Towards the end of the series both groups increased again.

Fish

- Weight: The year and birth year random effects (from the GAMMs of mean weight at age described in section 6.2) showed a diversity of change points with varying evidence across time and no clear pattern across series. Here, we focus on significant change points (greater than a threshold of 0.5; see Figure 7.5) that occurred for the following: blue whiting year effect in 1990 and birth year effect in 2005; mackerel year effect in 1990; plaice in area 7e year effect in 1998 and in area 7j–k year effect in 1999; and sole birth year effect in 1971.
- Growth: Change points were detected for haddock growth year effects (from the GAMMs of otolith growth measurement described in section 6.3)



Figure 7.4. Change-point probabilities across series. Colour scales with dark purple denoting a probability of 1 and white denoting a probability of 0. Horizontal lines appear where no data exist for that series. CV, coefficient of variation.

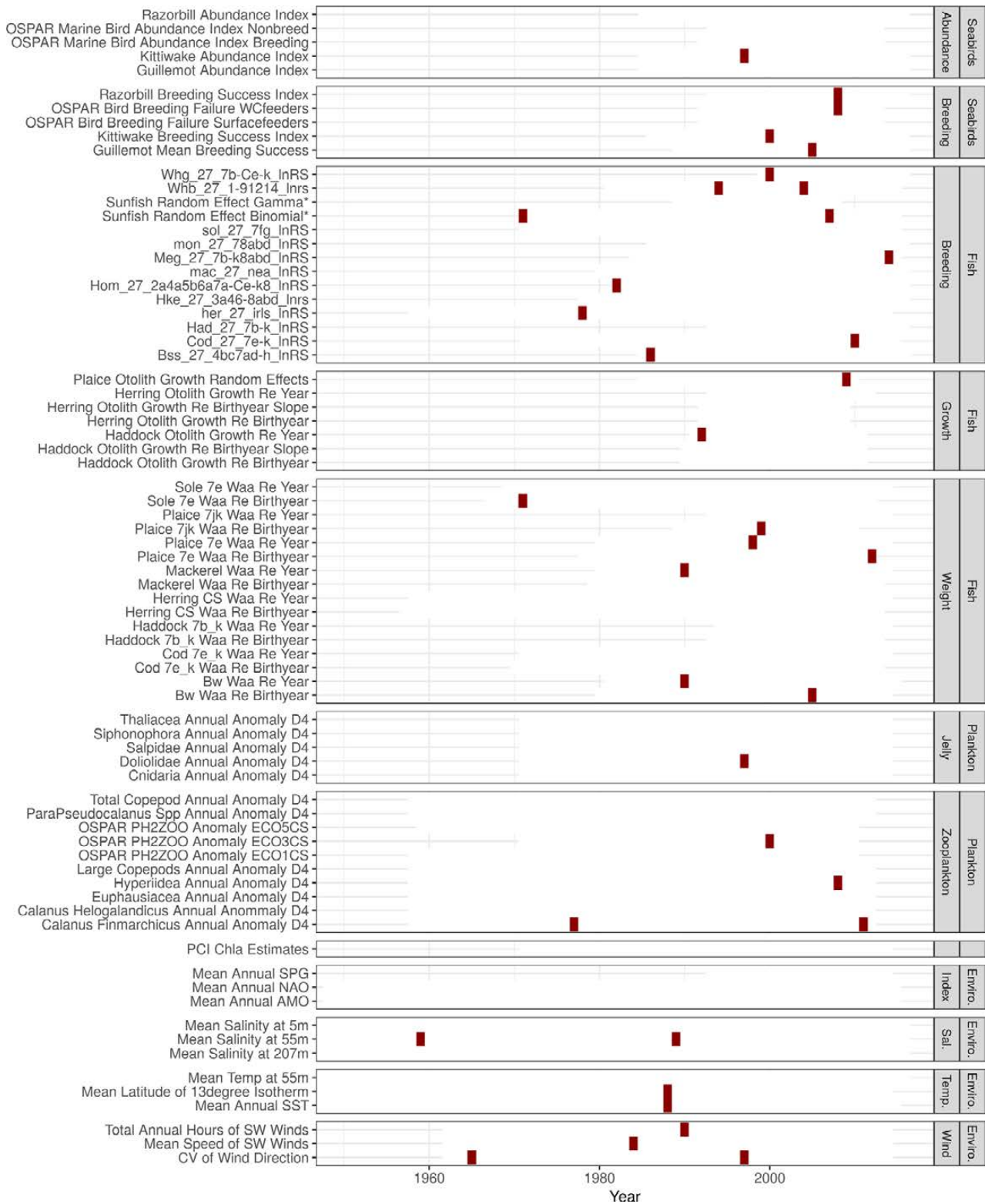


Figure 7.5. Change points across series. Each coloured cell represents a change-point probability greater than a threshold of 0.5. Horizontal lines appear where no data exist for that series. CV, coefficient of variation.

in 1992 and for plaice growth random effects in 2009.

- Breeding success: Similarly, fish breeding success displayed a diversity of change points across time, with change points occurring for whiting decrease in 2000; blue whiting increase in 1994 and subsequent decrease in 2004; megrim potential increase in 2014 followed by a rapid return; horse mackerel decrease at the beginning of the series in 1982; herring increase in 1978; cod decrease in 2010; and bass increase in 1986.

Seabirds

- Breeding success: Guillemot breeding success showed evidence for a change point in 2006 to lower levels. Kittiwake breeding success declined in 2000, whereas razorbill breeding success displayed a marked decrease in 2009. The OSPAR B3 indicator of marine bird breeding failure (water column feeders) also had a change point in 2009 to a higher index (more failures).
- Abundance: The kittiwake abundance index had a change point in 1998, showing a considerable decline.

7.3.3 Change-point summary

Average change points across all series demonstrate periods of coherent changes across environmental component series (Figures 7.6 and 7.7), with marked changes occurring in the late 1980s and mid-1990s. These changes are also reflected in changes in the single phytoplankton series presented here (*C. finmarchicus* annual anomaly; see Figure 7.1). For other ecosystem components important changes occur but are not tightly coupled or apparently cascading across series. For example, fish breeding success shows a consistently low background rate of change points across all series over time, which is also the case for zooplankton (*C. finmarchicus* annual anomaly; see Figure 7.6). Although the changes are not tightly coupled across series, it is critically important to note that these changes may be highly significant for given ecosystem components.

7.4 Discussion

The BOCPD algorithm provides a fully probabilistic framework to estimate run length probabilities and

distributions for the posterior distribution of the states across time (see Figures 7.1–7.3). A probabilistic framework provides quantified evidence for change points over time and, as such, is of central utility to informing cross-system monitoring of environmental and biological series. In this section, the main results are briefly discussed, caveats highlighted and future ideas presented.

7.4.1 Change-point evidence and synchronicity

Evidence for change points was present in each group and ecosystem component. This ranged from a low to non-negligible probability of change points for some series to high probabilities of change points above the threshold (see Figures 7.4 and 7.5). We can therefore say that the Celtic Sea system as represented by monitored series is highly dynamic and undergoes changes over varying timescales.

Tightly coupled environmental changes occurred around the late 1980s and early to mid-1990s (see Figures 7.4–7.7). Importantly, the series studied represent temperature, salinity and wind drivers, all of which are critically important components of the environmental conditions experienced by the biological ecosystem components.

We did not observe evidence of simultaneous or cascading changes in the filtered run length probabilities from the biological series (see Figures 7.4 and 7.5). There may be a number of methodological and mechanistic reasons for this:

- Methodological:
 - Currently, filtered run length probabilities are used with a lag. For some series this lag may be too short to demonstrate a given change. Smoothed run length probabilities that are obtained by hindcasting the system could alter this and potentially show more coherent changes across species. We doubt that the results will change radically from the smoothed probabilities, but this is presented as a possibility.
 - The model is sensitive to the priors on the variance parameters. It is possible that more subtle changes have been missed because of prior assumptions. Again, smoothed run length distributions would address this but, in addition, robust ways of specifying the priors without

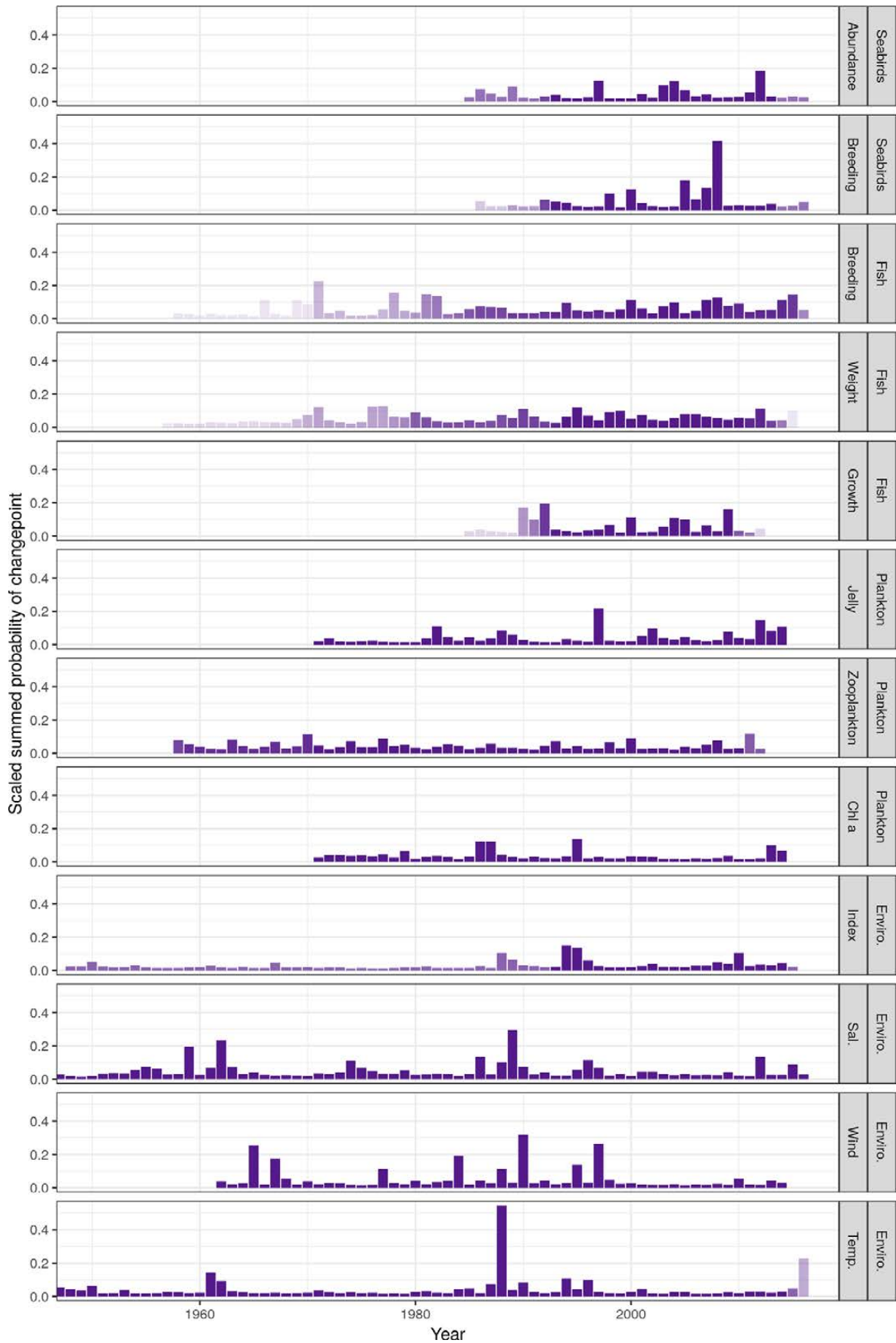


Figure 7.6. Average change-point probability across all series present in a given year. The opacity of each bar represents the proportion of series from a given group present in a given year (termed coverage).

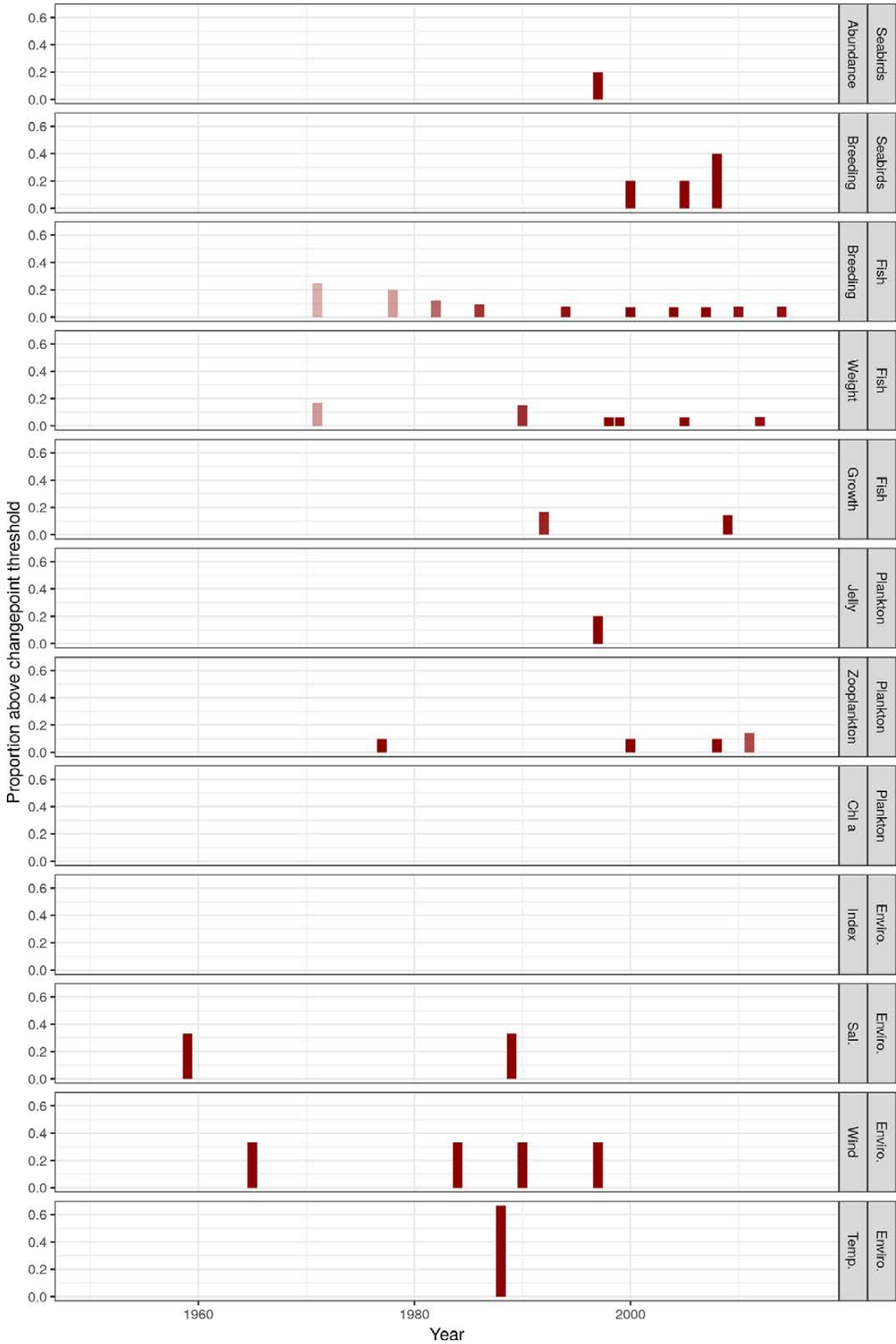


Figure 7.7. Proportion of series above a threshold of 0.5 in a given year. The opacity of each bar represents the proportion of series from a given group present in a given year (termed coverage).

biasing the results of the model should be developed.

- Observation window – from a time series perspective even the longest series are relatively short. It may be that the system has not been observed for long enough or that the resolution of the observation is too coarse to observe synchronous change.
- Mechanistic:
 - The Celtic Sea is a relatively open system, connected by a contiguous continental shelf and a dynamic open hydrography. Such openness may preclude synchronous changes across all series, which are additional to local forcing under the influence of external forcing.
 - We observe synchronicity in changes in environmental series; density-dependent and top-down effects in a diverse system may result in different community effects from system-wide cascading or synchronous change.
 - Complex non-linear dynamics are expected to show change points and regime shifts (Sugihara *et al.*, 2012) in communities. It is also possible that complex dynamics alter our expectations of cascading or synchronous changes across series.
 - Although the biological series observed do not appear to display coherent changes across series, we stress the importance of methodological improvements that may affect this result and also highlight the important result that changes clearly do occur for many series and that this has important consequences for management.

7.4.2 *Caveats*

An important caveat to the analyses presented is the absence of a hindcasted run length probability distribution. This absence is purely technical, with the attempted implementations not working as expected. It is anticipated that this can be improved before peer-review publication of the results. Notwithstanding, we present the filtered results that use the data to a given point in the time series and that are critically important in the online (i.e. real-time) detection of change points.

Development of improved priors would also assist in the performance of the filtering stage of the algorithm. This could simply be robust versions of those algorithms implemented to deal with spikes when

specifying priors from summary measures of the limits of the data.

Although the present algorithm works on the states (here, the absolute values of the series), it has some difficulty working with data with clear trends (see Figure 7.2). It would also be of interest to investigate the rate of change of selected series over time in which we identify change points not in the level but in the rate of change. Preliminary attempts to do so were hampered by a high level of variability, resulting in highly variable rates of change. Although it should in theory be possible for this to be identified in the model as a change in variance (volatility), a better approach might be to adopt the standard in functional data analysis of pre-smoothing the data before differencing (Ruppert *et al.*, 2003) while estimating breakpoints in the rate of change. Adopting an approach of monitoring both the state and the rate of change for change points would form a powerful additional framework using data already collected.

7.4.3 *Future development*

To fully realise the potential of the algorithms developed, it is important that the data are continually updated and results reported. This would enable:

- monitoring and reporting on change across series at various aggregation levels (e.g. Figures 7.1, 7.4 and 7.7) and thresholds;
- continual methodological development to produce accurate evidence to support management decisions, in particular multivariate extensions in which the number of run length distributions can be lower than the number of series;
- a “go-to” location for further scientific development (e.g. hypothesis development) and management development;
- the development of a modular framework that is transferrable to other systems.

It is important to recognise that abrupt changes have and will occur in the Celtic Sea and that methods to analyse such changes have been developed, coupled with ways of communicating such changes at various levels of aggregation. In a future of further predicted change we consider such frameworks vital for providing cutting-edge advice on sustainable management.

8 Overall Recommendations

- *Sustain long-term datasets.* The project highlights the value of long-term biological datasets for understanding ecosystem change. Some of the datasets used within the project were collected outside national data collection programmes and yet they are useful for ecosystem monitoring and could contribute to assessing progress towards conservation targets (e.g. under the MSFD). For example, the sunfish time series, sourced and digitised as part of this project, is collected largely by volunteers as part of a seabird monitoring programme and provides a presence/absence and abundance indicator for a fish species that is not adequately assessed by fisheries monitoring programmes. As a potential indicator of increasing jellyfish abundance and more widespread ecosystem change, this time series could contribute to MSFD monitoring under Descriptors 1 (Biodiversity) and 4 (Food webs). The need for a balanced and integrated ocean-observing system has been highlighted by the European Marine Board (Benedetti-Cecchi *et al.*, 2018). At a national level, long-term support should be provided to maintain extended ecological time series and to integrate them with data resources from national monitoring programmes.
- *Implement statistical methods for handling observer time series.* The European Marine Board has highlighted the value of citizen science initiatives for enhancing observation capacity while also increasing public awareness of the importance of biological observation, building public confidence in the scientific process and fostering connectedness with the marine environment (Benedetti-Cecchi *et al.*, 2018). Data from citizen science programmes are more prone to sources of imprecision and bias than data collected through rigorous scientific surveys. Appropriate statistical treatment of these data can account for this error to effectively detect the underlying long-term trends in the time series and can also be used to refine the design of observer programmes. In this study, the analysis of the sunfish time series showed that sunfish detections per unit effort increased as observer number and watch duration increased. The value of the Cape Clear observer programme for monitoring sunfish in the Celtic Sea could be enhanced by ensuring that observer numbers and watch duration are maintained at as high a level as possible. It is recommended that the statistical approaches to observer data applied within this project are implemented more broadly to maximise the value of national observer datasets for informing management decisions. This could be achieved by involving statisticians in the design of citizen science initiatives and the subsequent analysis of time series.
- *Preserve biochronological material from national fisheries monitoring programmes.* Under the MSFD, the demographic characteristics of fish populations (including age/size structure and growth) should be maintained at levels that are indicative of a healthy population and not adversely affected by anthropogenic pressures. However, for demographic indicators, pressure–state relationships are complex and subject to natural and climate-related variability, and no targets or reference points have been established (Marine Institute, 2015). Climate-driven changes in demographics are of particular concern for the future management of fisheries and marine ecosystems and the need to examine the most likely changes in growth under future climate scenarios is recognised (DAFM, 2019). Understanding the complex relationships between fish growth, climate and fishing requires detailed individual-level data that capture inherent variability in the response. Otolith growth measurements are particularly valuable in this respect because they describe how an individual fish has responded to its environment throughout its life cycle. This project demonstrates how the analysis of individual growth histories in otoliths can be used to partition intrinsic sources of variability from environmental and fishing-related effects. Extended otolith biochronologies capture long-term changes in growth and can help to predict future response to climate change. Every year large numbers of fish otoliths and scales are

collected as part of national fisheries monitoring programmes to derive individual age estimates, which are subsequently aggregated to produce population-level estimates of size and abundance at age. Currently, the rich individual-level data contained in these structures are underutilised and systems for curating the material are lacking. It is recommended that the preservation of these valuable archives is prioritised to make them available for research into climate- and fishing-related influences on fish demographics.

- **Monitor changes in wind-driven circulation and larval dispersal.** The Climate Change Sectoral Adaptation plan for the seafood sector states that “continued monitoring of the spatial distributions of commercially exploited fish stocks is essential to support future management” (DAFM, 2019). This study demonstrates how changes in wind-driven circulation can influence dispersal to nursery grounds, with consequences for the distribution of adult stocks. Oceanographic simulations coupled with field studies of larval distribution can provide an early warning of potential changes to the distribution of adult fish stocks and should be incorporated into fisheries monitoring programmes. To support this, better knowledge of small-scale local oceanographic processes is needed, as well as field evidence of larval behaviours.
- **Monitor changes in jellyfish abundance and associated food web effects.** The pronounced increase in the abundance of jellyfish (calycophoran siphonophores only) in the Celtic Sea since the late 1990s has consequences for the food web structure and ecosystem service provisioning. Indeed, Haberlin *et al.* (2019) (see Chapter 4) found that siphonophores can at times contribute up to 42% of the total zooplankton biomass (mg C m^{-3}). Furthermore, the warm water gelatinous community of the Celtic Sea typically had an approximately 40% greater gelatinous biomass than the cold water gelatinous community, and therefore jellyfish in warm water communities may have a greater predatory

impact on commercial fish species (Haberlin *et al.*, 2019). As the CPR record provides a time series of relative abundance for some jellyfish groups, it could contribute to the development of broadscale food web indicators under the MSFD. However, jellyfish indices from the CPR samples need to be compared with traditional plankton surveys in order to fully resolve what species are being captured. For example, under tipping points we have begun a retrospective examination of historical mackerel eggs survey data samples from the Celtic Sea. Comparison of these data with historical CPR data will provide the much-needed clarification on what the CPR samples represent in terms of jellyfish other than calycophoran siphonophores. However, it is vital for Ireland to start building jellyfish time series that are independent of the CPR data so that we can examine whether or not there are increases in the different gelatinous groups, many of which are not effectively sampled by the CPR survey (e.g. large scyphozoans and salps). It is recommended that some measure of the contribution of jellyfish to zooplankton be incorporated into food web indicators as these are developed. A recent study has highlighted that over half of recent food web models using EcoPath have not included a jellyfish group (Lamb *et al.*, 2019).

- **Incorporate change-point detection into ecosystem monitoring.** The BOCPD framework presented here provides a means of condensing high volumes of complex ecosystem data into a single coherent analysis of ecosystem change points, allowing shifts to be rapidly identified and effectively communicated at various levels of aggregation. Incorporation into ongoing monitoring programmes would ensure that data are continually updated and results reported. This approach could be applied to ecosystem indicators that have already been prioritised for monitoring and could be used to identify variables that display significant shifts with societal consequences and might warrant inclusion within a Framework for Ocean Observing (Lindstrom *et al.*, 2012).

References

- Adams, R.P. and MacKay, D.J., 2007. *Bayesian Online Change-point Detection*. Technical report. University of Cambridge, Cambridge, UK.
- Aeberhard, W.H., Flemming, J.M. and Nielsen, A., 2018. Review of state-space models for fisheries science. *Annual Review of Statistics and its Application* 5: 215–235.
- Akoglu, E., Salihoglu, B., Libralato, S., Oguz, T. and Solidoro, C., 2014. An indicator-based evaluation of Black Sea food web dynamics during 1960–2000. *Journal of Marine Systems* 134: 113–125.
- Alheit, J., Licandro, P., Coombs, S., Garcia, A., Giraldez, A., Santamaria, M.T.G., Slotte, A. and Tsikliras, A.C., 2014. Atlantic Multidecadal Oscillation (AMO) modulates dynamics of small pelagic fishes and ecosystem regime shifts in the eastern North and Central Atlantic. *Journal of Marine Systems* 131: 21–35.
- Alheit, J., Groger, J., Licandro, P., McQuinn, I.H., Pohlmann, T. and Tsikliras, A.C., 2019. What happened in the mid-1990s? The coupled ocean-atmosphere processes behind climate-induced ecosystem changes in the Northeast Atlantic and the Mediterranean. *Deep-Sea Research Part II: Topical Studies in Oceanography* 159: 130–142.
- Alvarez-Fernandez, S., Lindeboom, H. and Meesters, E., 2012. Temporal changes in plankton of the North Sea: community shifts and environmental drivers. *Marine Ecology Progress Series* 462: 21.
- Andersen, T., Carstensen, J., Hernandez-Garcia, E. and Duarte, C.M., 2009. Ecological thresholds and regime shifts: approaches to identification. *Trends in Ecology & Evolution* 24: 49–57.
- Arai, M.N., 1988. Interactions of fish and pelagic coelenterates. *Canadian Journal of Zoology* 66: 1913–1927.
- Archibald, D. and James, M.C., 2016. Evaluating inter-annual relative abundance of leatherback sea turtles in Atlantic Canada. *Marine Ecology Progress Series* 547: 233–246.
- Audzijonyte, A., Fulton, E., Haddon, M., Helidoniotis, F., Hobday, A.J., Kuparinen, A., Morrongiello, J., Smith, A.D.M., Upston, U. and Waples, R.S., 2016. Trends and management implications of human-influenced life-history changes in marine ectotherms. *Fish and Fisheries* 17: 1005–1028.
- Barner, A.K., Johnson, A., Hettinger, A., Osterback, A.-M.K., Focht, B., Mahoney, B., et al., 2017. Long-term studies contribute disproportionately to ecology and policy. *Bioscience* 67: 271–281.
- Baudron, A.R., Needle, C.L. and Marshall, C.T., 2011. Implications of a warming North Sea for the growth of haddock, *Melanogrammus aeglefinus*. *Journal of Fish Biology* 78: 1874–1889.
- Baumann, H., Hinrichsen, H.H., Mollmann, C., Koster, F.W., Malzahn, A.M. and Temming, A., 2006. Recruitment variability in Baltic Sea sprat (*Sprattus sprattus*) is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 2191–2201.
- Baxter, E.J., Walne, A.W., Purcell, J.E., McAllen, R. and Doyle, T.K., 2010. Identification of jellyfish from Continuous Plankton Recorder samples. *Hydrobiologia* 645: 193–201.
- Beaugrand, G. and Reid, P.C., 2012. Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. *ICES Journal of Marine Science* 69:1549–1562.
- Beaugrand, G., Ibanez, F. and Reid, P.C., 2000. Spatial, seasonal and long-term fluctuations of plankton in relation to hydroclimatic features in the English Channel, Celtic Sea and Bay of Biscay. *Marine Ecology Progress Series* 200: 93–102.
- Beaugrand, G., Luczak, C. and Edwards, M., 2009. Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Global Change Biology* 15: 1790–1803.
- Beaugrand, G., Harlay, X. and Edwards, M., 2014. Detecting plankton shifts in the North Sea: a new abrupt ecosystem shift between 1996 and 2003. *Marine Ecology Progress Series* 502: 85–104.
- Benedetti-Cecchi, L., Crowe, T., Boehme, L., Boero, F., Christensen, A., Grémare, A., Hernandez, F., Kromkamp, J.C., Nogueira Garcia, E., Petihakis, G., Robidart, J., Sousa Pinto, I. and Zingone, A., 2018. Strengthening Europe's capability in biological ocean observations. In Muñiz Piniella, Á., Kellett, P., Larkin, K. and Heymans, J.J. (eds), *Future Science Brief 3 of the European Marine Board*. European Marine Board, Ostend, Belgium.

- Bernreuther, M., Herrmann, J.P., Peck, M.A. and Temming, A., 2013. Growth energetics of juvenile herring, *Clupea harengus* L.: food conversion efficiency and temperature dependency of metabolic rate. *Journal of Applied Ichthyology* 29: 331–340.
- Berrow, S., Whooley, P., O’Connell, M. and Wall, D., 2010. *Irish Cetacean Review (2000–2009)*. Irish Whale and Dolphin Group. Kilrush, Co. Clare, Ireland.
- Berx, B. and Payne, M.R., 2017. The Sub-Polar Gyre Index – a community data set for application in fisheries and environment research. *Earth System Science Data* 9: 259–266.
- Biggs, R., Carpenter, S.R. and Brock, W.A., 2009. Turning back from the brink: detecting an impending regime shift in time to avert it. *Proceedings of the National Academy of Sciences of the United States of America* 106: 826–831.
- Bird, T.J., Bates, A.E., Lefcheck, J.S., Hill, N.A., Thomson, R.J., Edgar, G.J., Stuart-Smith, R.D., Wotherspoon, S., Krkosek, M., Stuart-Smith, J.F., Pecl, G.T., Barrett, N. and Frusher, S., 2014. Statistical solutions for error and bias in global citizen science datasets. *Biological Conservation* 173: 144–154.
- Black, B.A., Matta, M.E., Helsler, T.E. and Wilderbuer, T.K., 2013. Otolith biochronologies as multidecadal indicators of body size anomalies in yellowfin sole (*Limanda aspera*). *Fisheries Oceanography* 22: 523–532.
- Boero, F., Kraberg, A.C., Krause, G. and Wiltshire, K.H., 2015. Time is an affliction: why ecology cannot be as predictive as physics and why it needs time series. *Journal of Sea Research* 101: 12–18.
- Brander, K.M., 2007. The role of growth changes in the decline and recovery of North Atlantic cod stocks since 1970. *ICES Journal of Marine Science* 64: 211–217.
- Brander, K.M., Dickson, R.R. and Edwards, M., 2003. Use of Continuous Plankton Recorder information in support of marine management: applications in fisheries, environmental protection, and in the study of ecosystem response to environmental change. *Progress in Oceanography* 58: 175–191.
- Breen, P., Cañadas, A., Cadhla, O.Ó., Mackey, M., Scheidat, M., Geelhoed, S.C.V., Rogan, E. and Jessopp, M., 2017. New insights into ocean sunfish (*Mola mola*) abundance and seasonal distribution in the northeast Atlantic. *Scientific Reports* 7(1): 2025.
- Brodeur, R.D., Suchman, C.L., Reese, D., Miller, T. and Daly, E., 2008. Spatial overlap and trophic interactions between pelagic fish and large jellyfish in the northern California Current. *Marine Biology* 154: 649–659.
- Brophy, D. and Danilowicz, B.S., 2002. Tracing populations of Atlantic herring (*Clupea harengus*, L.) in the Irish and Celtic Seas using otolith microstructure. *ICES Journal of Marine Science* 59: 1305–1313.
- Brophy, D. and Danilowicz, B.S., 2003. The influence of pre-recruitment growth on subsequent growth and age at first spawning in Atlantic herring (*Clupea harengus*, L.). *ICES Journal of Marine Science* 60: 1103–1113.
- Brophy, D., Danilowicz, B.S. and King, P.A., 2006. Spawning season fidelity in sympatric populations of Atlantic herring (*Clupea harengus*). *Canadian Journal of Fisheries and Aquatic Sciences* 63: 607–616.
- Brunel, T. and Dickey-Collas, M., 2010. Effects of temperature and population density on von Bertalanffy growth parameters in Atlantic herring: a macro-ecological analysis. *Marine Ecology Progress Series* 405: 15–28.
- Burke, N., Brophy, D., Schon, P.J. and King, P.A., 2009. Temporal trends in stock origin and abundance of juvenile herring (*Clupea harengus*) in the Irish Sea. *ICES Journal of Marine Science* 66: 1749–1753.
- Burthe, S.J., Henrys, P.A., Mackay, E.B., Spears, B.M., Campbell, R., Carvalho, L., Dudley, B., Gunn, I.D.M., Johns, D.G., Maberly, S.C., May, L., Newell, M.A., Wanless, S., Winfield, I.J., Thackeray, S.J. and Daunt, F., 2016. Do early warning indicators consistently predict nonlinear change in long-term ecological data? *Journal of Applied Ecology* 53: 666–676.
- Chelton, D.B., 1984. Commentary: short-term climatic variability in the Northeast Pacific Ocean. In Pearcy, W. (ed.), *The Influence of Ocean Conditions on the Production of Salmonids in the North Pacific*. Oregon State University Press, Corvallis, OR, pp. 87–99.
- Clark, J.S., 2007. *Models for Ecological Data, an Introduction*. Princeton University Press, Princeton, NJ.
- Coad, J.O., Hussy, K., Farrell, E.D. and Clarke, M.W., 2014. The recent population expansion of boarfish, *Capros aper* (Linnaeus, 1758): interactions of climate, growth and recruitment. *Journal of Applied Ichthyology* 30: 463–741.
- Colebrook, J.M., 1979. Continuous plankton records – seasonal cycles of phytoplankton and copepods in the North Atlantic ocean and the North Sea. *Marine Biology* 51: 23–32.
- Conover, D.O. and Munch, S.B., 2002. Sustaining fisheries yields over evolutionary time scales. *Science* 297: 94–96.
- Costanza, R., d’Arge, R., deGroot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., Oneill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. and vandenBelt, M., 1997. The value of the world’s ecosystem services and natural capital. *Nature* 387: 253–260.

- Cox, S.L., Miller, P.I., Embling, C.B., Scales, K.L., Bicknell, A.W.J., Hosegood, P.J., Morgan, G., Ingram, S.N. and Votier, S.C., 2016. Seabird diving behaviour reveals the functional significance of shelf-sea fronts as foraging hotspots. *Royal Society Open Science* 3(9).
- Cragg, J.G., 1971. Some statistical models for limited dependent variables with application to the demand for durable goods. *Econometrica* 39: 829–844.
- Crain, C.M., Kroeker, K. and Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters* 11: 1304–1315.
- Cunningham, R.B. and Lindenmayer, D.B., 2005. Modeling count data of rare species: some statistical issues. *Ecology* 86: 1135–1142.
- DAFM (Department of Agriculture, Food and the Marine), 2019. *Agriculture, Forest and Seafood: Climate Change Sectoral Adaptation Plan*. DAFM, Dublin.
- Deschepper, I., Lyons, K., Lyashevskaya, O. and Brophy, D., 2019. Biophysical models reveal the role of tides, wind, and larval behaviour in early transport and retention of Atlantic herring (*Clupea harengus*) in the Celtic Sea. *Canadian Journal of Fisheries and Aquatic Sciences* 77: 90–107.
- Desobry, F., Davy, M. and Doncarli, C., 2005. An online Kernel change detection algorithm. *IEEE Transactions on Signal Processing* 53: 2961–2974.
- Doyle, T., Houghton, J., Buckley, S., Hays, G. and Davenport, J., 2007. The broad-scale distribution of five jellyfish species across a temperate coastal environment. *Hydrobiologia* 579: 29–39.
- Eason, T., Garmestani, A.S. and Cabezas, H., 2014. Managing for resilience: early detection of regime shifts in complex systems. *Clean Technologies and Environmental Policy* 16: 773–783.
- Edwards, M., Beaugrand, G., Hays, G.C., Koslow, J.A. and Richardson, A.J., 2010. Multi-decadal oceanic ecological datasets and their application in marine policy and management. *Trends in Ecology & Evolution* 25: 602–610.
- Edwards, M., Beaugrand, G., Helaouet, P., Alheit, J. and Coombs, S., 2013. Marine ecosystem response to the Atlantic Multidecadal Oscillation. *PLOS ONE* 8: e57212.
- Elith, J., Leathwick, J.R. and Hastie, T., 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* 77: 802–813.
- Elliott, K.C., Cheruvilil, K.S., Montgomery, G.M. and Soranno, P.A., 2016. Conceptions of good science in our data-rich world. *Bioscience* 66: 880–889.
- Enfield, D.B., Mestas-Nuñez, A.M. and Trimble, P.J., 2001. The Atlantic Multidecadal Oscillation and its relation to rainfall and river flows in the continental US. *Geophysical Research Letters* 28: 2077–2080.
- EU (European Union), 2008. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). OJ L 164, 25.6.2008, p. 19–40.
- Farley, S.S., Dawson, A., Goring, S.J. and Williams, J.W., 2018. Situating ecology as a big-data science: current advances, challenges and solutions. *Bioscience* 68: 563–576.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. and Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35: 557–581.
- Frafjord, K., Bakken, T., Kubicek, L., Ronning, A.H. and Syvertsen, P.O., 2017. Records of ocean sunfish *Mola mola* along the Norwegian coast spanning two centuries, 1801–2015. *Journal of Fish Biology* 91: 1365–1377.
- Friedman, J.H., 2001. Greedy function approximation: a gradient boosting machine. *Annals of Statistics* 29: 1189–1232.
- Gascuel, D., Coll, M., Fox, C., Guenette, S., Guitton, J., Kenny, A., Knittweis, L., Nielsen, J.R., Piet, G., Raid, T., Travers-Trolet, M. and Shephard, S., 2016. Fishing impact and environmental status in European seas: a diagnosis from stock assessments and ecosystem indicators. *Fish and Fisheries* 17: 31–55.
- Good, S.A., Martin, M.J. and Rayner, N.A., 2013. EN4: quality controlled ocean temperature and salinity profiles and monthly objective analyses with uncertainty estimates. *Journal of Geophysical Research: Oceans* 118: 6704–6716.
- Gremillet, D., White, C.R., Authier, M., Doremus, G., Ridoux, V. and Pettex, E., 2017. Ocean sunfish as indicators for the “rise of slime”. *Current Biology* 27: R1263–R1264.
- Greve, W., 1994. The 1989 German Bight invasion of *Muggiaea atlantica*. *ICES Journal of Marine Science* 51: 355–358.

- Griffen, B.D., Belgrad, B.A., Cannizzo, Z.J., Knotts, E.R. and Hancock, E.R., 2016. Rethinking our approach to multiple stressor studies in marine environments. *Marine Ecology Progress Series* 543: 273–281.
- Groffman, P., Baron, J., Blett, T., Gold, A., Goodman, I., Gunderson, L., Levinson, B., Palmer, M., Paerl, H., Peterson, G., Poff, N., Rejeski, D., Reynolds, J., Turner, M., Weathers, K. and Wiens, J., 2006. Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems* 9: 1–13.
- Guenette, 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.
- Haberlin, D., Raine, R., McAllen, R. and Doyle, T.K., 2019. Distinct gelatinous zooplankton communities across a dynamic shelf sea. *Limnology and Oceanography* 64: 1802–1818.
- Hamilton, J.D., 1989. A new approach to the economic-analysis of nonstationary time-series and the business-cycle. *Econometrica* 57: 357–384.
- Harma, C., Brophy, D., Minto, C. and Clarke, M., 2012. The rise and fall of autumn-spawning herring (*Clupea harengus*, L.) in the Celtic Sea between 1959 and 2009: temporal trends in spawning component diversity. *Fisheries Research* 121–122: 31–42.
- Harvey, A.C., 1990. *Forecasting, Structural Time Series Models and the Kalman Filter*. Cambridge University Press, Cambridge, UK.
- Hastie, T., Tibshirani, R. and Friedman, J., 2009. *Elements of Statistical Learning*. Springer, New York, NY.
- Hastings, A. and Wysham, D.B., 2010. Regime shifts in ecological systems can occur with no warning. *Ecology Letters* 13: 464–472.
- Hays, G.C., Doyle, T.K. and Houghton, J.D.R., 2018. A paradigm shift in the trophic importance of jellyfish? *Trends in Ecology & Evolution* 33: 874–884.
- Hinrichsen, H.-H., Dickey-Collas, M., Huret, M., Peck, M.A. and Vikebø, F.B., 2011. Evaluating the suitability of coupled biophysical models for fishery management. *ICES Journal of Marine Science* 68: 1478–1487.
- Hinrichsen, H.H., Hussy, K. and Huwer, B., 2012. Spatio-temporal variability in western Baltic cod early life stage survival mediated by egg buoyancy, hydrography and hydrodynamics. *ICES Journal of Marine Science* 69: 1744–1752.
- Hollowed, A.B., Bond, N.A., Wilderbuer, T.K., Stockhausen, W.T., A'Mar, Z.T., Beamish, R.J., Overland, J.E. and Schirripa, M.J., 2009. A framework for modelling fish and shellfish responses to future climate change. *ICES Journal of Marine Science* 66: 1584–1594.
- Holmes, E.E., Ward, E.J. and Wills, K., 2012. MARSS: Multivariate Autoregressive State-Space models for analyzing time-series data. *The R Journal* 4(1).
- Holmes, E.E., Ward, E.J. and Wills, K., 2018. MARSS: Multivariate Autoregressive State-Space Modeling. R version 3.10.10. Available online: <https://cran.r-project.org/web/packages/MARSS/index.html> (accessed 16 April 2020).
- Hosia, A., Falkenhaus, T. and Naustvoll, L.J., 2014. Trends in abundance and phenology of *Aurelia aurita* and *Cyanea* spp. at a Skagerrak location, 1992–2011. *Marine Ecology Progress Series* 498: 103–115.
- Houghton, J., Doyle, T., Davenport, J. and Hays, G., 2013. The ocean sunfish, *Mola mola*: insights into distribution, abundance and behaviour in the Irish and Celtic Seas. *Journal of the Marine Biological Association of the United Kingdom* 86: 1237–1243.
- Huang, B., Thorne, P.W., Banzon, V.F., Boyer, T., Chepurin, G., Lawrimore, J.H., Menne, M.J., Smith, T.M., Vose, R.S. and Zhan, H.M., 2017. NOAA Extended Reconstructed Sea Surface Temperature (ERSST), version 5. NOAA National Centers for Environmental Information. <https://doi.org/10.7289/V5T72FNM>.
- Hughes, T.P., Bellwood, D.R., Folke, C., Steneck, R.S. and Wilson, J., 2005. New paradigms for supporting the resilience of marine ecosystems. *Trends in Ecology & Evolution* 20: 380–386.
- Hurrell, J.W., 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* 269: 676–679.
- Husebo, A., Slotte, A. and Stenevik, E.K., 2007. Growth of juvenile Norwegian spring-spawning herring in relation to latitudinal and interannual differences in temperature and fish density in their coastal and fjord nursery areas. *ICES Journal of Marine Science* 64: 1161–1172.
- Huwer, B., Hinrichsen, H.H., Hüsey, K. and Eero, M., 2016. Connectivity of larval cod in the transition area between North Sea and Baltic Sea and potential implications for fisheries management. *ICES Journal of Marine Science* 73: 1815–1824.
- ICES (International Council for the Exploration of the Sea), 2017a. *Herring Assessment Working Group for the Area South of 62 Deg N (HAWG)*. 14–22 March 2017, ICES CM 2017/ACOM:07. ICES, Copenhagen.

- ICES (International Council for the Exploration of the Sea), 2017b. *Report of the Working Group on Celtic Seas Ecoregion (WGCSE)*. 9–18 May 2017, ICES CM 2017/ACOM:13. ICES, Copenhagen.
- ICES (International Council for the Exploration of the Sea), 2017c. *Report of the Working Group on Southern Horse Mackerel, Anchovy and Sardine (WGHANSA)*. 24–29 June 2017, ICES CM 2017/ACOM:17. ICES, Bilbao, Spain.
- ICES (International Council for the Exploration of the Sea), 2017d. *Report of the Working Group on Widely Distributed Stocks (WGWIDE)*. 30 August–5 September 2017, ICES CM 2017/ACOM:23. ICES, Copenhagen.
- Isaac, N.J.B., van Strien, A.J., August, T.A., de Zeeuw, M.P. and Roy, D.B., 2014. Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution* 5: 1052–1060.
- Ito, S.I., Rose, K.A., Megrey, B.A., Schweigert, J., Hay, D., Werner, F.E. and Aita, M.N., 2015. Geographic variation in Pacific herring growth in response to regime shifts in the North Pacific Ocean. *Progress in Oceanography* 138: 331–347.
- Jaynes, E.T., 2003. *Probability Theory: The Logic of Science*. Cambridge University Press, Cambridge, UK.
- Joint, I., Wollast, R., Chou, L., Batten, S., Elskens, M., Edwards, E., Hirst, A., Burkill, P., Groom, S., Gibb, S., Miller, A., Hydes, D., Dehairs, F., Antia, A., Barlow, R., Rees, A., Pomroy, A., Brockmann, U., Cummings, D., Lampitt, R., Loijens, M., Mantoura, F., Miller, P., Raabe, T., Alvarez-Salgado, X., Stelfox, C. and Woolfenden, J., 2001. Pelagic production at the Celtic Sea shelf break. *Deep-Sea Research Part II: Topical Studies in Oceanography* 48: 3049–3081.
- Jones, P.D., Jonsson, T. and Wheeler, D., 1997. Extension to the North Atlantic oscillation using early instrumental pressure observations from Gibraltar and south-west Iceland. *International Journal of Climatology* 17: 1433–1450.
- Kelling, S., Hochachka, W.M., Fink, D., Riedewald, M., Caruana, R., Ballard, G. and Hooker, G., 2009. Data-intensive science: a new paradigm for biodiversity studies. *Bioscience* 59: 613–620.
- Kideys, A. and Romanova, Z., 2003. Distribution of gelatinous macrozooplankton in the southern, Black Sea during 1996–1999. *Marine Biology* 142: 623.
- Kideys, A.E., 2002. *Ecology. Fall and rise of the Black Sea ecosystem*. *Science* 297: 1482–1484.
- Krkosek, M. and Drake, J.M., 2014. On signals of phase transitions in salmon population dynamics. *Proceedings of the Royal Society B: Biological Sciences* 281: 20133221.
- Lamb, P.D., Hunter, E., Pinnegar, J.K., Doyle, T.K., Creer, S. and Taylor, M.I., 2019. Inclusion of jellyfish in 30+ years of Ecopath with Ecosim models. *ICES Journal of Marine Science* 76: 1941–1950.
- Lambert, C., Pettex, E., Doremus, G., Laran, S., Stephan, E., Van Canneyt, O. and Ridoux, V., 2017. How does ocean seasonality drive habitat preferences of highly mobile top predators? Part II: The eastern North-Atlantic. *Deep-Sea Research Part II: Topical Studies in Oceanography* 141: 133–154.
- La Sorte, F.A. and Fink, D., 2017. Projected changes in prevailing winds for transatlantic migratory birds under global warming. *Journal of Animal Ecology* 86: 273–284.
- Lauria, V., Attrill, M.J., Pinnegar, J.K., Brown, A., Edwards, M. and Votier, S.C., 2012. Influence of climate change and trophic coupling across four trophic levels in the Celtic Sea. *PLOS ONE* 7(10).
- Law, R., 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science* 57: 659–668.
- Layer, K., Hildrew, A.G., Jenkins, G.B., Riede, J.O., Rossiter, S.J., Townsend, C.R. and Woodward, G., 2011. Long-term dynamics of a well-characterised food web: four decades of acidification and recovery in the broadstone stream model system. *Advances in Ecological Research* 44: 69–117.
- Leathwick, J.R., Elith, J., Francis, M.P., Hastie, T. and Taylor, P., 2006. Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. *Marine Ecology Progress Series* 321: 267–281.
- Leeney, R.H., Witt, M.J., Broderick, A.C., Buchanan, J., Jarvis, D.S., Richardson, P.B. and Godley, B.J., 2012. Marine megavertebrates of Cornwall and the Isles of Scilly: relative abundance and distribution. *Journal of the Marine Biological Association of the United Kingdom* 92: 1823–1833.
- Lees, K., Pitois, S., Scott, C., Frid, C. and Mackinson, S., 2006. Characterizing regime shifts in the marine environment. *Fish and Fisheries* 7: 104–127.
- Lett, C., Verley, P., Mullon, C., Parada, C., Brochier, T., Penven, P. and Blanke, B., 2008. A Lagrangian tool for modelling ichthyoplankton dynamics. *Environmental Modelling & Software* 23: 1210–1214.
- Lindley, J.A. and Daykin, S., 2005. Variations in the distributions of *Centropages chierchiae* and *Temora stylifera* (Copepoda: Calanoida) in the north-eastern Atlantic Ocean and western European shelf waters. *ICES Journal of Marine Science* 62: 869–877.

- Lindstrom, E., Gunn, J., Fischer, A., McCurdy, A. and Glover, L.K., 2012. *A Framework for Ocean Observing*. By the Task Team for an Integrated Framework for Sustained Ocean Observing, UNESCO 2012 (revised in 2017), IOC/INF-1284 rev.2. Available online: <https://unesdoc.unesco.org/ark:/48223/pf0000211260> (accessed 16 April 2020).
- Llopiz, J.K., Cowen, R.K., Hauff, M.J., Ji, R.B., Munday, P.L., Muhling, B.A., Peck, M.A., Richardson, D.E., Sogard, S. and Sponaugle, S., 2014. Early life history and fisheries oceanography: new questions in a changing world. *Oceanography* 27: 26–41.
- Lorden, G., 1971. Procedures for reacting to a change in distribution. *Annals of Mathematical Statistics* 42: 1897–1908.
- Luczak, C., Beaugrand, G., Jaffre, M. and Lenoir, S., 2011. Climate change impact on Balearic shearwater through a trophic cascade. *Biology Letters* 7: 702–705.
- Lynch, D., 2011. Biological changes in Celtic Sea and southwest of Ireland herring, based on a long-term data archival project. MSc Thesis. Trinity College Dublin, Dublin.
- Mace, G.M., Hails, R.S., Cryle, P., Harlow, J. and Clarke, S.J., 2015. Towards a risk register for natural capital. *Journal of Applied Ecology* 52: 641–653.
- McGinty, N., Johnson, M.P. and Power, A.M., 2014. Spatial mismatch between phytoplankton and zooplankton biomass at the Celtic Boundary Front. *Journal of Plankton Research* 36: 1446–1460.
- Macias, D., Garcia-Gorriz, E. and Stips, A., 2013. Understanding the causes of recent warming of Mediterranean waters. How much could be attributed to climate change? *PLOS ONE* 8(11).
- McQuatters-Gollop, A., 2012. Challenges for implementing the, Marine Strategy Framework Directive in a climate of macroecological change. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 370: 5636–5655.
- Marine Institute, 2015. *Marine Strategy Framework Directive: Article 11 Monitoring Programmes Report*. Available online: <https://www.housing.gov.ie/sites/default/files/migrated-files/en/Publications/Environment/Water/FileDownload%2C43582%2Cen.pdf> (accessed 16 April 2020).
- Martinez, I., Ellis, J.R., Scott, B. and Tidd, A., 2013. The fish and fisheries of Jones Bank and the wider Celtic Sea. *Progress in Oceanography* 117: 89–105.
- Matta, M.E., Helser, T.E. and Black, B.A., 2018. Intrinsic and environmental drivers of growth in an Alaskan rockfish: an otolith biochronology approach. *Environmental Biology of Fishes* 101: 1571–1587.
- Moellmann, C. and Diekmann, R., 2012. Marine ecosystem regime shifts induced by climate and overfishing: a review for the Northern Hemisphere. *Advances in Ecological Research* 47: 303–347.
- Morrongiello, J.R. and Thresher, R.E., 2014. A statistical framework to explore ontogenetic growth variation among individuals and populations: a marine fish example. *Ecological Monographs* 85: 93–115.
- Morrongiello, J.R., Thresher, R.E. and Smith, D.C., 2012. Aquatic biochronologies and climate change. *Nature Climate Change* 2: 849–857.
- Moss, R.H., Meehl, G.A., Lemos, M.C., Smith, J.B., Arnold, J.R., Arnott, J.C., *et al.*, 2013. Hell and high water: practice-relevant adaptation science. *Science* 342: 696–698.
- Muttill, N. and Chau, K.W., 2007. Machine-learning paradigms for selecting ecologically significant input variables. *Engineering Applications of Artificial Intelligence* 20: 735–744.
- Myers, R.A. and Mertz, G., 1998. Reducing uncertainty in the biological basis of fisheries management by meta-analysis of data from many populations: a synthesis. *Fisheries Research* 37: 51–60.
- Nakamura, I., Goto, Y. and Sato, K., 2015. Ocean sunfish rewarm at the surface after deep excursions to forage for siphonophores. *Journal of Animal Ecology* 84: 590–603.
- Neuheimer, A.B. and Taggart, C.T., 2010. Can changes in length-at-age and maturation timing in Scotian Shelf haddock (*Melanogrammus aeglefinus*) be explained by fishing? *Canadian Journal of Fisheries and Aquatic Sciences* 67: 854–865.
- Neuheimer, A.B., Thresher, R.E., Lyle, J.M. and Semmens, J.M., 2011. Tolerance limit for fish growth exceeded by warming waters. *Nature Climate Change* 1: 110–113.
- Nielsen, E., Bagge, O. and MacKenzie, B.R., 1998. Wind-induced transport of plaice (*Pleuronectes platessa*) early life-history stages in the Skagerrak-Kattegat. *Journal of Sea Research* 39: 11–28.
- Olden, J.D., Lawler, J.J. and Poff, N.L., 2008. Machine learning methods without tears: a primer for ecologists. *Quarterly Review of Biology* 83: 171–193.
- OSPAR (OSPAR Commission), 2017a. *Changes in Phytoplankton Biomass and Zooplankton Abundance. Intermediate Assessment 2017*. Available online: <https://oap.ospar.org/en/ospar-assessments/intermediate-assessment-2017/biodiversity-status/habitats/plankton-biomass/> (accessed 16 April 2020).

- OSPAR (OSPAR Commission), 2017b. *Marine Bird Breeding Success or Failure. Intermediate Assessment 2017*. Available online: <https://oap.ospar.org/en/ospar-assessments/intermediate-assessment-2017/biodiversity-status/marine-birds/marine-bird-breeding-success-failure/> (accessed 16 April 2020).
- OSPAR (OSPAR Commission), 2017c. *Marine Bird Abundance. Intermediate Assessment 2017*. Available online: <https://oap.ospar.org/en/ospar-assessments/intermediate-assessment-2017/biodiversity-status/marine-birds/bird-abundance/> (accessed 16 April 2020).
- Pacariz, S., Bjork, G. and Svedang, H., 2014. Interannual variability in the transport of fish eggs in the Kattegat and Oresund. *ICES Journal of Marine Science* 71: 1706–1716.
- Pace, M.L., Carpenter, S.R., Johnson, R.A. and Kurtzweil, J.T., 2013. Zooplankton provide early warnings of a regime shift in a whole lake manipulation. *Limnology and Oceanography* 58: 525–532.
- Page, E.S., 1955. A test for a change in a parameter occurring at an unknown point. *Biometrika* 42: 523–527.
- Palsson, J. and Astthorsson, O., 2016. New and historical records of the ocean sunfish *Mola mola* in Icelandic waters. *Journal of Fish Biology* 90: 1126–1132.
- Panfili, J., Pontual, H.D., Troadec, H. and Wright, P.J.E., 2002. *Manual of Fish Sclerochronology*. IFREMER-IRD, Brest, France.
- Perälä, T. and Kuparinen, A., 2015. Detecting regime shifts in fish stock dynamics. *Canadian Journal of Fisheries and Aquatic Sciences* 72: 1619–1628.
- Perälä, T.A., Swain, D.P. and Kuparinen, A., 2017. Examining nonstationarity in the recruitment dynamics of fishes using Bayesian change point analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 74: 751–765.
- Perretti, C.T. and Munch, S.B., 2012. Regime shift indicators fail under noise levels commonly observed in ecological systems. *Ecological Applications* 22: 1772–1779.
- Perry, R.I., Cury, P., Brander, K., Jennings, S., Mollmann, C. and Planque, B., 2010. Sensitivity of marine systems to climate and fishing: concepts, issues and management responses. *Journal of Marine Systems* 79: 427–435.
- Peterman, R.M., Pyper, B.J. and Grout, J.A., 2000. Comparison of parameter estimation methods for detecting climate-induced changes in productivity of Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences* 57: 181–191.
- Peters, D.P.C., Havstad, K.M., Cushing, J., Tweedie, C., Fuentes, O. and Villanueva-Rosales, N., 2014. Harnessing the power of big data: infusing the scientific method with machine learning to transform ecology. *Ecosphere* 5(6): 67.
- Petitgas, P., Rijnsdorp, A.D., Dickey-Collas, M., Engelhard, G.H., Peck, M.A., Pinnegar, J.K., Drinkwater, K., Huret, M. and Nash, R.D.M., 2013. Impacts of climate change on the complex life cycles of fish. *Fisheries Oceanography* 22: 121–139.
- Pineda, J., Hare, J.A. and Sponaugle, S., 2007. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* 20: 22–39.
- Pinnegar, J.K., Jennings, S., O'Brien, C.M. and Polunin, N.V.C., 2002. Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. *Journal of Applied Ecology* 39: 377–390.
- Potter, I.F., Galuardi, B. and Howell, W.H., 2011. Horizontal movement of ocean sunfish, *Mola mola*, in the northwest Atlantic. *Marine Biology* 158: 531–540.
- Potts, J.M. and Elith, J., 2006. Comparing species abundance models. *Ecological Modelling* 199: 153–163.
- Poulard, J.C. and Blanchard, F., 2005. The impact of climate change on the fish community structure of the eastern continental shelf of the Bay of Biscay. *ICES Journal of Marine Science* 62: 1436–1443.
- Purcell, J. and Arai, M.N., 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia* 451: 27–44.
- Pyper, B.J. and Peterman, R.M., 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 2127–2140.
- Python Software Foundation, 2019. Python language reference version 2.7. Available online: <http://www.python.org> (accessed 16 April 2020).
- Raitsos, D.E., Walne, A., Lavender, S.J., Licandro, P., Reid, P.C. and Edwards, M., 2013. A 60-year ocean colour data set from the continuous plankton recorder. *Journal of Plankton Research* 35: 158–164.
- R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available online: <https://www.R-project.org/> (accessed 16 April 2020).
- Reeves, J., Chen, J., Wang, X.L., Lund, R. and Lu, Q.Q., 2007. A review and comparison of changepoint detection techniques for climate data. *Journal of Applied Meteorology and Climatology* 46: 900–915.

- Reyers, M., Moemken, J. and Pinto, J.G., 2016. Future changes of wind energy potentials over Europe in a large CMIP5 multi-model ensemble. *International Journal of Climatology* 36: 783–796.
- Rijnsdorp, A.D., Peck, M.A., Engelhard, G.H., Möllmann, C. and Pinnegar, J.K., 2009. Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science* 66: 1570–1583.
- Ripley, B. and Lapsley, M., 2017. RODBC: ODBC database access. R package version 1.3-15. <https://cran.r-project.org/web/packages/RODBC/index.html> (accessed 16 April 2020).
- Rodionov, S. and Overland, J.E., 2005. Application of a sequential regime shift detection method to the Bering Sea ecosystem. *ICES Journal of Marine Science* 62: 328–332.
- Rodionov, S.N., 2004. A sequential algorithm for testing climate regime shifts. *Geophysical Research Letters* 31: L09204.
- Rountrey, A.N., Coulson, P.G., Meeuwig, J.J. and Meekan, M., 2014. Water temperature and fish growth: otoliths predict growth patterns of a marine fish in a changing climate. *Global Change Biology* 20: 2450–2458.
- Roxburgh, T., 2012. *A Guide to Implementing the Ecosystem Approach through the Marine Strategy Framework Directive*. PISCES (Partnerships Involving Stakeholders in the Celtic Sea Ecosystem). WWF–UK, Woking, UK.
- Ruppert, D., Wand, M.P. and Carroll, R.J., 2003. *Semiparametric Regression* (Vol. 12). Cambridge University Press, Cambridge, UK.
- Ruzicka, J.J., Daly, E.A. and Brodeur, R.D., 2016. Evidence that summer jellyfish blooms impact Pacific Northwest salmon production. *Ecosphere* 7: e01324.
- SAHFOS (Sir Alister Hardy Foundation for Ocean Science), 2012. Phytoplankton biomass and total copepod abundance to support Marine Strategy Framework Directive indicator, PH2. SAHFOS, Plymouth. <https://doi.org/10.7487/2015.355.1.935>.
- SAHFOS (Sir Alister Hardy Foundation for Ocean Science), 2017. Monthly averaged data for phytoplankton colour index and gelatinous zooplankton species (standard area, D.4) 1971–2016 as recorded by the Continuous Plankton Recorder. SAHFOS, Plymouth. <https://doi.org/10.7487/2017.226.1.1074>.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. and Walker, B., 2001. Catastrophic shifts in ecosystems. *Nature* 413: 591–596.
- Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held, H., van Nes, E.H., Rietkerk, M. and Sugihara, G., 2009. Early-warning signals for critical transitions. *Nature* 461: 53–59.
- Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V., van de Koppel, J., van de Leemput, I.A., Levin, S.A., van Nes, E.H., Pascual, M. and Vandermeer, J., 2012. Anticipating critical transitions. *Science* 338: 344–348.
- Smolinski, S. and Mirny, Z., 2017. Otolith biochronology as an indicator of marine fish responses to hydroclimatic conditions and ecosystem regime shifts. *Ecological Indicators* 79: 286–294.
- Sotillo, M.G., Cailleau, S., Lorente, P., Levier, B., Aznar, R., Reffray, G., Amo-Baladron, A., Chanut, J., Benkiran, M. and Alvarez-Fanjul, E., 2015. The MyOcean IBI Ocean Forecast and Reanalysis Systems: operational products and roadmap to the future Copernicus Service. *Journal of Operational Oceanography* 8: 63–79.
- Southward, A.J., Boalch, G.T. and Maddock, L., 1988. Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th-century. *Journal of the Marine Biological Association of the United Kingdom* 68: 423–445.
- Spencer, M., Mieszkowska, N., Robinson, L.A., Simpson, S.D., Burrows, M.T., Birchenough, S.N.R., Capasso, E., Cleall-Harding, P., Crummy, J., Duck, C., Eloire, D., Frost, M., Hall, A.J., Hawkins, S.J., Johns, D.G., Sims, D.W., Smyth, T.J. and Frid, C.L.J., 2012. Region-wide changes in marine ecosystem dynamics: state-space models to distinguish trends from step changes. *Global Change Biology* 18: 1270–1281.
- Stenseth, N.C., Ottersen, G., Hurrell, J.W., Mysterud, A., Lima, M., Chan, K.S., Yoccoz, N.G. and Adlandsvik, B., 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society B: Biological Sciences* 270: 2087–2096.
- Stephenson, R.L., Power, M.J., Laffan, S.W. and Suthers, I.M., 2015. Tests of larval retention in a tidally energetic environment reveal the complexity of the spatial structure in herring populations. *Fisheries Oceanography* 24: 553–570.
- Stevens, D., Richardson, A.J. and Reid, P.C., 2006. Continuous Plankton Recorder database: evolution, current uses and future directions. *Marine Ecology Progress Series* 316: 247–255.
- Suding, K.N., Gross, K.L. and Houseman, G.R., 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution* 19: 46–53.

- Sugihara, G. and May, R.M., 1990. Nonlinear forecasting as a way of distinguishing chaos from measurement error in time-series. *Nature* 344: 734–741.
- Sugihara, G., May, R., Ye, H., Hsieh, C.-H., Deyle, E., Fogarty, M. and Munch, S., 2012. Detecting causality in complex ecosystems. *Science* 338: 496–500.
- Swain, D.P., Sinclair, A.F. and Hanson, J.M., 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proceedings of the Royal Society B: Biological Sciences* 274: 1015–1022.
- Thorson, J.T. and Minto, C., 2014. Mixed effects: a unifying framework for statistical modelling in fisheries biology. *ICES Journal of Marine Science* 72: 1245–1256.
- Thys, T.M., Ryan, J.P., Dewar, H., Perle, C.R., Lyons, K., O’Sullivan, J., Farwell, C., Howard, M.J., Weng, K.C., Lavaniegos, B.E., Gaxiola-Castro, G., Bojorquez, L.E.M., Hazen, E.L. and Bograd, S.J., 2015. Ecology of the ocean sunfish, *Mola mola*, in the southern California current system. *Journal of Experimental Marine Biology and Ecology* 471: 64–76.
- Ting, M.F., Kushnir, Y. and Li, C.H., 2014. North Atlantic multidecadal SST oscillation: external forcing versus internal variability. *Journal of Marine Systems* 133: 27–38.
- Toresen, R. and Ostvedt, O.J., 2000. Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. *Fish and Fisheries* 1: 231–256.
- UNEP (United Nations Environment Programme), 2006. *Marine and Coastal Ecosystems and Human Well-being: A Synthesis Report Based on the Findings of the Millennium Ecosystem Assessment*. UNEP World Conservation Monitoring Centre, Cambridge, UK.
- Valde, L., Lopez-Urrutia, A., Cabal, J., Alvarez-Ossorio, M., Bode, A., Miranda, A., Cabanas, M., Huskin, I., Anadon, R., Alvarez-Marques, F., Llope, M. and Rodriguez, N., 2007. A decade of sampling in the Bay of Biscay: what are the zooplankton time series telling us? *Progress in Oceanography* 74: 98–114.
- van der Sleen, P., Dzaugis, M.P., Gentry, C., Hall, W.P., Hamilton, V., Helser, T.E., Matta, M.E., Underwood, C.A., Zuercher, R. and Black, B.A., 2017. Long-term Bering Sea environmental variability revealed by a centennial-length biochronology of Pacific ocean perch *Sebastes alutus*. *Climate Research* 71: 33–45.
- van Nes, E.H., Arani, B.M.S., Staal, A., van der Bolt, B., Flores, B.M., Bathiany, S. and Scheffer, M., 2016. What do you mean, “tipping point”? *Trends in Ecology & Evolution* 31: 902–904.
- van Walraven, L., Mollet, F.M., van Damme, C.J.G. and Rijnsdorp, A.D., 2010. Fisheries-induced evolution in growth, maturation and reproductive investment of the sexually dimorphic North Sea plaice (*Pleuronectes platessa*, L.). *Journal of Sea Research* 64: 85–92.
- Vikebo, F., Sundby, S., Adlandsvik, B. and Fiksen, O., 2005. The combined effect of transport and temperature on distribution and growth of larvae and pelagic juveniles of Arcto-Norwegian cod. *ICES Journal of Marine Science* 62: 1375–1386.
- Waggitt, J.J., Cazenave, P.W., Howarth, L.M., Evans, P.G.H, van der Kooij, J. and Hiddink, J.G., 2018. Combined measurements of prey availability explain habitat selection in foraging seabirds. *Biology Letters* 14(8).
- Walker, J. and Taylor, P.D., 2017. Using eBird data to model population change of migratory bird species. *Avian Conservation and Ecology* 12: 4.
- Williams, R., Conway, D.V.P. and Hunt, H.G., 1994. The role of copepods in the planktonic ecosystems of mixed and stratified waters of the European shelf seas. *Hydrobiologia* 293: 521–530.
- Zolck, M., Brophy, D., Mohn, C., Minto, C. and McGrath, D., 2015. Bio-physical model provides insight into dispersal of plaice (*Pleuronectes platessa*, L.) from putative spawning grounds to nursery areas on the west coast of Ireland. *Journal of Sea Research* 99: 61–73.
- Zuur, A., Ieno, E.N. and Smith, G.M., 2007. *Analyzing Ecological Data*. Springer Science & Business Media. New York, NY.
- Zuur, A.F., Fryer, R.J., Jolliffe, I.T., Dekker, R. and Beukema, J.J., 2003a. Estimating common trends in multivariate time series using dynamic factor analysis. *Environmetrics* 14: 665–685.
- Zuur, A.F., Tuck, I.D. and Bailey, N., 2003b. Dynamic factor analysis to estimate common trends in fisheries time series. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 542–552.

Abbreviations

AAC	Age at capture
AMO	Atlantic Multi-decadal Oscillation
BOCPD	Bayesian online change-point detection
CPR	Continuous Plankton Recorder
CSF	Celtic Sea front
df	Degrees of freedom
DFA	Dynamic factor analysis
DVM	Diel vertical migration
EWI	Early warning indicator
G	Green
GAMM	Generalised additive mixed model
GBRT	Gradient boosting regression tree
GES	Good Environmental Status
ICES	International Council for the Exploration of the Sea
JNCC	Joint Nature Conservation Committee
MSFD	Marine Strategy Framework Directive
NAO	North Atlantic Oscillation
NG	No green
PCI	Phytoplankton Colour Index
PG	Pale green
RI	Randomisation at the level of individual
RY	Randomisation at the level of year
SAHFOS	Sir Alister Hardy Foundation for Ocean Science
SPG	Sub-Polar Gyre Index
SSB	Spawning stock biomass
SST	Sea surface temperature
STARS	Sequential <i>t</i> -test analysis of regime shifts
TSB	Total stock biomass
VPG	Very pale green

AN GHNÍOMHAIREACHT UM CHAOMHNÚ COMHSHAOIL

Tá an Gníomhaireacht um Chaomhnú Comhshaoil (GCC) freagrach as an gcomhshaoil a chaomhnú agus a fheabhsú mar shócmhainn luachmhar do mhuintir na hÉireann. Táimid tiomanta do dhaoine agus don chomhshaoil a chosaint ó éifeachtaí díobhálacha na radaíochta agus an truaillithe.

Is féidir obair na Gníomhaireachta a roinnt ina trí phríomhréimse:

Rialú: Déanaimid córais éifeachtacha rialaithe agus comhlionta comhshaoil a chur i bhfeidhm chun torthaí maithe comhshaoil a sholáthar agus chun díriú orthu siúd nach gcloíonn leis na córais sin.

Eolas: Soláthraimid sonraí, faisnéis agus measúnú comhshaoil atá ar ardchaighdeán, spriocdhírthe agus tráthúil chun bonn eolais a chur faoin gcinnteoireacht ar gach leibhéal.

Tacaíocht: Bimid ag saothrú i gcomhar le grúpaí eile chun tacú le comhshaoil atá glan, táirgiúil agus cosanta go maith, agus le hiompar a chuirfidh le comhshaoil inbhuanaithe.

Ár bhFreagrachtaí

Ceadúnú

Déanaimid na gníomhaíochtaí seo a leanas a rialú ionas nach ndéanann siad dochar do shláinte an phobail ná don chomhshaoil:

- saoráidí dramhaíola (*m.sh. láithreáin líonta talún, loisceoirí, stáisiúin aistriúcháin dramhaíola*);
- gníomhaíochtaí tionsclaíocha ar scála mór (*m.sh. déantúsaíocht cógaisíochta, déantúsaíocht stroighne, stáisiúin chumhachta*);
- an diantalmhaíocht (*m.sh. muca, éanlaith*);
- úsáid shrianta agus scaoileadh rialaithe Orgánach Géinmhodhnaithe (*OGM*);
- foinsí radaíochta ianúcháin (*m.sh. trealamh x-gha agus radaiteiripe, foinsí tionsclaíocha*);
- áiseanna móra stórála peitрил;
- scardadh dramhuisece;
- gníomhaíochtaí dumpála ar farraige.

Forfheidhmiú Náisiúnta i leith Cúrsaí Comhshaoil

- Clár náisiúnta iniúchtaí agus cigireachtaí a dhéanamh gach bliain ar shaoráidí a bhfuil ceadúnas ón nGníomhaireacht acu.
- Maoirseacht a dhéanamh ar fhreagrachtaí cosanta comhshaoil na n-údarás áitiúil.
- Caighdeán an uisce óil, arna sholáthar ag soláthraithe uisce phoiblí, a mhaoirsiú.
- Obair le húdarás áitiúla agus le gníomhaireachtaí eile chun dul i ngleic le coireanna comhshaoil trí chomhordú a dhéanamh ar líonra forfheidhmiúcháin náisiúnta, trí dhírú ar chiontóirí, agus trí mhaoirsiú a dhéanamh ar leasúchán.
- Cur i bhfeidhm rialachán ar nós na Rialachán um Dhramhthrealamh Leictreach agus Leictreonach (DTLL), um Shrian ar Shubstaintí Guaiseacha agus na Rialachán um rialú ar shubstaintí a idíonn an ciseal ózóin.
- An dlí a chur orthu siúd a bhriseann dlí an chomhshaoil agus a dhéanann dochar don chomhshaoil.

Bainistíocht Uisce

- Monatóireacht agus tuairisciú a dhéanamh ar cháilíocht aibhneacha, lochanna, uisce idirchriosacha agus cósta na hÉireann, agus screamhuisecí; leibhéal uisce agus sruthanna aibhneacha a thomhas.
- Comhordú náisiúnta agus maoirsiú a dhéanamh ar an gCreat-Treoir Uisce.
- Monatóireacht agus tuairisciú a dhéanamh ar Cháilíocht an Uisce Snámha.

Monatóireacht, Anailís agus Tuairisciú ar an gComhshaoil

- Monatóireacht a dhéanamh ar cháilíocht an aeir agus Treoir an AE maidir le hAer Glan don Eoraip (CAFÉ) a chur chun feidhme.
- Tuairisciú neamhspleách le cabhrú le cinnteoireacht an rialtais náisiúnta agus na n-údarás áitiúil (*m.sh. tuairisciú tréimhsiúil ar staid Chomhshaoil na hÉireann agus Tuarascálacha ar Tháscairí*).

Rialú Astaíochtaí na nGás Ceaptha Teasa in Éirinn

- Fardail agus réamh-mheastacháin na hÉireann maidir le gáis ceaptha teasa a ullmhú.
- An Treoir maidir le Trádáil Astaíochtaí a chur chun feidhme i gcomhar breis agus 100 de na táirgeoirí dé-ocsaíde carbóin is mó in Éirinn.

Taighde agus Forbairt Comhshaoil

- Taighde comhshaoil a chistiú chun brúnna a shainiú, bonn eolais a chur faoi bheartais, agus réitigh a sholáthar i réimsí na haeráide, an uisce agus na hinbhuanaitheachta.

Measúnacht Straitéiseach Timpeallachta

- Measúnacht a dhéanamh ar thionchar pleananna agus clár beartaithe ar an gcomhshaoil in Éirinn (*m.sh. mórfheananna forbartha*).

Cosaint Raideolaíoch

- Monatóireacht a dhéanamh ar leibhéal radaíochta, measúnacht a dhéanamh ar nochtadh mhuintir na hÉireann don radaíocht ianúcháin.
- Cabhrú le pleananna náisiúnta a fhorbairt le haghaidh éigeandálaí ag eascairt as tairmí núicléacha.
- Monatóireacht a dhéanamh ar fhorbairtí thar lear a bhaineann le saoráidí núicléacha agus leis an tsábháilteacht raideolaíochta.
- Sainseirbhísí cosanta ar an radaíocht a sholáthar, nó maoirsiú a dhéanamh ar sholáthar na seirbhísí sin.

Treoir, Faisnéis Inrochtana agus Oideachas

- Comhairle agus treoir a chur ar fáil d'earnáil na tionsclaíochta agus don phobal maidir le hábhair a bhaineann le caomhnú an chomhshaoil agus leis an gcosaint raideolaíoch.
- Faisnéis thráthúil ar an gcomhshaoil ar a bhfuil fáil éasca a chur ar fáil chun rannpháirtíocht an phobail a spreagadh sa chinnteoireacht i ndáil leis an gcomhshaoil (*m.sh. Timpeall an Tí, léarscáileanna radóin*).
- Comhairle a chur ar fáil don Rialtas maidir le hábhair a bhaineann leis an tsábháilteacht raideolaíoch agus le cúrsaí práinnfhreagartha.
- Plean Náisiúnta Bainistíochta Dramhaíola Guaisí a fhorbairt chun dramhaíl ghuaiseach a chosaint agus a bhainistiú.

Múscail Feasachta agus Athrú Iompraíochta

- Feasacht comhshaoil níos fearr a ghiniúint agus dul i bhfeidhm ar athrú iompraíochta dearfach trí thacú le gnóthais, le pobail agus le teaghlaigh a bheith níos éifeachtúla ar acmhainní.
- Tástáil le haghaidh radóin a chur chun cinn i dtithe agus in ionaid oibre, agus gníomhartha leasúcháin a spreagadh nuair is gá.

Bainistíocht agus struchtúr na Gníomhaireachta um Chaomhnú Comhshaoil

Tá an ghníomhaíocht á bainistiú ag Bord Iáinimseartha, ar a bhfuil Ard-Stiúrthóir agus cúigear Stiúrthóirí. Déantar an obair ar fud cúig cinn d'Oifigí:

- An Oifig um Inmharthanacht Comhshaoil
- An Oifig Forfheidhmithe i leith cúrsaí Comhshaoil
- An Oifig um Fianaise is Measúnú
- Oifig um Chosaint Radaíochta agus Monatóireachta Comhshaoil
- An Oifig Cumarsáide agus Seirbhísí Corparáideacha

Tá Coiste Comhairleach ag an nGníomhaireacht le cabhrú léi. Tá dáréag comhaltáí air agus tagann siad le chéile go rialta le plé a dhéanamh ar ábhair inní agus le comhairle a chur ar an mBord.

Ecosystem Tipping Points: Learning from the Past to Manage for the Future



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Identifying pressures

Ecosystem change can occur abruptly in a non-linear fashion until a tipping point is reached and the ecosystem shifts to an alternative state. After a regime shift, the ecosystem may not return to its previous state, even when an external pressure is removed or reduced. This makes it difficult to predict ecosystem responses to human impacts and to identify appropriate indicators and targets for ecosystem-based management. The tipping points project aimed to collate and integrate datasets describing the Celtic Sea ecosystem, to use these data to quantify how physical and biological ecosystem components have changed in recent decades and to establish relationships between ecosystem responses and external pressures.

Informing policy

Environmental legal instruments such as the Marine Strategy Framework Directive (MSFD) and the OSPAR Convention prioritise holistic ecosystem-based management approaches. The dynamic nature of marine ecosystems makes the determination of ecosystem status, the identification of appropriate indicators and the setting of targets particularly challenging. The analysis of long-term environmental and biological datasets can support the implementation of the MSFD and other ecosystem management approaches by providing a historical context for changes in indicators, allowing natural short-term variability to be separated from long-term trends, regime shifts to be detected and links between ecosystem components to be identified. The ultimate goal for researchers, managers and policymakers is to develop early warning indicators that signal an approaching threshold before it is reached, allowing management to respond to avert a regime shift.

Developing solutions

A primary objective of the project was to develop analytical tools for detecting step changes and to use these tools to determine if ecological tipping points have occurred in the Celtic Sea ecosystem. Significant progress was made in the early detection of ecosystem change points using the Bayesian online change-point detection algorithm.

The results from the project show that there has been considerable change in the physical environment in the Celtic Sea, primarily associated with ocean warming. While a simultaneous regime shift across the ecosystem was not detected, there is strong evidence that change has occurred across multiple taxa and trophic levels in the Celtic Sea ecosystem over the last 50 years, which has important consequences for management.