

Imperial College London
Department of Life Sciences

Understanding human impacts on aquatic ecosystems: quantitative approaches to size-based community indicators

Georgina Adams

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Supervised by Daniel Reuman, Simon Jennings and Samraat Pawar

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Declaration

I declare that the work submitted in this thesis is my own and that any other material is appropriately referenced.

Any co-authors, and their respective contributions, are included at the beginning of each chapter.

Georgina L Adams

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Abstract

Body size is a fundamental property of organisms that underpins the structure and function of aquatic communities. Human impacts such as climate or fishing can significantly alter the size structure of ecological communities. This thesis aimed to understand further the effect of those impacts on properties of size-based indicators in real communities, by examining trends at levels of organisation or scales that have not been studied in detail before. To do this, various quantitative approaches were developed that allowed 1) trends in size-based indicators to be decomposed into contributions of constituent parts, and 2) significance of indicators and trends in indicators to be appropriately assessed. Results revealed important features of community size structure that should be considered when assessing trends in indicators. A study of the response of body size to warming in a diatom community did not support the commonly held idea that reduced body size is a universal response to warming at either the species or community levels. Results further demonstrated that overall community trends in body size are not wholly representative of the responses of the components that made up the community. This was further supported by results from decomposing a size-based fisheries indicator, where the overall trend in the indicator was an average of wildly diverging contributions of both species and geographic locations. The methods developed also allowed finer structure of the size spectrum in the North Sea fish community to be examined, and found empirical evidence of biologically meaningful deviations in the overall size structure over time. Finally, the methods developed for assessing significance provided a useful tool for analysing the components of size-based indicators and their response to human pressures, and offer a solution for detecting significant trends in indicators calculated from trawl survey sampling data that has applications for management of marine systems.

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Chapter 1. Introduction

1.1. Size-structuring of aquatic ecosystems

Body size is a key determinant of an organism's biology and ecology (Peters 1983; Cohen *et al.* 2003; Brown *et al.* 2004) and this is fundamental to the structure and functioning of aquatic ecosystems (Woodward *et al.* 2005; Hildrew *et al.*, 2007). At the individual level, almost all properties of organisms are a function of their body size, including metabolic rate and energy use or production (Brown & Gillooly, 2003; Brown *et al.*, 2004; Marquet *et al.*, 2005; Woodward *et al.*, 2005), as well as life history traits such as reproduction, growth and development (Hildrew *et al.*, 2007). The metabolic theory of ecology developed by Brown *et al.* (2004) links these individual level processes to the structure of populations, communities and ecosystems. In marine systems where predation is strongly size-dependent, and where organisms can grow through many orders of magnitude during their life cycle occupying different trophic levels as they grow (Jennings *et al.*, 2001), it is predominantly predator-prey interactions related to body size which underpin the structure and function of marine food webs (Cohen *et al.*, 1993; Barnes *et al.*, 2010). For instance, smaller predator prey size ratio is characteristic of more stable environments and food chains are longer when ratios are small (Jennings & Warr, 2003). Community structure is therefore largely determined by the body sizes of individuals and their interactions, and many studies and models of trophic interactions and food webs are based on body size (e.g. Cohen *et al.*, 2003; Reuman & Cohen 2004; Woodward *et al.*, 2005; Brose *et al.*, 2006; Petchey *et al.*, 2008; Cozar *et al.*, 2008; Reuman *et al.*, 2009; Hartvig *et al.*, 2010).

Body size scales with abundance in ecology (White *et al.*, 2007; Lewis *et al.*, 2008; Ulrich, 2008). The size range of aquatic organisms spans at least 20 orders of magnitude, categorised from very small bacteria up to the largest whales, that decrease in abundance with increased size (Sheldon *et al.*, 1972; Kerr & Dickie, 2001). Such a size structure is a common feature of many ecosystems, but is ubiquitous in aquatic systems (Sheldon *et al.*, 1972). A regular size spectrum occurs as the result of predation processes and energy transfer in food chains, which are dependent on body size (Sheldon *et al.*, 1972; Dickie *et al.*, 1987; Thiebaut &

Dickie, 1993). Kerr and Dickie (2001) analysed size spectra in many aquatic ecosystems, both freshwater and marine, to demonstrate that the spectrum is linear in many systems and the slope is remarkably consistent. The size spectrum is constructed by binning individuals or groups of organisms into size classes and statistically describing the relationship of log abundance or biomass versus log size class (spectra are commonly referred to as size spectra generally, or abundance or biomass spectra when calculated using those metrics). The resulting linear relationship corresponds to a power law dependence of abundance in each size class on the central body size in that class (Marquet *et al.*, 2005).

The slope of the spectrum, and therefore the exponent of the underlying power-law, is frequently found to be around -1 in non-exploited communities (Boudreau & Dickie, 1992; Kerr & Dickie, 2001; Jennings & Mackinson, 2003). However, the intercept of the slope varies between systems, and is indicative of different environmental conditions which determine the overall biomass density (Boudreau & Dickie, 1992). The size structure of communities is usually stable in the absence of pressures on the system, but influences of changing climate or exploitation on the community can alter the structure (Kerr & Dickie, 2001; Brose *et al.*, 2012). Size spectra and body size are often used as general indicators of an ecosystem (Petchey & Belgrano, 2010) and changes in size spectra and other size-based properties of communities and ecosystems are often linked to environmental pressures (Hildrew *et al.*, 2007; Yvon-Durocher *et al.*, 2011; Jochum *et al.*, 2012; O’Gorman *et al.*, 2012). Shifts in the size structure of communities are the main focus of this thesis.

1.2. Climate effects on the size structure of communities

Temperature increase is widespread across the globe (IPCC, 2007) and anthropogenic climate change has been shown to have wide ranging and profound effects on ecological communities (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Parmesan, 2006). These climate induced effects are expected to have consequences for the functioning of ecosystems and to result in species extinctions at local and global scales (Thomas *et al.*, 2004; Parmesan, 2006). Observed effects of climate warming on populations and communities include changes in phenology (Edwards & Richardson, 2004; Menzel *et al.*, 2006), shifts in distributional ranges

to higher latitudes and altitudes (Hickling *et al.*, 2006; Parmesan, 2006), and alterations in size composition towards smaller body sizes (Daufresne *et al.*, 2009; Sheridan & Bickford, 2011).

Smaller sizes at warmer temperatures are expected and rules explaining these observations have previously been described for different levels of biological organisation. At the individual level, the temperature-size rule states that body size at a fixed age or developmental stage is smaller at warmer temperatures for ectotherms (Atkinson, 1994; Atkinson & Sibly, 1997), and results from a plastic response at the individual level. At the population level, James' rule states that the mean body size of a species will be smaller at warmer temperatures (James, 1970; Blackburn *et al.*, 1999). At the community level, Bergmann's rule states that larger species tend to be found at higher latitudes, and therefore at colder temperatures (Blackburn *et al.*, 1999; Angilletta *et al.*, 2004; Millien *et al.*, 2006; Georg & Christian, 2011), so the converse can be described as smaller species tend to be found at lower latitudes and warmer temperatures. In a meta-analysis using both experimental and survey data, Daufresne *et al.* (2009) suggested that the shift towards smaller body sizes could be a universal rule for ectotherms in aquatic ecosystems. They further speculated that this rule was general across all biological scales, and that the metabolic theory of ecology (Brown *et al.*, 2004) could explain the underlying processes that lead to this generality. However, the existence of such a general rule depends on temperature-body size effects at those levels being in agreement, and thus the three temperature-size rules outlined above being related to each other and in agreement.

Body size shifts have been linked to temperature and climate warming across a wide range of taxa, and it is generally the case that warmer conditions do tend to favour smaller organisms (Atkinson, 1994; Daufresne *et al.*, 2009; Sheridan & Bickford, 2011). Examples have been shown for taxa as diverse as mammals (Yom-Tov *et al.*, 2010), birds (Gardner *et al.*, 2009), insects (Tarone *et al.*, 2011), zooplankton (Stelzer, 2002) and phytoplankton (Atkinson *et al.*, 2003). However, examples of larger or unchanged sizes at warmer temperatures also exist, but these responses are far less commonly reported (Sheridan & Bickford, 2011). Most of these studies have focussed on just one or a few species, and responses of whole communities to recent warming have not been explicitly tested, even though it is increasingly important to

understand how climate change affects communities or assemblages (Woodward *et al.*, 2010a). This is addressed by work in Chapter 2 of this thesis.

1.3. Impacts of climate and fishing in marine systems

The rest of the thesis (Chapters 3, 4 and 5) focuses on size structure in marine communities, specifically in the North Sea, which are impacted by both climate and fishing pressures.

Sea surface temperature increase in the North Sea has rapidly accelerated in recent years, 10 times faster than average (EEA, 2008). In addition, North Sea winter bottom temperature has already increased by 1.6 degrees over 25 years (MCCIP 2006). European shelf seas are warming faster than the global average (MCCIP 2006), and around the UK coast the sea surface temperature is expected to rise by another 1.5 to 4 degrees within this century, especially in the southern North Sea.

Effects of this warming, such as species range shifts, have already been detected in the North Sea. More southerly species have moved into the North Sea (Beare *et al.*, 2004) as temperatures have warmed. Dulvy *et al.* (2008) found that latitudinal response to warming was heterogeneous with abundant thermal specialists shifting northwards, and small southerly species that have their northern range boundary in the North Sea shifting south. The stronger effect was a depth response of fish moving deeper on average by 3.6 metres a decade, which is comparable to the altitudinal response observed in terrestrial systems (Parmesan & Yohe, 2003). Commercially important species such as cod and plaice have shifted in their distributions due to both fishing and climate (Engelhard *et al.*, 2011, 2014), with climate forcing a more northwards shift. Warming is also likely to be responsible for a shift towards smaller body sizes in the North Sea (Baudron *et al.*, 2014), due to changes in temperature and oxygen. However, these effects are difficult to disentangle from the large impacts of fishing on the North Sea fish community.

Fishing has had large impacts on marine communities worldwide. Industrialised fisheries have been shown to reduce community biomass by 80% over 15 years of exploitation (Myers & Worm, 2003) and this decline in large predators extends beyond the coastal regions where

fishing takes place into the global oceans. In the North Sea, fishing is estimated to have reduced biomass by up to 90% of pre-exploitation levels (Blanchard & Jennings, 2004). The North Sea has been extensively fished over the last century (Hall 1999), except for a reduction in effort during WW2. This did not result in a population recovery during this period, or in a rapid decline after post-war fishing resumed (Daan 1990; Hall 1999) suggesting that recovery times of fish communities to reduced fishing pressure are long. These long recovery times are also reflected in models where size structure takes decades to recover from fishing impacts (Fung *et al.*, 2013), as the effects of fishing are incorporated into size structure over long periods of time (Rossberg, 2012). The global distribution of fisheries has shifted in recent years, and Europe's share of worldwide fishing effort has decreased (Watson & Pauly, 2013). Fishing effort has reduced in the North Sea since 2000 as a result of management policies (Greenstreet *et al.*, 2012a) and landings have reduced by more than 50% since the peak of fishing effort in the 1970s (Gascuel *et al.*, 2014), but the recovery of the size structure may take longer.

Various size-based indicators have been proposed for monitoring responses of North Sea fish communities as part of an ecosystem approach to fisheries (Nicholson & Jennings, 2004; Jennings, 2005; Jennings & Dulvy, 2005; Shin *et al.*, 2005; Shin *et al.*, 2010; Borja *et al.*, 2011; Greenstreet *et al.*, 2012). Indicators are chosen for their responsiveness to pressures and for their ability to be measurable (ICES 2014). They include the slope of the size spectrum, which has been shown to respond to fishing pressure in the North Sea by becoming steeper as larger fish are removed from the community by fishing (Rice & Gislason, 1996; Shin *et al.*, 2005) and as prey are released in smaller size ranges (Heath, 2005). Another recently adopted indicator is the large fish indicator (LFI) which measures the proportion of biomass of large fish in the community (Greenstreet *et al.* 2011). Each of these indicators is the focus of a chapter in this thesis, as they are both responsive to fishing and climate pressures (Blanchard *et al.*, 2005; Shephard *et al.*, 2011a) and are complex in the information they convey about size structure in community ecology.

1.4. Aims of the thesis

The main aim of the thesis is to investigate the effects of human impacts on the size structure of aquatic ecosystems, at levels of organisation or detail that are not commonly examined in empirical studies. Trends in community body size are explored in both freshwater and marine systems, using size-based community indicators to represent the overall size structure of the system. Trends in these indicators are often averaged or aggregated and do not consider the component effects that contribute to the community-level indicator, whether that is on a spatial, temporal or organisational scale. The motivation for the studies in this thesis come from trying to understand how the effects and responses to anthropogenic pressures at different levels of organisation or at different scales can contribute to an observed overall trend in real ecological communities. Several quantitative approaches are taken to achieve this, by disentangling components in order to determine the levels or scales at which an effect is detectable and the relative contribution influential on the community indicator. Another important consideration of the thesis is that empirical studies such as these rely on ecological data that may include large levels of sampling variation. I address this by developing appropriate resampling methods to distinguish real ecological effects from sampling artefacts. Resampling methods have widely been applied in ecology and evolution to test for significance (Crowley, 1992), but I adapt them for the specific data used.

Chapter 2 examines the universality of the temperature-size rules in an assemblage of freshwater diatoms. Effects of climate on communities has not been as widely studied as on populations and individuals (Woodward *et al.*, 2005). I aim to address this by studying the overall community response to warming, but also identifying the components driving that response. The study system used is a geothermally heated set of streams that allow for a unique test of the effects of temperature change on body size and community structure in a real system without the interactions of other confounding environmental variables. Species and community responses to temperature effects are studied simultaneously and the mechanisms of size structure shifts are disentangled to determine the relative importance of intraspecific and interspecific processes to trends in the overall community structure.

The rest of the chapters shift focus to the marine environment, specifically the North Sea. Trends in size-based indicators are examined using a combination of quantitative approaches designed to reveal significant detail that is often overlooked in other empirical studies of these indicators. Chapter 3 develops two simple approaches to systematically determine the relative effects of the underlying components that contribute to community indicators. Firstly, a decomposition of an indicator or linear trend of an indicator over time into component parts, and secondly, a resampling based method that allows appropriate confidence intervals to be assigned to the component parts. The study considers the contributions of both species and space to overall trends in the large fish indicator, a widely used and tested community indicator that seeks to capture the size-based response of the fish community to fishing pressures. In combination, the two methods should provide insight into the driving components of community size structure over time.

Chapter 4 makes further use of the resampling method to examine finer scale structure of the community size spectrum in the North Sea than is currently documented in empirical studies. Size spectra in this region are often computed and averaged over large temporal scales, but the methods developed in the thesis allow smaller scale processes to be detected. Theoretical models of size spectra that have previously been formulated for both whole and partial food webs have predicted pulses in biomass that move through the spectrum when an ecosystem is subject to fishing pressure. Chapter 4 aims to determine whether this type of pulse exists in the North Sea size spectrum, as is expected from the history of heavy exploitation in the region.

The resampling based methods used in previous chapters to determine significance of results are further developed in Chapter 5. Community indicators are often reported without an appropriate measure of significance, and as such, can have limited meaning when year to year changes in indicator values are needed to inform management. I adapt a simple resampling method so that it is specific to the sampling design of fish trawl surveys, and is easy to apply to a wide range of indicators and trends.

Chapter 2. Diatoms can be an important exception to temperature-size rules at species and community levels of organisation

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Abstract

Climate warming has been linked to an apparent general decrease in body sizes of ectotherms, both across and within taxa, especially in aquatic systems. Smaller body size in warmer geographic regions has also been widely observed. Since body size is a fundamental determinant of many biological attributes, climate-warming-related changes in size could ripple across multiple levels of ecological organisation. Some recent studies have questioned the ubiquity of temperature-size rules, however, and certain widespread and abundant taxa, such as diatoms, may be important exceptions. This chapter tested the hypothesis that diatoms are smaller at warmer temperatures using a system of geothermally heated streams. There was no consistent relationship between size and temperature at either the population or community level. These field data provide important counterexamples to both James’ and Bergmann’s temperature-size rules, respectively, undermining the widely held assumption that warming favours the small. This study provides compelling new evidence that diatoms are an important exception to temperature-size rules for three reasons: 1) it uses many more species

than prior work; 2) it examines both community and species levels of organisation simultaneously; 3) it works in a natural system with a wide temperature gradient but minimal variation in other factors, to achieve robust tests of hypotheses without relying on laboratory setups, which have limited realism. In addition, results show that interspecific effects were a bigger contributor to whole-community size differences, and are probably more ecologically important than more commonly studied intraspecific effects. These findings highlight the need for multispecies approaches in future studies of climate warming and body size.

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2.1. Introduction

Body size is a key determinant of organism physiological traits and functional roles within an ecosystem (Peters, 1983; Cohen *et al.*, 2003; Brown *et al.*, 2004; Woodward *et al.*, 2005). Numerous studies have linked temperature and climate warming with changes in body size across taxa, with an apparent trend that warmer conditions tend to favour smaller organisms (Atkinson 1994; Daufresne *et al.* 2009; Sheridan & Bickford 2011; Yom-Tov *et al.* 2010; Gardner *et al.* 2009; Tarone *et al.* 2011; Stelzer 2002; Atkinson *et al.* 2003). Examples of larger or unchanged sizes at warmer temperatures also exist, but these are far less commonly reported (Sheridan & Bickford, 2011). Temperature-size relationships have ramifications for ecological interactions and the structure and functioning of communities, such that warming-induced changes in organism size and its consequences have been called one of the most far-reaching consequences of climate change (Daufresne *et al.*, 2009).

The general trend of smaller sizes at warmer temperatures has been separated conceptually into three well-known relationships, which are related to each other but are distinct in detail: Bergmann's rule (1847), James' rule (1970), and the temperature-size rule (Atkinson, 1994, 1995). Bergmann's rule states that larger species tend to be found at higher latitudes, and therefore at colder temperatures (Blackburn *et al.*, 1999; Angilletta *et al.*, 2004; Millien *et al.*, 2006; Georg & Christian, 2011). James' rule is an intraspecific version of Bergmann's rule (Blackburn *et al.*, 1999) and states that the mean body size of a species will be smaller at warmer temperatures. The temperature-size rule states that size at a fixed age or developmental stage is smaller in warmer temperatures for ectotherms (Atkinson, 1994; Atkinson & Sibly, 1997), and results from a plastic response at the individual level. This study focuses on Bergmann's and James' rules.

Recent work suggests that, for ectotherms in aquatic environments, the trend of smaller sizes at warmer temperatures is sufficiently widespread, in both experimental and survey data, that it may be a universal rule (Daufresne *et al.*, 2009). Daufresne *et al.* (2009) also suggested that "... a common mechanism (or set of mechanisms) links size structure and thermal energy at all biological scales" (p. 12790) and speculated that the metabolic theory of ecology (Brown *et al.*, 2004) could be implicated in such an explanation, although they did not explore or test

possible mechanisms in detail. Crucially, this depends on temperature-body size effects at those levels being in agreement. The analyses of Daufresne *et al.* (2009) are far-reaching and compelling, but the true universality and the underlying mechanisms behind the effects they describe require further research. Such potential mechanisms may be illuminated as much by exceptions as to any agreements with general trends.

Diatoms represent an ideal group of model organisms to test these ideas, as past research on warming-related body-size changes has produced mixed results. The term body size is used throughout the chapter in place of cell size, since it is understood in its broader sense in the application of the temperature-size rules. Diatoms are found in almost all aquatic systems (Smol & Stoermer, 2010) and account for around 23% of the world's total primary production (Snoeijs *et al.*, 2002). They play a key role in aquatic food web structure because their cell size can influence the flow of energy to higher trophic levels, as well as influencing an ecosystem's carbon cycle (Smetacek, 1999; Yvon-Durocher *et al.*, 2010; O'Gorman *et al.*, 2012). There is equivocal evidence that diatoms follow the temperature-size rule in controlled temperature studies at the intraspecific level (Montagnes & Franklin, 2001; Atkinson *et al.*, 2003). At the community level, shifts have been observed towards smaller primary producer species at warmer temperatures in both mesocosm experiments (Lewandowska & Sommer, 2010; Yvon-Durocher *et al.*, 2011; Peter & Sommer, 2012) and natural ecosystems (Li *et al.*, 2009; Winder *et al.*, 2009; Barnes *et al.*, 2010b), as predicted by Daufresne *et al.* (2009). However, exceptions have also been found (Atkinson, 1995; O'Gorman *et al.*, 2012; R  ger & Sommer, 2012) and if diatoms (and other single-celled organisms) do not conform to the rule of smaller body sizes at warmer temperatures, then they are very important exceptions. The first and main goal of this chapter is to determine to what extent diatoms exhibit decreases in body size at the community level (Bergmann's rule) and intraspecifically (James' rule), under warming.

It is critically important to understand how climate change affects whole assemblages or communities, yet most studies have examined just one or a few species (Woodward *et al.*, 2010a). There are three routes by which an overall community size difference between systems at different temperatures or different levels of another abiotic factor could be realised (Figure 2.1), and to my knowledge the relative contributions of these routes to size shifts in

actual communities have never been determined. These routes are conceptually similar to those outlined by Daufresne *et al.* (2009) at the population and community levels. First, *intraspecific size shifts* (Figure 2.1b) occur when the body sizes of individual species respond similarly to temperature, as in James' rule, such that the response will be reflected in a shift in the community mean body size. The other two mechanisms are types of compositional shift, as in Bergmann's rule. These can be manifested by *species relative abundance differences* (Figure 2.1c), where species of different mean size differ in relative abundance in systems at different temperatures, or in the more extreme form of *species turnover* (Figure 2.1d) due to local extinctions or invasions. Turnover may occur spatially among systems along a temperature gradient (e.g. after O’Gorman et al., 2012) or temporally, if warming occurs over time. The second goal of this chapter will be to assess the relative importance of these three contributors to community size shifts in diatoms.

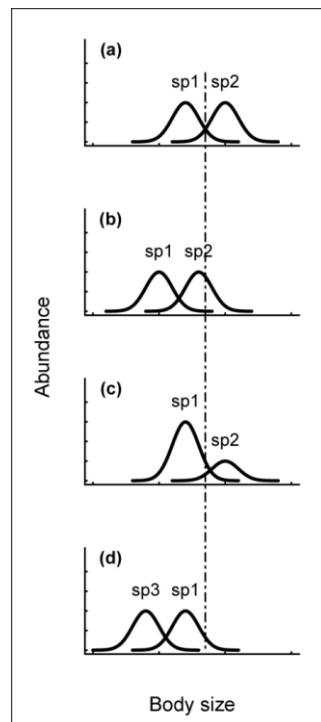


Figure 2.1: Plots showing conceptual differences among possible causes of overall community size changes with warming, for a two-species community. Compared to the reference distribution (a), community mean size could decrease from either the mean size of individual species decreasing (b), the relative abundance of small species increasing (c), species turnover effects (d), or a combination. The dashed line shows the mean body size in the reference distribution (a), and is for reference. Changes toward larger sizes could occur as well via the same three distinct routes or a combination. The abbreviation “sp” is for “species”.

The few studies that have examined phytoplankton or phytobenthos community responses to warming have had one or both of two common limitations that this study avoids: either they have been conducted in controlled mesocosm or microcosm environments (Lewandowska & Sommer, 2010; Rüger & Sommer, 2012), which have limited realism (Friberg *et al.*, 2009), or they have been conducted over large latitudinal (Morán *et al.*, 2010) or temporal (Winder *et al.*, 2009) scales, introducing dispersal constraints and confounding environmental covariates. To overcome these limitations, this study used a system of geothermally heated streams in Iceland that span a 20°C difference in temperature whilst being no more than 2 km apart (Figure 2.2).

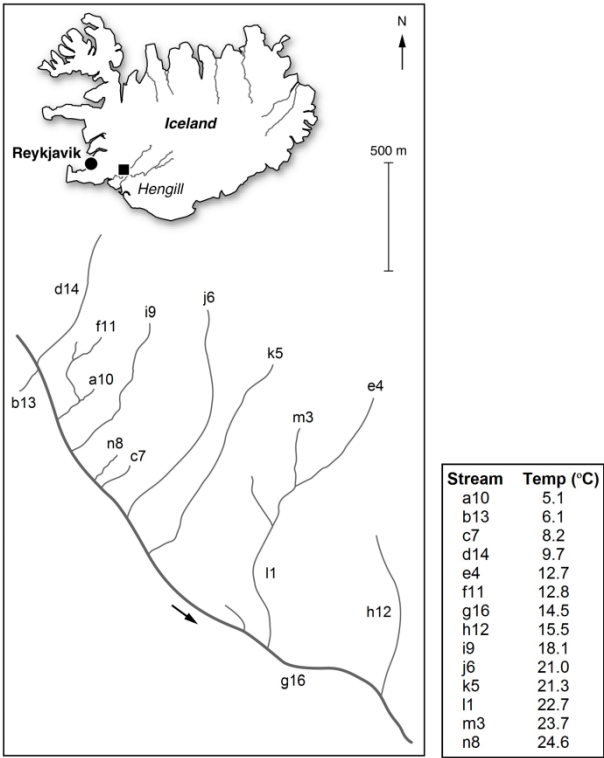


Figure 2.2: Map of the Hengill system within Iceland. Streams used are labelled using the numbering system outlined in Methods. The table shows mean August 2008 temperatures for the streams. The arrow is water flow direction.

The diatom assemblages of 14 streams within this catchment were sampled *in situ*, providing a rare natural experiment that allows us to capture the effects of warming on real, complex systems, without the confounding effects introduced by biogeography, and with minimal possibility for confounding effects of other environmental variables besides temperature (see

Methods, Table A.1 and Figure A.1 in Appendix A.1 for more details; Woodward *et al.* 2010b). Previous studies carried out at this site (e.g. Friberg *et al.* 2009; Woodward *et al.* 2010b; O’Gorman *et al.* 2012) and at other geothermal sites (e.g. Lamberti & Resh 1985) have shown that this form of warming is a reasonable proxy for climate change.

This chapter addresses two specific questions for each of the two research goals: 1a) For each species, how is mean body size per stream related to stream temperature, and how consistently is decreased size observed at warmer temperatures? 1b) How is mean body size of the diatom community in each stream related to stream temperature? 2a) What is the relative importance of intraspecific body size shifts and species compositional shifts in producing whole-community size shifts (i.e. the relative importance of Bergmann’s rule and James’ rule)? 2b) What is the relative importance of species relative abundance shifts and species turnover effects with temperature? This study is the first I know of both to address systematically the nature of size shifts for multiple diatom species in a natural ecosystem, and to examine the relative importance of both intraspecific and species compositional changes for community size shifts.

2.2. Materials and methods

2.2.1. Study site

The study was done in the geothermal Hengill region of Iceland (64°03'N, 021°18'W, 350–420 meters above sea level). The area contains multiple indirectly heated streams that are tributaries to the same main stem and which all lie within 2 km of one another, such that dispersal constraints are negligible across the whole system (Figure 2.2; see O’Gorman *et al.* 2012 for a more detailed site description). Stream water temperatures are altered by geothermal warming from deep below the streambed. Temperature is the major determinant of the taxonomic composition of assemblages of both primary and secondary producers across the streams (Woodward *et al.*, 2010b; Gudmundsdóttir *et al.*, 2011). These features enable us to isolate the effects of temperature on diatom community composition and size structure. Fourteen streams in the system were used for this study (Figure 2.2), spanning

about 5-25°C. This stream system was the subject of previous work (Woodward *et al.*, 2010b; Gudmundsdóttir *et al.*, 2011; O’Gorman *et al.*, 2012), in which the streams were named numerically. I have changed notation slightly so it is easier to distinguish between warm and cold streams. Streams used are labelled with the letters a-n in order from the coldest to the warmest stream, followed by the number used in the original system, so it is easier to compare with previous work.

2.2.2. Environmental variables other than temperature

A broad suite of physical and chemical variables were measured in the streams in August 2008, concurrently with the diatom sampling (see Woodward *et al.* 2010b; Demars *et al.* 2011; O’Gorman *et al.* 2012 for detailed methods). These variables included the major macronutrients (e.g. nitrate, ammonium, orthophosphate), ions (e.g. Ca^{2+} , K^+ , Na^+ , Cl), trace elements (e.g. Si), pH and conductivity (see Table A.1 in Appendix A.1). Besides temperature and a few variables directly linked to it by physico-chemical processes, all water chemistry and environmental variables were broadly similar among the streams and not strongly related to temperature (Friberg *et al.* 2009; Woodward *et al.* 2010b; Demars *et al.* 2011; O’Gorman *et al.* 2012; Table A.2 in Appendix A.1). Among those that are driven by physical laws that apply to all systems, dissolved oxygen concentrations declined with temperature, but the % saturation was independent of temperature across the gradient. The other two exceptions are silicon (Si) and K^+ concentrations, which increased with temperature, reflecting the increased chemical weathering of rocks. These two abiotic variables are unlikely to have ecological significance for the diatom assemblages at Hengill because Si is found in concentrations at least one order of magnitude above what is typically considered to be limiting in freshwaters (White *et al.*, 1999; Dalai *et al.*, 2002; Dupré *et al.*, 2003) and potassium (K) is thought to be unlikely to limit growth in natural waters (Hynes, 1970; Jaworski *et al.*, 2003; Talling, 2010). Algal production in these streams is (co)limited by N and P (Friberg *et al.*, 2009), as is typical of freshwater ecosystems, but concentrations of these macronutrients were not strongly related to temperature and there was very little variation across the catchment: total variation was <0.1% of the range for European streams (Woodward, G. *et al.* 2012 and also Figure A.1 in Appendix A.1).

2.2.3. Diatom sampling

Sampling took place in August 2008. Five stones were selected randomly from each stream. Potential in-stream and between-stream habitat heterogeneity was minimised by sampling from riffles. Stones were representative of the typical size of cobbles on the surface of the armoured layer and were similar sizes in each stream. Algal scrapes were collected from the whole upper (projected) surface of each stone using a toothbrush. The stone area sampled was recorded and samples were analysed separately. Samples were preserved immediately in Lugol's solution, and a fixed volume of the sample solution was subsequently acid-digested and mounted on microscope slides (after O’Gorman *et al.* 2012). Relative abundance of diatom species was determined by counting individuals present in a 100µm wide transect across the centre of the slide and calculating $\frac{c_i}{C}$ where C is the total number of individuals counted per stream, and c_i is the total number of individuals found of species i .

2.2.4. Diatom identification and measurements

Diatom species that accounted for the top 95% of abundance in each stream were measured for size: the remainder were grouped together and designated as a single group, 'other', for later use in resampling schemes. There were several species outside the 95% abundance group but these were always very rare. Within each stream, for every species and for the 'other' group, ten individuals per group were selected for size measurement along a transect starting at the centre of the slide, using an Olympus BH2 microscope. Samples for the 'other' group were taken as the first ten individuals found on a slide that were outside the top 95% for that stream. For some groups, 10 samples could not be found; in those cases as many were found as possible. Samples from 'other' were also identified to species level. Broken or obscured valves were not used. Individuals selected for size measurement were photographed in valve view with a high resolution Canon digital SLR camera. Any individuals that were lying out of focus had multiple images taken and were rendered in Helicon Focus (Helicon Soft Ltd., 2011). Images were taken at a magnification of x1000, except for a few very large individuals where x400 was used. Diatoms were identified using the species definitions and nomenclature of Krammer & Lange-Bertalot (volumes 2.1-2.4, 1986-1991). Classifications beyond the species level were not used.

Measurements were taken in ImageJ (Abramoff *et al.*, 2004) for valve length and maximum valve width. Diatom size is sometimes estimated using cell volume, using dimensions taken from diatoms in both valve view and girdle view (Hillebrand *et al.*, 1999). In this study, projected (cross-sectional) valve area was used because measurements of individual diatoms were required, and because each single diatom was lying in either valve or girdle view. This is a reliable measurement of body size as diatom cell volume is strongly correlated with valve length (Snoeijs *et al.*, 2002; Finkel *et al.*, 2009a) and valve area incorporates valve length as well as the additional information of valve width, and hence is likely to be even better correlated with volume. Valve area (μm^2) was calculated using a standard geometric shape for each genus as described in Hillebrand *et al.* (1999), with a few exceptions where the shape of the species in the Hengill region was distinctly different from the described shape for the genus. Table A.3 and Figure A.2 in Appendix A.2 justify the exceptions, showing that the new shape modifications improved accuracy.

2.2.5. Statistical analysis: intraspecific patterns

To determine the relationship between temperature and body size within individual species, the intraspecific analysis considered every species that was present in two or more streams. Linear regressions were carried out for each species, of temperature against body size of individuals. A Bonferroni correction for multiple tests was applied: p-values were multiplied by 31, the number of tests. Size data were $\log_{10}$ -transformed for this and all analyses.

During the asexual part of their life cycle, diatom cells progressively reduce in size (Edlund & Stoermer, 1997). Since the study system used here is a natural experiment where the sampled individuals could be at any stage of their life cycle, this phenomenon could potentially be contributing to any cell size differences observed. However, this vegetative cell size reduction is not uniform and in pennate diatoms the width of the valve decreases proportionally far less than the length (Round *et al.*, 1990). Thus, the intraspecific analysis was repeated using only valve width as the measure of body size, as a way of determining whether the diatom life cycle could have confounded the results.

2.2.6. Statistical analysis: whole community analysis

Average diatom size for each stream was calculated using a simple weighted mean. If k_α is the number of species present in stream α (including the ‘other’ group as a single ‘species’ for this count), $n_{\alpha i}$ is the number of samples taken of species i (cells measured, usually 10), $a_{\alpha i}$ is the relative abundance of species i in stream α , $s_{\alpha ij}$ is the $\log_{10}$ size measured for individual j of species i , and $\bar{s}_{\alpha i} = \sum_{j=1}^{n_{\alpha i}} \frac{s_{\alpha ij}}{n_{\alpha i}}$ is the average $\log_{10}$ size of species i in α , then the abundance-weighted mean size for α is $M_\alpha = \sum_{i=1}^{k_\alpha} a_{\alpha i} \bar{s}_{\alpha i}$. The $a_{\alpha i}$ are relative abundances, so they sum to 1 across all species (including ‘other’ as a species). Confidence intervals of the abundance-weighted mean were calculated using a resampling method (Crowley, 1992); for each stream M_α was calculated for a resampled dataset 10,000 times and from those took 95% confidence intervals, as follows. The resampled dataset was obtained by first resampling the original size data for each species $n_{\alpha i}$ times with replacement (including ‘other’ as a species), and second, recalculating the relative abundance of each species by resampling, with replacement, the original diatom count data C times using multinomial trials with probabilities proportional to the c_i for the species (including ‘other’).

2.2.7. Statistical analysis: partitioning the causes of community size change

The analysis partitioned the causes of community size change in two ways: first, by determining whether intraspecific effects or compositional shifts are the main contributor to whole-community size differences; and second by determining if compositional shifts are mostly due to differences in relative abundances of species or species turnover.

The proportional contribution of intraspecific effects to whole-community size differences was determined by calculating the size difference one would expect between any two streams, α and β , if there were no differences in community composition, and comparing this to the observed size differences between α and β in average diatom size (computed as described above). To remove compositional effects, the analysis first considered only species that were present in both α and β . To remove effects of differences in the relative abundance of species between α and β , which is a compositional effect, $a_{\alpha\beta i}$ was calculated as $\frac{a_{\alpha i} + a_{\beta i}}{2}$, the average relative abundance of species i in α and β . Then, if $k_{\alpha\beta}$ is the number of species in common

between α and β , the size difference one would expect due only to intraspecific effects is

$$\Delta_{\alpha\beta}^{INTRA} = \sum_{i=1}^{k_{\alpha\beta}} a_{\alpha\beta i} (\bar{s}_{\beta i} - \bar{s}_{\alpha i})$$

The overall average community size difference between streams α and β is $\Delta_{\alpha\beta}^{COMM} = M_{\beta} - M_{\alpha}$ and so the proportional contribution of intraspecific effects is $\Delta_{\alpha\beta}^{INTRA} / \Delta_{\alpha\beta}^{COMM}$. In the case where there are no compositional differences between streams α and β , $\Delta_{\alpha\beta}^{INTRA} = \Delta_{\alpha\beta}^{COMM}$. $\Delta_{\alpha\beta}^{INTER}$ was calculated as $\Delta_{\alpha\beta}^{COMM} - \Delta_{\alpha\beta}^{INTRA}$.

There are three possible outcomes to this analysis. If the result is negative then the intraspecific size difference was in a different direction to the overall community size difference and so the observed direction of body size difference between α and β is solely due to compositional shifts which overcame contrasting shifts in individual species; in other words, $\Delta_{\alpha\beta}^{INTER}$ had opposite sign and larger magnitude than $\Delta_{\alpha\beta}^{INTRA}$. If the result is 1 or above, then the overall community size difference is solely due to intraspecific size differences which overcame competing compositional shifts; in other words, $\Delta_{\alpha\beta}^{INTER}$ had opposite sign and smaller magnitude than $\Delta_{\alpha\beta}^{INTRA}$. If the result is between 0 and 1 then the overall community size difference is due to a mixture of intraspecific size differences and compositional shifts, and the value indicates the proportional contribution of $\Delta_{\alpha\beta}^{INTRA}$. In that case, $\Delta_{\alpha\beta}^{INTER}$ and $\Delta_{\alpha\beta}^{INTRA}$ have the same sign.

To provide illustration of the methods using simplified two-species examples, Table 2.1 gives calculations of $\Delta_{\alpha\beta}^{INTRA}$ and $\Delta_{\alpha\beta}^{COMM}$ for comparisons between a reference stream (α) and other streams (β_i); the three outcomes described above are shown. In all cases the average community body size decreases from stream α to stream β_i and $\Delta_{\alpha\beta}^{COMM}$ is negative, but the causes of the decrease are different. Examples (a) and (b) show the simplest examples, where only one cause of community size change is contributing. In (a) there is no change in the relative abundance of species between streams, only changes in the $\log_{10}$ size, therefore only intraspecific effects are contributing to the community size difference and $\Delta_{\alpha\beta}^{INTRA} = -1$ and $\Delta_{\alpha\beta}^{INTRA} / \Delta_{\alpha\beta}^{COMM} = 1$. In (b) there is no change in the $\log_{10}$ size of species, only in the relative

Stream	Species 1		Species 2		Species 3		$\Delta_{\alpha\beta}^{INTRA}$	$\Delta_{\alpha\beta}^{COMM}$	$\Delta_{\alpha\beta}^{INTRA}/\Delta_{\alpha\beta}^{COMM}$	Result
	abun- dance	log ₁₀ size ($\bar{s}_1$)	abun- dance	log ₁₀ size ($\bar{s}_2$)	abun- dance	log ₁₀ size ($\bar{s}_3$)				
α	7	2	3	3	-	-				
(a) β_1	7	1	3	2	-	-	-1	-1	1	ALL INTRA
(b) β_2	8	2	2	3	-	-	0	-0.1	0	ALL COMP
(c) β_3	8	1	2	2	-	-	-1	-1.1	0.91	91% INTRA
(d) β_4	6	1	4	2	-	-	-1	-0.9	1.11	ALL INTRA
(e) β_5	9	2	1	4	-	-	0.2	-0.1	-2	ALL COMP
(f) β_6	-	-	3	4	7	1	0.3	-0.4	-0.75	ALL COMP

Table 2.1: Examples of calculations for $\Delta_{\alpha\beta}^{COMM}$ and $\Delta_{\alpha\beta}^{INTRA}$ between streams α and β . Each example illustrates a difference from stream α on either 1) a change of log size for one or both species, 2) a shift in the relative abundances of the species, 3) a different species being present, or 4) a combination of these. $\Delta_{\alpha\beta}^{COMM}$ is calculated for a two-species system as $M_\beta - M_\alpha = (a_{\beta 1} \bar{s}_{\beta 1} + a_{\beta 2} \bar{s}_{\beta 2}) - (a_{\alpha 1} \bar{s}_{\alpha 1} + a_{\alpha 2} \bar{s}_{\alpha 2})$, where $a_{\alpha i}$ and $a_{\beta i}$ are the relative abundances of species i in streams α and β . $\Delta_{\alpha\beta}^{INTRA}$ is calculated as $\frac{a_{\alpha 1} + a_{\beta 1}}{2} (\bar{s}_{\beta 1} - \bar{s}_{\alpha 1}) + \frac{a_{\alpha 2} + a_{\beta 2}}{2} (\bar{s}_{\beta 2} - \bar{s}_{\alpha 2})$. There is only one species in common between α and β so $\Delta_{\alpha\beta}^{INTRA} = \frac{a_{\alpha 2} + a_{\beta 2}}{2} (\bar{s}_{\beta 2} - \bar{s}_{\alpha 2})$.

abundances of the species; therefore only compositional effects are contributing and $\Delta_{\alpha\beta}^{INTRA} = 0$ and $\Delta_{\alpha\beta}^{INTRA}/\Delta_{\alpha\beta}^{COMM} = 0$. Examples (c) to (f) illustrate a mixture of causes contributing to the difference in average community size between the streams. In (c) there is a decrease in the log₁₀ size of each species, and also a shift in the relative abundance towards species 1, the smaller species. Therefore both intraspecific and compositional effects are occurring in the same direction. $\Delta_{\alpha\beta}^{INTRA}/\Delta_{\alpha\beta}^{COMM} = 0.91$, so intraspecific effects are responsible for 91% of the average size difference between streams. In (d) there is the same decrease in log₁₀ size as in (c) but the shift in the relative abundance is in the opposite direction towards species 2, the larger species. In this case, intraspecific effects and compositional effects are acting in opposite directions, so $\Delta_{\alpha\beta}^{INTRA}/\Delta_{\alpha\beta}^{COMM} = 1.11$: intraspecific effects overcame compositional effects and are the only cause of the overall size decrease. In (e) there is an increase in log₁₀ size of species 2, and a shift in relative abundance towards species 1. This is the opposite of

example (d): $\Delta_{\alpha\beta}^{INTRA}/\Delta_{\alpha\beta}^{COMM} = -2$, and compositional effects overcame intraspecific effects. Example (f) shows the same outcome from the analysis as (e) with $\Delta_{\alpha\beta}^{INTRA}/\Delta_{\alpha\beta}^{COMM} = -0.75$, but in this case the compositional effects are due to species 3, a smaller species, replacing species 1. Turnover is the cause of the size decrease between the streams, rather than relative abundance shifts as in (e).

To assess the types of compositional shift that may be contributing to differences in body size this analysis considered the presence and absence of species (all species found in the streams, including those in the ‘other’ group) between streams and their relative abundances in the streams. The proportion of compositional change from stream α to stream β that was represented by species turnover, as opposed to species relative abundance shifts, was calculated as the sum of the relative abundances of the species that were present in α but not detected in β . If the main compositional difference between streams is mostly because of species turnover, then these values will be close to 1. If the main compositional differences are due to relative abundance shifts, then the values will be close to 0.

Intraspecific effects are the main contributor to changes in overall community size differences from one stream to another when the index $\Delta_{\alpha\beta}^{INTRA}/\Delta_{\alpha\beta}^{COMM}$ is greater than 0.5, and species turnover is the main contributor to compositional shifts when the index of the previous paragraph is greater than 0.5. Thus, the total fraction of all possible pairwise comparison values among streams that were greater than 0.5 in each analysis indicates the number of cases in which intraspecific effects or species turnover, respectively, are relatively more important, and characterizes the importance of these effects in the whole system. Again, confidence intervals were calculated for these measures using a resampling method. Data were resampled 1000 times according to the same scheme used for calculating confidence intervals for average community size, and all pairwise comparisons between streams were recalculated for each surrogate dataset created in this way. For each resampling, the total number of comparisons that showed a >50% contribution of $\Delta_{\alpha\beta}^{INTRA}$, or species turnover, was counted, and 95% confidence intervals for these numbers were taken as quantiles from the resulting distributions. All computations were carried out in the R programming language (version 2.14.1; R Development Core Team 2010).

2.3. Results

75 species were detected across the 14 streams of the study, and a total of 20,835 individual diatoms were counted to get relative abundance estimates and 2,006 diatoms were measured for body size.

2.3.1. Intraspecific size changes

There were 31 diatom species present in two or more streams, and these were used in the intraspecific analysis. Temperature appeared to have a significant effect on the body size of some diatoms. The slopes of intraspecific regressions (Table 2.2, Figure A.3 in Appendix A.3) revealed that the effect of temperature on $\log_{10}$ body size was species-specific, with increasing temperature having a negative effect in 16 cases (seven significant with $p < 0.05$) and a positive effect in 15 cases (five significant with $p < 0.05$). Seven relationships were significant at the 5% level after Bonferroni correction: 3 negative slopes (corrected $p = 0.0022$, $p = 0.0114$ and $p = 0.0266$) and 4 positive slopes (corrected $p = 0.0026$, $p = 0.0015$, $p = 0.0101$ and $p = 0.0029$). If species were excluded which only occurred in two streams, there were 26 species remaining, 15 with negative slope (3 significant with $p < 0.05$) and 11 with positive slope (3 significant with $p < 0.05$). Five relationships were significant at the 5% level after Bonferroni correction, 3 negative and 2 positive. If species were excluded which only occurred in three or fewer streams, 24 species remained, 14 with negative slopes (3 significant) and 10 with positive slopes (3 significant). Again, 5 were Bonferroni significant, 3 negative and 2 positive. Regardless of the details on how significance is judged or including versus excluding species that occurred in few streams, results are about evenly divided between species with increasing and decreasing slopes: no consistent influence of temperature across species was apparent.

Since results showed effects in opposite directions, in order to see whether there was a significant average effect of temperature on body size among species, a combined p-value for the 31 regressions was calculated using a weighted Stouffer's method (Stouffer *et al.*, 1949; Whitlock, 2005). Under a null hypothesis of diatom species not reducing in body size with increased temperature, the combined p-value was not significant ($p = 0.186$), so there was no average tendency for species to decrease in

Species	num. streams	Slope	R ²	p-value	Bonferroni corrected p-value
<i>Achnanthes lanceolata</i>	13	-0.0014	0.0039	0.48597845	1
<i>Amphora inariensis</i>	6	-0.0084	0.1114	0.01116087*	0.34598697
<i>Amphora pediculus</i>	6	-0.0046	0.0842	0.02450351*	0.75960881
<i>Caloneis lauta</i>	2	0.0029	0.0123	0.64100834	1
<i>Cocconeis pediculus</i>	4	0.0379	0.0849	0.08944546	1
<i>Cocconeis placentula</i>	10	-0.0013	0.0017	0.68446086	1
<i>Cymbella sinuata</i>	2	0.0325	0.5866	0.00008266***	0.00256246**
<i>Diatoma mesodon</i>	7	-0.0091	0.0879	0.01267111*	0.39280441
<i>Epithemia sorex</i>	3	-0.0097	0.0598	0.20974975	1
<i>Epithemia turgida</i>	8	-0.0003	0	0.96022789	1
<i>Fragilaria arcus</i>	2	0.0259	0.6105	0.00004755***	0.00147405**
<i>Fragilaria capucina</i>	14	0.0014	0.0061	0.35911286	1
<i>Fragilaria construens</i>	2	0.0338	0.097	0.2083153	1
<i>Fragilaria pinnata</i>	8	0.002	0.0076	0.48555925	1
<i>Gomphonema clavatum</i>	4	0.0125	0.345	0.00032597***	0.01010507*
<i>Gomphonema clevei</i>	4	0.0066	0.0986	0.07517861	1
<i>Gomphonema parvulum</i>	6	-0.01	0.0355	0.25732075	1
<i>Gomphonema type D</i>	8	0.0015	0.0065	0.50645964	1
<i>Melosira varians</i>	8	0.0343	0.1896	0.00009458***	0.00293198**
<i>Meridion circulare</i>	10	-0.0117	0.1618	0.00007049***	0.00218519**
<i>Navicula atomus</i>	4	-0.0007	0.0017	0.79776186	1
<i>Navicula minima</i>	13	0.0005	0.0011	0.71545164	1
<i>Navicula placentula</i>	6	-0.0091	0.2076	0.00036827***	0.01141637*
<i>Nitzschia dissipata</i>	4	0.0122	0.0242	0.37999347	1
<i>Nitzschia fonticola</i>	2	-0.0458	0.0645	0.32545121	1
<i>Nitzschia inconspicua</i>	3	0.0147	0.1694	0.08971087	1
<i>Nitzschia palea</i>	8	0.0096	0.0857	0.00885657**	0.27455367
<i>Nitzschia paleacea</i>	9	-0.0061	0.0336	0.09739664	1
<i>Rhoicosphenia abbreviata</i>	5	-0.0298	0.2253	0.00085866***	0.02661846*
<i>Rhopalodia gibba</i>	5	-0.0154	0.1626	0.00406858**	0.12612598
<i>Synedra ulna</i>	10	-0.0012	0.0016	0.72143697	1

Table 2.2: Summary of slopes and p-values from intraspecific body-size versus temperature analysis for 31 diatom species. num.streams is the number of streams in which each species was found; since most species' body sizes were measured for 10 individuals per stream, the number of points used in each regression was close to 10 times num.streams. Corrected p-values are Bonferroni corrected. Stars represent levels of significance: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***). Authorities for these and all species names are listed in Table A.4 in Appendix A.2.

size with increasing temperature. If species that occurred in only two streams were excluded from the analysis, the combined p-value was still not significant ($p = 0.113$), nor was it significant if those that occurred in three or fewer streams were excluded ($p = 0.112$). Two-tailed analogues of the above tests, which tested the null hypothesis that diatom species' sizes do not depend systematically on temperature, on average, had double the p-values reported above (Whitlock, 2005) and hence were also not significant. Thus there was no overall tendency for species to decrease or increase in size with increasing temperature.

The repeated intraspecific analysis using only valve width as the measure of body size gave similar results (Table A.5), so the lack of clear and consistent body size trends observed using valve area could not be ascribed to an artefact of the diatom reproductive cycle.

2.3.2. Whole-community size changes

Figure 2.3 shows that there is no clear relationship between temperature and body size at the community level. Both linear and quadratic regressions of mean $\log_{10}$ valve area against temperature, with weighting by inverse variances of mean $\log_{10}$ valve area estimates applied, were not significant ($p = 0.2628$ and $p = 0.3785$ respectively).

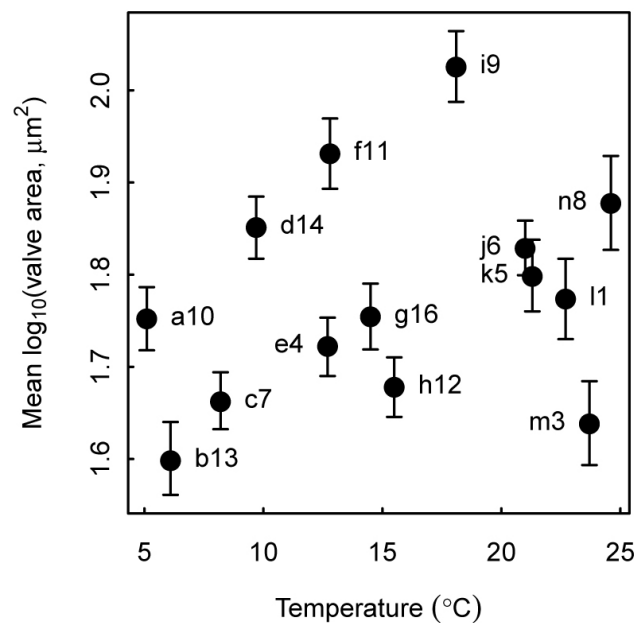


Figure 2.3: Mean body sizes of diatoms in the fourteen sampled streams, with 95% confidence intervals of the means, plotted against temperature.

In Figure 2.3 streams h12 and m3 appear to be possible outliers, but repeating the linear and quadratic regression analyses without those streams also gave insignificant results ($p = 0.0981$ and $p = 0.1742$ respectively). Thus there was no strong effect of temperature on community body size for diatoms in these streams, contradicting Bergmann's rule. If body size shifts in diatoms were a strong and general pattern, then across the large temperature gradient that was used ($\sim 20^\circ\text{C}$) one would expect to see significant relationships in these results for community-level and species-level patterns. The fact that these were not seen, contradicts the supposed universality of the temperature-size relationships.

2.3.3. Intraspecific effects versus compositional shifts

Compositional shifts were the main causes of the overall differences in average community body size. Of 91 pairwise comparisons between average community body size in the fourteen streams (Table A.8 in Appendix A.4), 51 showed that the observed difference in average community body size was solely due to compositional shifts (negative values of $\Delta_{\alpha\beta}^{INTRA}/\Delta_{\alpha\beta}^{COMM}$), and only four showed that the difference was solely due to intraspecific size change (values equal to 1 or above). Thirty-six were due to a mixture of the two mechanisms (values between 0 and 1), but of these 36, the average contribution of intraspecific size change to overall community change in body size was 21.8%, with a range from 0.28% to 84.4%. Only five of these 36 comparisons showed that intraspecific size differences were the main mechanism (over 50% contribution), and therefore only nine of 91 comparisons, total, indicated a greater role for intraspecific effects than compositional shifts; 95% confidence intervals for this count based on resampling were 7 to 16, the entire range of which was much less than half of the 91 pairwise comparisons made. In 55 of the comparisons, intraspecific and interspecific effects were acting in opposite directions, and in 36 they were acting in the same direction. Figure 2.4 shows that intraspecific effects were the dominant contributor to community body size in only nine of the 91 comparisons, and this mostly occurred when the direction of the size shift between the streams was negative.

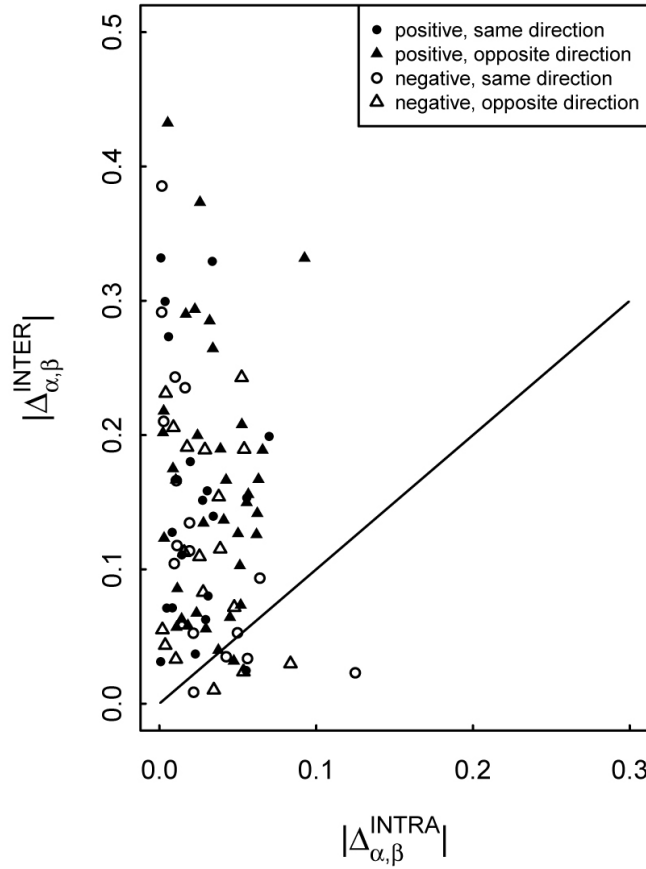


Figure 2.4: Relative importance of intraspecific and interspecific shifts in producing overall community size shifts in pairwise comparisons among streams, represented using $|\Delta_{\alpha\beta}^{INTRA}|$ vs $|\Delta_{\alpha\beta}^{INTER}|$ for 91 pairwise comparisons. Recall that $\Delta_{\alpha\beta}^{INTER} = \Delta_{\alpha\beta}^{COMM} - \Delta_{\alpha\beta}^{INTRA}$. A 1:1 line divides the plot; points above the line represent pairwise comparisons where interspecific effects were the greater contributor to community size differences, and points below the line represent pairwise comparisons where intraspecific effects were the greater contributor. Triangles represent pairwise comparisons where intraspecific and interspecific effects were acting in opposite directions, and circles where they were acting in the same direction. Solid points represent pairwise comparisons where $\Delta_{\alpha\beta}^{COMM}$ was positive, so body size increased with temperature between the two streams, and open points where $\Delta_{\alpha\beta}^{COMM}$ was negative.

2.3.4. Relative abundance shifts versus species turnover

Species relative abundance differences were the main cause of compositional shifts, rather than species turnover. Pairwise comparisons between streams (Table A.9 in Appendix A.4) showed species turnover contributed 0.5 - 71.7% of the difference in species composition, and the average contribution of species turnover was 14.8%. Out of 182 comparisons, only 34

showed species turnover contributing >25%, and only 6 showed species turnover contributing >50% (95% confidence intervals based on resampling were 6 to 11), and the comparisons with the highest level of species turnover were between streams with larger temperature differences. Because relative abundance differences were the main contributor to compositional shifts, and compositional shifts were the main cause of average community size differences, relative abundance differences were the main contributor to overall community size differences.

2.3.5. Other abiotic variables

For comparison, the same analyses as done for temperature were repeated for many of the other abiotic variables listed in Table A.1 in Appendix A.1, although the ranges of variation in those variables were small among the streams (Table A.6, Table A.7, Table A.10 and Figure A.4 in Appendix A). The comparison with temperature patterns provided additional evidence that temperature does not drive strong, consistent size changes in diatom size. For instance, intraspecific regressions of cell size against pH (Table A.6 and Table A.7 in Appendix A.3) were Bonferroni significant for two positive slopes and two negative slopes; recall that only four positive slopes and three negative slopes were Bonferroni significant using temperature. For silicate, there were five Bonferroni significantly positive slopes and a single negative one. Results were similar for other abiotic variables: temperature was not exceptional either in having an unusually large number of species showing a significant size response, nor in the consistency of response directions (positive or negative). Plots of average community diatom size versus abiotic variables sometimes showed stronger patterns for other variables than they did for temperature (e.g. pH; Table A.10 and Figure A.4 in Appendix A, compared to Figure 2.3). These results are remarkable because temperature variation across the streams was large and variation in the other abiotic variables was small; if temperature was driving consistent and substantial size variation in diatoms, one would expect observed effects under such circumstances to be stronger for temperature than for the other variables.

Tests were also carried out to assess whether temperature explained significantly more variation in community mean $\log_{10}$ sizes across streams when combined with other abiotic variables than was explained by those other variables alone, finding that it did not. When

models containing predictors temperature and pH, temperature and silicate, and temperature and K, respectively, were compared using F-tests to models with predictors pH, Si, and K, respectively, results were non-significant in any case ($p = 0.347, 0.670, 0.737$, respectively). Even though temperature variation across the streams was large and variation in other abiotic variables was small, temperature was less important in driving size variation in diatoms than some of the other variables.

Comparisons between intraspecific effects and compositional shifts and between relative abundance shifts and species turnover were substantially the same regardless of the abiotic variable used. The analogue of Figure 2.4 in which another abiotic variable is used in place of temperature looks the same as Figure 2.4 itself, but with the shading of some points changing. Changes just mean a pair of streams, α and β , in which temperature increased from α to β happened to show a decrease from α to β for the abiotic variable used in place of temperature – this change in no way affects the conclusion that compositional shifts were more important than intraspecific shifts. Computations of fractions of relative abundance shifts contributed by turnover also did not depend on the choice of abiotic variable.

2.4. Discussion

In a comprehensive study of diatoms in a natural community, this study provided evidence that commonly reported temperature-size relationships do not hold universally for diatoms. At both the intraspecific and community levels, results do not support the hypothesis of smaller body size under warmer conditions, undermining the generality of Bergmann's and James' rules and claims that reduced body size is a universal ecological response to warming in aquatic systems (Daufresne *et al.*, 2009). Diatoms are a very important exception to these general tendencies because they are abundant, widespread and play a global role in carbon cycling and primary production. The results also showed that community-level body-size shifts across gradients of temperature or other abiotic variables are determined largely by interspecific effects, with the most important of these being shifts in the relative abundances of species. Intraspecific size changes, which are commonly studied in single-species laboratory experiments, played a much smaller role in the field, highlighting the need for whole-

community *in situ* studies for understanding the effects of climate change in natural multispecies systems (Woodward *et al.*, 2010a).

At the community level, results showed that average diatom cell size does not decrease with temperature. This was unexpected given previous findings in which a shift towards smaller single-celled primary producers with increased warming was observed (Li *et al.*, 2009; Winder *et al.*, 2009; Lewandowska & Sommer, 2010; Morán *et al.*, 2010; Yvon-Durocher *et al.*, 2011; Peter & Sommer, 2012). The data from this chapter instead provide evidence supporting some more recent studies that suggest that shrinking body size is not a universal response to increasing temperature (Gardner *et al.*, 2011; R  ger & Sommer, 2012).

Across the literature there are inconsistent results from studies of individual or few diatom species (intraspecific) responses to temperature, with some studies supporting conformity of diatoms to James' rule and others claiming they are an exception. Most studies, however, have only considered a small number of diatom or phytoplankton species. Results from this study go beyond earlier work because of the number of species studied, and therefore provide convincing evidence that diatoms cannot generally or usually be seen to conform to James' rule. Some older studies show that diatom or phytoplankton cell volume can increase with increasing temperature (Durbin, 1977; Thompson *et al.*, 1992), but these measured just one and eight species, respectively. More recent studies have shown diatom cell volume decreasing 4% for every $^{\circ}\text{C}$ increase in temperature (Montagnes & Franklin, 2001) in a study of ten phytoplankton species (eight diatoms), with similar findings reported by Peter & Sommer (2012) for eleven species of phytoplankton (six diatoms). Both Byllaardt & Cyr (2011) and R  ger & Sommer (2012) concluded that individual diatom species can show an exception to James' rule, although they measured only three freshwater and seven marine species, respectively. In contrast, this study measured effects of temperature on body size for most of the abundant species present in the diatom community, a total of 31 diatom species. In addition, this approach was comprehensive in examining all diatoms that comprised the overwhelming majority of the abundance of a set of natural communities.

It is not well understood why most ectotherms might follow the established temperature-size rules, and several mechanisms have been proposed (Atkinson & Sibly, 1997; Partridge &

Coyne, 1997). Exceptions to general trends, such as those described here, may help illuminate mechanisms. Several mechanisms that may explain shrinking body size are discussed in Sheridan & Bickford (2011), but one of the main explanations put forward invokes changes in the metabolic rate of ectotherms: metabolic rate increases with temperature (Brown *et al.*, 2004), so at warmer temperatures, and if resource levels stay the same, growth will be limited and organisms will become smaller to compensate for the increased metabolic demand. However, under these conditions, it seems at least as likely that species will decrease in population size instead of body size, due to increased competition for resources; only if smaller individuals are better competitors for the limited resources, and only if this advantage is accentuated at higher temperatures, would the competitive balance be expected to tip in favour of smaller organisms with warming. It is not clear, *a priori*, whether this is the case in the Icelandic stream system, but experimental manipulations could be used to explore this possible explanation for size changes (or lack thereof, in the system of this study). A recent modelling study of Reuman *et al.* (2014a) explored the mechanics of a change in relative competitive abilities of differently sized phytoplankton species with warming, parameterising a nutrient competition and growth model in terms of phytoplankton cell size and ambient temperature. Results suggested that accentuated competitive ability of small phytoplankton cells for nutrient uptake and growth in warmer environments might explain decreased observed plankton sizes in some warmer environments. The model assumed one of several parameterisations for how cell mortality depends on body size and temperature. Whether those assumptions hold in the stream system of this study is not known, but investigating the relationship between that model and conditions in the field may illuminate the explanatory power of the model. Such an investigation may also illuminate the importance of top-down control for helping determine diatom size patterns with temperature in this and other stream systems. The dominant grazers in the system are the snails *Radix peregra* (syn. *balthica*), which do indeed increase in abundance across the temperature gradient (Woodward *et al.*, 2010b; O’Gorman *et al.*, 2012). These are very efficient grazers that feed by “bulldozing” entire biofilms in a non-size-selective way; such grazing may favour faster-growing species, which tend to be smaller. The model of Reuman *et al.* (2013) also suggests the rate at which non-size-specific grazing mortality increases with temperature may be implicated in whether competition for nutrients among size classes favours larger or

smaller cells, or neither, under warming. Thus further exploration of the Icelandic stream system in relation to the model may help illuminate temperature-size patterns in phytoplankton and phytobenthos and variation in these patterns.

Other proposed mechanisms of shrinking under warming relate to alterations in the physical environment caused by temperature change. Winder & Sommer (2012) suggested that phytoplankton will shift towards smaller species because, as water temperature increases and weakens mixing in the water column, small species that sink at a slower rate will be more dominant. This is the explanation given for results in Winder *et al.* (2009), where there is a shift towards smaller species of diatoms over time in lakes experiencing warming. Some previous studies showing a shift towards smaller diatoms examined in ocean ecosystems (Li *et al.*, 2009; Morán *et al.*, 2010) or deep lakes (Winder *et al.*, 2009) where stratification may be the most important factor controlling size distributions (Winder & Sommer, 2012). This chapter sampled benthic (not planktonic) diatoms from shallow streams, where factors such as grazing and competition for resources may be more important, and sinking rates and stratification are irrelevant (Moss *et al.*, 2003; Finkel *et al.*, 2009b). Hence the fact that smaller cells were not observed in warmer streams here, is consistent with the ideas of Winder & Sommer (2012). Another proposed mechanism for shrinking with warming is that changes in water temperature alter levels of dissolved oxygen, leading to acidification and altered iron levels which may affect phytoplankton cell sizes (Shi *et al.*, 2010; Forster *et al.*, 2012). Since these chemical changes do not occur in the stream system used in this study, the fact that size shifts are not observed is consistent with the ideas of Shi *et al.* (2010) and Forster *et al.* (2012).

Most phytoplankton or phytobenthos studies focus on the response of isolated individual species to temperature in the laboratory; however, experimental studies focussing on one or a few species do not provide evidence that global warming favours small diatom species, since the response to temperature seen in laboratory studies is invariably due to intraspecific shifts (Atkinson *et al.*, 2003), and these effects were of secondary importance in the natural communities examined here to community-compositional shifts. Therefore, measuring changes in body size of diatom species in natural communities provides a more realistic picture, revealing greater complexity in the community setting. More recently, other studies have started to test the proposed universal rule of Daufresne *et al.* (2009) that there is a shift

towards smaller species with increased warming in aquatic communities, with a few considering body size change of phytoplankton or phytobenthos at a community level (Winder *et al.*, 2009; Lewandowska & Sommer, 2010; Peter & Sommer, 2012; R ger & Sommer, 2012). Future studies should build on the species- and community-level responses of body size to warming demonstrated here, either through natural gradients or experimental manipulations of temperature in real, complex ecosystems, in order to help disentangle the most important factors determining differences in community structure under warming. Only by understanding the mechanisms underpinning the exceptions to general rules in ecology can the true predictability of future climate warming responses be promoted.

Chapter 3. New approaches to decomposing trends in community indicators reveal that the large fish indicator represents an average of divergent quantities and is sensitive to details of computation

Abstract

Community indicators are used to describe changes in the state of ecological communities. They are usually calculated from monitoring data collected at defined intervals, often annually. These indicators provide a univariate summary of complex multivariate phenomena. However, this can mean that different changes in the community lead to the same responses in the indicator: a challenge of multiple meanings. Sampling variation in the data also creates a challenge of detecting ecologically significant trends. This chapter addresses these challenges for community indicators, with a focus on the large fish indicator (LFI) which is often used to describe trends in the state of fish communities. The LFI expresses 'large' fish biomass as a proportion of total fish biomass and is calculated from species-size-abundance data collected on annual fish community surveys. The average trend in the LFI is decomposed into components, and demonstrates significant heterogeneity in species' and spatial contributions. Very few species and locations drove inter-annual trends and the influence of species and locations varied markedly among seasons (spring and autumn surveys). To assess significance of component trends, a resampling based method was developed to generate "surrogate" data sets. This method is used to calculate confidence intervals for the LFI estimates, but can be applied to any other metric based on the survey data. The new approach for decomposing community indicators and generating confidence intervals makes it possible to extract more information on drivers of a 'headline' indicator and can be generalised to assess the strengths and weaknesses of other community and biodiversity indicators based on species-size-abundance data. Values of community indicators will also vary in space and time when fish are moving in and out of a survey area. The approach taken in this chapter makes it possible to systematically identify the species and

sampling locations responsible for these effects. Analysis of the effects of indicator components on headline indicator values is highly recommended, because it helps to ensure that managers are not misled by divergent component signals.

3.1. Introduction

Ecological indicators can be defined as variables or indices of a phenomenon, and are widely used for environmental assessment, reporting, and management support (Rice, 2003). Indicators typically provide information on the status and trends of ecosystem components and attributes, usually those which are sensitive to human and environmental impacts. They are therefore often used in marine systems to describe the effects of climate or fishing pressure on the composition or function of a marine community or a subset of that community (Shin *et al.*, 2005, 2010). These indicators range from those that summarise responses of a set of species to those that describe changes in properties resulting from direct and indirect interactions of many species. In order to provide reliable information on the effects that human and environmental pressures have on communities, the response of the indicator should be sensitive and specific to the pressure (Rice & Rochet 2005; Fulton *et al.* 2005; Rombouts *et al.* 2013). In practice, community indicators have been proposed, and often adopted, more quickly than they have been evaluated, leading to the risk that changes in values are uninformative about community responses to pressure and leading to challenges to their legitimacy (e.g. Branch *et al.*, 2010).

Values of most community indicators are determined by the relative numbers or biomass of species and/ or body sizes in the community. This poses the first of several challenges to the interpretation of these indicators; that they provide a univariate summary of a complex, multivariate, ecological phenomenon. This summary is sought by indicator developers because it provides simplicity, but it also means that multiple and potentially different changes in community structure or function may result in the same overall change in an indicator value. This will be referred to as the *challenge of multiple meanings*. For this reason, it seems that any ‘headline’ community indicator will almost always need to be used and interpreted in conjunction with a suite of component indicators, that help to decompose

the properties of the community that account for changes in the ‘headline’ indicator. Unfortunately, community indicators are often used or reported in isolation (e.g. Shephard *et al.*, 2013; ICES, 2014) and without the explanatory decomposition to reveal which of a number of possible community changes is causing an observed change in the indicator. Decomposing an indicator to identify drivers is not the same as using multiple unrelated indicators to describe the community. This is because constituent indicators are chosen to illuminate the causes of changes in the ‘headline’ indicator.

Another challenge to interpretation of community indicators is that reported trends are often based on annual point estimates (Rice & Gislason 1996; Blanchard *et al.* 2005; Greenstreet *et al.* 2012; ICES 2014). Such estimates may vary between years due to sampling variation, in addition to variation due to the timing and location of sampling. This will be referred to as the *challenge of statistical significance*. This shortcoming can often be attributed to the challenges of sampling communities over large spatial and temporal extents. It also results from the use of data from surveys that were not originally designed to measure trends on a community level, but were used for assessment of a few species. Commonly used marine data sets are taken from trawl surveys where compromise designs are adopted to fulfil multiple needs. Statistically formal and correct approaches to determining the effects of sampling variation and whether changes and trends in community indicators are significant are still not widely used. In many cases they are not developed or used owing to the complexity of large-scale and long-term community sampling designs, which makes it difficult to work out appropriate statistical tests and assess sampling variation.

Several size-based community indicators have been developed to evaluate changes in marine communities and food webs in response to fishing and environmental pressures (Shin *et al.*, 2005). The large fish indicator (LFI) is one simple and widely tested and recommended indicator that has been adopted to describe changes in the state of fish communities and their responses to fishing. It is a ratio of the biomass of large fish to the biomass of small fish caught in survey trawls (Greenstreet *et al.*, 2011; a precise definition is given in “Methods”). The LFI is designed to show changes in the size structure of the community and thus provide more information than would be gleaned from the study of individual species. It is also assumed to be relatively robust to the changing dynamics of individual species (Greenstreet *et*

al., 2011; Houle *et al.*, 2012). The LFI is expressed as a ratio to reduce the sensitivity of the indicator to changes in primary production as opposed to fishing, based on the assumption that the ratio is less influenced by overall changes in system productivity than the absolute biomass of small or large fishes (ICES 2014).

The LFI is unlikely to be immune from the challenges of multiple meanings and statistical significance. These may limit the value of the LFI as a community indicator for assessing status and trends. This study investigates the extent and consequences of these challenges for the LFI in the North Sea, and how a decomposition of the indicator by species, space and time informs interpretation of trends. Although differences in the contributions of individual species to the LFI have been recognised (Shephard *et al.*, 2011b; Greenstreet *et al.*, 2012b), a systematic approach to determine how each species included in the indicator contributes to trends has not been developed. Since the LFI is now being used or considered as an indicator of the state of biodiversity and food webs in the North Sea (Greenstreet *et al.*, 2011) and other areas including the Celtic Sea (Shephard *et al.*, 2011b), North East Atlantic (Modica *et al.*, 2014; Defra, 2014), and Mediterranean (Edelist *et al.*, 2014) it is timely to assess the performance of this indicator and potential for improving interpretation.

The value of the North Sea LFI has been reported to increase in recent years (Fung *et al.*, 2012; Greenstreet *et al.*, 2012b) suggesting the proportion of large fish has increased. But this overall trend may be made up of contributions of different magnitudes, or even different signs, for different regions of the North Sea, or for different species residing in the North Sea. The LFI has also been reported for smaller sub-regions in the North Sea (ICES, 2014; Engelhard *et al.*, 2015) and Celtic Sea (Shephard *et al.*, 2011a), but since the LFI is calculated as a ratio, this does not accurately inform which sub-regions contribute to overall changes. The decomposition of trends by space that is developed in this study allows either sub-regions or species that dominate trends to be identified.

Given constraints on sampling resources, LFI time-series are usually based on data from trawl surveys that are conducted just once each year. For the North Sea, the data used to generate estimates of the LFI come from the Quarter 1 (Q1; first 3 months of the year) International Bottom Trawl Surveys (ICES 2012). The use of sampling data from discrete annual surveys

means that the effects of seasonality cannot be addressed. For discrete annual surveys the structure of the community in any defined time window may be influenced by seasonal changes in movement, migration and phenology. The time when fish in given species and size-classes are accessible to sampling methods may change from year to year. Data from the longer-running Q1 IBTS is usually used in preference to the shorter Q3 time-series and management targets for the North Sea LFI are based on values calculated from the Q1 data. Within either time-series, changes in phenology may lead to variation in the LFI, especially as the North Sea is an open system, with fishes migrating in and out to the North and South through the course of the year (Daan *et al.*, 1990). Values of indicators calculated from each of these (Q1 and Q3) surveys may therefore reflect seasonal differences in the timing of the survey, rather than true trends in abundance or community composition. Comparison between results using Q1 and Q3 data may provide insight into the extent of seasonal changes and their effects on values and trends in the LFI.

This chapter aims to address the challenges of multiple meanings and statistical significance in community indicators, with a focus on the factors driving changes in the LFI, as well as several specific biological questions that are relevant to the management of North Sea fisheries. 1) Are some species more dominant than others in driving trends in the LFI, and do different species contribute with different signs, as well as different magnitude, to changes in the LFI, so that overall LFI trends are not representative of all species? 2) Do trends differ spatially across the North Sea, and do different regions contribute differently to overall LFI trends, so that overall trends are not representative of all areas? 3) Are there seasonal differences in LFI trends (Q1 vs. Q3), revealing the possibility that apparent LFI trends are confounded by phenological shifts? And 4) how do interactions between species, space, and season affect the previous three questions?

The approach developed to answer these questions involves decomposing the LFI into constituent parts to address the challenge of multiple meanings, and using a novel resampling-based statistical tool to address the challenge of statistical significance. Combining these approaches allows more information to be extracted from a 'headline' indicator to determine causes of change and to show which components of an indicator are contributing significantly

to overall trends. The approach can be generalised to assess the strengths and weaknesses of other community indicators based on species-size-abundance data.

3.2. Materials and methods

3.2.1. LFI decomposition

The LFI is defined for IBTS data from the North Sea as the proportion of biomass in a set of trawls consisting of fish over a given length threshold, L , typically 40cm. It is therefore a sum of the biomass of “large” fish (defined as those over L in length) in each species, divided by the total biomass of fish in the trawls. If B is the total biomass of all fish in the trawls, B_L is the total biomass of fish greater than L in length, then the LFI is:

$$LFI_L = \frac{B_L}{B} = \frac{\sum_{i=1}^n B_{L,i}}{B} = \sum_{i=1}^n \frac{B_{L,i}}{B} = \sum_{i=1}^n LFI_{L,i}, \quad \text{Equation 1}$$

where n is the total number of species, $B_{L,i}$ is the large fish biomass for species i , and $LFI_{L,i}$ is the contribution of the i^{th} species to the LFI. The total LFI is the sum of the species LFI contributions. Species with no large fish will have a zero contribution to the overall sum, although they contribute biomass to the denominator, B .

If a trend in the LFI is computed using an ordinary linear regression of LFI against year, then the slope of the trend can be decomposed into the sum of slopes for each species: $S_{LFI} = \sum_i S_{LFI,i}$, where S_{LFI} is the slope of the regression of the LFI against year and $S_{LFI,i}$ is the slope of the regressions of the $LFI_{L,i}$ against year (see Appendix B.1 for a proof). In other words, the LFI and trends in the LFI decompose by species in a similar way. The slope of the regression of the LFI against year is referred to throughout as the “slope of the LFI.”

It is straightforward to show (Appendix B.1) that the LFI, as well as the slope of the regression of the LFI against year, can be decomposed not only with respect to species, but with respect to any other factor, or combination of factors. This study also considers decompositions of LFI trend slopes by spatial location ($1^\circ \times 1^\circ$ grid cell), and by both spatial location and species simultaneously. Decompositions by both spatial location and species

simultaneously can be summed over grid cells, or over species, to recover the decompositions solely by species, or by grid cell, respectively.

The summands $LFI_{L,i}$ in equation 1 have the quantity B in their denominators, equal to the total biomass of all fish caught in the set of trawls used, and (typically) not equal to the total biomass of fish of species i in those trawls. Likewise, the summands in the decomposition of the LFI by grid cell share the same denominator, B , that is not equal to the total biomass of fish captured in trawls that occurred in that grid cell. Thus the summands in the decomposition of the LFI by grid cell are not equal to the LFI values that would be computed by considering the grid cells in isolation, and likewise for decompositions of LFI slopes. For instance, the LFI computed for the whole North Sea is not the sum of the LFI computed using only data from trawls occurring south of 55°N and the LFI computed using only data from trawls occurring north of 55°N - the use of a whole-sea denominator in the whole-sea LFI complicates matters.

Similar decompositions for the total large fish biomass were also computed. Because the LFI is a ratio, changes in the LFI may be due to changes in large fish biomass, small fish biomass, or both. Decomposing the large fish biomass (the numerator in the LFI) allows us to interpret whether the numerator (large fish) or the denominator (small fish) drives trends in the LFI. Since a single additive metric (total biomass) is decomposed in this case, the contribution of each component to the overall trend is simply the independently-computed trend for that component, unlike for the LFI.

3.2.2. Resampling data to obtain confidence intervals

For assessing significance of values and trends from the IBTS data, in this chapter and further chapters, I developed a resampling method specific to trawl catch data. I used the method to produce “surrogate” (i.e., resampled) IBTS data sets. Confidence intervals for any statistic calculated from the IBTS data can be computed by calculating the same statistic on the surrogate data sets and generating percentiles. The original IBTS data comprises one row for each species in each length category in each haul. To produce the surrogate data sets, resampled catch rates were generated 1000 times for each species in each length category in

each haul. This was achieved by generating surrogate catch numbers from a Poisson distribution, where the total number of fish actually caught was used as the expected catch (the expected value of the Poisson distribution). The resampling method is described in more detail as part of Chapter 5 .

For each indicator (e.g. LFI) calculated from the resampled data, confidence intervals were estimated by calculating the metric for each surrogate dataset, and then taking percentiles from the resulting distribution of indicator values. By resampling the data in this way, rather than using a bootstrapping method that resamples at the level of entire hauls (e.g. the method used by Shephard *et al.*, 2012 for the LFI in the Celtic Sea), the spatial structure of the IBTS survey is preserved. This allows appropriate confidence intervals to be assigned to components of spatial decompositions and ensure that the variation captured can reliably be attributed to variation in the sampling of individuals. The surrogate datasets generated are representative of repeated sampling, as if the IBTS surveys had been carried out in exactly the same way in the same locations, but multiple times. The method does assume that deviations from expectation are independent for each species in each length category in each haul, or that this is an adequate approximation (see Chapter 5). Confidence intervals were 95% for all analyses.

3.2.3. Data

The data used in this chapter was trawl survey data from the North Sea Q1 and Q3 IBTS (ICES 2014). The IBTS survey is a spatially structured sampling survey across the North Sea which records the number of fish caught by length category for each species in each haul, a more detailed description of the data is in Appendix D.1. The time series used was for the years 1991 to 2013, which were the years for which data were available for both quarters. The data were cleaned to remove erroneous entries (Daan, 2001; Fung *et al.*, 2012; Appendix D.1), and to include only grid cells that were sampled in both quarters. To ensure that the spatial extent was comparable in each year, any grid cell that had more than 2 years with no haul data in either quarter was excluded from the data (Greenstreet *et al.*, 2012). Grid cells in the Kattegat and Skagge rat regions were also excluded, as is standard when processing IBTS data given that the ecology and biogeography of these regions is heavily influenced by

processes and pressures in the Baltic Sea. The remaining catch data were averaged over ICES rectangles (the spatial unit of stratification in the IBTS survey design, 0.5° latitude by 1° longitude) and then over $1^{\circ} \times 1^{\circ}$ grid cells for the spatial component of the analysis. Because different cleaning methods are known to affect the values of indicators calculated from the IBTS data (Greenstreet *et al.*, 2012), previously reported LFI values were compared to the LFI values used in this analysis (Figure B.1 in Appendix B.2) and found to differ in magnitude due to the specific cleaning details, but they showed the same overall trend.

3.2.4. Ancillary analyses

Several ancillary analyses were completed to make sure that results did not depend on arbitrary choices. The large fish indicator is usually calculated using catch per unit area (cpua, unit area is m^2 and determined by the area swept by the trawl gear) as the measure of abundance. This was adopted for the main analysis, but I also repeated the analysis using catch per unit effort (cpue, unit effort is defined as one hour). Catchability corrections for most species (Fraser *et al.*, 2007) were applied to both cpua and cpue for comparison in an alternative analysis, but not used in the analysis presented in the main text because they are not available for all species and are not completely independent of the trawl data. A large fish cut off of 40cm was used, as is defined for the North Sea LFI, but ancillary analyses also considered other cut-offs of 35cm and 45cm. The IBTS data are sometimes subsetted by removing pelagic species (as they are not part of the bottom dwelling community and are not so readily caught by the IBTS trawl gears) or by removing individuals under 20cm in length (which may be under-sampled by the IBTS trawl or may be more sensitive to changes in phenology). Both sets of restrictions were included in alternative analyses, but not adopted in the main analysis. The LFI time series obtained from choices used in the main analysis was compared to previously reported LFI trends (Figure B.9 in Appendix B.2) to check consistency; trends were similar although values of the LFI were lower overall due to inclusion of smaller and pelagic species.

3.3. Results

3.3.1. Species decomposition of the LFI slope

There was significant heterogeneity in contributions from species to the overall slope of the LFI with a general pattern of a few species contributing a large proportion of the LFI slope, and the rest contributing very little (Figure 3.1, Figure B.2 in Appendix B.2). Species contributions differed substantially in magnitude and also in sign, and this heterogeneity in species contributions was significant (i.e., supported by the confidence intervals computed from the resampled data sets). For instance, many species were found for which contributions to the overall slope were significantly positive, and many others were found for which contributions were significantly negative (Figure 3.1). Positive contributions varied over 5.3 orders of magnitude, and negative contributions varied over 4.5 orders of magnitude. The largest positive contribution to the overall slope in Q1 (9.35×10^{-4}) came from saithe, *Pollachius virens*, and the largest-magnitude negative contribution (-5.19×10^{-4}) from cod, *Gadus morhua*. In Q3, the largest positive contribution was 8.52×10^{-4} , again from saithe; the largest-magnitude negative contribution was -1.20×10^{-4} , from tope, *Galeorhinus galeus*. In Q1 the absolute LFI slope contributions of saithe and cod together were 50% of the sum of absolute slope contributions of all species (Figure B.2 in Appendix B.2). However, to reach 95% of the sum, 16 species were needed. Thus even though the LFI slope was dominated by a few species, it still captured information from a larger proportion of the fish community. In Q3, the absolute LFI slope contributions of saithe and cod together were 41% of the sum of absolute slope contributions of all species; to reach 95% of the sum, 16 species were again needed.

3.3.2. Spatial decomposition of the LFI slope

The contribution of grid cells to LFI slope varied strongly across the North Sea, both in magnitude and direction. A few grid cells contributed a large proportion of LFI slope, with the rest contributing relatively little (Figure 3.2). There were more positive (red in Figure 3.2) contributions in the north-west of the North Sea and in coastal areas, and more negative (blue in Figure 3.2) contributions in the central North Sea. This pattern was also apparent when

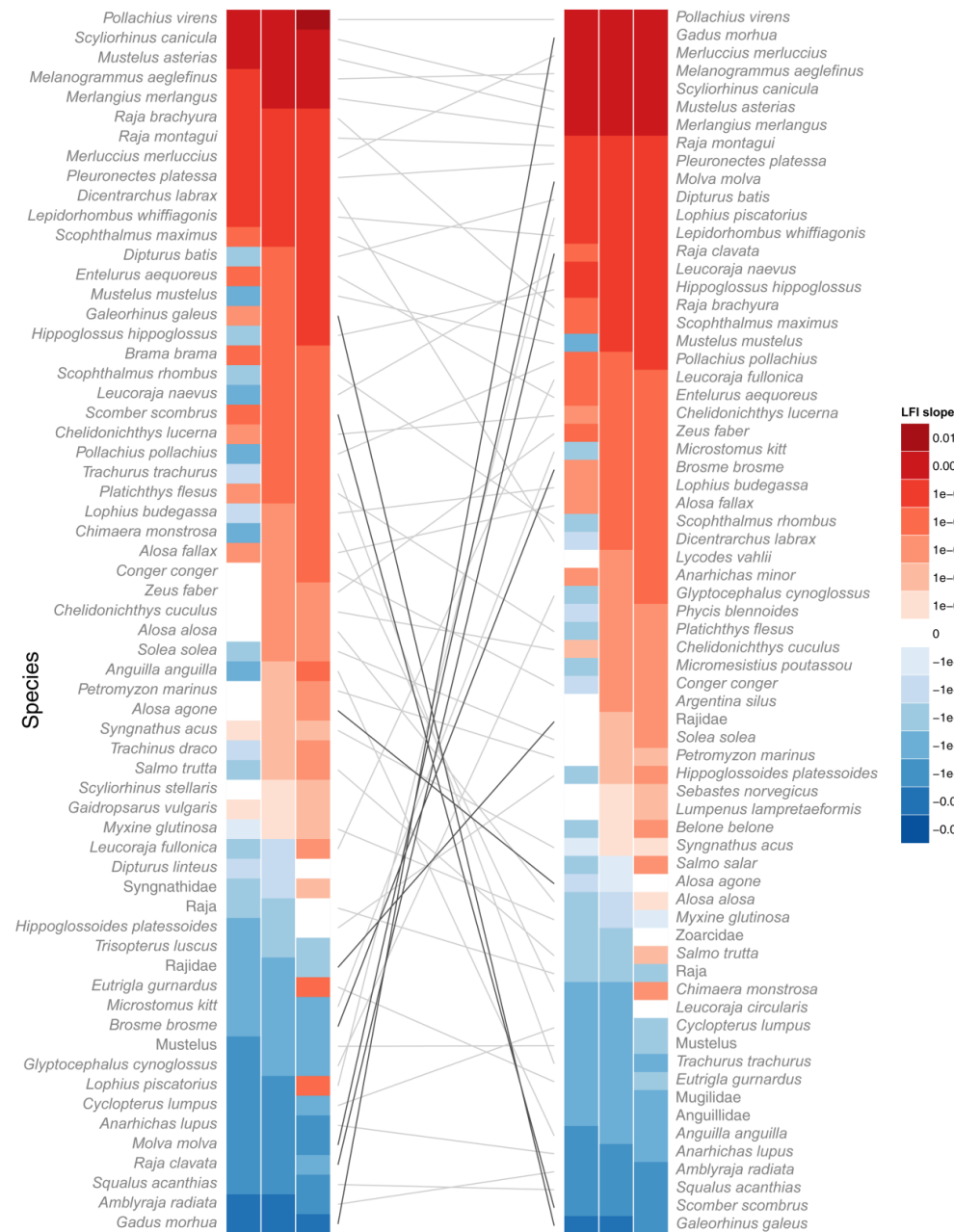


Figure 3.1: Decomposition of the large fish indicator slope (S_{LFI}) by species. The block of three vertical colour scales on the left of the plot shows Q1 results and the block on the right shows Q3 results. Within each block the central colour scale shows the point estimate of the LFI contribution for that species, the left colour scale shows the lower 95% confidence interval bound based on 1000 resampled datasets, and the right colour scale shows the upper 95% confidence interval bound. For all scales the colour ramp is linked to a log scale, with reds representing a positive contribution to the overall slope and blues a negative contribution (see colour bar at right). Species were ordered by contribution from positive to negative, separately in each quarter. Lines join species for which individuals $>40\text{cm}$ were sampled in both quarters, to facilitate comparisons of whether species

contributed similarly or differently to the LFI slope in the two quarters. Dark grey lines link species that have switched from either a significant negative contribution to a significant positive contribution or vice versa.

comparing the lower and upper confidence intervals for each grid cell, so the general pattern is unlikely to be driven by chance sampling variations. A few grid cells towards the north of the North Sea and two close to the English Channel made a dominant contribution to the trend (Figure B.5 in Appendix B.2), suggesting that an overall trend for the North Sea could be easily influenced by changes in just one or two grid cells.

3.3.3. Seasonal comparison of LFI slopes

The overall LFI slope in Q1 was 1.22×10^{-3} (CI 1.06×10^{-3} , 1.38×10^{-3}), and in Q3 was 3.06×10^{-3} (CI 2.96×10^{-3} , 3.17×10^{-3}). The confidence intervals did not overlap between quarters, therefore Q3 had a significantly different, more positive slope compared to Q1, and the LFI showed quicker recovery using Q3 data. To illustrate the meaning of this quantitative difference between quarters, hypothetically assume that changes in LFI were due solely to changes in biomass of large fish (i.e., assume that small fish biomass showed no trend over the period 1991-2013). In this case, large fish biomass would have increased by 1.7% over the period of measurement; and in Q3, large fish biomass would have increased by 5%. If, alternatively, the assumption was that changes in LFI were due solely to changes in small fish biomass (i.e. assume that large fish biomass showed no trend over the period of measurement), then small fish biomass decreased by 1.67% in Q1, and by 4.7% in Q3.

3.3.4. Interactions between season and species

Contributions of species to the overall positive LFI slope in each quarter were similar across quarters for some species, but markedly different for others, indicating an interaction between species decomposition and quarters where several species contributed very differently to the LFI slope in Q1 than in Q3 (Figure 3.1, black lines). The most marked example of species-level Q1-vs.-Q3 differences is provided by cod: this species was the largest-magnitude negative contributor to the LFI slope in Q1, but the second-largest positive contributor in Q3. Its contribution was significantly negative in Q1 and significantly positive in Q3. The tope

shark (*G. galeus*) and the Atlantic mackerel (*Scomber scombrus*) are additional examples: they were the two most negative contributors to the LFI slope in Q3, but were both positive contributors in Q1. Other species also switched their direction of contribution between quarters (Figure 3.1). Species which contributed similarly to LFI in both quarters include saithe (*P. virens*, the largest positive contributor in both quarters) and haddock (*Melanogrammus aeglefinus*, the fourth-largest positive contributor in both quarters).

Seasonal (Q1 vs Q3) differences in individual species contributions to LFI slopes were not necessarily related to seasonal differences in species' contributions to large fish biomass slopes (Figure B.3 in Appendix B.2). Some species had a contribution to the LFI slope that was opposite in sign to its trend in total large fish biomass. For example, one important contributor, haddock (*M. aeglefinus*), had a strong positive contribution to the LFI slope in both quarters, but the large haddock biomass slope only reflected this in Q3; the slope was negative in Q1. This resulted from the overall (negative) trend in biomass (and small fish biomass) in Q1 having a larger magnitude than the (also negative) trend in large haddock biomass. Since haddock are very abundant in the North Sea, this resulted in a large positive contribution to the LFI. This was not the case for all species; most trends in the LFI were consistent with trends in large fish biomass. For cod, its switch from a negative to a positive LFI contribution between quarters was reflected by the same switch in the slope of total large cod biomass.

3.3.5. Interactions between season and space

Contribution of grid cells to the overall LFI slope differed between seasons (Figure 3.2, Figure 3.3). There were more positive contributions in the north-west of the North Sea, and more negative contributions in the centre, for both Q1 and Q3, but the tendency was more pronounced in Q3 (Figure 3.2). Difference in LFI slope contributions between quarters show that some grid cells in the south switched from a positive to a negative contribution from Q1 to Q3, while some grid cells in the north did the opposite (Figure 3.3). This spatial pattern of more positive contributions in the northern region of the North Sea was significant (Figure 3.2) for the grid cells with the largest contributions. This was generally consistent with increases in total large fish biomass in those regions (Figure B.4 in Appendix B.2), with the

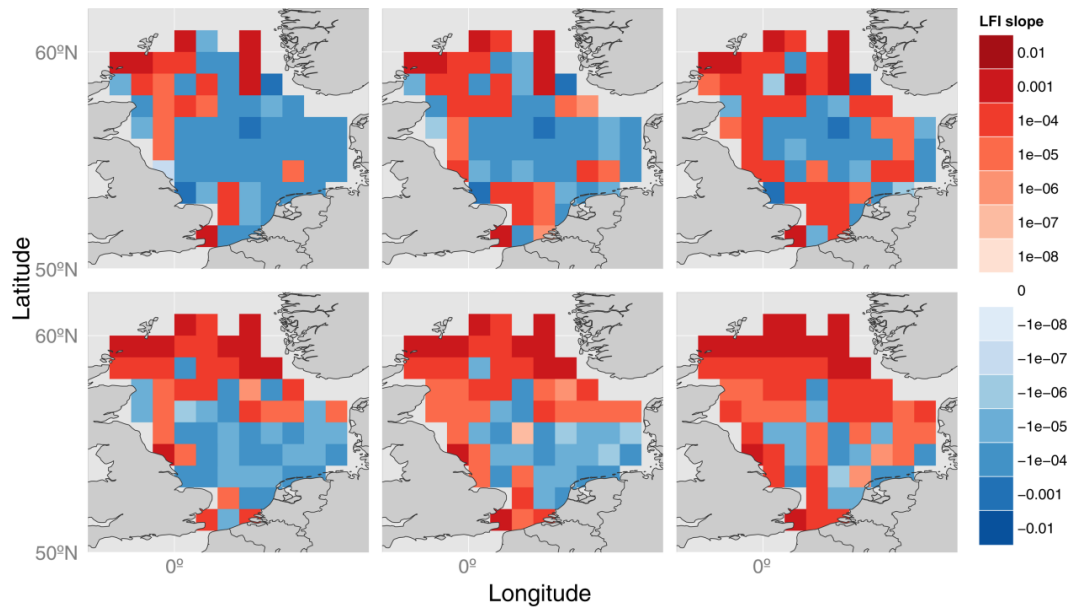
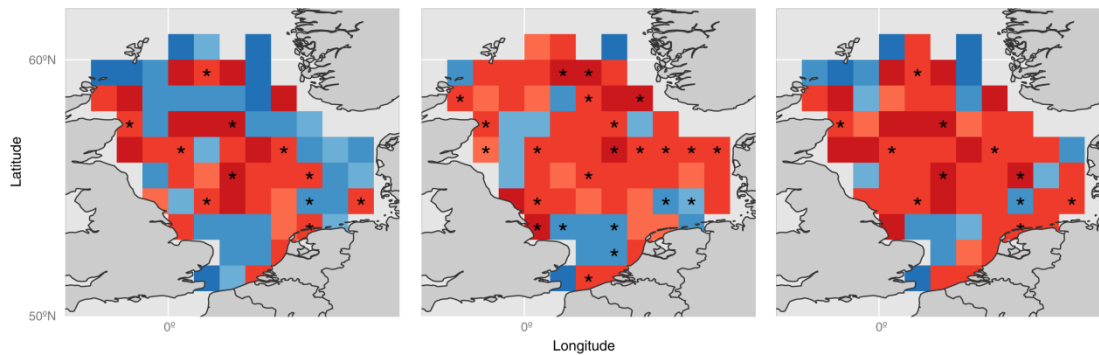


Figure 3.2: Decomposition of the LFI slope by $1^\circ \times 1^\circ$ grid cells. The first row of panels shows the decomposition for Q1 data, the second row for Q3 data. The middle column in each row is the point estimate, the left column is the lower 95% confidence interval bound based on 1000 resampled datasets, and the right column is the upper 95% confidence interval bound. Colours are based on a log scale, reds representing positive contributions to the overall slope and blues negative contributions.



*Uses legend in Figure 3.2 above

Figure 3.3: Seasonal difference in the decomposition of the LFI slope by $1^\circ \times 1^\circ$ grid cell. Differences were calculated by subtracting the Q1 slope contribution for each grid cell (Figure 3.2, top panels) from the Q3 slope contribution (Figure 3.2, bottom panels) in the cell. The middle plot shows point estimates, the left plot is lower 95% confidence interval bounds based on 1000 resampled datasets, and the right plot the upper 95% confidence interval bounds. Values are shown on a log scale, red representing a positive difference in the contribution between seasons (a contribution that was larger in Q3 than in Q1), and blue a negative difference. Stars identify grid cells that showed a change in the direction of contribution between seasons - starred red cells switched from negative in Q1 to positive in Q3, whereas starred blue cells switched from positive in Q1 to negative in Q3.

exception of grid cell 1×60 in both quarters. However, as in Q1, only a few grid cells, mostly towards the northern edge of the North Sea, made a large contribution to the overall LFI slope in Q3 (Figure B.5 in Appendix B.2). Although the same group of grid cells, with the exception of grid cell 1×51 in Q3, made the largest contributions in each quarter, there was a mix of positive and negative contributions in these cells in Q1 but only positive contributions in Q3. These differences between quarters mean that the difference in the overall slope can be accounted for by the more positive contributions of grid cells in Q3.

3.3.6. Interactions between species and space

When the LFI slope was decomposed by species and by grid cell, species did not contribute in the same way consistently over space (Figure B.6 and Figure B.7 in Appendix B.2). Very few species that were present in more than two grid cells contributed to the LFI slope in the same direction in all of those cells. There was also heterogeneity in the magnitude of the contribution across grid cells within a species. For example, the grid cell 1×51 near the English Channel made a large positive contribution in Q1 that was driven largely by an increase in biomass of large *Scyliorhinus canicula* (lesser spotted dogfish), a species that has a distribution across the whole North Sea but was abundant in that one grid cell. It can also be seen that the northernmost grid cells that dominated the LFI slope (cells 3×60, 0×60, 3×59, -2×59, -3×59; see Figure 3.2, Figure B.5 in Appendix B.2), are driven by saithe (*P. virens*) or cod (*G. morhua*) which were the dominant species in those grid cells in both quarters. Cod had the largest overall negative contribution to the LFI slope in Q1, but it was not consistently negative across space; in two of the northernmost grid cells where it was positive, it was the largest driver of the overall positive slope in those cells (-2×59, -3×59).

The decomposition of the LFI slope by both species and grid cell also allows the examination of the spatial contribution of each of the abundant and commercially important species that were shown to be some of the main drivers of overall trends (Figure 3.1; saithe, cod, haddock, whiting and hake). Maps of contributions to the LFI slope for these five species (Figure 3.4) showed that these species contributed differently in different regions of the North Sea. Saithe, although only present in the northern part of the North Sea, showed a similar general tendency to that in the overall spatial decomposition in Q1, with positive

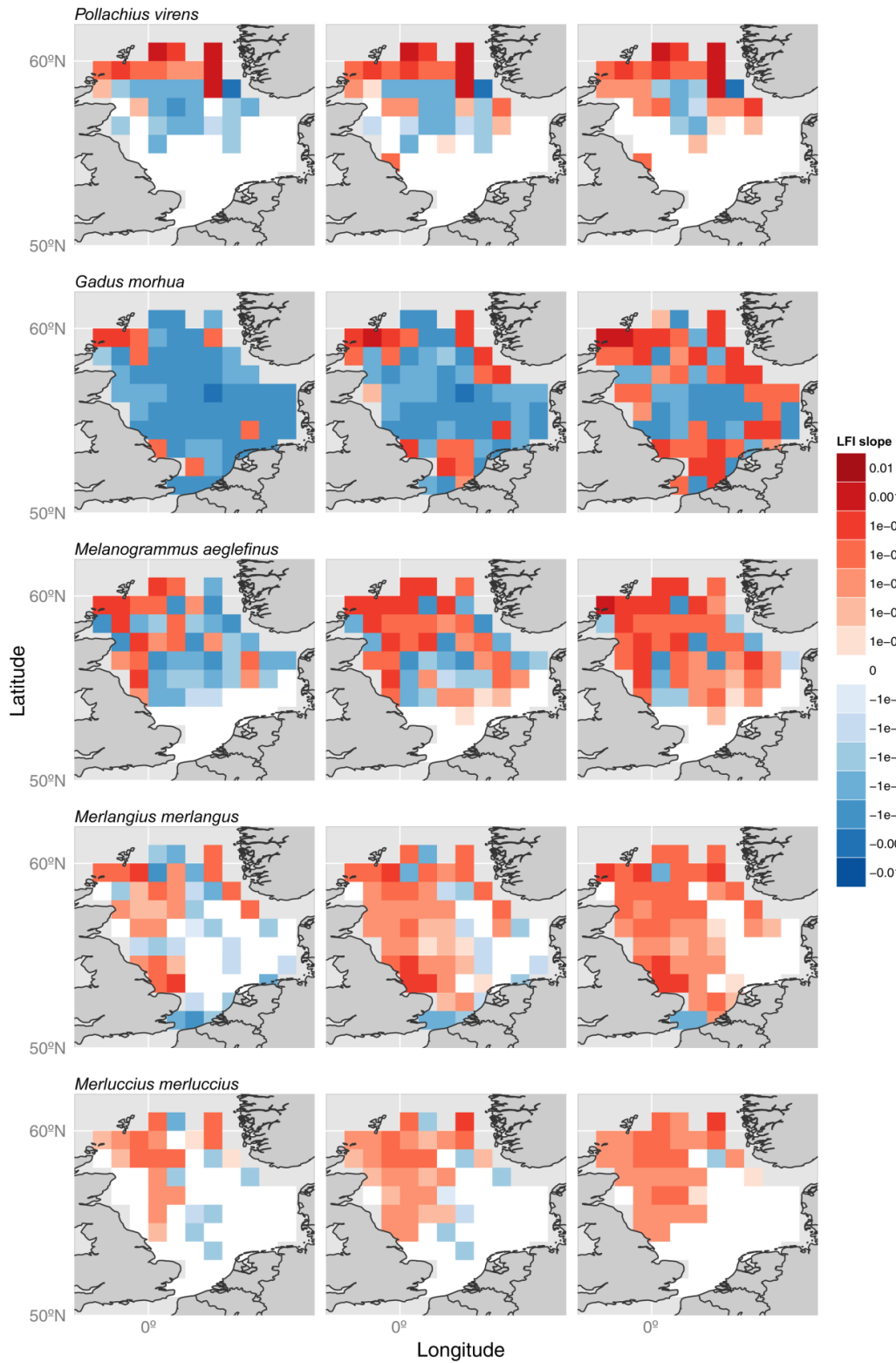


Figure 3.4: Decomposition of the LFI slope over time (1991-2013), by 1°x1° grid cell in Q1, for each of five species that are abundant and make a large contribution to the value of the LFI (*Pollachius*

virens, *Gadus morhua*, *Melanogrammus aeglefinus*, *Merlangius merlangus* and *Merluccius merluccius*). (Q3 results in Figure B.8 in Appendix B.2) The middle column in each row of panels is the point estimate from the data, the left column is the 2.5% lower confidence interval bound based on 1000 resampled datasets, and the right column the 97.5% upper confidence interval bound. Values are represented on a log scale, red represents a positive contribution to the overall slope and blue a negative contribution. White cells represent a contribution of zero to the overall slope: they are either grid cells in which surveys were carried out but no large fish from that particular species were found (in the middle column), or cells where the confidence limit is zero.

contributions in the northernmost grid cells and more negative contributions towards the centre region. The other species deviate from this pattern slightly; cod showed the same negative tendency in the central region while this extended further northwards than for other species (but not in Q3, Figure B.8 in Appendix B.2, where the contribution of cod was positive in more grid cells), and haddock, whiting and hake had more positive contributions in the western region of the North Sea. The lower and upper confidence intervals show similar patterns within species, so the observed patterns were likely to be significant.

Overall, results in all the aforementioned analyses were robust to alternative calculations using a combination of different measures of catch rates, fish length cut-offs, and to the exclusion of pelagic species.

3.4. Discussion

The challenges of multiple meanings and statistical significance both complicate the interpretation of the LFI when assessing status and trends. The methods developed in this chapter confirmed this and offered remedies. There was significant heterogeneity in species' and spatial contributions to the overall trend in the LFI that has not been previously reported. The novel approach to addressing the two challenges allowed more information to be extracted from the 'headline' indicator to help determine causes of change in the indicator through time and to show which indicator components are contributing most to overall trends, and how.

It was previously recognised that LFI values and trends were driven by a few abundant species (Greenstreet *et al.*, 2012b). The decomposition of the LFI by species confirmed this, and the approach additionally allowed for systematic identification and assessment of the

species that had the largest contribution, and in which direction. Since very few species made a significant contribution to the overall values and trend of the LFI, and the status of the main contributory species is already assessed in single-species stock assessments, the LFI seems to provide little additional information on the state of the North Sea that would not be obtained from the proportion of large fishes in assessed stocks. Interestingly, although saithe and cod were found to drive overall trends in the LFI, their effects were opposing in Q1, and when cod switched to a positive contribution in Q3, the annual rate of increase in the LFI was correspondingly greater. A value of the indicator calculated from stock assessment data should not show this bias, as the assessment seeks to represent the population rather than the proportion of the population in the survey area at the time of the survey. It is a common aspiration that community indicators complement species indicators by describing the outcome of interactions among species and the combination of species' direct and indirect responses to human and environmental pressures. However, the results from this study have shown that the LFI is largely describing the population fluctuations in just a few species.

Trends in the LFI are not spatially consistent, with more positive contributions in the north west and in coastal areas. While North-Sea-wide trends in the LFI are usually reported (Defra, 2014; Greenstreet *et al.*, 2011; Fung *et al.*, 2012) these trends belie regional differences and are driven by just a few grid cells. It has been noted before that the inclusion of survey catches in just one ICES rectangle ($1^{\circ} \times 0.5^{\circ}$ grid cell) could lead to a different interpretation of trends in the North Sea wide LFI estimate (Greenstreet *et al.*, 2012; Sundelof *et al.*, 2013; this rectangle was omitted from the analysis in this chapter). One study (Greenstreet *et al.*, 2012) re-reported trends in the LFI without omitting an ICES rectangle outside the intended study area, and consequently the trend in the LFI showed less of a recovery than when that rectangle had been included. The rectangle was populated by a productive and to some extent spatially isolated cod subpopulation which contained a very high proportion of large individuals in relation to the North Sea as a whole (Sundelof *et al.*, 2013). Even when this rectangle was excluded, results of the decomposition by species showed that the abundance of large saithe or cod drives much of the trend in the North Sea LFI. The decomposition by both species and space has also shown that changes in the abundance of a non-abundant species such as the lesser spotted dogfish, in just one grid cell, may contribute greatly to

overall trends. That fluctuations in catches in just one grid cell or rectangle can influence values of the LFI so strongly is a concern when the LFI is supposed to be an indicator of the status of the entire North Sea.

Although the LFI is identified as a community or food web indicator (ICES, 2014), values of the LFI are mostly determined by the abundance of a few large species in a few areas. In fact, the trends in large fish biomass in the North Sea in Q1 can be adequately described by just considering the biomass of seven species in ten grid cells (Figure B.9 in Appendix B.2). This suggests that the interaction of species and space is important to consider when assessing the validity of the LFI or other indicators. If overall values or trends in an indicator are dominated by small populations of certain species, then management efforts concentrated on those populations could greatly affect the value of the indicator and be misinterpreted as improving conditions across the whole ecosystem. These issues are only identified by decomposing the LFI into its components and examining the relationship between the value of the LFI and the values of components. Users commonly aspire to identify community indicators that show trends on large geographical scales, and yet the methods used here have shown that the LFI is strongly dominated by changes in the fish community in a very small region of the North Sea. Interpretation of the ‘headline’ LFI for the North Sea would be enhanced by information on spatially disaggregated trends, as also reported for the Celtic Sea by Shephard *et al.* (2012) and Greenstreet (unpublished, in ICES, 2014). The methods presented here can inform the debate on deciding where those regions might be.

Another issue that was addressed was the effect of seasonal variation. The resampling based methods used captures random variation in small differences in the location and timings of sampling effort, but not the differences likely to be seen in fish abundance between seasons which are more strongly influenced by migrations, growth and phenology. Comparing trends in the LFI between Q1 and Q3 highlighted the extent of seasonal variability. While the overall slope of the LFI was positive in both quarters, it increased more rapidly in Q3. Spatial contributions tended to be greater and more positive across both quarters in the northern areas of the North Sea, suggesting that populations with range centres outside the North Sea may be driving trends for the North Sea as a whole. Cod is one of the most significant contributors in both quarters, but switched from making a negative contribution in Q1 to a

positive one in Q3, which corresponded with changes in large cod biomass. Reasons for this switch are unclear; the contribution of cod had greater magnitude around the boundaries of the North Sea, especially in the north, which might suggest migration of large cod into the North Sea in Q3 from more northerly latitudes where cod are larger (Neuenfeldt *et al.*, 2013). However, cod populations in the northern region of the North Sea have been shown to have limited movement and stay within the survey area (Neat *et al.*, 2014) throughout the year. My results show that these northern cod populations are largely determining the trends in the LFI in both quarters, suggesting that a possible behavioural difference in cod populations in these sub-regions is the main reason for the faster recovery of the LFI in Q3.

In general, the main results of this study highlight a number of issues about survey design and the geographical areas chosen in analyses that are used to report the status of fish communities. Even locations such as the North Sea that are partly bounded by land are strongly linked by currents and seasonal migrations of fauna to the North Atlantic and Norwegian Sea, the Baltic Sea and the English Channel (Daan *et al.*, 1990). At any point in time, community composition will be determined by fauna resident in the North Sea and by fauna that are present seasonally. This confounds the understanding of trends in species' abundance in surveys (Blanchard *et al.*, 2009), and will have knock-on effects on attempts to measure trends in community structure. Further, competition, predation and other interactions that structure the community will be transient and dynamic owing to seasonal movements. The apparent effects of fisheries in the North Sea on community composition will also vary in space and time when fauna are moving in and out of the survey area. The approaches developed in this chapter allow the effects of choosing different times and geographical areas of analysis to be assessed, and to identify the species and sampling locations responsible for these effects.

There are plans to use indicators such as the LFI to guide management decision making, but I have demonstrated that the challenge of multiple meanings complicates the interpretation of trends in the LFI. By decomposing the LFI into its components, it is possible to show which species and areas contribute most to the observed trends. If the LFI is to be meaningfully interpreted, this study suggests that these steps are necessary. Simple indicators are useful because they reduce a complex food web into a metric that can be compared to itself or to a

set benchmark relatively straightforwardly. However, I have shown that it is more meaningful to consider component parts of these indicators and to reintroduce a bit more complexity in order to understand the main drivers behind the ‘headline’ indicator. By introducing component indicators alongside existing indicators, management efforts could be more targeted towards regions or species that are not recovering but likely to be overlooked when only considering a ‘headline’ indicator. Introducing such component indicators complicates interpretation for managers, but the added insight far outweighs this as management efforts will not be misguided by misleading headline indicators, and it is unavoidable that drivers of overall trends need to be identified and addressed. Further, introducing a method to assess significance of indicator values and trends is necessary to have confidence in these component indicators, so that management effort is based upon real effects and not sampling noise. The types of indicators that these methods can be applied to is generally limited to abundance based indicators. This is because the resampling based method cannot account for variation in species diversity, and the decomposition as it is presented here can only be applied to indicators with additive components. However, the general approach of systematically identifying significant driving components of indicators is useful and necessary to understand and manage larger ecosystems.

Chapter 4. The abundance spectrum is not linear and that reflects the ecology of marine systems

Abstract

The abundance spectrum, which describes the relationship between organism abundance and body size in a community or ecosystem, is frequently used to monitor the state of marine communities. The overall structure of the spectrum is commonly approximated as linear. The resulting slope is used as an indicator of change in the system, as the slope steepens with common exploitations, which usually target larger individuals. This chapter explores the degree to which linearity of the abundance spectrum is an approximation by examining in detail any deviations from linearity present in the spectrum of the demersal fish community in the North Sea. A novel method of assigning confidence intervals to abundance values is used to determine that there are, in fact, significant departures from a linear slope, which are consistent over time and constitute ‘stationary bumps’ in the spectrum that span a body mass ratio of around 4.5. A lagged correlation approach is also used to detect ‘transient bumps’ that move up through the spectrum over time, with a speed of propagation that moves a bump through a mass ratio of around 1.5 per year. The transient bumps propagate for 5 or 6 years before they diffuse. Results indicate the departures from linearity and the abundance spectrum are not just artefacts of sampling variation, and strongly suggest that bumps have ecological and potentially management meaning. The size of bumps may offer another metric for monitoring change in community structure, along with the basic slope of the abundance spectrum. Transient bumps indicate that if pulses in abundance at smaller size classes are detected they can be assumed to move to larger size classes with a certain speed, possibly allowing fluctuations in abundance of larger fish in future years to be predicted.

4.1. Introduction

In aquatic food webs, the body size of an organism is more fundamental to its abundance and other aspects of its ecology than is its taxonomy (Peters, 1983; Jennings *et al.*, 2001; Woodward *et al.*, 2005; Hildrew *et al.*, 2007). For instance, in marine systems, predation is strongly size dependent and this largely determines the transfer of energy through food webs from primary producers up to larger marine animals (Sheldon *et al.*, 1972). Predator-prey interactions in such systems, where predators are usually larger than their prey, are dependent on body size and this underpins the structure and function of communities (Cohen *et al.*, 1993; Blanchard *et al.*, 2009; Barnes *et al.*, 2010a). Marine organisms can grow through many orders of magnitude, and so occupy different trophic levels during their life cycle (Jennings *et al.*, 2001). Thus, at the community level, the trophic level of organisms is more accurately indicated by body size than species identity (Jennings *et al.*, 2001, 2002).

Marine communities are therefore often described by the abundance spectrum (Kerr & Dickie, 2001), a method that quantifies the community solely using body sizes of organisms, regardless of their taxonomy. The abundance spectrum is most commonly constructed by binning individuals into size bins and statistically describing the relationship of log abundance versus log size class. The log abundance of individuals in each size group tends to decrease with size, and the resulting slope of the spectrum has been shown empirically to be consistently linear across many systems (Kerr & Dickie, 2001). This linear relationship corresponds to a power law dependence of abundance in each size class on the central body size in that class (Marquet *et al.*, 2005). The slope of the spectrum, and therefore the exponent of the underlying power-law, is frequently found to be around -1 in non-exploited communities (Boudreau & Dickie, 1992; Kerr & Dickie, 2001; Jennings & Mackinson, 2003), meaning that as size increases by a factor of 10, the abundance decreases by a factor of 10^{-1} .

The slope of the abundance spectrum is considered to be a robust indicator of community structure in most marine systems (Pope *et al.*, 2006). Both the slope and intercept of the spectrum can vary due to the underlying natural variation in ecological and environmental conditions, and can be strongly influenced by climate change and fishing which makes them useful as indicators of anthropogenic impacts (Blanchard *et al.*, 2005). The slope responds

both directly and indirectly to fishing pressures. It becomes steeper as fishing intensity increases due to the direct removal of larger organisms from the population at the higher end of the size spectrum (Shin *et al.*, 2005), and also through the resulting shifts in the community structure (Daan *et al.*, 2005; Heath, 2005) at the lower end of the size spectrum. In a heavily exploited ecosystem such as the North Sea, the slope of the abundance spectrum has decreased over time as larger fish are removed by fishing (Rice & Gislason, 1996; Gislason & Rice, 1998). Therefore the slope of the spectrum is a simple metric that can be used to indicate the health of an ecosystem, and is commonly used as one of a suite of size-based community indicators in fisheries management (Boudreau *et al.*, 1991; Jennings *et al.*, 2001).

However, the use of the slope and intercept as the primary indicators of the abundance spectrum assumes that the abundance spectrum is always linear, or that deviations from linearity are minor and contain no meaningful information. It is possible, though rarely previously explored, that departures from linearity in the abundance spectrum contain information that reflects system ecology and may ultimately be used to inform management. Exploring this possibility is the aim of this study.

The assumption of linearity is an important aspect of how the abundance spectrum is typically used. Spectra have been computed across multiple trophic levels in marine ecosystems and many empirical studies exist that try to determine the slope in different systems (Kerr & Dickie, 2001; Zhou, 2006). There have also been a number of modelling approaches that try to derive further properties of the spectrum based on its underlying linear structure (Brown & Gillooly, 2003; Benoît & Rochet, 2004; Brown *et al.*, 2004; Andersen & Beyer, 2006; Law *et al.*, 2009; Blanchard *et al.*, 2010; Datta *et al.*, 2010; Hartvig *et al.*, 2010; Rochet & Benoît, 2011). Linearity is expected from a combination of processes of growth, mortality and predator-prey interactions. However, fluctuations of biomass have been observed in some empirical spectra (Boudreau & Dickie 1992; Kerr & Dickie 2001). These fluctuations appear as deviations from the overall slope and are seen when the spectra are computed over multiple trophic levels with large size ranges from phytoplankton up to large predators. In fisheries management, the slope of the size spectra is considered for fishes only and spans a much smaller size range across fewer trophic levels. Domes of biomass have also been detected in fish spectra over multiple years in both lake and marine systems (Duplisea

et al., 1997; Kerr & Dickie, 2001); the domes were made up of a variety of species but showed uniformity across years. I refer to deviations from linearity that show uniformity across time as *stationary bumps* in the abundance spectrum (Figure 4.1a-c). Stationary bumps may be ecologically meaningful if they really exist, i.e., if stable and consistent deviations from linearity are indeed a permanent feature of the spectrum through time. But stationary bumps have been insufficiently explored empirically in the North Sea.

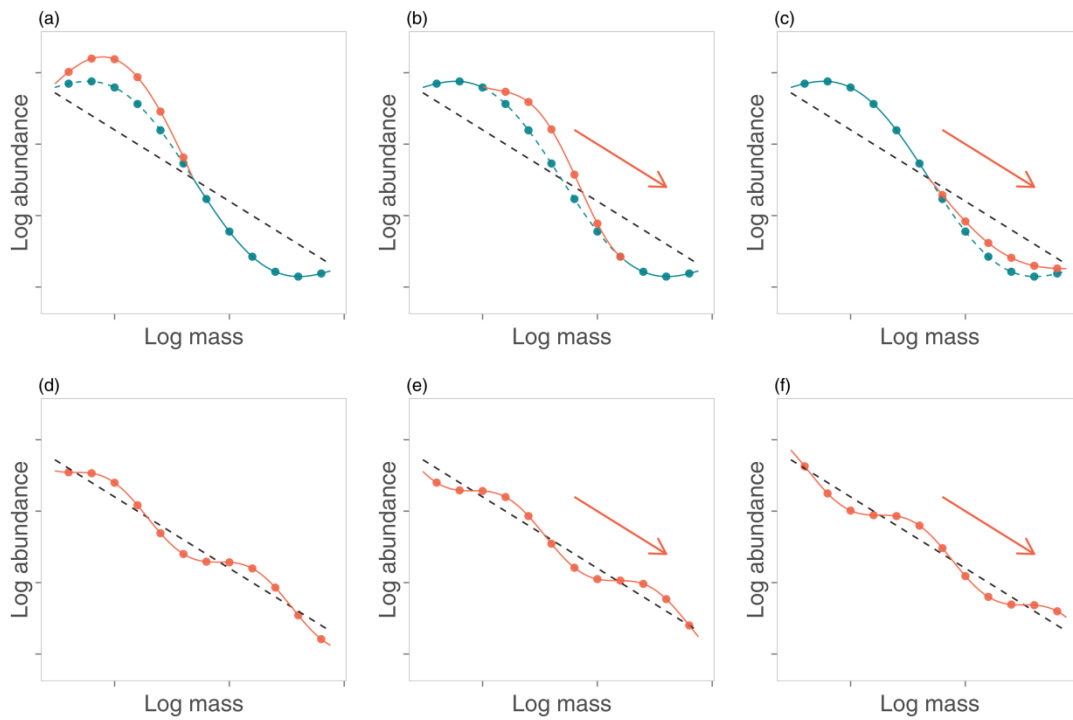


Figure 4.1: A conceptual example of how both stationary and transient bumps may appear in the abundance spectrum, where log mass is plotted against log abundance. The dashed black line represents the expected linear slope of the spectrum. Coloured points show deviations of individual size classes from that slope, and solid coloured lines show the appearance of the overall spectrum. Each column represents a different time period. The first row (a-c) shows the appearance of both stationary (green) and transient (orange) bumps in the spectrum. The stationary bumps are the same in each time period, whereas the transient bumps appear at different size classes in the different time periods. Arrows indicate the direction of movement of the transient bumps from smaller to larger mass bins in this example. Transient bumps can ‘sit’ on top of the stationary bumps (a-c), or they can exist in the spectrum alone (d-f). In the first case, the peaks and troughs in abundance remain centred around the same size classes through time, but reduce or increase in magnitude depending on the movement of the transient bump. In the second case, the peaks and troughs appear at different size classes through time.

In addition to stationary bumps in the spectrum, there is also the possibility of *transient bumps*. I use this term to refer to deviations from the time-averaged structure of the abundance spectrum that appear for smaller periods of time. Transient bumps seem likely to either move up and through the spectrum due to growth of the organisms comprising the bumps; and/or to become damped out through time by other processes including predation, fishing and differential growth rates of organisms. Transient bumps may be the only cause of deviations from linearity within a year, in which case the structure of the spectrum will change through time as they move (Figure 4.1c-e), or they may occur in addition to stationary bumps and ‘lie’ on top of them (Figure 4.1a-c). There are very few empirical studies that specifically look for evidence of bumps moving through the spectrum, but models have predicted them within marine communities under the influence of fishing pressure (Benoît & Rochet, 2004; Andersen & Pedersen, 2010; Rochet & Benoît, 2011). These models have shown pulses that propagate both up and down the spectrum through multiple trophic levels, from plankton up to large predators.

In this chapter I explore the presence of both stationary and transient bumps in the abundance spectrum of fish over the size range sampled by trawl surveys in the North Sea. By using an empirical approach and considering fish over a smaller size range than is usually represented in model-based studies, the methods used in this chapter should be able to detect smaller-scale interactions independent of the overall slope of the spectrum. Because the fish in this size range are only likely to comprise one trophic level, any transient bumps that are observed would be more closely related to growth of animals up through the size classes. Therefore observing variations in abundance in this size range may be useful for fisheries management, as being able to identify the characteristics of both stationary and transient bumps at this scale would mean more specific predictions could be made about the abundance of larger fish in future years. Crucially, the use of the resampling-based method developed in other chapters of this thesis allows the assessment of statistical confidence in any observed deviations from linearity or bumps moving through the spectrum at any spatial or temporal scale. It is only with the availability of such methods that fine scale structure in the abundance spectrum can be effectively explored; without methods that take into account sampling variation, any smaller features of the spectrum could not previously be attributed

statistical confidence. The specific aims of this chapter are to answer the following questions: 1) do stationary bumps exist in the abundance spectrum in the North Sea, and to what extent are nonlinearities of the spectrum stable over time; 2) do transient bumps exist in the spectrum, how large are they, and how quickly do they move up through the spectrum and/or dissipate. This will allow further understanding of the impacts of fishing on the size structure and abundance of fish as they grow over time.

4.2. Methods

4.2.1. IBTS data and surrogate data

For this chapter International Bottom Trawl Survey (IBTS) data from quarter 1 (Q1) only was used, as this had the longest time series available (34 years from 1980-2013). Data were cleaned as described in Appendix D.1 but without restricting the data to only those grid cells and years that were also present in the quarter 3 (Q3) data set. This resulted in different grid cells being included for this analysis; Figure D.1 in Appendix D.1 shows which grid cells were included. More years of data were included in this analysis than in previous chapters due to more earlier years of data being available for Q1, starting from 1980. The IBTS survey before 1980 was conducted using a variety of trawl gears, but had mostly been standardised by 1980. A few hauls carried out since 1980 had used an older version of the gear and those were removed for this analysis. The same surrogate IBTS data sets were used for calculating confidence intervals as were used in other chapters. All confidence intervals are 95% throughout the analysis.

4.2.2. Size classes

The IBTS data is naturally binned into length classes due to the way the fish are measured in the survey; fish are classified by 1cm size bins except for herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) which are measured to the nearest 5mm. Because of this, abundance spectra calculated from the IBTS have commonly used length as the unit of size. However, in other studies of size spectra, mass is preferred as the metric of body size (Jennings *et al.*, 2007)

as body mass largely determines the metabolic rate of organisms and their role in food webs (Brown *et al.*, 2004). Models of size spectra also use body mass or asymptotic body mass of fish (Andersen & Beyer, 2006; Blanchard *et al.*, 2009; Andersen & Pedersen, 2010) to describe how abundance scales with size. The analyses in this chapter therefore use mass as the measurement of body size.

In fish, length scales with body mass within a species. IBTS length classes were converted to mass using species-specific length-weight regression coefficients (Silva *et al.*, 2013) (Table D.1 in Appendix D.1) in the form $w = al^b$, taking l as the mid-point of the 1cm or 5mm length class. Species without recorded weight-length relationships were calculated using $a=0.01$ and $b=3$, the standard regression coefficients for fish (Blanchard *et al.*, 2005; ICES, 2014). This mapped each species-length class to a mass. The morphology of the fish species in the data vary significantly from flat-fish to round fish, so the animals in any length class can potentially span a wide range of masses. Masses were re-binned into 30 $\log_{10}$ -equal bins. Using log mass bins shows less bias in estimates of the slope than linear binning (White *et al.*, 2008), because the distribution of points in the spectrum are not biased towards the larger end of the size range.

4.2.3. Abundance spectrum and detection of stationary bumps

In order to investigate deviations from linearity and stationary bumps, first data was aggregated over all years to construct a time-averaged abundance spectrum. Because the resampling methods provide confidence intervals for each bin in the abundance spectrum, statistical confidence of deviations can be assessed visually. Then spectra were also plotted for each year from 1980-2013 to see if any non-linear characteristics were a constant feature of the spectrum through the years, which would indicate stable stationary bumps.

The abundance spectrum was plotted with $\log_{10}$ mass bins on the x-axis and $\log_{10}$ mean catch rate on the y-axis. Data were aggregated over space, or over space and time, so mean catch rate was used as the measure of abundance. Mean catch rate was calculated as the mean catch per unit effort (cpue, where unit effort is defined as one hour) per ICES rectangle ($1^\circ \times 0.5^\circ$ grid cell) as there was some variation in the number of rectangles sampled in each year.

For averaged spectra where data were aggregated over both space and time, the mean catch rate was calculated as the mean cpue per ICES rectangle per year. The central value of each $\log_{10}$ mass bin was taken as the midpoint of the bin on the log scale. The largest mass bins in some years contained no data because large fish are rare and the largest size was only found in very recent years. These bins were excluded from the analysis in those years because $\log(0)$ is undefined. Confidence intervals of the mean catch rate for each log mass bin were taken from the distribution of mean catch rates calculated for each of the 1000 surrogate data sets (see Chapter 5 for a detailed description of the methods used to calculate the surrogate data sets). The slope of the spectrum, when needed for comparison, was fitted using ordinary linear regression on the log-transformed values of mass and mean catch rate. Confidence intervals were taken from the distribution of fitted slopes from abundance spectra of the 1000 surrogate data sets.

The slope was fitted for size bins between a restricted log mass range from 2 to 4. Larger size bins were excluded due to very low catch rates for large species that could become zero in the surrogate data sets. Larger individuals are rare or able to outswim the trawl gear and are therefore under-sampled in the survey data. Because of this, the large size classes are also likely to have very wide confidence intervals of their mean catch rate. The smaller size bins are also likely to underestimate abundance due to small fish being under-sampled by the trawl gear because they are able to swim through the mesh opening in the net (ICES 2012). The log mass range of 2 to 4 roughly corresponds to fish between length ranges for which it is reasonable to assume fish are sampled accurately by the gear.

Stationary bumps were detected as deviations from a linear slope fitted by linear regression. Because the analysis used log equal mass bins, the slope is the estimate of $\lambda+1$ rather than the exponent of the underlying power law, λ . Other methods have been suggested as preferred methods for fitting a power law to the data but these were not appropriate for this analysis. White *et al.* (2008) found that binning methods performed poorly compared to using maximum likelihood approaches for estimating λ . However, these approaches rely on a continuous distribution such as the Pareto distribution. This is appropriate for mass-abundance scaling in most cases since masses of organisms come from a continuous distribution, but not for the IBTS which has naturally binned size classes. A discrete Pareto

distribution exists, and it is also possible to adapt the truncated Pareto distribution for binned data, which would then be appropriate for the binned length classes in the IBTS. The choice of log mass bin used here complicates this, as the data have been taken from a binned distribution, had a continuous function applied to them and then been re-binned. Another consideration is that this analysis does not depend on the value of the estimate of the slope, but instead looks at deviations from the slope. Thus, the method of fitting a linear slope to the data is unlikely to affect the detection of stationary bumps.

4.2.4. Lagged correlations and the detection of transient bumps

To test whether transient bumps were detectable in the abundance spectrum I used methods based on correlations lagged by size class. Let $\alpha_m(t)$ be the abundance (mean catch rate) in mass bin m through time, t , where here m is an index for the mass bin, not the actual mass itself. Then define the “mass-lagged” correlation as $c_{m,m+l_m} = \text{cor}(\alpha_m(t), \alpha_{m+l_m}(t))$, which does not depend on t . If transient bumps exist, then whenever $\alpha_m(t)$ is larger (respectively, smaller) than average, one expects $\alpha_{m+l_m}(t)$ for a small lag l_m to also be larger (respectively, smaller), i.e., one expects a positive $c_{m,m+l_m}$. Furthermore, the decline in $c_{m,m+l_m}$ for larger values of l_m will indicate the typical size of transient bumps. For example, if the value of $c_{m,m+l_m}$ is positive for all m , across values of l_m from 0 up to 2, then the size of the transient bump is 3 mass bins. To see the average size of the transient bumps, $\overline{c_{m,m+l_m}}$ was computed as the average correlation over m , and plotted against l_m to display the magnitude of correlation at each l_m . Correlations used were Pearson correlation coefficients. Confidence intervals were calculated, as usual, for each correlation using the 1000 surrogate datasets. This approach measures transient bumps regardless of whether stationary bumps exist because stationary bumps manifest in the time averages of the $\alpha_m(t)$, whereas correlations measure departures through time of the $\alpha_m(t)$ from their averages and whether these are related.

To calculate if and how long it takes for the transient bump to propagate through the spectrum, the same correlation method was used but also incorporated time lags, l_t . The correlations were then calculated as $c_{m,m+l_m}(l_t) = \text{cor}(\alpha_m(t), \alpha_{m+l_m}(t + l_t))$, for each m and l_m as before, and for a range of time lags. If the transient bump propagates through the

spectrum with time, one would expect to see $c_{m,m+l_m}(l_t) > c_{m,m}(l_t)$ for some $l_m > 0$ if $l_t > 0$. The value of l_m that tends to maximize $c_{m,m+l_m}(l_t)$ indicates to what extent a transient bump typically moves in time l_t . To see this, $\overline{c_{m,m+l_m}}(l_t)$ was plotted against l_m for each of several l_t , where the average here is computed across m . If bumps propagate then the maximum value of $\overline{c_{m,m+l_m}}(l_t)$ is expected to occur for larger l_m at larger l_t , and in particular to occur for positive l_m when l_t is positive. To determine to what extent transient bumps move versus dissipate through time, the extent to which the maximal values of $\overline{c_{m,m+l_m}}(l_t)$ (maximum computed across l_m) declined with increasing l_t was examined – fast declines correspond to rapid dissipation of transient bumps, whereas slow declines mean bumps travel up the spectrum more or less intact. Again, confidence was assigned using surrogates.

4.3. Results

4.3.1. Deviations from linearity

The abundance spectrum showed significant deviations from linearity. Figure 4.2 shows that for data aggregated and averaged over time and space in the North Sea, most abundance values fell significantly below or above the fitted slope of the spectrum. This was consistent across slopes fitted for different ranges of size bins (Figure C.1 in Appendix C.1). The specific deviations from linearity observed in the restricted mass range were small, but they were well outside the variation that can be explained from sampling noise alone. Even within the restricted mass range there were values that deviated significantly from the spectrum slope. Specifically, log mass classes from about 2 to about 2.5 (100g to about 316g) were more abundant than expected from linearity of the abundance spectrum, classes from about 2.5 to 3.5 (about 316g to 3162g) were less abundant than expected, and mass classes from 3.5 to 4 (about 3162g to 10000g) were more abundant.

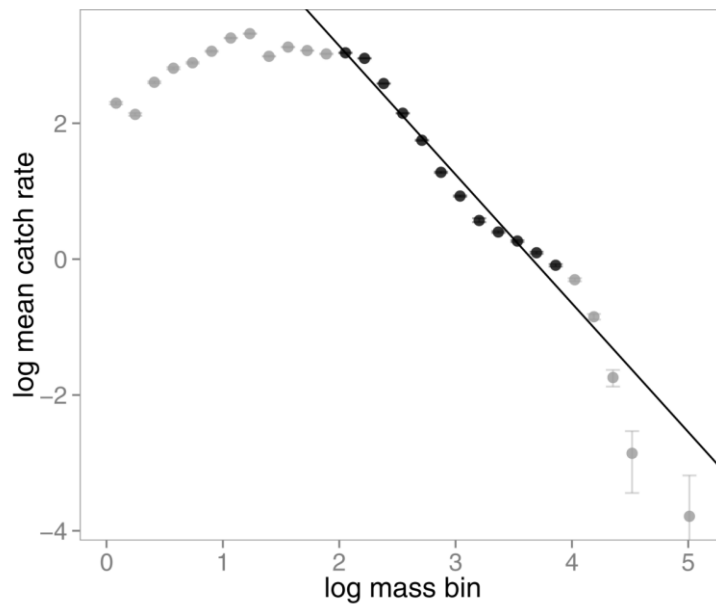


Figure 4.2: Abundance spectrum for the North Sea, computed from data aggregated over 34 years (1980-2013). Log mass (g) is plotted against log mean yearly catch rate (cpue). The slope is fitted through mass bins by ordinary linear regression. Light grey points show the values excluded from the slope fit, which were the log size bins outside the range 2 to 4 (see Figure C.1 in Appendix C.1. for justification of the choice of mass bins included). Confidence intervals on the abundance in each mass bin were calculated from the 1000 surrogate data sets.

4.3.2. Stationary bumps in the spectrum

Deviations from a linear abundance spectrum slope were consistent across years. The slope of the spectrum became steeper over time which is consistent with previous results for the North Sea (Rice & Gislason, 1996; Daan *et al.*, 2005); Figure 4.3 shows the abundance spectrum for three years with significantly different slopes. In each of these years, and across almost all of the other years (Figure C.2 in Appendix C.2), the same pattern observed in the time-averaged spectrum was seen; log size bins in the middle of the 2-4 range had below the abundance expected from linearity, and size classes at either side of the range had above-expected abundance. There was some variation around the number of size bins that fell into the middle range in each year, but the general pattern was remarkably consistent. The consistency is especially notable because it persists in light of the major change in slope of the abundance spectrum, from -1.61 to -2.27 over the period. This suggests that the deviations from linearity are stationary bumps in the spectrum, even more stable than the overall slope of the spectrum when one computes slope using standard methods (linear regression).

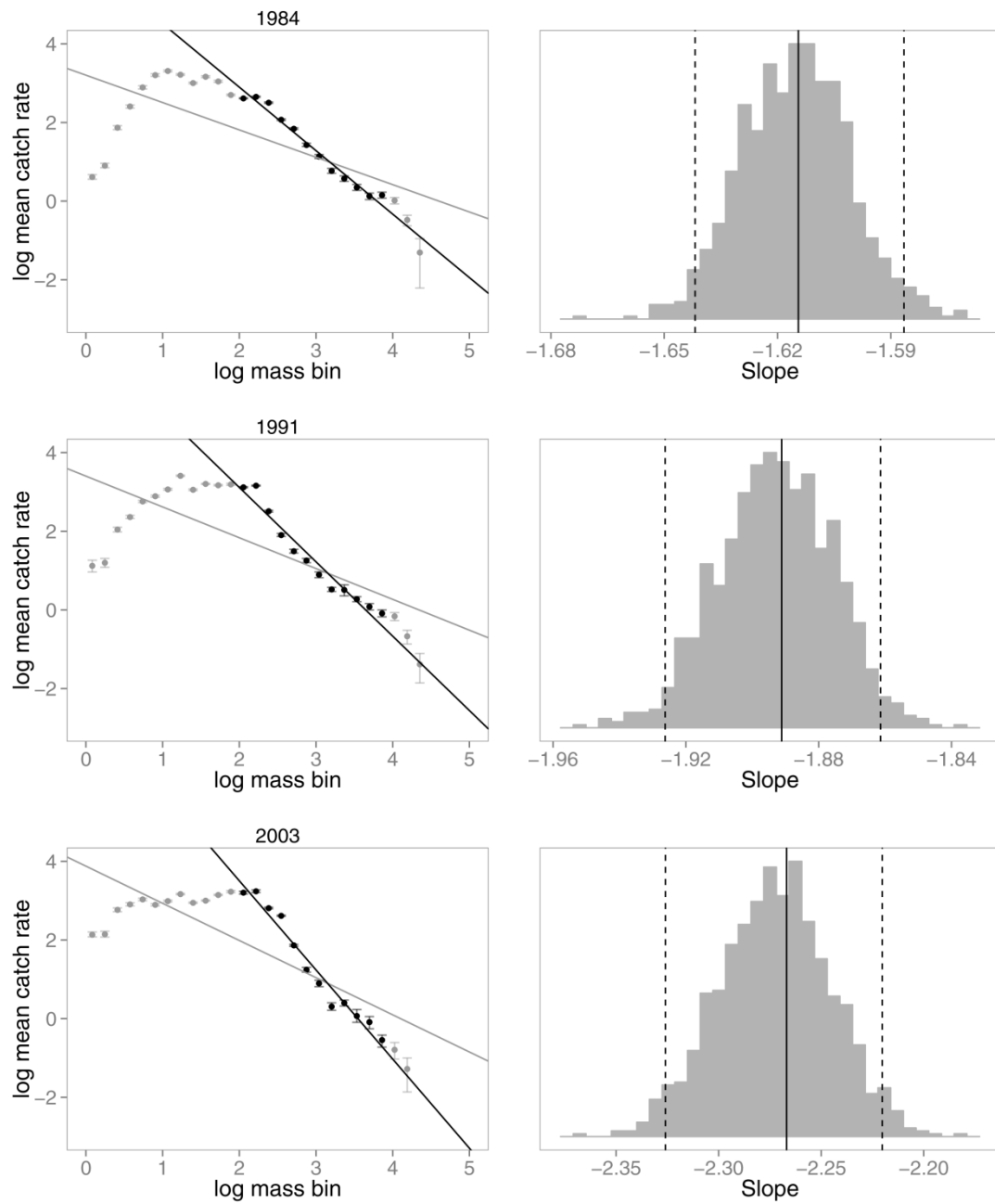


Figure 4.3: Abundance spectra in the North Sea for a selection of years (1984, 1996 and 2003). Years were chosen based on the slope of the abundance spectrum in the restricted mass range of 2 to 4; 1984 had the shallowest slope, 2003 the steepest, and 1996 was in the middle of the range of slope values. Log mass (g) is plotted against log mean catch rate (cpue). Confidence intervals on the abundance in each mass bin were calculated from the 1000 surrogate data sets. Histograms show the distribution of fitted slopes within the restricted mass range (2 to 4) calculated for each of the 1000 surrogate data sets, with dashed lines indicating the lower and upper confidence interval of the slope (solid line). Spectra for other years can be seen in Figure C.1 in Appendix C.1.

4.3.3. Transient bumps in the spectrum

Transient bumps were detected in the abundance spectrum with a typical log size lag of 0.66, or four mass bins, corresponding to a mass ratio of about 4.5 between the leading and trailing edges of the transient bump. Values of $c_{m,m+l_m}$ (for $l_t = 0$) were consistently and significantly positive for l_m between 0 and 3 (Figure 4.4). This gap of four mass bins (including the boundary bins) corresponds to a mass ratio of 4.53 (4 bins times a bin width on the $\log_{10}$ scale of 0.164). These transient bumps exist on top of the stationary bumps demonstrated in the previous section, and they constitute the year-to-year variation in the spectrum. Figure 4.5a also illustrates the size of the bump spanning four mass bins.

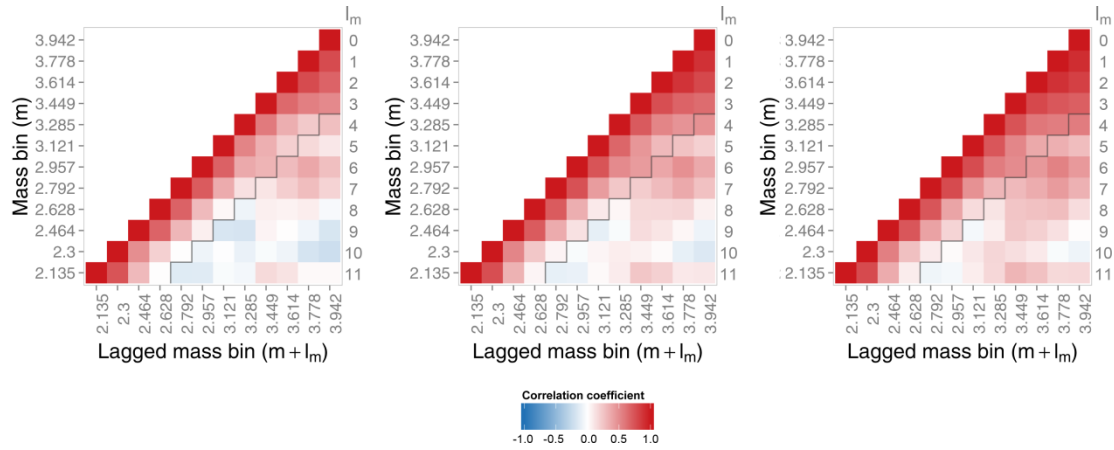


Figure 4.4: Correlations of abundance (mean catch rate) of fish in log mass bins in the range 2-4, calculated for each mass lag, l_m . Correlations were calculated across all 34 years (1980-2013), with time lag $l_t = 0$. Correlations from the real data are in the central plot, the left plot is the lower confidence interval taken from coefficient values calculated from the 1000 surrogate data sets, the right plot is the upper confidence interval. The values represented are Pearson correlation coefficients and range from 1 (red) to -1 (blue), with white meaning a value of 0. Only correlations calculated for positive l_m are shown here, and are plotted from a smaller mass bin (y-axis) to a larger mass bin (x-axis). Each diagonal represents a different value of l_m from 0 to 11; the black line indicates the value of l_m at which correlations above the line were positive for all mass bins.

The transient bumps moved up through the spectrum, propagating roughly at an average rate of one $\log_{10}$ mass units per year for five or six years before they dissipated. Peaks of plots of $\overline{c_{m,m+l_m}}(l_t)$ versus l_m (Figure 4.5) occurred at larger mass lags, l_m , for larger time lags, l_t (recall that the mean in $\overline{c_{m,m+l_m}}(l_t)$ is computed over m). Peaks were apparent for five or six

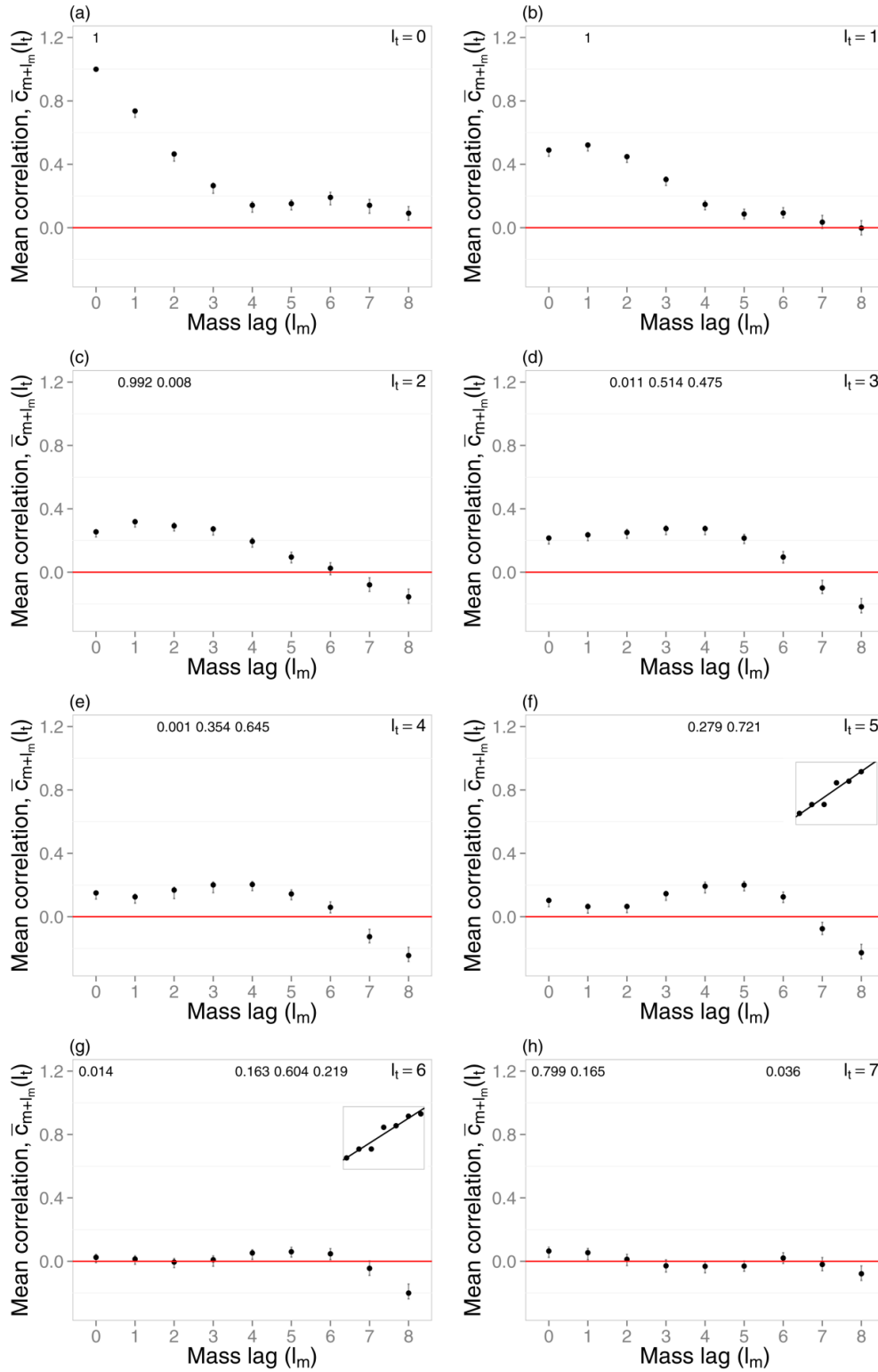


Figure 4.5: Mean correlation coefficient values, $\bar{c}_{m,m+l_m}(l_t)$, plotted against each value of l_m from 0 to 8 (each diagonal in Figure 4.4 with more than 3 mass bin comparisons to average across), for each

time lag, l_t , from 0 to 7 (a-h). Confidence intervals are taken from the distribution of mean values, $\overline{c_{m,m+l_m}}(l_t)$, of correlation coefficients calculated from the 1000 surrogate data sets. The numbers above peak values of $\overline{c_{m,m+l_m}}(l_t)$ for each mass lag l_m indicate the proportion of surrogate values of $\overline{c_{m,m+l_m}}(l_t)$ that were maximal at each l_m . Red lines are at a correlation coefficient of zero. Inset plots at $l_t = 5$ and $l_t = 6$ show a linear regression through $\overline{c_{m,m+l_m}}(l_t)$ against l_m .

years (i.e., l_t up to five or six) but did not occur for larger l_t (Figure 4.5). Values of $\overline{c_{m,m+l_m}}(l_t)$ tended to decrease as l_t increased, corresponding to dissipation of transient bumps as they propagate through the spectrum. Speed of progression of transient bumps was assessed (Figure 4.5 caption, insets on panels f and g) by estimating the rate of progression of maxima of the plots of $\overline{c_{m,m+l_m}}(l_t)$ with increasing l_t , which moved at a rate of around 1 mass bin per year (a mass ratio of 1.46).

4.4. Discussion

Significant deviations from linearity are present in the abundance spectrum, and take forms which are interpretable and probably convey substantial ecological meaning. Using the resampling methods developed in this thesis was the key to allowing meaningful and interpretable deviations to be distinguished from sampling variation in the trawl survey data. Stationary bumps were found across all sizes in the range 100g to 10kg, with some ranges showing more abundance than expected from a linear expectation, and accordingly some ranges showing less abundance compared to that expectation. This was remarkably consistent from year to year even in the face of substantial changes in the more commonly tracked slope of the abundance spectrum, although with some variation around the size and width of each bump. As the slope of the spectrum decreases over time, stationary bumps are still present and follow the same basic pattern. Analysis of the size of these bumps and the underlying processes that cause them to be permanent features of the North Sea fish size spectrum may offer an extra metric of community structure that can be monitored in this ecosystem, alongside the slope. Models of size-structured communities are often based on the assumption of a linear slope and don't consider the underlying structure of the real data. Understanding size spectra of real communities may benefit from further exploration of these features.

Built on top of this apparently permanent non-linear structure, there were also transient bumps that propagated up the spectrum. These bumps spanned a size-lag width of 0.66 on a log scale, representing a mass ratio of around 4.5 between edges of the bump. The bumps propagated at a speed of roughly 1 mass category per year, for around 5 or 6 years before they dissipated. On average, this suggests that pulses in abundance are detectable for 6 years in the spectrum before they become damped. The damping could occur because fish have grown to their maximum size and abundance in larger size categories drops off as individuals mature and approach their asymptotic size with a slowed growth rate, or in the case of larger fish, have grown out of the range of sizes that were considered in the analysis. It is also possible that some damping occurs as larger individuals are removed from the community by fishing. The results here showed that size classes that are closer together tend to be more correlated within the same year, but correlations lagged over time showed positive correlations with larger size classes, and in some cases negative correlations with even larger size classes. This is consistent with models where perturbations in abundance or biomass cause waves to move through the spectrum, and result in gaps in the exploited size range with peaks and valleys in the adjacent sizes (Rochet & Benoît, 2011).

The stationary bumps detected in the North Sea in this chapter are consistent with previous studies. Evidence of stationary bumps in biomass spectra has previously been detected in a range of systems over particular ranges of body size (Kerr & Dickie, 2001). These bumps can exist at two levels. Firstly, at the ecosystem level, domes of biomass have been shown centred around distinct trophic groups such as phytoplankton, zooplankton, and fish (Kerr & Dickie, 2001). Within these trophic groups, there can also exist a secondary structure with smaller domes in biomass across smaller size ranges. Such domes have been shown in fish spectra from exploited regions such as the Scotian shelf (Duplisea *et al.*, 1997), the northern North Sea, and George's Bank (Kerr & Dickie, 2001), and these domes were consistent over time periods ranging from 10 to 30 years. Kerr and Dickie (2001) suggested that these secondary biomass domes are likely to be a common property of community size spectra, since the domes have been found in major multi-species systems, persist through time, and even cluster around the same range of body sizes across systems. This is further supported by the results of this chapter, which have shown that stationary bumps in the spectrum are still a feature of

the North Sea fish community in recent years, and are significant departures from the expected linearity of the slope. The fact that bumps or domes have been detected previously using data in systems with different survey design suggests that they are a real feature of fish communities (Kerr & Dickie, 2001), and this is confirmed here by the use of appropriate methods to assess the significance of the bumps.

Theoretical justification for the existence of stable, permanent bumps in the spectrum has been developed (Thiebaut & Dickie 1993). The Thiebaut-Dickie model is based on predator-prey interactions and results in a series of stationary biomass domes, where the spacing of the domes is related to the body sizes of predators and their prey. Thus, the stationary bumps detected here in the North Sea fish community are likely to be a permanent feature of the spectrum that manifest from underlying processes at the individual level, and be dependent on predator-prey mass ratios in the system. Boudreau & Dickie (1992) suggested that stationary bumps in the spectrum at individual trophic positions must depend on small-scale processes, and perturbations in individual food-chain elements would result in year-to-year changes of the bumps. This may explain the variation around the stationary bumps that was detected in the annual spectra, and therefore the transient bumps that were also detected. Further analysis using the same correlation methods but with the time-averaged abundance spectrum structure removed from the year-to-year variation would allow the dynamics of the transient bumps to be assessed in isolation from the underlying stationary structure.

The transient bumps detected here were over a small size range, and may be reflecting a smaller part of a trophic cascade that propagates through the entire size spectrum. Trophic cascades have been shown to exist in exploited marine systems and delay the recovery of a system or individual species (Babcock *et al.*, 2010; Frank *et al.*, 2011). Models of biomass pulses that move through multiple trophic groups have shown that cascades are likely to be induced by top-down influences of fishing pressure that destabilise the size spectrum (Benoît & Rochet, 2004; Rochet & Benoît, 2011). These models describe a wave where peaks move down the spectrum, but are damped rapidly. Models of fish community spectra have also shown trophic cascades caused by fishing (Andersen & Pedersen, 2010; Houle *et al.*, 2012); when the larger fish were targeted selectively by fishing, then reduction of biomass in those

size categories caused cascades that propagated through the spectrum with peaks that became damped the further they moved from the targeted trophic level (Andersen & Pedersen, 2010). However, these models are resolved for multiple trophic levels, whereas the analysis of transient bumps in this chapter concentrated on only the small range of sizes available from trawl survey data. While it is possible that the transient bumps detected here were induced by fishing, the movement was in an upwards direction through the spectrum to larger sizes and not down through trophic levels as in the models. This suggests that the movement of the bumps seen here at this smaller scale is due more to the growth of the animals, in addition to the possible influence of cascades through the larger spectrum and processes outside the range of sizes considered here.

The time it takes for transient bumps to move through the spectrum may then be the result of many underlying causes, but is probably largely dependent on growth. Each mass bin in the spectrum contains animals of different asymptotic sizes, meaning that individuals within each size range are growing at different rates. A possible further analysis would be to determine the species driving the propagation of the bumps, categorised by their asymptotic size. Andersen & Beyer (2006) derived a model where abundance in a size class can be determined by asymptotic size in size-structured communities. Using this, and diversity spectrum theory where the number of asymptotic sizes in a size class is also strongly size structured (Reuman *et al.*, 2014b), proportions of asymptotic sizes in each size class can be predicted and an average growth rate calculated for each mass bin. This would allow the asymptotic sizes that contribute to the movement of the bumps to be determined. In previous empirical studies where stationary bumps in the spectrum were found, the species that made up the domes of biomass were not major replacements of one species group by another in the Scotian shelf (Duplisea *et al.*, 1997), but in the North Sea they were made up of consistent changes in species (Kerr & Dickie, 2001). Further work should also examine whether the stationary bumps detected here are composed of the same species over time or whether the bumps exist regardless of species composition and are more a function of size. Understanding which types of species make up the stationary bumps and which drive the transient bumps may have consequences for fisheries; if abundance in small size groups in the North Sea

increases but does not comprise the larger species that can grow and move up to further size classes, then abundance at the larger end of the size spectrum will not recover.

This chapter has shown that the abundance spectrum is significantly non-linear in the North Sea, and that this non-linearity results from both stationary bumps in the underlying structure of the spectrum, and transient bumps that move up through the spectrum with time. Stationary bumps are consistent with previous size spectra studies in both lake and marine communities (Kerr & Dickie, 2001), but the detection of transient bumps and the speed at which they propagate in the fish community size spectrum is new. The transient bumps detected here may be indicative of unstable communities that are more sensitive to environmental change. Further analysis of non-linear characteristics of abundance spectra in the North Sea is needed to understand the underlying dynamics and the potential for outside influences to change the state of the ecosystem.

Chapter 5. A simple resampling method for assessing significance of trawl-survey based community indicators and trends.

Abstract

Size-based ecosystem indicators are often used to inform fisheries management, but variability in the survey data they are calculated from is often not assessed. In addition, trends in ecosystem indicators are commonly studied in order to further understand long term impacts of fishing and environmental change on community structure, but whether those apparent trends are just artefacts of sampling are often not investigated. Methods to account for variability in trawl survey data have been proposed before, but are sometimes inconsistent and often not implemented because of their complexity and statistical appropriateness only for limited circumstances. I develop a more appropriate version of these methods, based on resampling, that 1) preserves the trawl-survey design, 2) is applicable to almost any indicator that can be calculated from typical trawl survey data, 3) can be used at any level of disaggregation of the data, and 4) does not require the user to undertake complex mathematics or statistics. The method uses parametric bootstrapping to create surrogate versions of the North Sea IBTS trawl survey data which are then used to calculate confidence intervals for point estimates or trends in indicators. In addition to the principal result which consists of the method itself and tools to aid in its implementation by others, I illustrate several benefits of applying the method using trawl survey data from the North Sea: 1) the method shows that sampling variation is not greater than year to year variability across various size-based indicators of community structure; 2) confidence intervals can be assigned to general trends in indicators; and 3) I suggest ways of applying the method to perform model selection between different models of trends in indicators. The new resampling method is simple to apply but potentially valuable for obtaining greater confidence in assessments based on indicators calculated from trawl survey data.

5.1. Introduction

Trawl surveys are carried out by research vessels in many marine regions (Walsh, 1996) to monitor the abundances of populations and the composition of marine communities. They also provide an alternative data set to fisheries stock assessments for use in assessing trends in diversity and abundance related to fishing and climate. These surveys are increasingly important for the management of marine resources, as an ecosystem approach to fisheries management is being adopted in many systems (Hall & Mainprize, 2004; Pikitch *et al.*, 2004; Shephard *et al.*, 2013), and community indicators calculated from trawl survey data are now commonly used for management purposes in exploited marine ecosystems. Although trawl surveys provide important and valuable data for evaluating the state of marine ecosystems, the levels of sampling variability and other forms of variability present in the data means that there exists substantial uncertainty in values of the indicators, which complicates their interpretation for management. It has been suggested that management strategies are slow to respond to ecosystem indicators at least in part because of this variability, and a lack of knowledge on when to interpret observed changes in an indicator as meaningful and actionable (Browman *et al.*, 2005; Dambacher *et al.*, 2009).

Indicators are often reported with no confidence intervals or levels of significance, which means that changes from year to year cannot be accurately evaluated as representing meaningful trends, as opposed to sampling variation or other stochastic variation. For example, in the North Sea, many abundance-based species and community indicators are calculated from the International Bottom Trawl Survey (IBTS) data in order to evaluate the state of the demersal fish community (Jennings & Dulvy, 2005; Greenstreet *et al.*, 2012b; ICES, 2012; ICES, 2014) without sampling variation being taken into account. Another example is the large fish indicator (LFI), which is currently attracting a lot of attention as a size-based community indicator as it conveys information about the size structure of the fish community and the response to fishing pressure (Greenstreet *et al.*, 2011, 2012b; Fung *et al.*, 2012; Engelhard *et al.*, 2015). However, values of the LFI that have been reported for the North Sea lack confidence intervals, and trends are evaluated by comparing values between years, or on their size relative to some management target value.

The principal goal of this chapter is to provide a practical method for associating statistical confidence with calculations of ecosystem indicators based on trawl survey data. The approach is based on resampling of the trawl survey data set, and enables the calculation of confidence intervals for both indicator values in a single year, and for trends in indicator values. Although the methods could be, in principle, applied or adapted to any trawl survey data set, the focus here is on application to the IBTS data set in the North Sea. North Sea fisheries are of interest to a large number of European countries, and the IBTS is a long-running, widely used dataset that has a standardised and stable sampling design. The IBTS comprises both quarter 1 (Q1) and quarter 3 (Q3) sampling surveys, both of which will be used here.

Although sampling variability and statistical confidence are often not considered when trawl survey data are used to assess the state of ecosystems, there have been some past resampling-based approaches applied specifically to trawl survey data (Smith & Gavaris, 1993; Smith, 1997; Trenkel & Rochet, 2003; Shephard *et al.*, 2012). The method developed for the IBTS here fills a different niche from the earlier methods. The other methods are typically either, 1) inappropriate for the survey design used, 2) applicable in a constrained set of circumstances, or 3) require that users be mathematically or statistically sophisticated. The approach taken for the IBTS in this chapter remedies these shortcomings. Comparisons between this approach and existing approaches will be made at length in the Discussion.

This chapter develops and advocates a resampling based method of including statistical confidence in indicators based on IBTS data, and in trends based on these indicators. The method should be applicable to a wide variety of indicators and metrics of the North Sea demersal fish community, and should be applicable by users not having high levels of mathematical or statistical sophistication. In addition to introducing the method, the application is illustrated by answering questions about the nature of sampling variability in community indicators based on IBTS data from the North Sea: 1) What is the relative size of statistical sampling variation in indicators and year-to-year variability in those indicators, i.e. are the year-to-year variations in indicators meaningful or produced purely by sampling variation? 2) Are differences between trends in indicators based on Q1 data significantly different from trends based on Q3 data? 3) Can the resampling method be used to perform

model selection among different candidate models for how indicator values change over time. The answers to these questions may have implications for management in the North Sea, but the main focus throughout this chapter is on the method itself, and the benefits of assigning confidence to community indicators and trends. It is a simple and easily applied approach, and is expected to be a highly useful tool not only for the illustrative questions addressed, but also for a wide variety of other applications.

5.2. Methods

5.2.1. Data

North Sea International Bottom Trawl Survey (IBTS) data was downloaded from the ICES data service DATRAS (datras.ices.dk). A description of the data can be found in Appendix D.1. Data were cleaned following methods described in Appendix D.1. Data from both quarter 1 (Q1) and quarter 3 (Q3) surveys were used, for the years 1991-2013, in order to compare trends between quarters to assess seasonal variability.

The specific structure of the IBTS data is important to the resampling method. Firstly, the survey is stratified by ICES rectangle ($1^\circ \times 0.5^\circ$ grid cell). The survey design aims to carry out at least two hauls in each rectangle per year, so that catch rates can be averaged to give a mean catch rate per rectangle. In reality, the number of valid hauls per rectangle varies between years depending on factors such as weather conditions or the time or duration of the haul. The resampling method must respect this spatial structure and the multiple and varying number of hauls carried out in each rectangle by resampling within each haul, not within or across rectangles. Secondly, each row/entry of the IBTS data comprises the number of individuals caught in a length category of a species in a haul (Table 5.1). In order for the resampling method to approximate repeated survey effort, it should resample on this unit, i.e. on the actual number of fish caught by species-length category within a haul. This requires being able to resample from the raw number of individuals caught, however, this is complicated by the IBTS data available on DATRAS sometimes not reporting raw catch numbers but instead reporting scaled up numbers due to necessary subsampling of catches

(Table 5.1 row 2). It is common in the IBTS for large numbers of individuals of abundant species to be caught in each haul, so subsamples of the catch are taken as not every individual can be counted or measured. Subsampling factors are either reported or can be calculated from the data, and these are needed to transform recorded catch rates back into raw catch numbers per species-length category, in the cases where raw catch numbers were not available in the data. Taking any subsampling factors into account is important for the resampling procedure, as this process of scaling up catch numbers based on subsamples is likely to result in the sampling variation being greatly inflated for large catches. Thus, cleaning the data to recover subsampling factors is needed to accurately reproduce the true levels of sampling variation, and was carried out as described in Appendix D.1.

Species	Total catch	No. individuals measured	Subfactor (reported)	Length class (cm)	Catch at length (recorded)	Subfactor (corrected)	Catch at length (true)	cpue
<i>Limanda limanda</i>	15	15	1	14	2	1	2	4
<i>Merlangius merlangus</i>	178	89	1	15	50	2	25	100

Table 5.1: Example rows of the IBTS data, taken from the Q1 survey data.

5.2.2. Description of resampling method and surrogate datasets

Based on the specific structure of the IBTS data described above, I developed a resampling based method that used parametric bootstrapping to obtain surrogate IBTS data sets. Various resampling methods exist for estimating bias and uncertainty in sampled ecological data (Crowley, 1992), but parametric bootstrapping has distinct advantages over other types of resampling for the analysis of management indicator values and trends. Other methods include permutation testing, which provides p-values and is used to answer questions related to hypothesis testing, and jack-knifing, which provides bias-corrected estimates and is most commonly used for detecting outliers in the data. Neither of these approaches would be suitable for providing confidence intervals on indicator values calculated from a large dataset such as the IBTS. In contrast, bootstrapping approaches estimate variability at the level of the sampling process and could provide confidence intervals on any metric that can be calculated from the data. The bootstrapping approach can then be extended to calculate confidence intervals for trends in the data as a way of assessing significance. Bootstrapping can be

parametric or non-parametric, and results in the creation of surrogate datasets. The non-parametric bootstrap resamples directly from the data with replacement, so that the surrogate datasets contain repeated data and may not include all species, size categories, or locations as the original data, depending on the unit of resampling chosen. The parametric bootstrap resamples from values in the data using a statistical distribution so that the surrogate datasets may not contain the same values as the original data, but do retain the overall structure. Since the general idea was that the surrogate datasets should represent repeated sampling effort, that is, as if the IBTS survey were carried out in the North Sea multiple times in each haul location simultaneously, the parametric bootstrap was most appropriate. Resampling in this way means that surrogate datasets can be used in exactly the same way as the original data; whichever value, indicator or trend is calculated from the original data can also be calculated for each of the surrogate data sets, which then provides a distribution of values from which confidence intervals can be drawn.

The resampling was carried out as follows. For each haul in each location and year, the true number of individuals caught in each species-length category was calculated using either the recorded or corrected subsampling factor (in cases where no subsampling occurred and every individual caught was measured, a subsampling factor of 1 was used). The example IBTS data in Table 5.1 illustrates this process: the true catch-at-length was derived by dividing the recorded catch at length by the corrected subsampling factor. The resulting column (Catch at length (true)) contains the values that were used to resample from in the data. Using the true catch number as the resampling unit is crucial, because it means that the sampling variation in the catch numbers is captured before being scaled up by the subsampling factor, which will amplify variation in the resampled data as in the real data.

A parametric bootstrap was then calculated by drawing values from a Poisson distribution, where the parameter was taken as the true catch-at-length. This method of resampling makes some assumptions about the data; that the sampling variability in the data was due to by chance catching a different distribution of individuals in any given haul, and that the number of individuals caught in any species-length category (out of the whole population available for sampling) can be described by a Poisson distribution.

The resampled catch-at-length numbers were used to produce surrogate IBTS data sets. Resampled catch-at-length values were generated 1000 times for each species-length category in each haul (i.e. for each row of the IBTS data set). Resampled values were then multiplied by the corrected subsampling factor where required, and converted into a catch rate (cpue; catch per unit effort) averaged by haul duration (usually 30 minutes). Surrogate data sets were then cleaned in the same way as for the IBTS data described in Appendix D.1. This resulted in 1000 surrogate datasets with the exact same spatial distribution and species composition as the original IBTS data, with catch numbers drawn from the same species-length distribution as in the original data, but now with sampling variation built in at the level of individual organisms captured.

5.2.3. Confidence intervals and indicators calculated

To illustrate the resampling methods, five size-based indicators were chosen to assess the levels of sampling variation present in the IBTS data Table 5.2. The indicators were calculated for both Q1 and Q3 IBTS data, over a time series of 23 years, and confidence intervals were assigned to the point estimate of each indicator value in each year using the surrogate data sets. To examine the extent to which sampling variation affects average trends, ordinary linear regressions were fitted to the indicator values over time. Taking p-values from ordinary linear regressions does not constitute a statistically valid approach to assess significance of a trend, as sampling variation in the indicator estimates may vary from year to year, and may be non-independent, contrary to standard assumptions of ordinary linear regression. The surrogate data sets were used to calculate confidence intervals for the slope of the linear regression, which is a more appropriate estimate of the significance of the linear trends.

Confidence intervals can be calculated from the surrogate data sets for any indicator value or trend that is required. The process is demonstrated in Figure 5.1. For the analysis of indicator values, the method of calculating the indicator was simply repeated for each of the 1000 surrogate data sets, resulting in a distribution of 1000 indicator values from which percentiles were drawn. Similarly, for trends, linear regression slopes were fitted to the yearly indicator values for each surrogate data set, and confidence intervals taken from the distribution of

surrogate slopes. Confidence intervals were always taken as 95% limits from the distribution. Two point estimates of indicator values were considered significantly different if their confidence intervals did not overlap. A trend was considered to be significantly non-zero if its lower confidence limit was above zero for positive trends, or its upper confidence limit was below zero for negative trends.

Indicator	Calculation		Source
Mean length (abundance weighted)	$\frac{\sum_i L_i}{N} = \frac{\sum_i C_i L_i}{\sum_i C_i}$	C_i is the catch rate (cpua) for species-length category i , and L_i is the midpoint of the length category.	Trenkel and Rochet (2003), Nicholson and Jennings (2004), Houle <i>et al.</i> (2012)
Mean weight (abundance weighted)	$\frac{\sum_i W_i}{N} = \frac{\sum_i C_i W_i}{\sum_i C_i}$	C_i is the catch rate (cpua) for species-length category i , and W_i is the weight calculated from the midpoint of the length category.	Nicholson and Jennings (2004), Piet and Jennings (2005), Shin <i>et al.</i> (2010)
LFI	$\frac{\sum B_{L>40cm}}{\sum B}$	$B_{>40cm}$ is the biomass of individuals over 40cm in length, and B is the biomass of all individuals.	Greenstreet <i>et al.</i> (2011)
LSI	$\frac{\sum B_{L_{max}>85cm}}{\sum B}$	$B_{L_{max}>85cm}$ is the biomass of species with a maximum length over 85cm, and B is the biomass of all species	Shin <i>et al.</i> (2010), Shephard <i>et al.</i> (2012), Houle <i>et al.</i> (2012)
Abundance spectrum slope		Linear regression slope of log mass against log catch rate (cpue, see Chapter 4 Methods).	Nicholson and Jennings (2004), Piet and Jennings (2005), Shin <i>et al.</i> (2010).

Table 5.2: Suite of five indicators tested for sampling variability and Q1 and Q3 trends. The indicators were chosen for their current use as indicators in both research and management contexts, and for their ability to be calculated directly from the trawl survey data. Sources of indicators are listed, they have all also been calculated for the IBTS in various ICES reports (ICES 2014). The LFI calculation was the same as in Chapter 3, and the abundance spectrum slope was calculated as in Chapter 4.

5.2.4. Toward model selection

I also made an initial step towards using the surrogate datasets for model testing. Models tested were linear, using ordinary linear regression. For comparison between models, a leave-one-out regression approach was used to determine model fit. With this approach, a model with any number of parameters can be compared to another, as follows: a model was fitted n times (n = number of years) leaving out one year each time, and the value of the indicator in the missing year was predicted from that model. Predicted values were subtracted from the values observed in the data, then averaged (mean squared error) to obtain an error estimate

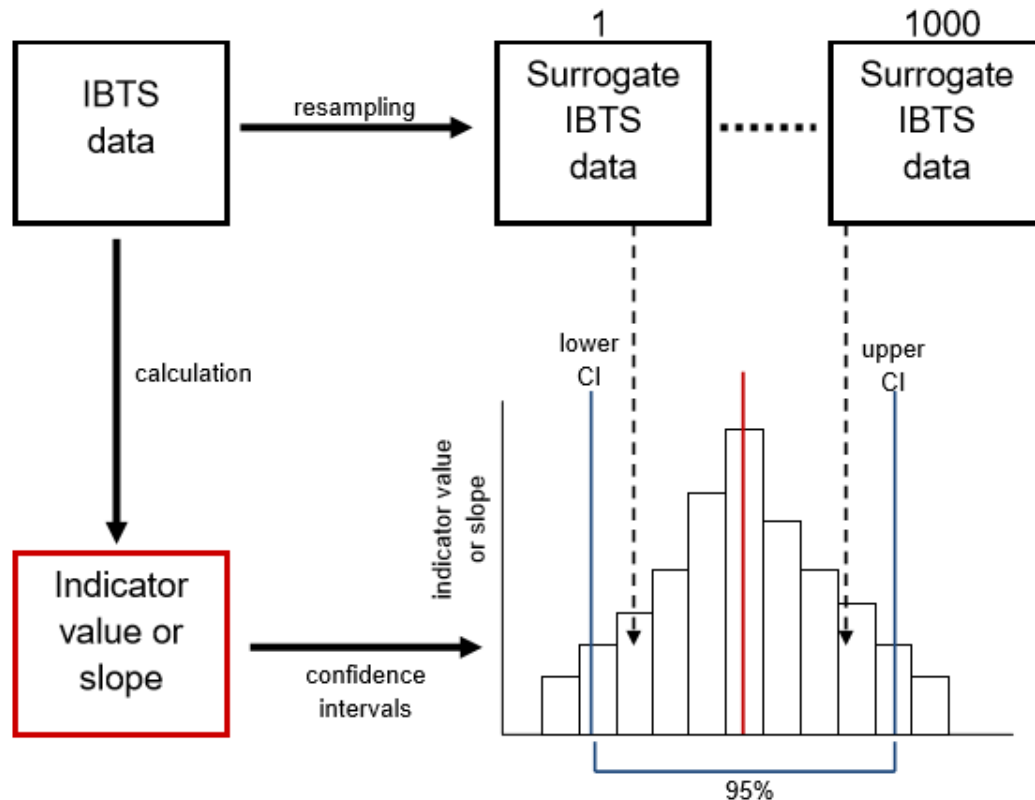


Figure 5.1: Flow chart to illustrate the process of calculating confidence intervals for either a value of an indicator, or a trend in an indicator. The same calculation that is performed on the IBTS data to obtain the indicator value or trend value is carried out in the same way on each of the 1000 surrogate IBTS data sets. Those surrogate values form a distribution from which confidence intervals of any size can be drawn, shown here as 95% limits.

of the model. Error estimates were calculated for both models tested, and compared within each of the surrogate datasets to give 1000 model fit comparisons.

To illustrate this method, two different linear models were fitted to the LFI. The LFI has previously been shown to have decreased over time before increasing again around the year 2000, corresponding with changes in fishing effort in the North Sea (Engelhard *et al.*, 2015). The example therefore modelled a split linear regression trend, with a fixed break point at the year 2001 (and for comparison, repeated with the year 2000) based on looking at trends in the version of the data used in this analysis. The significance of the split linear regression model was checked first to ensure that the negative slope and the positive slope were both significant, and then that model was compared to a linear regression slope through all years.

5.3. Results illustrating the methods

5.3.1. Sampling variation in indicator values

Indicator values generally showed more variation between years than is accounted for by sampling variation (Figure 5.2). This was consistent across the suite of indicators, which ranged from simple metrics of mean size to more complex size-structure based indicators of the community. This was true for both Q1 and Q3 values of the indicators, with no obvious difference in sampling variability between seasons.

Confidence intervals around point estimates were sometimes larger in some years than others, indicating more uncertainty in the indicator value in those years. For example, the year 1991 in Q3 generally showed more sampling variability than other years. This was the first year that the survey was standardised and carried out in Q3, and less hauls (around 30% of hauls in other years) were carried out. The larger variation in 1991 was not present for values of the LFI and closely related LSI, which might be due to those indicators being calculated as proportions so reduced sampling effort has less of an effect on the estimated value. The estimates of mean weight also had some years that had considerably larger confidence intervals than in other years; 1996 and 2013 in Q1 and 2007 in Q3.

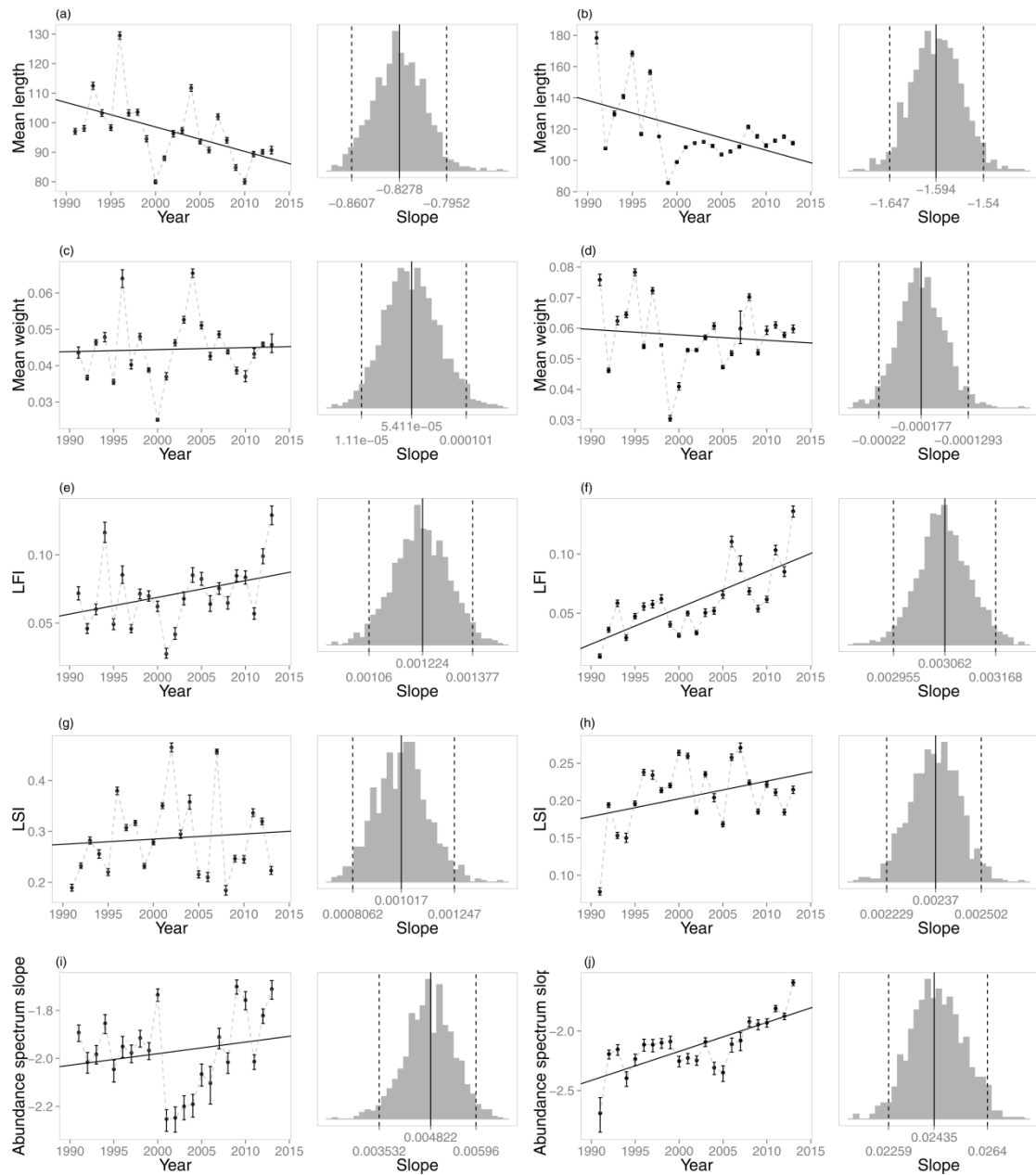


Figure 5.2: Indicator values for five different community indicators from 1991-2013, with 95% confidence intervals calculated from 1000 surrogate datasets, for Q1 (a,c,e,g,i) and Q3 (b,d,f,h,j). Trend lines are linear regression slopes fitted to the data, and histograms show the distribution of slopes calculated for the surrogate datasets. Dashed lines indicate the 95% confidence intervals of the slope (solid line). Mean length is measured in mm, and mean weight in kg.

The abundance spectrum slope showed the most uncertainty in values between years, in both Q1 and Q3 there were periods of 3 or 4 years with no significant change in the indicator. This could be because there was no real change in the indicator value in those years, but may

also be reflecting the nature of the indicator. The abundance spectrum slope is altered by changes in abundance in each of the size classes used to estimate the slope, so sampling variability in each of those size classes may be amplified in the overall metric.

5.3.2. Indicator trends and seasonal comparisons

Trends in all indicators were significant based on confidence intervals of the slopes (Figure 5.2); however, some average linear trends were small in magnitude and averaged over considerable year-to-year differences in indicator values. For example, mean weight in Q1 had a very small positive overall trend, but some yearly values deviated wildly from the average.

In addition, seasonal trends in some indicators were significantly different in magnitude. This is expected in some cases, for example the negative trend in mean length is twice as large in Q3 than in Q1, due to the growth of fish between Q1 and Q3. The spring survey in Q1 is carried out when most fish have just spawned so the lengths and masses of fish are smaller on average than in Q3 when younger fish have had time to grow (and thus their catchability by the trawl gear increased). Fish also move into and out of the region between seasons which could affect the overall mean size, but most of the difference in magnitude of trends is likely to be due to growth.

The LFI and the LSI had significantly more positive trends in Q3 than in Q1, even though values of the indicator were similar (LFI) or less overall (LSI) in Q3. Trends in the abundance spectrum slope showed an overall increase in the value of the slope, meaning the slopes became less steep over time. This is in contrast to previous studies where the abundance spectrum slope steepened over time in Q1 IBTS data (Rice & Gislason, 1996; Nicholson & Jennings, 2004), but those studies included earlier years where values of the slope were less steep. Q3 values were steeper than in Q1, but the trend was significantly greater in magnitude, suggesting a faster recovery in Q3.

5.3.3. Model selection example

The trend in the LFI in Q1 was split into two different linear trends, with a fixed split point at the year 2001 or 2000 (Figure 5.3). The negative trend was significant when the split point was 2001, but not 2000. The model testing was therefore carried out for the case where the LFI has two slopes split at 2001, and compared to the average trend over all years as shown in Figure 5.2. The split regression model was preferred in 72.5% of cases, meaning the model was a better fit than an overall linear regression, but not significantly better.

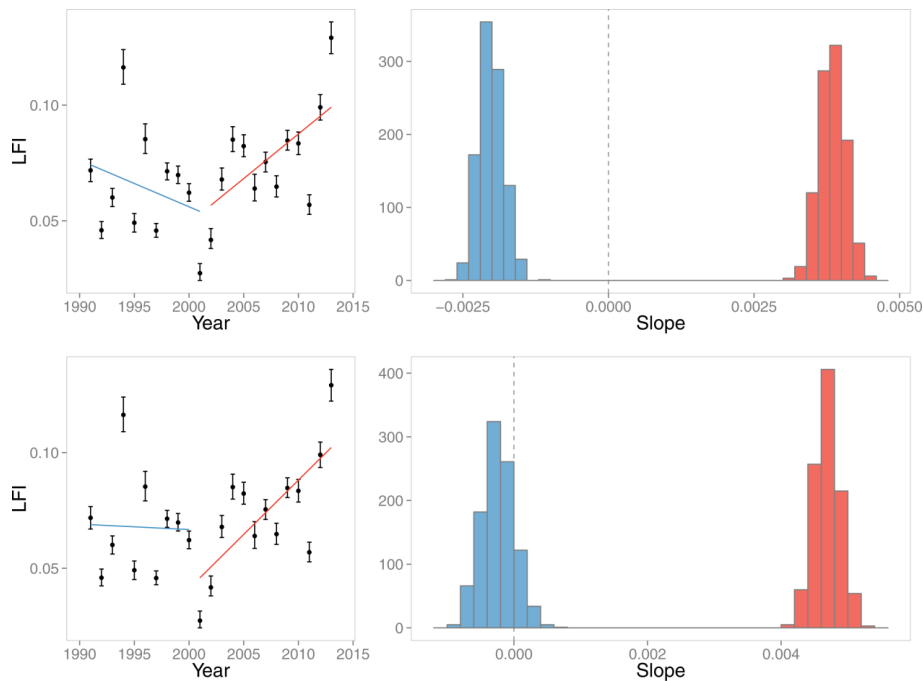


Figure 5.3: LFI values for Q1 plotted against year (1991-2013) with 95% confidence intervals as in Figure 5.2. Linear regression trends split at the year 2001 (first row) and the year 2000 (second row) are represented by blue lines for a negative trend and red lines for a positive trend. Histograms show the distribution of slopes for each trend (red for positive, blue for negative) calculated from the 1000 surrogate datasets.

5.4. Discussion

The resampling method developed in this chapter is an improvement on previous resampling based approaches that have been applied to trawl survey data. Its main strengths are that it is simple to understand and use, and easy to apply to many indicators and trends that can be calculated from the IBTS data. The approach respects the underlying structure of the survey

design in order to create surrogate datasets that more accurately represent repeated sampling effort. It is also compatible with any cleaning procedures or data aggregation that may be applied to the data, so has wide usability. The method as developed here is specific to the IBTS data, but could easily be used with any trawl survey design that includes raw catch data or where raw catch data could be calculated. This is an important consideration of the method, which is not only the parametric bootstrap approach adopted, but also the treatment of the data to obtain the values on which resampling is carried out.

5.4.1. Assessing statistical sampling variability using the methods

Results from applying the methods to a range of size-based community indicators showed that statistical sampling variability is generally not the main cause of year-to-year variability in indicator values calculated from the IBTS data. In addition, there was no seasonal difference in the amount of sampling variability present in the indicator values. Therefore indicator values are varying significantly between years, although the cause of that variation could be due to other types of sampling variation not detected by these methods. Trawl survey data often shows inter-annual variability in catch estimates because timings may vary between surveys, and locations can vary slightly from year to year. This type of sampling variation is known to affect indicator calculations (Trenkel & Rochet, 2003; Blanchard *et al.*, 2007), in addition to stochastic sampling variation. Changes in the relative timing and location of monitoring (e.g. with phenological and environmental change) means that individual hauls may vary in their catch depending on the animals that are available for sampling at that moment. This type of sampling variation in the data is more complex to account for as it is based on biological and not random processes, and further work is needed to determine levels of variability caused by such processes. However, it is still important to determine how much of the variation seen between years in indicator values is attributable to statistical sampling variation, and results here suggest it is not large compared to overall inter-annual variation when calculated over the whole region.

Trends in indicators, although calculated as average linear trends through indicator values that varied significantly in direction between years, were significant within statistical sampling variation. The power of trawl survey data to capture trends has been assessed before, and it

was found that longer time series (over 10 years) were needed to accurately describe trends because of the high variability in the data (Trenkel & Rochet, 2003; Nicholson & Jennings, 2004), which is reflected here in significant trends calculated over 23 years. Further analysis using the surrogate datasets could test how long a time series is needed before trends become non-significant due to statistical sampling variation. There was no seasonal difference in the levels of sampling bias, but trends differed significantly in magnitude between Q1 and Q3 for some indicators. This is an interesting application of the method, as the choice of period used for sampling has previously been shown to alter the perception of the structure and dynamics of a community (Trenkel, 2004). In the North Sea, Q1 data is usually used for the assessment of indicators, but results here suggest that using Q3 data instead may lead to a different interpretation of the performance of the indicator over time.

A number of previous studies have applied methods for calculating confidence intervals for trawl-survey-based indicators, mostly in the Celtic Sea. These studies adopted various bootstrapping methods that resampled by haul (Shepherd *et al.* 2012; ICES 2014), by length distribution (ICES 2007), or by abundance or biomass estimate (Trenkel & Rochet, 2003). These methods generally resulted in very wide confidence intervals that overlapped between years for the indicator(s) they were applied to, due to various shortcomings of the methods. The method used by Shepherd *et al.* (2012) was applied to values of the LFI in the Celtic Sea and subsequently used in an ICES report (2014) for the LFI in the North Sea. They used a non-parametric bootstrapping approach that resampled among hauls with replacement. This method ignored the spatial structure of the trawl survey sampling design by creating surrogate datasets with varying spatial distributions and biases depending on which hauls were included. Resampling hauls with replacement also means some hauls will be sampled more frequently than others, thus confidence limits are likely to be biased by hauls with particularly large or unusual catches (Smith, 1997). Prior to the LFI application, ICES (2007) had described a non-parametric bootstrapping procedure for Database of Trawl Surveys (DATRAS) data (including the IBTS) that resampled within hauls. This method retained the length distributions of a species such that any stochastic variation in numbers of individuals caught within a species or length category in a haul was not accounted for by the resampling. In addition, for the IBTS, because relatively few hauls are carried out within each stratum,

they recommended that hauls be pooled into larger sub-regions of the North Sea which meant that not only was the spatial resolution of the survey removed in the resampled data, but that local community structure was also lost. Finally, the methods used by Trenkel and Rochet (2003) for the Celtic Sea trawl survey data included parametric bootstrapping based on a lognormal or gamma distribution, which is similar to the methods developed in this chapter. However, their approach used individual estimates of abundance or biomass, which meant the data had already been treated before being resampled and thus was restricted to use with indicators based on those particular abundance and biomass estimates. The resampling methods developed in this chapter address all of these shortcomings, and are thus more useful for general application.

5.4.2. Limitations and suggestions for further testing of the methods

Further work needs to be done to assess the performance of the resampling approach compared to other methods. A few studies exist that compare bootstrap methods for assessing uncertainty in fisheries data (Smith & Gavaris, 1993; Smith, 1997; Patterson *et al.*, 2001; Hoyle & Cameron, 2003). The first (Smith & Gavaris 1993) compared the accuracy of abundance methods using bottom trawl survey data in the North West Atlantic. They modified bootstrapping methods to resample from the data and compared that to a parametric bootstrap using a lognormal distribution, which gave similar results. In a later study, three bootstrapping methods for North American groundfish trawl surveys, with methods appropriate to stratified sampling, were compared, including parametric and non-parametric (Smith 1997). It was determined that non-parametric bootstrapping is not a valid method for complex survey designs and stratified random designs because the sampling intensity may vary between strata, and sampling with equal probability within each stratum means that not all aspects of the sampling scheme are captured. This should not generally affect the IBTS because sampling is supposed to be homogenous across the spatial grid used, however there is some variation in the number of hauls carried out in each location from year to year. The use of a parametric bootstrap is also recommended for calculating confidence intervals from large ecological datasets by Crowley (1992). Thus, the parametric bootstrap is likely to be appropriate for the IBTS over the non-parametric bootstrap, but methods other than

bootstrapping could have been applied to assess significance. For example, permutation testing could have been carried out to assign a p-value to the difference in indicator values between years, or to trends, but the applications of the method are more limited. One advantage of a p-value over confidence intervals would be to increase ease of interpretation for management; confidence intervals applied to indicator values are simple to interpret when comparing values year-on-year, but are less easy to interpret when applied to a trend. However, it would also increase complexity as users would be required to carry out the statistics on each trend they wanted to analyse. The main advantage of bootstrapping is that it creates surrogate datasets which are straightforward to create and only require the user to repeat their existing analysis for each surrogate. The parametric bootstrap assesses sampling variability in trawl survey data in an appropriate way by incorporating it at the level of each haul which preserves the sampling structure of the data, and the resulting confidence intervals are simple to apply and interpret for a wide variety of applications.

One disadvantage of the parametric bootstrap, however, is that it assumes an underlying statistical distribution of the data. A non-parametric bootstrap would remove the need for assumptions to be made about the distribution of the data, but has other limitations, as discussed previously. Both Smith (1997) and Patterson *et al.* (2001) suggested that care should be taken when using bootstrap methods on surveys of complex designs, and when choosing the underlying statistical distribution to use in parametric bootstrapping. The Poisson distribution was chosen for the parametric bootstrap because it is typically used for count data and is appropriate for the IBTS data for a few reasons. Firstly, the Poisson distribution has only one parameter, the mean or expected number of counts (λ) in a given time period, which allows the count value of the catch per species-length category in each haul to be used as the resampling unit. Secondly, the distribution is discrete, and bounded on the left by zero, ensuring that resampled catch values are positive integers as expected. The resampled values can take any positive integer value since the distribution has no upper limit, but the probability of obtaining values far from the mean is unlikely; at small values of λ the distribution skews right but as λ increases it resembles the shape of the normal distribution. In addition, any species-length category can be resampled as zero, although it is unlikely for those with higher catch rates, so rare species or outliers in size may be absent in the surrogate

datasets. These properties of the Poisson distribution make it simple to apply, and suitable for assessing sampling variability in the number of fish caught in a trawl survey. However, some assumptions made about the distribution of fish in the trawl path may not hold for the IBTS data. The variance of the Poisson distribution is the same as the mean, which assumes a random spatial fish distribution, but some fish species may exhibit schooling behaviour and follow a non-Poisson distribution (Trenkel & Skaug, 2005). This assumption should be further tested and the data compared to other possible distributions to assess the validity of using a Poisson distribution. Another assumption is that the number of fish in each species-length category is independent, but it is likely that the presence or absence of individuals of one species or size will influence the presence or absence of individuals of another species or size due to predation, competition, or other behaviour. These behavioural traits, including schooling of fish, would need to be incorporated into a more complex resampling scheme in order to more accurately replicate the IBTS data, reducing the ease of its application to trawl survey data for management purposes.

The trends examined in this chapter were limited to linear trends. Fulton *et al.* (2005) suggested that for indicators to be informative, they should observe a linear correlation with ecological attributes. However, Houle *et al.* (2012) found that non-linear responses are also important because the indicators they studied, including the LFI, didn't show a proportional change with a reduction of fishing effort over time. Curved fits have been applied to trends in indicators in other studies (Trenkel & Rochet, 2003; Houle *et al.*, 2012) and further analyses could assess this for the IBTS data using the surrogate datasets to assign confidence. This further work could extend to the model testing approach that was applied as another use of the resampling methods. Results illustrated the potential for model testing by showing that a split slope model was preferred to an overall linear slope for the LFI in Q1, as determined in other work (Engelhard *et al.*, 2014). Being able to compare models using the surrogate data may be a more appropriate method for assessing trends based on trawl survey data, and incorporating methods for non-linear models would offer further potential. However, the model testing approach suggested here is probably not optimal, and needs to be further developed and compared to other model testing approaches such as AIC to test performance (Babu, 2011).

5.4.3. Conclusions

Comparison of indicator values to previous years is necessary to understand the response of a community to management (Rossberg, 2013), however, this is difficult when estimates of significance or confidence are not reported. I have developed a method that allows confidence intervals to be calculated for almost any indicator derived from trawl survey data, which is widely applicable and simple to implement. Resampling methods have previously been applied to fisheries data, but the wide variety of methods that have been used before are either complex or inappropriate. The bootstrapping approach adopted here more accurately replicates repeated sampling effort and significance can be assessed at smaller spatial scales or for different components of the data, leading to a broader range of applications. The ease of application should be appealing to fisheries management because it is understandable and the resulting significance values are easy to interpret.

Although the resampling method has limitations, such as not capturing other types of sampling variation in the fish community related to variation in survey timings and locations, it enables statistical sampling variation to be taken into account when assessing indicators. Testing of the method is needed to understand the effect of the assumptions made, and alternative approaches could be considered such as choosing a different distribution for the parametric bootstrap, or using different methods for calculating confidence intervals (Smith, 1996). Further uses of the method for assessing trends in indicators are not fully developed, but have potential to allow different trends to be simply and meaningfully assessed. The method depends on trawl survey data where the true number of individuals caught in each species-length category is available in the data or able to be calculated (i.e. raw data is available and not just aggregated or corrected data). It also has limited use for assessing significance of some diversity indices such as species richness, as rare species not caught by the trawl gear cannot be accounted for. However, the surrogate datasets produced using the resampling method allow potential users to apply significance to almost any size or abundance based indicator, for use with whichever cleaning methods or subset of the data they require. This is a valuable tool for advocating adoption of these types of methods to more meaningfully interpret and assess performance of management indicators.

Chapter 6. Discussion

The aims of the thesis were to investigate the effects of human impacts on community size structure in aquatic ecosystems, and to understand how averaged trends in size-based indicators are composed of effects at different levels or across smaller scales. The approaches I took in the thesis to do this revealed several important results that have implications for further study of community responses to anthropogenic change, and for management of marine systems. This section will summarise main results from previous chapters, and suggest ideas for further work.

6.1. Impact of warming on community structure

Most studies of the effects of temperature on body size focus on just a few species. Chapter 2 addressed this by studying the effects of warming on a natural diatom community, and decomposed the community level effect to determine whether intraspecific or interspecific effects drove the overall patterns. The work went beyond previous studies by considering the entire range of species in the community, and found that diatoms are an important exception to temperature-size rules at both the intraspecific and community level, undermining the supposed generality of Bergmann's and James' rules. Further, the response at the community level was determined largely by community-compositional shifts, and not intraspecific effects, which were heterogeneous and showed no overall trend. The temperature range of the streams in the study system was much larger than the expected increases in global or even polar temperatures due to climate change, and no overall shift in body size was found. However, the results still highlight the likely mechanisms of community response to warming, which is by shifts in community composition, rather than intraspecific changes in body size. The results demonstrated here suggest that future studies of temperature effects on communities should consider the responses of the entire community in order to understand the full impact that increased warming is likely to have on community size structure.

The methods used in Chapter 2 allowed the relative contributions of intraspecific versus interspecific effects to be determined. Similar methods could be applied to other data, including the IBTS trawl survey data used in the analyses in later chapters of the thesis. Temperature-size responses have been assessed for fish in marine ecosystems and found that fish decrease in size with warming (Cheung *et al.*, 2012), or decrease in asymptotic size (Baudron *et al.*, 2014). The modelling approach used by Cheung *et al.* (2012) predicted that half of the future warming-induced reduction in body size would be due to changes in distribution and abundance, and the other half changes in physiology. Some fish species have been shown to shift in distribution due to climate in the North Sea, both northwards and with depth (Dulvy *et al.*, 2008; Engelhard *et al.*, 2014; Rutterford *et al.*, 2015). The study by Rutterford *et al.* (2015) used the IBTS data to inform a predictive model that found that future fish distributions are likely to be constrained by depth in warming seas, and not shifted northwards. A more empirical approach could be applied to the IBTS data to understand how community body size, rather than species, has changed with warming in the North Sea over the last 30 years. However, the effects of fishing would need to be taken into consideration, and the approach from Chapter 2 developed to partition responses based on climate and fishing.

6.2. Trends in marine community indicators and implications for management

The general approach of decomposing an overall trend into component parts that was taken in Chapter 2 was also applied in Chapter 3. Trends in the large fish indicator (LFI) were decomposed into species and spatial contributions, and similarly to Chapter 2, results showed that the overall community trend was an aggregation of heterogeneous contributions. Important commercial species showed differing contributions to trends in the LFI, and some species, including cod, switched in the direction of their contribution between seasons. The magnitude of species contributions also varied significantly, with just a few species contributing to the overall trend. The LFI may not be an appropriate indicator for assessing the state of the community if the indicator trend can be so greatly influenced by a small

number of species. This was further supported in results from the spatial decomposition of trends, where only a few grid cells determined the overall trend.

Results from Chapter 3 have implications for management of the North Sea fish community, as reported trends in the LFI appear as though the whole region is recovering when in fact they may just be reflecting the recovery of a few species in a few small regions. This suggests that headline indicators should always be accompanied by their component indicators so that more informed management decisions can be made. Further work could develop and identify appropriate component indicators for other headline indicators, such as Chapter 3 did for the LFI. This thesis concentrated on size-based indicators, but the problem of aggregation in community metrics has previously been highlighted for diversity indices (King & Baker, 2010). That study found that aggregate community diversity indices were not as responsive to environmental gradients due to mixed signals from the contributing taxa, and they also advocated the need to understand responses of species that contribute to the community indicator.

Chapter 4 investigated changes in the structure of the North Sea fish community abundance spectrum over time. Significant deviations from linearity were present in the abundance spectrum. These deviations were consistent over time, and comprised both stationary and transient bumps in the spectrum. As the slope of the spectrum decreased over time, stationary bumps were still present and followed the same basic pattern. The size of the stationary bumps could therefore be used as another indicator of community change, alongside the slope of the spectrum. Transient bumps were detected in the spectrum, as predicted by size spectrum theory based on perturbations caused by fishing, and moved through the spectrum towards larger masses of fish. The bumps were detected over a small range of masses but were significant, and the approach used allowed both the size of the bump and its speed of propagation to be determined. The transient bumps detected may also have applications in fisheries management, as knowing the speed of propagation would allow pulses in abundance in small size classes to be tracked and potentially predict the future abundance of fish in larger size classes.

A possible further analysis was suggested in the Discussion of Chapter 4 that would allow the determination of the species driving the propagation of the bumps, categorised by their asymptotic size. Understanding which species (asymptotic sizes) are driving the bumps would offer further insight into the dynamics of the abundance spectrum, and again provide useful information that is usually lost when considering aggregated community indicators. Chapter 3 results illustrated that spatial aggregation could also confound interpretation of community indicators. The analyses in Chapter 4 were calculated over the region of the whole North Sea, but as the IBTS data is spatially structured, abundance spectra could be computed at smaller spatial scales. Deviations from linearity in the abundance spectrum may only appear at larger spatial scales, or stationary and transient bumps may have different characteristics in different regions depending on the fish populations occupying them. Detection of transient bumps was also aggregated over time. Trends can only be detected from trawl survey data over relatively long time series (Nicholson & Jennings, 2004), but Worm & Branch (2012) suggest that it is important to look at how exploited populations and communities respond to more recent perturbations caused by the reduction of fishing effort. A time lagged approach as used in Chapter 4 to detect transient bumps could be applied over shorter time periods to test if there is a difference in response, and the resampling based methods would allow significance of trends to be determined.

6.3. Resampling based methods for assessing uncertainty in community indicators

The resampling method, which was developed specifically for the trawl survey data to obtain surrogate datasets, proved useful for determining the significance of component trends calculated from disaggregated data in Chapter 3, and was crucial for detecting deviations from linearity in the abundance spectrum in Chapter 4. In Chapter 5, these methods were developed further and advocated as a simple approach that could easily be adopted by groups working with the IBTS data that need to be able to assess significance of indicator values and trends. Specific results from this chapter were not extensive but illustrated the application of the methods. Statistical sampling variation was found to be small in comparison

to other inter-annual variation in indicator values, and this was consistent across a range of indicators, and between seasons. However, the method is limited to detecting only statistical variation caused by stochastic processes during the survey, and not other sampling variation that occurs because of variation in timings and locations of surveys, or phenological events that alter the availability of fish when the trawl is carried out. Further work would need to be done to assess this more complex type of variability in the data.

Analysis of trends in indicators in Chapter 5 showed that average linear trends were significantly different in magnitude between seasons. Seasonal variability has been shown to affect trends in indicators as much as the difference between trawled and protected areas does, in a study carried out in the Mediterranean (Sweeting *et al.*, 2009). Chapter 3 results also showed a significant seasonal difference in not only the overall LFI trend, but in the contributions of species between seasons. This seasonal variability was only able to be detected as significant by using the surrogate datasets.

An initial application of the surrogate datasets to model testing was applied to trends in the LFI, and found that a linear regression split at the year 2000 was a better, but not significantly better, fit to the data than an overall average trend. Using the surrogate datasets for model testing has potential, but more development is needed. The resampling method itself also requires further testing against other resampling methods to assess its performance. However, the parametric bootstrapping approach has distinct advantages over previous methods of applying confidence intervals to indicators calculated from trawl survey data. It is appropriate for the structure of the data, and preserves the spatial design of the survey, allowing spatial components to be assessed for significance as applied in Chapter 3 for the LFI. It is also simple to use, and applicable to almost any indicator that can be calculated from the IBTS data. Chapters 3 and 4 used the methods to reveal useful and interesting results that have wider implications for the assessment of indicators of size structure in the North Sea fish community. Chapter 5 further advocates the use of the method when comparing indicator values and trends. The surrogate datasets were needed for the particular analyses applied in this thesis, but are also potentially useful for wider use in management and fisheries research.

6.4. Conclusion

Assessing the effects of human impacts on community size structure requires the use of size-based community indicators. Results have shown that such indicators are likely to be misinterpreted if both species and community levels of the indicator are not considered simultaneously. Other components such as spatial and temporal aggregation are also likely to affect interpretation of indicator values and trends. The methods and approaches used in the thesis to decompose indicators and trends, to examine finer detail in the abundance spectrum, and to assess levels of sampling variation, have all allowed for more meaningful interpretation of community indicators. These approaches could be adopted more widely to provide more detailed assessments of the responses of communities to climate change and fishing.

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Appendices

Appendix A

A.1. Environmental data in streams

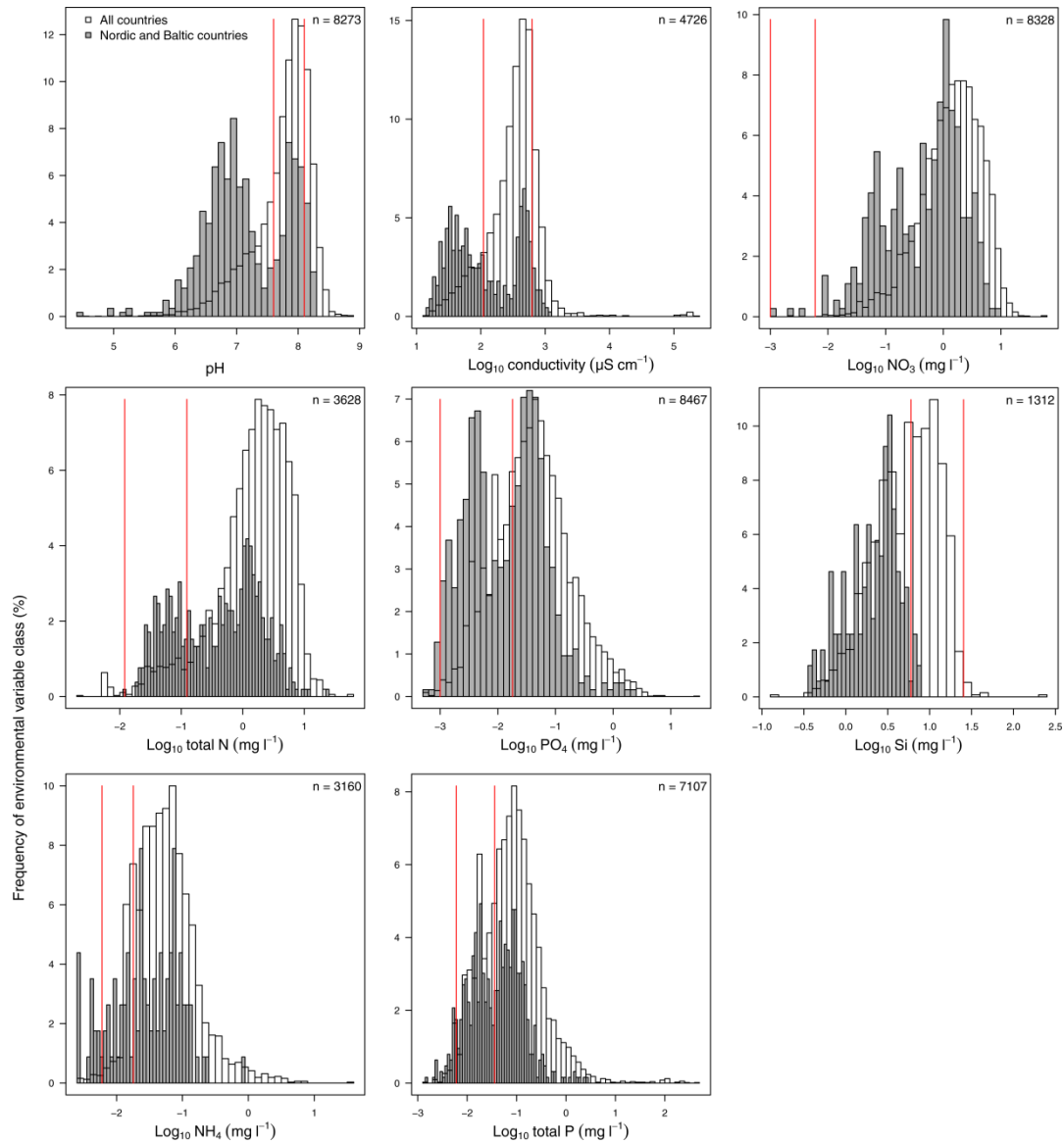


Figure A.1: Comparison of the range of abiotic variables at Hengill, Iceland (red lines) to observed ranges in 32 other European countries (white bars). Values for 8 Nordic and Baltic states are also shown (grey bars) for a more direct comparison with northern latitude ecosystems. Data on water chemistry from 11,251 running waters from across Europe (sample sizes for each variable are given on each panel) were collated from the European Environment Agency (EEA) database (extracted from databases held at <http://www.eea.europa.eu/data-and-maps> on 1st April 2013). The figure

highlights how Hengill falls well within the range of abiotic variables found across Europe, with only nitrate occurring at the low end of this continental-level gradient.

Table A.1: Table showing the values for abiotic variables measured in each stream in August 2008, ordered by mean stream temperature. Temp = temperature in °C; pH is unitless; Cond = conductivity in $\mu\text{S cm}^{-1}$; all other environmental parameters are given in mg l^{-1} . DOC = dissolved organic carbon; DO = dissolved oxygen; TN = total nitrogen; TP = total phosphorous.

Stream	Temp	pH	Cond	DOC	DO	NH ₄	NO ₃	TN
a10	5.1	7.7	129	0.314	11.7	0.006	0.002	0.054
b13	6.1	7.6	201	0.294	11.1	0.018	0.001	0.114
c7	8.2	7.6	110	0.208	11.4	0.010	0.001	0.012
d14	9.7	8.1	254	0.403	10.7	0.010	0.003	0.123
e4	12.7	7.7	153	0.465	10.7	0.008	0.006	0.041
f11	12.8	8.0	624	0.581	9.9	0.009	0.001	0.085
g16	14.5	7.9	249	0.318	11.1	0.015	0.003	0.068
h12	15.5	7.9	223	0.618	8.1	0.012	0.005	0.098
i9	18.1	8.1	262	0.263	8.5	0.008	0.004	0.036
j6	21.0	8.1	283	0.317	8.6	0.011	0.002	0.016
k5	21.3	8.0	282	0.427	8.0	0.006	0.006	0.032
l1	22.7	7.8	294	0.767	8.2	0.009	0.003	0.062
m3	23.7	7.9	275	0.226	7.1	0.013	0.004	0.019
n8	24.6	8.1	300	0.330	6.8	0.009	0.006	0.014

Stream	PO ₄	TP	Ca ²⁺	K ⁺	Mg ²⁺	Na ²⁺	Si	Cl ⁻	SO ₂ ⁴⁻
a10	0.010	0.018	20.1	0.3	4.7	11.0	6.0	6.6	3.8
b13	0.001	0.006	28.4	0.5	8.9	15.1	9.9	7.2	5.9
c7	0.012	0.025	14.1	0.5	4.1	10.6	7.0	7.7	1.5
d14	0.001	0.010	35.9	0.5	8.5	17.5	11.4	6.4	5.8
e4	0.001	0.008	20.3	0.3	5.1	7.4	9.8	7.6	2.9
f11	0.001	0.015	32.4	2.5	29.5	123.8	25.4	5.7	0.2
g16	0.003	0.020	30.5	1.1	8.8	22.0	15.7	6.7	5.8
h12	0.001	0.011	25.1	1.4	7.7	19.6	17.6	7.0	2.6
i9	0.018	0.036	26.9	1.5	6.6	34.6	17.9	6.6	2.7
j6	0.007	0.028	29.8	2.2	6.4	37.0	19.7	6.5	4.6
k5	0.002	0.019	31.1	2.2	6.7	36.8	19.8	6.3	4.8
l1	0.003	0.015	30.8	1.4	7.6	29.0	18.6	6.5	4.9
m3	0.009	0.028	29.5	1.8	6.5	29.9	19.6	6.4	6.4
n8	0.012	0.031	28.2	2.6	5.5	37.5	20.2	6.3	3.5

Table A.2: Summary of correlation analysis results for mean stream temperature tested against 16 other abiotic variables measured in the fourteen streams. Cond = conductivity; DOC = dissolved organic carbon; DO = dissolved oxygen. Correlation coefficients (r) are Pearson's correlation coefficients. Corrected p-values are Bonferroni corrected and stars represent levels of significance: p<0.05 (*), p<0.01 (**), p<0.001 (***). (***). P-values were obtained making the standard assumptions of Pearson correlation, but results were similar when p-values were instead calculated by comparing correlation results from data to results from 10000 appropriately randomised datasets.

Abiotic variable	p-value	r	Corrected p-value
pH	0.0255*	0.5927	0.4079
Cond	0.2643	0.3203	1
DOC	0.5218	0.1871	1
DO	2.76e-06***	-0.9219	0.00004***
NH ₄	0.5973	-0.1548	1
NO ₃	0.0346*	0.5668	0.5530
Total N	0.0569	-0.5196	0.9099
PO ₄	0.5096	0.1925	1
Total P	0.0454*	0.5418	0.6806
Ca ²⁺	0.1529	0.4032	1
K ⁺	0.0012**	0.7736	0.0187*
Mg ²⁺	0.7198	-0.1054	1
Na ²⁺	0.4727	0.2093	1
Si	0.0016**	0.7596	0.0260*
Cl ⁻	0.1170	-0.4383	1
SO ₂ ⁴⁻	0.5183	0.1887	1

A.2. Diatom species and size calculations

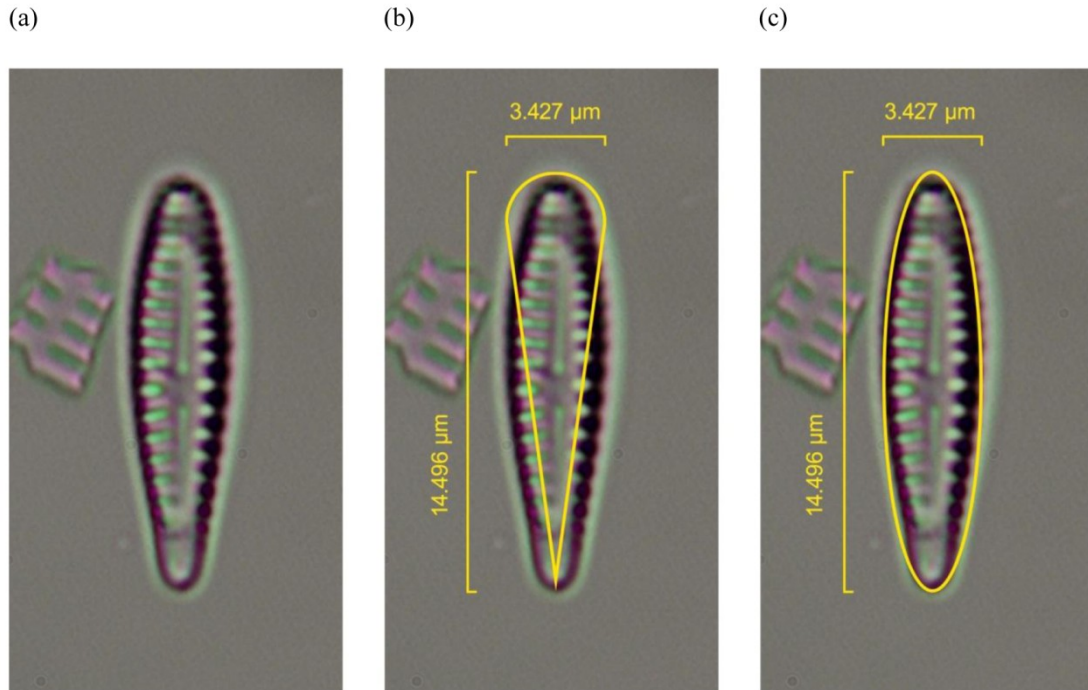


Figure A.2: Photographs illustrating shape approximations of a diatom species (*Rhoicosphenia abbreviata*) that showed an unusual valve outline in the Icelandic streams: a) photograph of one individual from stream n8; b) the same photograph with the suggested shape approximation in Hillebrand *et al.*, (1999) and c) the photograph with the shape approximation used in this study. For every diatom species that showed a shape deviation from the generic shape approximation described in Hillebrand *et al.* (1999) a more appropriate shape approximation was decided for that species using standard shapes that could easily be calculated using width and length measurements, such as the ellipse shown in (c). To be certain that the new shape approximations were more accurate, the new and old shape approximations were compared with the actual area of the diatom valve for a sample of individuals (one individual per species per stream; Table A.3). Actual valve area was calculated in Image J using the outline of the valve; valve area using the shape approximations was calculated using valve width and length measurements.

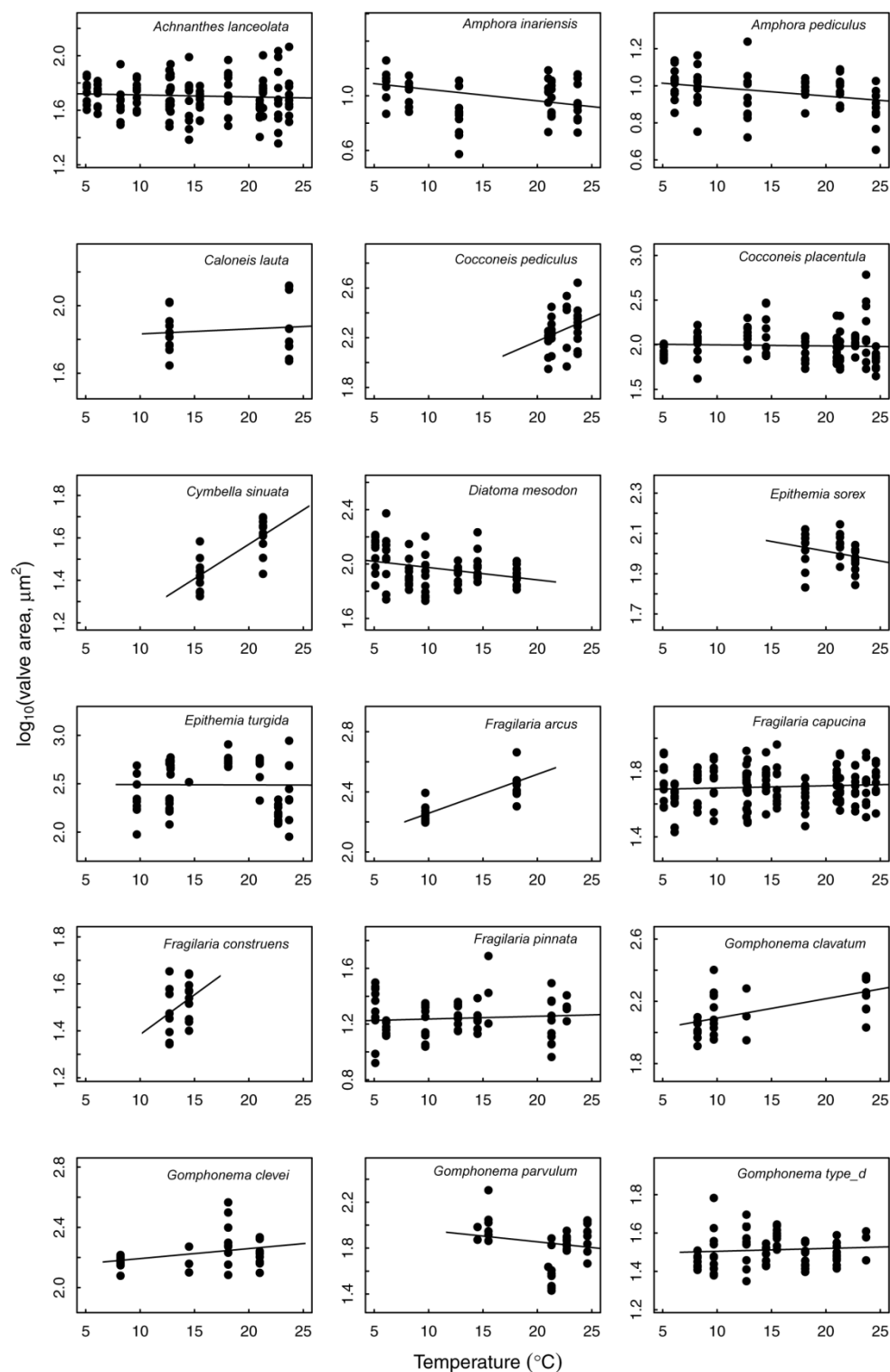
Table A.3: Actual diatom valve area compared with estimates of valve area using linear measurements and shape approximations, for diatom species with an unusual valve shape. Thirteen species showed an unusual valve shape compared to that described for their genus in Hillebrand *et al.* (1999). For twelve of these species the new shape approximation was on average a better estimate of the actual valve area than when using the original shape approximation. For one species (*Eunotia bilunaris*) it was not possible to use width and length measurements to calculate the area using the original shape approximation, but the new area shape approximation is a good estimate of the actual area for that species.

Species	Stream	Actual valve area (μm^2)	Width (μm)	Length (μm)	Original volume shape approximation	Original area shape approximation	Original estimated area	New area shape approximation	New estimated area	Best shape approximation
<i>Eunotia bilunaris</i>	b13	51.26	3.33	16.10	Sickle shaped prism	-	-	Rectangle	53.53	-
<i>Eunotia bilunaris</i>	m3	49.27	2.66	22.26	Sickle shaped prism	-	-	Rectangle	59.14	-
<i>Gomphonema angustatum</i>	i9	71.74	5.35	17.81	Gomphonemoid	Petal	51.78	Ellipse	74.90	New
<i>Gomphonema clavatum</i>	c7	105.77	5.18	24.88	Gomphonemoid	Petal	68.30	Ellipse	101.27	New
<i>Gomphonema clavatum</i>	m3	233.87	8.50	35.36	Gomphonemoid	Petal	256.66	Ellipse	236.03	New
<i>Gomphonema clavatum</i>	e4	139.35	6.57	28.35	Gomphonemoid	Petal	160.10	Ellipse	146.34	New
<i>Gomphonema clavatum</i>	d14	96.17	5.70	20.89	Gomphonemoid	Petal	99.39	Ellipse	93.57	New
<i>Gomphonema clevei</i>	c7	175.36	6.14	33.36	Gomphonemoid	Petal	107.78	Ellipse	160.85	New
<i>Gomphonema clevei</i>	i9	241.87	6.82	46.86	Gomphonemoid	Petal	166.31	Ellipse	250.82	New
<i>Gomphonema clevei</i>	j6	210.66	6.56	39.85	Gomphonemoid	Petal	235.28	Ellipse	205.32	New
<i>Gomphonema clevei</i>	g16	175.59	6.43	38.44	Gomphonemoid	Petal	222.12	Ellipse	194.19	New
<i>Gomphonema parvulum</i>	n8	92.26	5.67	24.43	Gomphonemoid	Petal	73.81	Ellipse	108.75	New
<i>Gomphonema parvulum</i>	k5	28.23	3.65	9.92	Gomphonemoid	Petal	20.01	Ellipse	28.45	New
<i>Gomphonema parvulum</i>	l1	65.53	5.16	18.22	Gomphonemoid	Petal	50.77	Ellipse	73.79	New
<i>Gomphonema parvulum</i>	j6	42.86	4.22	13.88	Gomphonemoid	Petal	47.76	Ellipse	46.00	New
<i>Gomphonema parvulum</i>	h12	68.54	5.02	18.18	Gomphonemoid	Petal	75.97	Ellipse	71.69	New
<i>Gomphonema parvulum</i>	g16	91.36	6.03	19.70	Gomphonemoid	Petal	96.79	Ellipse	93.39	New
<i>Gomphonema type D</i>	c7	32.33	3.59	10.67	Gomphonemoid	Petal	21.03	Ellipse	30.13	New
<i>Gomphonema type D</i>	i9	28.44	3.32	10.45	Gomphonemoid	Petal	18.91	Ellipse	27.24	New
<i>Gomphonema type D</i>	m3	36.86	4.40	12.84	Gomphonemoid	Petal	44.73	Ellipse	44.37	New
<i>Gomphonema type D</i>	e4	42.28	3.90	12.64	Gomphonemoid	Petal	40.03	Ellipse	38.68	Old
<i>Gomphonema type D</i>	j6	33.98	3.64	10.93	Gomphonemoid	Petal	31.73	Ellipse	31.24	Old
<i>Gomphonema type D</i>	h12	46.07	4.44	13.12	Gomphonemoid	Petal	46.26	Ellipse	45.73	Old
<i>Gomphonema type D</i>	d14	28.47	3.29	10.69	Gomphonemoid	Petal	28.57	Ellipse	27.59	Old
<i>Gomphonema type D</i>	g16	31.30	3.71	10.47	Gomphonemoid	Petal	30.50	Ellipse	30.53	New
<i>Meridion circulare</i>	m3	109.46	5.47	26.48	Gomphonemoid	Petal	126.77	Ellipse	113.86	New
<i>Meridion circulare</i>	e4	125.38	5.21	32.75	Gomphonemoid	Petal	154.08	Ellipse	133.95	New
<i>Meridion circulare</i>	a10	128.90	5.56	29.37	Gomphonemoid	Petal	144.56	Ellipse	128.29	New
<i>Meridion circulare</i>	h12	74.32	4.27	23.28	Gomphonemoid	Petal	88.32	Ellipse	78.05	New
<i>Meridion circulare</i>	d14	144.87	4.09	43.37	Gomphonemoid	Petal	167.07	Ellipse	139.18	New
<i>Meridion circulare</i>	g16	69.02	5.42	17.73	Gomphonemoid	Petal	78.33	Ellipse	75.55	New
<i>Nitzschia dissipata</i>	b13	93.26	4.60	27.57	Prism on parallelogram	Parallelogram	126.90	Ellipse	99.67	New
<i>Nitzschia dissipata</i>	e4	18.68	2.91	10.45	Prism on parallelogram	Parallelogram	30.39	Ellipse	23.87	New
<i>Nitzschia dissipata</i>	h12	77.34	3.78	25.51	Prism on parallelogram	Parallelogram	96.37	Ellipse	75.69	New
<i>Nitzschia dissipata</i>	d14	81.28	2.99	30.92	Prism on parallelogram	Parallelogram	92.58	Ellipse	72.71	New
<i>Nitzschia dissipata</i>	g16	64.44	3.40	24.48	Prism on parallelogram	Parallelogram	83.26	Ellipse	65.39	New
<i>Nitzschia fonticola</i>	e4	65.63	3.72	24.28	Prism on parallelogram	Parallelogram	90.21	Ellipse	70.85	New
<i>Nitzschia fonticola</i>	h12	34.54	2.61	16.29	Prism on parallelogram	Parallelogram	42.51	Ellipse	33.39	New
<i>Nitzschia inconspicua</i>	c7	13.71	2.76	6.23	Prism on parallelogram	Parallelogram	17.21	Ellipse	13.52	New
<i>Nitzschia inconspicua</i>	d14	14.63	2.70	7.20	Prism on parallelogram	Parallelogram	19.47	Ellipse	15.29	New
<i>Nitzschia inconspicua</i>	g16	20.55	2.54	9.11	Prism on parallelogram	Parallelogram	23.09	Ellipse	18.14	New
<i>Nitzschia palea</i>	l1	36.45	2.36	20.46	Prism on parallelogram	Parallelogram	48.37	Ellipse	37.99	New
<i>Nitzschia palea</i>	f11	33.30	2.38	17.08	Prism on parallelogram	Parallelogram	40.69	Ellipse	31.96	New
<i>Nitzschia palea</i>	m3	73.94	3.17	28.32	Prism on parallelogram	Parallelogram	89.78	Ellipse	70.51	New
<i>Nitzschia palea</i>	e4	47.67	2.60	25.91	Prism on parallelogram	Parallelogram	67.29	Ellipse	52.85	New
<i>Nitzschia palea</i>	j6	38.58	2.57	19.07	Prism on parallelogram	Parallelogram	49.09	Ellipse	38.55	New
<i>Nitzschia palea</i>	h12	120.40	3.66	37.55	Prism on parallelogram	Parallelogram	137.44	Ellipse	107.95	New
<i>Nitzschia palea</i>	d14	52.29	2.42	25.70	Prism on parallelogram	Parallelogram	62.17	Ellipse	48.83	New
<i>Nitzschia palea</i>	g16	45.95	2.54	23.78	Prism on parallelogram	Parallelogram	60.31	Ellipse	47.37	New
<i>Nitzschia paleacea</i>	k5	55.25	2.73	26.82	Prism on parallelogram	Parallelogram	73.25	Ellipse	57.53	New
<i>Nitzschia paleacea</i>	f11	38.67	2.13	20.94	Prism on parallelogram	Parallelogram	44.53	Ellipse	34.97	New
<i>Nitzschia paleacea</i>	l1	28.21	1.95	16.93	Prism on parallelogram	Parallelogram	33.06	Ellipse	25.97	New
<i>Nitzschia paleacea</i>	i9	27.73	2.73	14.19	Prism on parallelogram	Parallelogram	38.78	Ellipse	30.46	New
<i>Nitzschia paleacea</i>	m3	77.27	2.61	37.21	Prism on parallelogram	Parallelogram	97.27	Ellipse	76.39	New
<i>Nitzschia paleacea</i>	e4	64.57	2.15	35.34	Prism on parallelogram	Parallelogram	66.48	Ellipse	59.59	Old
<i>Nitzschia paleacea</i>	h12	32.64	1.96	22.75	Prism on parallelogram	Parallelogram	44.49	Ellipse	34.94	New
<i>Nitzschia paleacea</i>	d14	39.48	1.84	25.32	Prism on parallelogram	Parallelogram	46.63	Ellipse	36.62	New
<i>Nitzschia paleacea</i>	g16	50.46	2.24	29.30	Prism on parallelogram	Parallelogram	65.68	Ellipse	51.58	New
<i>Rhoicosphenia abbreviata</i>	n8	40.01	3.43	14.50	Gomphonemoid	Petal	26.51	Ellipse	39.01	New
<i>Rhoicosphenia abbreviata</i>	i9	106.48	4.98	26.95	Gomphonemoid	Petal	70.60	Ellipse	105.35	New
<i>Rhoicosphenia abbreviata</i>	k5	77.68	4.37	22.38	Gomphonemoid	Petal	51.60	Ellipse	76.77	New
<i>Rhoicosphenia abbreviata</i>	l1	49.28	3.21	20.41	Gomphonemoid	Petal	34.22	Ellipse	51.45	New
<i>Rhoicosphenia abbreviata</i>	m3	67.30	4.86	19.54	Gomphonemoid	Petal	80.67	Ellipse	74.64	New

Table A.4: Species found in the fourteen streams that were used for analysis, listed with their species authorities. Two taxa that were sampled could not be identified to species level. The first was called Gomphonema Type D; it is very likely that it belongs in the Gomphonema genus and is distinct from other Gomphonema species in the streams. The second was called Pinnularia spp.; it is very likely that it belongs in the Pinnularia genus, and it was only found in one stream.

Species	Authority
<i>Achnanthes grana</i>	Hohn & Hellermann
<i>Achnanthes lanceolata</i>	(Brébisson) Grunow
<i>Achnanthes minutissima</i>	Kützing
<i>Achnanthes stolidia</i>	(Krasske) Krasske
<i>Amphora inariensis</i>	Krammer
<i>Amphora ovalis</i>	(Kützing) Kützing
<i>Amphora pediculus</i>	(Kützing) Grunow
<i>Caloneis lauta</i>	Carter & Bailey-Watts
<i>Cocconeis pediculus</i>	Ehrenberg
<i>Cocconeis placentula</i>	Ehrenberg
<i>Cymbella minuta</i>	Hilse
<i>Cymbella sinuata</i>	Gregory
<i>Diatoma mesodon</i>	(Ehrenberg) Kützing
<i>Diploneis ovalis</i>	Hilse (Cleve)
<i>Epithemia sorex</i>	Kützing
<i>Epithemia turgida</i>	(Ehrenberg) Kützing
<i>Eunotia bilunaris</i>	(Ehrenberg) Mills
<i>Fragilaria arcus</i>	(Ehrenberg) Cleve
<i>Fragilaria capucina</i>	Desmazières
<i>Fragilaria construens</i>	(Ehrenberg) Grunow
<i>Fragilaria pinnata</i>	Ehrenberg
<i>Fragilaria virescens</i>	Ralfs
<i>Frustilia vulgaris</i>	(Thwaites) De Toni
<i>Gomphonema angustatum</i>	Kützing
<i>Gomphonema clavatum</i>	Ehrenberg
<i>Gomphonema clevei</i>	Fricke
<i>Gomphonema parvulum</i>	Kützing
<i>Gomphonema type D</i>	
<i>Melosira varians</i>	Agardh
<i>Meridion circulare</i>	(Greville) Agardh
<i>Navicula atomus</i>	(Kützing) Grunow
<i>Navicula cryptotenella</i>	Lange-Bertalot
<i>Navicula gallica</i>	(W. Smith) Lagerstedt
<i>Navicula minima</i>	Grunow
<i>Navicula placentula</i>	(Ehrenberg) Grunow
<i>Navicula tripunctata</i>	(O.F.Müller) Bory de Saint- Vincent
<i>Navicula variostrata</i>	Krasske
<i>Navicula viridula</i>	(Kützing) Kützing
<i>Nitzschia aequorea</i>	Hustedt
<i>Nitzschia dissipata</i>	(Kützing) Grunow
<i>Nitzschia fonticola</i>	Grunow (Grunow)
<i>Nitzschia inconspicua</i>	Grunow
<i>Nitzschia palea</i>	(Kützing) W. Smith
<i>Nitzschia paleacea</i>	Grunow
<i>Pinnularia spp.</i>	
<i>Rhoicosphenia abbreviata</i>	(Agardh) Lange-Bertalot
<i>Rhopalodia gibba</i>	(Ehrenberg) O. Müller
<i>Surirella angusta</i>	Kützing
<i>Synedra ulna</i>	Ehrenberg

A.3. Additional results: intraspecific



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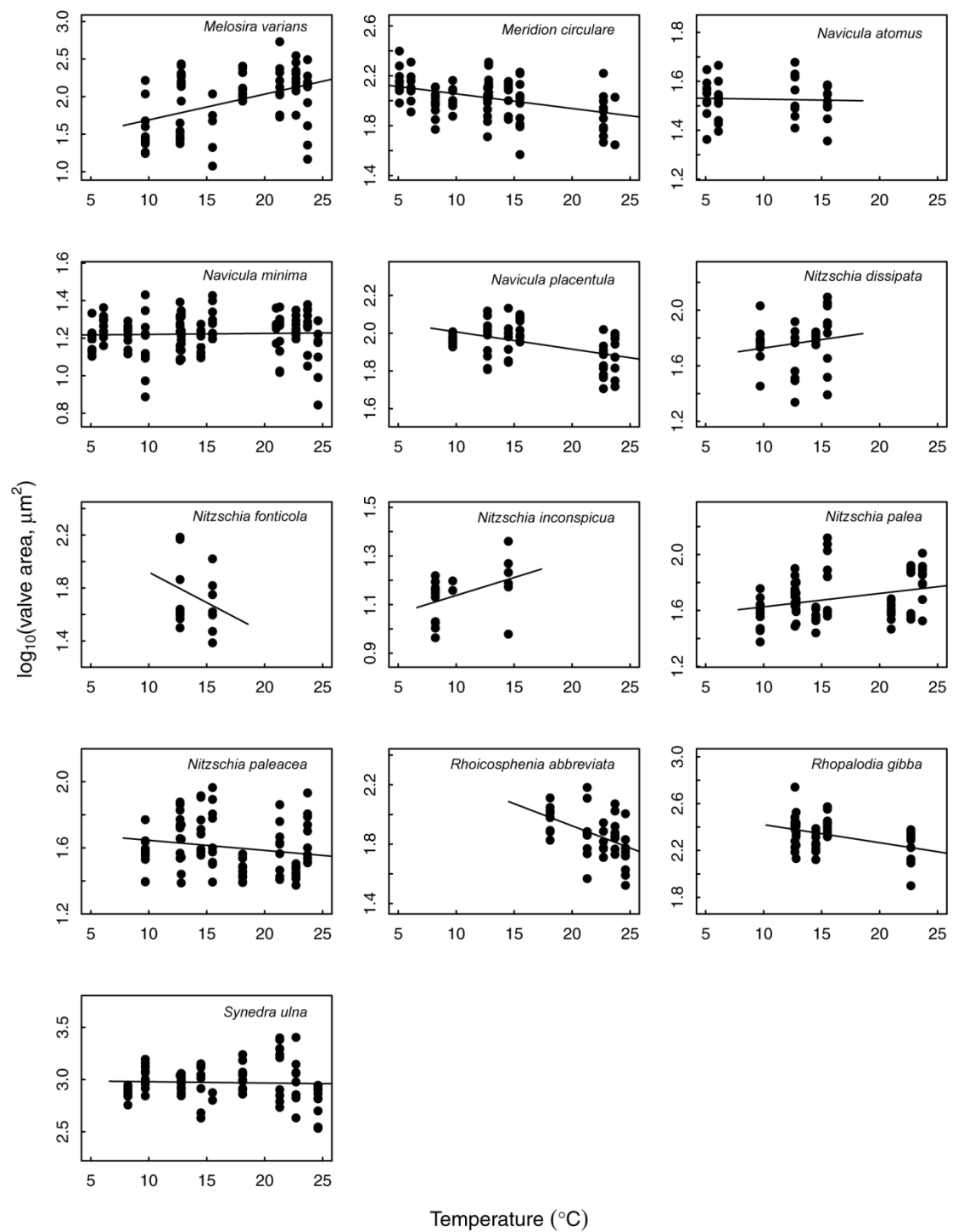


Figure A.3: Linear regression plots of temperature against $\log_{10}$ valve area for 31 diatom species that were present in at least 2 of the sampled streams.

Table A.5: Slopes and p-values from linear regressions of temperature against log₁₀ valve width for 31 species of diatom found in at least 2 of the sampled streams. Corrected p-values are Bonferroni corrected and stars represent levels of significance: p<0.05 (*), p<0.01 (**), p<0.001 (***).

Species	num. streams	Slope	R2	p-value	Corrected p-value
<i>Achnanthes lanceolata</i>	13	-0.0008	0.0088	0.2947	1
<i>Amphora inariensis</i>	6	-0.0021	0.0303	0.1957	1
<i>Amphora pediculus</i>	6	-0.001	0.0153	0.3456	1
<i>Caloneis lauta</i>	2	0.0036	0.0739	0.2464	1
<i>Cocconeis pediculus</i>	4	0.0204	0.0923	0.0760	1
<i>Cocconeis placentula</i>	10	-0.0006	0.0013	0.7169	1
<i>Cymbella sinuata</i>	2	0.0155	0.5588	0.0002***	0.0047**
<i>Diatoma mesodon</i>	7	-0.0017	0.0188	0.2578	1
<i>Epithemia sorex</i>	3	-0.0057	0.069	0.1770	1
<i>Epithemia turgida</i>	8	0.0004	0.0003	0.8836	1
<i>Fragilaria arcus</i>	2	0.0035	0.1931	0.0526	1
<i>Fragilaria capucina</i>	14	0.0022	0.0269	0.0527	1
<i>Fragilaria construens</i>	2	0.0102	0.0432	0.4076	1
<i>Fragilaria pinnata</i>	8	-0.0004	0.0022	0.7077	1
<i>Gomphonema clavatum</i>	4	0.0058	0.2936	0.0011**	0.0350*
<i>Gomphonema clevei</i>	4	0.001	0.0178	0.4598	1
<i>Gomphonema parvulum</i>	6	-0.0555	0.524	0.00000028***	0.0000087***
<i>Gomphonema type</i>	D	8	0.0039	0.1473	0.0010**
<i>Melosira varians</i>	8	0.0171	0.1896	0.0001***	0.0029**
<i>Meridion circulare</i>	10	0	0	0.9866	1
<i>Navicula atomus</i>	4	0.0001	0.0001	0.9531	1
<i>Navicula minima</i>	13	0.0013	0.0236	0.0872	1
<i>Navicula placentula</i>	6	-0.0037	0.2454	0.0001***	0.0028**
<i>Nitzschia dissipata</i>	4	0.002	0.0046	0.7036	1
<i>Nitzschia fonticola</i>	2	-0.0227	0.0553	0.3634	1
<i>Nitzschia inconspicua</i>	3	0.0004	0.0009	0.9049	1
<i>Nitzschia palea</i>	8	0.0008	0.0035	0.6027	1
<i>Nitzschia paleacea</i>	9	-0.0013	0.0067	0.4609	1
<i>Rhoicosphenia abbreviata</i>	5	-0.0118	0.2238	0.0009***	0.0279*
<i>Rhopalodia gibba</i>	5	-0.0032	0.0484	0.1288	1
<i>Synedra ulna</i>	10	-0.0009	0.0081	0.4177	1

Table A.6: Intraspecific analysis for abiotic variables pH, Si, K, NO₃, NH₄, Total N, PO₄ and Total P. Slopes and p-values are from linear regressions of the abiotic variable against mean log₁₀ valve area, for 31 species of diatoms found in at least 2 of the sampled streams. Corrected p-values are Bonferroni corrected and stars represent levels of significance: p<0.05 (*), p<0.01 (**), p<0.001 (***).

Abiotic variable	Species	num. streams	Slope	R2	p-value	Corrected p-value
pH	<i>Achnanthes lanceolata</i>	13	-0.0018	0	0.9794	1
	<i>Amphora inariensis</i>	6	-0.3956	0.1979	0.00053***	0.0157593*
	<i>Amphora pediculus</i>	6	-0.1366	0.0758	0.0332*	0.9974817
	<i>Caloneis lauta</i>	2	0.1597	0.0123	0.641	1
	<i>Cocconeis pediculus</i>	4	-0.4741	0.1075	0.0545	1
	<i>Cocconeis placentula</i>	10	-0.1708	0.0207	0.1528	1
	<i>Cymbella sinuata</i>	2	1.8849	0.5866	0.000083***	0.0024798**
	<i>Diatoma mesodon</i>	7	-0.1668	0.0642	0.0343*	1
	<i>Epithemia sorex</i>	3	0.2295	0.1404	0.0495*	1
	<i>Epithemia turgida</i>	8	0.8731	0.258	0.000006***	0.0001842***
	<i>Fragilaria arcus</i>	2	NA	0	NA	NA
	<i>Fragilaria capucina</i>	14	0.0318	0.0026	0.5481	1
	<i>Fragilaria construens</i>	2	0.3043	0.097	0.2083	1
	<i>Fragilaria pinnata</i>	8	-0.024	0.0009	0.8124	1
	<i>Gomphonema clavatum</i>	4	0.2695	0.1476	0.0273*	0.8179845
	<i>Gomphonema clevei</i>	4	0.1953	0.1584	0.0218*	0.6545091
	<i>Gomphonema parvulum</i>	6	-0.1906	0.0147	0.4679	1
	<i>Gomphonema type</i>	D	8	-0.01	0.0005	0.8534
	<i>Melosira varians</i>	8	0.5615	0.0375	0.0959	1
	<i>Meridion circulare</i>	10	0.036	0.0015	0.7183	1
	<i>Navicula atomus</i>	4	-0.0576	0.0067	0.6154	1
	<i>Navicula minima</i>	13	-0.0885	0.0231	0.091	1
	<i>Navicula placentula</i>	6	0.1025	0.0154	0.3571	1
	<i>Nitzschia dissipata</i>	4	0.2414	0.0368	0.2773	1
	<i>Nitzschia fonticola</i>	2	-0.6418	0.0645	0.3255	1
	<i>Nitzschia inconspicua</i>	3	0.2217	0.1549	0.1061	1
	<i>Nitzschia palea</i>	8	-0.435	0.1261	0.0013**	0.0396801*
	<i>Nitzschia paleacea</i>	9	-0.364	0.0887	0.0062**	0.1874952
	<i>Rhoicosphenia abbreviata</i>	5	0.0034	0	0.9871	1
	<i>Rhopalodia gibba</i>	5	0.0207	0.0002	0.9187	1
	<i>Synedra ulna</i>	10	0.1164	0.0119	0.3257	1
Si	<i>Achnanthes lanceolata</i>	13	0.0001	0	0.9808	1
	<i>Amphora inariensis</i>	6	-0.0136	0.2609	0.000049***	0.0015221**
	<i>Amphora pediculus</i>	6	-0.0044	0.0681	0.0439*	1
	<i>Caloneis lauta</i>	2	0.0033	0.0123	0.641	1
	<i>Cocconeis pediculus</i>	4	-0.0568	0.0224	0.3911	1
	<i>Cocconeis placentula</i>	10	0.0025	0.0052	0.4743	1
	<i>Cymbella sinuata</i>	2	0.0857	0.5866	0.000083***	0.00256246**

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	<i>Diatoma mesodon</i>	7	-0.0066	0.039	0.1011	1
	<i>Epithemia sorex</i>	3	0.0193	0.0346	0.343	1
	<i>Epithemia turgida</i>	8	0.0218	0.174	0.0003***	0.00918716**
	<i>Fragilaria arcus</i>	2	0.0335	0.6105	0.000048***	0.00147405**
	<i>Fragilaria capucina</i>	14	-0.0009	0.0019	0.6056	1
	<i>Fragilaria construens</i>	2	0.0103	0.097	0.2083	1
	<i>Fragilaria pinnata</i>	8	0.0007	0.0005	0.8532	1
	<i>Gomphonema clavatum</i>	4	0.0178	0.4045	0.00007***	0.00215481**
	<i>Gomphonema clevei</i>	4	0.0069	0.1115	0.0575	1
	<i>Gomphonema parvulum</i>	6	-0.0507	0.1153	0.037	1
	<i>Gomphonema type</i>	D	8	0.002	0.0123	0.3601
	<i>Melosira varians</i>	8	0.0522	0.3993	<2.2e-16***	<2.2e-16***
	<i>Meridion circulare</i>	10	-0.0002	0.0001	0.9346	1
	<i>Navicula atomus</i>	4	-0.0026	0.0205	0.3785	1
	<i>Navicula minima</i>	13	0.001	0.0032	0.5295	1
	<i>Navicula placentula</i>	6	-0.0069	0.0623	0.0612	1
	<i>Nitzschia dissipata</i>	4	0.0183	0.1035	0.0636	1
	<i>Nitzschia fonticola</i>	2	-0.0165	0.0645	0.3255	1
	<i>Nitzschia inconspicua</i>	3	0.0112	0.1874	0.0728	1
	<i>Nitzschia palea</i>	8	0.0035	0.0106	0.367	1
	<i>Nitzschia paleacea</i>	9	-0.0095	0.0607	0.0248*	0.76752838
	<i>Rhoicosphenia abbreviata</i>	5	-0.0724	0.176	0.0037**	0.11475425
	<i>Rhopalodia gibba</i>	5	-0.0026	0.0087	0.5235	1
	<i>Synedra ulna</i>	10	0.0005	0.0003	0.8848	1
K	<i>Achnanthes lanceolata</i>	13	-0.0001	0	0.9964	1
	<i>Amphora inariensis</i>	6	-0.1064	0.2571	0.00006***	0.00176669**
	<i>Amphora pediculus</i>	6	-0.0411	0.1125	0.0088**	0.27292772
	<i>Caloneis lauta</i>	2	0.0213	0.0123	0.641	1
	<i>Cocconeis pediculus</i>	4	-0.13	0.0647	0.1404	1
	<i>Cocconeis placentula</i>	10	-0.0176	0.0046	0.5026	1
	<i>Cymbella sinuata</i>	2	0.2356	0.5866	0.000083***	0.00256246**
	<i>Diatoma mesodon</i>	7	-0.046	0.0209	0.2325	1
	<i>Epithemia sorex</i>	3	0.0865	0.1402	0.0496*	1
	<i>Epithemia turgida</i>	8	0.1675	0.2429	0.000013***	0.00039246***
	<i>Fragilaria arcus</i>	2	0.2179	0.6105	0.000048***	0.00147405**
	<i>Fragilaria capucina</i>	14	-0.0013	0.0001	0.9099	1
	<i>Fragilaria construens</i>	2	0.0761	0.097	0.2083	1
	<i>Fragilaria pinnata</i>	8	0.0008	0	0.9753	1
	<i>Gomphonema clavatum</i>	4	0.1275	0.304	0.00088***	0.02733487*
	<i>Gomphonema clevei</i>	4	0.0373	0.0513	0.205	1
	<i>Gomphonema parvulum</i>	6	-0.076	0.0511	0.1724	1
	<i>Gomphonema type</i>	D	8	0	0	0.9979
	<i>Melosira varians</i>	8	0.3275	0.3716	0.00000001***	0.00000031***
	<i>Meridion circulare</i>	10	0.0121	0.0029	0.6117	1
	<i>Navicula atomus</i>	4	-0.0277	0.027	0.3108	1
	<i>Navicula minima</i>	13	-0.001	0.0001	0.9294	1

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	<i>Navicula placentula</i>	6	-0.0441	0.0524	0.0869	1
	<i>Nitzschia dissipata</i>	4	0.1278	0.1011	0.0668	1
	<i>Nitzschia fonticola</i>	2	-0.1167	0.0645	0.3255	1
	<i>Nitzschia inconspicua</i>	3	0.1394	0.1459	0.1178	1
	<i>Nitzschia palea</i>	8	0.0123	0.0031	0.6271	1
	<i>Nitzschia paleacea</i>	9	-0.0473	0.038	0.0775	1
	<i>Rhoicosphenia abbreviata</i>	5	-0.141	0.1751	0.0038**	0.11790943
	<i>Rhopalodia gibba</i>	5	-0.011	0.003	0.7068	1
	<i>Synedra ulna</i>	10	-0.0226	0.01	0.3687	1
NO3	<i>Achnanthes lanceolata</i>	13	-0.2492	0	0.9728	1
	<i>Amphora inariensis</i>	6	-16.093	0.0325	0.1798	1
	<i>Amphora pediculus</i>	6	-9.4507	0.04	0.1257	1
	<i>Caloneis lauta</i>	2	-15.966	0.0123	0.641	1
	<i>Cocconeis pediculus</i>	4	17.675	0.0339	0.2896	1
	<i>Cocconeis placentula</i>	10	-27.086	0.056	0.0178*	0.55152565
	<i>Cymbella sinuata</i>	2	188.49	0.5866	0.000083***	0.00256246**
	<i>Diatoma mesodon</i>	7	-19.092	0.055	0.0507	1
	<i>Epithemia sorex</i>	3	28.017	0.1834	0.0230*	0.71247889
	<i>Epithemia turgida</i>	8	-52.909	0.0929	0.0098**	0.30266044
	<i>Fragilaria arcus</i>	2	217.91	0.6105	0.000048***	0.00147405**
	<i>Fragilaria capucina</i>	14	7.7439	0.0157	0.1406	1
	<i>Fragilaria construens</i>	2	-20.29	0.097	0.2083	1
	<i>Fragilaria pinnata</i>	8	8.5085	0.0127	0.367	1
	<i>Gomphonema clavatum</i>	4	42.184	0.2073	0.0078**	0.24032037
	<i>Gomphonema clevei</i>	4	46.115	0.2531	0.0028**	0.08815222
	<i>Gomphonema parvulum</i>	6	-16.501	0.0156	0.4546	1
	<i>Gomphonema type</i>	D	8	20.9695	0.1597	0.0006***
	<i>Melosira varians</i>	8	-80.767	0.1095	0.0037**	0.1158
	<i>Meridion circulare</i>	10	-32.154	0.1193	0.0007***	0.02307392*
	<i>Navicula atomus</i>	4	1.9582	0.0028	0.7468	1
	<i>Navicula minima</i>	13	-4.9876	0.0084	0.3081	1
	<i>Navicula placentula</i>	6	24.711	0.0792	0.0340*	1
	<i>Nitzschia dissipata</i>	4	-23.462	0.0267	0.3555	1
	<i>Nitzschia fonticola</i>	2	128.35	0.0645	0.3255	1
	<i>Nitzschia inconspicua</i>	3	45.203	0.1895	0.071	1
	<i>Nitzschia palea</i>	8	35.392	0.1105	0.0028**	0.08579002
	<i>Nitzschia paleacea</i>	9	31.284	0.0774	0.0109*	0.33690645
	<i>Rhoicosphenia abbreviata</i>	5	-35.541	0.076	0.0638	1
	<i>Rhopalodia gibba</i>	5	23.128	0.0821	0.0460*	1
	<i>Synedra ulna</i>	10	4.5006	0.0021	0.6787	1
NH4	<i>Achnanthes lanceolata</i>	13	-3.1618	0.0058	0.3963	1
	<i>Amphora inariensis</i>	6	17.796	0.1535	0.0026**	0.07992141
	<i>Amphora pediculus</i>	6	4.1558	0.0216	0.263	1
	<i>Caloneis lauta</i>	2	6.3862	0.0123	0.641	1
	<i>Cocconeis pediculus</i>	4	0.5334	0.0001	0.9553	1
	<i>Cocconeis placentula</i>	10	24.968	0.1163	0.0005***	0.01597616*

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	<i>Cymbella sinuata</i>	2	-31.415	0.5866	0.000083***	0.00256246**
	<i>Diatoma mesodon</i>	7	3.8226	0.0128	0.3512	1
	<i>Epithemia sores</i>	3	-28.017	0.1834	0.0230*	0.71247889
	<i>Epithemia turgida</i>	8	0.5655	0	0.9742	1
	<i>Fragilaria arcus</i>	2	-108.96	0.6105	0.000048***	0.00147405**
	<i>Fragilaria capucina</i>	14	-2.8964	0.007	0.3249	1
	<i>Fragilaria construens</i>	2	8.6955	0.097	0.2083	1
	<i>Fragilaria pinnata</i>	8	-5.9214	0.0336	0.1409	1
	<i>Gomphonema clavatum</i>	4	44.431	0.2526	0.0029**	0.08904037
	<i>Gomphonema clevei</i>	4	-21.756	0.1462	0.0281*	0.87122741
	<i>Gomphonema parvulum</i>	6	46.223	0.3497	0.000092***	0.00286471**
	<i>Gomphonema type</i>	D	8	2.0408	0.0027	0.6699
	<i>Melosira varians</i>	8	-35.048	0.0341	0.1127	1
	<i>Meridion circulare</i>	10	1.673	0.0014	0.725	1
	<i>Navicula atomus</i>	4	-2.3772	0.0202	0.3814	1
	<i>Navicula minima</i>	13	5.0587	0.027	0.067	1
	<i>Navicula placentula</i>	6	4.9552	0.0128	0.4015	1
	<i>Nitzschia dissipata</i>	4	22.042	0.0806	0.1038	1
	<i>Nitzschia fonticola</i>	2	-32.089	0.0645	0.3255	1
	<i>Nitzschia inconspicua</i>	3	16.726	0.1459	0.1178	1
	<i>Nitzschia palea</i>	8	-4.4693	0.0037	0.5962	1
	<i>Nitzschia paleacea</i>	9	15.736	0.0705	0.0152*	0.47273109
	<i>Rhoicosphenia abbreviata</i>	5	-0.6197	0.0001	0.9478	1
	<i>Rhopalodia gibba</i>	5	-5.62	0.01	0.4946	1
	<i>Synedra ulna</i>	10	-10.07	0.0187	0.2176	1
Total N	<i>Achnanthes lanceolata</i>	13	0.2533	0.0042	0.4708	1
	<i>Amphora inariensis</i>	6	0.6072	0.0191	0.3058	1
	<i>Amphora pediculus</i>	6	0.4294	0.0229	0.248	1
	<i>Caloneis lauta</i>	2	-1.4514	0.0123	0.641	1
	<i>Cocconeis pediculus</i>	4	1.6636	0.0292	0.3264	1
	<i>Cocconeis placentula</i>	10	1.5837	0.0391	0.0486*	1
	<i>Cymbella sinuata</i>	2	-2.8559	0.5866	0.000083***	0.00256246**
	<i>Diatoma mesodon</i>	7	0.3103	0.0078	0.4674	1
	<i>Epithemia sores</i>	3	-2.6829	0.2079	0.0148*	0.45747103
	<i>Epithemia turgida</i>	8	-1.6702	0.0537	0.0517	1
	<i>Fragilaria arcus</i>	2	-2.5047	0.6105	0.000048***	0.00147405**
	<i>Fragilaria capucina</i>	14	-0.3434	0.0126	0.1865	1
	<i>Fragilaria construens</i>	2	2.2544	0.097	0.2083	1
	<i>Fragilaria pinnata</i>	8	-0.5438	0.0176	0.2887	1
	<i>Gomphonema clavatum</i>	4	0.1067	0.0013	0.8398	1
	<i>Gomphonema clevei</i>	4	1.2914	0.0383	0.2749	1
	<i>Gomphonema parvulum</i>	6	2.0172	0.1117	0.0402*	1
	<i>Gomphonema type</i>	D	8	0.5144	0.059	0.0427*
	<i>Melosira varians</i>	8	-2.7063	0.0551	0.0427*	1
	<i>Meridion circulare</i>	10	0.8674	0.0362	0.0693	1
	<i>Navicula atomus</i>	4	-0.4734	0.0347	0.2498	1

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	<i>Navicula minima</i>	13	0.1313	0.0023	0.5942	1
	<i>Navicula placentula</i>	6	1.0006	0.114	0.0102*	0.31697779
	<i>Nitzschia dissipata</i>	4	1.2899	0.0488	0.2093	1
	<i>Nitzschia fonticola</i>	2	-2.2518	0.0645	0.3255	1
	<i>Nitzschia inconspicua</i>	3	1.0016	0.1369	0.1307	1
	<i>Nitzschia palea</i>	8	-0.5983	0.0176	0.2439	1
	<i>Nitzschia paleacea</i>	9	-0.2718	0.0033	0.606	1
	<i>Rhoicosphenia abbreviata</i>	5	1.5696	0.0251	0.293	1
	<i>Rhopalodia gibba</i>	5	1.1985	0.0278	0.252	1
	<i>Synedra ulna</i>	10	0.9837	0.0397	0.071	1
PO4	<i>Achnanthes lanceolata</i>	13	0.6854	0.0007	0.7714	1
	<i>Amphora inariensis</i>	6	2.2997	0.0034	0.6686	1
	<i>Amphora pediculus</i>	6	-1.4239	0.0078	0.502	1
	<i>Caloneis lauta</i>	2	3.9914	0.0123	0.641	1
	<i>Cocconeis pediculus</i>	4	-1.1374	0.0005	0.8988	1
	<i>Cocconeis placentula</i>	10	-8.6991	0.0531	0.0211*	0.6333786
	<i>Cymbella sinuata</i>	2	188.49	0.5866	0.000083***	0.0024798**
	<i>Diatoma mesodon</i>	7	-1.0984	0.0027	0.6703	1
	<i>Epithemia sorex</i>	3	1.0564	0.0099	0.6153	1
	<i>Epithemia turgida</i>	8	18.696	0.1789	0.00024***	0.0071391**
	<i>Fragilaria arcus</i>	2	12.818	0.6105	0.000048***	0.0014265**
	<i>Fragilaria capucina</i>	14	-0.5672	0.0007	0.749	1
	<i>Fragilaria construens</i>	2	30.434	0.097	0.2083	1
	<i>Fragilaria pinnata</i>	8	6.9597	0.0242	0.2124	1
	<i>Gomphonema clavatum</i>	4	-3.9036	0.0174	0.4638	1
	<i>Gomphonema clevei</i>	4	8.8223	0.1633	0.0197*	0.5899428
	<i>Gomphonema parvulum</i>	6	8.042	0.037	0.2475	1
	<i>Gomphonema type</i>	D	8	-4.4506	0.107	0.0057**
	<i>Melosira varians</i>	8	17.82	0.0694	0.0224*	0.6719
	<i>Meridion circulare</i>	10	0.2763	0.0001	0.9458	1
	<i>Navicula atomus</i>	4	1.4114	0.0052	0.6598	1
	<i>Navicula minima</i>	13	-2.7757	0.0141	0.1873	1
	<i>Navicula placentula</i>	6	-14.27	0.1502	0.0029**	0.0867693
	<i>Nitzschia dissipata</i>	4	21.991	0.0084	0.6056	1
	<i>Nitzschia fonticola</i>	2	NA	0	NA	NA
	<i>Nitzschia inconspicua</i>	3	-9.2132	0.1802	0.0791	1
	<i>Nitzschia palea</i>	8	5.4968	0.0101	0.3789	1
	<i>Nitzschia paleacea</i>	9	-7.6717	0.0733	0.0133*	0.3994572
	<i>Rhoicosphenia abbreviata</i>	5	4.4544	0.0314	0.2388	1
	<i>Rhopalodia gibba</i>	5	-80.732	0.3069	0.000036***	0.0010914**
	<i>Synedra ulna</i>	10	-5.7454	0.0394	0.0722	1
Total P	<i>Achnanthes lanceolata</i>	13	-0.3412	0.0004	0.8164	1
	<i>Amphora inariensis</i>	6	-4.6539	0.0451	0.1129	1
	<i>Amphora pediculus</i>	6	-1.923	0.0322	0.1701	1
	<i>Caloneis lauta</i>	2	1.5966	0.0123	0.641	1
	<i>Cocconeis pediculus</i>	4	-3.8733	0.0187	0.4332	1

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<i>Cocconeis placentula</i>	10	-5.3115	0.0336	0.0678	1
<i>Cymbella sinuata</i>	2	23.561	0.5866	0.000083***	0.00256246**
<i>Diatoma mesodon</i>	7	-1.633	0.0146	0.3193	1
<i>Epithemia sorex</i>	3	1.6728	0.0393	0.312	1
<i>Epithemia turgida</i>	8	13.259	0.2562	0.000007***	0.0002077***
<i>Fragilaria arcus</i>	2	8.3812	0.6105	0.000048***	0.00147405**
<i>Fragilaria capucina</i>	14	0.2943	0.0006	0.7832	1
<i>Fragilaria construens</i>	2	5.0724	0.097	0.2083	1
<i>Fragilaria pinnata</i>	8	2.3508	0.0081	0.4718	1
<i>Gomphonema clavatum</i>	4	1.9995	0.014	0.5113	1
<i>Gomphonema clevei</i>	4	11.235	0.2829	0.0014**	0.04479314*
<i>Gomphonema parvulum</i>	6	-0.7892	0.001	0.8483	1
<i>Gomphonema type D</i>	8	-2.8145	0.1117	0.0047**	0.1453
<i>Melosira varians</i>	8	17.53	0.1672	0.00027***	0.00835853**
<i>Meridion circulare</i>	10	-0.9873	0.0015	0.7171	1
<i>Navicula atomus</i>	4	0.719	0.0018	0.7937	1
<i>Navicula minima</i>	13	-1.4375	0.012	0.2232	1
<i>Navicula placentula</i>	6	-5.0093	0.1094	0.0120*	0.37054827
<i>Nitzschia dissipata</i>	4	8.2189	0.0331	0.3028	1
<i>Nitzschia fonticola</i>	2	-42.785	0.0645	0.3255	1
<i>Nitzschia inconspicua</i>	3	-6.7049	0.0938	0.2165	1
<i>Nitzschia palea</i>	8	-0.6939	0.001	0.7812	1
<i>Nitzschia paleacea</i>	9	-4.0237	0.0516	0.0389*	1
<i>Rhoicosphenia abbreviata</i>	5	3.0752	0.0232	0.3125	1
<i>Rhopalodia gibba</i>	5	-15.178	0.1839	0.0021**	0.06544503
<i>Synedra ulna</i>	10	-3.8554	0.0333	0.0989	1

Table A.7: Summary of regression slopes from (Table 2.2 and Table A.6), showing the total number of positive and negative slopes, positive and negative slopes with $p < 0.05$ and positive and negative slopes with Bonferroni-corrected $p < 0.05$

Abiotic Variable	All Slopes		Significant Slopes		Bonferroni corrected	
	Positive	Negative	Positive	Negative	Positive	Negative
Temperature	15	16	5	7	4	3
pH	16	14	6	5	2	2
Si	18	13	5	4	5	1
K	15	16	6	3	5	1
NO3	17	14	10	4	3	1
NH4	17	14	5	4	2	2
Total N	19	12	4	4	0	2
PO4	17	13	5	5	3	1
Total P	14	17	5	4	5	0

A.4. Additional results: community

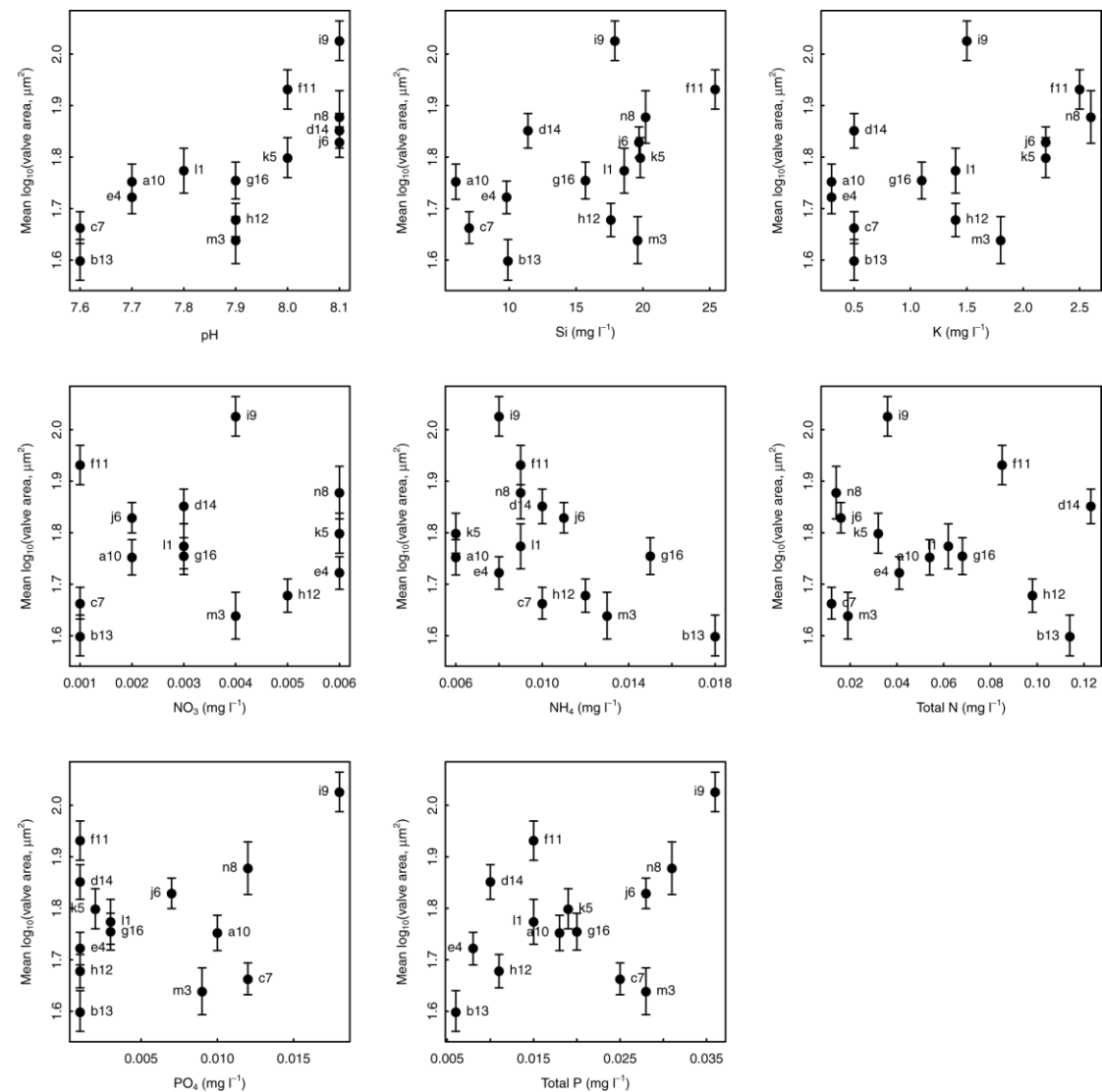


Figure A.4: Community-level plots showing mean $\log_{10}$ valve area for 8 different abiotic variables in the fourteen streams, analogous to Figure 2.3 in the main text.

Table A.8: Matrix showing the proportion of the total community size change between streams that is due to intraspecific effects. Each value is a pairwise comparison between streams α and β , calculating the size change one would expect to see due to intraspecific effects as a percentage of the overall average community size difference between the streams, $\Delta_{\alpha\beta}^{INTRA}/\Delta$. The matrix shows only upper triangle values as the matrix is symmetric.

	a	b	c	d	e	f	g	h	i	j	k	l	m	n
a	-	0.1246	0.6249	-0.5721	1.7914	0.1537	-16.8708	0.2912	-0.0617	-0.6561	-0.2373	-2.4133	0.0832	0.1145
b	-	-	-0.9684	-0.1268	-0.3433	0.0028	-0.0672	0.1031	-0.0125	-0.1481	0.0982	-0.1388	-0.4554	0.0207
c	-	-	-	0.1611	0.3826	0.2600	0.3198	3.0254	0.0927	-0.0522	0.0601	0.2787	-1.9884	-0.0129
d	-	-	-	-	0.0868	0.6912	-0.1634	-0.1020	0.1973	-0.4639	-0.0368	0.5485	0.0127	-1.1347
e	-	-	-	-	-	0.2665	0.0232	-0.3243	0.0118	-0.2643	0.0608	-0.9984	-0.3046	-0.3390
f	-	-	-	-	-	-	0.0608	0.0395	-0.5920	0.4849	0.1443	0.4064	0.0049	1.5522
g	-	-	-	-	-	-	-	-0.5074	-0.0836	-0.1543	-0.5409	-2.3370	-0.3259	-0.5350
h	-	-	-	-	-	-	-	-	-0.0746	-0.2587	-0.0251	-0.4289	-0.0941	-0.0116
i	-	-	-	-	-	-	-	-	-	-0.0455	-0.0177	0.0650	0.0041	0.8441
j	-	-	-	-	-	-	-	-	-	-	0.7168	-0.5082	-0.2757	-0.2906
k	-	-	-	-	-	-	-	-	-	-	-	1.4167	-0.1817	-0.7884
l	-	-	-	-	-	-	-	-	-	-	-	-	-0.3994	-0.6093
m	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.3872
n	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table A.9: Matrix showing the total relative abundance of species in stream α (labelled in the rows) not found in stream β (labelled in the columns; see Methods). Each value represents the proportional contribution of species turnover to overall species compositional differences between streams.

	a	b	c	d	e	f	g	h	i	j	k	l	m	n
a	0	0.0417	0.0254	0.0048	0.0060	0.0091	0.0054	0.0284	0.0260	0.2958	0.0387	0.0526	0.0296	0.0405
b	0.0334	0	0.0409	0.1438	0.1378	0.0238	0.0349	0.1478	0.0423	0.3302	0.0371	0.1493	0.1568	0.0509
c	0.0332	0.4097	0	0.0541	0.0897	0.0356	0.0360	0.1458	0.0288	0.2219	0.2711	0.3100	0.0973	0.2439
d	0.1061	0.1700	0.0662	0	0.0423	0.0646	0.0591	0.0343	0.0271	0.4773	0.0838	0.0678	0.0726	0.1429
e	0.1236	0.2712	0.1525	0.0598	0	0.1342	0.0676	0.0714	0.1380	0.3909	0.2181	0.1477	0.0907	0.3156
f	0.1208	0.3343	0.0449	0.0266	0.0256	0	0.0118	0.3028	0.0123	0.1203	0.0227	0.0232	0.0863	0.0700
g	0.1107	0.2611	0.1144	0.0351	0.0443	0.1042	0	0.1125	0.1181	0.2740	0.1393	0.1439	0.0913	0.2122
h	0.1296	0.2438	0.0926	0.0504	0.0576	0.0998	0.0484	0	0.1255	0.2407	0.2253	0.0751	0.0936	0.2994
i	0.1426	0.7166	0.1442	0.0561	0.4365	0.0418	0.0865	0.2037	0	0.0856	0.1156	0.3986	0.4378	0.4964
j	0.0960	0.5144	0.0736	0.0252	0.2283	0.0438	0.0196	0.1463	0.0457	0	0.1463	0.1966	0.2022	0.4651
k	0.3592	0.2836	0.2033	0.2602	0.3365	0.2428	0.1819	0.2716	0.2555	0.0963	0	0.0649	0.0883	0.1940
l	0.5626	0.2645	0.2251	0.1937	0.2367	0.0824	0.0731	0.1995	0.0916	0.3248	0.0371	0	0.1067	0.2448
m	0.1090	0.2042	0.0673	0.0267	0.0557	0.0638	0.0731	0.1079	0.0487	0.0870	0.0313	0.0487	0	0.0893
n	0.6897	0.6405	0.0596	0.0460	0.5559	0.0669	0.0115	0.1567	0.0627	0.0157	0.0052	0.0199	0.2623	0

Table A.10: Summary of p-values from linear and quadratic regressions of log₁₀ mean valve area against 9 different abiotic variables. Corrected p-values are Bonferroni corrected and stars represent levels of significance: p<0.05 (*), p<0.01 (**), p<0.001 (***).

Abiotic variable	Linear regression				Quadratic regression		
	Slope	R ²	p-value	Corrected p-value	R ²	p-value	Corrected p-value
Temperature	0.0058	0.1032	0.2628	1	0.1619	0.3785	1
pH	0.4484	0.5759	0.0016**	0.0148*	0.6002	0.0065**	0.0581
Si	0.0097	0.2523	0.0672	0.6048	0.2680	0.1799	1
K	0.0659	0.2295	0.0830	0.7473	0.2445	0.2139	1
NO ₃	4.0969	0.0045	0.8195	1	0.0701	0.6707	1
NH ₄	-16.4759	0.2181	0.0923	0.8303	0.2533	0.2006	1
TotalN	-0.1710	0.0034	0.8439	1	0.0206	0.8920	1
PO ₄	6.0221	0.0835	0.3165	1	0.2702	0.1768	1
TotalP	5.4506	0.1874	0.1221	1	0.2333	0.2320	1

Appendix B

B.1. Proof of LFI slope decomposition

The slope of an ordinary linear regression can be calculated and decomposed as follows:

$$\begin{aligned} slope &= \frac{\sum x_i y_i - \frac{1}{n} \sum x_i \sum y_i}{\sum x_i^2 - \frac{1}{n} (\sum x_i)^2} = \frac{\sum_j^N \sum_i^n x_i y_{ij} - \frac{1}{n} \sum x_i \sum_j^N \sum_i^n y_{ij}}{\sum x_i^2 - \frac{1}{n} (\sum x_i)^2} \\ &= \sum_j^N \frac{\sum x_i y_{ij} - \frac{1}{n} \sum x_i \sum y_{ij}}{\sum x_i^2 - \frac{1}{n} (\sum x_i)^2} \end{aligned}$$

Where x_i is the explanatory variable (year), y_i is the dependent variable (LFI value), and n is the number of observations. If N is the number of components contributing to y_i , and y_{ij} is the LFI value for component j , then the slope is decomposed to the sum of the slopes for each component, j . In terms of the LFI, this can be written as:

$$slope = \frac{\sum x_i \frac{B_L}{B} - \frac{1}{n} \sum x_i \sum \frac{B_L}{B}}{\sum x_i^2 - \frac{1}{n} (\sum x_i)^2} = \sum_j^N \frac{\sum x_i \frac{B_{L,j}}{B} - \frac{1}{n} \sum x_i \sum \frac{B_{L,j}}{B}}{\sum x_i^2 - \frac{1}{n} (\sum x_i)^2}$$

Where $\frac{B_L}{B}$ is the LFI value calculated as the total biomass of large fish B_L divided by the total biomass of all fish, B . Then $\frac{B_{L,j}}{B}$ is the LFI contribution of component j , the sum of biomass of large fish in component j divided by the total biomass of all fish, B .

B.2. Additional results

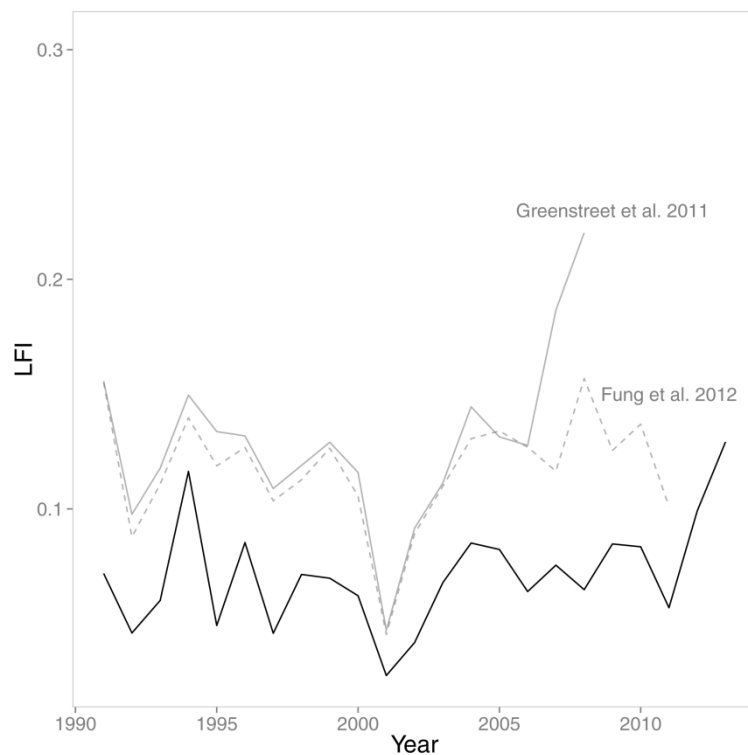


Figure B.1: LFI values between 1991 and 2013 for Q1 IBTS data, as calculated using the cleaning methods detailed in Appendix D.1 (black line), together with Q1 LFI values taken from two previously published studies of the LFI in the North Sea (Greenstreet *et al.* 2011 (grey solid line) and Fung *et al.* 2012 (grey dashed line)). LFI trends calculated using data cleaned for analysis in this chapter are similar to previously reported trends, but LFI values are lower overall, due to the inclusion of smaller individuals and pelagic species in the LFI denominator.

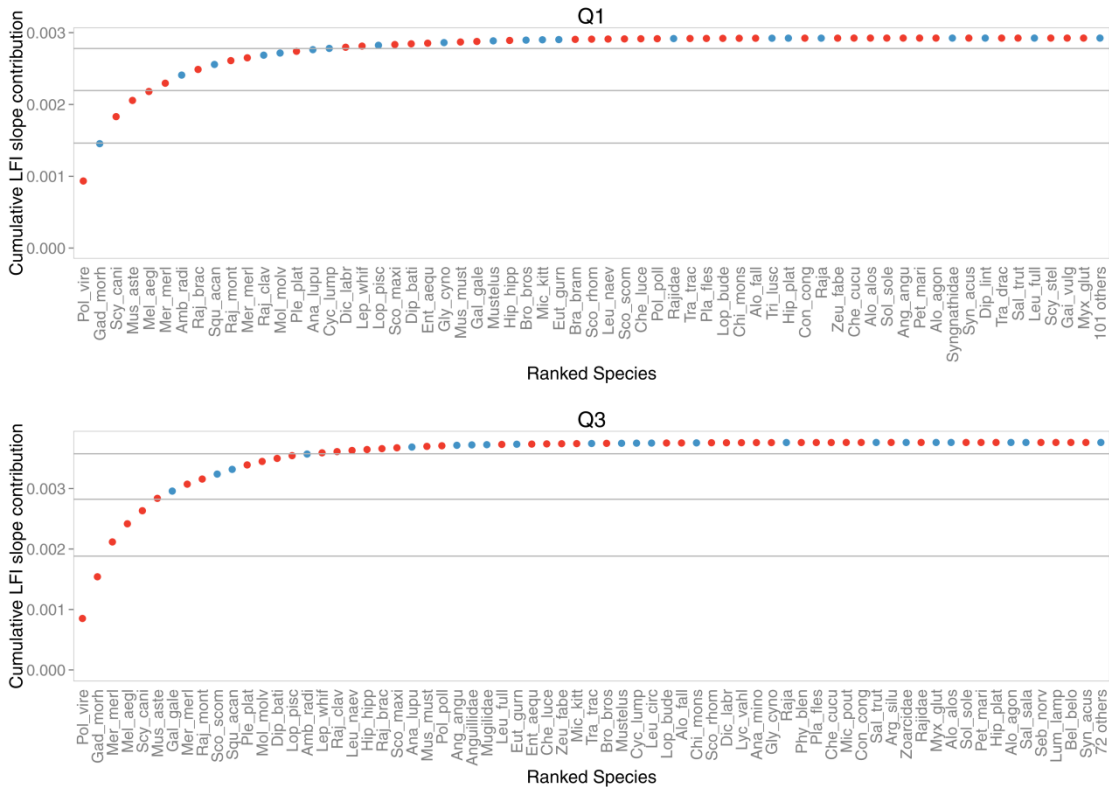


Figure B.2: Ranked contributions to the slope of the LFI, decomposed by species. Values are on a linear scale, and are absolute values of the slope contribution for each species, ranked in size from largest to smallest. Red points represent a positive contribution, blue a negative one. Horizontal lines show 50%, 75% and 95% of the sum of the absolute values of all contributions. Species names are truncated, a list of species is in Table D.1 in Appendix D.1.

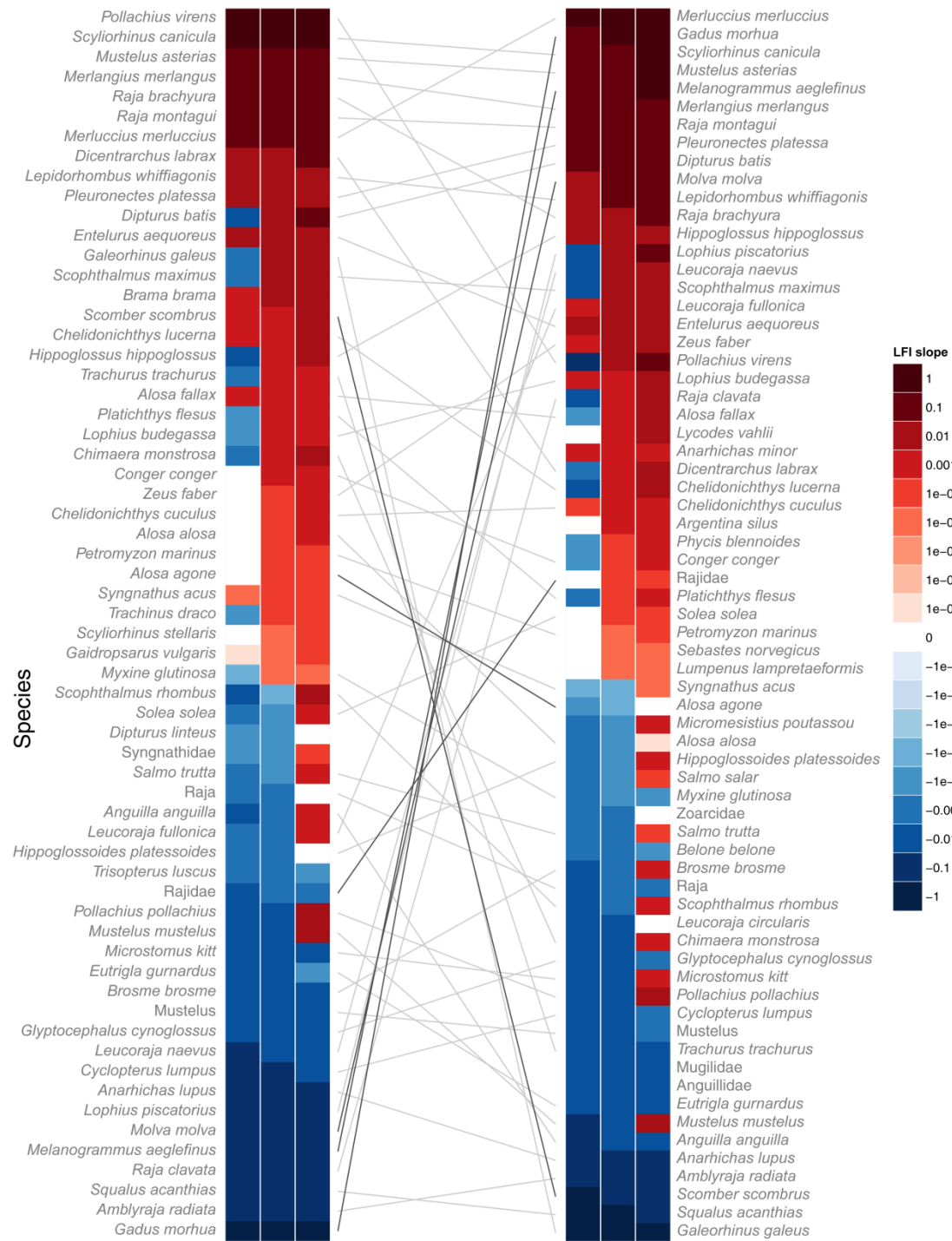


Figure B.3: Decomposition of the total large fish biomass slope over time (1991-2013), by species. Analogous to Figure 3.1, but calculated using large fish (> 40cm in length) biomass totals for each species rather than the LFI which is weighted by the biomass of all fish. Unlike the LFI decomposition, these components are independent of each other and represent independently calculated slopes for each species, as well as contributions to an overall slope. The block of three

vertical colour scales on the left of the plot shows Q1 results and the block on the right shows Q3 results. Within each block the central colour scale shows the point estimate of the LFI, the left colour scale the 2.5% lower confidence interval based on 1000 resampled datasets, and the right colour scale the 97.5% upper confidence interval. Values are represented on a log scale, red represents a positive slope and blue a negative slope. Lines are between species that have large fish present in both quarters, where dark grey lines link species that have switched significantly from either a negative slope to a positive one or vice versa.

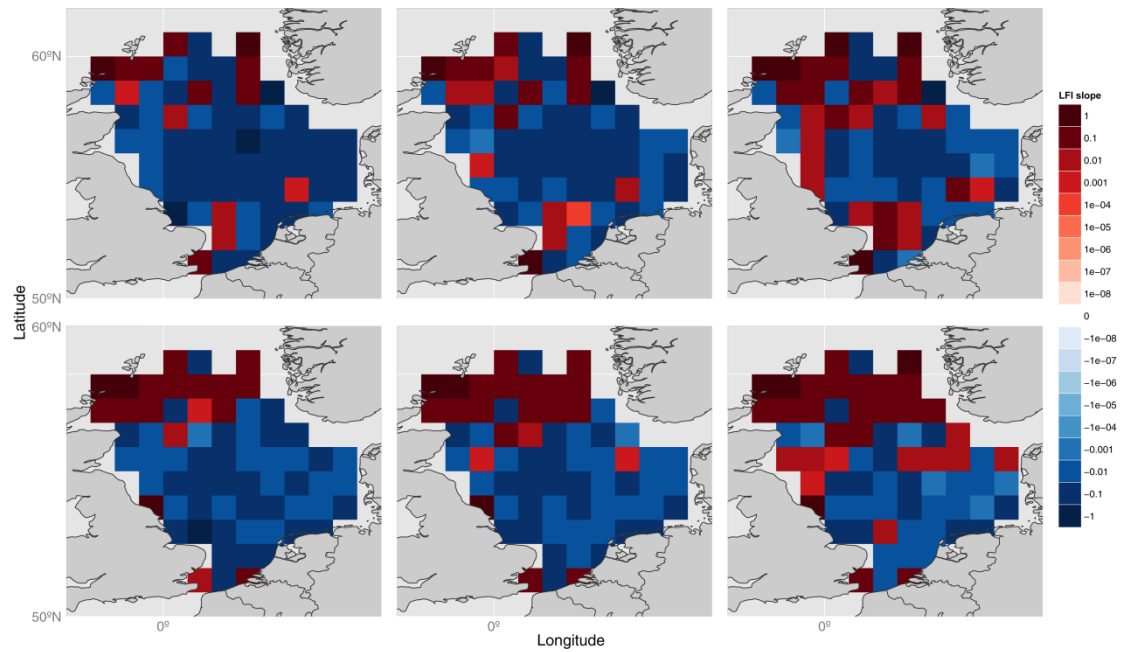


Figure B.4: Decomposition of the total large fish biomass slope over time (1991-2013), by $1^\circ \times 1^\circ$ grid cell. This is analogous to Figure 3.2 but calculated using large fish ($> 40\text{cm}$ in length) biomass totals for each species rather than the LFI which is weighted by the biomass of all fish. Unlike the LFI decomposition, these components represent slopes of values calculated independently using only data from each grid cell, not just contributions to an overall slope. The first row shows the decomposition for Q1 data plotted on a map of the North Sea, the second row for Q3 data. The middle column in each row is the point estimate from the data, the left column is the 2.5% lower confidence interval bound based on 1000 resampled datasets, and the right column the 97.5% upper confidence interval bound. Values are represented on a linear scale, red represents a positive contribution to the overall slope and blue a negative contribution.

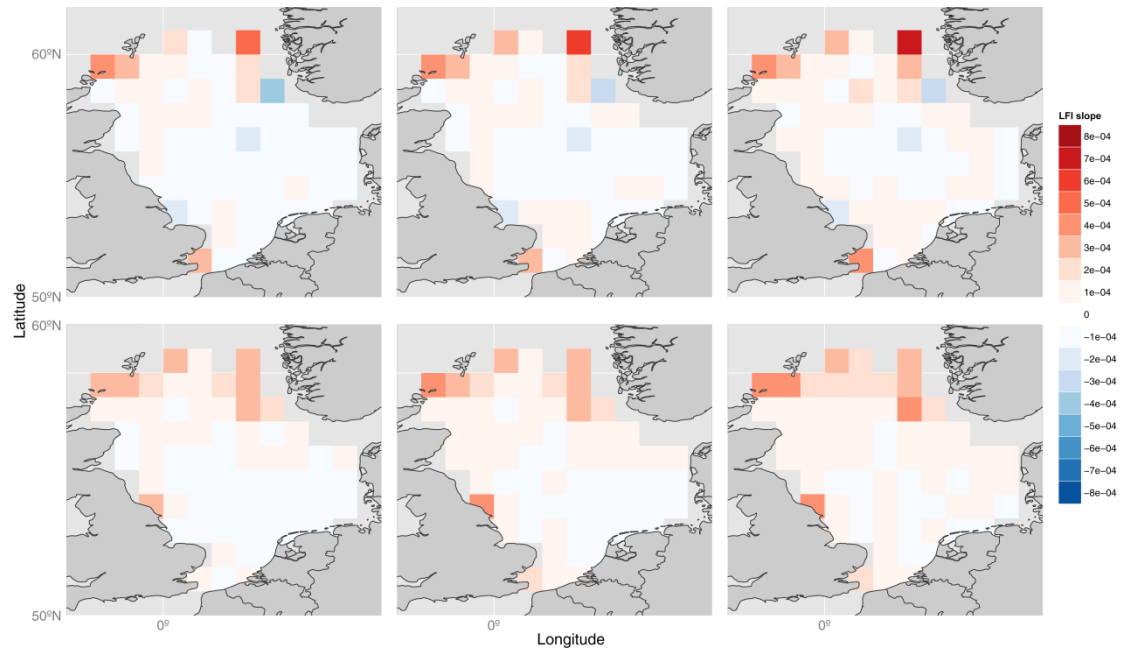


Figure B.5: Decomposition of the LFI slope over time (1991-2013), by $1^\circ \times 1^\circ$ grid cell. This is analogous to Figure 3.2, but the colours are now on a linear scale to highlight the difference in the magnitude of contributions across grid cells. The first row shows the decomposition for Q1 data plotted on a map of the North Sea, the second row for Q3 data. The middle column in each row is the point estimate from the data, the left column is the 2.5% lower confidence interval based on 1000 resampled datasets, and the right column the 97.5% upper confidence interval. Red represents a positive contribution to the overall slope and blue a negative contribution.

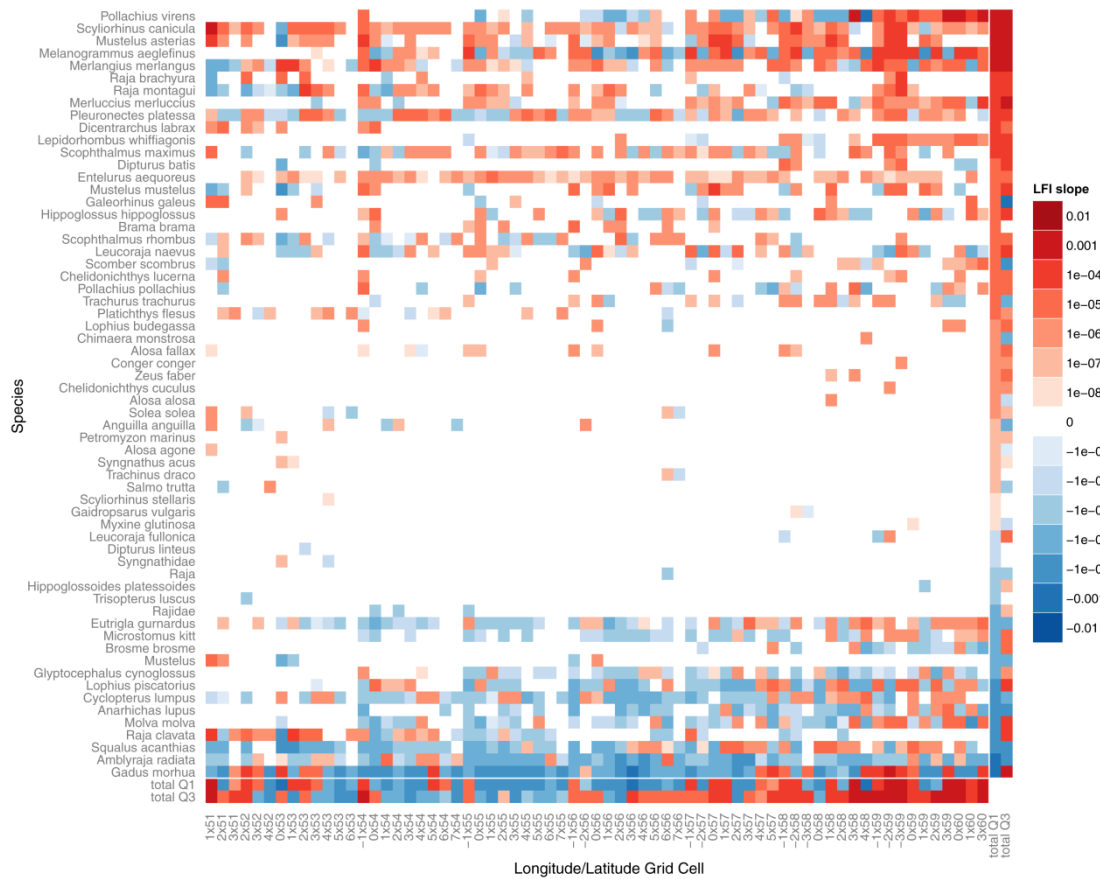


Figure B.6: Q1 data for heat map showing the decomposition of the LFI slope over time (1991-2013) by both species and by $1^\circ \times 1^\circ$ grid cell. Values are represented on a log scale, red represents a positive contribution to the overall slope and blue a negative contribution. Species are ordered on the y-axis by magnitude of contribution from positive to negative. Grid cells are ordered on the x-axis from lower latitude bands to higher latitude bands. Total columns show the sum of contributions across all grid cells for each species, the first column is for the quarter represented by the plot, the second for the species total in the opposite quarter to enable comparison (if a species has a contribution in both quarters). These species totals are the same as in Figure 3.1. Total rows show the sum of contributions across all species for each grid cell, the first column is for the quarter represented by the plot, the second for the grid cell total in the opposite quarter to enable comparison. These totals for each grid cell are the same as in Figure 3.2.

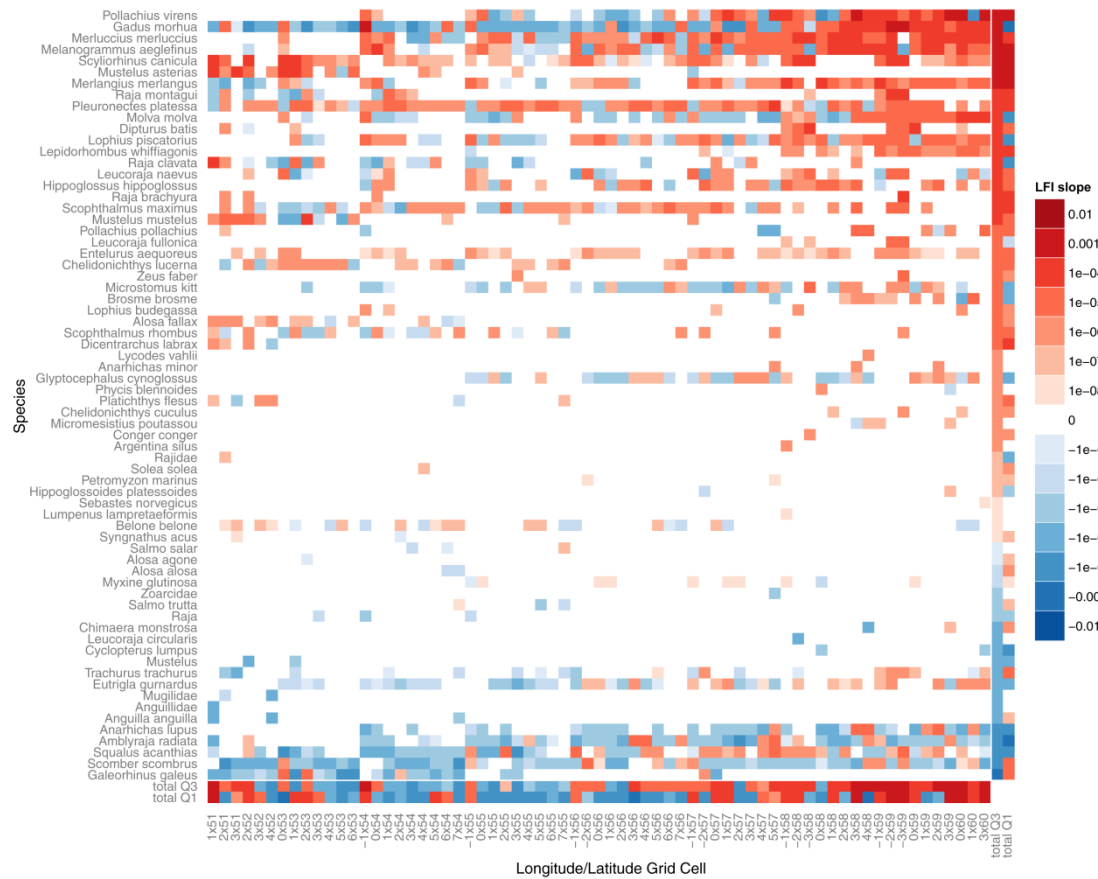


Figure B.7: Q3 data for heat map showing the decomposition of the LFI slope over time (1991-2013) by both species and by $1^\circ \times 1^\circ$ grid cell. Values are represented on a log scale, red represents a positive contribution to the overall slope and blue a negative contribution. Species are ordered on the y-axis by magnitude of contribution from positive to negative. Grid cells are ordered on the x-axis from lower latitude bands to higher latitude bands. Total columns show the sum of contributions across all grid cells for each species, the first column is for the quarter represented by the plot, the second for the species total in the opposite quarter to enable comparison (if a species has a contribution in both quarters). These species totals are the same as in Figure 3.1. Total rows show the sum of contributions across all species for each grid cell, the first column is for the quarter represented by the plot, the second for the grid cell total in the opposite quarter to enable comparison. These totals for each grid cell are the same as in Figure 3.2.

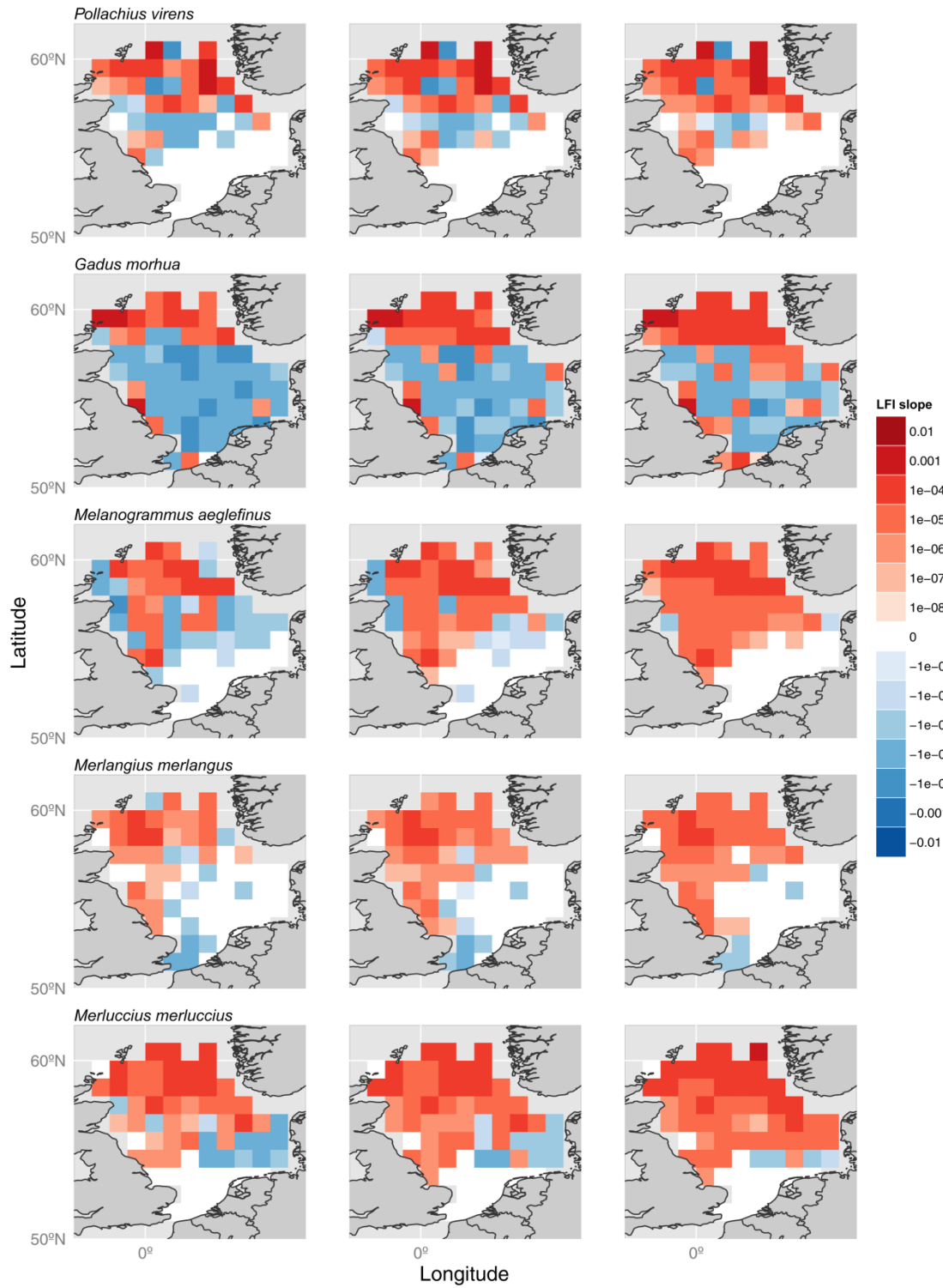


Figure B.8: Decomposition of the LFI slope over time (1991-2013), by 1°x1° grid cell in Q3, for each of five species that are abundant and make a large contribution to the value of the LFI (*Pollachius virens*, *Gadus morhua*, *Melanogrammus aeglefinus*, *Merlangius merlangus* and *Merluccius merluccius*). The middle column in each row of panels is the point estimate from the data, the left

column is the 2.5% lower confidence interval bound based on 1000 resampled datasets, and the right column the 97.5% upper confidence interval bound. Values are represented on a log scale, red represents a positive contribution to the overall slope and blue a negative contribution. White cells represent a contribution of zero to the overall slope: they are either grid cells in which surveys were carried out but no large fish from that particular species were found (in the middle column), or cells where the confidence limit is zero.

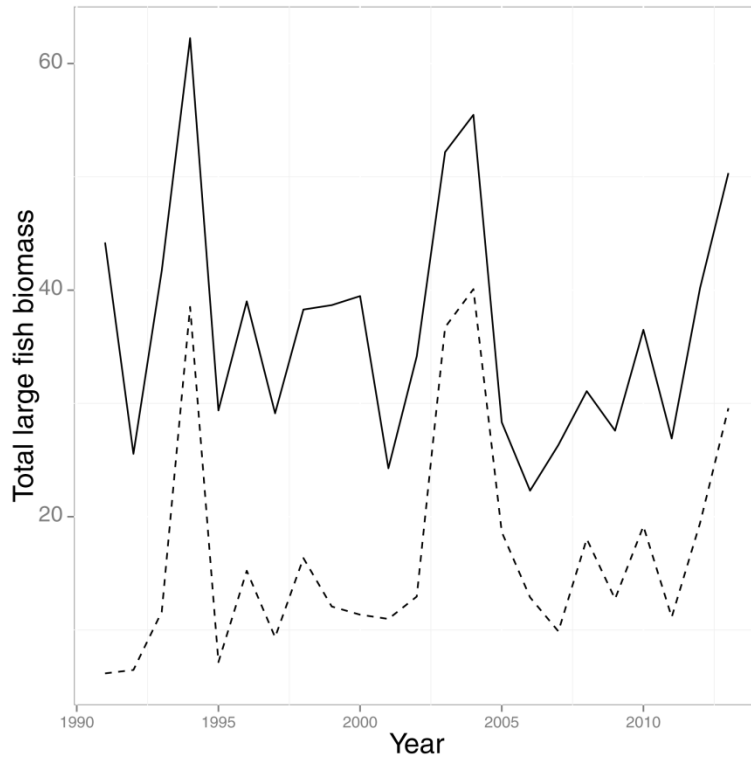
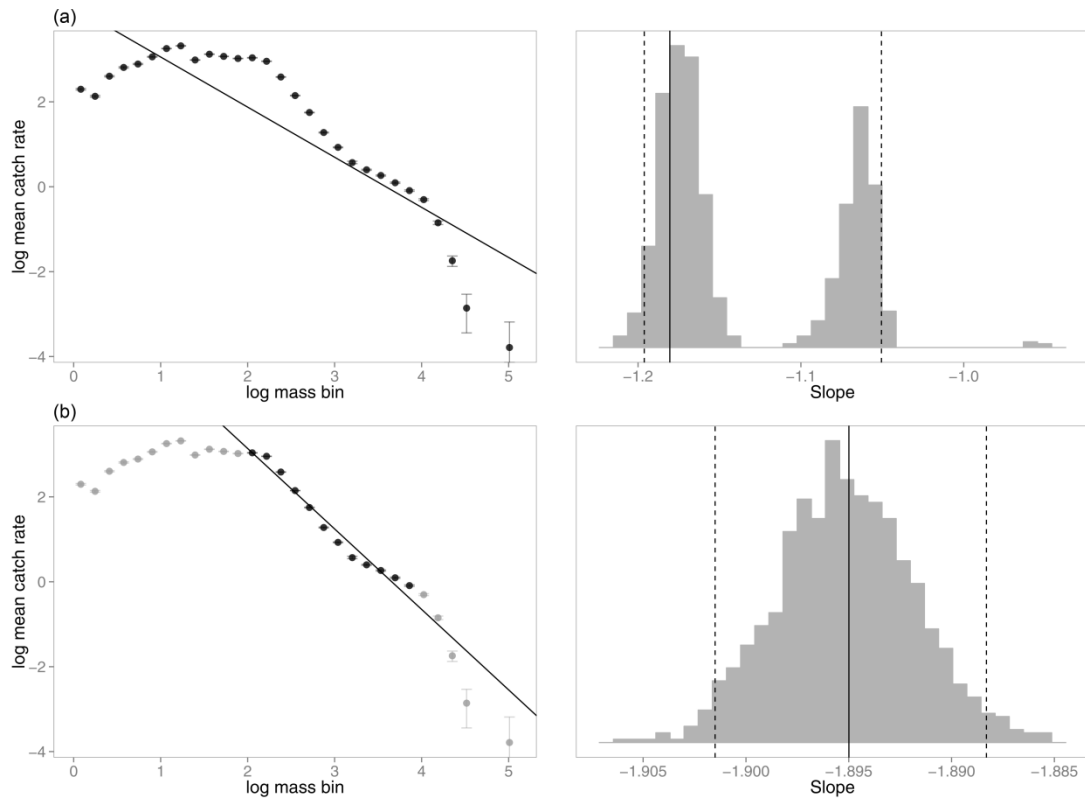


Figure B.9: Large fish biomass plotted against time (1991-2013) for all species in the whole North Sea (solid line) and a selection of species and grid cells (dashed line). Large fish biomass is the total biomass (based on cpu area) of fish above 40cm summed over all species and grid cells in each case. The species and grid cells in the selection represent the largest contributors to the LFI (an absolute value of their slope greater than 1×10^{-4}). The species are: *Gadus morhua*, *Amblyraja radiata*, *Merlangius merlangus*, *Melanogrammus aeglefinus*, *Mustelus asterias*, *Scyliorhinus canicula* and *Pollachius virens*. The grid cells are: 1x51, 0x53, 3x56, 3x58, 4x58, -2x59, -3x59, 3x59, 0x60, 3x60.

Appendix C

C.1. Slopes in different mass ranges

Slopes that included the largest bins (a,c) showed a bimodal distribution of surrogate slopes. Excluding these large size classes, the distribution of surrogate slopes became unimodal (b,d). The smaller size bins caused the slope to become shallower as they are lower in abundance than would be expected if the spectrum was linear (d). The restriction of log mass bins to a range between 2 and 4 showed the most appropriate range for assessing the linear section of the spectrum. This range was therefore chosen as the range of mass bins used in the main analyses.



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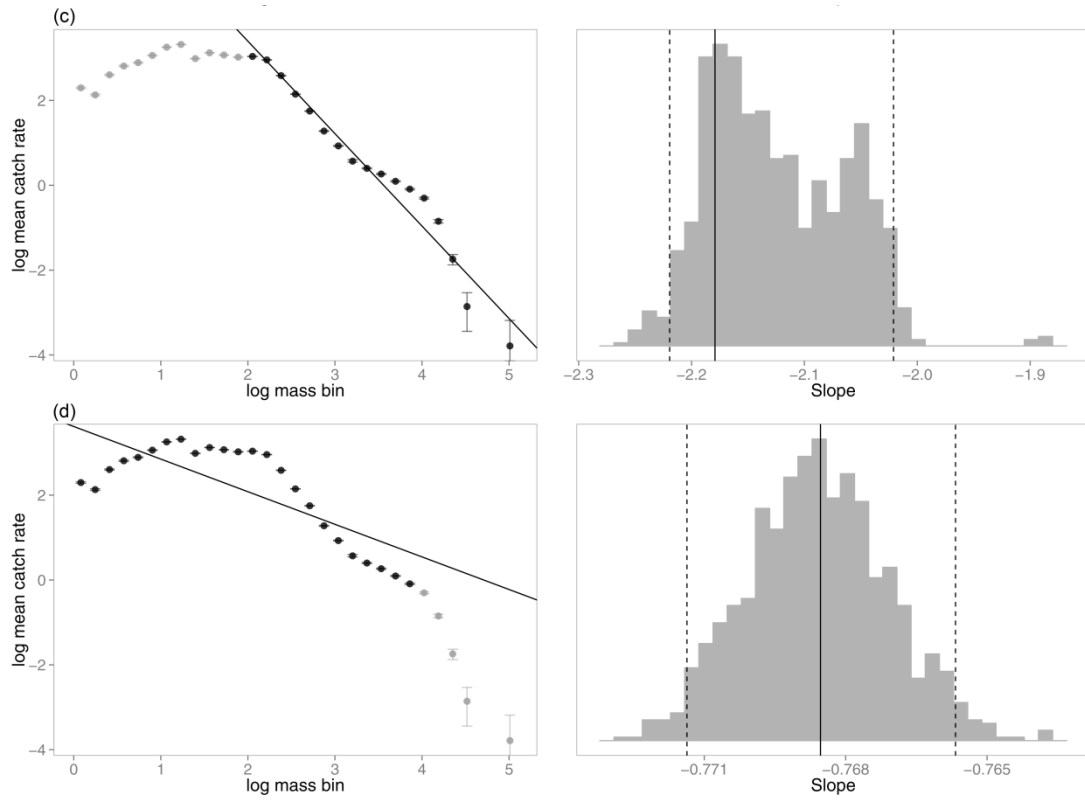
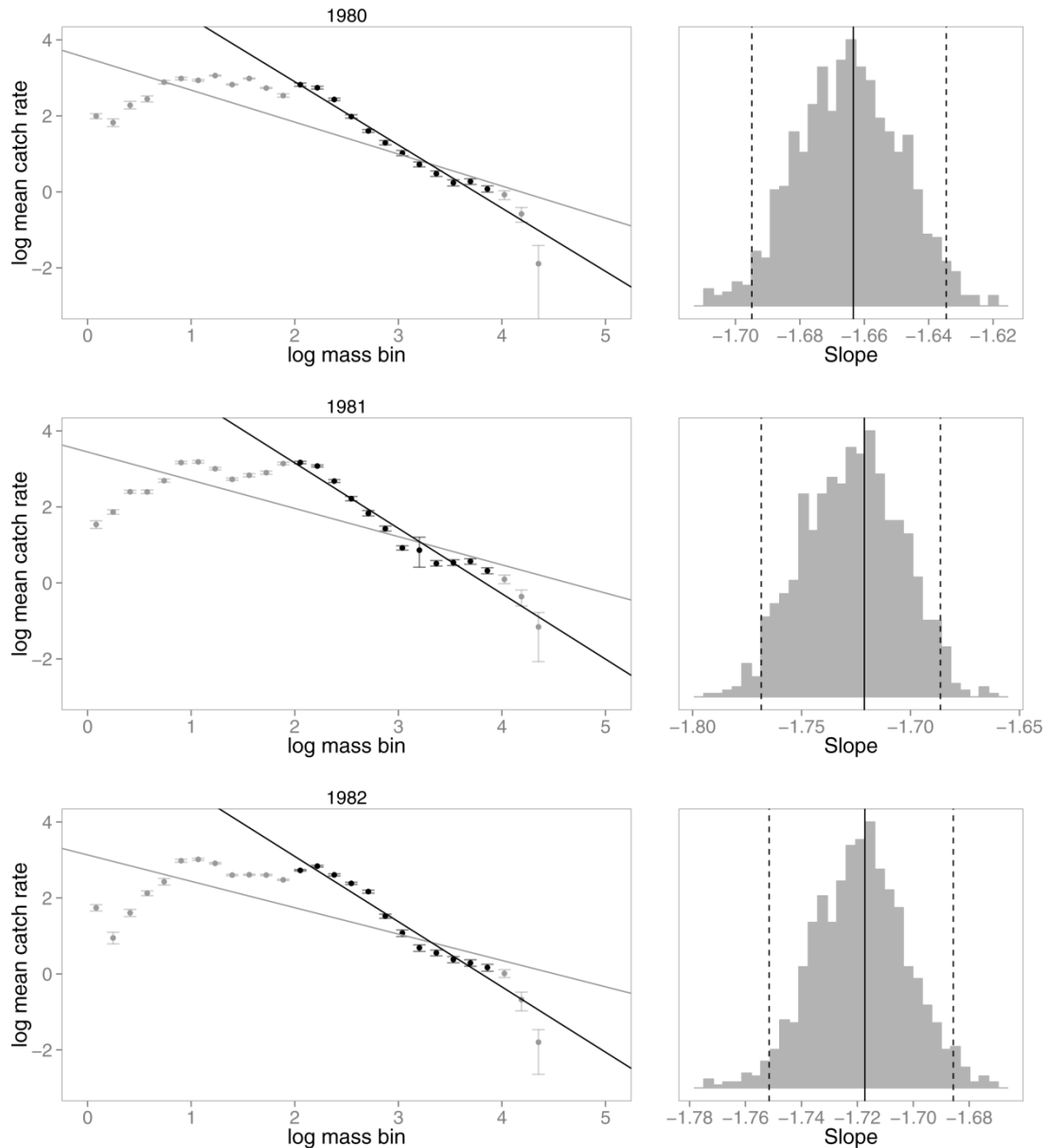


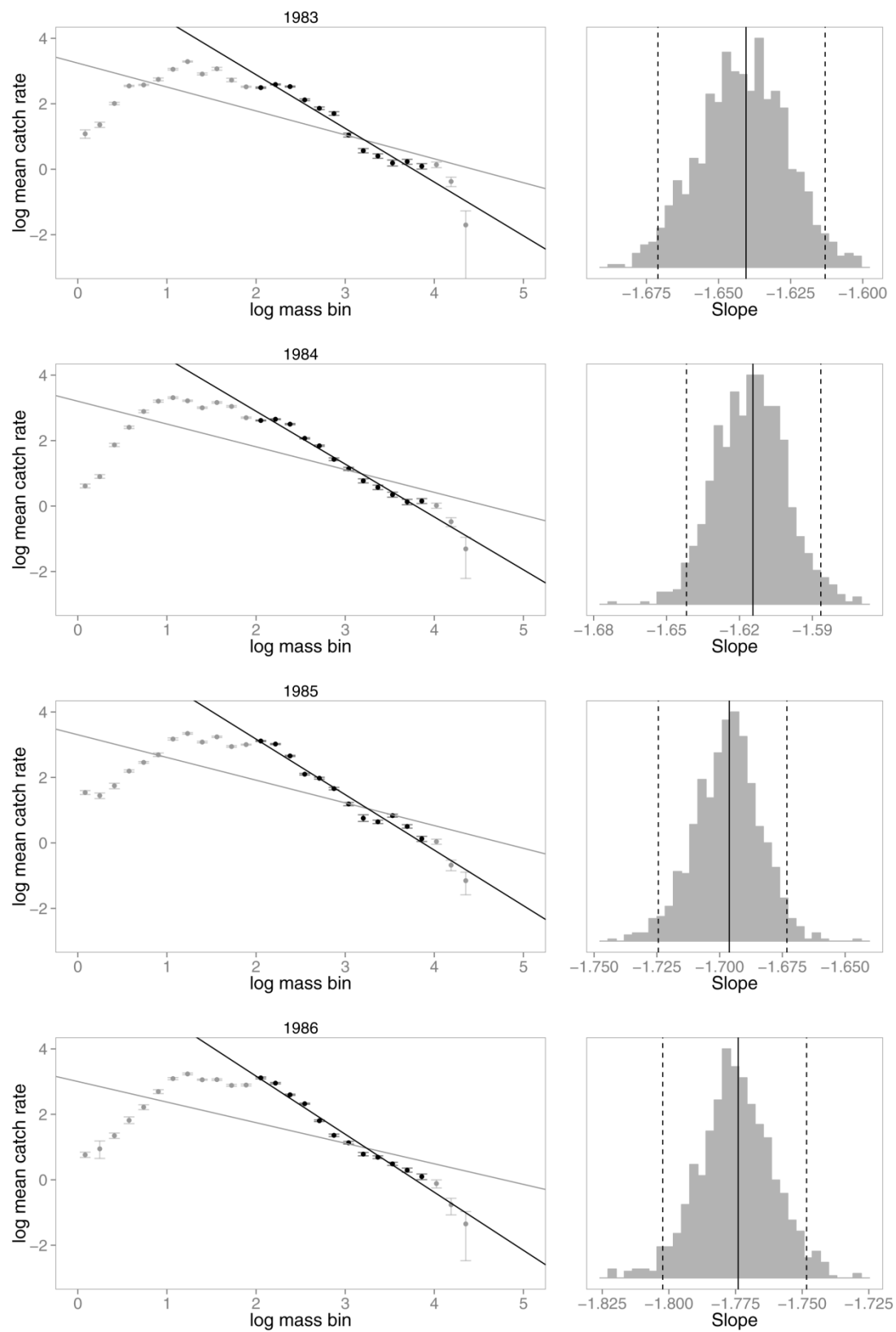
Figure C.1: Abundance spectrum for the whole North Sea, computed from data aggregated over 34 years (1980-2013). Log mass (g) is plotted against log mean yearly catch rate (cpue). The slope is fitted through mass bins by ordinary linear regression, the slope fit included different ranges of log mass bins; all mass bins (a), mass bins in the range 2 to 4 (b), the exclusion of small mass bins below 2 (c), and the exclusion of large mass bins above 4 (d). Light grey points show the values excluded from the slope fit. Histograms show the distributions of fitted slopes within each range of masses for each of the 1000 surrogate data sets, with dashed lines indicating the lower and upper confidence interval of the slope (solid line).

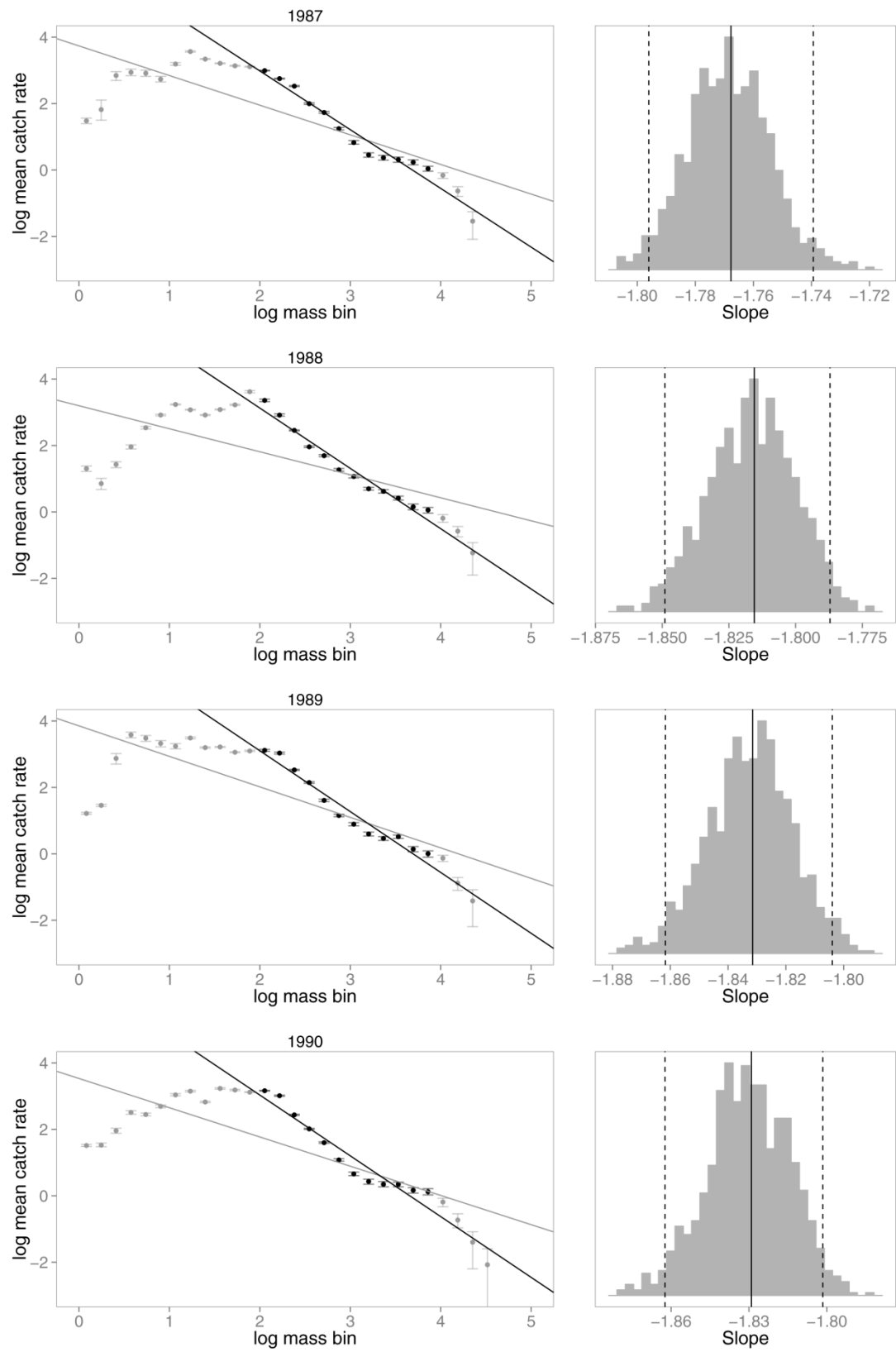
C.2. Spectra in individual years

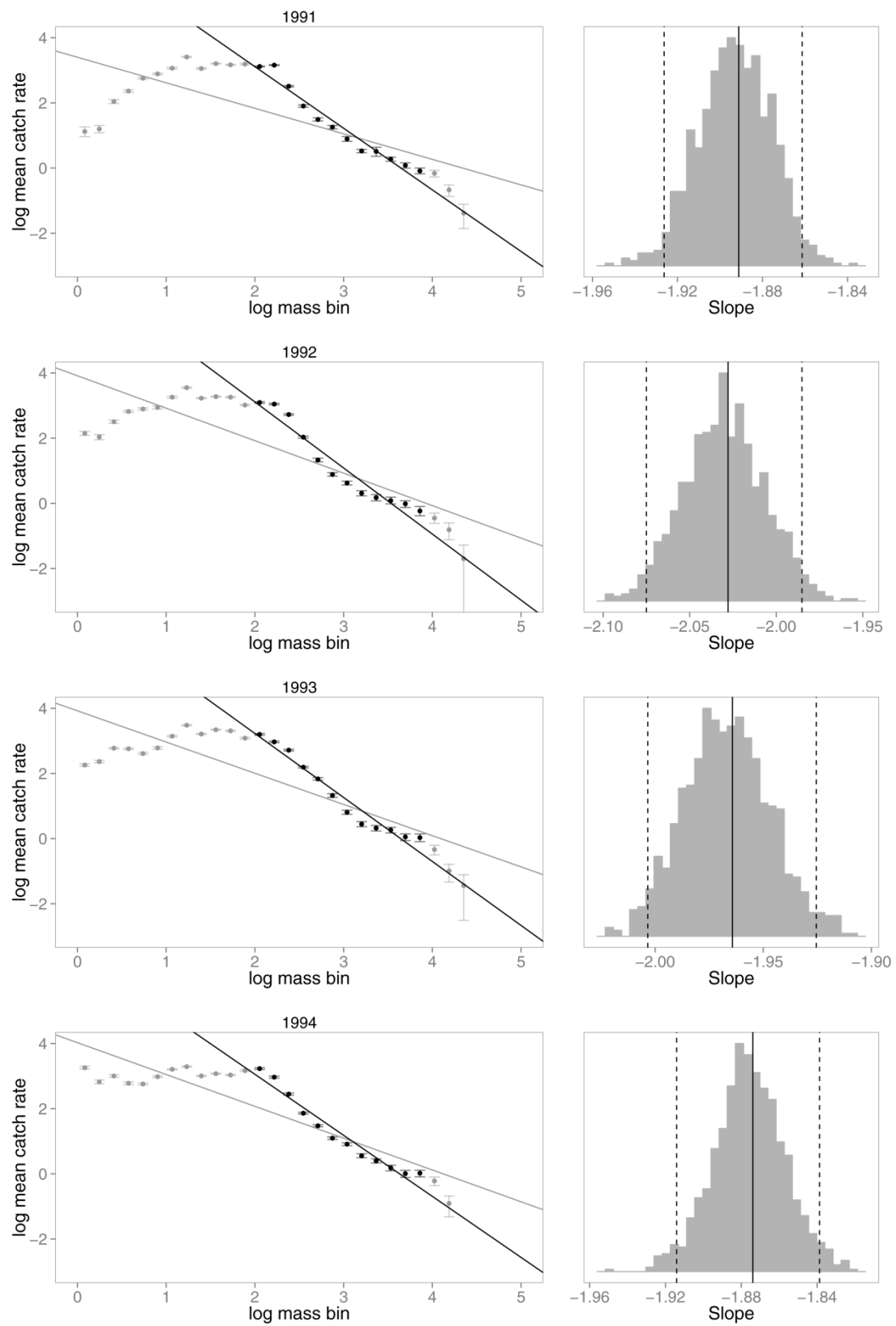
Figure C.2: Abundance spectra for the whole North Sea plotted for each year from 1980 to 2013. Log mass (g) is plotted against log mean catch rate (cpue). Confidence intervals on the abundance in each mass bin were calculated from the 1000 surrogate data sets. Histograms show the distribution of fitted slopes within a restricted log mass range (2 to 4), calculated for each of the 1000 surrogate data sets, with dashed lines indicating the lower and upper confidence interval of the slope (solid line).

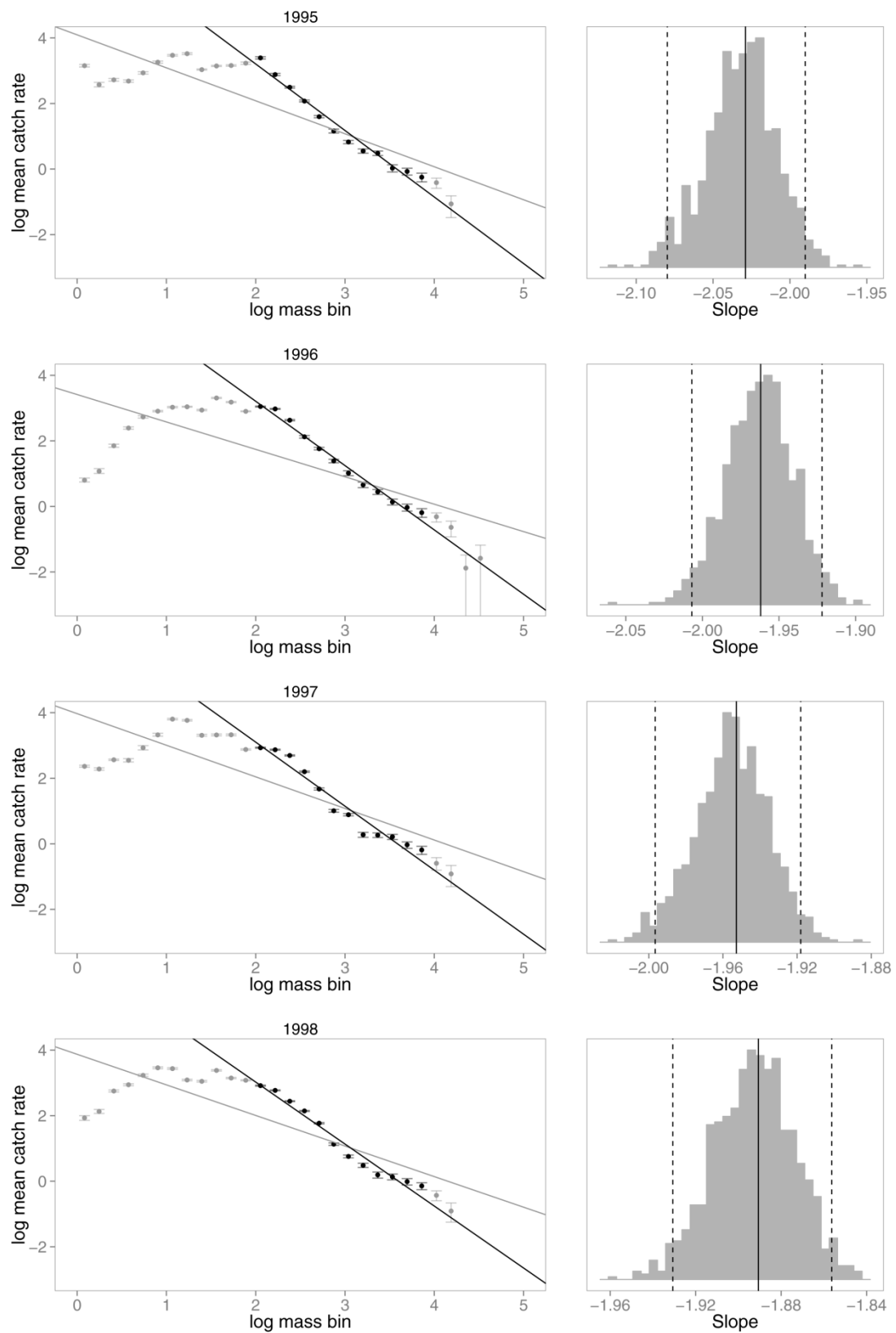


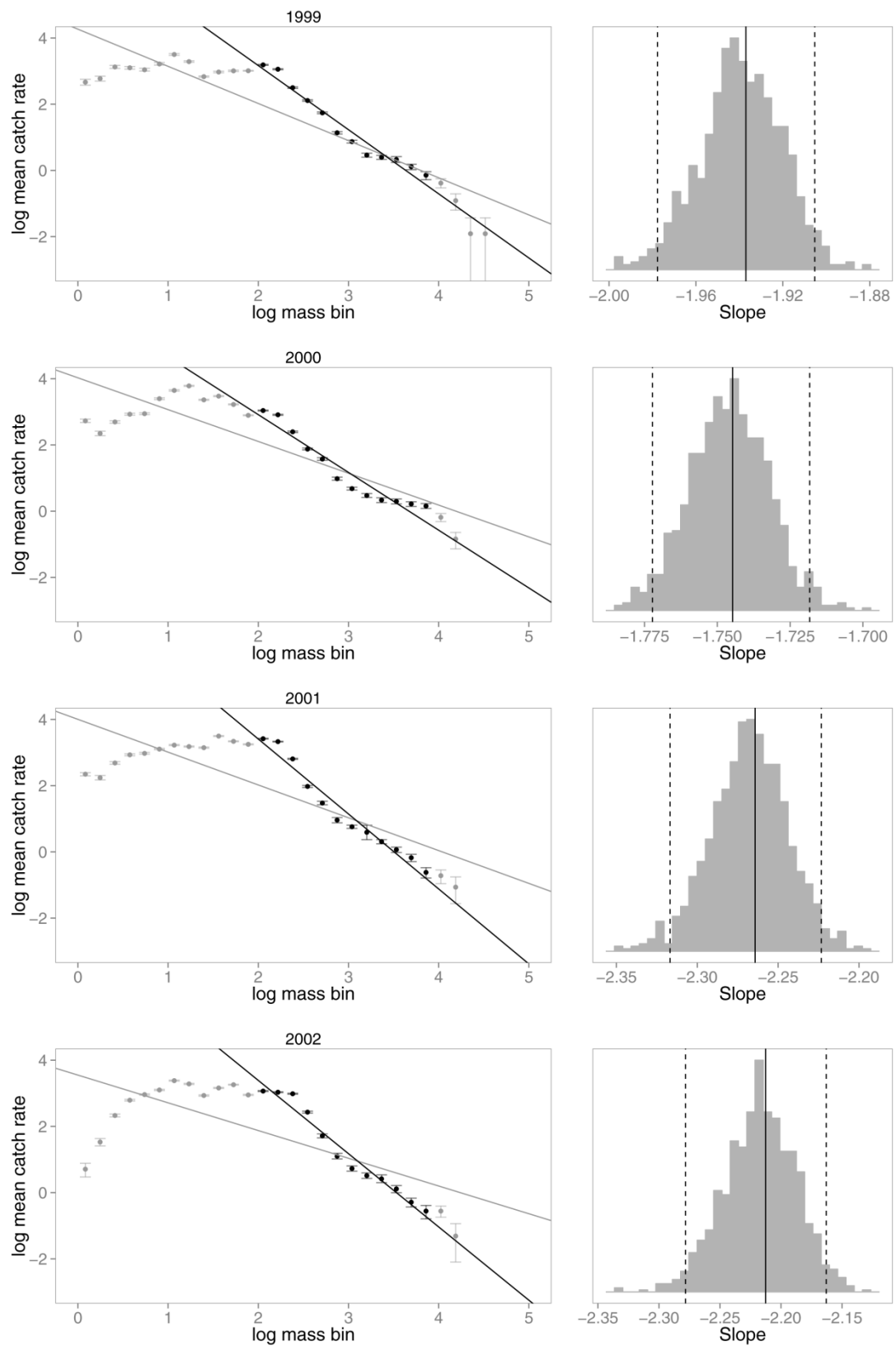
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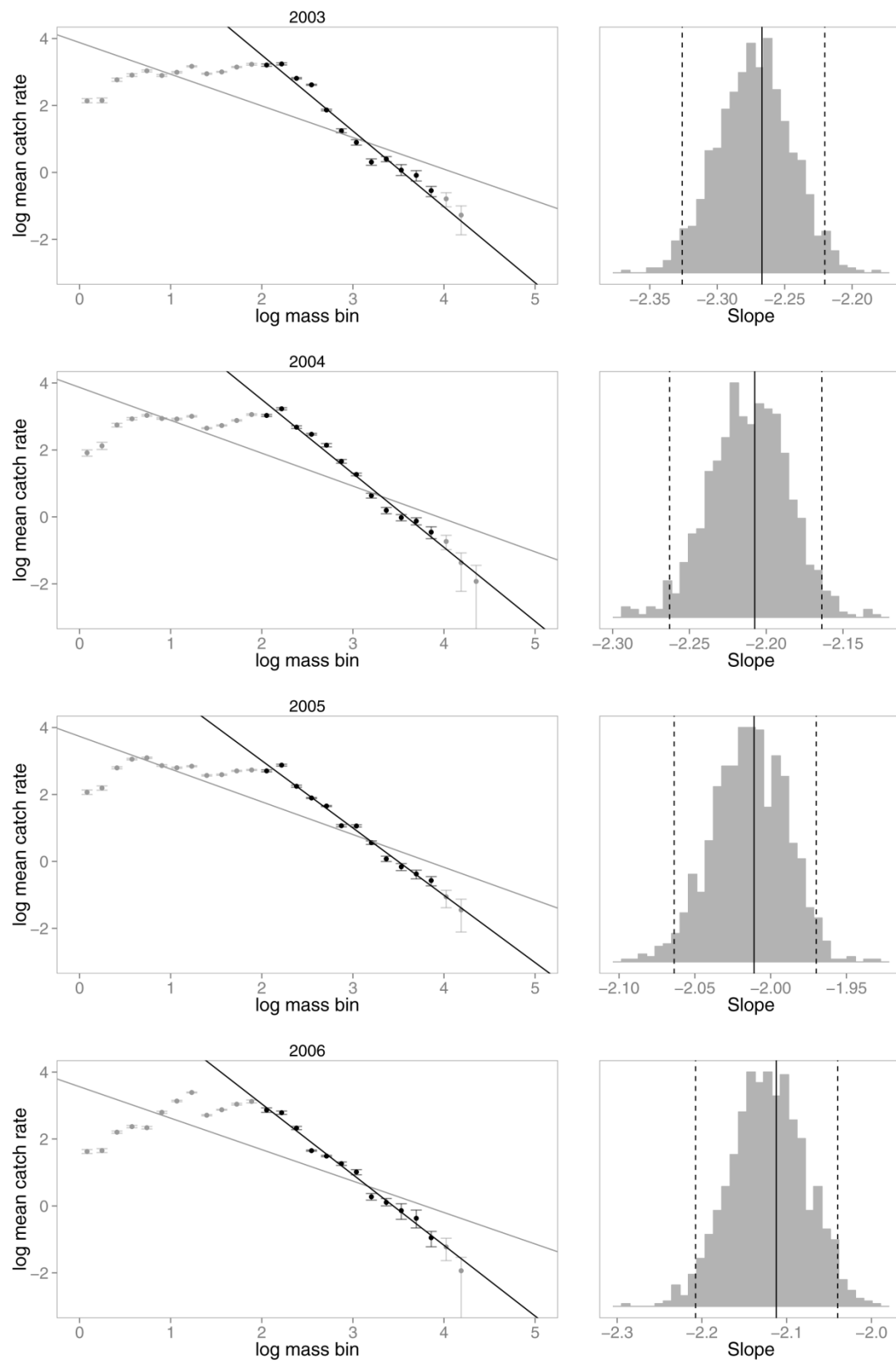


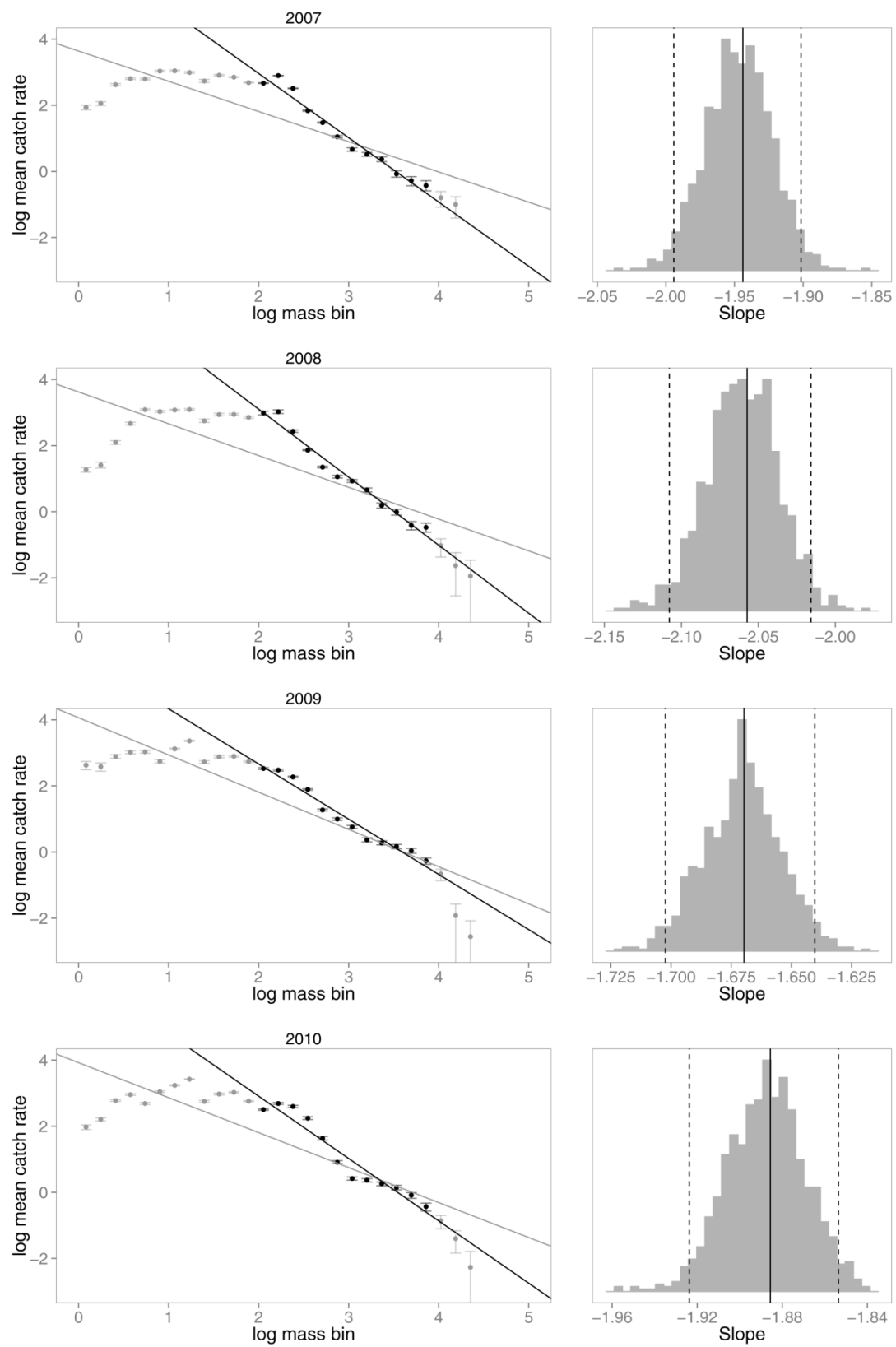


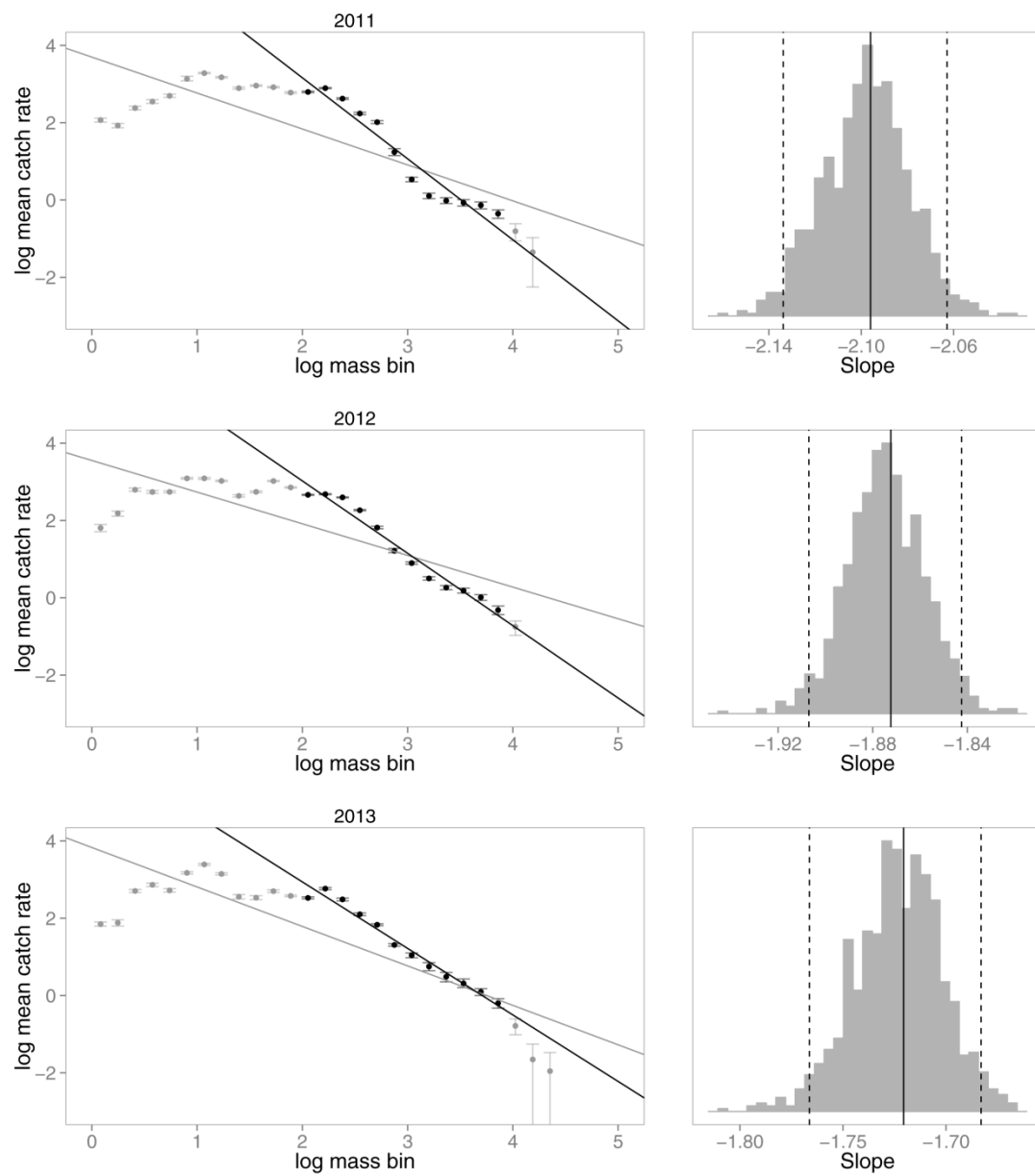












Appendix D

D.1. IBTS data cleaning methods

Data description

The International Bottom Trawl Survey (IBTS) is an annual survey carried out in the North Sea (ICES 2012), and is managed by ICES (International Council for the Exploration of the Seas). It originated as an international herring survey in the 1960s to assess juvenile herring, but gradually changed in design as it was realised that data on other species was also being collected and could be valuable. In the early 1990s, surveys carried out in the North Sea by various countries were combined with this older survey to form the quarter 1 (Q1) IBTS, and a further survey in quarter 3 (Q3) was added. Q1 is carried out in the spring, Q3 in the autumn. Two further quarterly surveys were added between 1991-1996 in Q2 and Q4, but I do not use these for analysis in any chapter of this thesis due to the very short time series available. The main objective of the survey is to provide standardised abundance data that can be used to assess community properties and examine spatial and temporal trends in the North Sea fish assemblages, independently of fisheries stock assessment data. There are currently 8 nations that contribute to the survey; England, Scotland, France, Netherlands, Norway, Sweden, Denmark, and Germany.

The IBTS surveys collect length and age data for all finfish species of the North Sea, and more recently for some shellfish and cephalopod species. The analyses in this thesis use only the length data set, and consider only fish species. The length distributions of each species are recorded for each haul towed, as follows: the catch is sorted by species (identified to species level where possible, but some genus or family level groups are also present in the data) and then by length. Length is measured to the nearest 1cm for all fish species except sprat and herring, which are measured to the nearest 0.5cm. This creates a naturally binned length distribution in the data. The number of individuals caught in each length category for each species is recorded.

The sampling design of the IBTS is stratified into ICES rectangles (1° longitude by 0.5° latitude) that each cover an area of roughly 30 x 30 nautical miles. The aim is to have two ships from different countries sample within each rectangle in a survey, so that at least two hauls per rectangle are carried out per year. The path trawled by the vessel within each rectangle usually varies from year to year; a number of defined, safe to trawl routes are available and are randomly selected from in most cases, but a small number of countries always trawl the same route so that some of the rectangles are sampled in the same place every year. Each trawl is 30 minutes in length and has been standardized since 1978 for all countries, except Scotland which carried out 1 hour trawls until 1998. All trawl lengths and locations are recorded in the IBTS data.

The IBTS is an otter trawl survey. The trawl gear used has been standardized for all countries since 1983 to the use of the GOV gear, with surveys carried out between 1978 and 1983 gradually changing over to that gear. The trawl operates by being towed by the vessel along the ground (at a standardized speed of 4 knots), meaning that each trawl is carried out at a different depth, dependent on the location in the North Sea. The depth and speed of each trawl are recorded in the survey. The GOV trawl gear primarily targets demersal species, as it operates at the level of the sea bed. The mesh openings in the nets of the gear are 20mm, so that very small individuals are not adequately sampled by the gear since they are able to swim through the openings. Larger individuals are also not adequately sampled by the GOV as they can outswim the gear and avoid being caught (ICES 2012).

Data cleaning

IBTS data was downloaded from the ICES data service for trawl surveys (DATRAS; datras.ices.dk) on 08/10/2013 for Q1 and 13/02/2014 for Q3. The data were cleaned following the IBTS survey manual (ICES 2012), Daan (2001) and Fung *et al.* (2012), with some updated adjustments and modifications that were needed for the analyses carried out in this thesis. The cleaning process I used is detailed below. The IBTS survey is known to contain errors, mostly due to the differences between countries in species identification and sampling (Daan, 2001). Where possible I tried to make the process of cleaning and removing errors as automated as possible, so that cleaning methods could be applied in exactly the same way to

Q1 and Q3 IBTS data, to the surrogate data sets, and be robust to the addition of data from future years.

Species – length records

Species names were assigned from the WoRMS (World Register of Marine Species; www.marinespecies.org) and ITIS (Integrated Taxonomic Integration System; www.itis.gov) databases using R package *taxize* (Chamberlain and Szocs 2013); individuals in the survey are identified to species level where possible and genus, family or occasionally order where not. All non-fish species (shellfish, cephalopods) were removed from the dataset. Length categories are supposed to be recorded in 1cm intervals for all fish except herring and sprat, but some vessels recorded some fish species to 1mm intervals. To ensure consistency across all vessels, lengths were standardised to 1cm intervals for all fish species except herring and sprat (which were standardised to 5mm categories). Individual records where incorrect lengths had been recorded were removed in the following way: any individual that was recorded as being over 10% longer than the maximum length recorded for its species (obtained from a list of North Sea maximum lengths by species on FishBase (www.fishbase.org) on 12/12/2013) was discarded from the data. This was consistent with individual records that lay far outside of the rest of the length distribution for that species in the data, and resulted in the removal of 262 records from Q1 and 135 from Q3.

For the calculation of most size-based metrics, body mass is needed. Because the survey only records length of individuals, length categories were converted to mass using species specific length-weight regressions where possible (Table D.1; ICES 2014), and the standard regression coefficients of 0.01 and 3 for fish elsewhere (Blanchard *et al.*, 2005; ICES, 2014). Less than 10% of biomass was estimated using the standard regression coefficients (ICES 2014). The specific length-weight regression coefficients came from (Silva *et al.*, 2013) which is the most up to date and comprehensive list of species-specific regressions available for the North Sea. The mid-point of the length interval for each species-length category was used in the regression.

Some indicators and studies suggest that pelagic species should be removed (Greenstreet *et al.*, 2011; Shephard *et al.*, 2011b) as they don't form part of the demersal community that is

sampled by the GOV trawl gear. However, they are an important part of the North Sea fish community and several very abundant and important small species (sprat, herring) are considered to be pelagic. I left those species in for the main analyses in each chapter, but carried out alternative analyses with pelagic species removed for the calculation of the LFI for comparison.

Some small individuals are usually removed from the data as they are under-sampled by the gear (ICES 2012), but the length or weight cut-off used tends to vary and could potentially remove a lot of the data. I left in all small species, but again for the analysis of the LFI, repeated the analysis with small (less than 200cm in length) species removed. In Chapter 4, all main analyses only considered species within a mass range that is adequately sampled by the gear.

Calculation of catch rates

In the downloaded catch data, for large hauls the catch had been subsampled by species according to weight and a subsampling factor was recorded. In other catches, the number of fish had been counted accurately, but only a subsample had been measured for length. In both cases, the number of individuals measured in each length class was scaled up by a subsampling factor. For some data, subsampling factors had been incorrectly recorded or were absent, so corrected estimates of actual numbers of fish measured per length category were obtained by calculating the corrected subsampling factor as the total catch column divided by the number of individuals measured. Subsampling factors taken by weight were checked by dividing the total catch weight by the measured weight.

Catch rate per unit effort (cpue; unit effort is one hour) was then calculated for each length category per species per haul; hauls are typically 30 minutes in duration but there is some variation in the data. Catch rate per unit area (cpua; unit area is per m²) was calculated following Fraser *et al.* (2007) to obtain catch rates that were corrected for the area swept by the gear in each haul, which varies by depth and by the speed of the vessel. Catch rates were then averaged over hauls in each ICES rectangle; the survey requires two hauls to be carried out in each ICES rectangle, but there is sometimes variation in the number of valid hauls per rectangle per year.

Catchability corrections

Because the GOV gear is known to under-sample smaller individuals (ICES 2012), catchability corrections have previously been derived for North Sea fish grouped by body type and applied to the data (Yang, 1982; Sparholt, 1990). These don't account for variations among and within species, however, and catchability can vary based on specific life stage or size of the individual. Fraser *et al.* (2007) expanded the catchability corrections to account for the differences of catchability within a species by length. The result of applying the species-length corrections is an increase in the proportion of biomass of small fish (Fraser *et al.*, 2007). These catchability corrections were derived from the differences in catch rates in the Q3 IBTS survey and in a Dutch beam trawl survey (BTS) also carried out in Q3. The BTS uses a different gear to the IBTS and catches several small demersal species not found in the IBTS, as they are not caught at all by the GOV gear. This method of calculating catchability corrections still relies on trawl survey data from the BTS, which likely comes with its own gear bias. They are also solely based on Q3 surveys, when fish have grown and individuals are larger in size overall. It has also been shown that catchability can vary between seasons for some large important species (haddock, cod; Harley & Myers 2001). Therefore, catchability corrections from the Q3 data are unlikely to be appropriate for the fish sampled in the Q1 survey, and seem likely to introduce a different bias to the one they are supposed to be correcting for. For these reasons, the main analyses using IBTS data in the thesis do not use catchability corrections. Alternative analyses with the corrections applied were carried out in Chapter 3 for comparison.

Spatial extent and aggregation

Inconsistencies in survey design from year to year can cause variability in the catch numbers and therefore any indicators (Piet & Jennings, 2005). Consistent spatial sampling is important as different areas may have different populations that can influence values of the indicator (Shin *et al.*, 2005). In order to make the data comparable temporally and spatially, ICES rectangles were grouped into 1x1 degree grid cells, and any grid cell with missing hauls in more than 2 years was discarded (Greenstreet *et al.*, 2012c). The same grid cells were included in every year. For results that compare Q1 with Q3, Q1 data was restricted to the same grid cells as in Q3, which is a more limited survey both spatially and temporally. The

IBTS is sampled in areas that are typically defined as being outside of the North Sea region (Kattegat and Skaggeerrat) so ICES rectangles in these areas were removed from the data. Maps with the grid cells included in each analysis are shown in Figure D.1 (Chapter 3 and 5 analyses with both Q1 and Q3) and Figure D.1 (Chapter 4 analysis that included only Q1).

Invalid hauls

Hauls towed at night, or with a duration of less than 15 minutes were removed from the data (ICES 2012, Petrakis 2001).

Table D.1: Species in the IBTS survey, with truncated species names as used in some plots. Species-specific weight-length regression coefficients from Silva et al. (2013) are listed as a and b, used in the form $W=aL^b$, where W is weight and L is length. Values of 0.01 and 3 were used where no species-specific coefficients were available. The final column indicates which survey the species was present in, Q1, Q3 or both.

Species	Truncated species name	a	b	Quarter
Acentronura		0.01	3	Q1
<i>Agonus cataphractus</i>	Ago_cata	0.0232	2.5916	Q1, Q3
Alosa		0.01	3	Q1
<i>Alosa agone</i>	Alo_agon	0.01	3	Q1, Q3
<i>Alosa alosa</i>	Alo_alos	0.00492	3.20165	Q1, Q3
<i>Alosa fallax</i>	Alo_fall	0.01	3	Q1, Q3
<i>Amblyraja radiata</i>	Amb_radi	0.0107	2.94	Q1, Q3
Ammodytes		0.01	3	Q1, Q3
<i>Ammodytes marinus</i>	Amm_mari	0.0017	3.1828	Q1, Q3
<i>Ammodytes tobianus</i>	Amm_tobi	0.01	3	Q1, Q3
Ammodytidae		0.01	3	Q1, Q3
Anarhichadidae		0.01	3	Q1
<i>Anarhichas lupus</i>	Ana_lupu	0.0046	3.1849	Q1, Q3
<i>Anarhichas minor</i>	Ana_mino	0.01	3	Q3
<i>Anguilla anguilla</i>	Ang_angu	0.01	3	Q1, Q3
Anguillidae		0.01	3	Q3
<i>Aphia minuta</i>	Aph_minu	0.01	3	Q1, Q3
Argentina		0.01	3	Q1, Q3
<i>Argentina silus</i>	Arg_silu	0.01	3	Q1, Q3
<i>Argentina sphyraena</i>	Arg_sphy	0.0053	3.0534	Q1, Q3
Arnoglossus		0.01	3	Q1
<i>Arnoglossus imperialis</i>	Arn_impe	0.007	3.0541	Q1, Q3
<i>Arnoglossus laterna</i>	Arn_late	0.0198	2.6673	Q1, Q3
<i>Atherina presbyter</i>	Ath_pres	0.01	3	Q1
<i>Belone belone</i>	Bel_belo	2.00E-04	3.442	Q1, Q3
Blenniidae		0.01	3	Q1
Bothidae		0.01	3	Q1
<i>Brama brama</i>	Bra_bram	0.01	3	Q1
<i>Brosme brosme</i>	Bro_bros	0.00514	3.189	Q1, Q3
Buglossidium		0.01	3	Q1

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<i>Buglossidium luteum</i>	Bug_lute	0.0157	2.9092	Q1, Q3
<i>Callionymidae</i>		0.01	3	Q1, Q3
<i>Callionymus</i>		0.01	3	Q1
<i>Callionymus lyra</i>	Cal_lyra	0.021	2.647	Q1, Q3
<i>Callionymus maculatus</i>	Cal_macu	0.0369	2.2653	Q1, Q3
<i>Callionymus reticulatus</i>	Cal_reti	0.0296	2.3367	Q1, Q3
<i>Capros aper</i>	Cap_aper	0.0549	2.6322	Q1, Q3
<i>Chelidonichthys cuculus</i>	Che_cucu	0.0089	3.0257	Q1, Q3
<i>Chelidonichthys lucerna</i>	Che_luce	0.0106	2.9846	Q1, Q3
<i>Chimaera monstrosa</i>	Chi_mons	0.01	3	Q1, Q3
<i>Ciliata mustella</i>	Cil_must	0.01	3	Q1
<i>Ciliata septentrionalis</i>	Cil_sept	0.0092	2.9846	Q1, Q3
<i>Clupea harengus</i>	Clu_hare	0.0026	3.3687	Q1, Q3
<i>Conger conger</i>	Con_cong	2.00E-04	3.5789	Q1, Q3
<i>Cottidae</i>		0.01	3	Q1
<i>Crystallogobius linearis</i>	Cry_line	0.01	3	Q1, Q3
<i>Ctenolabrus rupestris</i>	Cte_rupe	0.015	3.0403	Q1, Q3
<i>Cyclopteridae</i>		0.01	3	Q1
<i>Cyclopterus lumpus</i>	Cyc_lump	0.0587	2.939	Q1, Q3
<i>Dicentrarchus labrax</i>	Dic_labr	0.0103	3.0047	Q1, Q3
<i>Diplecogaster bimaculata</i>	Dip_bima	0.0589	1.8205	Q1
<i>Dipturus batis</i>	Dip_bati	0.0038	3.1201	Q1, Q3
<i>Dipturus linteus</i>	Dip_lint	0.01	3	Q1
<i>Echiichthys vipera</i>	Ech_vipe	0.0186	2.8398	Q1, Q3
<i>Echiodon drummondii</i>	Ech_drum	0.01	3	Q1, Q3
<i>Enchelyopus cimbrius</i>	Enc_cimb	0.008	2.8377	Q1, Q3
<i>Engraulis encrasicolus</i>	Eng_encr	0.005	3.1072	Q1, Q3
<i>Entelurus aequoreus</i>	Ent_aequ	8.00E-04	2.5939	Q1, Q3
<i>Eutrigla gurnardus</i>	Eut_gurn	0.0091	2.9772	Q1, Q3
<i>Gadiculus argenteus</i>	Gad_arge	0.016	2.7931	Q1, Q3
<i>Gadus morhua</i>	Gad_morh	0.0098	3.0109	Q1, Q3
<i>Gaidropsarus</i>		0.01	3	Q1
<i>Gaidropsarus mediterraneus</i>	Gai_medi	0.0133	2.8387	Q1
<i>Gaidropsarus vulgaris</i>	Gai_vulg	0.0051	3.1481	Q1, Q3
<i>Galeorhinus galeus</i>	Gal_gale	0.0038	3.0331	Q1, Q3
<i>Gasterosteidae</i>		0.01	3	Q1
<i>Gasterosteus aculeatus</i>	Gas_acul	0.01	3	Q1, Q3
<i>Glyptocephalus cynoglossus</i>	Gly_cyno	0.0033	3.2048	Q1, Q3
<i>Gobiidae</i>		0.01	3	Q1, Q3
<i>Gobius</i>		0.01	3	Q1
<i>Gobius cobitis</i>	Gob_cobi	0.01	3	Q1
<i>Gobius niger</i>	Gob_nige	0.0056	3.3081	Q1, Q3
<i>Gymnammodytes semisquamatus</i>	Gym_semi	0.0489	2.0911	Q1, Q3
<i>Helicolenus dactylopterus</i>	Hel_dact	0.0104	3.09109	Q1, Q3
<i>Hippoglossoides platessoides</i>	Hip_plat	0.0105	2.9029	Q1, Q3
<i>Hippoglossus hippoglossus</i>	Hip_hipp	0.0023	3.3796	Q1, Q3
<i>Hyperoplus</i>		0.01	3	Q1, Q3
<i>Hyperoplus immaculatus</i>	Hyp_imma	0.0056	2.8225	Q1, Q3
<i>Hyperoplus lanceolatus</i>	Hyp_lanc	0.0087	2.6262	Q1, Q3
<i>Labrus bergylta</i>	Lab_berg	0.0127	3.1048	Q1
<i>Labrus mixtus</i>	Lab_mixt	0.0069	3.2084	Q1
<i>Lampetra fluviatilis</i>	Lam_fluv	0.01	3	Q1, Q3
<i>Lepadogaster</i>		0.01	3	Q1
<i>Lepidorhombus whiffiagonis</i>	Lep_whif	0.0058	3.0736	Q1, Q3
<i>Leptoclinus maculatus</i>	Lep_macu	0.01	3	Q3
<i>Lesueurigobius friesii</i>	Les_frie	0.0641	2.1122	Q1
<i>Leucoraja circularis</i>	Leu_circ	0.01	3	Q1, Q3
<i>Leucoraja fullonica</i>	Leu_full	0.0033	3.098	Q1, Q3
<i>Leucoraja naevus</i>	Leu_naev	0.0036	3.1399	Q1, Q3
<i>Limanda limanda</i>	Lim_lima	0.0171	2.8468	Q1, Q3

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Liparis		0.01	3	Q1
<i>Liparis liparis</i>	Lip_lipa	0.01	3	Q1, Q3
<i>Liparis montagui</i>	Lip_mont	0.01	3	Q1, Q3
Lophiidae		0.01	3	Q1
<i>Lophius budegassa</i>	Lop_bude	0.0259	2.8575	Q1, Q3
<i>Lophius piscatorius</i>	Lop_pisc	0.0266	2.8614	Q1, Q3
<i>Lumpenus lampretaeformis</i>	Lum_lamp	0.0342	1.9847	Q1, Q3
<i>Lycenchelys sarsii</i>	Lyc_sars	0.01	3	Q3
<i>Lycodes gracilis</i>	Lyc_grac	0.01	3	Q3
<i>Lycodes vahlii</i>	Lyc_vahl	0.01	3	Q1, Q3
<i>Maurolucus muelleri</i>	Mau_muel	0.1149	1.6065	Q1, Q3
<i>Melanogrammus aeglefinus</i>	Mel_aegl	0.0083	3.0473	Q1, Q3
<i>Merlangius merlangus</i>	Mer_merl	0.0082	3.0059	Q1, Q3
<i>Merluccius merluccius</i>	Mer_merl	0.006	3.0363	Q1, Q3
<i>Micrenophrys lilljeborgii</i>	Mic_lill	0.01	3	Q1
<i>Microchirus variegatus</i>	Mic_vari	0.0185	2.8546	Q1, Q3
<i>Micromesistius poutassou</i>	Mic_pout	0.0047	3.1074	Q1, Q3
<i>Microstomus kitt</i>	Mic_kitt	0.0106	3.0419	Q1, Q3
<i>Molva dypterygia</i>	Mol_dypt	0.01	3	Q1
<i>Molva molva</i>	Mol_molv	0.0036	3.108	Q1, Q3
Mugilidae		0.01	3	Q1, Q3
<i>Mullus barbatus</i>	Mul_barb	0.01	3	Q1, Q3
<i>Mullus surmuletus</i>	Mul_surm	0.0092	3.1048	Q1, Q3
Mustelus		0.01	3	Q1, Q3
<i>Mustelus asterias</i>	Mus_aste	0.01	3	Q1, Q3
<i>Mustelus mustelus</i>	Mus_must	0.01	3	Q1, Q3
<i>Myoxocephalus quadricornis</i>	Myo_quad	0.01	3	Q1
<i>Myoxocephalus scorpioides</i>	Myo_scor	0.01	3	Q1, Q3
<i>Myoxocephalus scorpius</i>	Myo_scor	0.0273	2.8524	Q1, Q3
<i>Myxine glutinosa</i>	Myx_glut	0.0167	2.2466	Q1, Q3
<i>Nerophis ophidion</i>	Ner_ophi	0.01	3	Q1
<i>Osmerus eperlanus</i>	Osm_eper	0.01	3	Q1, Q3
<i>Pagellus erythrinus</i>	Pag_eryt	0.01	3	Q1
<i>Pegusa lascaris</i>	Peg_lasc	0.008	3.1282	Q1
<i>Petromyzon marinus</i>	Pet_mari	3.00E-04	3.4046	Q1, Q3
<i>Pholis gunnellus</i>	Pho_gunn	0.0138	2.4873	Q1, Q3
<i>Phrynorhombus norvegicus</i>	Phr_norv	0.01	3	Q1, Q3
<i>Phycis blennoides</i>	Phy_blen	0.0051	3.1469	Q1, Q3
<i>Platichthys flesus</i>	Pla_fles	0.0244	2.7853	Q1, Q3
<i>Pleuronectes platessa</i>	Ple_plat	0.0151	2.8876	Q1, Q3
<i>Pollachius pollachius</i>	Pol_poll	0.0076	3.0686	Q1, Q3
<i>Pollachius virens</i>	Pol_vire	0.0085	3.0242	Q1, Q3
Pomatoschistus		0.01	3	Q1, Q3
<i>Pomatoschistus microps</i>	Pom_micr	0.01	3	Q1
<i>Pomatoschistus minutus</i>	Pom_minu	0.0062	3.173	Q1, Q3
<i>Pomatoschistus pictus</i>	Pom_pict	0.0073	3.02	Q1
Raja		0.01	3	Q1, Q3
<i>Raja brachyura</i>	Raj_brac	0.0027	3.258	Q1, Q3
<i>Raja clavata</i>	Raj_clav	0.0045	3.0961	Q1, Q3
<i>Raja montagui</i>	Raj_mont	0.0041	3.1152	Q1, Q3
<i>Raja undulata</i>	Raj_undu	0.004	3.1346	Q1
Rajidae		0.01	3	Q1, Q3
<i>Raniceps raninus</i>	Ran_rani	0.0062	3.2667	Q1, Q3
<i>Salmo salar</i>	Sal_sala	0.01	3	Q3
<i>Salmo trutta</i>	Sal_trut	0.01	3	Q1, Q3
<i>Sardina pilchardus</i>	Sar_pilc	0.0053	3.1619	Q1, Q3
<i>Scomber scombrus</i>	Sco_scom	0.0014	3.544	Q1, Q3
<i>Scophthalmus maximus</i>	Sco_maxi	0.0149	3.0791	Q1, Q3
<i>Scophthalmus rhombus</i>	Sco_rhom	0.014	3.0096	Q1, Q3
<i>Scyliorhinus canicula</i>	Scy_cani	0.0022	3.1194	Q1, Q3

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<i>Scyliorhinus stellaris</i>	Scy_stel	0.0045	3.0155	Q1, Q3
<i>Sebastes norvegicus</i>	Seb_norv	0.01	3	Q1, Q3
<i>Sebastes viviparus</i>	Seb_vivi	0.0115	3.1369	Q1, Q3
<i>Sepia officinalis</i>	Sep_offi	0.01	3	Q1, Q3
<i>Solea solea</i>	Sol_sole	0.008	3.0499	Q1, Q3
Soleidae		0.01	3	Q1
Sparidae		0.01	3	Q1
<i>Spinachia spinachia</i>	Spi_spin	0.01	3	Q1
<i>Spondyliosoma cantharus</i>	Spo_cant	0.0148	3.0044	Q1, Q3
<i>Sprattus sprattus</i>	Spr_spra	0.0088	2.9193	Q1, Q3
<i>Squalus acanthias</i>	Squ_acan	0.0017	3.208	Q1, Q3
Stichaeidae		0.01	3	Q1, Q3
<i>Symphodus melops</i>	Sym_melo	0.01	3	Q1
Syngnathidae		0.01	3	Q1, Q3
Syngnathus		0.01	3	Q1
<i>Syngnathus acus</i>	Syn_acus	6.00E-05	3.527	Q1, Q3
<i>Syngnathus rostellatus</i>	Syn_rost	1.00E-04	3.414	Q1, Q3
<i>Syngnathus typhle</i>	Syn_typh	0.01	3	Q1
<i>Taurulus bubalis</i>	Tau_buba	0.0161	3.0785	Q1, Q3
<i>Trachinus draco</i>	Tra_drac	0.0087	2.9231	Q1, Q3
<i>Trachurus trachurus</i>	Tra_trac	0.0105	2.9622	Q1, Q3
<i>Trachyrincus murrayi</i>	Tra_murr	0.01	3	Q1
Triglidae		0.01	3	Q1, Q3
<i>Trigloporus lastoviza</i>	Tri_last	0.017	2.8685	Q1, Q3
<i>Triglops murrayi</i>	Tri_murr	0.01	3	Q1, Q3
<i>Trisopterus esmarkii</i>	Tri_esma	0.01	3	Q1, Q3
<i>Trisopterus luscus</i>	Tri_lusc	0.0151	2.9459	Q1, Q3
<i>Trisopterus minutus</i>	Tri_minu	0.0117	2.9452	Q1, Q3
Zeiformes		0.01	3	Q1
<i>Zeugopterus punctatus</i>	Zeu_punc	0.0206	3.024	Q1, Q3
<i>Zeugopterus regius</i>	Zeu_regi	0.0129	3.2052	Q1
<i>Zeus faber</i>	Zeu_fabe	0.0399	2.7536	Q1, Q3
<i>Zoarcas viviparus</i>	Zoa_vivi	0.0417	2.2532	Q1, Q3
Zoarcidae		0.01	3	Q3

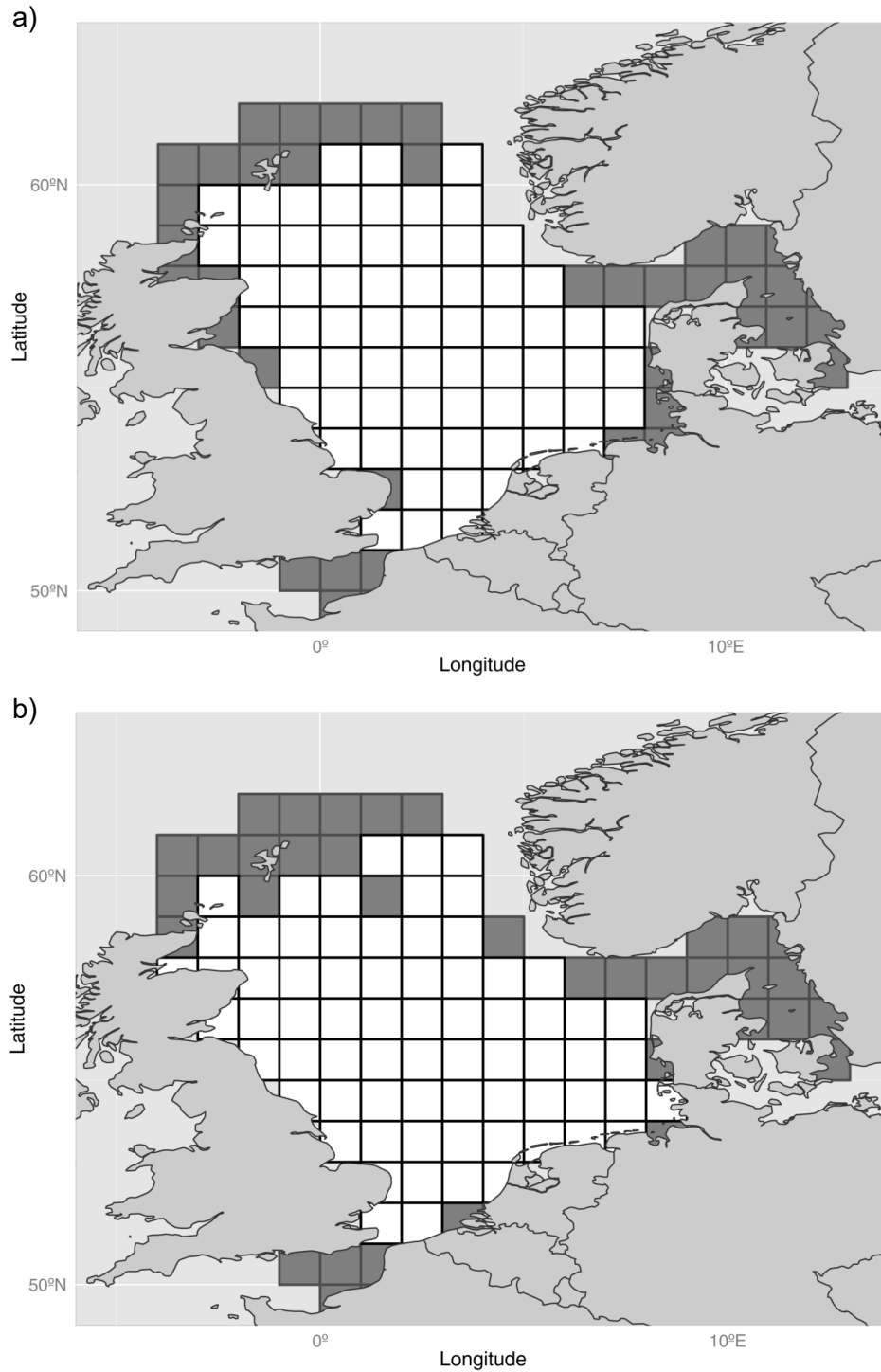


Figure D.1: Map of the North Sea showing 1° x 1° grid cells included in analyses in Chapters 3 and 5 (a) and Chapter 4 (b), highlighted in white. Excluded grid cells are shown in dark grey. Grid cells in (a) were selected as those which had no more than 2 missing years of data per grid cell in the years 1991-2013, across both Q1 and Q3 IBTS data. Grid cells in (b) had no more than 2 missing years of data per grid cell in the years 1980-2013 in Q1 data.