

Modelling changes in the growth, maturity, and abundance  
of fish in Scottish waters.

PhD Thesis

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# Abstract

The quantity of fish that may be sustainably harvested from the oceans depends upon how abundant they are and, less obviously, on their rate of growth, the sizes they can attain and the sizes at which they begin reproducing. This thesis investigates whether fish stocks in Scottish waters have exhibited long term changes in growth rates, maturation scheduling or abundance. The Firth of Clyde was of particular interest, so fish stocks from this region were considered separately in each chapter.

Scientific bottom trawl survey data were used to examine changes in growth rates and maturation scheduling. Trends in growth rates were determined by calculating time series of mean lengths-at-age and von Bertalanffy growth parameters. Probabilistic maturation reaction norms were used to investigate trends in maturation. The von Bertalanffy growth parameters and maturation indices were regressed against sea-surface temperature data and abundance indices derived from the survey data to determine whether trends in these variables were responsible for changes in growth and maturation. Demersal fish species were considered in chapters 2 and 3, and pelagic fish species were considered in chapter 4. Long term declines in growth rates and lengths-at-maturation were observed in several species.

A length based stock assessment model was developed in chapter 5. Information on the length structure of stocks was provided by survey samples instead of catch-at-length data which is typical for such models, so the model presented here should be widely applicable since many different species are sampled by surveys. Model output was compared with existing results derived from more conventional age based models. The results were encouraging; Bayesian implementations, in particular, returned output very similar to the existing age based models.

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# Chapter 1

## Introduction

### 1.1 Overview

Fish are an important component of human diets. Recent studies indicate that fish, molluscs and other crustaceans account for about 13.8–16.5% of the animal protein consumed globally by humans (WHO, 2002). Fishing practises developed over centuries, from local subsistence fishing using relatively basic technologies and small boats, into a lucrative global industry that utilises sophisticated fishing gears and vessels. Advances in technology allowed seafood to be preserved and transported over large distances for trade, so fish have become increasingly important, not simply as food, but as a commodity. The quantity of fish harvested from the oceans has risen to satisfy increasing demand from the ever-expanding human population. The number of fish in the ocean is, of course, finite, so intensive fishing can endanger fish populations and the amount that may be harvested is limited.

There is evidence that historical harvest of fish and shellfish from coastal regions around the world has dramatically altered ecosystems, primarily by reducing the abundance of large species — including mammals, fish and invertebrates (Jackson et al., 2001). The industrialisation of fishing over the last century has increased the rate at which fish are harvested and expanded the range of vessels, so transformations observed in coastal ecosystems have spread outwards into the oceans and the impact of fishing has never been as high as it is currently (Martins et al., 2012). Many productive fish-

eries have declined or collapsed in recent decades due to overfishing. Species that are targeted by fisheries, and those caught as bycatch, are at risk of overexploitation that can cause declines in abundance. This can lead to the extirpation of fish populations. Fishing-induced declines in the abundance of harvested species may also have cascading effects through the food web, so fishing can have indirect consequences for myriad species regardless of whether those species are harvested by fisheries. Declines in the abundance of fish and changes to the species complement in marine ecosystems are detrimental to human populations and fisheries which rely on an abundance of fish for sustenance and profit.

Aside from altering the abundance of ocean life, fishing can also influence the growth rates and maturation timings of harvested fish stocks. When such fishing-induced changes are observed it is typical for maturation to occur at increasingly young ages with passing generations (Law, 2000; Jørgensen et al., 2007). Changes in growth tend to be more variable, but long term declines in the growth rate of fish from harvested stocks are observed more frequently than increases in growth rate. There are numerous mechanisms for changes in growth and maturation — both natural and anthropogenic — but since declines in growth rate and decreases in age and/or length at maturation are often associated to the level of exploitation, it seems that fishing practises have played a vital role in altering the growth and maturation of many exploited stocks (Dunlop et al., 2009). The size of an individual is of crucial importance in many ecosystem interactions, so pervasive declines in growth rates can disrupt the balance of ecosystems and have a wide range of negative effects on marine and terrestrial animals. For example, massive declines in sea bird populations are thought to be associated with declines, not only in the abundance, but also the size and nutritional quality of fish and sandeels. When entire fish stocks begin to expedite maturation it is an indication that the stock is under stress and trying to rapidly replenish itself, and since increasingly early maturation has been observed in fish stocks prior to their collapse (Trippel, 1995), it should be considered as a warning to reassess and alter fishing practises. It is important to monitor changes in the growth and maturation of fish stocks, not only for conservation and ecosystem restoration purposes, but also for assessing the sustainability of fisheries,

and ensuring the continued profitability of fisheries and the supply of fish for human consumption.

The Firth of Clyde sea, to the west of Scotland, is a region that has recently attracted a lot of media and scientific attention. It was claimed that decades of overfishing the Clyde had depleted the fish stocks to such an extent that the region was now a ‘marine desert’ where no fish species existed in sufficient number to sustain a commercial catch (Thurstan and Roberts, 2010). These claims were later found to be a little misleading, as the Clyde still contains lots of fish and is certainly not a marine desert, but fish stocks would not be able to sustain commercial catches due to the fact that very few large fish remain in the Clyde (Heath and Speirs, 2012). The Clyde, in many ways, is typical of a heavily exploited coastal ecosystem, and the fish stocks have exhibited a substantial transformation in accordance with what may be expected as a result of intensive fishing.

This thesis is a study of changes in the growth, maturation and abundance of fish in Scottish waters. Since there is currently a great deal of interest in the Firth of Clyde ecosystem, fish from the Clyde are considered separately within each chapter of this thesis. The following sections of the introduction provide some background information about the Firth of Clyde fishery, changes in the growth and maturation of fish and how these are measured, and methods for assessing the abundance of fish stocks. The final section of the introduction provides a synopsis for each chapter of the thesis.

## 1.2 Development of the Firth of Clyde fishery

The Firth of Clyde is a fjord, reaching over 100 km into the southwest coast of Scotland (fig. 1.1). The Firth of Clyde has a centuries-long history of fishing. Advances in fishing gears and vessels, and a succession of fishery management regulations have altered the fishery and the fish stocks of the Clyde. The harvesting of Clyde fish has diminished exploitable stocks so that the fin-fish fishery is no longer viable, and fishery profits are now based almost entirely on shellfish, particularly *Nephrops* (*Nephrops norvegicus*). Thurstan and Roberts (2010) used landings data from 1854 to 2009 and historical accounts to describe the history of fishing on the Clyde and its effects on the fish

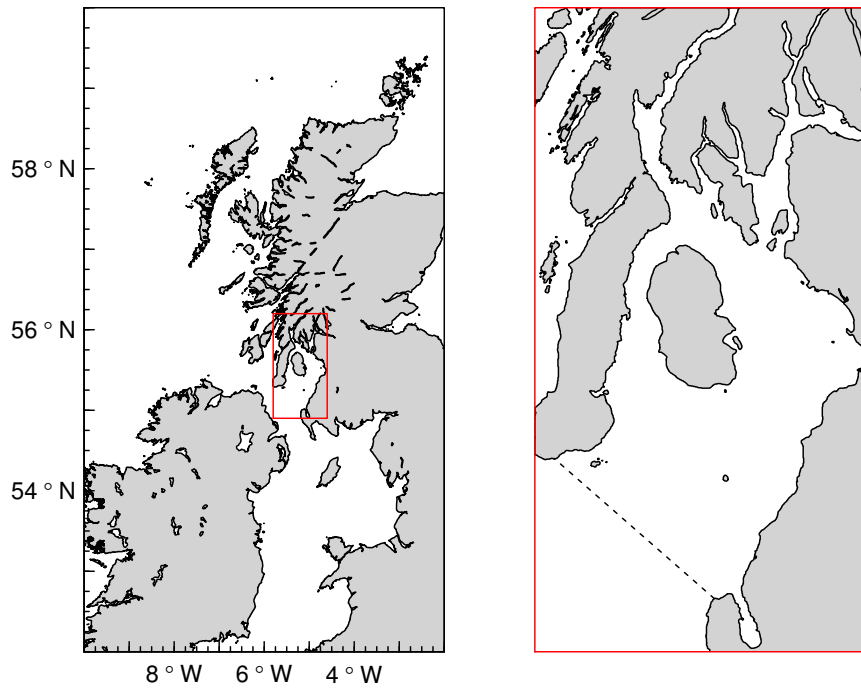


Figure 1.1: The dashed line marks the entrance to the Firth of Clyde.

community from the early 1800s until 2009. A study by Jones et al. (2016) used anecdotal evidence from fishers and parliamentary commissions of enquiry to describe the history of the mid-west and southeast Scottish fisheries in the 19<sup>th</sup> century, and used landings and fishing effort data to derive trends in the catch per unit effort (an index of abundance) of herring (*Clupea harengus*) and whitefish between 1845 and the mid 1880s. The mid-west region included the Firth of Clyde, and Jones et al. (2016) specifically discuss the Clyde throughout their paper. The studies by Thurstan and Roberts (2010) and Jones et al. (2016), and references therein, are drawn on throughout this section to describe the history of fishing on the Clyde.

Herring were, historically, the mainstay of the Firth of Clyde fishery. Landings of the seasonally abundant herring far exceeded the landings of other fish species from Clyde until the latter half of the 20<sup>th</sup> century. Throughout most of the 19<sup>th</sup> century the provincial fleet consisted of small rowing and sailing boats that fished for herring

with drift, trammel, and seine nets. Drift and trammel nets are static fishing gears which were set in the water column or across the seabed and retrieved after a day or more. Seine nets are mobile gears which were deployed from two vessels that circled the net around shoals of fish before drawing it closed at the bottom. Seine nets were first used in the Clyde in 1838 to harvest herring from Loch Fyne, which had long been a productive fishing ground. The introduction of seine nets created disputes between fishers operating drift and trammel nets and those operating the less passive seines. Seine nets were capable of harvesting huge quantities of fish in a single haul, putting boats using drift or trammel nets at a disadvantage. It was also argued that seines indiscriminately caught undersized, unmarketable fish, and that they destroyed the spawn of herring and other fish species. Seine netting was banned in 1851, but the ban was largely enforced by local drift and trammel net fishers and was ineffective as seine netting continued nonetheless. The ban on seine netting, as well as all other fishing regulations, were repealed in 1867, allowing fishers freedom to choose preferred fishing methods, and the use of seine nets became more prevalent throughout the Clyde. Huge quantities of herring continued to be landed throughout the 19<sup>th</sup> century, particularly from 1880 onwards, by which time most of the provincial fleet had adopted seine nets to target herring. The catch of herring per unit effort increased over the second half of the 19<sup>th</sup> century, suggesting that the abundance of herring had increased during this time, although this could have been partially due to the greater efficiency of seine netting. By the start of the 20<sup>th</sup> century, the seasonal herring fishery had been considered a failure in some important fishing grounds for several years, although the harvest of herring was still the most profitable part of the Clyde fishery.

Many demersal fish species such as cod, dab and flounder were also harvested from the Clyde during the 19<sup>th</sup> century. These species tended to be targeted during the summer months when herring did not form large shoals. Demersal fish were caught with lines, static nets and traps throughout most the 19<sup>th</sup> century, although a small number of vessels harvested these fish with bottom trawling gear. Trawling gears were towed by small sailing vessels, and many parts of the Clyde were inaccessible to trawls as they required areas of fairly smooth ground, free of obstacles that could impede movement of

the gear. The number of vessels fishing the Clyde with trawling gear increased greatly during the mid 1880s when steam powered trawlers came into regular use. Steam powered trawlers were much more efficient than sailing vessels as they could haul greater quantities of fish and could reliably tow in adverse weather conditions; they were also less hindered by uneven ground, so more of the Clyde became accessible to trawlers. Many fishers expressed concerns about trawling; a Clyde boat-owner interviewed in 1887 stated that ‘...if beam trawling is allowed to go on unchecked, the chief fishing banks in the Clyde (already greatly exhausted) will soon be so destroyed that for many years the yield will not meet the working expenses’ (Campbell, 1887). The catch composition, and resulting discarding practises, of trawling vessels worried some fishers; large species such as ‘dog-fish and skate’ were regularly caught, along with ‘a great amount of small fish . . . there were more small than big fish, and they were usually thrown overboard’ (Hannah, 1887). The size of marketable fish caught from the Clyde was thought to be in decline, and many linked this to trawling. A District Fishery Officer expressed his views on beam trawling in the Clyde when interviewed in 1887, ‘...takes have fallen off very much of late, and the fish now got are generally very much smaller in size than formerly, and altogether the aspect of things appear to indicate that beam trawling has injured this fishery very considerably’ (Bain, 1887). A ban on trawling within the Clyde was imposed on vessels over 8 tonnes in 1889 to protect valuable fish stocks from further declines in abundance or size composition — sailing vessels under 8 tonnes were still allowed to trawl in regions further than 3 nautical miles from the coast. The ban benefited fishers using more traditional fishing methods since competition from the trawling sector was greatly reduced, and fewer trawls interfered with static fishing gears.

Herring continued to be the most economically important species to the Clyde fishery during the first half of the 20<sup>th</sup> century. Annual landings of herring between 1920 and 1960 were typically on par with, and sometimes significantly greater (peaking at > 40000 t in 1932), than annual landings between 1860 and 1900 (which tended to be in the range of 10000–20000 t). Technological advances improved fisher’s ability to locate herring, and helped to sustain the high quantity of landings throughout most

of the 20<sup>th</sup> century, despite stock depletion in some key fishing grounds. Increased use of motorised boats facilitated longer and more regular fishing trips. Locating shoals of herring became less laborious in the 1930s, when the adoption of feeler-wires enabled fishers to feel when herring were present instead of relying on sight. Echo location devices that could locate shoals of herring were introduced in the 1950s. Concerns continued to be raised about the small size of herring caught from the Clyde, and it was determined in 1936 that the Clyde herring fishery was dependent on immature herring from successive year classes, and that sporadic recruitment accounted for the large fluctuations in annual landings. By the late 1950s, shoals of herring were observed much less frequently, and annual landings were consistently under 10000 t. The mid-water pair trawl was invented in the 1960s, allowing diffuse (non-shoaling) herring populations to be harvested effectively, and seine netting for Clyde herring was gradually replaced. The mid-water trawls also caught lots of large marketable demersal fish, which formed a valuable part of the bycatch. Landings of herring declined from 1970 onwards, and although landings quotas were introduced in 1976, the herring fishery did not recover. By this time herring were not the most profitable component of the Clyde fishery, but most fishers were targeting demersal fish, *Nephrops* and other shellfish, and the fishery remained profitable.

The Clyde fishery for *Nephrops* began to expand in the 1950s due to increasing demand and market price, and because *Nephrops* were an abundant alternative target species to herring. This fishery consisted of vessels equipped with seine nets, and small (under 8 tonnes) trawling vessels towing nets with mesh sizes narrow enough to retain the target *Nephrops*; these vessels also caught large amounts of demersal fish. The ban on vessels over 8 tonnes trawling within the Clyde was partially lifted in 1962, when these vessels were permitted to trawl in areas further than three nautical miles from the coast. This allowed further exploitation of the *Nephrops* stocks, which were increasing in importance to fishers as the herring fishery was failing. As trawlers increased in size and power, they were able to exploit rocky and uneven areas that were previously inaccessible under the trawling regulations. The introduction of ‘rock-hopper’ trawling gears further opened new fishing grounds to trawling. Most of the Clyde fishing fleet

adopted demersal trawling throughout the 1960s, and most of those still targeting herring were using mid-water trawls. Despite declines in herring landings, the traditional mainstay of Clyde fishers, the fishery entered a boom period due to high demersal fish landings. Landings of the main commercial demersal stocks all increased immediately after large vessels were permitted to trawl the Clyde. For most of these species, however, the period of high landings was fleeting. There was a boom-bust fishery for Clyde saithe (*Pollachius virens*), the landings of which increased from < 500 t per year during the early 1960s to almost 7000 t in 1974 — landings then plummeted. There was a similar story for haddock (*Melanogrammus aeglefinus*), for which landings initially increased, but were in decline just a few years after large scale trawling had commenced. Total landings of demersal fish increased to a peak in 1973 due to the increased use of demersal trawls, but began to decline thereafter as landings of each demersal species declined one after another. The landings of most commercially important demersal fish species had fallen by the early 1980s. Large vessels were permitted to trawl within three nautical miles of the coast from 1984 in an effort to sustain the high landings, but this was unsuccessful and demersal fish landings continued to decline. Vessels equipped with nets fine enough to target *Nephrops* accounted for most of the trawling effort in the Clyde, and further increases in trawling effort were biased towards *Nephrops* gear. *Nephrops* had become the most profitable component of the fishery by the mid 1980s, and the Clyde *Nephrops* fishery swelled as demersal fish landings plummeted. The abundance of *Nephrops* was thought to have increased in response to reductions in the number of predators in the environment, and the quantity of *Nephrops* landings has sustained the profitability of the Clyde fishery into the 21<sup>st</sup> century. Demersal fish landings were a negligible part of the fishery profit by 2005, by which time almost all fishing effort was targeted at *Nephrops* and other shellfish.



### **1.3 Transformation of the Firth of Clyde demersal fish community**

Landings data and historical testimonials were used by Thurstan and Roberts (2010) to review how the Clyde fishery and fish stocks have changed over time. The collapse of the demersal fish stocks followed shortly after the 3 mile limit on bottom trawling was rescinded in 1984, and it was suggested that this coastal area of refuge helped to sustain fish landings until this time. The steep declines in the landings of demersal fish indicated that Clyde stocks had become less productive and could no-longer sustain a commercial catch (Thurstan and Roberts, 2010), and that many species which were once abundant had become extirpated within the Clyde. Landings data, however, do not represent the abundance of fish, but instead show only what has been retained from catches. This means that landings data do not account for the portion of the catch that is discarded. Landings data are also subject to bias caused by changes in fishing gears and locations, market demand for certain species and changes in fishery management. Inferences about changes in the state of the fish community that are based solely on landings data are therefore subject to a wide range of biases, and should be treated with some caution. Data from routine survey samples are not subject to the same biases associated with landings data, and should provide a more accurate representation of what fish are present within the surveyed region. A study by Heath and Speirs (2012) that was based on data from research vessel bottom trawl samples also concluded that the Clyde demersal fish community had undergone a transformation — since the trawling ban was repealed in 1962 — to a state where few marketable-sized fish remained. Although the Clyde could no-longer sustain a commercial catch of demersal fish, Heath and Speirs (2012) demonstrated that the demersal community remained productive after the collapse in landings. Small fish, under minimum landing sizes, and non-target species were sampled by the surveys, so the research based on this data provided a more complete analysis of the nature of the transformation in the demersal community.

Heath and Speirs (2012) examined trends in several length-based indices and measures of diversity to assess changes in the condition of the demersal fish community. Community mean length and the proportion of the demersal fish biomass comprising of individuals greater than 40 cm long were among the length-based indices studied. The diversity indices considered by Heath and Speirs (2012) were the cumulative number of new species to appear in the survey samples, species richness (the number of species sampled per 20 tows) and species evenness (a measure of how evenly biomass was distributed among different species). It was found that, although landings had declined to negligible levels by the mid 2000s, demersal fish remained highly abundant within the Clyde. Estimates of the total biomass of demersal fish during 1927–1960 and 2000–2009 were similar, and declines in total biomass were not evident. What had changed, however, was the proportion of that biomass comprising of fish that were greater than 40 cm in length. The biomass of fish larger than 40 cm declined after the resumption of industrial trawling; these biomass estimates fluctuated for the first 20 years before falling into terminal decline from the early 1980s, and large individuals became increasingly rare within the Clyde. The biomass comprising of individuals smaller than 40 cm increased when the trawling ban was lifted, and has consistently been greater than it was pre 1960; it appeared to increase substantially again from about 1990. The shift in length structure was evident from the trend in community mean length, which was consistently estimated to be greater than 50 cm in 1927–1960, but had declined to around 20 cm by the 2000s. Demersal white-fish currently form a negligible part of the landings from the Clyde fishery due to the fact that few marketable-sized fish remain; the Clyde, however, is still a productive ecosystem and continues to sustain a large stock of small-bodied demersal fish. Heath and Speirs (2012) found no change in species richness, so the number of demersal fish species present within the Clyde does not appear to have changed. Species evenness, on the other hand, was estimated at a maximum during the late 1920s and '30s, had decreased by the 1960s, and then declined steeply between 1980 and 2000. During 1920–1959, 13 species accounted for 95% of the demersal fish biomass, and about 31% of this comprised of spurdog (*Squalus acanthius*), thornback rays (*Raja clavata*) and tope (*Galeorhinus galeus*), all large and predatory species.

The abundance of these large species declined when industrial trawling recommenced — spurdog accounted for about 4% of the demersal biomass in 1960–1979, thornback rays and tope were each less than 1 % — and the biomass began to comprise more of smaller species, particularly whiting (*Merlangius merlangus*). The relative abundance of other large species, cod (*Gadus morhua*), saithe, and hake (*Merluccius merluccius*) also declined, but the decrease in the relative abundances of saithe and cod lagged the increased trawling effort. Saithe became relatively abundant (about 18% of demersal biomass) during 1960–1979, and their abundance dropped off thereafter; the relative abundance of cod also increased (to about 24% of demersal biomass) in 1980–1994, then fell to less than 3% of the demersal biomass from 1995 onwards; and the relative abundance of hake declined steadily from 14% of demersal biomass in 1920–1959 to < 2% from 1995 onwards. The decline in species evenness was so severe that 1 species, whiting, accounted for 87% of the demersal fish biomass during 1995–2004, when 95% of the biomass was invested in just 4 species. Species evenness then increased from 2005–2009, when 8 species accounted for 95% of the demersal biomass, although whiting was still by far the most abundant species at 72% of the biomass. Although species evenness increased from the mid 2000s, the majority of the biomass was still invested in 1 species, and the main species complement consisted of relatively small-bodied species — whiting and haddock accounted for 84% of the biomass in 2005–2009, another 4% was attributed to Norway pout (*Trisopterus esmarki*) and a further 8% was distributed between cod, hake, poor cod (*Trisopterus minutus*), plaice (*Pleuronectes platessa*), and long rough dab (*Hippoglossoides platessoides*). The demersal fish biomass of the Clyde is as high now as it was in 1927–1960, but the abundance of large bodied species has declined, and the biomass now consists of small individuals and relatively small bodied species. Despite the encouraging sign of increased species evenness since the targeted demersal fishery ceased in 2005, the Clyde community has yet to show signs of returning to a state in which large, marketable fish are once more abundant.

## 1.4 Potential contributory factors to transformation of the Clyde fish community

Fishing pressure sustained over centuries, culminating in a decades-long period of intense industrial trawling, has resulted in large fish becoming rare within the Clyde. Although this occurred as a direct consequence of selectively removing large individuals, there are a range of other factors that may have contributed to the decline and current scarcity of large fish. Most of these factors, such as habitat degradation and loss of diversity, are related to fishing activity, but other anthropogenic and environmental influences that may have contributed to declines in large fish abundance include changes in pollution levels and climate.

The use of bottom trawls and dredges has damaged and homogenised vast areas of seabed in sublittoral regions throughout the world (Watling and Norse, 1998). Dragging heavy trawls over the seabed can crush marine plants and crustacean colonies that provide habitat for myriad other species. The most extensive maerl beds in Europe are to be found off the west coast of Scotland, and maerl is present within the Firth of Clyde (Hall-Spencer, 2001). Maerl is a form of coralline algae that provides habitat for invertebrates and juveniles of commercial fish species. Scallop dredging has caused long-lasting damage to maerl beds in the Clyde: a single sweep of the gear over a previously undisturbed area was demonstrated to greatly reduce live maerl coverage, and there was no evidence of recovery after four years undisturbed (Hall-Spencer and Moore, 2000). The lack of recovery within this time was due to the extremely slow growth rate of maerl — 1 mm per year is typical in European waters (Hall-Spencer, 2001). Loss of maerl beds and other structurally complex habitats may have inhibited recruitment for some fish species that favour these habitats as juveniles. Trawls reduce the abundance and diversity of epifauna, particularly immobile species, and since trawls plough into soft sediments they also excavate infauna and destroy burrows and tubes (Bergman and Hup, 1992; Hinz et al., 2009; van Denderen et al., 2014). Detachment from the seabed or losing a burrow is fatal to many species, and these may only be able to recolonise a trawled region after reproduction and resettlement. The destruction of

complex habitats and the resulting reductions in abundance and diversity of epifauna can restrict food availability for demersal fish, and may lead to a regime change where pelagic fish increase in abundance while only small or poor-condition demersal fish remain (Choi et al., 2004). It is possible that when large trawlers began fishing within 3 miles of the coast they quickly destroyed valuable and diverse habitats, reducing food availability for demersal fish. This may have prevented fish from growing to large sizes, or encouraged large individuals to migrate to find richer feeding grounds. The amount of time required for an area of seabed to recover from being trawled depends on the substrate type; the species complement prior to and after trawling; species regeneration time; and frequency of further trawling during the recovery (Watling and Norse, 1998). Some slow-forming habitats, like maerl beds, will likely take decades, or even centuries, to fully recover from severe trawling damage, and many benthic organisms may struggle to recover within the homogenised, low-diversity environment. Most of the physical damage to habitats occurs the first time an area is trawled, and further trawling incurs more damage, so bottom trawling in ecologically complex areas must cease entirely in order for those areas to regenerate. A fully protected marine reserve was established in the Firth of Clyde (Lamlash Bay, Isle of Arran) in 2008 to aid regeneration of local habitats and promote increases in the abundance of commercially important fish and shellfish near Lamlash Bay (Axelsson et al., 2009). Both juvenile and large scallops have increased in abundance within the marine reserve and in nearby areas due to the regeneration of habitats formed by seaweeds and hydroids (Howarth et al., 2015). A Regulating Order application to manage the Clyde shell-fisheries was prepared by the Sustainable Inshore Fisheries Trust and submitted to the Scottish Government in October 2015; the proposal was to impose spatial restrictions on fishing activity, particularly trawling and dredging, in 28% of the Firth of Clyde area to allow regeneration of habitats for the benefit of fish species and the fishery (SIFT, 2015). Unfortunately this proposal was rejected by the Scottish Government in 2016.

Selective harvest of large individuals and large-bodied species reduces predation pressures on smaller fish, which may increase in abundance as a consequence. Consistent with a pattern that has been documented in fisheries around the world (Bianchi

et al., 2000), it was large species, particularly spurdog, that were the first to decline in abundance once industrial trawling was permitted within the Clyde. This will have reduced predation mortalities on many fish species and may have had a cascading effect through the food web (Pace, 1999). As large species and individuals become increasingly rare, the abundance of smaller fish species often increases until they also begin to suffer deleterious effects from the fishery (Myres and Worm, 2003), or approach the carrying capacity of their environment. There is some evidence of this having happened in the Clyde community: saithe were relatively abundant in 1960–1979, and cod were relatively abundant in 1980–1994 (Heath and Speirs, 2012). It may be that both of these species, released from predation pressures, increased in abundance until they too succumbed to fishing pressure. The demersal fish species that has been best able to tolerate and adapt to intense trawling in the Clyde was whiting, a relatively small species that has increased in abundance to replace spurdog as the biggest contributor to total demersal biomass. Releases in predation pressure upon whiting may have enabled the population to grow and subsequently suppress the populations of larger species through competition in the larval and juvenile stages (Rowlands et al., 2006; Shaw et al., 2008), or through predation on the larvae and juveniles of other species. The transformation of the Clyde demersal community to a state where only small fish are common may be a regime shift that is difficult to reverse if small species are now inhibiting the recovery of larger species, particularly since the complex habitats that larvae and juveniles of the larger species would seek for refuge from predation have degraded or disappeared due to trawling in the Clyde.

Altered predation rates through the disproportionate harvest of large-bodied fish not only affect abundances of various species, but may also influence behavioural, reproductive- and growth-related traits of prey populations (de Roos and Persson, 2002; Madin et al., 2015). Changes in predation can therefore influence typical growth rates of individuals in prey populations, inducing either increases or decreases in the numbers of large fish present in the prey populations. Fishing itself, is a form of predation, and can also have strong influences on the growth of harvested species. Thus fishing not only removes large individuals from the community, but can also cause changes in

the growth rates of the fish that remain. Changes to the growth rates and maturation schedules of demersal fish in the Firth of Clyde community may be partially responsible for the current scarcity of large individuals. Much of this thesis is concerned with investigating whether the growth rates and maturation schedules of fish from the Clyde and neighbouring regions have changed over time, so more detail on the theory and evidence for changes in the growth rates and maturation schedules of fish is provided in the following section.

## **1.5 Phenotypic plasticity and heritability of growth and maturation in fish**

Growth can consist of increases in body length or weight, termed somatic growth, or increases in gonadal mass which is called reproductive growth. Throughout this thesis the terms growth or growth rate refer to somatic growth unless otherwise specified. The growth rate of an individual is its change in size per unit time, describing how size is related to age. Measures of growth rate in fish are length or weight increments per unit time; increases in length are irreversible, whereas weight may increase or decrease as energy reserves are stored or depleted. Growth — both somatic and reproductive — is controlled by the amount of resources (energy and nutrients) acquired by an individual, and how those resources are allocated among competing physiological demands (Enberg et al., 2012). The energy from digested food is partitioned among various functions: basal maintenance, growth and reproduction (Roff, 1983). Basal maintenance includes all functions other than somatic or reproductive growth, including digestion, immune defence, healing, cognition and movement. These energy costs for vital functions must be met for an individual to survive. Surplus energy can then be allocated to growth and reproduction. Juveniles may allocate all surplus energy into somatic growth. Growth rates tend to decrease once fish mature because some fraction of surplus energy, the reproductive investment, is used for gonadal growth, migrations and mating. Fish that invest heavily in reproduction do so at the expense of suppressed growth rate since proportionally less energy will be allocated to growth. Reproductive investment generally

increases as fish age, so growth rates tend to decline as fish grow larger, but fecundity increases (Stearns, 1992). The rate of structural growth (increases in length) becomes negligible as fish approach their maximum length, at which time surplus energy is mostly invested in reproduction and reserves. Besides from the allocation of resources to physiological functions, somatic and reproductive growth is also controlled/limited by the amount of resources acquired by an individual (Reznick et al., 2000). This depends on a range of factors including the abundance and nutritional quality of available food, competition for that food, and the foraging behaviour of the individual (Enberg et al., 2012). Correlations exist between these factors, and foraging behaviour may be influenced by other aspects of the environment such as predation pressures (Dill and Fraser, 1984; Lima and Dill, 1990). Somatic and reproductive growth are therefore influenced by a range of interacting processes affecting both the acquisition and allocation of resources.

Strategies of resource acquisition and allocation, influencing growth and reproductive investment, change as individuals age, grow and mature (Jørgensen and Fiksen, 2005). These strategies can also change in response to a range of variables other than the life stage of the individual. Such changes are called phenotypic plastic responses to the environment or the condition of the individual. Phenotypic plasticity allows animals of the same genotype to express a range of phenotypes, including various physiological or behavioural traits. This allows fish species to thrive in various different environments, and also enables individuals to adapt to short term changes in conditions. It is useful to distinguish between three aspects of the environment: (1) the ancestral environment, where conditions have remained stable over generations and populations have adapted over time through natural selection; (2) the macro-environment, current conditions collectively experienced by whole populations; (3) the micro-environment, the specific conditions experienced by each individual within a population (Dieckmann and Heino, 2007). Phenotypic plastic change occurs regularly within individuals, as they continually adapt to their own micro-environments. Plastic changes in growth or maturation can become apparent at the population level when most individuals respond similarly to some change in the macro-environment. Any change to the environment



that persists over generations alters the ancestral environment, and populations may adapt to these long term changes through selection on phenotype expression. We will first summarise why individuals exhibit plasticity in growth and maturation, before considering population level plasticity and heredity.

Strategies of partitioning resources between basal maintenance, growth and reproduction may vary considerably between individuals, and each individual may alter their strategy in response to changes in their own micro-environment. The energy demands of various basal maintenance functions fluctuate periodically, for example, the energy required for digestion will increase when a food item is swallowed (Tandler and Beamish, 1979), limiting the energy that may be expended on other activities (Arnott et al., 2006; Suzuki et al., 2010). The energy allocated to basal maintenance must also be able to increase greatly in certain circumstances, such as energy expended on rapid movement to avoid predators, energy required to heal an injury, or increased maintenance costs of parasitism. The partitioning of resources between maintenance, growth and reproduction is therefore necessarily flexible, and this flexibility allows the allocation of energy to different functions to vary in response to changes in the environment and the current needs of the individual. Maximising fitness (lifetime reproductive success) within the environment is thought to be the motive for all phenotypic changes (Stearns, 1992), so plastic changes in growth or maturation are the result of improving individual fitness.

The compensatory growth response, above average growth rates following periods of poor growing conditions, indicates that growth rates can vary considerably and are typically well below the physiologically feasible maximum (Ali et al., 2003). Given that large individuals are less vulnerable to predation and starvation, are strong competitors for food and territory resources, and have higher fecundity, one might expect typical growth rates to be higher. Despite the benefits of being large, growing to a large size takes time and energy, and although rapid growth hastens the advantages of a large size, it may not always be the strategy that maximises fitness. Growing quickly could require increased foraging times that would raise predation risks, or allocating more energy into growth which could reduce fecundity and potentially have a range of deleterious consequences to basal functions (negatively affecting health). The compensatory

growth response shows that individuals are able to accelerate their growth, but the fact that growth rates are typically well below the maximum suggests that rapid growth is a risky means of attaining a large size (Metcalf and Monaghan, 2001).

The proportion of surplus energy an individual uses for reproduction instead of growth may vary within or between spawning seasons, and some individuals may even ‘decide’ to skip spawning in some years (Jørgensen et al., 2005; Rideout and Tomkiewicz, 2011). Plastic changes in reproductive investment are the result of a bet-hedging exercise where individuals have made a ‘choice’ intended to increase fitness, either by producing lots of offspring during the next spawning season at the expense of slowed growth, or by investing little in reproduction to maximise growth and, if the individual survives, increasing size and fecundity in subsequent spawning seasons. There is also plasticity in maturation, that is the age and size at which juveniles become mature (Barot et al., 2004b). Juvenile fish can grow more quickly than adults because they do not expend energy on reproduction, so an individual that, given its size and age, could mature, may opt to delay maturation until it has become larger. Again, plasticity in maturation optimises fitness, so individuals are likely to delay maturation only if there is a good chance of surviving to reproduce in subsequent years, and conversely, maturation may occur earlier if survival likelihood is poor.

The amount of energy available to an individual for growth and reproduction depends on the resources it acquires, and resource intake rate may vary with food abundance, competition and foraging strategy (Enberg et al., 2012). In general, increased time spent foraging will increase the energy available for growth and reproduction but raises the risk of predation and parasitism (Stephens et al., 2007). Foraging strategies are chosen to balance these risks and benefits, resulting in some energy acquisition rate that limits somatic and reproductive growth. Individuals may be able to maintain a stable resource intake rate despite changes to food abundance or competition by altering foraging strategies, but this may not be desirable if the risks become too great. Potential changes to growth and reproduction due to altered food abundance could therefore be mitigated by plasticity in behaviour, but this may not always occur since altered foraging strategies incur other costs to fitness.

In summary, the phenotypes expressed by an individual are ‘chosen’ to maximise fitness. Some phenotypes pertaining to growth and reproduction can change plastically in response to variations in the environment or the condition of the individual. The somatic growth rate, maturation schedule and reproductive investment of individuals are flexible, and tuned to the specific environment each individual experiences.

Observing plasticity in individuals is possible in laboratory conditions, where the responses of individual fish to environmental changes can be monitored, but phenotypic plasticity is only observable in wild fish at the population level. There is variation in phenotype expression within populations, as individuals do not necessarily adopt the same strategies. Some phenotypes will tend to optimise fitness more effectively than others. This may cause some bias in adopted strategies, becoming evident in the population as a whole when the majority of individuals express a similar phenotype — maturation at small sizes for instance. Spatially distinct populations are likely to exhibit differences in phenotype expression if their environments differ. For example, populations from cold regions tend to have slower average growth rates but attain larger maximum lengths than those in warmer climates (Angilletta et al., 2004); populations inhabiting regions where food is unevenly distributed or low in abundance may exhibit considerable competitiveness or tenacious foraging behaviours (Ward et al., 2006); a population subjected to high mortality rates may tend to increase reproductive investment or expedite maturation relative to other populations with greater survivorship (Gunderson, 1997). Variation in phenotype expression between distinct populations is a result of individuals from each population adopting traits that best suit their particular environment. This variation may not always be entirely due to plastic responses to the environment, but can also have a genetic basis (Gall, 1983). If a population has inhabited a region for many generations, then the process of selection on phenotypes may alter the gene pool as sub-optimal traits are selected out of the population. Thus, selection for and against certain heritable phenotypes can cause populations to evolve. Differences in phenotype expression between spatially distinct populations are due to plastic responses to differences in the environments and selection on certain phenotypes; the extent to which the differences are genetic depends on the strength of selection, the

heritability of the phenotype, and the length of time over which selection has occurred (Law, 2000).

Average growth rates or maturation timings may, however, be similar among spatially distinct populations inhabiting regions where differences in environmental conditions might be expected to have caused some divergence in these traits (Conover and Schultz, 1995). This phenomenon, termed counter gradient variation, can occur when individuals are able to adapt their strategies of resource acquisition and allocation enough to oppose environmental influences. This has been observed in Atlantic silver-side, as populations from northerly regions with short growing seasons have average growth rates that are equivalent to those of southern populations experiencing a relatively long growing season (Conover and Present, 1990). Interestingly, when these fish were sampled from the separate populations and raised under laboratory conditions, the individuals originating from the northerly region grew more quickly. This indicated that the differences in growth rate had a genetic component, i.e. that the northerly population exhibited more rapid growth as a result of evolving within a less favourable ancestral environment.

Phenotypic plasticity in growth or maturation becomes evident within a single population when average growth rates or maturation timings change over time; these changes may occur as a gradual trend, as an abrupt change, or as interannual fluctuations. Population-wide shifts in growth rates and maturation schedules can be caused by changes to the environment. If some environmental change were to improve the fitness associated with certain phenotypes relative to others, then it is likely that the fitter phenotypes would become more prevalent in the population. If the environmental change persisted over generations, then plastic responses of the population may become genetically encoded via selection on heritable phenotypes, causing the population to evolve towards the phenotypes that most improve fitness in the altered environment. Food availability, mortality rates, and temperature are among the factors most liable to induce change in growth rates, reproductive investment, and maturation timings.

Temperature is directly related to the metabolic rates of poikilotherms, so may influence the amount of surplus energy available for growth and reproduction (Peters,

1983). Rises in temperature have been linked to observed declines in average growth rates and typical maximum sizes within several distinct populations (Daufresne et al., 2009; Baudron et al., 2014). Furthermore, the growth of fish has been predicted to change in response to globally increasing temperatures so that large individuals will become increasingly uncommon worldwide (Cheung et al., 2012). Temperature variations may also alter maturation schedules; this can occur either as a secondary effect of altered growth, or independently of temperature-induced changes in growth (Kuparinen et al., 2011). High temperatures are usually associated with early maturation at young ages, whereas low temperatures are usually associated with delayed maturation (Berrigan and Charnov, 1994).

Fishing pressure has been linked to observed trends in the growth (e.g. Bianchi et al., 2000; Law, 2000; Olsen et al., 2004; Shin et al., 2005; Swain et al., 2007; Darimont et al., 2009) and maturation (e.g. Grift et al., 2007; Mollet et al., 2007; Sharpe and Hendry, 2009; Wright et al., 2011; Marty et al., 2014) of many different populations. The precise nature of these trends is varied and can depend upon many factors including the species; whether that species is targeted by the fishery; the type of fishing gears used; and the duration of harvesting. Fishing-induced changes in the average growth and maturation of a population can result from the direct or secondary effects of fishing: the direct effect of fishing is to increase the mortality rate of harvested populations, whereas secondary effects include all environmental changes that occur as a consequence of fishing. Secondary responses in growth or maturation are often caused by fishing altering the amount of food that is available to a population. Bottom trawling gear can plough as deep as 30 cm into soft substrates (Linnane et al., 2000), excavates infauna and makes them more vulnerable to predation by fish. This can increase food availability for some species resulting in increased growth rates. Such increases in growth rate are typically observed in bottom dwelling flatfish species (Hiddink et al., 2008). The food available to each individual in a population may also increase after harvesting due to reduced competition. The primary effect of fishing is the removal of fish, which increases the mortality rate of harvested populations. The mesh of fishing nets are designed to allow small fish to escape while retaining larger individuals, so the

mortality due to fishing is biased towards fish at the large end of the population length distribution — this is the opposite of natural mortality through predation (Conover, 2007; Allendorf and Hard, 2009). Since the likelihood of being caught increases with size, the fitness of a heavily fished population would improve by investing more into reproduction, suppressing growth rates and expediting maturation, and these changes are often observed in harvested populations. Since fishing applies a disproportionately high mortality on large individuals, it selects for early maturation and traits associated with small size and slow adult growth. Fishing-induced selection for early maturation may be particularly severe when the size range of targeted fish includes the typical size at maturation, because late maturing individuals are more likely to be caught while still juveniles. Furthermore, fishing does not need to be size-selective to induce genetic change in maturation, since uniformly increasing mortality rates across all sizes will select for earlier maturation (Law, 2007). Fishing mortality rates often greatly exceed natural mortality rates (Mertz and Myres, 1998), so the selection pressures due to fishing can be strong, and there is convincing evidence that size-selective fishing practises can cause rapid evolution of maturation schedules and growth (Jørgensen et al., 2007; Fenberg and Roy, 2008; Dunlop et al., 2009). ‘The question is not whether such evolution will occur, but how fast fishing practises bring about evolutionary changes and what the consequences will be’ (Jørgensen et al., 2007).

## **1.6 Measuring changes in the growth rates and maturation schedules of fish**

Measuring the growth rates and maturation schedules of individuals, and relating these traits to environmental conditions, is most accurately accomplished with fish raised in artificial laboratory conditions. The size of fish reared in captivity may be measured at regular intervals to precisely determine rates of growth throughout the fishes lifetime, and various stages of maturity can be accurately associated with length, weight and age, as well as other indices of condition. Laboratory experiments usually maintain a regular environment, perhaps altering only one variable (e.g. temperature) throughout the

duration of the experiment in order to investigate the influence that particular variable has upon growth or maturation, or any other trait under investigation. Experiments using fish reared in captivity have provided a great deal of insight into how various conditions influence growth rates (e.g. Cridland, 1962; Silliman, 1975; Imsland et al., 2005; Craig et al., 2006; Walsh et al., 2006) and maturation (e.g. Karlsen et al., 1995; Norberg et al., 2004; Skæraansen et al., 2006; Uusi-Heikkilä et al., 2011). There is obviously more variation in environmental conditions in natural ecosystems, and there is never any guarantee that fish in the wild will respond to environmental changes similarly to captive fish. Thus, in order to measure how environmental change affects the growth and maturation of wild fish it is necessary to examine fish that live in natural (albeit exploited) ecosystems.

There are essentially two main methods for measuring changes in the growth of wild fish: analyses of survey data samples that provide time series of length and age measurements, and tagging studies that examine the growth of individuals. Tagging studies investigating growth involve capturing live fish, taking measurements of their length and/or weight, affixing a distinctive tag to each individual and then releasing them back into the wild. With luck, a sizeable proportion of the tagged fish will be recaptured in the future so that they can be remeasured to find out how much they have grown since they were released. There are a range of difficulties associated with tagging studies: they can be expensive to conduct (Hammer and Blankenship, 2001); recapture rates can be low (Björnsson et al., 2011); tagging can be injurious to fish (Nichol and Chilton, 2006); and crucially for growth studies, being encumbered by a tag can inhibit growth rates (Bégout Anras et al., 2003). Tagging studies provide lots of useful information on the growth rates of fish (e.g. Shackell et al., 1997), however, due to the associated difficulties, measuring changes in growth is more readily accomplished through examining time series of survey data.

Data collected from scientific trawl surveys can be used to estimate the typical growth rates and maturation schedules of sampled populations. Estimating growth rates usually relies on measurements of both the length and age of sampled fish — although in some instances growth rates may be estimated from length data alone

(Bhattacharya, 1967). It is straightforward to measure the length of fish, but determining their age is more challenging. There are several techniques for deducing the age of fish by detecting and counting contrasting bands in hard parts of the body, most often it is otoliths (a calcareous deposit in the ear) or scales that are examined (Campana, 2001). Since measuring age is more difficult and costly than measuring length, it is usual for only a length-stratified subsample of fish to be aged — unless there are very few fish present in the sample, in which case every individual may be aged. When survey data that specifies the age and length of sampled fish is available, the distributions of lengths at each age can be used to calculate typical growth rates within a population. Maturation schedules can be assessed using survey data that provides measurements of age and/or length as well as maturity status. The maturity stage of individuals can be gauged by visual inspection of the gonads, and like age data, maturity data typically forms a subset of the full survey sample because maturity is also more costly and time consuming to measure than length. While age and length are continuous, monotonically increasing variables, maturity status is discrete and varies periodically in adults of iteroparous species. Maturity data is therefore classified into several stages, but the precise classifications often lack consistency between surveys, species and sexes. As this lack of consistency can cause difficulties, Brown-Peterson et al. (2011) suggest that the following maturity scale should be adopted as standard due to its applicability to all species and both sexes: (1) immature (juveniles yet to develop functioning gonads); (2) developing (period of gonadal growth prior to spawning season); (3) spawning capable; (4) regressing (period of depletion and diminution of gonads once spawning is complete); and (5) regenerating (sexually mature but reproductively inactive between spawning seasons). Sufficiently long time series of survey data allow long-term (over several cohorts, or generations) trends in average growth rates and maturation schedules to be measured. Time series data on environmental variables can then be compared to any detected trends in growth or maturation in attempts to determine possible causes for the trends.

Growth curves may be fitted to age-length data to represent expected growth trajectories. This means that growth may be considered in terms of the parameters as-



sociated with the growth curve instead of in terms of expected lengths for each age. If there are several age groups within the data then fitting a parameterised growth curve and interpreting the parameters can be easier and more intuitive than considering the mean lengths-at-age (Hernandez-Llamas and Ratkowsky, 2004). The growth curve that is most commonly applied to model the growth of fish is the von Bertalanffy curve,  $\bar{L}(a) = L_\infty (1 - \exp(-k(a - t_0)))$  (where  $\bar{L}$  is expected length and  $a$  is age) (von Bertalanffy, 1934). There are three parameters in the von Bertalanffy growth equation;  $L_\infty$ , the average maximum (asymptotic) length;  $k$ , the von Bertalanffy growth rate; and depending on the parameterisation, either  $t_0$  or  $L_0$ , which are the theoretical age when length equals 0 or the initial length when age equals 0 respectively. The von Bertalanffy growth model is derived on biological grounds, more specifically, assumptions about energy intake rates, energy allocation, and length-weight relationships. According to theory, the asymptotic length,  $L_\infty$ , depends on the amount of food that is ingested, while the growth rate,  $k$ , depends on metabolic rates (Gurney and Nisbet, 1998). When investigating the causes of changes in growth it can be more useful and informative to consider how environmental variables relate to the von Bertalanffy growth parameters instead of expected lengths at age. Given the theory underlying the derivation of the von Bertalanffy growth equation, it is reasonable to expect changes in food availability to impact more upon  $L_\infty$  than  $k$ , whereas changes in temperature, or any changes influencing metabolic rates, are likely to impact more heavily on  $k$ . That being said, as variation in growth often allows length- or weight-age data to be equally well fitted by a range of different growth curves, in practice  $L_\infty$  and  $k$  are usually highly correlated. This correlation may cause difficulties when relating either  $L_\infty$  or  $k$  to covariates.

Maturity is most often assumed to be dependent on age and/or size. The most common method for assessing the ages and lengths of mature individuals in a population involves deriving age- or length-based maturity ogives that specify the proportion of fish that are mature at a given age or length — this is usually done by modelling the proportions with a logistic curve (e.g. Jørgensen, 1990; Chen and Paloheimo, 1994; Morgan and Colbourne, 1999). If maturity data is available for a sufficiently long period

then trends in the proportion of the population that is mature at age or length become evident through the maturity ogive approach. Results based on the ogive method can be subject to biases because the proportions mature given age or length can vary in response to factors that are independent of maturation propensity (e.g. changes in the relative mortality rates of immature and mature individuals, or changes in growth rate). Trends in the proportion of a population that is mature given age or length are therefore not necessarily due to changes in the ages or lengths at which fish first become mature. The method of probabilistic maturation reaction norms (PMRNs) alleviates some the problems associated with the ogive method (Heino et al., 2002). Instead of estimating the proportions that are mature given age or length, PMRNs are used to estimate the probability of maturation given age and length, i.e. the probability that a mature fish is a first-time spawner, having just transitioned from juvenile to adult. Since fish are first-time spawners only once during their lives, PMRNs estimate the probability of a single event. This means that, unlike the ogive approach, PMRN maturation indices should be unaffected by short-term changes in mortality regimes. Furthermore, changes in growth rate are accounted for automatically because PMRNs assume that maturation is dependent upon both length and age. PMRN descriptions of maturation extend easily to higher dimensions by adding more explanatory variables other than length or age, e.g. weight or temperature (Grift et al., 2007; Uusi-Heikkilä et al., 2011). Since PMRNs are a relatively unbiased estimator of maturation propensity they can provide some indication as to whether changes in maturation schedules have a genetic basis, provided that trends in influential environmental variables have been taken into account.

## 1.7 Length-structured stock assessments

Stock assessments models use numerical data to derive useful information about harvested fish stocks. The information that can be derived for a particular stock depends on the type of data that is available and the type of model that is used, but all stock assessments return information about the historical and current stock size, as well as trends in recruitment (the influx of fish to the exploitable stock) and fishing mortality

rates. Stock assessment models may also be used to predict how various harvesting strategies could influence the future abundance of the stock. Information derived from stock assessments may be used to help inform fishery management authorities about the history and present status of harvested stocks, and about potential, or probable, outcomes of changes in management. Single-species stock assessments can be broadly categorised into three classes: surplus production models, age-structured models, and length-structured models (Haddon, 2011). The simplest of these are the surplus production models because they represent abundance by the total stock biomass which does not take into account the age or size structure of the stock. Most surplus production models consider all individuals within the stock to be identical to each other because distinguishing features, such as age or length, are not modelled — there are a few exceptions where biomass is segregated by sex (e.g. Prager and Goodyear, 2001). These models tend to have a modest number of parameters, which is good for model parsimony (Cotter et al., 2004), but ecologically important aspects of the stock structure are excluded so the biological realism of these simple models is limited. In light of recent calls for more biologically realistic stock assessment models (Kuparinen et al., 2012), it would be preferable to assess stocks with age- or length-structured models when possible.

Most contemporary stock assessments applied to fish species are integrated statistical stage-structured models. Here, ‘integrated’ refers to the use of multiple sources of data, and ‘statistical’ implies that probability distributions are used to model the data. Stage-structured models applied to fish species are almost always based the age structure of the stock (e.g. Deriso et al., 1985; Punt et al., 2001; Methot and Wetzel, 2013). Mortality and fecundity are strongly correlated to body size, and therefore also age. As fish grow they generally become more fecund and increasingly capable of producing fit offspring, while becoming less vulnerable to predation and more vulnerable to fisheries. Representing this knowledge within stock assessment models improves their biological realism and allows other useful information, such as trends in age-dependent mortalities and within-age-group abundances, to be derived. This information may help guide fishery management decisions, and indeed may be of critical importance as increased

variability in abundance, instances of stock collapse and failures of collapsed stocks to recover have each been linked to declines in the relative abundance of old and large fish (e.g. Beamish et al., 2006; Hsieh et al., 2006; Hixon et al., 2014). This is because old and large fish contribute most to recruitment, and populations consisting primarily of young, inexperienced spawners may struggle to produce new recruits in numbers sufficient to replenish the stock. The abundance of old and large fish can be monitored using stage-structured models, which is important because the long-term sustainability of many fisheries may depend on the preservation of these individuals within stocks (Berkeley et al., 2004b; Hixon et al., 2014).

Age-structured models can be fitted using data that provides information about the age of fish in the stock; this can be either age data from survey samples or, more commonly, fishery catch-at-age data (Cook, 2013). Age data is costly and time consuming to collect, so it is typically only available for the most commercially valuable fish species. This precludes the application of age-structured stock assessments for less valuable species that are rarely, if ever, aged. It is important to be able to assess stocks that lack age data because species that are not aged may still form valuable components of the fishery catch, and other species that are neither targeted nor particularly valuable may nonetheless be present regularly in bycatch. As time series of age data are not available for the vast majority of fish species, assessments of trends in the abundance of most stocks are typically conducted with surplus production models or, less commonly, length-structured models. Although some recent stock assessment studies have used relatively simple length-structured models, have focussed on length-based sustainable harvest indices, or have estimated trends in length-at-age within the model (e.g. O'Farrell and Botsford, 2005; Pope et al., 2006; Froese et al., 2008; Klaer et al., 2012; Mäntyniemi et al., 2013), applications of integrated statistical length-structured models remain uncommon (see Mäntyniemi et al., 2015, for a notable exception). Length-structured models are, however, in frequent use for assessing invertebrate stocks (Punt et al., 2013).

Length-structured models offer an alternative to age-structured models, and have the same advantages associated with monitoring the structure of fish stocks. In fact,

since mortality and fecundity are thought to be primarily size-dependent, length-structured models should in principle be more biologically realistic than age-structured models. The basic form of integrated statistical length-structured stock assessment models was presented by Sullivan et al. (1990). Conceptually, the main difference between age- and length-structured models is that the latter requires the growth of fish to be modelled explicitly. This is because growth rates tend to decrease as age and size increase, and there may be considerable variation between the growth rate of individuals. These issues do not present problems for age-structured models because all fish age at the same constant rate. However, in order to calculate biomasses, age-structured models often need to convert age into size, and this is typically done by specifying some fixed growth parameters — although some assessments may estimate growth parameters within the model (Francis, 2016). Length-structured assessments typically model growth by way of a growth transition matrix that specifies the probabilities of growing from each initial length to each final length per unit time (Punt et al., 2016). Biomasses can be calculated from length-structured models using species-specific allometric length-weight relationships — these tend to be less variable and controversial than length-age relationships. Temporal trends in growth rate can have significant influences on stock sizes and should therefore be included within assessments, but due to difficulties incorporating changes in growth into stock assessments few studies consider growth as temporally variable (Patterson et al., 2001).

Fitting a length-structured model requires either fishery catch-at-length data or length data from surveys. Landings-at-length data is made available for some stocks through market sampling programs, but this data is typically only collected for the most commercially important species. Discards-at-length — the other component of catch-at-length data — may be estimated from discard observer programs. Most length-structured stock assessment that have been applied to fish species have used catch-at-length data to inform the model about the structure of the stock (e.g. Sullivan, 1992), but this kind of data is lacking for many harvested stocks. Scientific trawl surveys are routinely conducted in many regions with active fisheries, and these surveys provide information on the length structure of many stocks that are not aged and for which

fishery stage-structured data does not exist. The length-structured model presented in chapter 5 of this thesis relies solely on survey length samples to inform the model about the length structure of the stock, and is also fitted to data on the total annual landings and (optionally) discards. As these data are widely available for many fish stocks, this model could theoretically be used to assess stocks that would otherwise require simpler surplus production models

## 1.8 Summary of thesis

Chapters 2–4 of this thesis are analyses of time series of bottom trawl survey data with information on age, length and maturity. The principal aim of these chapters was to determine whether temporal changes could be observed in the growth rates and maturation schedules of several fish species within Scottish waters. Since the Firth of Clyde was a region of particular interest, data collected from the Clyde were considered separately so that changes in the growth and maturation strategies of Clyde populations could be compared to those of their neighbours in the Scottish western shelf sea and in the North Sea. Observed changes in growth rates and maturation schedules were compared with trends in abundance indices derived from the survey samples and trends in temperature in efforts to explain why growth and/or maturation had changed in some populations.

Chapter 2 examines changes in the growth rates of five demersal fish species in the west of Scotland, and has been published as an original research paper in the journal ‘Fisheries Research’ (Hunter et al., 2016). The species considered were cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), Norway pout (*Trisopterus esmarkii*) and saithe (*Pollachius virens*). Age and length data from survey samples were used to generate distributions of lengths-at-age so that temporal trends in mean length-at-age could be derived. The von Bertalanffy growth model was fitted to successive cohorts to derive time series of asymptotic lengths,  $L_\infty$ , and von Bertalanffy growth rates,  $k$ . The mean lengths of several age groups were observed to have declined in four of the populations sampled from the western shelf sea, either steadily or over a brief interval since the 1980s. Long term trends in growth could only

be derived for four species within the Clyde, of which three exhibited declines in growth rate. The rates at which growth rate declined were considerably greater in populations from the Clyde compared to those from the rest of the western shelf sea. Few of the temporal trends in the von Bertalanffy growth parameters were related to abundance or temperature, and it appears that fishing has been responsible for the declines in growth rate and current scarcity of large demersal fish in the seas to the west of Scotland.

Chapter 3 involved assessing changes in the typical ages- and lengths-at-maturation for three demersal species from the west of Scotland, and has been published as an original research paper in the journal 'Fisheries Research' (Hunter et al., 2015). The species considered were cod, haddock and whiting. The probabilistic maturation reaction norm (PMRN) method was used to relate maturation propensity to the combination of age and length. PMRNs were fitted to successive cohorts to form time series of maturation indices. Ages-at-maturation were found to be relatively young compared to populations of the same species from other regions. West of Scotland cod, haddock, and whiting were maturing before the fish had time to grow large, and within-age-group lengths-at-maturation had declined in most of the populations since the 1980s. As with the declines in growth rates, trends of decreasing lengths-at-maturation were most rapid within the Clyde populations. Again, there was little evidence that these trends in maturation were related to abundance or temperature. Thus, in the absence of explanatory environmental trends, the declines in lengths-at-maturation assessed using PMRNs suggest that these populations have been evolving to reach maturity at progressively smaller lengths, most likely in response to size-selective fishing practises.

Chapter 4 presents similar analyses of bottom trawl survey data that examines trends in the growth rates and maturation schedules of three pelagic species from the west of Scotland and the North Sea. The species considered were herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and mackerel (*Scomber scombrus*). The results for these pelagic species were more varied than those of the demersal species. Depending on the region considered, both long-term increases and decreases in growth rates and within-age-group lengths-at-maturation were observed within the same species. However, similarly to several demersal fish populations, growth rates of these pelagic

species have also tended to decline in the west of Scotland populations, and decreases were particularly severe within the Clyde. This chapter has been written in the form of an independent research paper and will be submitted for consideration by a peer reviewed scientific journal in the near future.

Chapter 5 presents a widely applicable length-structured stock assessment model that is an extension of the model of Sullivan et al. (1990), and details the results of applying the model to west of Scotland demersal fish stocks. The species considered were cod, haddock and whiting. The results were compared with those of existing age-structured assessments to determine whether the two different model types produce similar estimates of stock size, recruitment and mortality rates. The length-structured model produced results that were similar to the age-structured model that is currently used to provide management advice for these stocks (ICES, 2013b). This was encouraging, so the length-structured model was then applied to stocks within the Firth of Clyde. The Clyde fish stocks are not currently assessed, so the results of the length-structured model may prove useful in future management of the Clyde stocks. That being said, since there are no other stock assessments to compare with, the model results should be treated with caution. This chapter has been written in the form of an independent research paper. This will also be submitted to a scientific journal in due course, but still requires some further work.



## Chapter 2

# Investigating trends in the growth of five demersal fish species from the Firth of Clyde and the wider western shelf of Scotland

### 2.1 Introduction

The Firth of Clyde is a large semi-enclosed body of water in the south-west coast of Scotland that has a long history of fishing. Vessels over eight tonnes were prohibited from trawling in the Clyde from 1889–1962 in order to protect dwindling fish stocks, particularly herring (Thurstan and Roberts, 2010). The declining seine net fishery for herring led to the ban on trawling being lifted in 1962 to allow for the exploitation of demersal fish, *Nephrops* and scallops in areas further than three miles from the coast. Landings of demersal fish then increased rapidly, reaching a maximum in 1973 before falling into decline (Hislop, 1986). Trawling within three miles of the coast was permitted from 1984 in an attempt to sustain the high catch levels. Landings then

rose in 1985, but continued to decline thereafter (McIntyre et al., 2012). Responding to diminishing demersal fish catches, increasing numbers of fishing vessels began to directly target *Nephrops* during the 1990s. The targeted demersal fishery had stopped by 2005, effectively being replaced by the *Nephrops* fishery. Since 2005 landings of demersal fish have come primarily from the *Nephrops* fishery bycatch.

The Clyde demersal fish community has undergone considerable changes since large vessels began trawling. A recent analysis of bottom trawl survey data over 1927–2009 revealed temporal trends in several community-level length related indices (Heath and Speirs, 2012). They found that the onset of trawling was associated with a steep decline in the mean length of demersal fish, over all species, which decreased from approximately 40 cm in 1960 to an all time low of 20 cm in 2009. Some of the changes were driven by shifts in species abundance. There was an even distribution of species in the period 1920–1959, with thirteen different species — including large predators like spurdog (*Squalus acanthius*) and tope (*Galeorhinus galeus*) — accounting for 95% of the total demersal biomass. Species evenness reached a minimum during 1995–2004, when 95% of the biomass was attributable to only four species, with whiting (*Merlangius merlangus*) alone, accounting for 87% of the biomass. Species evenness has since increased, with the majority of the biomass being distributed among eight different species during 2005–2009. However, it is relatively small species such as Norway pout (*Trisopterus esmarkii*) and poor cod (*Trisopterus minutus*) that have begun to contribute more to total biomass, and whiting remains by far the most abundant species. Total demersal biomass in 2009 was approximately equal to the pre-trawling biomass, so demersal fish are still abundant in the Clyde, but few of them are large and the majority are whiting.

The length structure of the Clyde demersal fish community has shown little sign of recovery since the targeted fishery closed, and this may be due to a number of different reasons. If the *Nephrops* fleet is imposing a sufficiently large mortality on the demersal community through discarded bycatch, then the length distribution may become truncated (Jackson et al., 2001; Conover and Munch, 2002). Determining the impact of the *Nephrops* fleet will require investigating the recent discarding practices of

the fishery. Additionally, trawling and dredging damage the sea floor, homogenising the habitat and disrupting benthic creatures (Auster and Langton, 1999), many of which are integral components of the diets of demersal fish. Damage to the sea floor may have resulted in large fish migrating from the Clyde to seek out more suitable feeding grounds. Finally, physiological changes in the fish themselves may also be responsible for the continued lack of large individuals. If growth rates have decreased then fish will be relatively small for their age and may never attain a large size. To determine if Clyde fish are indeed growing more slowly, we investigate temporal trends in the mean length-at-age and von Bertalanffy growth parameters of cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), Norway pout (*Trisopterus esmarkii*) and saithe (*Pollachius virens*). The von Bertalanffy growth model describes length-at-age in terms of an asymptotic length,  $L_\infty$ , and a growth rate,  $k$ . Length-at-age depends on growth history, so changes in growth rate may refer to either changes in length-at-age, which is a combination of  $L_\infty$  and  $k$ , or to changes in  $k$ . To avoid ambiguity, the  $k$  notation will be used whenever it is specifically the von Bertalanffy growth rate that is being referred to.

Growth rate is a plastic trait which can vary in response to environmental conditions such as food availability (Overholtz, 1989; Lorenzen and Enberg, 2002) and water temperature (Jørgensen, 1992; Brander, 1995; Daufresne et al., 2009). Surplus energy is used for growth and reproduction, so fish are able to grow more rapidly during periods of high food availability. Food availability for each individual depends primarily upon prey abundance, but also on competition (Ward et al., 2009). Increased competition for food generally decreases its availability to each individual, so fluctuations in year class strength may cause variations in growth (Lorenzen and Enberg, 2002). Water temperature is one of the primary environmental factors that influence growth. Fish from cold regions tend to grow more slowly than those experiencing a warm climate, however they generally live longer and attain larger body sizes (Angilletta et al., 2004). Short-term variation in growth rates may be induced by fluctuations in water temperature, and long term trends of increasing temperature have been shown to decrease the typical maximum lengths of some species (Baudron et al., 2014).

Growth rates have been shown to be modestly heritable with naturally large genetic variability (Gjedrem, 1983; Carlson and Seamons, 2008), so can evolve in response to selective pressures (Conover and Munch, 2002; Enberg et al., 2012). Small fish are more vulnerable to predation than larger individuals as they are easier to swallow and are slower swimmers (Scharf et al., 2000), so within a cohort of young fish, an individual with above average growth rate is more likely to survive predation than its peers. Therefore predation selects for rapid initial growth. Trawling nets employ a wide mesh that is designed to allow small fish to escape (Armstrong et al., 1990), disproportionately increasing the mortality rate of large individuals and generating a selective pressure to oppose that caused by predation (Edeline et al., 2007). If fishing mortality rates are high, and particularly if length distributions are truncated near the mean maturation length, then populations can potentially lose genetic variability in growth rates as fast growing fish are more likely to be caught as juveniles, or after relatively few spawning seasons as adults (Trippel, 1995; Jørgensen et al., 2007). Boldness and competitive ability are often related to growth, so fishing may also select for slow growth by imposing a selection differential on boldness (Biro and Post, 2008). The rate of fishery-induced losses in genetic variability will increase with fishing mortality rate, and relatively isolated populations will be most severely affected (Law, 2000). Growth can therefore evolve in response to fishing, at a pace determined by the heritability coefficient of growth, the fishing intensity, and the reproductive time scale of the species in question. The reversal of changes caused by fisheries induced evolution of growth has been predicted to take as long, or longer, than the initial changes (Law, 2000; Conover et al., 2009).

For our study, age-length distributions for demersal species were derived from bottom trawl survey data (1980–2012) to investigate temporal trends in mean length-at-age and fit von Bertalanffy growth curves to successive cohorts (von Bertalanffy, 1934). We aimed to determine if expected lengths-at-age have changed, and to describe any changes in terms of the asymptotic length,  $L_\infty$ , and growth rate,  $k$ . The  $L_\infty$  and  $k$  parameters were regressed against sea-surface temperature, estimated year-class strength and time, to determine the extent to which these variables have influenced growth. Sig-

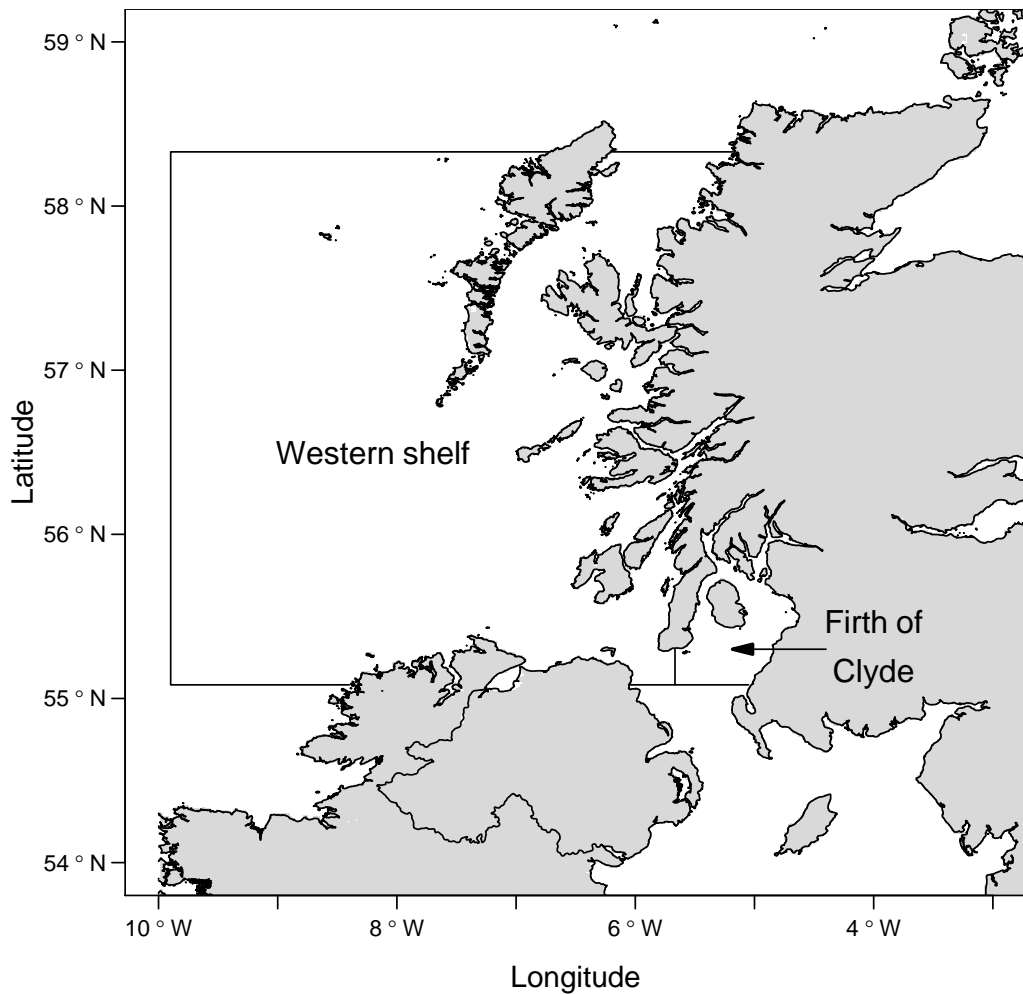


Figure 2.1: The Firth of Clyde and western shelf regions.

nificant relationships to temperature or year-class strength would indicate that changes in growth were plastic responses to environmental conditions that ought to revert if conditions were to change back to a prior state. A significant temporal trend may indicate that the growth parameters were responding to some other environmental variables, or that they have been evolving.

Clyde populations were compared to those in the wider west coast of Scotland to determine if any changes in the mean length-at-age and growth parameters of Clyde fish were typical of the wider region or particularly extreme. The two regions considered were the Firth of Clyde and western shelf (fig. 2.1). Mixing of the demersal populations between these regions is thought to be limited, as there is evidence indicating

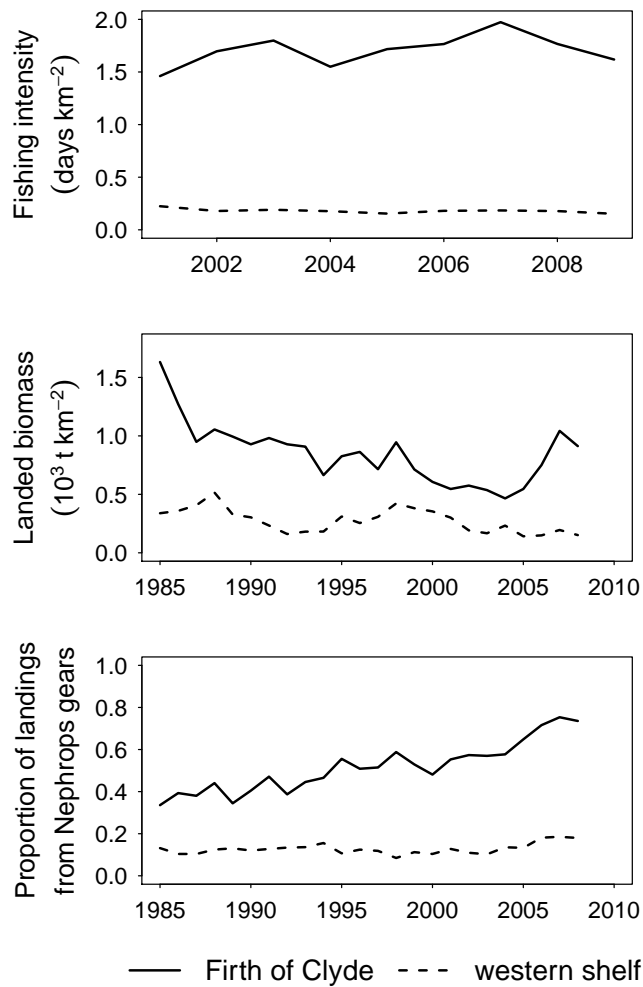


Figure 2.2: Differences in the Clyde and western shelf fisheries. Top: annual fishing intensity of UK bottom trawling vessels over 10 m long from 2001 until 2009. Total landings were calculated as the sum of the landed biomass of all species from all demersal and *Nephrops* trawls. Middle: total landings divided by the area of the region. Bottom: proportion of the total landings caught by *Nephrops* trawls.

that immigration into the Clyde is uncommon (Brander, 1975; Connolly and Officer, 2001); that some populations are resident within the Clyde (Wright et al., 2006); that Clyde demersal fish tend to spawn within the confines of, or close to, the Clyde (Hislop, 1986); and that the isolation of the Clyde is sufficient for the demersal community to

display independent local responses to exploitation, and potentially also to environmental fluctuations (Heath and Speirs, 2012). Regional differences in growth should therefore be examinable with survey data, and may be the result of differences in the local environment. Fishing intensity has been greater in the Clyde than western shelf, and the proportion of vessels that trawl with finer mesh nets to target *Nephrops* has risen steadily in the Clyde and is much greater than in the western shelf (fig. 2.2). If fishing has been driving trends in growth then we would expect changes in the Clyde populations to be more severe. Thus, if growth has changed significantly over time then regional comparisons may provide evidence to indicate whether the trends were due to fishing.

## 2.2 Material and Methods

### 2.2.1 The data

International Bottom Trawl Survey data from the Scottish west coast (SWC-IBTS) were used in this analysis (ICES, 2015). The samples were collected using grande ouverture verticale (GOV) nets and spanned the years 1985–2012. Fisheries Research Services (FRS) demersal trawl survey data were also used, resulting in time series spanning 1980–2012. The bulk of the dataset was length data, which consisted of annual random samples of fish where the total length of each individual had been measured and rounded down to the nearest centimetre. Some of these fish were also aged, by examination of otoliths for annual growth rings, creating a length-stratified age-length data subset. The average annual sample sizes and proportions of the samples that were aged are shown in table 2.1. Most of the data had been collected during quarters one and four of the year. To reduce variability in length-at-age, which improves the accuracy of the analysis by creating more distinct peaks in the length frequency distributions, we considered data from quarter one only. We chose quarter one because sample sizes were larger than in quarter four, and there were fewer missing years.

Annual stock assessments of ICES area VIa provide fishing mortality rate estimates for cod, haddock and whiting. However, since ICES area VIa includes both of the

regions considered in this paper, these estimates could not be used to evaluate regional differences. We therefore used fishing effort data (Marine Scotland Science) and landings data collected in the finer spatial scale of ICES statistical rectangles to assess regional differences in fishing activity and size selectivity.

Annual mean summer (June, July and August) sea-surface temperatures were calculated using the Keppel pier, Millport, dataset (University Marine Biological Station, Millport, 1949–) for the Clyde, and the Hadley Centre HadISST1 dataset (Rayner et al., 2003) for the western shelf. Mean summer temperature was calculated as the mean of mean monthly temperatures based on daily readings. Local temperature data for the years 1988, 1996 and 2003 were missing from the HadISST1 dataset, so the mean summer temperature for these years was assumed to be the average of the mean summer temperature for the preceding and subsequent years.

## 2.2.2 Estimating age-at-length

Estimating von Bertalanffy growth parameters requires age-length data, so the age of each individual in the length data was estimated. This was done by analysing the annual length and age-length frequency distributions from the length and age data respectively, using the methods of Martin and Cook (1990) as follows. This method was applied to each year of data individually, so variables are subscripted with  $y$  to indicate year. Length-at-age was assumed to be normally distributed such that modelled length frequency distributions consisted of several overlapping normal distributions, each corresponding to a different age class. The probability,  $q_y(l|a)$ , that an individual is of

Table 2.1: The ‘sample size’ columns show the mean number of fish present in the annual samples, with the range shown in parenthesis. The ‘proportion aged’ columns show the proportion of the sampled fish that were aged, averaged over years, with the range in parenthesis. Years without data have been excluded. FC and WS stand for the Firth of Clyde and the western shelf.

Species	Sample size		Proportion aged	
	FC	WS	FC	WS
Cod	29 (3–225)	81 (6–241)	0.921 (0.316–1)	0.769 (0.186–1)
Haddock	141 (1–775)	7404 (989–20716)	0.622 (0.201–1)	0.089 (0.002–0.402)
Whiting	4799 (731–14978)	10396 (1092–29303)	0.056 (0.005–0.461)	0.068 (0.013–0.296)
Norway pout	242 (3–1122)	61548 (1761–145530)	0.169 (0.015–0.865)	0.009 (0.001–0.043)
Saithe	123 (1–699)	84 (2–929)	0.658 (0.133–1)	0.746 (0.100–1)



length  $l$ , given its age,  $a$ , can then be written as

$$q_y(l|a) = \frac{1}{s_y(a)\sqrt{2\pi}} \int_l^{l+w} \exp\left(-\frac{1}{2}\left(\frac{x - m_y(a)}{s_y(a)}\right)^2\right) dx \quad (2.1)$$

where  $m_y(a)$  and  $s_y(a)$  are the mean and standard deviation of length at age  $a$ , and  $w$  is the width of the length intervals. Upon making this assumption, the length and age-length frequency distributions may be expressed solely in terms of the following parameters.

$$p_y(a) = \text{proportion of fish aged } a \quad (2.2)$$

$$m_y(a) = \text{mean length of fish aged } a \quad (2.3)$$

$$s_y(a) = \text{standard deviation of length at age } a \quad (2.4)$$

Let  $p_y(l, a)$  be the probability of a randomly selected fish being of length  $l$  and age  $a$ . This can be written in terms of eqs. (2.2) to (2.4) as  $p_y(l, a) = p_y(a) q_y(l|a)$ . The probability of being in length class  $l$  is  $p_y(l) = \sum_{a=1}^{A_y} p_y(l, a)$ , where  $A_y$  is the maximum age of fish within the samples. The expected length frequency distribution,  $f_y(l)$ , can now be written as  $f_y(l) = N_y p_y(l)$ , where  $N_y$  is the total number of sampled fish.

Let annual age-length keys be defined by  $q_y(a|l)$ , the probability of age,  $a$ , given length,  $l$ . Since  $p_y(l, a) = p_y(l) q_y(a|l)$ , the age-length keys can be written as

$$q_y(a|l) = \frac{p_y(l, a)}{p_y(l)}. \quad (2.5)$$

Let  $n_y(l)$  be the number of fish that were sub-sampled for age in length class  $l$ . The expected age distribution of fish from sub-sample  $n_y(l)$  is given as  $n_y(l, a) = n_y(l) q_y(a|l)$ . Thus, the expected length and age-length frequency distributions can both be expressed in terms of eqs. (2.2) to (2.4). The observed length and age-length frequency distributions,  $\hat{f}_y(l)$  and  $\hat{n}_y(l, a)$ , were assumed to follow multinomial distributions,  $\hat{f}_y(l) \sim \text{Multi}(N_y, p_y(l))$  and  $\hat{n}_y(l = i, a) \sim \text{Multi}(n_y(i), q_y(a|i))$ , so that eqs. (2.2) to (2.4) could be estimated by maximum likelihood to yield age-length keys given by

eq. (2.5). Maximising the likelihood is equivalent to minimising

$$2 \sum_{l=1}^{L_y} \hat{f}_y(l) \log \left( \frac{\hat{f}_y(l)}{f_y(l)} \right) + 2 \sum_{l=1}^{L_y} \sum_{a=1}^{A_y} \hat{n}_y(l, a) \log \left( \frac{\hat{n}_y(l, a)}{n_y(l, a)} \right) \quad (2.6)$$

where  $L_y$  is the maximum length within the samples (Schnute and Fournier, 1980). Equation (2.6) is the objective function that was minimised to estimate  $p_y(a)$ ,  $m_y(a)$  and  $s_y(a)$ .

Minimising eq. (2.6) required the parameters to be given some initial values. The initial values of  $p_y(a)$  and  $m_y(a)$  were calculated directly from the age data. Due to the scarcity of old fish, values of  $s_y(a)$  calculated directly from the age data were often underestimated in the older age groups. We assumed that  $s_y(a)$  would increase linearly with  $m_y(a)$  and fitted linear models,  $\tilde{s}(a) = \alpha_0 + \alpha_1 \tilde{m}(a)$ , where  $\tilde{\cdot}$  indicates values calculated from age data from all years combined, to generate more reasonable initial values for  $s_y(a)$  in the older age groups. The initial values were then calculated as  $s_y(a) = \alpha_0 + \alpha_1 m_y(a)$ . In order to acquire physically meaningful estimates, the minimisation procedure constrained the parameters such that  $p_y(a)$ ,  $m_y(a)$  and  $s_y(a) \geq 0$  and  $\sum_{a=1}^{A_y} p_y(a) \leq 1$ .

Once the best fitting values  $p_y(a)$ ,  $m_y(a)$  and  $s_y(a)$  were found, age-length keys could be derived from eq. (2.5). The ages of all fish in the length data were estimated by multiplying the observed length frequency distributions through the age-length keys to obtain matrices,  $M_{a,l,y} = q_y(a | l) \text{diag}(\hat{f}_y(l))$ , in which entries specified the number of individuals at each age and length, after rounding to the nearest whole fish. These numbers at age and length matrices were then transformed to give age-length frequency distributions for cohorts,  $c$ , instead of years,  $M_{a,l,c}$ . Vectors specifying the length,  $l_{i,c}$ , and age,  $a_{i,c}$ ,  $i \in \{1, \dots, N_c\}$ , of each of the  $N_c$  sampled fish were extracted from  $M_{a,l,c}$  and used to estimate the von Bertalanffy growth parameters.

### 2.2.3 Estimating growth parameters

The von Bertalanffy growth model was fitted to the age-length data for successive cohorts

$$l_{i,c} = L_{\infty c} (1 - \exp(-k_c (a_{i,c} - t_{0c}))) + \varepsilon_{i,c}, \quad \varepsilon_{i,c} \sim N(0, \sigma_c^2) \quad (2.7)$$

assuming that errors were i.i.d. and normal. We used OpenBUGS, via the R package R2OpenBUGS, to estimate the  $L_{\infty c}$ ,  $k_c$  and  $t_{0c}$  parameters because it produced fewer spurious results than other R functions such as non-linear least squares (nls) and it automatically provided credible intervals for the estimates. Priors for  $L_{\infty c}$  and  $k_c$  were specified as gamma distributions, and the priors for  $t_{0c}$  were normally distributed. The error variances,  $\sigma_c^2$ , were given wide ranging uniform priors. The gamma distribution describes positive variables and provided a sensible choice for the priors, but other less informative priors such as uniform distributions could have been used instead. The parameters for each prior distribution were found by fitting the probability density functions to the range of growth parameter values provided for each species in the online database fishbase.org (Froese and Pauly, 2015). The prior parameter values for each species are shown in table 2.2. Three over-dispersed MCMC chains were run simultaneously for each cohort. Convergence was tested for with Gelman and ACF plots, as well as visually with trace plots of the MCMC chains. Simulations were run until convergence was reached, the number of iterations ranged from  $10^5$  to  $10^7$  depending on the pattern of growth of the cohort and the sample sizes, with more data-heavy cohorts requiring a longer run time. Cohorts with growth patterns closely matching von Bertalanffy growth required fewer iterations than those whose growth was more poorly described by the von Bertalanffy curve. The simulations were run on a computer with 8 GB of RAM and four Intel (R) Core (TM) i5-3570 processors, although simulations were run sequentially so that only one of the cores were used. The total run-time taken to generate growth parameter estimates for each cohort for all five species in both regions was approximately two months, however, if all four cores were used then the time taken would have been reduced greatly. The OpenBUGS output consisted of estimates of the growth parameters,  $L_{\infty c}$ ,  $k_c$  and  $t_{0c}$ , the standard

deviation of each parameter, MCMC error and 95% credible intervals.

#### 2.2.4 Trends in mean length-at-age and the growth parameters

The age-length data,  $M_{a,l,y}$ , estimated following section 2.2.2, were used to fit linear models

$$l_j = \beta_{a_j} + \gamma_{a_j} y_j \quad (2.8)$$

where  $j$  indexes individuals. These were independently fitted to each species within each region, to estimate trends in mean length-at-age. Age,  $a_j$ , was treated as a categorical variable, so fitting eq. (2.8) resulted in separate estimates of  $\beta_{a_j}$  and  $\gamma_{a_j}$  for each age group. The  $\gamma_{a_j}$  terms are the estimated linear rates of change of length within age groups, which were used as a measure of the average annual change in mean length-at-age, and to estimate the total change in mean length-at-age over the time series.

The estimated growth parameters,  $L_{\infty c}$  and  $k_c$ , were independently regressed against the year of birth of the cohort,  $Y_c$ , and against combinations of  $Y_c$ , estimated year class strength,  $N_{0,c}$ , and the mean summer temperature experienced by each cohort during the first three years of growth,  $T_c$ ,

$$P_c = \delta_0 + \delta_1 Y_c + \delta_2 N_{0,c} + \delta_3 T_c + \delta_4 N_{0,c} T_c \quad (2.9)$$

where  $P_c$  is either  $L_{\infty c}$  or  $k_c$ . To reduce the impact of poorly estimated growth parameters, these regressions were weighted by the inverse standard deviations of the growth parameter estimates. Parameters were excluded from eq. (2.9) using a stepwise

Table 2.2: Parameterisation of prior distributions;  $L_{\infty}$  and  $k$  were gamma distributed and  $t_0$  was normally distributed.

Species	$L_{\infty}$		$k$		$t_0$	
	shape	rate	shape	rate	mean	st. dev.
Cod	13.3	0.12	5.3	27.1	-0.35	0.51
Haddock	27.6	0.40	8.7	36.2	-0.52	0.48
Whiting	15.3	0.33	3.2	9.2	-0.98	1.08
Norway pout	50.9	2.4	8.3	13.9	0.0	1.5
Saithe	26.0	0.22	8.1	55.7	-0.78	0.57

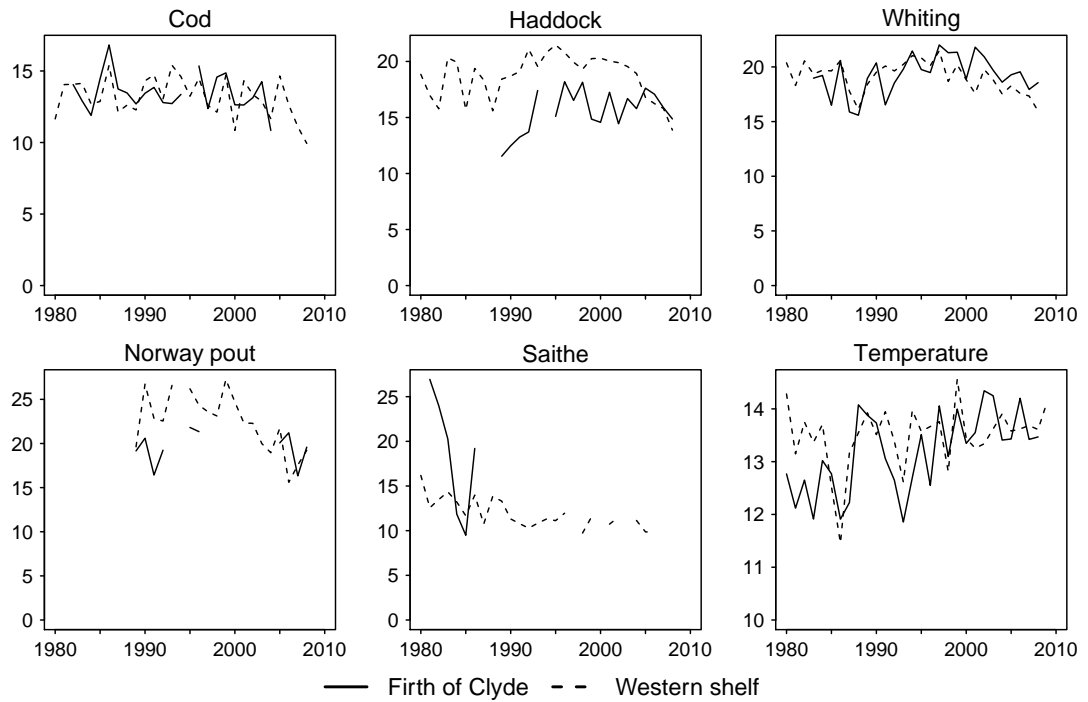


Figure 2.3: Time series of estimated log year-class strength (numbers per km<sup>2</sup>) for each species, as well as temperature (°C).

AIC procedure, and the interaction term,  $N_{0,c} T_c$ , was retained only if it was significant ( $p < 0.05$ ). Catchability-at-length estimates for North Sea GOV trawl surveys (Fraser et al., 2007) were used to estimate the actual number of fish in the path swept out by the trawling gear. An abundance-at-age index,  $N_{a,c}$ , was then created for each cohort by dividing the number of fish at each age — which were in the path of the gear — by the total area swept out during the year that age group was sampled. The year class strength,  $N_{0,c}$ , was then estimated by fitting a simple survivorship model

$$\log(N_{a,c}) = \log(N_{0,c}) - Z_c a \quad (2.10)$$

where the gradient,  $Z_c$ , denotes estimated mortality rate. Time series of temperature and the estimated log year class strength are shown in fig. 2.3.

## 2.3 Results

### 2.3.1 Age-length data

Annual age-length data sets were generated by calculating the probability of age given length and assigning an age to each individual in the length data. This involved estimating time series of mean lengths,  $m_y(a)$ , standard deviation of lengths,  $s_y(a)$ , and the proportions,  $p_y(a)$ , within each age group, following section 2.2.2. The results are summarised in fig. 2.4. Comparing the estimated age-length data between regions, it is apparent that age groups four and above, from each of the five species considered, have been relatively poorly sampled within the Clyde. This indicates that the proportion of the Clyde populations that consist of these older individuals is lower than in the western shelf. It may, however, be a consequence of less representative surveys within the Clyde.

### 2.3.2 Trends in mean length-at-age

Table 2.3 shows the results of the linear regressions of length-at-age against time (eq. (2.8)). The changes in mean length-at-age predicted from eq. (2.8), and time series of estimated mean lengths-at-age are plotted in fig. 2.5.

Mean lengths declined significantly over time in most age groups of Clyde haddock, the exception being age group four. The decreases in length ranged from  $5.0 \pm 0.6$  cm in age group one to  $20.0 \pm 2.2$  cm in age group three during 1985–2011; the mean length of age group five decreased by  $9.3 \pm 4.7$  cm over 2004–2010. Lengths-at-age also declined in western shelf haddock in age groups two and above, but at markedly slower rates than in the Clyde. Decreases in mean length in western shelf haddock ranged from  $1.5 \pm 0.1$  cm to  $9.7 \pm 0.3$  cm during 1980–2011 in age groups two and five respectively.

Declines in mean length were observed in all age groups of Clyde and western shelf whiting, apart from age group five in the western shelf. Decreases in length within the Clyde ranged from  $3.7 \pm 0.1$  cm to  $15.1 \pm 2.2$  cm in age groups one and four during 1980–2011 and 1980–2007 respectively; in the western shelf the decreases in the lengths of these age groups were  $2.9 \pm 0.1$  cm and  $4.6 \pm 0.2$  cm during 1980–2011.

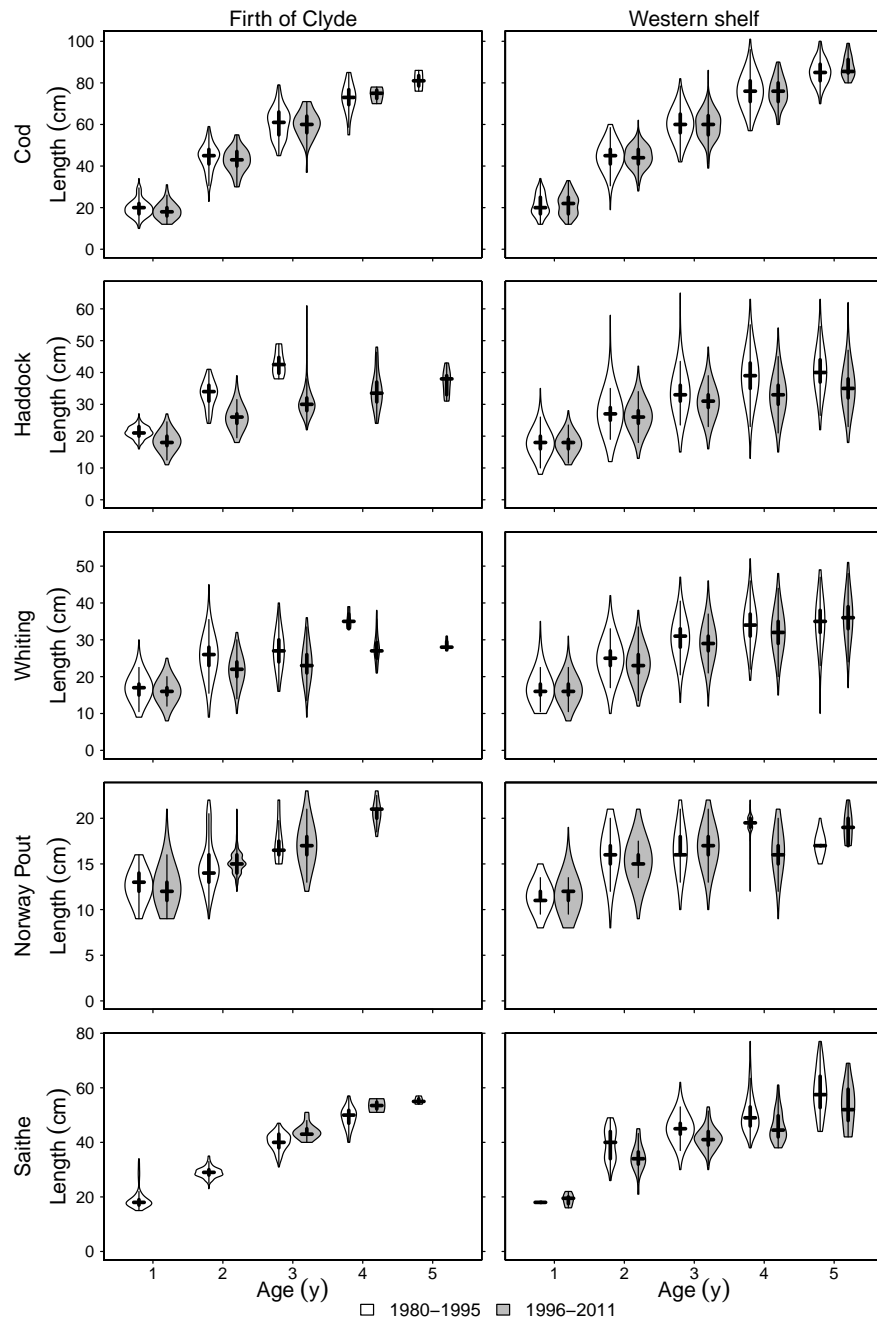


Figure 2.4: Violin plots of the estimated age-length data produced from section 2.2.2, grouped by periods 1980–1995 and 1996–2011. Horizontal lines indicate median length at age. Thick vertical lines show the interquartile range of length-at-age, and the narrower vertical lines show the range of the data excluding outliers (defined as 1.5 times the interquartile size in either direction). Violins extending beyond the vertical lines indicate the presence of outlying values. Within each period, the width of the violins are proportional to the quartic root of the sample size to indicate proportions at age. Age groups greater than five have been omitted.

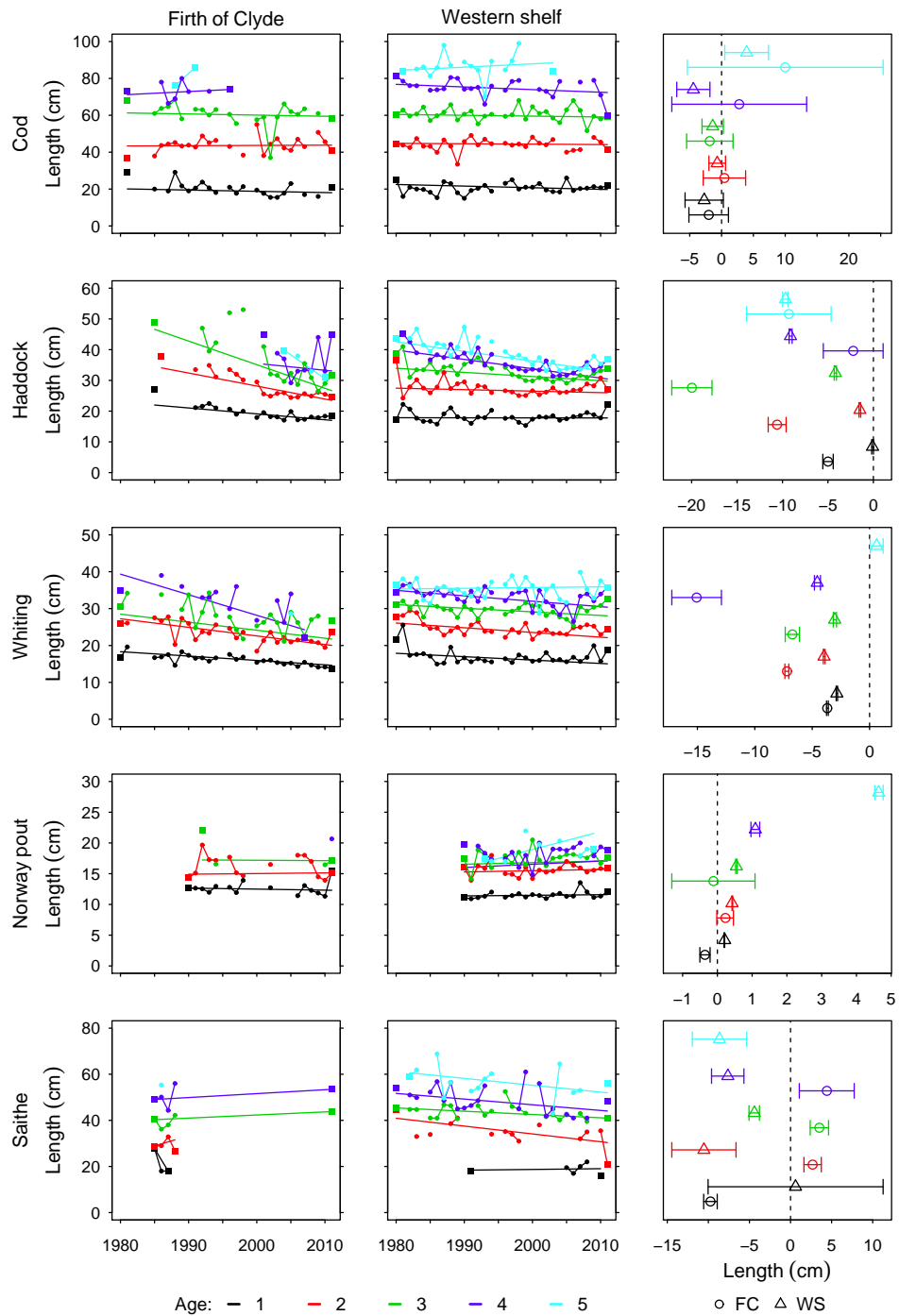


Figure 2.5: Points show mean length-at-age, calculated from the estimated age-length data. Square symbols are the estimates corresponding to the first and final years in the time series. Straight lines are regression lines from eq. (2.8). Plots in the column to the right show the total change in mean length between the first and final years, with 95% confidence intervals, predicted from eq. (2.8). FC and WS stand for the Firth of Clyde and western shelf.



The mean lengths of all age groups of Norway pout from the western shelf have increased significantly over time, by amounts ranging from  $0.2 \pm 0.01$  cm in age group one to  $4.6 \pm 0.1$  cm in age group five during 1990–2011 and 1993–2009 respectively. There were no such increases in the lengths of Clyde Norway pout, in fact, there has been a small but significant decrease of  $0.4 \pm 0.1$  cm in the mean length of age group one during 1990–2011.

Mean lengths of western shelf saithe in age groups two and above declined over time; the largest decrease of  $10.5 \pm 3.9$  cm was observed in age group two during 1980–2011. Most of the data for Clyde saithe were restricted to 1985–1988 (fig. 2.5), so long term trends in length-at-age could not be calculated, and consequently the significant trends reported in table 2.3 for Clyde saithe should be considered spurious.

### 2.3.3 Growth parameters

Figure 2.6 shows the von Bertalanffy growth parameters that were estimated by using OpenBUGS to fit the model described in section 2.2.3 to the estimated age-length data. The extent to which  $L_\infty$  and  $k$  changed over the time series was calculated from the

Table 2.3: The linear rate of change of mean length-at-age in units of  $\text{cm y}^{-1}$ , with 95% confidence intervals shown below in parenthesis. Significant trends are indicated in bold. FC and WS stand for the Firth of Clyde and western shelf.

Species	Region	Age 1	Age 2	Age 3	Age 4	Age 5
Cod	FC	-0.067 (-0.171, 0.036)	0.015 (-0.096, 0.126)	-0.062 (-0.183, 0.060)	0.185 (-0.521, 0.891)	3.333 (-1.792, 8.459)
	WS	-0.088 (-0.185, 0.009)	-0.022 (-0.064, 0.020)	-0.045 (-0.099, 0.009)	<b>-0.143</b> (-0.227, -0.059)	<b>0.179</b> (0.023, 0.335)
Haddock	FC	<b>-0.192</b> (-0.214, -0.170)	<b>-0.424</b> (-0.463, -0.384)	<b>-0.768</b> (-0.853, -0.683)	-0.222 (-0.551, 0.107)	<b>-1.550</b> (-2.325, -0.775)
	WS	-0.003 (-0.006, 0.0003)	<b>-0.048</b> (-0.051, -0.045)	<b>-0.135</b> (-0.139, -0.131)	<b>-0.304</b> (-0.309, -0.298)	<b>-0.312</b> (-0.322, -0.303)
Whiting	FC	<b>-0.119</b> (-0.121, -0.116)	<b>-0.232</b> (-0.238, -0.227)	<b>-0.217</b> (-0.237, -0.197)	<b>-0.558</b> (-0.638, -0.478)	NA
	WS	<b>-0.092</b> (-0.094, -0.090)	<b>-0.128</b> (-0.130, -0.125)	<b>-0.098</b> (-0.102, -0.093)	<b>-0.147</b> (-0.155, -0.138)	<b>0.020</b> (0.002, 0.038)
Norway pout	FC	<b>-0.017</b> (-0.024, -0.010)	0.011 (-0.0008, 0.022)	-0.006 (-0.069, 0.057)	NA	NA
	WS	<b>0.0099</b> (0.0094, 0.0104)	<b>0.0204</b> (0.0200, 0.0209)	<b>0.026</b> (0.025, 0.027)	<b>0.052</b> (0.046, 0.058)	<b>0.290</b> (0.283, 0.298)
Saithe	FC	<b>-4.873</b> (-5.286, -4.460)	<b>0.896</b> (0.544, 1.248)	<b>0.135</b> (0.092, 0.178)	<b>0.170</b> (0.041, 0.298)	NA
	WS	0.032 (-0.528, 0.593)	<b>-0.340</b> (-0.466, -0.214)	<b>-0.142</b> (-0.163, -0.122)	<b>-0.246</b> (-0.310, -0.183)	<b>-0.298</b> (-0.412, -0.184)

output of the regressions against time and shown in table 2.4.

#### 2.3.4 Environmental influences

The growth parameters were regressed against time series of estimated year class strength, average summer temperature over the first three years of growth, and cohort (fig. 2.3). The results of these regressions (table 2.4) are used in this section to describe how trends in temperature and year class strength may have influenced  $L_\infty$  and  $k$ .

The growth parameters of Clyde cod did not change significantly over time, so the best fitting models excluded the cohort variable. Temperature and year class strength, however, both appear to influence  $L_\infty$ , which tended to decrease as the temperature rose and increase with reducing year class strength. The growth rate of cod in the western shelf increased over time, the best fitting model included temperature and cohort, and temperature explained enough of the variation to make the cohort variable insignificant. The  $L_\infty$  parameter decreased over time, the best fitting model included cohort, year class strength, temperature and the interaction term, and all but cohort were significant. However, cohort accounted for a larger decrease in  $L_\infty$  than the combination of other variables.

Both  $L_\infty$  and  $k$  decreased over time in Clyde haddock. The decrease in  $L_\infty$  was not explained by trends in temperature or year class strength, but there was a significant relationship between  $k$  and year class strength. The predicted increase attributable to year class strength was an order of magnitude lower than the decreases associated with the cohort and temperature variables, and the cohort effect accounted for the largest change. Neither of the growth parameters changed linearly over time in western shelf haddock, and they showed no dependence on the environmental variables.

The growth parameters of Clyde whiting did not vary linearly with cohort, and the best fitting models were regressions of  $L_\infty$  against temperature, and  $k$  against year class strength. Only the rise in year class strength was significant, accounting for about half of the overall change in  $k$ . There were no linear relationships between the environmental variables and the growth parameters of western shelf whiting.

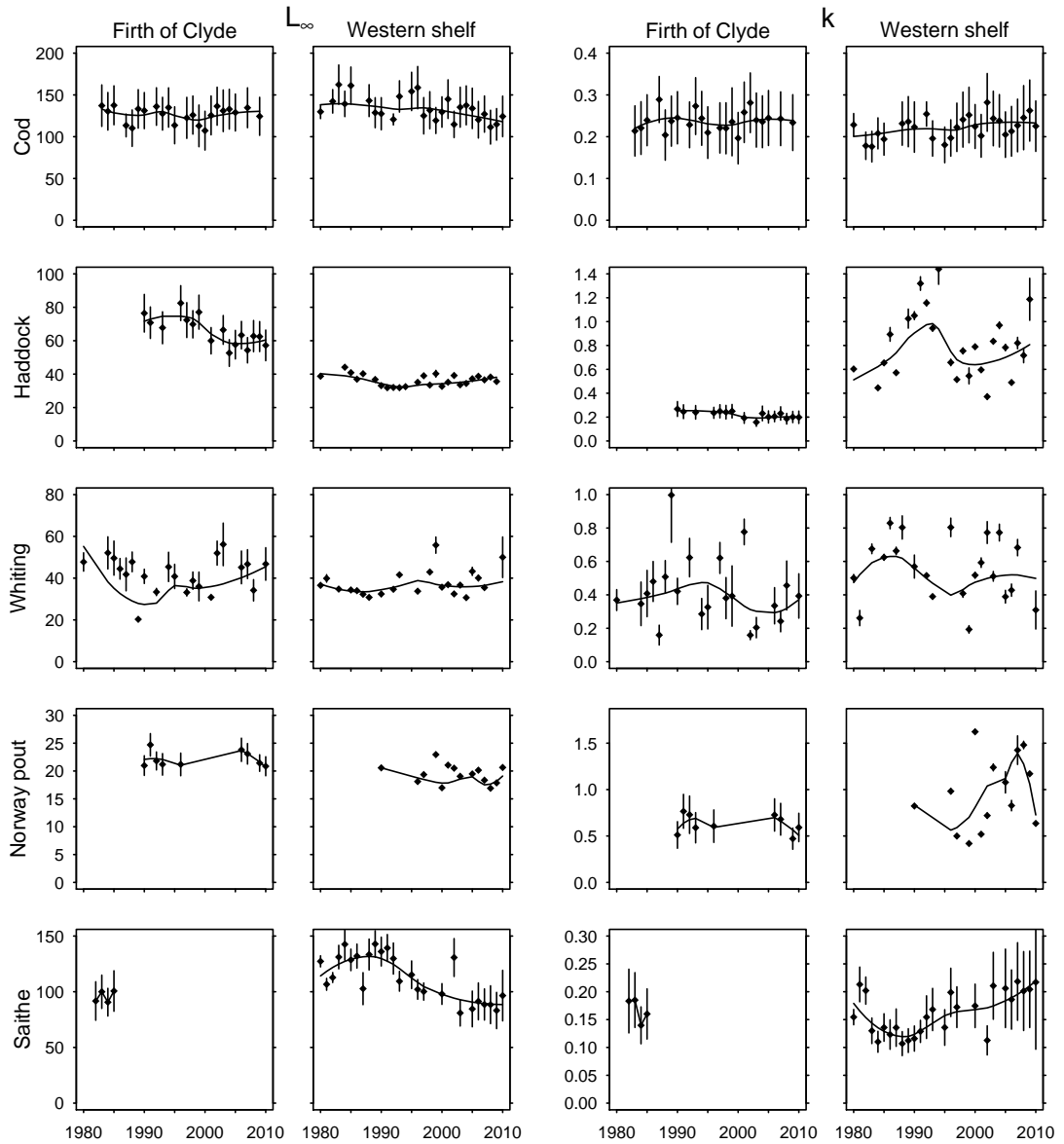


Figure 2.6: The estimated mean values and standard deviations of the von Bertalanffy growth parameters,  $L_\infty$  (cm) and  $k$  ( $y^{-1}$ ), plotted with loess smoothing curves. Asymptotic lengths in each region are shown in the two columns to the left, and growth rates in the the two rightmost columns.

### 2.3. Results

Table 2.4: The total changes in  $L_\infty$  (cm) and  $k$  ( $y^{-1}$ ) over the time periods shown, predicted from regressing against cohort only, are given with 95% confidence intervals in parenthesis. The ‘effect’ column shows the most informative combination of explanatory variables from eq. (2.9). The coefficients and standard errors for these variables, and their expected effect on the growth parameters are shown in the last two columns. The coefficients are rates of change of the growth parameters with respect to cohort, year class strength and temperature, in units of  $\text{cm } y^{-1}$ ,  $\text{cm } 10^{-3} \text{ km}^2$  and  $\text{cm } ^\circ\text{C}^{-1}$  for  $L_\infty$ , and  $y^{-2}$ ,  $y^{-1} 10^{-3} \text{ km}^2$  and  $y^{-1} ^\circ\text{C}^{-1}$  for  $k$ . Significant changes and linear trends are shown in bold. FC and WS stand for the Firth of Clyde and western shelf.

Group	Parameter	Total change	Effect	Coefficient (SE)	Resulting change
FC cod 1983–2009	$L_\infty$	-1.63 (-16.43, 13.18)	<b>year class strength</b>	<b>-4.60 (2.00)</b>	<b>2.19</b>
			<b>temperature</b>	<b>-7.44 (3.43)</b>	<b>-8.86</b>
	$k$	0.0067 (-0.0300, 0.0435)	year class strength	0.013 (0.0062)	-0.0068
WS cod 1980–2010	$L_\infty$	<b>-19.66</b> <b>(-36.31, -3.01)</b>	cohort	-0.55 (0.30)	-15.28
			<b>year class strength</b>	<b>-18600 (8500)</b>	<b>264.72</b>
			<b>temperature</b>	<b>-30.09 (10.35)</b>	<b>-20.24</b>
		<b>y. c. s. × temperature</b>	<b>1340 (626.6)</b>	<b>-253.67</b>	
	$k$	<b>0.036</b> <b>(0.0027, 0.0695)</b>	cohort	0.00095 (0.00064)	0.027
			temperature	0.017 (0.015)	0.011
FC haddock 1990–2010	$L_\infty$	<b>-19.47</b> <b>(-30.33, -8.72)</b>	<b>cohort</b>	<b>-0.97 (0.25)</b>	<b>-19.47</b>
	$k$	<b>-0.066</b> <b>(-0.109, -0.024)</b>	cohort	-0.0029 (0.0014)	-0.052
			<b>year class strength</b>	<b>0.0035 (0.0014)</b>	<b>0.0037</b>
			temperature	-0.026 (0.021)	-0.023
WS haddock 1980–2009	$L_\infty$	-4.11 (-9.12, 0.90)	cohort	-0.14 (0.084)	-4.11
	$k$	0.13 (-0.18–0.44)	no effect		
FC whiting 1980–2010	$L_\infty$	-0.98 (-14.95, 13.00)	temperature	-3.19 (3.69)	-4.74
	$k$	-0.11 (-0.42, 0.19)	<b>year class strength</b>	<b>-0.00052 (0.00019)</b>	<b>-0.058</b>
WS whiting 1980–2010	$L_\infty$	2.05 (-3.85, 7.95)	no effect		
	$k$	-0.12 (-0.39, 0.15)	temperature	-0.15 (0.095)	-0.091
FC Norway pout 1990–2010	$L_\infty$	-0.093 (-2.906, 2.721)	no effect		
	$k$	-0.053 (-0.265, 0.160)	cohort	0.016 (0.0066)	0.31
			temperature	-0.21 (0.010)	-0.21
WS Norway pout 1990–2010	$L_\infty$	-1.78 (-4.82, 1.26)	<b>cohort</b>	<b>-0.18 (0.051)</b>	<b>-3.59</b>
			<b>year class strength</b>	<b>-0.00027 (0.000078)</b>	<b>0.70</b>
		$k$	0.30 (-0.45, 1.05)	<b>cohort</b>	<b>0.035 (0.014)</b>
			<b>year class strength</b>	<b>0.000096 (0.000031)</b>	<b>-0.25</b>
FC saithe 1982–1985	$L_\infty$	4.24 (-33.49, 41.96)	no effect		
	$k$	-0.036 (-0.162, 0.090)	cohort	-0.012 (0.0098)	-0.036
WS saithe 1980–2010	$L_\infty$	<b>-38.13</b> <b>(-57.06, -19.20)</b>	<b>cohort</b>	<b>-1.44 (0.44)</b>	<b>-43.12</b>
			year class strength	-40.14 (41.64)	4.35
		$k$	0.044 (-0.007, 0.095)	cohort	0.0018 (0.0011)
			year class strength	0.14 (0.095)	-0.014

Since the growth parameter time series for Norway pout and saithe from the Clyde were sparse, there were no significant relationships with temperature or year class strength. Neither of the growth parameters of Norway pout from the western shelf trend linearly over time, although they both respond to decreases in year class strength, and are balanced by a cohort effect. In each case the largest change in the parameters was due to the cohort effect, which caused decreases in  $L_\infty$  and increases in  $k$ . The best fitting models for the growth parameters of western shelf saithe included the cohort and year class strength variables, but only the temporal trend in  $L_\infty$  was significant.

## 2.4 Discussion

### 2.4.1 Large reductions in lengths of Clyde fish

Length-at-age has declined in many distinct fish stocks around the world (Pope and Knights, 1982; Swain et al., 2007; Cheung et al., 2012; Audzijonyte et al., 2013; Baudron et al., 2014), and this has now been observed in demersal populations within the Firth of Clyde as well as throughout the Scottish western shelf sea. The rapid declines in the mean length of Clyde haddock in age groups one and above were due to significant declines in  $L_\infty$  and  $k$  (table 2.4); the growth rate decreased steadily throughout the time series, whereas the decrease in  $L_\infty$  occurred during 1998–2004 (fig. 2.6). Mean lengths-at-age of western shelf haddock declined most rapidly during 1994–2000 (fig. 2.5) when  $k$  decreased sharply; lengths-at-age were relatively stationary in 1980–1994 as the rise in  $k$  was balanced by declining  $L_\infty$  values. Long term decreases in both the  $L_\infty$  and  $k$  values of haddock only occurred within the Clyde population, resulting in the relatively large declines in length. Although linear trends in the growth parameters of Clyde whiting were not significant,  $L_\infty$  and  $k$  in cohorts from the second half of the time series both tended to be lower than in earlier cohorts, explaining the steady and rapid declines in mean length across all age groups. Decreases in lengths-at-age in western shelf whiting in age groups one to four were due to lower  $k$  values in the second half of the time series, as fig. 2.6 suggests an increase in  $L_\infty$  over time; this increase in  $L_\infty$  corresponds to the significant increase in the expected length of age group five. As

with haddock, declines in both the  $L_\infty$  and  $k$  values of whiting only occurred within the Clyde population, explaining the relatively large declines in length-at-age. Increases in the mean lengths of all age groups of western shelf Norway pout appear to have resulted from the rise in  $k$  between 1995 and the late 2000s (fig. 2.6). There was no such increase in the growth rate of Norway pout from the Clyde, and consequently, no increases in mean lengths-at-age. Decreases in the mean lengths of western shelf saithe in age groups two and above were due to the significant decline in  $L_\infty$  (table 2.4). The survey data — as well as landings data (Thurstan and Roberts, 2010) — indicate that saithe has become rare in the Clyde since the late 1980s, and the data available for this species was insufficient to analyse long term trends in growth.

Declines in length were much more pronounced in the haddock and whiting populations within the Clyde than in the western shelf region, and the lengths of Norway pout increased in the western shelf while remaining stationary — and actually decreasing in age group one — within the Clyde. This suggests that growth has been changing in response to environmental factors that differ between the two regions, or in response to fishing pressure.

#### 2.4.2 Why has growth changed?

Although changes in  $L_\infty$  and  $k$  were significantly related to temperature and year class strength in several groups, in most of those cases these two environmental variables only accounted for a small fraction of the observed overall changes. Most of the changes in  $L_\infty$  and  $k$  were attributable to a cohort effect, so it appears that declines in length-at-age have been due to some other environmental factors or fishing. Growth may vary in response to any environmental fluctuations that induce changes in resource acquisition and allocation (Enberg et al., 2012), but since temperature and food availability have the most direct effects (Nicieza and Metcalfe, 1997), our results imply that large changes in growth have been induced independently of environmental influences. Due to the long term nature of the declines in length, and regional differences in growth trends and the fisheries, we suggest that the changes may have been largely due to over fishing with size selective nets.

Trawl fishing disproportionately targets large individuals as they are unable to escape from the nets, so mean lengths-at-age are expected to decline when fishing commences in a region simply because more of the larger fish in each age group are removed from the population. If this were the only effect that fishing had on length distributions then declines in mean length-at-age would be expected to halt as populations approach new steady states under sustained fishing pressure. We have observed steady declines in length-at-age that have occurred over two to three decades, suggesting that the disproportionate removal of large fish has gradually reduced growth rates. The linear declines in length, that were particularly severe in Clyde haddock and whiting, are suggestive of a long term selective pressure favouring small sizes (Law, 2000; Sinclair et al., 2002b). This has been observed in other exploited populations (Ricker, 1981; Kirkpatrick, 1993; Law and Rowell, 1993; Haugen and Vøllestad, 2001; Sinclair et al., 2002a) and through experiments (Silliman, 1975; Walsh et al., 2006; Conover and Baumann, 2009), and can either be caused directly by fishing and environmental fluctuations, or indirectly through several potential secondary responses (Enberg et al., 2012).

When minimum landing sizes are well below  $L_\infty$  and a population is heavily fished, large and fast-growing individuals can become increasingly rare. This is because fish that grow quickly to a large  $L_\infty$  are more likely to be caught at a young age, so will often have fewer reproductive seasons than slower growing individuals; thus variability in maximum length can be reduced by selection against fish with large  $L_\infty$ . Since the Clyde is relatively enclosed and the influx of fish from other regions is limited (Brander, 1975; Connolly and Officer, 2001; Wright et al., 2006), genetic variability in growth may have been quickly depleted by intense fishing. It therefore seems likely that decades of size-selective trawl fishing in the Clyde has steadily reduced growth rates and maximum lengths such that the resident fish have evolved to become smaller. Declines in the length-at-age of haddock and whiting were more gradual within the western shelf populations. This can be readily explained by the regional differences in fishing intensity and the selectivity of the fishing gear, which will vary the strength of selection between regions (Law, 2000).

Fishing pressure was much greater in the Clyde than in the western shelf during

the 2000s (fig. 2.2). The comparatively low fishing intensity in the western shelf will reduce the severity of truncations in length distributions, allowing greater proportions of fast growing fish to survive to adulthood and pass on their genes. This may have resulted in the reduced rates of decline in the length-at-age of western shelf populations. The Clyde *Nephrops* fishery is substantial and trawls with fine 70 mm nets; finer nets catch greater proportions of small fish, so 70 mm nets will select for even smaller fish than the 100 mm nets that are used when demersal fish are the main target. The combination of greater fishing intensity and extensive use of 70 mm nets within the Clyde will result in comparatively high mortality rates, particularly in small individuals and small species. Of the five species that we have studied, Norway pout is the smallest, and lengths actually increased across all age groups in the western shelf population. The fishing regime of the western shelf does not seem to be selecting for smaller Norway pout, and may in fact be promoting increased growth rates through some secondary responses (Enberg et al., 2012). The heavy use of *Nephrops* trawling gear within the Clyde, however, appears to have been sufficient to suppress the increase in growth rate observed in Norway pout from elsewhere in the west of Scotland.

Fishing may also have selected for slow growth indirectly, by disproportionately targeting bold and competitive fish that tend to grow more quickly (Biro and Post, 2008), or by selecting for early maturation (Law, 2000). Since growth slows upon maturation, declines in length may also have been indirectly caused by trends in length-at-maturation. The length-at-maturation of Clyde haddock and whiting has been in decline (Hunter et al., 2015), so changing maturation schedules may have contributed to reductions in length. The trends in maturation, however, also appear to have been driven by fishing, so reductions in lengths are likely a combination of direct and indirect effects of fishing. Thus it appears as though trawl fishing in the west coast of Scotland has been selecting for slow growth in demersal species, causing long term reductions in lengths, and that relatively high fishing pressures and extensive use of *Nephrops* trawls has caused this to happen most rapidly in the Clyde.



## Chapter 3

# Fishery-induced changes to age and length dependent maturation schedules of three demersal fish species in the Firth of Clyde

### 3.1 Introduction

The Firth of Clyde is a large estuary in the west coast of Scotland that once supported substantial demersal fisheries for a range of species such as cod, haddock, saithe, whiting and hake (Ross et al., 2009). A ban on trawling for vessels over 15 m was repealed in 1962. Consequently, the landings of demersal fish quickly rose, peaking in 1973 before falling into decline (Hislop, 1986), reaching near-zero levels by 2005 when the fleet stopped targeting demersal fish. Fishing effort shifted away from demersal fish during the 1990s as more vessels began converting to exploit the abundant *Nephrops* stock, and since 2005 the Clyde demersal fish catch has been mostly bycatch from the *Nephrops* fishery.

Although the steep decline in demersal landings suggests that there are few fish left in the Clyde (Thurstan and Roberts, 2010), an analysis of survey data (Heath and Speirs, 2012) provides a more comprehensive view. Biomass estimates of the six main

commercial species; cod, hake, haddock, plaice, saithe and whiting indicate that the community biomass in the late 2000s was approximately double what it was pre-1960. This biomass however, now consists almost entirely of small fish that are less than 40 cm in length, and small species – predominately whiting – now dominate. Community mean length decreased sharply as fishing pressure was sustained, and large fish do not appear to have increased in number since the targeted demersal fishery ceased in 2005. In this paper we investigate potential trends in the age and length at maturation of cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) from the Firth of Clyde. Trends in maturation schedules may be related to some of the observed changes in length structure and species complement.

Maturation schedules are plastic and may vary in response to environmental conditions. Somatic growth slows when fish mature (Roff, 1983; Jobling, 1994), so those that mature early may remain relatively small for their age. Small individuals are usually more vulnerable to predation and may be out-competed for resources (Mittelbach, 1981), however, small fish are less vulnerable to size-selective trawling nets. If a population is heavily exploited then fish that mature at older ages and larger lengths are more likely to be caught before maturation, and early maturing fish may therefore contribute more to future recruitment. Thus, fish that mature late may benefit from a larger size and are generally capable of producing more viable offspring per season (Trippel, 1998; Berkeley et al., 2004; but see Marshall et al., 2010), although they are more likely to die before having the opportunity to reproduce, especially in heavily fished regions. Since somatic growth slows upon maturation, it is plausible that a shift towards early maturation is partially responsible for the scarcity of large individuals in the Clyde. The shift in species complement, towards smaller species, is an expected consequence of sustained size-selective fishing that may also be related to the adaptive nature of maturation schedules, since species with greater plasticity in maturation may be more resilient to fishing pressures.

Numerous studies have shown that the typical age and/or length at which fish are mature is decreasing in exploited stocks (Jørgensen, 1990; Trippel, 1995; Morgan and Colbourne, 1999; Kuparinen et al., 2009; Sharpe and Hendry, 2009; Audzijonyte et al.,

2013). Fish may be maturing increasingly early for a number of reasons. Maturation is largely dependent upon a combination of age and length, so changes in growth rates directly affect maturation schedules. Long term trends in environmental variables such as water temperature or food availability could cause long term trends in growth rates (Jørgensen, 1992), which in turn, would influence the expected age and length at maturation (Heino et al., 2002). Age and length at maturation may also exhibit phenotypic plastic changes in direct response to environmental conditions (Kraak, 2007; Marshall and McAdam, 2007), i.e. independently of growth. Fisheries alter the environment and population structure, so may also induce plastic changes in growth and maturation indirectly. As fitness-related traits, age and length at maturation have modest heritability (Mousseau and Roff, 1987), so if the size-selective pressures generated by fishing are strong then they may cause maturation schedules to evolve rapidly (Jennings et al., 1998; Law, 2000). Growth rates are also heritable and subject to selective pressures (Kinnison et al., 2011), so fishing may cause evolution in growth through selection on size and any factors pertaining to resource acquisition (Enberg et al., 2012), which could also affect age and length at maturation. A combination of these factors may apply to fisheries where changes in maturation schedules have been observed.

To account for the effect of fluctuating growth and mortality rates when evaluating trends in maturity schedules, we use probabilistic maturation reaction norms (PMRNs) (Heino et al., 2002). A PMRN is a function of length and age that estimates the probability that a fish, which was immature the previous year, will have matured, conditional upon it having survived. Temporal trends in maturation schedules are characterised by trends in the length at which there is a 50% probability of maturing. This length,  $L_{p50}$ , is calculated for each age group and used as a maturation index. The  $L_{p50}$  indices are calculated from conditional probabilities of a single event, first maturation given age and length. The potential for bias caused by variations in the relative mortality rates of immature and mature fish is therefore mostly removed when using PMRNs. The PMRN description of the maturation process also separates variations in growth rate from trends in maturation schedules, because different growth trajectories simply intersect the  $L_{p50}$  curve at different locations in the length-age plane. Temporal trends

in maturation schedules are indicated by the gradual movement of  $L_{p50}$  itself.

Maturation schedules may respond plastically to variation in factors such as social structure (Hobbs et al., 2004; Pauli and Heino, 2013) or temperature (Dhillon and Fox, 2004; Kraak, 2007; Tobin and Wright, 2011). By modelling estimated  $L_{p50}$  values against such factors, it is possible to estimate the extent to which long term differences in  $L_{p50}$  are attributable to various phenotypic plastic responses. Temporal trends in  $L_{p50}$  that remain – once potential influences of environmental variations have been accounted for – indicate changes to the maturation schedule itself and may be suggestive of change in the genetic composition of the population (Heino et al., 2002).

To investigate changes to the maturation schedules of Clyde cod, haddock and whiting, we have estimated time series of PMRNs over the period 1986-2009. Differences in the maturation timing of males and females have been examined by comparing PMRNs that were calculated separately for each sex. For fish that exhibited temporal trends in maturation lengths,  $L_{p50}$  estimates were regressed against trends in abundance and temperature to determine the extent of the change in  $L_{p50}$  that could be attributed to phenotypic responses to these factors. As exploited stocks have typically experienced declines in length at maturation, we expect to find that PMRN midpoints have decreased over time. Since males tend to mature earlier than females (Templeman and Bishop, 1979; Ajiad et al., 1999; Gerritsen et al., 2003), we also expect to find that  $L_{p50}$  values are lower in male fish.

The  $L_{p50}$  estimates of fish sampled from the Firth of Clyde are compared to those from the adjacent area to the north-west, referred to here as the western shelf (fig. 3.1). Fishing intensity was greater in the Clyde than in the western shelf during the 2000s (fig. 3.2). Unfortunately, effort data from 1985 to 2000 were unavailable in these two regions, but the total landed biomass per area (fig. 3.2) has been consistently greater in the Clyde since 1985, suggesting that fishing intensity has also been greater since this time. Thus, the Clyde populations are likely to have been subjected to a relatively high fishing mortality rate during the time period for which we estimate PMRNs. The main target species in the Clyde is *Nephrops*, so the majority of the Clyde trawlers use nets with a finer mesh size (between 70 mm and 100 mm) than vessels that target demersal

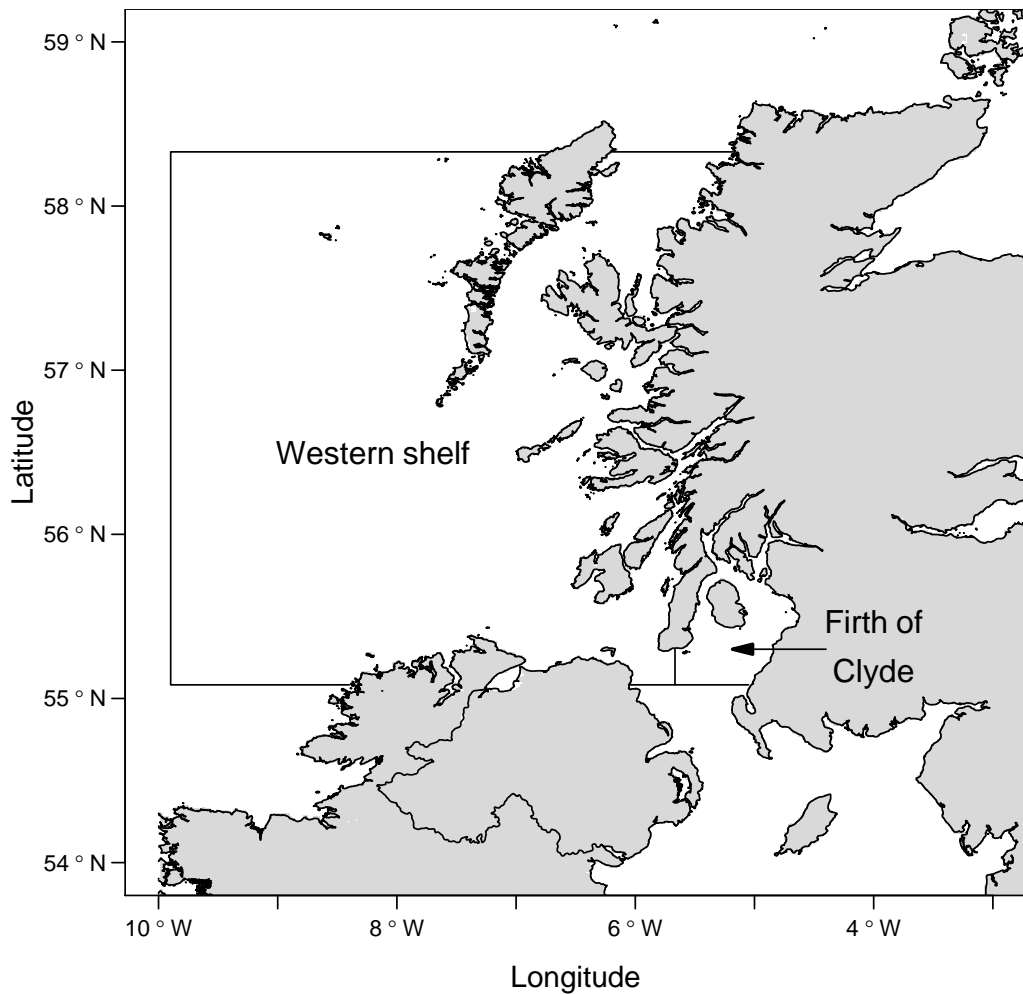


Figure 3.1: The two areas in the West of Scotland chosen for this analysis.

fish ( $\geq 100$  mm). *Nephrops* are also targeted in the western shelf, but the fishery in this region is more mixed. The proportion of the landed biomass from trawling vessels in each region that was caught using *Nephrops* gear is shown in fig. 3.2. Small fish are likely to be more vulnerable to the fishing gears in the Clyde than western shelf due to differences in the size-selectivity of the fisheries in these regions. If fishing has induced changes in maturation schedules then we would expect the affects to be more severe in regions of high fishing intensity, and where population length structures have been most severely truncated. We therefore expect to find that PMRN midpoints have declined at faster rates in the Clyde populations, because they are fished with relatively fine nets and have experienced greater fishing pressure. If rates of change in

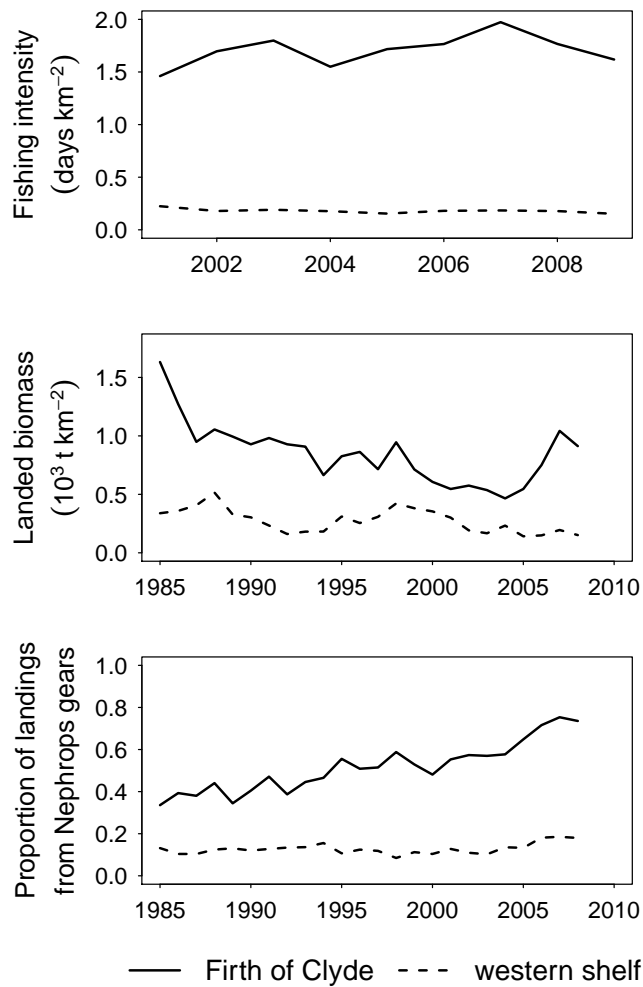


Figure 3.2: Differences in the Clyde and western shelf fisheries. Top: annual fishing intensity of UK bottom trawling vessels over 10 m long from 2001 until 2009. Total landings were calculated as the sum of the landed biomass of all species from all demersal and *Nephrops* trawls. Middle: total landings divided by the area of the region. Bottom: proportion of the total landings caught by *Nephrops* trawls.

$L_{p50}$  are indeed greater in the Clyde, and the trends are not explained by abundance or temperature variations, then it would suggest that fishing has been a key factor in changing maturation schedules.

## 3.2 Material and Methods

### 3.2.1 Data

In this analysis we used the International Bottom Trawl Survey data collected in the Scottish west coast (SWC-IBTS). These data detail the length, age, sex and maturity status of samples of fish and span the years 1986 to 2010. The length of each fish has been measured and rounded down to the nearest cm. Age has been determined by examination of otoliths for annual growth rings; sex and maturity status was determined by visual inspection of the gonads. We used data from only one quarter to reduce variability in length and maturity status at age, and chose the first quarter of the year because this is when most of the maturity data were collected – as gonads are swollen in preparation for spawning. Since the data were collected close to spawning times, when an individual's age has been recorded as  $a$  years old, that individual was alive for approximately  $12 \times a$  months. Pre-1990, maturity status was designated as either immature or mature, then following a five year gap in the data, fish sampled from 1995 onwards were designated as either immature, maturing, spawning or spent. We consolidated the maturity groupings of the post-1994 fish such that maturing, spawning and spent fish were all considered to be mature, thus bringing the later data in line with prior samples. Average annual sample sizes are shown in table 3.1.

There were few immature fish aged two or older present in the samples, particularly in the Clyde. As a PMRN specifies the probability of first maturation at age and length, it is conditional upon the fish being immature the previous year, and since old and immature fish were sparse, only age groups one and two could be analysed using PMRNs. The proportions of mature fish at each age are shown in table 3.2. For male whiting, and female cod and male haddock in the Clyde, we were able to calculate PMRNs for age group one fish only. The data for some cohorts were grouped where sample sizes were low. This allowed estimation of PMRNs for groups of cohorts prior to 1985, although confidence in these estimates was often low. Even when grouped into decade long intervals, the data for male cod was too limited to estimate PMRNs.

The age-sex-maturity data form a length-stratified subset of the larger length data

set. Annual abundance indices were derived from the length data by dividing the number of sampled fish by the total area swept out by the survey gear.

Annual mean summer (June, July and August) sea surface temperatures were calculated using the Keppel pier, Millport, data set for the Clyde, and the Hadley Centre HadISST1 data set for the western shelf. Mean summer temperature was calculated as the mean of mean monthly temperatures based on daily readings. Local temperature data for the years 1988, 1996 and 2003 were missing from the HadISST1 data set, so the mean summer temperature for these years was calculated as the average of the mean summer temperature for the preceding and subsequent years.

Annual stock assessments of ICES area VIa provide fishing mortality rate estimates. However, since ICES area VIa includes both of the regions considered here, these estimates could not be used to evaluate regional differences. For this reason, we used fishing effort data (Marine Scotland Science) and landings data collected in the finer spatial scale of ICES statistical rectangles to assess regional differences in fishing intensity and size-selectivity.

Table 3.1: Mean number of fish sampled for sex and maturity status each year. FC and WS stand for the Firth of Clyde and western shelf.

Region	Sex	Haddock	Whiting	Cod
FC	M	29	42	13
	F	27	46	8
WS	M	194	170	32
	F	284	189	28

Table 3.2: The percentage of sampled fish that were mature. These values have been calculated from data spanning the years 1986 to 2010.

Region	Sex	Haddock		Whiting		Cod		
		Age 1	Age 2	Age 1	Age 2	Age 1	Age 2	Age 3
FC	M	53.0	98.9	47.2	99.2	0.0	96.6	100
	F	3.6	92.7	12.4	98.9	0.0	60.9	97.8
WC	M	35.1	95.6	52.7	98.2	1.7	59.9	99.5
	F	2.1	85.2	23.0	96.0	0.0	38.9	86.2



### 3.2.2 Calculating PMRNs

The probability of an immature fish from cohort  $c$  maturing,  $m(a, l, c)$ , at  $a$  years old and  $l$  cm long was estimated with the following approximation (Barot et al., 2004).

$$m(a, l, c) = \frac{p(a, l, c) - p(a - 1, l - \Delta l, c)}{1 - p(a - 1, l - \Delta l, c)} \quad (3.1)$$

Annual growth increments,  $\Delta l = l(a, c) - l(a - 1, c)$ , and the probability of being mature,  $p(a, l, c)$ , were estimated with linear models

$$l(a, c) = \beta_{0,a} + \beta_{1,c} \quad (3.2)$$

$$\text{logit}(p(a, l, c)) = \beta_{0,c} + \beta_1 l + \beta_2 a + \beta_3 a l + \beta_{4,c} l + \beta_{5,c} a \quad (3.3)$$

where subscripted letters indicate which variables were treated as factors. Insignificant interaction terms were removed from eq. (3.3) to reduce standard errors and improve the model fit.

The  $L_{p50}$  index estimates the length at which an immature fish has a 50% probability of maturing, marking the midpoints of the PMRN. Time series of  $L_{p50,c}$  were estimated separately for each age.

$$\begin{aligned} \text{logit}(m(l, c)) &= \beta_{0,c} + \beta_1 l \\ L_{p50,c} &= \frac{-\beta_{0,c}}{\beta_1} \end{aligned} \quad (3.4)$$

By way of illustration, fig. 3.3 shows the PMRN calculated for the 1999 cohort (defined as the fish that were spawned in 1999) of western shelf haddock.

Confidence intervals for  $L_{p50,c}$  were generated by bootstrapping. The data were resampled 1000 times with replacement, stratifying by cohort, to generate distributions for  $L_{p50,c}$ . Confidence bounds were then set at the 95% percentiles of the bootstrapped distributions.

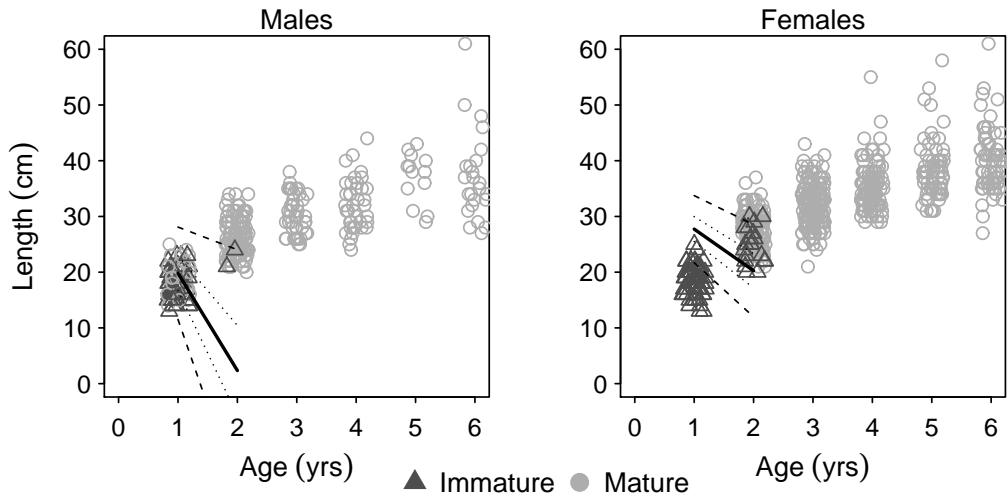


Figure 3.3: Western shelf haddock sampled from the 1999 cohort. The solid line is the reaction norm midpoint where the probability of a juvenile maturing is 50%. The dotted lines mark the range of lengths and ages for which the probability of maturing is 25% and 75%; similarly the dashed lines mark 5% and 95% maturation probabilities. The spread of points within age groups is jittering and does not indicate different ages.

### 3.2.3 Temporal trends and the significance of region and sex

Temporal trends in PMRN midpoints were assessed with linear models of  $L_{p50}$  against cohort

$$L_{p50,c} = \beta_0 + \beta_1 c \quad (3.5)$$

where cohort was treated as a continuous variable and the model was weighted by the inverse standard deviations of the bootstrapped estimates for  $L_{p50}$ . Significant trends in  $L_{p50}$  indicate that the lengths at which first maturation occurs have been changing over time.

Differences in  $L_{p50}$  values between the regions and sexes were evaluated with two simple linear models,  $L_{p50} = \beta_r$  and  $L_{p50} = \beta_s$ , where  $r$  and  $s$  indicate the factors region and sex. These models – also weighted by the inverse standard deviations of bootstrapped estimates of  $L_{p50}$  – show whether average  $L_{p50}$  values differed significantly between the regions or sexes.

### 3.2.4 Significance of temperature and abundance

In the populations that exhibited temporal trends in PMRN midpoints, we estimated the change in  $L_{p50}$  that was attributable to temporal trends in the temperature,  $T$ , and the surrounding population abundance,  $N$ , endured by newly recruited age-group zero fish with another weighted regression.

$$L_{p50} = \beta_0 + \beta_1 c + \beta_2 \log(N) + \beta_3 T \quad (3.6)$$

To eliminate potential collinearity between temperature, abundance and cohort, eq. (3.6) was performed as a principal component regression. Since we were aiming to explain long term trends in  $L_{p50}$  we only considered the effects of abundance or temperature if these variables also showed long term trends, as determined from linear models against cohort (see fig. 3.4). The magnitude of the difference in  $L_{p50}$  that was attributable to either abundance or temperature was calculated as the product of the linear rate of change in log abundance or temperature, the number of years in the time interval, and  $\beta_2$  or  $\beta_3$  from eq. (3.6).

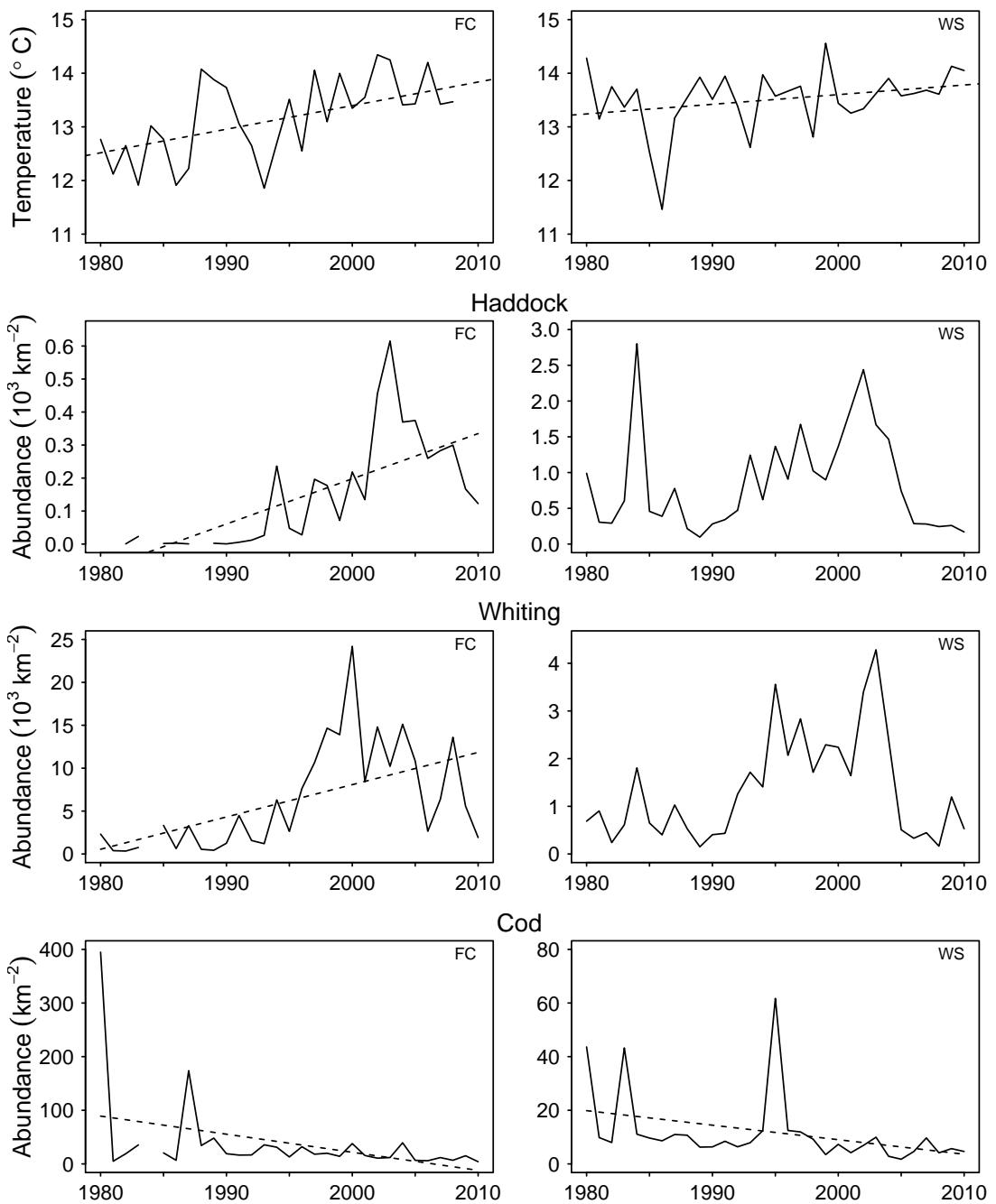


Figure 3.4: Time series of abundance and sea-surface temperature estimates, shown with linear trend lines whenever significant. Text inserted in the top right corner indicates region, where FC and WS stand for the Firth of Clyde and western shelf.

### 3.3 Results

#### 3.3.1 PMRN positions

The positioning of the PMRN curves were quite similar among most species-sex groups. In every instance in which  $L_{p50}$  could be estimated for both one and two year old fish, the PMRN sloped downwards so that, irrespective of length, maturation probability always increased with age. The PMRNs depicted in fig. 3.3 were fairly typical of the estimates for haddock. Age-length ranges corresponding to maturation probabilities between 5% and 95% tended to include most one year old males and the smallest of those two years old, and for females approximately the larger half of the one year old fish and the smaller half of those that were two years old. This corresponds well with table 3.2, which shows that nearly all of the haddock were mature at two years old, but maturation at age one occurred predominately in males. In general, the whiting PMRNs showed the same pattern as those of haddock;  $L_{p50}$  intersected one year old males and fell below the lengths of two year old males. The  $L_{p50}$  estimates for female whiting tended to coincide with the larger one year old fish and the smallest two year old fish. Almost all of the two year old whiting were mature, as were about half of the one year old males and a significant number of females (table 3.2). The positioning of the PMRNs were slightly different for female cod; the negative slopes were steeper,  $L_{p50}$  was greater than the lengths of one year old fish – which were immature – and tended to intersect the smaller two year old fish. This was caused by cod being immature at age one, and mostly maturing at two years old.

#### 3.3.2 Comparisons of $L_{p50}$ between sex and region

The average  $L_{p50}$  values of one year old haddock and whiting of both sexes, and one year old female cod from the Clyde, were significantly smaller than those of the western shelf (table 3.3). Regional differences in the magnitude of  $L_{p50}$  for age group two were insignificant in female haddock and whiting, and could not be evaluated for the other groups.

In each instance where it was possible to draw a comparison between males and

females, average  $L_{p50}$  values were significantly lower in the males. There were also differences in the rate of change of  $L_{p50}$  between the sexes. The  $L_{p50}$  values of one year old female haddock and whiting from the Clyde have decreased more rapidly than in the equivalent male fish. In one year old western shelf haddock,  $L_{p50}$  only decreased in the males, while for age group two the decrease was more rapid in the females.

### 3.3.3 Temporal trends in $L_{p50}$

Temporal trends in  $L_{p50}$  were assessed using eq. (3.5). We expected any declines in  $L_{p50}$  to vary in accordance with regional differences in fishing intensity and size-selectivity such that the most rapid declines would be seen in the Clyde populations.

Table 3.3 and fig. 3.5 shows that there were significant decreases in  $L_{p50}$  over time in all of the one year old haddock except western shelf females. For one year old Clyde males  $L_{p50}$  decreased by 6.0 cm (27%) from 1986 to 2009, it decreased by 11.3 cm (35%) in the females. In the western shelf,  $L_{p50}$  decreased by 3.9 cm (17%) in one year old males.

The  $L_{p50}$  values of two year old female haddock decreased by 11.7 cm (38%) and 7.3 cm (28%) in the Clyde and western shelf respectively from 1986 to 2009. Since so few two year old Clyde fish were immature,  $L_{p50}$  time series could not be calculated for two year old males, and the decline was not significant in two year old males from the western shelf.

There were declines in  $L_{p50}$  for all of the one year old whiting. In the Clyde,  $L_{p50}$

Table 3.3: Results obtained from section 2.3. The top section shows the linear rates of change in  $L_{p50}$  over time ( $\text{cm y}^{-1}$ ) with the standard errors in parenthesis, significant trends are shown in bold. The bottom two sections indicate significant differences in PMRN midpoints between regions and the sexes (e.g. FC < WS means that  $L_{p50}$  is lower in Clyde fish than in western shelf fish). ND = not done, these entries show where too few immature fish were present to calculate PMRNs. NS = not significant.

Region	Sex	Haddock		Whiting		Cod	
		Age 1	Age 2	Age 1	Age 2	Age 1	Age 2
FC	M	<b>-0.26 (0.064)</b>	ND	<b>-0.22 (0.039)</b>	ND	ND	ND
	F	<b>-0.50 (0.079)</b>	<b>-0.52 (0.067)</b>	<b>-0.32 (0.097)</b>	<b>-0.28 (0.073)</b>	<b>-0.68 (0.259)</b>	ND
WS	M	<b>-0.14 (0.041)</b>	-0.11 (0.204)	<b>-0.10 (0.025)</b>	ND	ND	ND
	F	0.07 (0.051)	<b>-0.27 (0.085)</b>	<b>-0.10 (0.043)</b>	<b>-0.14 (0.060)</b>	<b>-0.74 (0.095)</b>	<b>-0.72 (0.091)</b>
	M	FC < WS	ND	FC < WS	ND	ND	ND
	F	FC < WS	NS	FC < WS	NS	FC < WS	ND
FC		M < F	ND	M < F	ND	ND	ND
WS		M < F	M < F	M < F	M < F	ND	ND

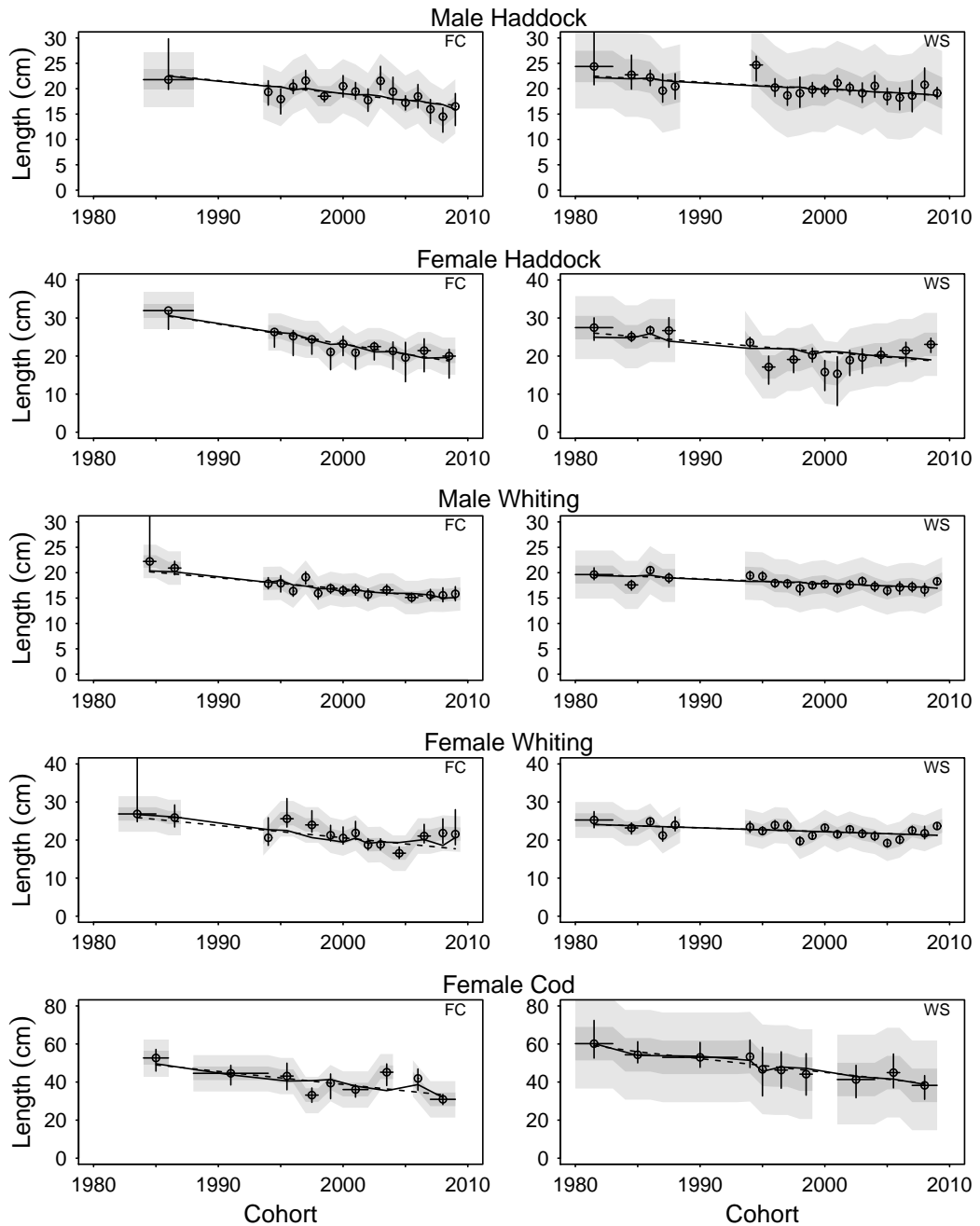


Figure 3.5: PMRN midpoints evaluated for the age groups that were best estimated (age two for WS cod and female haddock, age one otherwise). Vertical lines indicate bootstrapped 95% confidence intervals. Horizontal lines show the range of cohorts used for each  $L_{p50}$  estimate. The grey polygons represent maturation envelopes – dark grey =  $L_{p25} \rightarrow L_{p75}$ , light grey =  $L_{p05} \rightarrow L_{p95}$ . Significant linear temporal trends in  $L_{p50}$  are shown with dashed lines. Trends in  $L_{p50}$ , calculated with the inclusion of abundance and temperature variables, are shown by solid lines. Text inserted in the top right corner indicates region, FC and WS stand for Firth of Clyde and western shelf.

decreased by 5.4 cm (27%) in males and by 8.2 cm (32%) in females from 1986 to 2009. The  $L_{p50}$  values of one year old western shelf whiting decreased by 2.8 cm (13%) in both males and females over the same time period.

The declines in  $L_{p50}$  for two year old female whiting were 7.1 cm (38%) and 3.9 cm (24%) in the Clyde and western shelf respectively. Time series of  $L_{p50}$  could not be calculated for two year old male whiting as so few of these fish were immature.

In the Clyde, the  $L_{p50}$  values of one year old female cod decreased by 15.6 cm (32%) from 1985 to 2008. Western shelf female cod had declining  $L_{p50}$  values from 1981 to 2008, with decreases of 19.6 cm (29%) and 19.1 cm (32%) for age groups one and two respectively. The maturity data for male cod was too sparse to estimate PMRNs, even when large numbers of cohorts were grouped together.

As expected, the declines in  $L_{p50}$  tended to be most rapid in the more heavily exploited Clyde populations (table 3.3). The only exception to this being 1 year old female cod, for which the regional difference in rate is slight.

### 3.3.4 Temperature and abundance effects

The degree to which temporal trends in the PMRN midpoints were explainable by trends in temperature or abundance was examined using eq. (3.6). We did not include the abundance variables for western shelf haddock or whiting because they did not have a significant linear trend (fig. 3.4).

Table 3.4 shows that trends in  $L_{p50}$  were not significantly related to abundance or temperature. For some groups, however, the inclusion of these variables explained enough of the variation in  $L_{p50}$  to make the cohort effect insignificant. This occurred in two year old female whiting from the western shelf, where the rising temperature accounted for 11% of the decrease in  $L_{p50}$ , and also in female Clyde whiting, where increasing abundance accounted for 29% of the decrease in  $L_{p50}$ . In each of these cases the cohort variable still explained most of the difference in  $L_{p50}$ .



Table 3.4: Results of the principal component regression eq. (3.6). The estimated rates of change of  $L_{p50}$  in response to changes in log abundance ( $\text{cm } 10^{-3} \text{ km}^2$ ) and temperature ( $\text{cm } ^\circ\text{C}^{-1}$ ) are shown, with associated standard errors, for the groups of fish that experience long term trends in these variables. The residual temporal rate of change in  $L_{p50}$  ( $\text{cm y}^{-1}$ ) is indicated by the cohort effect. The change in  $L_{p50}$ ,  $\Delta L_{p50}$  (cm), that is attributable to each variable is also shown. Significant variables are shown in bold. FC and WS stand for the Firth of Clyde and western shelf.

Group	Effect	Coefficient (SE)	p-value	$\Delta L_{p50}$
FC male haddock (age 1)	<b>cohort</b>	<b>-0.28 (0.083)</b>	<b>0.0062</b>	<b>-6.4</b>
	abundance	0.08 (0.587)	0.9379	0.2
	temperature	0.33 (0.642)	0.6131	0.2
FC female haddock (age 1)	<b>cohort</b>	<b>-0.54 (0.103)</b>	<b>0.0008</b>	<b>-12.2</b>
	abundance	0.41 (0.630)	0.5335	2.0
	temperature	-1.05 (0.909)	0.2822	-0.6
FC female haddock (age 2)	<b>cohort</b>	<b>-0.51 (0.102)</b>	<b>0.0010</b>	<b>-11.6</b>
	abundance	0.06 (0.655)	0.9332	0.3
	temperature	-0.92 (0.842)	0.3085	-0.5
FC male whiting (age 1)	<b>cohort</b>	<b>-0.20 (0.041)</b>	<b>0.0004</b>	<b>-4.8</b>
	abundance	-0.56 (0.417)	0.2004	-0.7
	temperature	0.11 (0.382)	0.7727	0.1
FC female whiting (age 1)	cohort	-0.19 (0.122)	0.1439	-4.9
	abundance	-1.31 (1.131)	0.2746	-2.3
	temperature	-0.58 (1.143)	0.6235	-0.8
FC female whiting (age 2)	cohort	-0.17 0.103	0.2220	-4.3
	abundance	-1.24 (1.092)	0.2723	-2.1
	temperature	-0.55 (0.908)	0.5557	-0.7
FC female cod (age 1)	cohort	-0.82 (0.326)	0.0534	-18.9
	abundance	-3.0 (5.243)	0.5926	1.8
	temperature	2.33 (4.082)	0.5922	2.3
WS male haddock (age 1)	<b>cohort</b>	<b>-0.12 (0.046)</b>	<b>0.0152</b>	<b>-3.4</b>
	temperature	-0.21 (0.639)	0.7450	-0.2
WS female haddock (age 2)	<b>cohort</b>	<b>-0.21 (0.095)</b>	<b>0.0455</b>	<b>-5.7</b>
	temperature	-0.86 (1.218)	0.4933	-0.6
WS male whiting (age 1)	<b>cohort</b>	<b>-0.09 (0.027)</b>	<b>0.0049</b>	<b>-2.4</b>
	temperature	-0.21 (0.357)	0.5558	-0.1
WS female whiting (age 1)	<b>cohort</b>	<b>-0.10 (0.047)</b>	<b>0.0418</b>	<b>-2.8</b>
	temperature	-0.01 (0.649)	0.9929	0.0
WS female whiting (age 2)	cohort	-0.12 (0.067)	0.1046	-3.2
	temperature	-0.60 (0.895)	0.5111	-0.4
WS female cod (age 1)	<b>cohort</b>	<b>-0.93 (0.105)</b>	<b>0.0001</b>	<b>-24.6</b>
	abundance	-1.67 (1.490)	0.3065	2.4
	temperature	4.36 (2.401)	0.1193	2.0
WS female cod (age 2)	<b>cohort</b>	<b>-0.94 (0.102)</b>	<b>&lt; 0.0001</b>	<b>-24.8</b>
	abundance	-1.90 (1.478)	0.2454	2.7
	temperature	4.48 (2.336)	0.1035	2.1

## 3.4 Discussion

### 3.4.1 Early maturation in west of Scotland fish

Haddock will typically mature when they reach ages of three years or older (Taylor and Stefánsson, 1999; Neuheimer and Taggart, 2010), at lengths ranging from about 30 cm to 60 cm in males and 40 cm to 70 cm in females (Devine and Heino, 2011). Whiting in the Irish Sea tend to reach maturity when they are two years old, but one year old mature males are not uncommon (Gerritsen et al., 2003); the length of whiting at maturity is usually about 18 cm to 24 cm in males and 22 cm to 25 cm in females (Gerritsen et al., 2003; Vallisneri et al., 2006). Age and length at maturation in cod populations tends to be in the range of three to five years old and 30 cm to 70 cm long (Olsen et al., 2005; Pardoe et al., 2009; Swain, 2010; Pérez-Rodríguez et al., 2013). The results presented here show that west coast haddock and cod have been maturing at unusually young ages and small lengths, and compare well with other studies of cod in the west coast of Scotland (Yoneda and Wright, 2004) and Irish Sea (Armstrong et al., 2004). The results for whiting are quite similar to those of the Irish Sea, although greater proportions of west coast whiting were mature at age one, and typical lengths at maturation became lower in the Clyde. The west of Scotland gadoid community appears to be dominated by fish that mature at very small lengths and young ages – with large numbers of whiting and haddock maturing at just one year old – and is a rather extreme example of plasticity in maturation.

### 3.4.2 Differences in maturation lengths between the sexes

In both regions, male haddock and whiting had a significantly greater probability of maturing than females of equivalent length and age. This is what was expected based on previous studies where females were shown to mature at older ages (Templeman and Bishop, 1979; Gerritsen et al., 2003). Females may take longer to mature because they need to divert more energy from somatic growth into reproduction and so require a longer juvenile period in which to grow larger before maturing (Miller and Kendall, 2009). Although maturation lengths were lower in males, rates of change in  $L_{p50}$  in

the Clyde have been more rapid in female fish. In the western shelf,  $L_{p50}$  declined at equal rates in male and female whiting, while for haddock the rate of decline in  $L_{p50}$  was greatest in one year old males and two year old females. The reasons for these differences in rate is unknown.

### 3.4.3 Distinctness of the Clyde populations

We see that average  $L_{p50}$  values tended to be lower in the Clyde populations (table 3.3). Young Clyde fish have therefore been more likely to mature at small lengths than fish from elsewhere in the Scottish west coast.

There is evidence suggesting that the Clyde populations are fairly self-contained, and that the commercially important species spawn within or close to the Clyde (Hislop, 1986). In particular, tag-recapture studies have indicated that Clyde cod are a resident population (Wright et al., 2006) subject to very low immigration (Brander, 1975; Connolly and Officer, 2001). Although whiting eggs and juveniles from the Scottish west coast mix into the North Sea, the exchange of adults is limited (Tobin et al., 2010), so west of Scotland whiting should be treated as a distinct population within which the Clyde estuary contains the greatest density of new recruits (de Castro et al., 2013). Differences in length-based indices also suggest that the Clyde demersal community is sufficiently isolated from neighbouring regions to display independent local responses to exploitation and, potentially, also to environmental fluctuations (Heath and Speirs, 2012). Differences between the maturation schedules of Clyde and western shelf fish may therefore be explained by regional differences in the environment and fishery.

### 3.4.4 Declines in lengths at maturation

Significant declines in PMRN midpoints were observed in every group except for one year old female, and two year old male haddock from the western shelf. Temporal trends in  $L_{p50}$  are not unique to cod, haddock and whiting in the Scottish west coast, but have also been observed in the North Sea (Wright et al., 2011; Marty et al., 2014), as well as in other species from several different regions (Grift et al., 2007; Jørgensen et al., 2007; Kuparinen and Merilä, 2007; Mollet et al., 2007; Hutchings and Fraser, 2008;

Sharpe and Hendry, 2009). We expected regional differences in the rate of change of  $L_{p50}$  to correspond with the regional difference in the fisheries such that fish in the Clyde would experience more rapid declines in  $L_{p50}$ .

The rate of decline in  $L_{p50}$  for one year old male whiting was approximately twice as rapid in the Clyde than in the western shelf, and about three times greater in the Clyde females. The rate of change in  $L_{p50}$  for one year old male haddock was about twice as great in the Clyde than in the western shelf, and decreases in the  $L_{p50}$  values of the one year old females were only observed in the Clyde. The regional difference in the rate of change of  $L_{p50}$  for one year old female cod was relatively small, and contrary to the overall pattern the decline was more rapid in the western shelf. We cannot compare regional differences in the rate of change of  $L_{p50}$  for two year old males since so few of them were juveniles, but we can compare the females. Declines in  $L_{p50}$  were approximately twice as rapid in two year old female haddock and whiting from the Clyde than those from the western shelf. Thus, the rates of decline in  $L_{p50}$  have indeed been greater in the more heavily fished Clyde than elsewhere in the west coast of Scotland.

### 3.4.5 Potential drivers of changing maturation lengths

Temporal trends in PMRN midpoints may be explained by various sources of growth-independent plasticity or by evolutionary changes in maturation (Dieckmann and Heino, 2007; Kraak, 2007; Marshall and McAdam, 2007; Heino and Dieckmann, 2008). Plastic changes to maturation schedules can be induced by rising temperatures (Dhillon and Fox, 2004; Tobin and Wright, 2011), or trends in abundance which may alter social structures (Hobbs et al., 2004; Pauli and Heino, 2013) and food availability (Reznick, 1993). Long-term trends in abundance and temperature have not explained the trends in PMRM midpoints and do not appear to have been driving the changes in maturation. The rise in temperature and increase in Clyde whiting abundance accounted for small decreases in  $L_{p50}$  for female Clyde whiting and two year old female western shelf whiting that were sufficient to reduce the significance of the cohort effect above the  $p = 0.05$  threshold, but the changes in  $L_{p50}$  were still predominately due to a cohort ef-

fect. The remaining significant declines in  $L_{p50}$  were all associated with a cohort effect. This suggests that lengths at maturation have declined in response to either one, or a combination of temporal trends in some other environmental conditions and fishing.

Regional differences in the rates of decline in  $L_{p50}$  are consistent with the hypothesis that fishing has been influencing maturation. PMRN midpoints declined most rapidly in the Clyde, where fishing intensity has been greatest. The Clyde fleet comprises mostly of *Nephrops* trawlers which use relatively fine nets, these nets are less selective and may exacerbate trends in maturation lengths through increased removal of immature fish. The discarding rates of fish from Clyde *Nephrops* vessels are high – particularly for whiting as it is very abundant – averaging 62% between 1982 and 1998 (Stratoudakis et al., 2001). The range of lengths discarded were 9-32 cm, 7-31 cm and 8-34 cm for haddock, whiting and cod respectively, with mean discarded lengths of 18.1 cm, 19.1 cm and 22.4 cm (Stratoudakis et al., 2001), so many immature fish must therefore have been caught and discarded. According to fisheries induced evolution theory, this will have generated a selective pressure to favour early maturation at small sizes. Although we cannot assert a causal link on the basis of these observations, it does appear likely that fishing is at least partially responsible for the reductions in lengths at maturation. This may have occurred directly through fisheries-induced evolution due to selection for small sizes, or indirectly through other potential consequences of fishing, e.g. relaxed social pressures due to disproportionate removal of large and mature fish. Further work is still required to determine the mechanisms driving the declines in  $L_{p50}$ .

#### 3.4.6 Limitations and assumptions

The annual data samples for cod were small in comparison to those collected for haddock and whiting, so the size of the cohort groups had to be larger in cod. Even when the data was split into a few large groups of cohorts it was still not possible to calculate PMRNs for male cod.

There were few immature fish aged two or older present in the data – particularly in the Clyde. It was therefore not possible to generate  $L_{p50}$  time series for two year old male whiting, male Clyde haddock or female Clyde cod. However, if the sample sizes

were large enough to capture more of these two year old fish in an immature state then it may have been possible to calculate  $L_{p50}$  values.

Estimating PMRNs using eq. (3.1) assumes that, for each age class, growth rate and mortality are not affected by maturity status (Barot et al., 2004). As growth slows upon maturation, maturity status certainly will affect growth, but differences are likely to be small within age classes. Differences in mortality between immature and mature fish within an age class may arise from differences in behaviour; for example, fishing populations that segregate according to maturity status may result in higher mortalities for the mature fish of an age class. However, the method has been shown to be robust to violations of the above assumptions (Barot et al., 2004).

### 3.4.7 Future work

In this study we have demonstrated that expected lengths at maturation have been declining in Scottish west coast cod, haddock and whiting, but we have not conclusively shown the mechanisms driving these changes. In order to determine why PMRN positions change over time it is necessary to account for the influence of variables known to influence maturation schedules. We considered trends in two environmental variables, abundance – perhaps influencing social structure and food availability – and temperature, and found that significant temporal trends in the PMRNs remained unexplained. However, as there are other potentially important factors that were neglected, this analysis could be expanded by the inclusion of more explanatory variables in eq. (3.6). Some possibilities are body condition and growth histories, either of which may influence maturation (Marteinsdottir and Begg, 2002; Morgan, 2004; Baulier et al., 2006; Morita and Fukuwaka, 2006), and time series of food availability. Trends in these variables may help to explain the increased likelihood of maturation at small lengths, but could not be considered in this study as the relevant data were not available.

In light of the apparent correlation between regional differences in the fisheries and the rate of change in  $L_{p50}$ , we suggest further investigation into the role of fishing. Time series of fishing mortality rates could be included in eq. (3.6), as well as interactions between fishing and the other environmental variables. If fishing mortality rates and a

greater number of environmental or physiological variables were included in eq. (3.6) then it may be possible to confirm if fishing explains some of the trends in  $L_{p50}$ , either directly or through interactions. The potential role of fisheries-induced evolution could also be assessed by calculating time series of selection differentials due to fishing (Law, 2000). Estimates of fishing gear selectivity and time series of fishing mortality rates in the Clyde will be needed to investigate how fishing may have been influencing maturation, so conducting stock assessments to derive these estimates will be a necessary first step.

Time series of PMRNs describe temporal changes to maturation propensity independently from potential changes in growth, so temporal trends in growth were not considered in this paper. Growth rates can vary in response to the same conditions as maturation schedules (Law, 2000) – environmental, physiological and selective conditions – and a similar investigation into the growth of fish from the Clyde and wider west coast of Scotland will complement this study.

### 3.4.8 Concluding remarks

Haddock, whiting and female cod in the Scottish west coast have been maturing at progressively smaller lengths and younger ages since 1986, and this has occurred most rapidly in the Clyde populations of haddock and whiting. As decreases in lengths at maturation can reduce lengths-at-age and maximum lengths by prematurely slowing growth rates, the steep decline in the abundance of large fish in the Clyde (Heath and Speirs, 2012) may be partially explained by these trends in maturation. Declines in Clyde landings coincided with decreases in large fish abundance, and typical catches increasingly consisted of small unmarketable individuals. Trawl fishing always truncates length structures, lowering the abundance of large fish, but if it has also been causing increasingly early maturation then the fishing process has induced a response which may have further reduced the probability of individuals growing to a large size. A reversal of these trends in maturation may promote increases in the abundance of large fish, which is needed if the Clyde demersal fishery is to be restored.

If fishing has caused the observed declines in  $L_{p50}$  then the amount of time since

Clyde vessels stopped targeting demersal fish – from 2005 – has been insufficient for a recovery. This may be due to *Nephrops* vessels continuing to catch large quantities of fish. If discarding levels of the *Nephrops* fleet have not reduced since the 1980s and 1990s then current fishing activity may be preventing lengths at maturation from increasing, this may also explain why the community length structure has not shown signs of improvement. Furthermore, if the changes in maturation schedules have been partially caused by evolutionary responses to size-selective fishing, then this process may be ongoing through the *Nephrops* fishery, and may even have been accelerated by the increased use of nets with smaller mesh sizes. If there is an evolutionary component to the declines in maturation lengths then increases in  $L_{p50}$  will be gradual and likely to require periods of time similar to the initial decreases (Law, 2000). Further work is still needed to determine why Clyde demersal fish have shown such rapid declines in length at maturation, and to assess means of reversing these trends.



## Chapter 4

# Examining the growth and maturation of three pelagic fish species from the North Sea and west of Scotland

### 4.1 Introduction

We have used bottom trawl survey data to investigate potential long term changes in the growth rates and age- and length-dependent maturation schedules of North Sea and west of Scotland herring (*Clupea harengus*), mackerel (*Scomber scombrus*) and sprat (*Sprattus sprattus*). Long term changes in growth and the maturation schedules of exploited fish stocks have occurred worldwide in many different species and locations. Changes to growth have been observed in Pacific salmon (Ricker, 1981), North Sea sole (de Veen, 1976), several cod stocks (e.g. Hanson and Chouinard, 1992; Rogers et al., 2010) and many other fish populations (Shackell et al., 2010; Cheung et al., 2012; Audzijonyte et al., 2013). Age and length at maturity have changed in North Sea plaice (Rijnsdorp, 1993), Norwegian halibut (Haug and Tjemsland, 1986), several cod and haddock stocks (e.g. Taylor and Stefánsson, 1999; Olsen et al., 2005; Pardoe et al., 2009; Neuheimer and Taggart, 2010) and in other fish stocks in the west and

east Atlantic (Trippel, 1995; Marty et al., 2014). In most instances, growth rates and expected ages and/or lengths at maturity have declined over time. Declines in the growth rates of harvested fish species are detrimental to fisheries because large individuals are the most valuable. There may be further, less direct, consequences for fisheries as changes in the growth rate and size at maturation of certain species can have a range of ecosystem effects (Woodward et al., 2005). For example, declines in the abundance and size of predatory fish can relax predation pressures and may result in increased abundance of prey species and trophic cascades (Casini et al., 2009; Shackell et al., 2010; Fauchald et al., 2011). Fecundity increases with body size (Roff, 2002), so declines in age and length at maturation may reduce the reproductive potential of populations and their capacity to recover from depletion (Murawski et al., 2001; Hixon et al., 2014). Furthermore, negative trends in age and length at maturation have been postulated as indicators of population stress and potential stock collapse (Trippel, 1995). An awareness of trends in growth and maturation schedules can therefore be useful for fisheries management, particularly with regards to potential yield estimation and evaluating stock sustainability under various harvest rates.

North Sea herring may be categorised into several distinct stocks based on spawning locations, but the majority can be considered as part of three main stocks, spawning in the north (around Shetland and the north east coast of Scotland), central (east coast of England) and southern (English channel and Southern Bight) North Sea (Daan et al., 1990). The northern and central stocks are autumn spawners, spawning from late July to September and from August to October respectively; the southern stock spawn during the winter, from November to January (MacKenzie, 1985). Besides from spawning location, herring stocks may be distinguished through differences in vertebrae number or otolith structure (Rosenberg and Palmén, 1981; Bird et al., 1986). These distinctions, however, may result from phenotypic responses to differences in environment (Hulme, 1995). Genetic studies have provided little evidence that herring stocks are discrete (Grant, 1984; Dahle and Eriksen, 1990), and individuals spawned by one stock may recruit to neighbouring stocks (McQuinn, 1997). Spring spawning herring are also present in the North Sea. These may be transported, as larvae, by the

northerly Atlantic current into the North Sea from spawning grounds to the west of Scotland (Heath and MacLachlan, 1987). Spring spawning herring from the Skagerrak and Kattegat seas, and west coast of Norway may also mix with the North Sea autumn spawners (Ruzzante et al., 2006).

The western herring stock is west of the British Isles, and is currently managed as four sub stocks that are defined by the location and timing of spawning (ICES, 2015). Adult herring from several spawning sites have been shown to originate from a range of nursery grounds (Geffen et al., 2011), so it appears that juveniles spawned in a particular location often recruit to adult stocks that spawn elsewhere. Larvae hatched offshore, in the vicinity of the strong northerly Atlantic current, tend to drift far from their spawn sites to nursery grounds in the North Sea, whereas larvae hatched inshore tend to remain within the Scottish west coast (Heath and MacLachlan, 1987; Heath et al., 1987). Tagging and parasite studies have not supported the concept of distinct stocks (Morrison and Bruce, 1981; MacKenzie, 1985), and otolith microchemistry analysis suggests that the western herring are essentially one stock with discrete spawning locations and timings (Geffen et al., 2011).

North Sea sprat are most abundant in the south, from the Southern Bight to the west coast of Denmark, but are also numerous along the English east coast and Moray Firth (Knijn et al., 1993). Spawning takes place throughout these regions from March until August, depending on temperature, with peak spawning during May and June (Wahl and Alheit, 1988). The German Bight is a nursery ground for juvenile sprat, and it has been suggested that counter-clockwise currents transport the pelagic eggs and larvae from a large area in the southern North Sea into the German Bight (Baumann et al., 2009). Sprat tend to spawn offshore in open water, then the larvae drift towards the coast, and juveniles are often abundant in estuarine or sea-loch environments (Cunningham, 1896). There is some evidence suggesting that sprat stocks from the German Bight, Kattegat and Celtic Sea are genetically distinct (Limborg et al., 2009), and that isolated stocks are present in Norwegian fjords. Detailed information about the stock structure and potential migrations of sprat from regions within the North Sea is somewhat lacking. Sprat are found all around the British and Irish coasts

(Wheeler, 1969), but less is known about the western sprat populations located west of the British Isles. The western sprat stock spawn in the spring and early summer (de Silva, 1973a). Currents transport larval sprat northwards, depositing many of them in estuarine regions and sea-lochs (de Silva, 1973b). These areas are nursery grounds for young sprat, which usually migrate to deeper waters once they have grown sufficiently.

Mackerel are widely distributed throughout the north-east Atlantic, and three distinct stocks are defined based on spawning location and timing; these are the North Sea stock; the western stock (west of British Isles and Celtic Sea); and the southern stock (Bay of Biscay) (Nesbø et al., 2015). The North Sea stock disperse throughout the entire North Sea to spawn during June and July, but spawning is concentrated in the center (Johnson, 1977). The western mackerel stock migrates south-west from the northern North Sea, along the continental shelf, to spawn in a huge area to the west and south-west of the British Isles from March until June (Reid et al., 2001; Uriarte and Lucio, 2001). Both of these stocks congregate in feeding grounds in the northern North Sea after spawning, and overwinter around the northern edge of the continental shelf (Jansen et al., 2012). The North Sea and western stocks mix during the autumn and winter, and individuals from one stock may often stray into the other (Jansen and Gislason, 2013).

We have used bottom trawl survey data collected from ICES areas IVa, IVb and VIa (fig. 4.1) to determine whether herring, sprat and mackerel stocks in the North Sea and west of Scotland have shown long term trends in mean length at age, or age and length at first maturation. Age-length distributions were derived for each species-region combination, and von Bertalanffy growth curves were fitted to successive cohorts (von Bertalanffy, 1934). Changes in mean length at age were described using time series of the estimated von Bertalanffy growth parameters. These are the asymptotic lengths,  $L_{\infty}$ ; the von Bertalanffy growth rates,  $k$ ; and the expected lengths at age zero (initial lengths),  $L_0$ . Changes in age and length dependent maturation were investigated using probabilistic maturation reaction norms (PMRNs) estimated for individual cohorts (Heino et al., 2002). The time series of the estimated growth parameters and  $L_{p50}$  maturation indices were regressed against sea-surface temperature, abundance es-

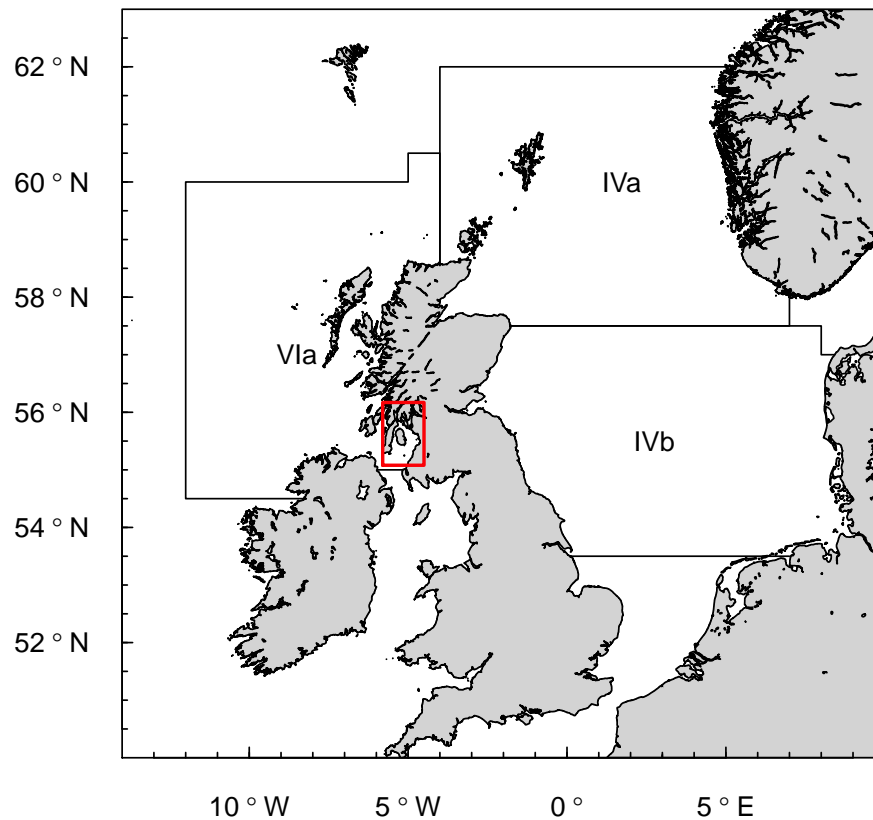


Figure 4.1: A map showing the ICES fishing areas considered. The Firth of Clyde, within area VIa, is highlighted in red. Areas IVa and IVb are referred to as the northern and southern North Sea in this paper.

timates and time, to determine the extent to which these variables influenced growth or maturation.

## 4.2 Materials and methods

### 4.2.1 The data

The International Bottom Trawl Survey (IBTS) data for the Scottish west coast and North Sea were used for this analysis (ICES, 2015). The IBTS data was extended backwards, where possible, by using bottom trawl survey data collected by Fisheries

Research Services (FRS). Data from ICES areas IVa, IVb and VIa were considered separately for herring and sprat. As some demersal fish species have shown localised changes in growth and maturation in the Firth of Clyde region within area VIa (Hunter et al., 2015, 2016), the Clyde was considered separately whenever possible, to determine if the pelagic fish species of the present study have undergone similar localised changes. Data from ICES areas IVa and IVb were grouped together to study North Sea mackerel, and data from area VIa was used to study the western stock, although the western stock is known to extend southwards far beyond area VIa. The time span of the data depended on region, species and quarter of the year — the longest running age data set was for herring in area IVb during quarter one, spanning 1966–2012.

Each of the IBTS and FRS data sets consisted of three components, namely, length, age and maturity data. The length data contained samples of fish where the length of each individual had been measured and rounded down to the nearest 1 cm (mackerel) or 0.5 cm (herring and sprat). The age and maturity data sets were length stratified sub samples of the length data, in which the age of each individual (in years) had been determined from counting the number of annual otolith rings. The recorded age depended on the number of winter growth rings observed on the otoliths, and the birthdays of fish were assumed to be on the January 1<sup>st</sup> nearest to the time the fish were spawned. Sprat, mackerel and spring spawned herring were therefore slightly younger than their recorded ages, and autumn spawned herring were not only slightly older than their recorded age, but also belonged to the previous year class to spring spawned fish of the same recorded age. The phrase ‘age group’ was used instead of ‘age’ throughout this paper to refer to the recorded ages of fish because of the discrepancies between the recorded and true ages. The maturity data contained information on the sex and maturity status of each individual, which had been determined by visual inspection of the gonads. The measures of maturity status differed between the IBTS and FRS surveys. The IBTS maturity scale was: (1) immature, (2) maturing, (3) spawning, (4) spent. The FRS maturity scale was: (1) juvenile, (2) virgin-maturing, (3–5) maturing, (6) spawning, (7) spent, (8) resting.

To reduce variability in both length and maturity status at age, we only used data

from one quarter of the year within each separate analysis. Data from quarter one were used exclusively for the growth analyses because, for most species and regions, the quarter one data were collected over a longer period and had fewer years with no data. Since there are two races of herring, the autumn and spring spawners, we used maturity data from quarters one and three to analyse the maturation of herring. It is preferable to study maturation using data collected during, or just prior to, the spawning season. Unfortunately, autumn spawning herring in area VIa and spring spawners in area IVb had to be analysed using data from quarters one and three respectively. In area VIa, this was because survey data were collected in quarters one and four, and only data collected during quarters one or three should be used to distinguish between spring and autumn spawning herring (see section 4.2.6). Whereas in area IVb, although maturity data were available in quarters one and three, IBTS data were available in all of the years covered by the FRS data, which prevented race determination in some fish due to the less informative IBTS maturity scale (again, see section 4.2.6). The mean size and the range of the annual samples for length, age and maturity for each species and region are shown in table 4.1.

Annual mean summer sea surface temperatures were calculated using the Hadley Centre HadISST1 data set (Rayner et al., 2003), except in the Firth of Clyde where the Keppel pier, Millport, data set was used (University Marine Biological Station, Millport, 1949–). Annual mean summer temperature in each region was calculated as the mean of mean monthly (June, July and August) temperatures over each measurement location within the region. In the Clyde, the mean annual temperature was calculated as the mean of mean monthly temperatures based on daily readings.

#### **4.2.2 Age-length keys**

Annual age-length keys were derived from the quarter 1 age data. These specify the distribution of ages within each length class, and were used to assign each fish in the length data to an age group. The age-length keys were derived following the method of Stari et al. (2010) which we now summarise. The following procedure was applied to each year of survey data separately, but we have omitted subscripts indicating year

as these are not relevant to the method. The probability that an individual is in age group  $a$  given that it is  $l$  cm long,  $p_a(l)$ , can be expressed as a continuation ratio

$$\theta_a(l) = \begin{cases} \frac{p_a(l)}{\sum_{i=a}^A p_i(l)} & a = 1, 2, \dots, A-1 \\ 1 - \sum_{a=1}^{A-1} \theta_a(l) & a = A \end{cases} \quad (4.1)$$

where  $A$  is the oldest age group. The likelihood of the age distribution at length  $l$ ,  $\mathbb{L}_l = \prod_{a=1}^A p_a(l)^{n_{a,l}}$ , can be written in terms of eq. (4.1) as

$$\mathbb{L}_l = \prod_{a=1}^{A-1} \theta_a(l)^{n_{a,l}} (1 - \theta_a(l))^{N_{a,l}} \quad (4.2)$$

where  $n_{a,l}$  is the number of fish of length  $l$  and age  $a$ , and  $N_{a,l} = \sum_{i=a+1}^A n_{i,l}$ . The continuation ratios were parameterised as logistic curves

$$\theta_a(l) = \frac{1}{1 + e^{\alpha_a + \beta_a l}} \quad (4.3)$$

so that  $\theta_a(l)$  could be estimated for each age group through logistic regressions estimating  $\alpha_a$  and  $\beta_a$ . The total likelihood,  $\mathbb{L} = \prod_{l=1}^L \mathbb{L}_l$ , can be expressed in terms of

Table 4.1: The mean number of fish sampled for length, age and maturity status each year, with the range shown in parenthesis. Years without data have been excluded. WS and FC stand for the western shelf and the Firth of Clyde.

Species	Region	Quarter	Length	Age	Maturity
Herring	IVa	1	59483 (2–507936)	743 (2–2304)	647 (1–1938)
	IVa	3	58613 (886–284888)	944 (234–1936)	972 (133–1733)
	IVb	1	288023 (9378–948674)	944 (234–1936)	972 (133–1733)
	IVb	3	221369 (979–677919)	1217 (172–2845)	1071 (113–2099)
	VIa	1	76911 (7213–330262)	1310 (187–2040)	1295 (181–2040)
	WS	1	73462 (4918–328476)	1113 (187–1762)	1105 (181–1725)
	FC	1	3491 (137–13552)	216 (78–338)	208 (76–315)
	Sprat	IVa	1	17714 (30–156346)	122 (6–277)
IVb		1	332975 (3663–1187217)	763 (16–2840)	434 (3–894)
VIa		1	9222 (208–23177)	215 (1–524)	
WS		1	7852 (394–21787)	178 (1–383)	
FC		1	1441 (23–11277)	92 (12–141)	
Mackerel	IVa & IVb	1	16308 (7–211942)	208 (6–542)	163 (6–509)
	VIa	1	98571 (39–394512)	560 (40–1014)	705 (344–912)



eq. (4.2) as

$$\mathbb{L} = \prod_{l=1}^L \mathbb{L}_l = \prod_{a=1}^{A-1} \prod_{l=1}^L \theta_a(l)^{n_{a,l}} (1 - \theta_a(l))^{N_{a,l}} = \prod_{a=1}^{A-1} \mathbb{L}_a \quad (4.4)$$

where  $L$  is the maximum length and  $\mathbb{L}_a$  is the likelihood of observing the length distribution of the age group  $a$  fish. Maximising eq. (4.4) produces estimates of  $\alpha_a$  and  $\beta_a$ , and hence  $\theta_a(l)$ . Age-length keys are the probability of age given length,  $p_a(l)$ , and can be derived from eq. (4.1).

$$p_a(l) = \begin{cases} \theta_1(l) & a = 1 \\ \theta_a(l) \prod_{i=1}^{a-1} (1 - \theta_i(l)) & a = 2, \dots, A-1 \\ \prod_{i=1}^{A-1} (1 - \theta_i(l)) & a = A \end{cases} \quad (4.5)$$

Matrices giving the number of individuals at age and length,  $M_{a,l}$  can then be calculated as

$$M_{a,l} = P_{a,l} f_l \quad (4.6)$$

where  $P_{a,l}$  is the matrix of  $p_a(l)$  and  $f_l$  is the vector of total numbers at length. These  $M_{a,l}$  matrices represent all of the fish present in the length data samples and the age group each individual was assigned to.

### 4.2.3 Von Bertalanffy growth parameters

The age-length data, derived following the method of the previous section, was used to generate time series of von Bertalanffy growth parameters that were estimated for successive cohorts. These were calculated by maximum likelihood, using a method from Kimura (1980), as follows.

The mean length at age of each cohort was assumed to follow a von Bertalanffy growth curve

$$\begin{aligned} l_{i,c} &= L_{\infty c} - (L_{\infty c} - L_{0c}) e^{-k_c a_{i,c}} + \epsilon_{i,c} \\ &= \mu(a_{i,c}) + \epsilon_{i,c} \end{aligned} \quad (4.7)$$

where the  $c$  subscripts indicate cohort;  $l_{i,c}$  and  $a_{i,c}$  denote the length and age of individual  $i$  from cohort  $c$ ;  $L_{\infty c}$ ,  $k_c$  and  $L_{0c}$  are the asymptotic length, the von Bertalanffy growth rate and length at age zero respectively; and  $\epsilon_{i,c}$  are independent  $N(0, \sigma_c^2)$  distributed errors. A sum of squares function was defined as

$$\mathcal{S}(L_{\infty c}, k_c, L_{0c}) = \sum_i \frac{n_{a_i,c}}{v_{a_i,c}^2} (\bar{l}_{a_i,c} - \mu(a_{i,c}))^2 \quad (4.8)$$

where  $n_{a_i,c}$  is the number of fish aged  $a_i$  in cohort  $c$ , and  $\bar{l}_{a_i,c}$  and  $v_{a_i,c}$  are the sample mean length and sample variance of length of fish aged  $a_i$  in cohort  $c$ . The log-likelihood, omitting the constant term, can now be written as

$$\mathcal{L}(L_{\infty c}, k_c, L_{0c}, \sigma_c^2) = -\frac{1}{2} N_c \ln(\sigma_c^2) - \frac{\mathcal{S}(L_{\infty c}, k_c, L_{0c})}{2\sigma_c^2} \quad (4.9)$$

where  $N_c$  is the total number of sampled fish. The maximum likelihood estimator for the error variance is given by

$$\hat{\sigma}_c^2 = \mathcal{S}(\hat{L}_{\infty c}, \hat{k}_c, \hat{L}_{0c}) / N_c \quad (4.10)$$

where hatted terms indicate the fitted parameters. The von Bertalanffy growth parameters were estimated numerically by minimising the negative log-likelihood.

Confidence intervals (Wald intervals) for  $\hat{L}_{\infty c}$ ,  $\hat{k}_c$  and  $\hat{L}_{0c}$  were derived from the resulting Hessian matrix,  $\mathbf{H}_c$  (Garthwaite et al., 1995). The standard errors of the parameters  $\hat{\boldsymbol{\theta}}_c = (\hat{L}_{\infty c}, \hat{k}_c, \hat{L}_{0c})$  were approximated as  $\text{s.e}(\hat{\theta}_{j,c}) = \sqrt{(-1/H_{j,j,c})}$ , where  $j = (1, 2, 3)$  indexes the growth parameters. Then 95% confidence intervals were estimated as

$$(\hat{\boldsymbol{\theta}}_c - 1.96 \text{s.e}(\hat{\boldsymbol{\theta}}_c), \hat{\boldsymbol{\theta}}_c + 1.96 \text{s.e}(\hat{\boldsymbol{\theta}}_c)). \quad (4.11)$$

#### 4.2.4 Probabilistic maturation reaction norms

The probability of an  $a$  year old,  $l$  cm long fish from cohort  $c$  reaching maturity,  $m(a, l, c)$ , was approximated as

$$m(a, l, c) = \frac{p(a, l, c) - p(a - 1, l - \Delta l, c)}{1 - p(a - 1, l - \Delta l, c)} \quad (4.12)$$

where  $p(a, l, c)$  is the probability of being mature and  $\Delta l$  is the average annual growth increment (Barot et al., 2004). Equation (4.12) specifies a PMRN for each cohort; that is the probability of first maturation for each combination of age and length. Annual growth increments,  $\Delta l = l(a, c) - l(a - 1, c)$ , and the probability of being mature were estimated from linear models.

$$l(a, c) = \beta_a + \beta_c \quad (4.13)$$

$$\text{logit}(p(a, l, c)) = \beta_{0,c} + \beta_1 l + \beta_2 a + \beta_{3,c} l + \beta_{4,c} a + \beta_5 l a + \beta_{6,c} l a \quad (4.14)$$

Cohort and age were both treated as categorical variables in eq. (4.13). Cohort was the only categorical variable in eq. (4.14). When using eq. (4.14) to model the probability of being of mature, it was usually not possible to fit the full model with all of the interaction terms. Non-significant terms were removed until the best fitting and most parsimonious models were determined.

PMRN midpoints,  $L_{p50}$ , are defined as regions in the length-age plane corresponding to a 50% probability of first maturation. When the growth trajectory of a juvenile fish intersects the curve formed by PMRN midpoints, that fish has a 50% probability of maturing. Time series of PMRN midpoints,  $L_{p50c}$ , were estimated separately for each age group as

$$\begin{aligned} \text{logit}(m(l, c)) &= \beta_{0,c} + \beta_1 l \\ L_{p50c} &= \frac{-\beta_{0,c}}{\beta_1} \end{aligned} \quad (4.15)$$

where cohort was treated as a categorical variable. These  $L_{p50c}$  time series were used to evaluate trends in within-age-group lengths at maturation. Confidence intervals

for  $L_{p50}$  estimates were generated by bootstrapping the maturity data. The data were resampled 1000 times with replacement, stratifying by cohort, to generate distributions for  $L_{p50}$  by repeating the above procedure with the bootstrapped data. Confidence intervals were set at the 95% percentiles of the bootstrapped distributions.

#### 4.2.5 Temporal trends, regional differences, and the influence of abundance and temperature

Linear models were used to assess whether any long term trends were present in mean length at age, the von Bertalanffy growth parameters and  $L_{p50c}$  values. These models were independently fitted to each species within each region. The gradient terms, specifying linear rates of change, were used to estimate differences over the full time series. The mean lengths of age groups 1–8 were regressed against year. The estimated growth parameters,  $L_{\infty c}$  and  $k_c$ , and  $L_{p50c}$  values for age groups 1–3 were independently regressed against the year of birth of the cohort,  $Y_c$ , and also regressed against combinations of  $Y_c$ , abundance estimates,  $N_c$ , and summer sea surface temperature,  $T_c$ ,

$$P_c = \beta_0 + \beta_1 Y_c + \beta_2 N_c + \beta_3 T_c + \beta_4 N_c T_c \quad (4.16)$$

where  $P_c$  is either  $L_{\infty c}$ ,  $k_c$  or  $L_{p50c}$ . Annual abundance estimates were derived by dividing the number of sampled fish by the proportion of the total regional area that was swept out by the survey trawl gear each year. The  $N_c$  and  $T_c$  variables were calculated as the mean abundance or temperature over the first three years of growth for cohort  $c$  when  $P_c = L_{\infty c}$  or  $P_c = k_c$ , and were the means over the first  $a$  years when  $P_c = L_{p50c}$  evaluated for age group  $a$ . Covariates were excluded from eq. (4.16) by selecting the models with the lowest AIC scores, and the interaction term,  $N_c T_c$ , was only included if it was significant ( $p < 0.05$ ). The trends in temperature and estimated abundance are shown in fig. 4.2. The statistical significance of regional differences in mean length at age,  $L_{\infty c}$ ,  $k_c$ , and  $L_{p50c}$  were determined with Nemenyi pairwise comparison tests.

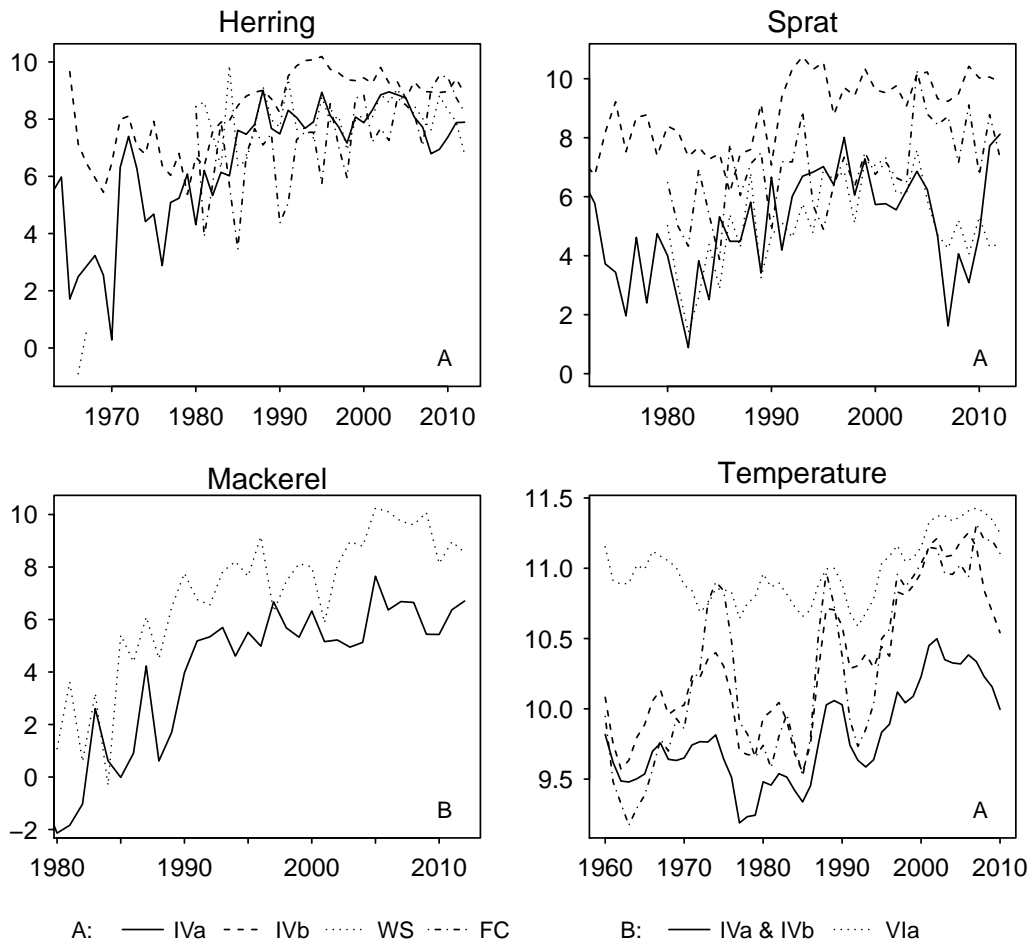


Figure 4.2: Time series of relative abundance and temperature. The abundance estimates are sampled numbers per km<sup>2</sup> of area swept by the survey gear, and have been log transformed. Units of temperature are °C. Text in the bottom right corners refer to the legends. WS and FC stand for the western shelf and Firth of Clyde.

#### 4.2.6 Categorising herring as spring or autumn spawners

The maturity status of sampled herring may be used to determine whether individuals were from spring spawning or autumn spawning stocks, provided that the samples were collected in the period from two months prior to spawning season until the peak of the spawning season (Bucholtz et al., 2008). Survey data collected in quarters one and three, prior to spring and autumn spawning, were used for this purpose. The eight stage maturity scale is: (1) virgin; (2) virgin with small gonads; (3–5) maturing; (6)

spawning; (7) spent; (8) recovering (McPherson et al., 2011). During quarter one, adult spring spawners will be maturing while the autumn spawners will be spent/recovering, so fish in maturity stages 3–6 can be classed as spring spawners, and those in stages 7–8 or 2 are autumn spawners. It is the reverse during quarter three, when fish in maturity stages 3–6 can be classed as autumn spawners, and those in stages 7–8 or 2 are spring spawners (Bucholtz et al., 2008). If a survey uses an eight stage maturity scale such as this, then the adult herring (stages 2–8) present in samples collected during quarters one or three may be categorised as belonging to spring or autumn spawning stocks.

The IBTS data set has not used this maturity scale, instead maturity was classed as: (1) juvenile; (2) maturing; (3) spawning; (4) spent. Spawning and spent individuals can be categorised as spring or autumn spawning as above. Stage 2 individuals, however, need to be split into two groups corresponding to stages 2 and 3–5 on the eight stage maturity scale. The FRS data set consisted of a collection of different surveys which included the IBTS data, so the maturity status of an individual within the FRS data set may have been recorded using the eight stage scale or the less informative IBTS scale. A ‘test’ data set that only used the eight stage maturity scale was obtained by extracting FRS data collected in years where the IBTS surveys were not conducted. Every mature fish (maturity stages 2–8) in this ‘test’ data set was then classed as spring or autumn spawning. The rest of this section describes how the remaining uncategorised herring were assigned to either spring spawning or autumn spawning stocks. The remaining uncategorised herring consisted of the juveniles (stage 1 on either scale) and fish recorded as maturity stage 2 in the IBTS data.

The recorded age of herring had been standardised so that the assumed birth-days were the nearest January 1st to the time of spawning, and age was measured by counting winter otolith rings. Therefore, within age groups, autumn spawned individuals will be approximately six months older — and often larger on average — than spring spawned fish. Plots of length distributions within age groups were often bimodal or highly skewed, suggesting the presence of both autumn and spring spawned fish. Mixture-normal distributions were fitted to the annual length distributions for age groups 1–4 to assess whether the non-normality could be due to differences in the

distributions of length at age of spring and autumn spawners. The expected within-age-group lengths of spring and autumn spawners were calculated from the time series of von Bertalanffy growth parameter estimates using approximate ‘true’ birthdays for each race — these ‘true’ birthdays were Jan. 1<sup>st</sup>  $\pm$  3 months. The expected lengths of each race and the mixed normal distributions were then overlaid on plots of the length frequency distributions. The expected lengths of spring and autumn spawners were a close match to the two peaks of the mixed normal distributions for many of the years where the distributions of length at age were bimodal or skewed. In these instances, the mixed normal distributions were used to specify the race of each individual not previously categorised via recorded maturity statuses. Thus, length frequency distributions combined with predicted lengths at age were used to categorise many of the juvenile (stage 1) and IBTS stage 2 herring as spring or autumn spawners. The FRS ‘test’ data set was then expanded to include these new individuals for which race had been specified.

The remaining juvenile and IBTS stage 2 fish were split into spring and autumn stocks by fitting GAMs to the ‘test’ data, modelling the probability of race against smooth functions of age,  $a$ , and length,  $l$ , and including year,  $y$ , area partitions of statistical rectangle,  $sr$ , and sex,  $s$ , as covariates whenever significant ( $p < 0.05$ ).

$$\text{logit}(p(\text{autumn, spring})) = \alpha_{sr} + \alpha_s + f(a, l) + y g(a, l) \quad (4.17)$$

The IBTS stage 2 fish were considered first, so the data used to fit the GAM consisted of all adults within the ‘test’ data, which were fish whose race had been specified. The GAMs were then fitted to juveniles from the ‘test’ data. The fitted GAMs were then used to specify the race of all the remaining uncategorised fish.

## 4.3 Results

### 4.3.1 Length at age

Time series of estimated mean lengths at age are plotted in fig. 4.3. The linear rates of change of mean length at age are shown in table 4.2, and used to calculate the total

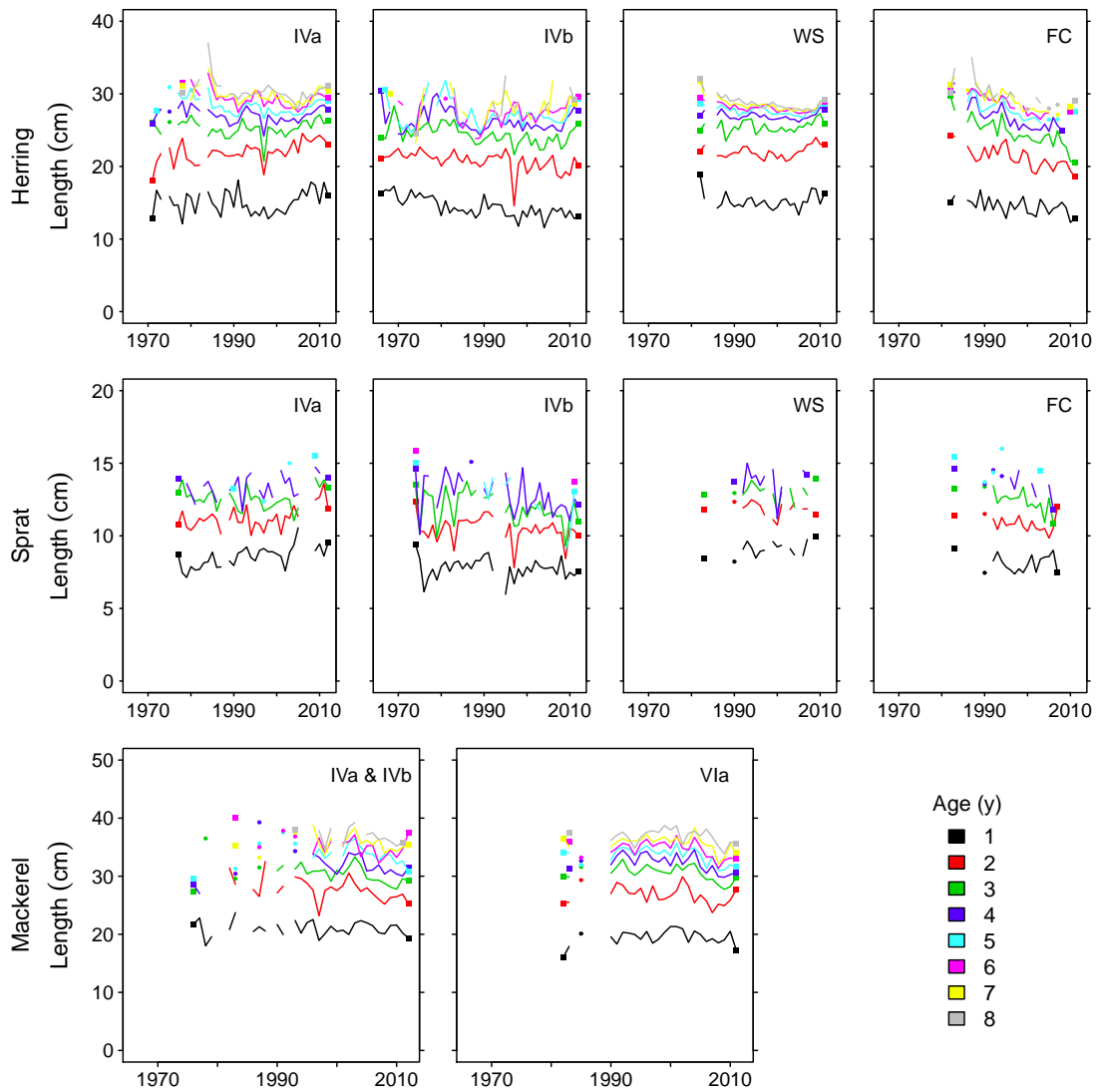


Figure 4.3: Temporal trends in mean length at age. Square symbols indicate the first and final years in the time series for each age group. Text at the top-right corner indicates region. WS and FC stand for the western shelf and the Firth of Clyde.

change in mean length at age over the full time series. The results of the Nemenyi pairwise comparisons are shown in table 4.3, these indicate whether there were significant regional differences in mean lengths at age.

The mean length of age group 2 herring in area IVa increased by  $2.9 \pm 1.2$  cm during 1971–2012; the mean length of age group 5 decreased by  $1.6 \pm 1.3$  cm during 1972–2012,



Table 4.2: The linear rate of change of mean length at age ( $\text{cm y}^{-1}$ ) calculated over the full time series, with 95% confidence intervals in parenthesis. Significant trends are shown in bold. WS and FC stand for the western shelf and the Firth of Clyde.

Species	Region	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8
Herring	IVa	0.023 (-0.019, 0.064)	<b>0.070</b> ( <b>0.040, 0.100</b> )	0.003 (-0.028, 0.034)	-0.013 (-0.040, 0.014)	<b>-0.040</b> ( <b>-0.072, -0.008</b> )	<b>-0.062</b> ( <b>-0.102, -0.023</b> )	-0.039 (-0.079, 0.0005)	<b>-0.058</b> ( <b>-0.109, -0.007</b> )
	IVb	<b>-0.073</b> ( <b>-0.093, -0.052</b> )	<b>-0.050</b> ( <b>-0.075, -0.024</b> )	<b>-0.045</b> ( <b>-0.070, -0.019</b> )	-0.026 (-0.058, 0.006)	-0.020 (-0.061, 0.021)	0.005 (-0.041, 0.051)	0.002 (-0.063, 0.067)	0.092 (-0.024, 0.209)
	WS	-0.011 (-0.064, 0.041)	0.030 (-0.006, 0.067)	0.028 (-0.010, 0.066)	-0.005 (-0.029, 0.019)	<b>-0.026</b> ( <b>-0.051, -0.0005</b> )	<b>-0.034</b> ( <b>-0.058, -0.009</b> )	<b>-0.068</b> ( <b>-0.099, -0.036</b> )	<b>-0.087</b> ( <b>-0.118, -0.056</b> )
	FC	<b>-0.065</b> ( <b>-0.109, -0.021</b> )	<b>-0.135</b> ( <b>-0.185, -0.085</b> )	<b>-0.207</b> ( <b>-0.255, -0.158</b> )	<b>-0.195</b> ( <b>-0.250, -0.140</b> )	<b>-0.171</b> ( <b>-0.227, -0.114</b> )	<b>-0.177</b> ( <b>-0.212, -0.141</b> )	<b>-0.173</b> ( <b>-0.218, -0.129</b> )	<b>-0.151</b> ( <b>-0.235, -0.066</b> )
Sprat	IVa	<b>0.047</b> ( <b>0.027, 0.066</b> )	<b>0.038</b> ( <b>0.013, 0.062</b> )	0.004 (-0.022, 0.029)	0.025 (-0.006, 0.055)	0.145 (-0.180, 0.469)			
	IVb	-0.009 (-0.029, 0.011)	-0.018 (-0.042, 0.006)	<b>-0.035</b> ( <b>-0.064, -0.006</b> )	<b>-0.047</b> ( <b>-0.081, -0.012</b> )	<b>-0.125</b> ( <b>-0.205, -0.045</b> )			
	WS	<b>0.037</b> ( <b>0.002, 0.073</b> )	-0.018 (-0.056, 0.019)	0.001 (-0.047, 0.049)	0.004 (-0.127, 0.135)				
	FC	-0.009 (-0.059, 0.041)	-0.031 (-0.073, 0.011)	<b>-0.089</b> ( <b>-0.137, -0.040</b> )	<b>-0.088</b> ( <b>-0.155, -0.021</b> )	-0.020 (-0.248, 0.208)			
Mackerel	IVa & IVb	-0.007 (-0.050, 0.036)	<b>-0.104</b> ( <b>-0.173, -0.035</b> )	-0.073 (-0.150, 0.002)	0.019 (-0.092, 0.130)	0.008 (-0.088, 0.103)	<b>-0.127</b> ( <b>-0.226, -0.029</b> )	-0.012 (-0.109, 0.085)	-0.097 (-0.249, 0.055)
	VIa	0.031 (-0.035, 0.096)	-0.049 (-0.126, 0.027)	<b>-0.064</b> ( <b>-0.125, -0.003</b> )	<b>-0.088</b> ( <b>-0.161, -0.014</b> )	<b>-0.067</b> ( <b>-0.132, -0.003</b> )	<b>-0.074</b> ( <b>-0.148, -0.0003</b> )	-0.059 (-0.123, 0.006)	-0.049 (-0.124, 0.025)

and the mean lengths of age groups 6 and 8 decreased by  $2.1 \pm 1.3$  cm and  $2.0 \pm 1.7$  cm during 1978–2012. In area IVb, the mean lengths of age groups 1–3 declined during 1966–2012, by  $3.4 \pm 0.9$  cm,  $2.3 \pm 1.2$  cm and  $2.1 \pm 1.2$  cm respectively. The mean lengths of western shelf herring in age groups 5–8 declined during 1982–2011; the magnitude of the declines ranged from  $0.8 \pm 0.7$  cm to  $2.5 \pm 0.9$  cm in age groups 5 and 8 respectively. Significant declines in mean length at age were observed in age groups 1–8 in the Firth of Clyde during 1982–2011; the magnitude of the declines ranged from  $1.9 \pm 1.3$  cm to  $6.0 \pm 1.4$  cm in age groups 1 and 3 respectively.

Herring in age groups 2–6 were significantly larger in area IVa than in IVb. Considered over the full time series, the mean lengths at age of Clyde and western shelf herring were not statistically different, but mean lengths at ages 2–4 were significantly smaller in the Clyde from 2000–2012 due to the more rapid decline in average growth rate.

The mean lengths of IVa sprat in age groups 1 and 2 increased by  $1.6 \pm 0.7$  cm and  $1.3 \pm 0.9$  cm during 1977–2012. In area IVb, the mean lengths of age groups 3–5 declined over time; the magnitude of the declines ranged from  $1.3 \pm 1.1$  cm during 1974–2012 to  $4.8 \pm 3.0$  cm during 1974–2011 in age groups 3 and 5 respectively. The mean length of western shelf sprat in age group 1 increased by  $1.0 \pm 0.9$  cm during 1983–2009. The mean length of Firth of Clyde sprat in age groups 3 and 4 decreased by  $2.0 \pm 1.1$  cm and  $2.0 \pm 1.5$  cm during 1983–2006.

Regional differences in the lengths at age of sprat resembled those observed in herring. Within the North Sea, age groups 1 and 2 were significantly larger in area IVa

Table 4.3: Results of the Nemenyi pairwise comparison tests, comparing mean length at age and the growth parameters between regions. Each entry shows a significant ( $p < 0.05$ ) difference, e.g., IVa>IVb in the  $L_\infty$  column means that  $L_\infty$  was larger in fish from area IVa than it was in IVb. WS and FC stand for the western shelf and the Firth of Clyde regions within area VIa.

Species	Mean length						Growth parameters		
	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	$L_\infty$	$k$	$L_0$
Herring		IVa>IVb	IVa>IVb	IVa>IVb	IVa>IVb	IVa>IVb	IVa>IVb	WS>IVa	IVa>FC
		WS>IVb	WS>IVb			IVa>WS	IVa>WS	FC>IVa	
						FC>IVb	IVa>FC		
Sprat	IVa>IVb	IVa>IVb	WS>IVb				FC>IVb	IVa>FC	
	WS>IVb	WS>IVb							
	WS>FC	WS>IVa							
		WS>FC							
Mackerel	IVa & IVb>VIa	IVa & IVb>VIa							

than IVb, and to the west of Scotland these age groups were larger in the western shelf region than in the Firth of Clyde.

The mean lengths of North Sea (areas IVa and IVb) mackerel in age groups 2 and 6 declined significantly by  $3.7 \pm 2.5$  cm during 1976–2012 and  $3.7 \pm 2.9$  cm during 1983–2012. In area VIa, significant declines in mean length were observed in age groups 3 and 5 during 1982–2011, and in age groups 4 and 6 during 1983–2011; the magnitude of the declines ranged from  $1.9 \pm 1.8$  cm to  $2.5 \pm 2.1$  cm in age groups 3 and 4 respectively. North Sea mackerel in age groups 1 and 2 were significantly larger than those from the west of Scotland, but lengths at age were similar in older age groups.

### 4.3.2 Growth parameters

Figures 4.4 to 4.6 show the von Bertalanffy growth parameters that were estimated for individual cohorts of herring, sprat and mackerel. The magnitude of changes in  $L_\infty$  and  $k$  were calculated from the output of the regressions against time and are shown in table 4.4. Significant regional differences in the growth parameters are shown in table 4.3.

### 4.3.3 Maturity at age

The proportions of sampled fish that were mature within each age group are shown in table 4.5. Figures 4.7 and 4.8 show how the proportions mature at age have changed over time.

### 4.3.4 Trends in $L_{p50}$

Time series of estimated  $L_{p50}$  values for cohorts of herring, sprat and mackerel are shown in figs. 4.9 and 4.10. The linear rates of change in  $L_{p50}$  for age groups 1–3 are shown in table 4.6, used to calculate the total change in  $L_{p50}$  values over the full time series. Significant regional differences in  $L_{p50}$  are shown in table 4.7.

The only group of herring from area IVa to exhibit a significant linear trend in  $L_{p50}$  over the full time series were autumn spawning, age group 2 males, for which  $L_{p50}$  declined by  $2.1 \pm 1.6$  cm between the 1988 and 2009 cohorts. In area IVb, the  $L_{p50}$

### 4.3. Results

Table 4.4: The total change in  $L_\infty$  (cm) and  $k$  ( $y^{-1}$ ) over the time periods shown, predicted from regressing against cohort only, is given in the ‘parameter’ column. The ‘effect’ column shows the most informative combination of explanatory variables from eq. (4.16). The coefficients and standard errors (SE) for these variables, and their expected effect on the growth parameters, are shown in the last two columns. The coefficients are rates of change; the units for the regressions involving  $L_\infty$  are  $\text{cm } y^{-1}$ ,  $10^{-3} \text{ cm km}^2$  and  $\text{cm } ^\circ\text{C}^{-1}$ , and those involving  $k$  are  $y^{-2}$ ,  $10^{-3} y^{-1} \text{ km}^2$  and  $y^{-1} ^\circ\text{C}^{-1}$  for cohort, abundance and temperature respectively. Significant temporal trends, and significant explanatory variable are highlighted in bold. WS and FC stand for the western shelf and the Firth of Clyde.

Group	Parameter	Effect	Coefficient (SE)	Resulting change
IVa herring 1970–2009	$L_\infty$ ( $-1.56 \pm 1.68$ )	cohort	-0.040 (0.021)	-1.56
	<b><math>k</math> (<math>0.16 \pm 0.15</math>)</b>	<b>cohort</b>	<b>0.0086 (0.0023)</b>	<b>0.34</b>
		<b>abundance</b>	<b>-0.063 (0.022)</b>	<b>-0.17</b>
IVb herring 1965–2007	$L_\infty$ ( $-0.69 \pm 2.44$ )	<b>abundance</b>	<b>16.94 (8.17)</b>	<b>48.23</b>
		<b>temperature</b>	<b>17.77 (7.19)</b>	<b>24.30</b>
		<b>abundance*temperature</b>	<b>-1.77 (0.81)</b>	<b>-73.19</b>
	<b><math>k</math> (<math>-0.18 \pm 0.16</math>)</b>	<b>temperature</b>	<b>-0.14 (0.041)</b>	<b>-0.19</b>
WS herring 1982–2007	$L_\infty$ ( $0.81 \pm 1.33$ )	temperature	1.25 (0.69)	0.94
	$k$ ( $-0.0027 \pm 0.24$ )	no effect		
FC herring 1985–2005	<b><math>L_\infty</math> (<math>-2.48 \pm 1.50</math>)</b>	<b>cohort</b>	<b>-0.12 (0.036)</b>	<b>-2.48</b>
	$k$ ( $-0.13 \pm 0.27$ )	abundance	-0.11 (0.063)	-0.17
IVa sprat 1976–2008	$L_\infty$ ( $-0.25 \pm 1.86$ )	no effect		
	$k$ ( $0.33 \pm 0.56$ )	no effect		
IVb sprat 1974–2009	$L_\infty$ ( $-0.56 \pm 2.14$ )	<b>cohort</b>	<b>0.10 (0.043)</b>	<b>3.55</b>
		<b>abundance</b>	<b>-1.69 (0.51)</b>	<b>-4.11</b>
	<b><math>k</math> (<math>-0.49 \pm 0.38</math>)</b>	<b>cohort</b>	<b>-0.030 (0.0084)</b>	<b>-1.06</b>
		<b>abundance</b>	<b>0.23 (0.099)</b>	<b>0.56</b>
WS sprat 1991–2003	$L_\infty$ ( $0.74 \pm 4.14$ )	<b>cohort</b>	<b>-0.32 (0.10)</b>	<b>-3.78</b>
		<b>abundance</b>	<b>2.99 (0.66)</b>	<b>4.52</b>
	$k$ ( $-0.16 \pm 0.82$ )	<b>abundance</b>	<b>-0.62 (0.17)</b>	<b>-0.93</b>
		temperature	0.96 (0.39)	0.75
FC sprat 1989–2003	$L_\infty$ ( $-4.71 \pm 5.46$ )	<b>cohort</b>	<b>-0.59 (0.13)</b>	<b>-8.27</b>
		<b>abundance</b>	<b>172.85 (29.53)</b>	<b>45.92</b>
		<b>temperature</b>	<b>127.10 (21.81)</b>	<b>147.57</b>
		<b>abundance*temperature</b>	<b>-15.84 (2.68)</b>	<b>-189.93</b>
	$k$ ( $0.30 \pm 0.51$ )	cohort	0.015 (0.0093)	0.21
		<b>abundance</b>	<b>-9.30 (2.16)</b>	<b>-2.47</b>
		<b>temperature</b>	<b>-6.76 1.60</b>	<b>-7.84</b>
		<b>abundance*temperature</b>	<b>0.87 (0.20)</b>	<b>10.40</b>
IVa & IVb mackerel 1985–2008	<b><math>L_\infty</math> (<math>-7.1 \pm 3.70</math>)</b>	<b>cohort</b>	<b>-0.31 (0.075)</b>	<b>-7.12</b>
	$k$ ( $0.27 \pm 0.33$ )	abundance	0.073 (0.040)	0.22
VIa mackerel 1981–2005	<b><math>L_\infty</math> (<math>-5.75 \pm 2.97</math>)</b>	<b>cohort</b>	<b>-0.52 (0.10)</b>	<b>-12.55</b>
		<b>abundance</b>	<b>1.11 (0.36)</b>	<b>6.80</b>
	<b><math>k</math> (<math>0.20 \pm 0.18</math>)</b>	<b>cohort</b>	<b>0.020 (0.0074)</b>	<b>0.47</b>
		abundance	-0.045 (0.026)	-0.27

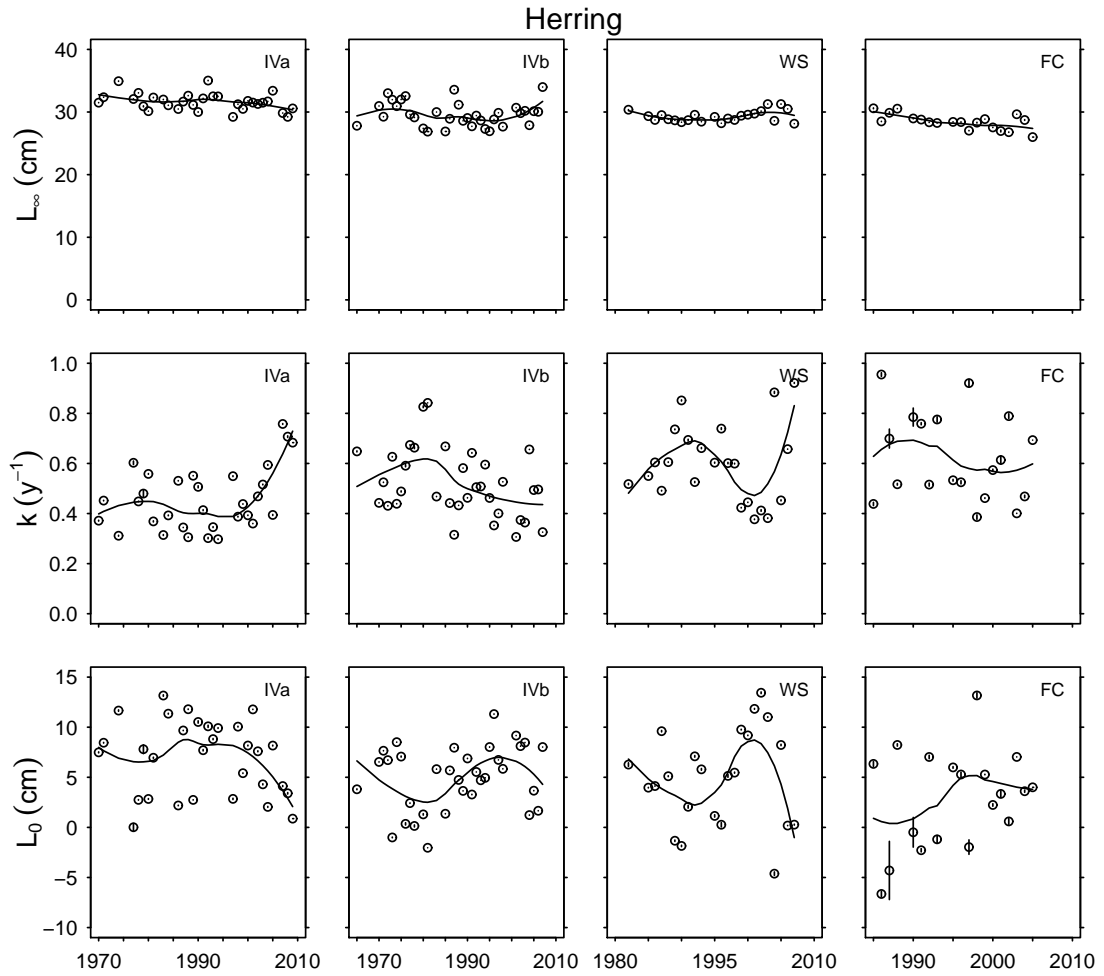


Figure 4.4: Von Bertalanffy growth parameters estimated for cohorts of herring, plotted with 95% confidence intervals and a loess smoothing curve. Text inserted in the top-right corner indicates region. WS and FC stand for the western shelf and Firth of Clyde.

values of spring spawning males in age groups 1–3 increased by  $3.1 \pm 2.0$  cm,  $2.6 \pm 1.8$  cm and  $2.0 \pm 1.4$  cm respectively, between the 1986 and 2008 cohorts; the  $L_{p50}$  values of the age group 2 females also increased by  $2.9 \pm 2.1$  cm during the same time. There were no significant linear trends in  $L_{p50}$  for autumn spawning herring from area IVb. In area VIa, the  $L_{p50}$  values of age group 3 spring spawning herring increased by  $1.6 \pm 1.0$  cm in the females and by  $1.4 \pm 1.1$  cm in the males, between the 1984/85 and 2008 cohorts. The  $L_{p50}$  values of VIa autumn spawning females increased by  $5.1 \pm 2.9$  cm,  $6.7 \pm 2.6$  cm and  $3.7 \pm 1.5$  cm in age groups 1–3.

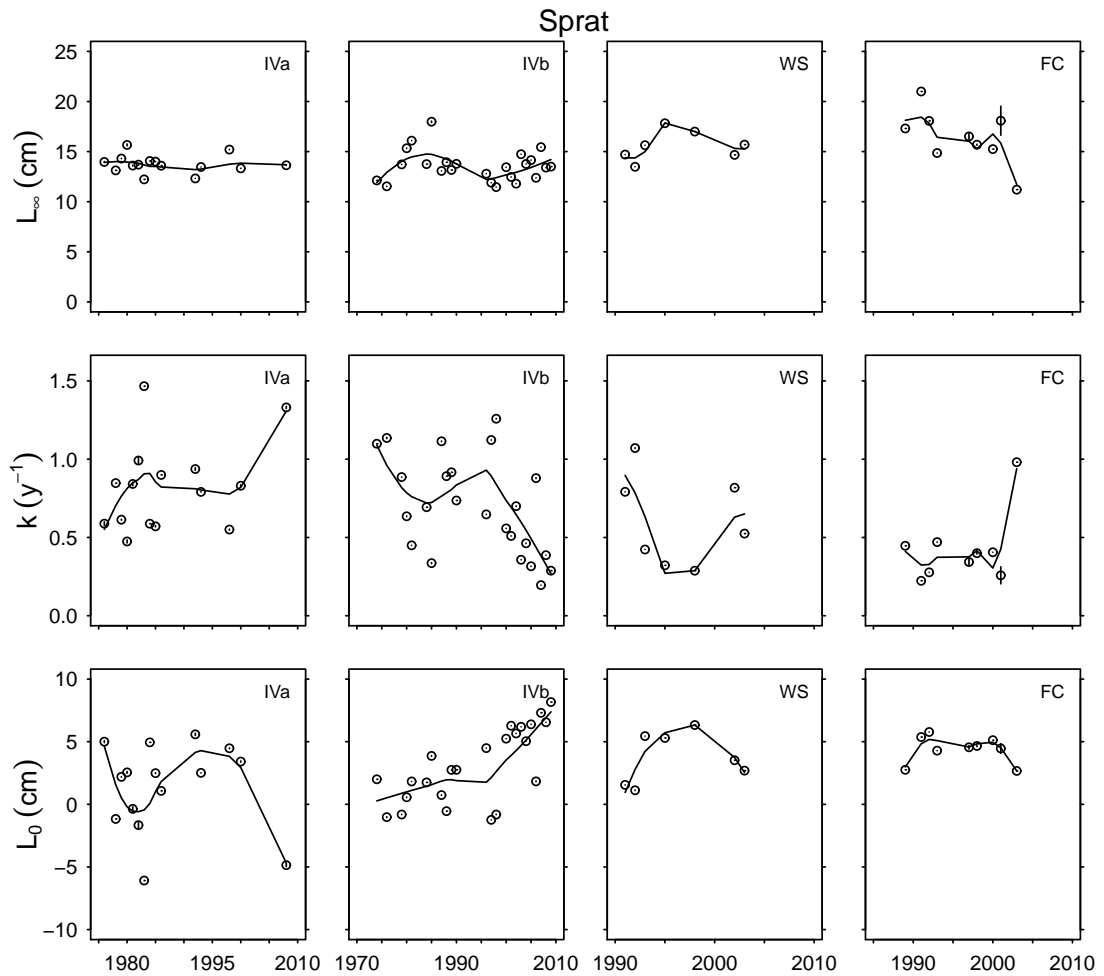


Figure 4.5: Von Bertalanffy growth parameters estimated for cohorts of sprat, plotted with 95% confidence intervals and a loess smoothing curve. Text inserted in the top-right corner indicates region. WS and FC stand for the western shelf and Firth of Clyde.

The  $L_{p50}$  values of IVa spring spawning male herring in age groups 1–3 were larger than those from areas IVb and VIa, so these IVb and VIa herring have been more likely to mature at small sizes. A similar result was obtained for the spring spawning females; the  $L_{p50}$  values observed in area IVa tended to be greater than those in area IVb for age groups 1 and 2, and greater than those in area VIa for age groups 1 and 3. The  $L_{p50}$  values of age group 2 autumn spawning herring were smallest in area IVb for both males and females.

There were no significant linear trends in the  $L_{p50}$  values of sprat. However,  $L_{p50}$

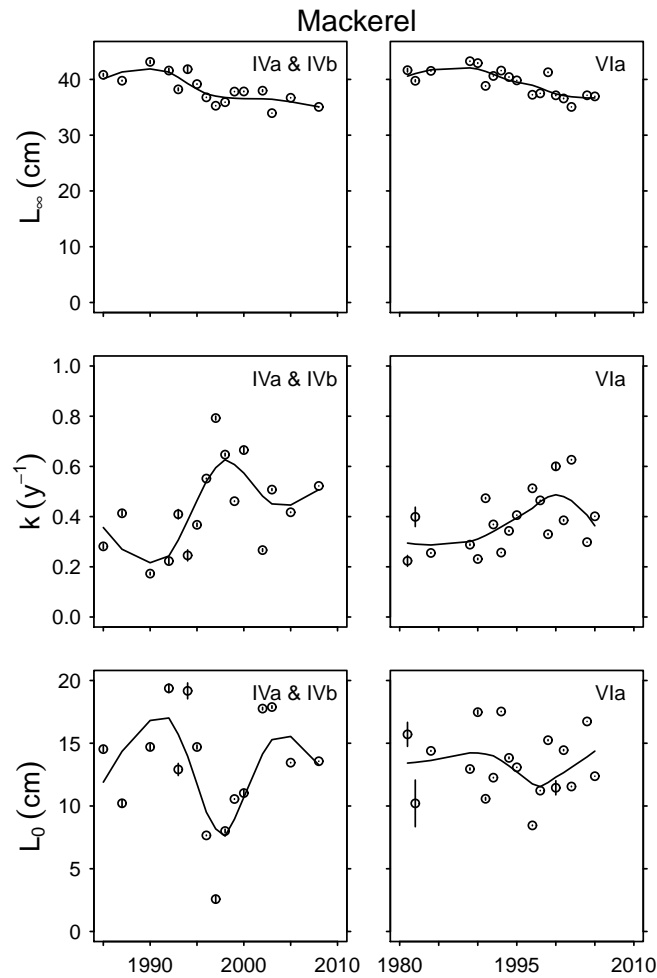


Figure 4.6: Von Bertalanffy growth parameters estimated for cohorts of mackerel, plotted with 95% confidence intervals and a loess smoothing curve. Text inserted in the top-right corner indicates region. WS and FC stand for the western shelf and Firth of Clyde.

tended to be larger in age group 1 males from area IVa than in those from area IVb, so these IVb sprat have been more likely to mature at small sizes.

The  $L_{p50}$  values of male mackerel from areas IVa and IVb declined by  $4.8 \pm 2.8$  cm between the 1982 and 2010 cohorts and by  $3.9 \pm 3.7$  cm between the 1984 and 2010 cohorts in age groups 1 and 2 respectively. The only significant linear trend in  $L_{p50}$  in VIa mackerel was an increase of  $2.7 \pm 2.3$  cm in age group 2 males between the 2004

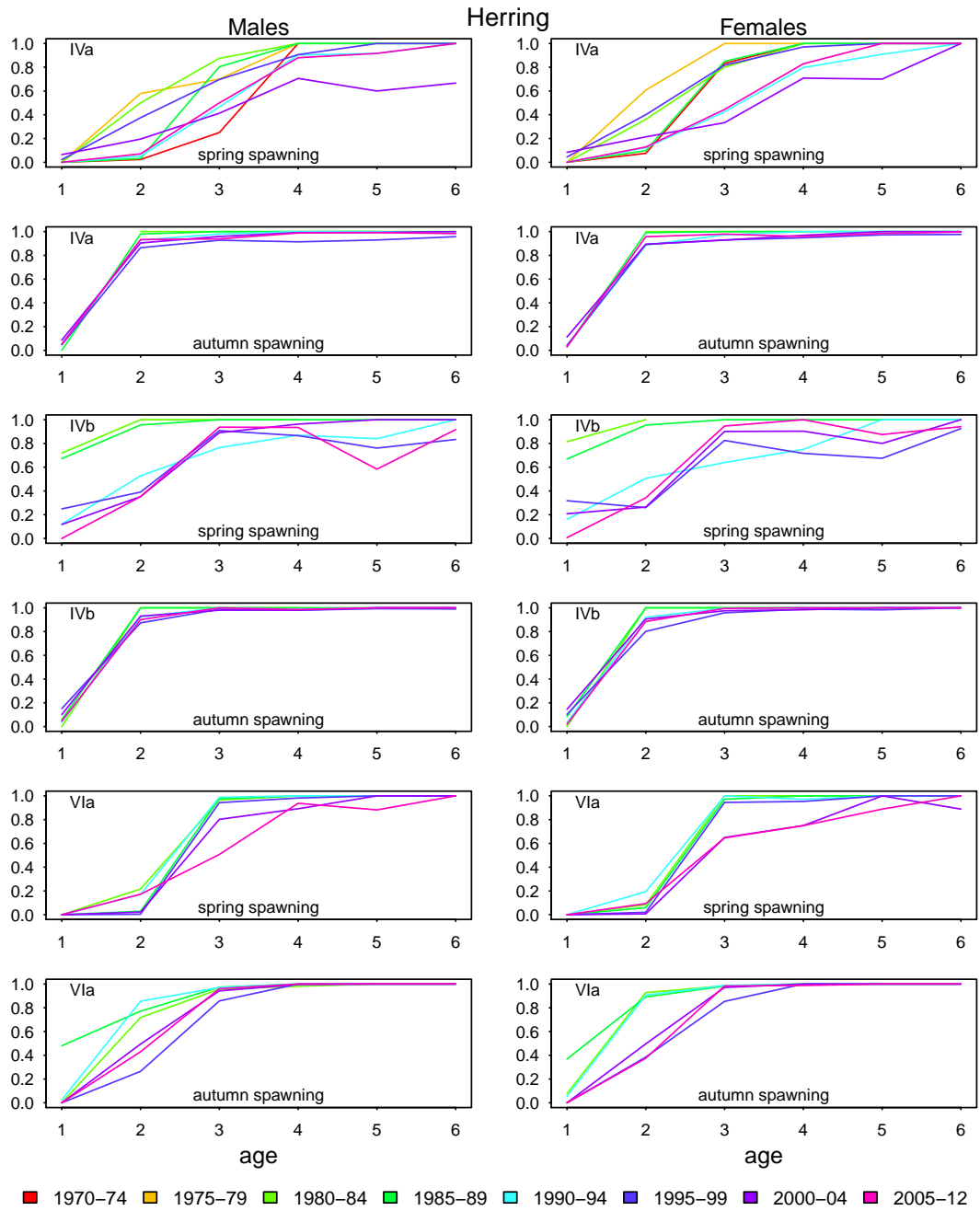


Figure 4.7: The proportion of sampled herring that were mature within each age group, averaged over intervals of five years. Text inserted in the top-left corner indicates region.



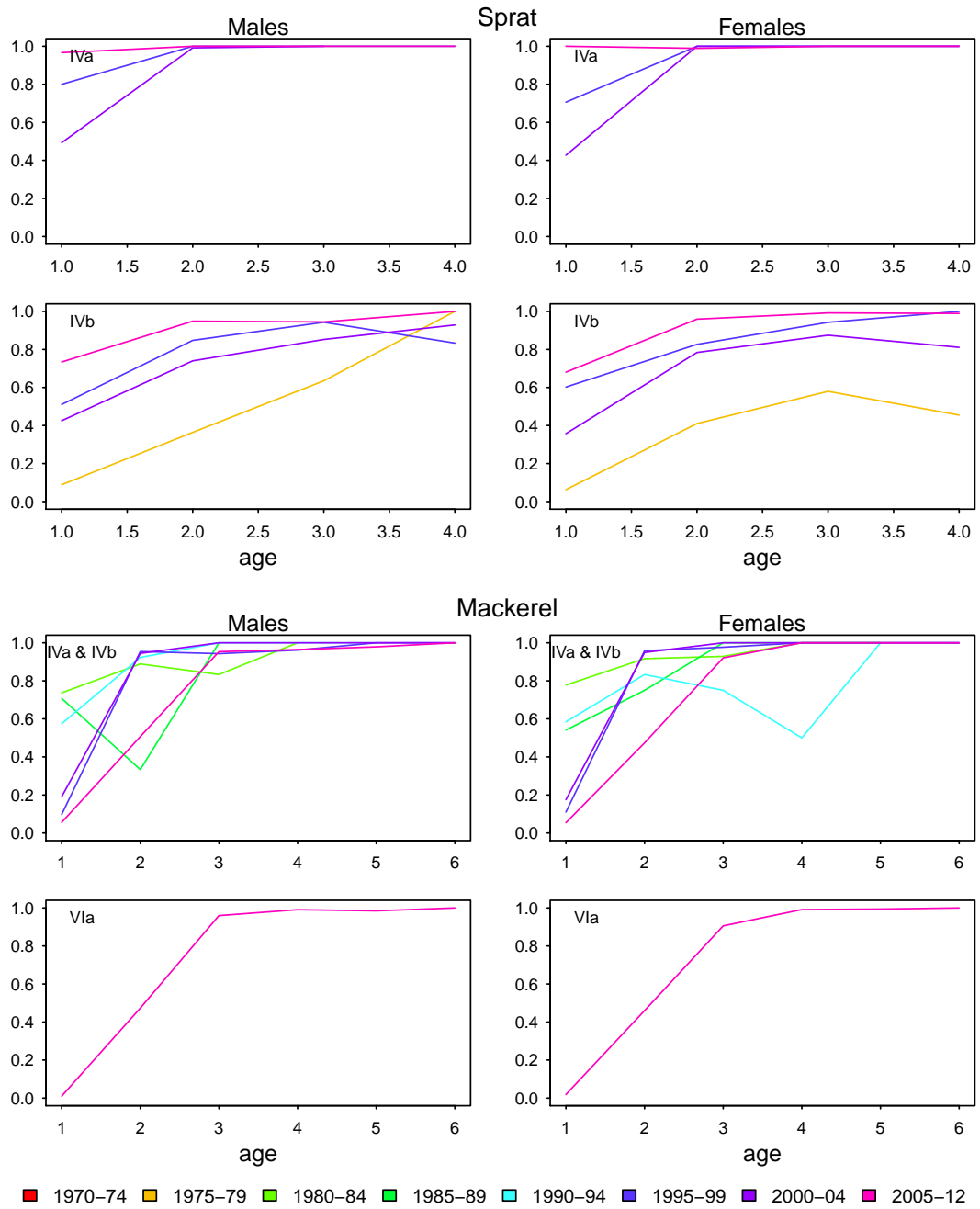


Figure 4.8: The proportion of sampled mackerel and sprat that were mature within each age group, averaged over intervals of five years. Text inserted in the top-left corner indicates region.

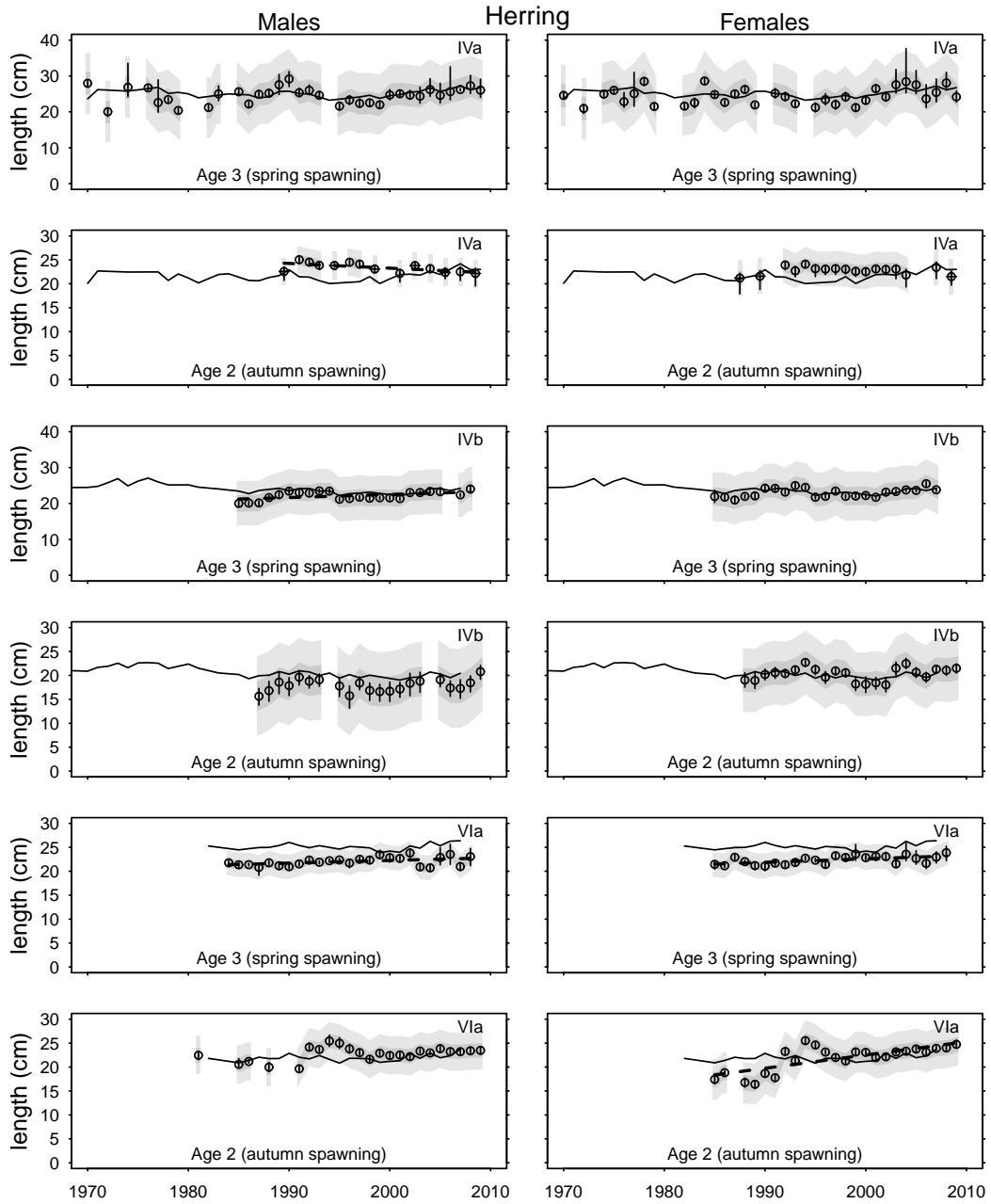


Figure 4.9: Time series of  $L_{p50}$  estimated for cohorts of herring, with 95% confidence intervals. The age groups with the most precise estimates of  $L_{p50}$  are shown. The light and dark grey polygons are maturation envelopes, representing  $L_{p05} \rightarrow L_{p95}$  and  $L_{p25} \rightarrow L_{p75}$  respectively. Thick dashed lines show significant linear trends. Thin solid lines show expected length based on the estimated growth parameters. Text inserted in the top-right corner indicates region.

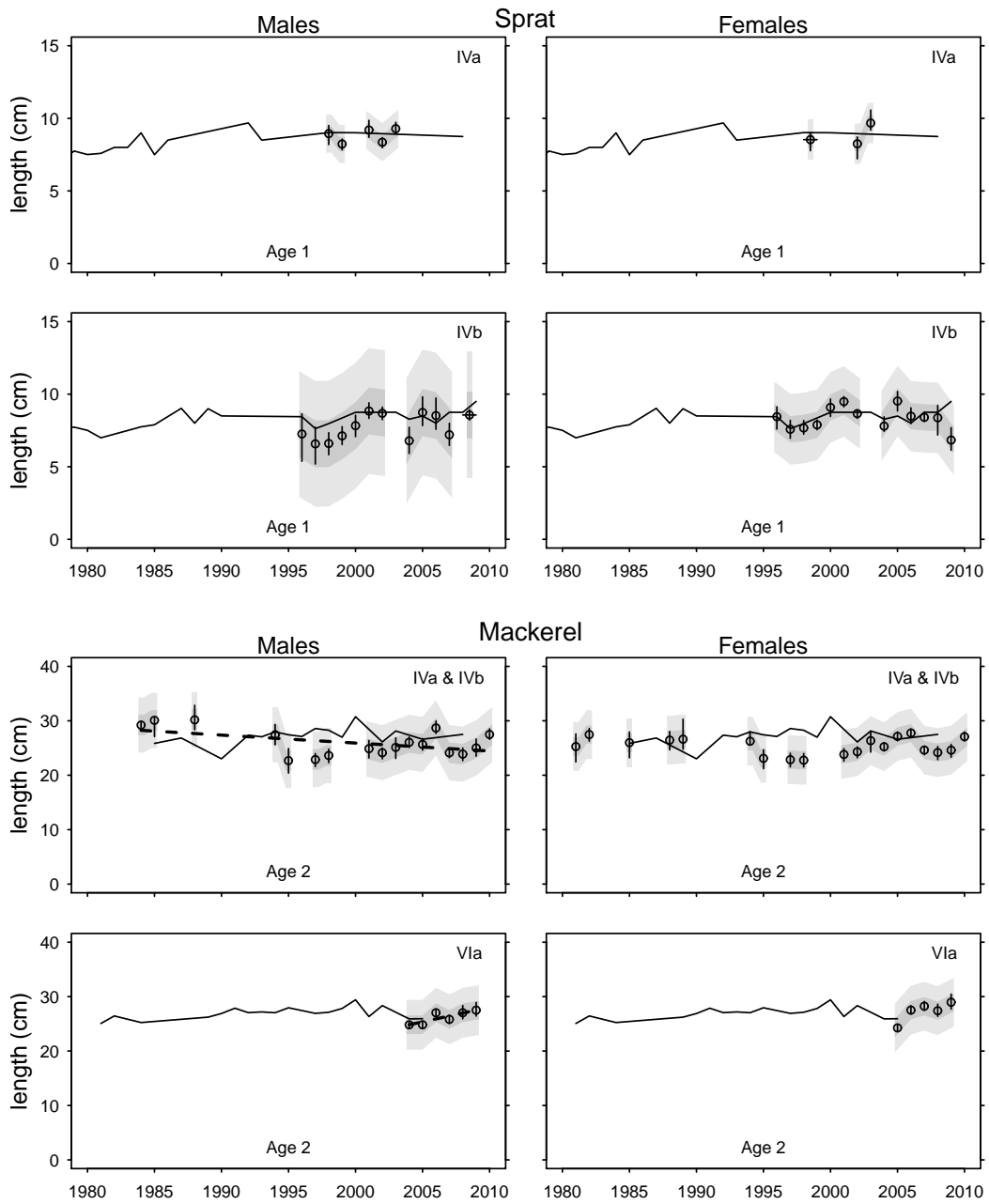


Figure 4.10: Time series of  $L_{p50}$  estimated for cohorts of mackerel and sprat, with 95% confidence intervals. The age groups with the most precise estimates of  $L_{p50}$  are shown. The light and dark grey polygons are maturation envelopes, representing  $L_{p05} \rightarrow L_{p95}$  and  $L_{p25} \rightarrow L_{p75}$  respectively. Thick dashed lines show significant linear trends. Thin solid lines show expected length based on the estimated growth parameters. Text inserted in the top-right corner indicates region.

and 2009 cohorts. The  $L_{p50}$  values of VIa female mackerel in age groups 1–3 were significantly greater than those from areas IVa and IVb, so female mackerel from the North Sea have been more likely to mature at small sizes.

#### 4.3.5 Influence of temperature and abundance on growth and maturation

The results of regressing the von Bertalanffy growth parameters and  $L_{p50}$  values against time, abundance and temperature are shown in tables 4.4 and 4.8. Figure 4.11 shows how the growth parameters and  $L_{p50}$  were related to abundance and temperature in instances where the interaction between these explanatory variables was significant.

The increase in abundance of IVa herring during 1970–2009 has acted to reduce  $k$ , however, the significant increase in  $k$  indicates that some other factor has had more influence on growth rate. There were no significant linear temporal trends in  $L_{p50}$  for

Table 4.5: The proportion of mature individuals present in the survey maturity data within age groups 1–6, calculated over the full study period. S and A indicate spring and autumn spawning herring.

Species	Region	Quarter	Sex	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
Herring (S)	IVa	1	M	0.02	0.21	0.70	0.89	0.93	0.96
			F	0.01	0.29	0.69	0.92	0.94	0.95
Herring (A)	IVa	3	M	0.06	0.96	0.98	0.98	0.92	0.92
			F	0.06	0.95	0.98	0.98	0.97	1
Herring (S)	IVb	3	M	0.21	0.50	0.90	0.90	0.85	0.91
			F	0.24	0.43	0.86	0.87	0.88	0.96
Herring (A)	IVb	3	M	0.08	0.91	0.99	0.98	1	1
			F	0.07	0.89	0.99	0.99	1	1
Herring (S)	VIa	1	M	0.00	0.12	0.8	0.96	0.96	1
			F	0.00	0.12	0.78	0.88	0.99	0.96
Herring (A)	VIa	1	M	0.02	0.53	0.97	1	1	1
			F	0.02	0.57	0.99	1	1	1
Sprat	IVa	1	M	0.69	1	1	1	1	1
			F	0.7	0.97	1	1	1	
Sprat	IVb	1	M	0.55	0.81	0.84	0.92	0.67	1
			F	0.49	0.81	0.87	0.87	1	1
Mackerel	IVa & IVb	1	M	0.30	0.70	0.96	0.92	0.94	1
			F	0.27	0.73	0.93	0.95	1	1
Mackerel	VIa	1	M	0.01	0.46	0.94	0.98	0.98	1
			F	0.02	0.43	0.91	0.98	1	1

4.3. Results

Table 4.6: Linear rates of change in  $L_{p50}$  over time ( $\text{cm y}^{-1}$ ), with 95% confidence intervals in parenthesis. Significant trends ( $p < 0.05$ ) are shown in bold. Spring and autumn spawning herring are indicated by (S) and (A).

Species	Region	Sex	Age 1	Age 2	Age 3
Herring (S)	IVa	M	-0.01 (-0.11, 0.10)	0.06 (-0.02, 0.14)	0.03 (-0.04, 0.10)
		F	0.06 (-0.08, 0.20)	0.04 (-0.06, 0.13)	0.04 (-0.03, 0.11)
Herring (A)	IVa	M	0.03 (-0.08, 0.14)	<b>-0.10 (-0.17, -0.02)</b>	
		F	0.05 (-0.06, 0.17)	0.00 (-0.07, 0.08)	
Herring (S)	IVb	M	<b>0.14 (0.05, 0.23)</b>	<b>0.12 (0.04, 0.20)</b>	<b>0.09 (0.02, 0.15)</b>
		F	0.11 (-0.01, 0.24)	<b>0.13 (0.04, 0.23)</b>	0.07 (-0.01, 0.15)
Herring (A)	IVb	M	0.03 (-0.03, 0.09)	0.05 (-0.04, 0.14)	
		F	0.03 (-0.04, 0.10)	0.04 (-0.06, 0.13)	
Herring (S)	VIa	M	0.01 (-0.03, 0.05)	0.01 (-0.02, 0.04)	<b>0.06 (0.01, 0.10)</b>
		F	0.03 (-0.0003, 0.07)		<b>0.07 (0.03, 0.12)</b>
Herring (A)	VIa	M	0.13 (-0.04, 0.31)	0.07 (-0.002, 0.15)	
		F	<b>0.22 (0.09, 0.34)</b>	<b>0.28 (0.17, 0.39)</b>	<b>0.16 (0.09, 0.22)</b>
Sprat	IVa	M	0.07 (-0.34, 0.48)		
		F	0.17 (-3.30, 3.64)		
Sprat	IVb	M	0.11 (-0.02, 0.24)		
		F	-0.01 (-0.13, 0.11)		
Mackerel	IVa & IVb	M	<b>-0.17 (-0.27, -0.07)</b>	<b>-0.15 (-0.29, -0.002)</b>	
		F	-0.07 (-0.17, 0.02)	-0.02 (-0.11, 0.06)	-0.06 (-0.17, 0.06)
Mackerel	VIa	M	0.27 (-1.22, 1.76)	<b>0.54 (0.07, 1.00)</b>	0.48 (-0.13, 1.09)
		F	0.37 (-0.85, 1.60)	0.93 (-0.27, 2.14)	-0.28 (-5.00, 4.45)

Table 4.7: Results of the Nemenyi pairwise comparison tests, comparing  $L_{p50}$  values between regions. Each entry shows a significant ( $p < 0.05$ ) difference, e.g., IVa>IVb in the Age 2 column means that  $L_{p50}$  was larger in age group 2 fish from area IVa than it was in IVb. Spring and autumn spawning herring are indicated by (S) and (A).

Species	Sex	Age 1	Age 2	Age 3
Herring (S)	M	IVa>IVb	IVa>IVb	IVa>IVb
		IVa>VIa	IVa>VIa	IVa>VIa
		VIa>IVb		
	F	IVa>IVb	IVa>IVb	IVa>VIa
		IVa>VIa		
		VIa>IVb		
Herring (A)	M		IVa>IVb	
			VIa>IVb	
	F		IVa>IVb	
			VIa>IVb	
Sprat	M	IVa>IVb		
Mackerel	F	VIa>IVa & IVb	VIa>IVa & IVb	VIa>IVa & IVb

spring spawning herring in area IVa, although increases in abundance were related to decreases in  $L_{p50}$  for age group 1 males and rising temperature was related to increases in  $L_{p50}$  for age group 2 males.

The decline in the growth rate,  $k$ , of IVb herring appears to be entirely attributable to rising temperature. The asymptotic length,  $L_{\infty}$ , did not change significantly over the full time series, although it tended to increase with rising temperature and decrease with rising abundance; the extent to which  $L_{\infty}$  was affected by changes in abundance or temperature depended on the combination of these two variables. The  $L_{p50}$  values of IVb spring spawning males in age groups 1 and 3, and IVb spring and autumn spawning females in age group 1 varied with interactions between abundance and temperature. In general, rises in either temperature or abundance caused increases in  $L_{p50}$  when the other variable was relatively low, and rises in either variable caused decreases in  $L_{p50}$  when the other variable was relatively large. However, the abundance–temperature interaction was relatively weak in the one year old spring spawners, so that the  $L_{p50}$  values of the males remained fairly stationary as temperature increased at high abundance, and  $L_{p50}$  decreased only slightly in the females as abundance increased at high temperatures.

The only significant linear trend in the growth parameters of herring from the west of Scotland was a decline in  $L_{\infty}$  for Clyde herring, but this was not related to abundance or temperature. PMRNs for the western herring stock were estimated using data from the whole of area VIa because the adult to juvenile ratio in the Clyde was too low to calculate PMRNs. The  $L_{p50}$  values of autumn spawning females in age groups 1 and 2 increased over time, but these increases appear to have been significantly inhibited by rises in temperature which acted to reduce  $L_{p50}$ .

Variations in the growth parameters and  $L_{p50}$  values of IVa sprat were not related to abundance or temperature, in fact, none of the  $L_{p50}$  time series for sprat in the regions considered were related to abundance or temperature. In IVb sprat,  $L_{\infty}$  decreased with a rise in abundance, but a significant cohort effect acting in the opposite direction prevented a large overall decline. The rise in abundance of IVb sprat acted to increase  $k$ , but a strong cohort effect resulted in a decline in  $k$ .

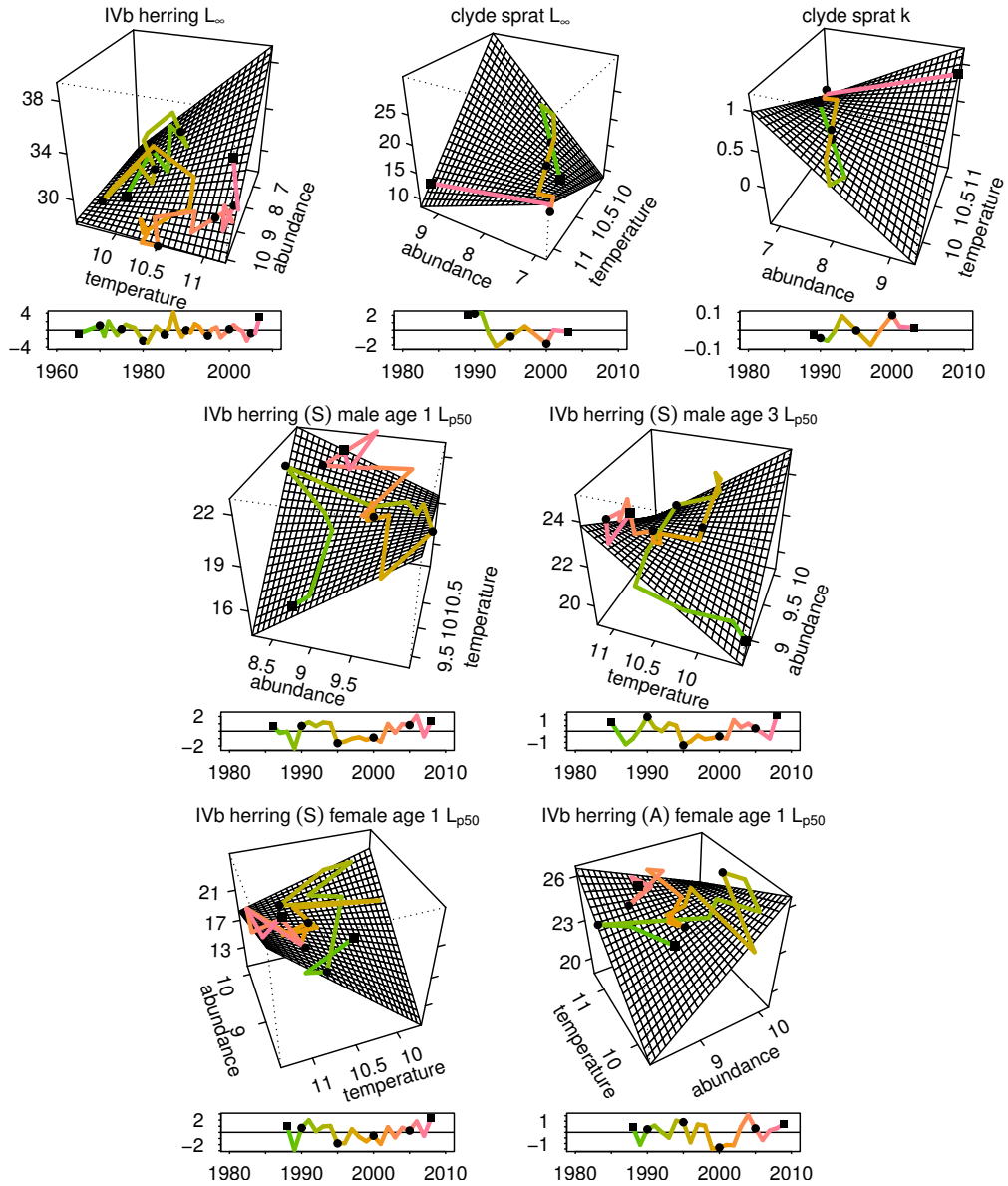


Figure 4.11: Surfaces show predicted values of  $L_\infty$ ,  $k$  or  $L_{p50}$  from regressions against abundance and temperature. The overlaid lines show the actual values of the  $L_\infty$ ,  $k$  and  $L_{p50}$  estimates. Differences between model predictions and the actual values are shown as time series in the sub-plots. Only groups with a significant abundance–temperature interaction are plotted. Spring and autumn spawning herring are indicated by (S) and (A).

The overall decline in  $k$  in western shelf sprat appears to be explainable in terms of variation in abundance and temperature;  $k$  decreased with increases in abundance and increased with rises in temperature, although the linear relation to temperature was not significant. The  $L_\infty$  values of western shelf sprat tended to increase with rising abundance, but  $L_\infty$  did not exhibit a long term trend as it was inhibited a significant cohort effect.

The  $L_\infty$  values of Clyde sprat declined in response to some cohort effect, while an interaction between abundance and temperature caused  $L_\infty$  to increase with rises in either variable while the other had a relatively low value, and decrease with rises in either variable when the other had a relatively large value. The growth rate,  $k$ , of Clyde sprat was related to an interaction between abundance and temperature so that increases in either variable when the other had a relatively low value caused declines in  $k$ , and increases in either variable when the other had a relatively large value resulted

Table 4.8: The estimated coefficients and standard errors (SE) from regressions of  $L_{p50}$  against cohort ( $\text{cm y}^{-1}$ ), temperature ( $\text{cm }^\circ\text{C}^{-1}$ ) and log abundance ( $\text{cm km}^2$ ), and the total change ascribable to each covariate. Significant linear trends are shown in bold. Groups for which there was no significant relationship between  $L_{p50}$  and temperature or abundance have been excluded. Spring and autumn spawning herring are indicated by (S) and (A).

Group	Age	Cohort range	Effect	Coefficient (SE)	Resulting change
IVa male herring (S)	1	1974–2009	<b>abundance</b>	<b>-0.72 (0.32)</b>	<b>-2.68</b>
			temperature	2.32 (1.39)	1.95
	2	1971–2009	<b>temperature</b>	<b>2.83 (1.07)</b>	<b>2.92</b>
IVb male herring (S)	1	1986–2008	<b>abundance</b>	<b>28.24 (11.76)</b>	<b>2.08</b>
			<b>temperature</b>	<b>26.00 (10.26)</b>	<b>35.66</b>
			<b>abundance*temperature</b>	<b>-2.64 (1.11)</b>	<b>-35.20</b>
	3	1985–2008	<b>abundance</b>	<b>41.76 (13.97)</b>	<b>0.52</b>
			<b>temperature</b>	<b>37.08 (12.26)</b>	<b>46.24</b>
			<b>abundance*temperature</b>	<b>-3.93 (1.35)</b>	<b>-45.11</b>
IVb female herring (S)	1	1988–2008	<b>abundance</b>	<b>67.28 (25.31)</b>	<b>-12.46</b>
			<b>temperature</b>	<b>60.75 (22.53)</b>	<b>55.18</b>
			<b>abundance*temperature</b>	<b>-6.25 (2.35)</b>	<b>-41.03</b>
IVb female herring (A)	1	1988–2009	<b>abundance</b>	<b>37.70 (15.69)</b>	<b>-10.48</b>
			<b>temperature</b>	<b>33.29 (13.95)</b>	<b>29.86</b>
			<b>abundance*temperature</b>	<b>-3.47 (1.46)</b>	<b>-18.91</b>
VIa female herring (A)	1	1986–2009	<b>cohort</b>	<b>0.43 (0.096)</b>	<b>9.97</b>
			<b>temperature</b>	<b>-5.23 (1.92)</b>	<b>-5.00</b>
	2	1985–2009	<b>cohort</b>	<b>0.54 (0.080)</b>	<b>12.99</b>
			<b>temperature</b>	<b>-7.56 (1.95)</b>	<b>-6.33</b>
IVa & IVb male mackerel	1	1982–2010	<b>abundance</b>	<b>-0.81 (0.14)</b>	<b>-4.94</b>
	2	1984–2010	<b>abundance</b>	<b>-0.76 (0.22)</b>	<b>-4.42</b>
VIa male mackerel	2	2004–2009	<b>temperature</b>	<b>19.93 (5.06)</b>	<b>2.41</b>



in increases in  $k$ . A cohort effect accounted for most of the increase in  $k$  for Clyde sprat, although this was not deemed significant.

The decline in the  $L_\infty$  parameter for North Sea mackerel was not related to abundance or temperature, but entirely due to a cohort effect. The increase in the growth rate,  $k$ , appears to be largely explained by rises in abundance, but this variable was not considered to be significant. Declines in the  $L_{p50}$  values of male North Sea mackerel in age groups 1 and 2 were attributable to increases in abundance.

The  $L_\infty$  values of VIa mackerel tended to increase with rises in abundance, but the overall decrease was due to some significant cohort effect. The model for the growth rate,  $k$ , included the abundance term, but this was insignificant, and the overall increase to  $k$  was due to a cohort effect. The increase in the  $L_{p50}$  values of age group 2 males was largely due to rises in temperature.

## 4.4 Discussion

### 4.4.1 Trends in growth

Trends in the length at age and growth parameters of North Sea herring differed between the north (IVa) and south (IVb). In area IVa, mean lengths of age groups 3–8 declined between the 1970s and early 2000s, then increased until 2012. This was reflected by the gradual decline in  $L_\infty$  throughout the time series, and the steep increase in  $k$  during the 2000s. The rise in  $k$  accounted for the increase in the mean length of age group 2, and the concurrent decrease in  $L_0$  accounted for the relatively stationary mean length of age group 1. In area IVb, the mean lengths of age groups 1–3 declined significantly over the full time series; these declines were most rapid between the late 1960s and 1990, and the lengths of age groups 3 and older appeared to be increasing by the late 2000s. These declines were emulated in the von Bertalanffy parameters by a decrease in  $k$ , which fell most rapidly in cohorts spawned during the 1980s. Increases in the lengths of older fish around 1980 and the mid 1990s were represented by large  $L_\infty$  values in the 1972–1976 and 1987–1988 cohorts. Herring in age groups 2–6 were significantly larger in area IVa than in IVb, and  $L_\infty$  was greater in area IVa. The lengths of IVb herring in

age groups 4–6 were consistently smaller than in area IVa throughout the time series, however, the lengths of age groups 1–3 were initially similar, but became smaller in area IVb as time progressed.

Excepting the well studied Baltic Sea populations, most research on the growth of east Atlantic herring (e.g. de Silva, 1973b; Heath et al., 1997; Johannessen et al., 2000) has focused on larval or juvenile growth without considering changes in the expected length of older individuals or describing growth in terms of the von Bertalanffy model. An exception is the meta-analysis by Brunel and Dickey-Collas (2010), in which von Bertalanffy growth parameters were estimated for 15 herring populations in the east and west Atlantic, and then related to sea surface temperature and stock density estimates. Brunel and Dickey-Collas (2010) estimated growth parameters ( $W_\infty$  = asymptotic weight,  $k$  and  $t_0$  = age at length of zero) for individual cohorts using acoustic survey data collected in June/July in the seas west and north of Scotland during 1993–2006 and in the North Sea during 1984–2006. They did not report temporal trends in the growth parameters, as their focus was on how growth was correlated with temperature and abundance, but instead provided mean values for the parameters. We can use allometric length-weight relationships to estimate  $L_\infty$  from  $W_\infty$  and, by calculating  $L_0$  (accounting for the difference in sampling times), we can compare the mean values of our parameter estimates to their results. We found that the 1984–2006 cohorts of herring sampled from areas IVa and IVb had mean growth parameter values of  $L_\infty = 31.6$  cm and 29.7 cm,  $k = 0.46$   $y^{-1}$  and  $0.52$   $y^{-1}$ ,  $L_0 = 6.9$  cm and 4.9 cm respectively, and the results of Brunel and Dickey-Collas (2010) — after transformation — were  $L_\infty = 33.1$  cm,  $k = 0.46$   $y^{-1}$  and  $L_0 = 6.6$  cm for herring in the whole of the North Sea. The mean of the growth rate and initial length parameters of IVa herring were a very close match, but IVb herring had smaller initial length and faster growth rate. The most striking difference in the growth parameter estimates is the relatively low values of  $L_\infty$  in the present study, which may be due to large individuals being poorly represented in samples from bottom trawl surveys compared with acoustic surveys. Using these mean parameter values to calculate expected length-at-age, we found that length-at-age in areas IVa and IVb was an average of 95% and

89% lower than the length-at-age predicted for the whole North Sea by the results of Brunel and Dickey-Collas (2010). Clausen et al. (2015) used acoustic survey data to derive von Bertalanffy growth parameter values of  $L_\infty = 29.7$  cm,  $k = 0.38$  y<sup>-1</sup> and  $t_0 = -1.94$  y ( $L_0 = 15.5$  cm) for autumn spawning North Sea herring in 2006–2011, however, since their data was collected from the Skagerrak and Kattegat, the sampled North Sea autumn spawners represented the eastern boundary of the stock.

There were also regional differences in the growth of the west of Scotland herring stock, where declines in length at age were most apparent in the Firth of Clyde. In the western shelf region, the slight decrease to  $L_\infty$  occurring in cohorts from the early 1980s to late 1990s accounted for declines in the mean lengths of age groups 5–8; the partial recovery of the lengths of these age groups in the late 2000s was represented by the slight increase to  $L_\infty$  in cohorts of the early 2000s. The mean lengths of younger fish were more stationary during most of the time series, although the lengths of age groups 2–4 also increased in the 2000s. In the Firth of Clyde, steady declines in mean length at age were observed in age groups 1–8 throughout the entire time series. This was represented by the steady decline in  $L_\infty$ . There were no significant differences in mean lengths at age between the western shelf and Clyde herring considered over the full time series, but mean lengths in age groups 1–4 were smaller in the Clyde during the 2000s.

We found that the 1985–2006 cohorts of western shelf and Clyde herring had mean growth parameter values of  $L_\infty = 29.5$  cm and 27.9 cm,  $k = 0.56$  y<sup>-1</sup> and 0.59 y<sup>-1</sup>,  $L_0 = 5.9$  cm and 3.9 cm respectively, and the results of Brunel and Dickey-Collas (2010) — after transformation — were  $L_\infty = 30.1$  cm,  $k = 0.69$  y<sup>-1</sup> and  $L_0 = 4.0$  cm for herring in the seas to the west and north of Scotland. As in the North Sea, the expected asymptotic lengths of western shelf and Clyde herring over 1993–2006 were smaller than those estimated previously from acoustic survey data. These mean parameter values show that the expected lengths of age groups 1–8 in western shelf and Clyde herring were estimated by the present study to be an average of 94% and 89% of the lengths-at-age predicted for west of Scotland herring by Brunel and Dickey-Collas (2010). Jennings and Beverton (1991) report von Bertalanffy growth parameters for

Clyde herring (estimated from unpublished data cited as “R. S. Bailey, DAFS, Marine Laboratory, Aberdeen pers. comm”) as  $L_\infty = 34.9$  cm,  $k = 0.41$   $y^{-1}$  and  $t_0 = -1.02$  y ( $L_0 = 11.9$  cm). The expected lengths of age groups 1–8, predicted from our growth parameter estimates for cohorts up to 1991, were an average of 87% of the lengths expected from Jennings and Beverton (1991).

There were differences between the trends in the growth of sprat from the northern and southern North Sea. In area IVa, length at age tended to increase over time. Increases to length at age were represented by increases in  $k$ ; the asymptotic length was quite stationary throughout the time series, and  $L_0$  fluctuated but decreased overall. In area IVb, the mean lengths at age of sprat increased during 1975–1992 before declining — mean lengths in age groups 3–5 decreased over the full time series. This was represented in the von Bertalanffy parameters by relatively large  $L_\infty$  values for cohorts spawned between the late 1970s and late 1980s, and a steep decline in  $k$  from 1995 — the increase in  $L_0$  from 1995 reflected the relatively stationary lengths of age group 1.

Compared to herring, the scientific literature for sprat is sparse, and there are few studies reporting on trends in the growth of sprat. Baltic Sea sprat are an exception, as studies on how trends in growth were related to food availability, intra-specific competition, temperature and salinity have been conducted (Cardinale et al., 2002; Möllmann et al., 2004). Existing studies on the growth of North Sea and west of Scotland sprat most often examined the growth of larvae or juveniles (e.g. de Silva, 1973b; Munk, 1993). Estimates of von Bertalanffy growth parameters have, however, been reported as  $L_\infty = 15$  cm,  $k = 0.503$   $y^{-1}$  and  $t_0 = -0.49$  y ( $L_0 = 3.3$  cm) in the North Sea (German EEZ) (Froese and Sampang, 2013). Our results indicate a lower asymptotic length and faster growth rate, as the mean parameter values for IVb sprat were  $L_\infty = 13.7$  cm,  $k = 0.82$   $y^{-1}$  and  $L_0 = 3.12$  cm.

The data for sprat from the west of Scotland were relatively sparse. Trends in length at age were examined from 1983 onwards, and growth parameters could only be estimated for 7 and 9 cohorts from the western shelf and the Firth of Clyde respectively. As observed in herring, there were clear differences in the trends of length at age between the western shelf and Clyde sprat. In the western shelf, the only significant trend in

mean length at age was an increase the length of age group 1. This appears to have been represented in the von Bertalanffy parameters by an increase in the initial length parameter,  $L_0$ , between the early 1990s and early 2000s — although the asymptotic length and growth rate parameters also fluctuate,  $L_\infty$  increases while  $k$  decreases. This was in contrast to the Clyde, where mean lengths at age tended to decrease in all age groups, with significant linear declines over the full time series observed in age groups 3 and 4. The von Bertalanffy parameters represented these trends as a decline in  $L_\infty$ .

The von Bertalanffy growth parameters have been reported as  $L_\infty = 14$  cm and 16.4 cm,  $k = 0.53\text{y}^{-1}$  and  $0.63\text{y}^{-1}$  for two groups of sprat to the west of England (Iles and Johnson, 1962). The mean values of the growth parameters derived in the present study for western shelf and Clyde sprat were similar,  $L_\infty = 15.6$  cm and 16.4 cm and  $k = 0.61\text{y}^{-1}$  and  $0.42\text{y}^{-1}$  respectively.

North Sea mackerel were poorly sampled by the survey until the late 1990s. The mean lengths of age groups 2 and older appear to have decreased during the 2000s. The relatively few estimates of mean length prior to about 1995 are not very informative as they suggest that mean lengths for age groups 2 and 6 used to be greater, while other age groups used to be smaller. These declines in length during the 2000s were represented by a decline in  $L_\infty$  that occurred around the 1995 cohort. The mean length of age group 1 was relatively stationary throughout the time series, and this was reflected in the von Bertalanffy parameters by rise in  $k$  as  $L_\infty$  declined.

The von Bertalanffy growth parameters of mackerel have previously been estimated as  $L_\infty = 39$  cm and  $k = 0.43\text{y}^{-1}$  in the North Sea (Ehrenbaum, 1923); and as  $L_\infty = 33.6$  cm and 42 cm,  $k = 0.837\text{y}^{-1}$  and  $0.238\text{y}^{-1}$  in the central and southern North Sea respectively (Nedelec, 1958). The mean values of our parameter estimates for North Sea mackerel were  $L_\infty = 38.2$  cm and  $k = 0.43\text{y}^{-1}$ , which are nearly identical to the results of Ehrenbaum (1923).

Apart from age group 1, lengths at age tended to decrease in mackerel from the west of Scotland — the declines were linearly significant in age groups 3–6. Lengths at age appeared to be fairly stationary during the 1990s and began to decrease in the early 2000s. This was emulated in the von Bertalanffy growth parameters by a decrease

in  $L_\infty$  and an increase in  $k$  between cohorts spawned in 1990 and 2000.

Previous studies have estimated the von Bertalanffy growth parameters of the western mackerel stock as  $L_\infty = 39.9\text{cm}$  and  $k = 0.36\text{y}^{-1}$  (Jennings et al., 1998);  $L_\infty = 37.4\text{cm}$  and  $k = 0.47\text{y}^{-1}$  in the Celtic Sea (Nedelec, 1958);  $L_\infty = 41.8\text{cm}$  and  $k = 0.43\text{y}^{-1}$  in the English Channel and Irish Sea (Steven, 1952). We found mean growth parameter values of  $L_\infty = 39.4\text{cm}$  and  $k = 0.38\text{y}^{-1}$  for mackerel in area VIa, which were a close match to the results of Jennings et al. (1998).

#### 4.4.2 Trends in maturation schedules

The  $L_{p50}$  values of IVa spring spawning herring did not change significantly over the time series, so maturation propensity given age and length appears to have remained fairly stationary. Variation in the proportions mature within each age group was therefore likely to be largely due to fluctuations in growth and mortality rates. The only significant trend in  $L_{p50}$  for autumn spawning IVa herring was a decrease observed in the age group 2 males during 1989–2009, which is interpreted as an increased probability of maturation for age group 2 males of equivalent length. However, the proportion of these fish that were mature decreased by 13% between 1989 and 1999, then increased by the late 2000s. This may have been due to the dip in mean length in the late 1990s.

Increases in the  $L_{p50}$  values of IVb spring spawning herring were observed in males in age groups 1–2 and females in age group 2, so maturation probability at length decreased over time for these fish. The large decrease in the proportions of these fish that were mature, occurring in 1985–1994, can be explained by these changes in the age- and length-dependent maturation schedules. The decreases in the proportions mature may have been exacerbated by the significant declines in length-at-age that were observed in IVb herring in age groups 1–3. There were no significant trends in the  $L_{p50}$  values of IVb autumn spawning herring. The declines in length-at-age may explain the small decreases in the proportion of IVb autumn spawners that were mature.

Jennings and Beverton (1991) report estimates of  $A_{50}$ , the age at which 50% of the stock is mature, for the Buchan (area IVa) and Banks (area IVb) stocks as  $A_{50} = 4\text{y}$  and  $A_{50} = 3\text{y}$  respectively (see Zijlstra, 1963; Parrish and Saville, 1965, for the original

studies). We found that most autumn spawning herring throughout the North Sea were immature in age group 1 and mature in age group 2. Accounting for the difference between the actual age of autumn spawned herring and the age-group index,  $A_{50}$  may be crudely approximated as 2 years old. There was more variation in the proportions mature within age groups for spring spawners;  $A_{50}$  was approximately 2–3 y in area IVa, and 2–2.5 y in area IVb. Our results for autumn spawned herring were similar to a recent  $A_{50}$  estimate (Vasilakopoulos et al., 2011), showing that  $A_{50}$  has decreased since the 1960s (Zijlstra, 1963; Parrish and Saville, 1965).

Within area VIa, the increase in the  $L_{p50}$  values of age group 3 spring spawning herring indicates that the probability of maturation at length has decreased, so maturation has been occurring at increasingly large lengths. The reduction in the proportion of these fish that were mature, occurring in the 2000s, may be explained by the increase in  $L_{p50}$ . Increases in  $L_{p50}$  were also observed in female autumn spawners in age groups 1–3. This resulted in declines in the proportions of these fish that were mature. There were no significant linear trends in the  $L_{p50}$  values of the male autumn spawners, although the proportions mature followed a similar trend to the females. Nonetheless,  $L_{p50}$  did increase over time in the males, reaching a maximum in the 1994 cohort, which explains the decreases in the proportions mature — this was most evident in age group 2.

Jennings and Beverton (1991) report results of earlier studies that estimated the ages at which 50% of the winter spawning Manx (Irish Sea) and spring spawning Clyde herring stocks were mature to be  $A_{50} = 3$  y and  $A_{50} = 2.5$  y respectively (see Brand, 1979, for the original study). More recently, herring in the south of area VIa have been found to be immature in age group 1 and mature in age group 2 (ICES, 2015). Our results indicated that  $A_{50}$  was approximately 2.5 y in spring and autumn spawners in area VIa during the 2000s, and that most fish had matured by age 3.5 y.

PMRNs could only be estimated for a few cohorts of IVa sprat, and trends in  $L_{p50}$  were not significant. Since so few  $L_{p50}$  estimates were available, it was not really possible to assess whether the increase in the proportion of mature fish in age group 1 during 1995–2012 was due to changes in maturation propensity. It does, however,

appear likely that the increase in the proportion mature in age group 1 was partially due to the increases in length at age.

A greater number of  $L_{p50}$  estimates were available for sprat in area IVb. Although there were no significant linear trends over the time series,  $L_{p50}$  increased to a maximum in both males and females during the early 2000s, causing decreases in the proportions mature within age groups. Then the proportions mature increased as  $L_{p50}$  decreased in the late 2000s.

Acoustic surveys conducted in the summer have shown that the majority of North Sea sprat in age groups 1 and above were mature (ICES, 2013a). An earlier study found that a small proportion of age group 1 North Sea sprat were mature, but that first maturation generally occurred at two years of age (Bailey, 1980). Our results agree with the more recent of these studies (ICES, 2013a), as we found that large proportions of the age group 1 sprat were mature. This suggests that maturation of North Sea sprat now occurs at younger ages than was common in the 1970s.

The proportion of North Sea mackerel that were mature in age group 1 decreased from well over 50% in 1980–1994 to below 20% from 1995 onwards. The  $L_{p50}$  values tended to decrease over time within each age group, representing increasing maturation propensity given age and length. The decreases in the proportions mature in age group 1 were therefore not explained by trends in  $L_{p50}$ . The decrease in the proportion of mature mackerel in age group 2 during the 2000s was also not explained by the negative trends in  $L_{p50}$ , however, the decline in the mean length of this age group may have resulted in fewer fish maturing.

PMRNs could only be estimated for a few cohorts of VIa mackerel during the 2000s, so long term changes in the maturation schedules could not be assessed. From the short time series of  $L_{p50}$  values, it appears as though the probability of maturation at length has decreased in some age groups — particularly in age group 2 males — but the time series are too short to draw any firm conclusions. The proportions mature at age in 2005–2012 were similar to the North Sea mackerel during the same period.

The age at which 50% of the north-east Atlantic (including the regions in the present study) mackerel stock is mature has been estimated as  $A_{50} = 2\text{y}$  (Vasilakopoulos et al.,



2011). The percentage mature in age groups 1–3 have been estimated as 0%, 37% and 100% in the North Sea, and 8%, 60% and 90% in the western stock (ICES, 2005). We found that over 50% of the age group 1 mackerel in the North Sea were mature pre-1995; this decreased to < 20% from 1995 onwards but did not reach 0%. Our results also show that approximately 40% of age group 2 North Sea mackerel were mature during 2005–2012, which was similar to previous estimates (ICES, 2005). However, we found that approximately 40% of age group 2 mackerel from area VIa were mature during 2005–2012; 20% less than previous estimates for the western stock. As expected (ICES, 2005), the majority of age group 3 mackerel in the North Sea and western stocks were found to be mature.

#### 4.4.3 Abundance and temperature variations

Only one of the significant temporal trends in  $L_\infty$  or  $k$  appear to have been caused by trends in abundance or temperature. The growth rate,  $k$ , of IVb herring decreased by  $0.18 \pm 0.16 \text{ y}^{-1}$  due to the average summer temperature increasing from 9.5–10 °C to 11 °C during 1965–2010 — the steepest decrease in  $k$  was concurrent with the steepest rise in temperature in the late 1980s. The remaining significant temporal trends in the growth parameters were all due to some unknown cohort effects, which caused decreases in the  $L_\infty$  values of several groups, and caused  $k$  to increase in IVa herring and VIa mackerel and decrease in IVb sprat. Although variations in abundance and temperature were significantly related to the trends in some of these parameters, the resulting changes were in the opposite direction to the stronger cohort effects, so merely acted to limit the amount that the growth parameters changed throughout the time series. There were four cases where the abundance and temperature variables were significantly related to growth parameters that did not have a temporal trend. Of these, the  $L_\infty$  parameter of IVb sprat tended to decrease in response to increases in abundance, and the remaining three involved interactions between abundance and temperature (fig. 4.11). Thus, variation in abundance and temperature accounted for some short term variation in  $L_\infty$  and  $k$ , but most of the long term temporal trends in the growth parameters appear to have been caused by other factors.

Brunel and Dickey-Collas (2010) found negative correlations between  $W_\infty$  and sea surface temperature in North Sea and west of Scotland herring, as well as positive correlations between  $W_\infty$  and year class strength and between  $k$  and temperature in North Sea herring. Our results differ, as the only significant relationships found in the growth parameters of herring were the negative correlations between  $k$  and temperature in area IVb, between  $k$  and abundance in area IVa, and the interaction consisting of mainly positive and mainly negative correlations between  $L_\infty$  and temperature and  $L_\infty$  and abundance respectively in area IVb.

The body condition (used as a growth index) of Baltic Sea sprat has been shown to be density dependent, such that it decreases with rises in abundance (Cardinale et al., 2002; Casini et al., 2014). Our results also show a degree of density dependence in the growth of sprat, since rises in abundance appeared to cause  $L_\infty$  to decrease in area IVb, and changes in abundance within the Clyde caused temperature-dependent increases and decreases to both  $L_\infty$  and  $k$ .

Several of the significant linear trends in  $L_{p50}$  appear to have been caused by trends in abundance and/or temperature. In area IVb, the  $L_{p50}$  values of age group 1 spring spawning male herring increased by  $3.1 \pm 2.0$  cm during 1986–2008, this was related to an interaction between abundance and temperature, but most of the increase was due to a rise in average summer temperature from  $10^\circ\text{C}$  in the mid 1980s to  $> 11^\circ\text{C}$  during some years in the late 2000s. Increases in abundance when temperatures were relatively high tended to reduce  $L_{p50}$ , and a decline was observed when abundance reached a maximum during the early 1990s. The trends in abundance and temperature accounted for 82% of the total increase in  $L_{p50}$ . The significant linear increase to  $L_{p50}$  in age group 2 spring spawning females from area IVb was not related to temperature or abundance, however, the non-significant increase of  $2.2 \pm 2.5$  cm in age group 1 was related to an interaction between abundance and temperature that was very similar to the males just discussed.

The increases in the  $L_{p50}$  values of age group 3 spring spawning herring in area VIa were not related to abundance or temperature. Neither were the increases observed in autumn spawning females in age groups 1–3, although the rising temperature appeared

to inhibit increases in  $L_{p50}$  for age groups 1–2 which were due to some unknown cohort effect.

Decreases of  $4.8 \pm 2.8$  cm and  $3.9 \pm 3.7$  cm in the  $L_{p50}$  values of male North Sea mackerel in age groups 1–2 appear to be entirely due to the increasing abundance. Rises in temperature may account for 89% of the  $2.7 \pm 2.3$  cm increase to  $L_{p50}$  in age group 2 male mackerel in area VIa, although there were only six  $L_{p50}$  estimates for this group so the relationship with temperature is tenuous.

There were other groups of herring and mackerel whose  $L_{p50}$  estimates did not trend significantly over time, but were nonetheless related to abundance and temperature. Much of the variation in the age and length dependent maturity schedules of these pelagic fish stocks can therefore be explained by fluctuations in abundance and temperature. Trends in these variables appear to have induced significant changes in age and length dependent maturation probabilities, both increases and decreases, in several of the groups considered.

Recent studies have shown that the timing of the spawning season in Norwegian herring (Langård et al., 2014) and North Sea mackerel (Jansen and Gislason, 2011) are strongly related to temperature, but research on the affects of temperature and abundance variations upon the age and/or length dependent maturation schedules of these species, in fact pelagic species in general, seems to be lacking.

#### 4.4.4 Other factors that may explain the trends

Growth and maturation schedules may respond to a variety of environmental changes other than abundance and temperature. Food availability is of particular importance. The amount of food that is available per individual is the main determinant of growth rate (Ward et al., 2009), and  $L_{\infty}$  is directly related to food intake (von Bertalanffy, 1934). Trends in the abundance of food can therefore cause changes to average maximum lengths. It is the availability of food per individual — not the abundance of food — that influences growth, so food abundance and population abundance interact, through intra-specific competition, to affect growth. Changes in length-at-age should not influence PMRN positions (Heino et al., 2002), however, food availability may affect

$L_{p50}$  values by altering the average condition (weight-at-length) of fish populations, as individuals in poor condition are more likely to delay maturation (Grift et al., 2007). We did not consider trends in food availability in this study, but doing so may lead to further insight on some of the unexplained temporal trends in the growth parameters and  $L_{p50}$ .

Species with overlaps in distribution and diet may compete for resources, so inter-specific competition may have influenced the growth of herring, sprat and mackerel. Sprat are planktivorous, feeding on copepods throughout their entire lives (Last, 1987). Herring are omnivorous, they feed exclusively on zoo-plankton until they grow large enough to handle larger prey items, at which point they may also consume small fish such as sprat (Last, 1987). Mackerel has the broadest diet range of the species considered here, feeding on a range of prey sizes from zoo-plankton to small fish, but has a preference for larger prey items (Pepin et al., 1987; Langøy et al., 2006). We might expect there to be significant competition for zoo-plankton between each of these three species, as well as competition for larger prey between herring and mackerel, so fluctuations in the abundance of any one of these species may influence the growth of the others through inter-specific competition. Mackerel tend to be larger than herring, they are also faster swimmers, more efficient plankton eaters, and usually have fuller stomachs (Debes et al., 2012), so are potentially the main competitor with herring within the northern North Sea. Mackerel are less abundant in the southern North Sea, where sprat are highly abundant, so sprat is probably a more significant competitor to herring in this region. It may be useful to consider the total abundance of competitors from multiple species as explanatory variables potentially affecting growth (e.g. Cardinale and Arrhenius, 2000; Casini et al., 2010).

Relaxation of predation pressures due to overfishing may induce changes in the growth of prey species (de Roos and Persson, 2002). Declines in the abundance of predatory demersal species may have reduced the mortality rates of the pelagic species considered here, particularly within the young age/small length classes. This could lead to increased abundance, greater competition, and consequent reductions in growth. Increased abundance of juveniles due to suppressed predation rates may also lead to

declines in condition and delayed maturation (Grift et al., 2007). In addition to reducing mortality rates, declines in predation can induce changes in the foraging behaviour of prey species (Madin et al., 2010), which may also influence growth rates. Predators can only consume prey that is within certain size-ranges (Persson et al., 1996), so fishing- and climate-induced declines in the size of predatory fish (Bianchi et al., 2000; Baudron et al., 2014) may have reduced the size at which prey species become invulnerable to the majority of predators, thus relaxing selective pressures to grow and mature quickly.

Fishing is size-selective, imposing a disproportionately high mortality rate upon large individuals, so fishing activity may have contributed directly to changes in the growth and maturation of the North Sea and west of Scotland herring, sprat and mackerel. Fishing lowers the abundance of harvested stocks, so may reduce competition for resources and potentially increase food-availability and growth rates. Fishing gears harvest large individuals, allowing smaller fish to escape, and therefore impose selective pressures that are opposite to those of predation. This may lead to decreased growth rates and early maturation through evolutionary processes, particularly when minimum landing sizes are close to typical sizes at maturation. Fisheries-induced evolution of growth and maturation is thought to have stronger effects on large species which mature at large sizes, than relatively small species. Since the pelagic fish considered here are small, compared to most demersal fish species in which fisheries-induced evolution is thought to have occurred, fishing is perhaps more likely to affect growth and maturation indirectly through altering the size-structures and abundances of predator populations. We therefore suggest that relating trends in the growth and maturation of North Sea and west of Scotland herring, sprat and mackerel to trends in inter-specific competition, and the abundance and average size of predator species, as a potentially useful extension to this study.

## Chapter 5

# Applying a length-based Bayesian stock assessment model to demersal stocks from the west of Scotland

### 5.1 Introduction

Most stock assessment models applied to commercially exploited stocks are integrated statistical stage-structured models. This means that the models are fitted to multiple sources of data, at least one of the data sources contains information about stock structure, and the data are modelled with likelihood functions. Stage-structured models applied to fish stocks are usually based on the age-structure of the stock (e.g. Deriso et al., 1985; Punt et al., 2001; Methot and Wetzell, 2013). Age-based stock assessments provide within-age-group estimates of abundance, mortality rates, and fishery and/or survey selectivity. The state variable in these models is abundance-at-age (either in terms of biomass or numbers), which is updated with successive time increments to generate time series of stock abundance. Since age increases uniformly with time, updating the state variable is a simple procedure; abundance at each age is reduced by an age-dependent mortality term then input into the next modelled age class, and an

influx of new recruits are added to the youngest age class. Fitting these models requires information about the age-structure of the stock. This could be in the form of fisheries data giving the catch in each age-class, or fisheries-independent survey data which can provide auxiliary information on abundance-at-age or may sometimes be used as the sole source of data (Cook, 2013). Fish may be aged by otolith or scale analysis, both of which are time consuming and costly procedures (Penttila, 1988a,b; Campana, 2001; Ross and Hüseyin, 2013). Due to difficulties ageing fish, age data tend to be collected only for the most commercially valuable stocks, since these contribute more to the economy and attract more scientific research. This means that conventional age-based models are somewhat limited in their applicability, as they can only be used to assess a minority of exploited stocks. Several contemporary age-based models incorporate length-age relationships that enable them to utilise length composition data (e.g. Methot and Wetzel, 2013), although there are difficulties associated with this (Punt et al., 2013).

Surplus production models and length-based models are assessment methods that do not rely upon considering age structure. Surplus production models track total stock biomass as the state variable, and update this by estimating mortalities and recruitment from catch data (Haddon, 2011). These models do not account for internal structuring of the population by age or size, and consider individuals within the stock as homogeneous. Modelling the life-stage of individuals within a stock provides greater realism and more information than simply considering the total abundance and overall mortality rate. It is therefore desirable to model population abundance in a structured form when assessing fish stocks (Kuparinen et al., 2012). Length-based stock assessments, that use abundance-at-length as the state variable, are an alternative to age-based models and offer the same benefits of greater precision in parameter estimates and more detailed information on how fishing affects stocks (see Sullivan et al., 1990, for the first integrated length-structured assessment model). Structuring by length instead of age increases model complexity as it becomes necessary to explicitly account for growth. This is due to variation in the growth of similarly aged fish, and growth slowing with age. Despite recent stock assessment studies using relatively simple length-based models, focussing on length-based sustainable harvest indices, or

estimating length-at-age within the model (e.g. O’Farrell and Botsford, 2005; Pope et al., 2006; Froese et al., 2008; Klaer et al., 2012; Mäntyniemi et al., 2013), integrated statistical length-structured models applied to fish stocks remain uncommon (the general model of Mäntyniemi et al., 2015, is an exception that can be tailored to be length structured).

The length-based model developed here is based on the model of Sullivan et al. (1990), but modifies it in several ways. The model of Sullivan et al. (1990) is fitted to fishery catch-at-length data and allows use of auxiliary information such as effort or survey data. Our length-based model is fitted to fishery data on the total biomass landed and discarded annually, as well as length measurements from bottom trawl survey samples. The data informing our model about the length-structure of the stock are provided by survey samples which, unlike fishery catch-at-length data, are widely available for many species in many different regions. Data on the annual total landings and estimates of discards are also widely available for many stocks. Thus, our model provides a useful extension of Sullivan et al. (1990) because it does not rely upon length-data from commercial fisheries, instead it is fitted to data that are regularly collected for a wide range of species. A further modification allows our model to account for temporal trends in the average growth rate of fish. As widespread declines in the size of marine fish have been reported (e.g. Bianchi et al., 2000; Shackell et al., 2010), allowing growth to vary over time should increase model realism and help to prevent biased estimates of stock biomass (Lorenzen, 2016). Time-varying growth was incorporated into our model by estimating growth parameters uniquely each year. The number of extra parameters required was limited by estimating the growth parameters using cubic splines with few node points, resulting in smoothly varying growth rates. We chose a spline representation for the growth parameters because it was a simple means of parameterising time-varying growth, but other methods such as random walks could be implemented instead (similarly to Wilberg and Bence, 2006, who used random walks to model time-varying catchability). The third major modification from the original Sullivan et al. (1990) model involved fitting our model using Bayesian methods. This allowed the uncertainty associated to each parameter and modelled quantity to be sim-



ply assessed via credible intervals, and also permitted greater flexibility in constraining the model through the prior distributions of each parameter.

The model has been tested by applying it to the west of Scotland (ICES area VIa) cod, haddock, and whiting stocks (fig. 5.1). The results of age-based time series analyses stock assessments are available for these three stocks (ICES, 2013b). The ICES (2013b) models were fitted to data on the landings and discards within each age group, and used survey age samples as auxiliary data. We fitted our model to the same catch data, but summed over age groups to acquire the total landings and discards; information on the stage-structure was given by the survey length-frequency distributions. By fitting to the same catch data, and making the same assumptions about natural mortality, the ICES (2013b) age-based model should provide a good reference point from which to gauge the effectiveness of our length-based model. If the estimates of trends in total abundance, recruitment, and mortality rates are in reasonable agreement with the existing age-based model, then this would indicate that our length-based model could be successfully applied to these west of Scotland stocks, and would suggest that the model may be more widely applicable.

We have also applied the model to the Firth of Clyde haddock and whiting stocks (fig. 5.1). Stock assessment results are not presently available for these Clyde stocks, so there is no alternative model with which to compare our results. The comparisons between the age- and length-based model results for the VIa stocks are therefore important for gauging the viability of the length-based results for the Clyde stocks. If there is good agreement between the age- and length-based models in area VIa then this will increase confidence in the results obtained for the Clyde stocks.

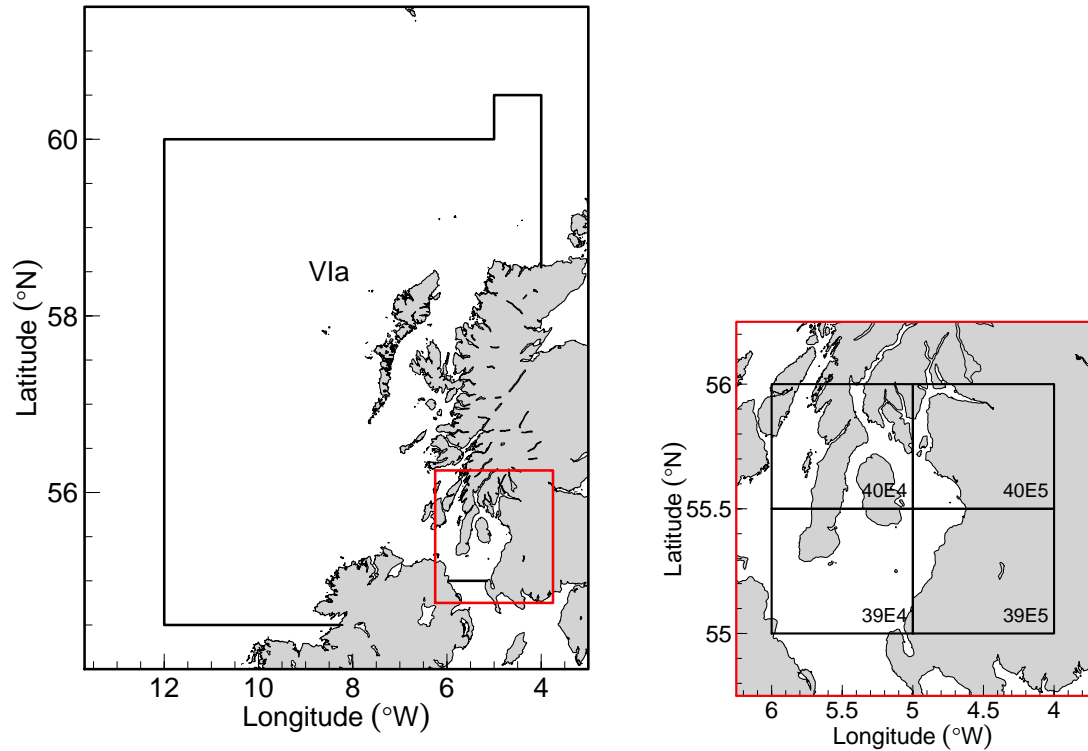


Figure 5.1: ICES area VIa to the west of Scotland, and the four statistical rectangles that encompass the Firth of Clyde.

## 5.2 Materials and methods

### 5.2.1 Data

The length-based model was fitted to bottom trawl survey data of length measurements (ICES, 2015) and data specifying the total biomass landed and discarded annually. The landed and discarded biomasses of cod, haddock, and whiting within ICES area VIa were provided in ICES (2013b). The survey samples were length frequency distributions specifying the number of fish within 1 cm length classes, where lengths had been rounded down to the nearest cm. Survey length data collected during quarter 1 were available for 1980–2014. Length data were also available for some earlier years (going back as far the 1960s), but were collected during quarters 3 or 4. The model was fitted to survey length data from quarter 1 only, because it provided larger sample sizes and

data from this quarter were collected consistently each year. The model was not fitted to length distribution data from multiple quarters of the year as growth would need to be modelled to vary seasonally, and recruitment would need to be chosen to occur during a specific quarter or possibly over multiple quarters; but this could be attempted in future work. The landings and discards data for area VIa spanned the years 1965–2012. The model was fitted to data from 1980 to 2012; years of catch data prior to 1980 were excluded because the model lacked the auxiliary survey data which provides a relative abundance index.

The landings and discards data, and age-based stock assessment results for ICES area VIa cod, haddock and whiting are presented in ICES (2013b). We have fitted the length-based model to the same catch data and have made the same assumptions about natural mortalities and length/weight relationships, so that our results may be comparable to the existing age-based model.

The survey data pertaining to the Firth of Clyde (ICES, 2015) was specified as data collected from within the statistical rectangles 39E4, 39E5, 40E4 and 40E5 (fig. 5.1). The biomass landed annually from the Clyde was also specified by these statistical rectangles, from landings data sourced from Marine Scotland. These landings data were available from 1985 to 2008. Data on the biomass of haddock and whiting that were discarded from the Clyde were not available. The discarded biomasses were instead approximated from information about the discarding practises of vessels equipped with *Nephrops* trawling gear (Stratoudakis et al., 2001); this information was founded upon observations from 106 fishing trips included in the Scottish discard sampling programme. Stratoudakis et al. (2001) provides the total landings and discards of fish,  $L_y^F$  and  $D_y^F$ , and *Nephrops*,  $L_y^N$  and  $D_y^N$ , from *Nephrops* vessels for the years  $y = 1982, \dots, 1998$ . The discarding rates,  $d_i^r$  ( $\text{kg h}^{-1}$ ), for 19 commonly caught fish species (where  $i$  indexes species) were also given. The proportion of fish discards that consisted of species  $i$  was calculated as  $d_i^p = \frac{d_i^r}{\sum_i d_i^r}$ . Then the discarded biomass of species  $i$  was estimated as  $D_y^i = d_i^p D_y^F$  for  $y = 1982, \dots, 1998$ . The discarded biomass in later years was estimated using landings data for *Nephrops*. Let  $p$  be the median of  $\frac{D_y^F}{L_y^N}$  ( $y = 1982, \dots, 1998$ ), then the total fish discards were estimated as  $D_y^F = p L_y^N$

( $y = 1999, \dots$ ), and species-specific discards as  $D_y^i = d_i^p D_y^F$ .

### 5.2.2 Model specification

The model process is a matrix recurrence relation that is composed of growth, survivorship, and recruitment components. The following section describes the derivation of each of these components, then the process equation is constructed. Parameters that are to be estimated directly by the model are denoted with hats ( $\hat{\cdot}$ ), as are model predicted values for the data.

#### Growth

Mean growth trajectories were assumed to follow a von Bertalanffy growth curve

$$\bar{l}(a) = \hat{L}_\infty \left( 1 - \exp \left( -\hat{k} (a - t_0) \right) \right) \quad (5.1)$$

where  $\bar{l}(a)$  is the expected length of an  $a$  year old individual,  $\hat{L}_\infty$  is the asymptotic length,  $\hat{k}$  is the von Bertalanffy growth rate, and  $t_0$  is the theoretical age at  $l = 0$ . Mean growth increments,  $\bar{\Delta l}$ , from arbitrary initial lengths,  $l$ , over a period,  $dt$ , can be written solely in terms of  $\hat{L}_\infty$  and  $\hat{k}$ .

$$\begin{aligned} \bar{\Delta l} &= l(a + dt) - l(a) \\ \implies \bar{\Delta l} &= \left( \hat{L}_\infty - l \right) \left( 1 - \exp \left( -\hat{k} dt \right) \right) \end{aligned} \quad (5.2)$$

Variation in growth is incorporated into the model by representing growth increments with log-normal distributions that are specified uniquely for each initial length. The probability density function for growth increments,  $\Delta l$ , from an initial length of  $l$  is

$$p(x = \Delta l \mid \mu_l, \sigma_l) = \frac{1}{x \sigma_l \sqrt{2\pi}} \exp \left( \frac{-(\ln(x) - \mu_l)^2}{2\sigma_l^2} \right) \quad (5.3)$$

where  $\mu_l$  and  $\sigma_l$  are the growth increment mean and standard deviation of the associated normal distribution. The standard deviation of growth increments,  $\Sigma_l$ , is calculated uniquely for each initial length as the product of  $\bar{\Delta l}$  and the coefficient of variation for

growth increments,  $\hat{c}\hat{v}^g$ , which is estimated by the model. The parameters for eq. (5.3) are then found as

$$\begin{aligned}\mu_l &= 2 \ln(\bar{\Delta}l) - \frac{1}{2} \ln(\Sigma_l^2 + \bar{\Delta}l^2) \\ \sigma_l &= \left( \ln(\Sigma_l^2 + \bar{\Delta}l^2) - 2 \ln(\bar{\Delta}l) \right)^{\frac{1}{2}}.\end{aligned}\quad (5.4)$$

Thus, growth is fully described by eq. (5.3) and three parameters,  $\hat{L}_\infty$ ,  $\hat{k}$  and  $\hat{c}\hat{v}^g$ .

Specifying growth in terms of log-normal distributions that are constrained by a von Bertalanffy curve has some immediate practical benefits because the modelled growth accurately represents properties of actual fish growth. Small fish increase in length more quickly than larger individuals, so mean growth increments should decrease as initial lengths increase. Variation in growth increments is also likely to decrease as fish grow towards the asymptotic length,  $L_\infty$ . Equation (5.2) ensures that mean growth follows a von Bertalanffy curve so that  $\bar{\Delta}l$  decreases as initial length increases, and variation in growth also decreases with increasing initial length since the standard deviation of growth increments is calculated as  $\Sigma_l = \hat{c}\hat{v}^g \bar{\Delta}l$ .

The probability of an individual growing from an initial length of  $l$  to a final length of  $l' \geq l$  is found by integrating eq. (5.3). This integration is performed for each combination of  $l$  and  $l' \geq l$ , to derive a lower triangular growth increment probability matrix,  $P_{l',l}$ .

$$P_{l',l} = \int_l^{l'+1} \frac{1}{x \sigma_l \sqrt{2\pi}} \exp\left(-\frac{(\ln(x) - \mu_l)^2}{2\sigma_l^2}\right) dx \quad (5.5)$$

Each column of  $P_{l',l}$  represents an initial length  $l$ , and shows the proportions of  $l$  cm long fish that grow to  $l' \geq l$  during time  $dt$ .

### Time varying growth

The growth of fish populations may change over time, indeed, it has been shown that changes in growth have occurred within the populations to which we have applied this model. Temporal trends in growth cannot be modelled when the von Bertalanffy growth parameters are assumed to be constant over time. Failing to account for the po-

tential of growth to change over time could result in poor estimates of abundance. For example, if growth rate were to trend monotonically over time then the model would estimate growth parameters such that predicted length-at-age would approximate actual length-at-age near the midpoint of the time series, and abundance may be poorly estimated near the start and end of the time series when growth was misspecified. Even if stock biomass estimates were accurate then fish numbers could be overestimated (underestimated) when model-predicted length-at-age was too low (high).

Time-varying growth has been incorporated into the model to attempt to overcome these potential problems. The  $\hat{L}_\infty$  and  $\hat{k}$  parameters were both modelled with cubic splines so that they could change smoothly over time. The splines were defined by three knot points, each of which was specified by the magnitude of the growth parameter and the year. The years chosen for the knot points were the first, last and middle years in the time series, and the growth parameter values at the knot points were estimated by the model. If  $\eta$  is the chosen number of knot points in the splines, then modelling time varying growth in this way requires an extra  $2(\eta - 1)$  parameters to be estimated — if only one of the growth parameters were modelled by a spline then there would be  $\eta - 1$  extra parameters to estimate. Since  $\hat{L}_\infty$  and  $\hat{k}$  take different values each year, the growth increment probability matrix needs to be calculated for each year, and becomes  $P_{l',l,y}$  with the addition of another dimension. This greatly reduces the speed of the model because calculating  $P_{l',l}$  is the most computationally expensive part of the process.

### **Mortality**

Mortality rate at length  $l$ , in year  $y$ , is denoted by  $Z_{l,y}$  and split into two components,  $Z_{l,y} = M_{l,y} + F_{l,y}$ , where  $M_{l,y}$  and  $F_{l,y}$  are the natural and fishing mortality rates respectively. It is assumed that  $F_{l,y}$  is separable, consisting of a length component,  $s_l^f$ , the selectivity of the fishery, and a year component,  $\hat{F}_y$ , the fishing mortality rate experienced by fish that are fully selected by the fishery. The selectivity term accounts for the fact that small fish are less likely to become trapped in nets than larger individuals,

and is parameterised as a logistic curve.

$$s_l^f = \frac{1}{1 + \exp\left(\frac{-\ln(9)(l - \hat{l}_{50}^f)}{\hat{\beta}^f}\right)} \quad (5.6)$$

The  $\hat{l}_{50}^f$  parameter represents the length at which 50% of fish entering the net are too large to escape, and the  $\hat{\beta}^f$  parameter is the 50% selection range ( $\hat{\beta}^f = l_{75}^f - l_{25}^f$ ) which describes how quickly the probability of escape changes with length. The catchability of the fishery is not explicitly represented within the model, so  $\hat{l}_{50}^f$  and  $\hat{\beta}^f$  will also vary in accordance with how available fish are to the fishery.

As natural mortality rate and fishing mortality rate are confounding variables, natural mortality rate is specified a priori. It may be set as a scalar,  $M_{l,y} = M$ , or given some functional dependence on length,  $M_{l,y} = M_l$ , such as the Lorenzen natural mortality curve (Lorenzen, 1996). We chose to set the natural mortality rate of haddock as a scalar,  $M = 0.2$ , and the natural mortality rate of whiting followed the Lorenzen mortality curve for natural ecosystems,  $M_l = 3W_l^{-0.288}$ , where  $W_l$  is weight at length  $l$  (weight at length was specified according to the allometric relationships given in Coull et al. (1989)). These natural mortality rates were chosen to match the values used in the ICES age-based model (ICES, 2013b) so that our results would be comparable to an existing assessment of these stocks.

### Recruitment

A matrix,  $R_{l,y}$ , stores the number of fish, within each length class, that recruit to the stock each year. This matrix was separated into length and year components,  $R_{l,y} = p_l \hat{R}_y$ , where  $p_l$  is the length distribution of recruits and  $\hat{R}_y$  are the total number of recruits in years  $y = 2, \dots, y_{\max}$ , where  $y_{\max}$  is the number of modelled years. A log-normal distribution was used to represent  $p_l$ , so the length distribution of recruits was described by two parameters, the mean length of recruits,  $\hat{l}^r$ , and the standard deviation of recruitment length on the associated normal distribution,  $\hat{\sigma}^r$ . Splitting the recruitment matrix in this way reduces the number of parameters within the model, but

means that the length distribution of recruits is constant over time. The mean length of recruits,  $\hat{l}^r$ , could be represented with splines, similarly to the von Bertalanffy growth parameters, in order to more fully represent time-varying growth. However, as the mean lengths of young fish vary less over time, we decided to keep  $\hat{l}^r$  constant in order to limit the number of model-estimated parameters.

### The process equation

The stock is described by a matrix of numbers-at-length,  $N_{l,y}$ . Given some initial population,  $N_{l,1}$ , numbers-at-length in future years is calculated as

$$N_{l',y+1} = P_{l',l,y} S_{l,y} P_{l,l,y} N_{l,y} + R_{l',y+1}, \quad y = 1, 2, \dots, y_{\max} - 1 \quad (5.7)$$

$$l = l_{\min}, \dots, l_{\max}$$

where  $S_{l,y} = \exp(-Z_{l,y})$  is the survivorship matrix;  $P_{l',l,y}$  is the growth increment probability matrix for  $dt = 0.5$  (eq. (5.5));  $y_{\max}$  is the number of modelled years; and the minimum and maximum modelled lengths are  $l_{\min}$  and  $l_{\max}$ . The  $N_{l,y}$  matrix is updated annually in four stages; a growing period over the first half of the year, reduction in numbers through mortality, growth for the remaining half of the year, and the addition of new recruits. Mortality rates are length-dependent, so small individuals become more vulnerable to the fishery as they grow throughout the year. The survivorship term was applied in the middle of each year to reduce numbers when individuals were at intermediate lengths, reducing potential bias in estimates of mortality rates and the length structure of predicted catches.

The initial population,  $N_{l,1}$ , was generated by estimating recruited numbers,  $\hat{R}_i^{\text{hist}}$  ( $i = 1, \dots, n^{\text{hist}}$ ), for the  $n^{\text{hist}}$  years up to and including the initial year,  $y = 2 - n^{\text{hist}}, \dots, 1$ . A vector,  $N_l^{\text{hist}}$ , was set equal to  $\hat{R}_1^{\text{hist}}$  and then updated  $n^{\text{hist}} - 1$  times using eq. (5.7) with  $\hat{R}_{2, \dots, n^{\text{hist}}}^{\text{hist}}$  and the growth and survivorship matrices for the initial year,  $P_{l',l,1}$  and  $S_{l,1}$ . The value of  $N_l^{\text{hist}}$  that resulted from the  $(n^{\text{hist}} - 1)^{\text{th}}$  iteration was taken as the initial population,  $N_{l,1}$ . We set  $n^{\text{hist}} = 4$ , as this value was large enough to generate initial populations whose length distributions resembled the survey data



in terms of number of visually distinct peaks. Recruited numbers equal  $\hat{R}_{n^{\text{hist}}}^{\text{hist}}$  in the initial year, so  $\hat{R}_y$  was estimated for  $y = 2, \dots, y_{\text{max}}$ .

### The observation equations

The model is fitted to data on the total biomass landed,  $L_y^B$ , and discarded,  $D_y^B$ , annually, and length frequency distributions from survey samples,  $N_{l,y}^v$ . Numbers-at-length in the catch,  $C_{l,y}$ , are estimated using the Baranov catch equation (Baranov, 1918) written in terms of length.

$$C_{l,y} = \frac{F_{l,y}}{Z_{l,y}} (1 - S_{l,y}) P_{l,y} N_{l,y} \quad (5.8)$$

The Baranov catch equation is used to describe the catch in most stock assessment models. It predicts the catch by calculating the proportion of deaths that were due to fishing, and multiplying this into the predicted number of deaths. The growth increment matrix was included in eq. (5.8) so that the catch was taken in the middle of each year, after fish had grown for six months. The catch consists of landings,  $L_{l,y}$ , and discards,  $D_{l,y}$ . The discards were considered as the sum of two components, length-dependent discards,  $D_{l,y}^{\text{len}}$ , and length-independent bulk discards,  $D_y^{\text{bulk}}$  (Heath and Cook, 2015). The biomass within the bulk discards was calculated as

$$D_y^{\text{bulk}} = \hat{p}_y^{\text{bulk}} \sum_l W_l C_{l,y} \quad (5.9)$$

where the model estimates  $\hat{p}_y^{\text{bulk}}$  to represent the proportion of the catch that is discarded independently of length, and  $W_l$  is the weight at length  $l$ . Allometric weight-at-length relationships were used to calculate  $W_l$  (Coull et al., 1989). The numbers present in the landings and length-dependent discards were calculated as

$$L_{l,y} = s_l^d (1 - \hat{p}_y^{\text{bulk}}) C_{l,y} \quad (5.10)$$

$$D_{l,y}^{\text{len}} = (1 - s_l^d) (1 - \hat{p}_y^{\text{bulk}}) C_{l,y} \quad (5.11)$$

where  $s_l^d$ , the retention fraction, specifies the proportion of the catch in length class  $l$  that is not discarded due to being undersized. The retention fraction was parameterised as a logistic curve

$$s_l^d = \frac{1}{1 + \exp\left(\frac{-\ln(9)(l - \hat{l}_{50}^d)}{\beta^d}\right)} \quad (5.12)$$

where  $\hat{l}_{50}^d$  is the length at which 50% of the catch is retained, and  $\beta^d$  is the 50% retention range ( $\beta^d = l_{75}^d - l_{25}^d$ ) which controls the rate of change of  $s_l^d$  with length. The data does not contain information on the length distribution of the catch so the model cannot sensibly estimate the retention fraction parameters without constraints. This is why the model does not estimate the retention range,  $\beta^d$ ; instead it is the retention fraction at  $l^d \ll$  minimum landing size,  $\hat{p}^d = s_l^d (l = l^d)$ , that is estimated and constrained to be small. The retention range can be recovered as  $\beta^d = \frac{\ln(9) (\hat{l}_{50}^d - l^d)}{\ln(1 - \hat{p}^d) - \ln(\hat{p}^d)}$ . The model-predicted total landed and discarded biomasses were calculated as

$$\hat{L}_y^B = \sum_l W_l L_{l,y}, \quad \hat{D}_y^B = D_y^{\text{bulk}} + \sum_l W_l D_{l,y}^{\text{len}}. \quad (5.13)$$

The numbers sampled by the survey were calculated as

$$\hat{N}_{l,y}^v = \hat{q} s_l^v A_y^p \exp(-\rho Z_{l,y}) N_{l,y} \quad (5.14)$$

where  $\hat{N}_{l,y}^v$  is the predicted numbers at length in the survey samples;  $s_l^v$  is the selectivity of the survey trawling gear;  $A_y^p$  is the proportion of the total area of the assessed region that was swept out by the survey in year  $y$ ;  $\hat{q}$  is the catchability; and  $\rho$  is the proportion of the year between January 1<sup>st</sup> and the average survey date. As swimming speed and stamina influence which fish are caught by survey trawls, and speed and stamina tend to increase with size, large fish may exhibit reduced catchability by more easily swimming ahead of trawling nets than smaller individuals (Winger et al., 1999, 2001; Fraser et al., 2007). This may explain why large fish often appear to be under-represented in the survey samples. The survey selectivity is parameterised as a gamma-type distribution

that can produce curves with a positive gradient at small lengths and a negative gradient at large lengths. This allows it to represent reduced catchability of larger individuals.

$$s_l^v = \left(\frac{l}{\hat{l}^v}\right)^{\frac{\hat{l}^v}{\beta^v}} \exp\left(\frac{\hat{l}^v - l}{\beta^v}\right) \quad (5.15)$$

The  $\hat{l}^v$  parameter is the mode, that is the length at which survey selectivity is at a maximum, and  $\beta^v$  controls the shape of the selectivity curve. In order to impose constraints on the survey selectivity that ensured realistic curves, the selectivity at  $l = l_{\min}$ ,  $\hat{p}^v = s_l^v(l = l_{\min})$  was estimated by the model and constrained to be small.

The  $\beta^v$  parameter was recovered as  $\beta^v = \frac{\hat{l}^v \left( \ln(l_{\min}) - \ln(\hat{l}^v) + 1 \right) - l_{\min}}{\ln(\hat{p}^v)}$ .

The area swept out by each individual survey tow was calculated as the product of the distance towed and the width of the net opening. The width of the net opening depends on whether the extra width of the wings is included. The wings attached to each side of the survey nets stir up sediment that steers some fish towards the centre of the gear. Following Fraser et al. (2007), the width of the net opening included the extra width of the wings when the model was fitted to haddock and whiting, but excluded the extra width of the wings when the model was fitted to cod. The total area swept out by the survey,  $A_y$ , was the sum of the areas swept out by each tow in year  $y$ . The proportion of the fishery area that was swept by the survey,  $A_y^p$ , equals  $A_y$  divided by the total area of the fishery. As the reliability of these area calculations is uncertain, particularly since fish may swim into or escape the survey tow path, part of the function of the catchability,  $\hat{q}$ , is to scale swept area and help reduce potential bias in  $A_y^p$ .

The numbers sampled by the survey,  $\hat{N}_{l,y}^v$ , is a function of the numbers in the population,  $N_{l,y}$ , and since the surveys do not take place at the beginning of the year, a mortality term,  $\exp(-\rho Z_{l,y})$ , was applied to  $N_{l,y}$  to reduce population numbers before calculating  $\hat{N}_{l,y}^v$ . The seasonality of growth rates prevents accounting for growth during time  $\rho$  in the same fashion, so this was neglected. This was reasonable given that the survey samples were collected in quarter one, and growth is minimal during winter.

### 5.2.3 Bayesian model fitting

We estimated the model parameters,  $\theta$ , using Bayesian methods. This enabled simple calculation of credible intervals for each parameter and each derived model quantity, and also allowed us to constrain the parameters through their prior distributions. The underlying assumption in Bayesian analyses is that  $\theta$  are not fixed, but are random quantities described by probability distributions. The best fitting parameters depend upon the data,  $Y$ , and are described by the posterior probability distribution,  $\pi(\theta | Y)$ . Baye's theorem (Bayes and Price, 1763; Lee, 2012) shows that  $\pi(\theta | Y)$  is proportional to the product of the likelihood of the data given the parameters,  $L(Y | \theta)$ , and the prior probability for each of the  $j$  parameters,  $p_j(\theta_j)$ . This allows calculation or approximation of the posterior distribution. Once the posterior distribution is found, parameters are sampled from it and input into the model to generate results. The prior probability distributions,  $p_j(\theta_j)$ , represent the expectations of the modeller prior to fitting the model, i.e., the parameter medians and ranges that the modeller believes to be likely or feasible. The prior distributions that were used are shown in table 5.1.

The posterior distribution is derived by updating the prior distributions using the data and a maximum likelihood approach. The data need to be assumed to follow some distributional forms in order for likelihood functions to be constructed. The biomass landed,  $L_y^B$ , and discarded,  $D_y^B$ , and the total numbers sampled by the survey,  $N_y^{\text{tot}} = \sum_l N_{l,y}$ , were assumed to be log-normally distributed

$$L_y^B = \hat{L}_y^B \exp(\varepsilon_y^L), \quad \varepsilon_y^L \sim \mathcal{N}\left(0, \left(\hat{c}v^L \hat{L}_y^B\right)^2\right) \quad (5.16)$$

$$D_y^B = \hat{D}_y^B \exp(\varepsilon_y^D), \quad \varepsilon_y^D \sim \mathcal{N}\left(0, \left(\hat{c}v^D \hat{D}_y^B\right)^2\right) \quad (5.17)$$

$$N_y^{\text{tot}} = \hat{N}_y^{\text{tot}} \exp(\varepsilon_y^N), \quad \varepsilon_y^N \sim \mathcal{N}\left(0, \left(\hat{c}v^N \hat{N}_y^{\text{tot}}\right)^2\right) \quad (5.18)$$

and were parameterised in terms of coefficients of variation,  $\hat{c}v^L$ ,  $\hat{c}v^D$  and  $\hat{c}v^N$  that were estimated within the model. Normalised length distributions from the survey,  $N_{l,y}^{\text{dist}} = \frac{N_{l,y}}{N_y^{\text{tot}}}$ , were modelled using a robust multinomial distribution so that the log-

## 5.2. Materials and methods

Table 5.1: The prior distributions used for the parameters estimated in the Bayesian stock assessment model.

Parameter	Distribution	Basis
$l_{50}^f$	Normal(35, 5) Cod	Symmetric distribution centred at minimum landing size. Large enough variance to allow wide range of values. <sup>a</sup>
	Normal(30, 5) Haddock	
	Normal(27, 5) Whiting	
$\beta^f$	Lognormal(1.263, 0.833)	Mean and standard deviation of prior distribution both equal 5. Expect fairly small value for selection range, but long tail allows large values. <sup>b</sup>
$l_{50}^d$	Normal(35, 1) Cod	Strongly informative prior to ensure length at 50% retention remains close to minimum landing size. <sup>a</sup>
	Normal(30, 1) Haddock	
	Normal(27, 1) Whiting	
$p^d$	Beta*(0.5, 3   0, 0.01)	The retention fraction, $p^d = s_l^d(l = l^d)$ , at small length, $l^d$ , was assumed to be low and constrained to less than 1%. Cod, $l^d = 25$ cm; haddock, $l^d = 20$ cm; whiting, $l^d = 20$ cm. <sup>c</sup>
$p_y^{\text{bulk}}$	Beta(0.5, 3)	The proportion of the catch that was discarded independently of size was expected to be low, but the prior, which was used in Heath and Cook (2015), permits large values.
$L_\infty$	Normal(140, 10) Cod	Based on estimates given in Hunter et al. (2016), the 5%–95% range of the priors include most values reported therein. Used for each separate node of the spline for $L_\infty$ . <sup>a</sup>
	Normal(45, 6) Haddock	
	Normal(40, 5) Whiting	
$k$	Lognormal(−1.540, 0.555) Cod	Chosen similarly to priors for $L_\infty$ . Mean and standard deviation of distribution equal 0.25 and 0.15 for cod, and equal 0.5 and 0.1 for haddock and whiting. <sup>b</sup>
	Lognormal(−0.713, 0.198) Haddock	
	Lognormal(−0.713, 0.198) Whiting	
$cv^g$	Beta*(5, 15   0, 0.4)	Informative prior ensures a fairly small coefficient of variation of growth increments that was constrained to be less than 0.4. <sup>c</sup>
$l^r$	Normal(19, 1.5) Cod	Informative prior for mean length of recruits, based on inspection of the observed survey length distributions. <sup>a</sup>
	Normal(16.9, 1.5) Haddock	
	Normal(15.6, 1.5) Whiting	
$\sigma^r$	Lognormal(−1.721, 0.472)	Mean and standard deviation of distribution equal 0.2 and 0.1 respectively. Allows a reasonable range of length distributions for recruits when combined with the restrictive prior for $l^r$ . <sup>b</sup>
$l^v$	Normal(45, 10) Cod	Symmetric distribution centred at arbitrary, but reasonable means, with large standard deviations to allow a wide range of values. <sup>a</sup>
	Normal(30, 8) Haddock	
	Normal(30, 8) Whiting	
$p^v$	Beta*(0.5, 3   0, 0.01)	Selectivity of the survey, $p^v = s_l^v(l = l_{\min})$ , at length $l_{\min}$ was assumed to be small, and constrained to be less than 1%. <sup>c</sup>
$q$	Beta*(18, 9   0, 1.5)	Informative prior for survey catchability has a mean of 1, and is constrained to be less than 1.5. Positive skew gives long left tail to represent expectation that $q$ is not greater than 1. <sup>c</sup>
$F_{y=1}$	Lognormal(−0.847, 0.555)	Mean and standard deviation equal 0.5 and 0.3 respectively. Permits a wide range of values for maximum fishing mortality rate in the initial year. <sup>b</sup>
$F_y$	Normal( $F_{y-1}$ , 0.1)	Maximum fishing mortality rate in years $y = 2, \dots, y_{\max}$ was centred at value of previous year, with a low s.d. to constrain fishing mortality rate to gradual inter-annual fluctuations. <sup>a</sup>
$R_y$	Lognormal( $\ln(\mu^R) - \frac{1}{2}(\sigma^R)^2, \sigma^R$ )	$\mu^R$ and $\sigma^R$ are model-estimated hyper-parameters. $\mu^R$ is the mean number of recruits. The hyper-prior for $\sigma^R$ has a mean and standard deviation that both equal 0.25. <sup>b,d</sup>
	$\mu^R \sim \text{Lognormal}(R^{\text{mean}}, R^{\text{sd}})$	
	$\sigma^R \sim \text{Lognormal}(-1.733, 0.833)$	
$cv^L$	Half-Normal(0, 0.5)	The coefficients of variation associated to the landings, discards and surveyed numbers were assumed to be small. The half-normal prior still permits fairly large values. <sup>a</sup>
$cv^D$		
$cv^N$		

<sup>a</sup> Parameterisations of normal and half-normal distributions were in terms of the mean and standard deviation.

<sup>b</sup> Log-normal distributions were parameterised in terms of the mean and s.d. of the underlying normal distribution.

<sup>c</sup> The Beta\*( $a, b | x^-, x^+$ ) distribution transforms the support of the Beta( $a, b$ ) distribution from (0, 1) to ( $x^-, x^+$ ).

Beta\*( $a, b | x^-, x^+$ ) =  $\frac{(x-x^-)^{a-1}(x^+-x)^{b-1}}{B(a,b)(x^+-x^-)^{a+b-1}}$  where  $B(a, b)$  is the beta function.

<sup>d</sup> VIa cod, ( $R^{\text{mean}}, R^{\text{sd}}$ ) = (15.937, 0.810); VIa haddock, ( $R^{\text{mean}}, R^{\text{sd}}$ ) = (18.240, 0.832); VIa whiting, ( $R^{\text{mean}}, R^{\text{sd}}$ ) = (18.679, 0.621); Clyde haddock, ( $R^{\text{mean}}, R^{\text{sd}}$ ) = (15.219, 0.849); Clyde whiting, ( $R^{\text{mean}}, R^{\text{sd}}$ ) = (17.311, 0.606).

likelihood of  $N_{l,y}^{\text{dist}}$  was given by

$$\mathcal{L}(N_{l,y}^{\text{dist}} | \boldsymbol{\theta}) = \ln \left( \exp \left( \frac{-w \left( N_{l,y}^{\text{dist}} - \hat{N}_{l,y}^{\text{dist}} \right)^2}{2 E_{l,y}} \right) + 0.01 \right) - \frac{1}{2} \ln (E_{l,y})$$

$$\text{where } E_{l,y} = \left( 1 - \hat{N}_{l,y}^{\text{dist}} \right) \hat{N}_{l,y}^{\text{dist}} + \frac{0.1}{n} \quad (5.19)$$

where  $n$  is the number of modelled length classes and  $w$  is the effective sample size used to weight the survey length data (Francis, 2011). As correlations within length or age distribution data are known to reduce effective sample sizes (Francis, 2011), we assumed that  $w$  was a small fraction of the actual annual average sample sizes ( $w = \frac{1}{1000 y_{\text{max}}} \sum_{y=1}^{y_{\text{max}}} N_y^{\text{tot}}$  for haddock and whiting, and  $w = \frac{1}{20 y_{\text{max}}} \sum_{y=1}^{y_{\text{max}}} N_y^{\text{tot}}$  for cod). These values of effective sample size were chosen fairly arbitrarily; following the rationale of (Francis, 2011), we selected low values for  $w$  so that abundance data took precedence over the length distribution data. More statistically sound methods for selecting  $w$  will be considered in future applications of this model.

The posterior distribution was approximated by fitting the model using STAN via the ‘rstan’ package in R (Stan Development Team, 2016). STAN is a programming language that facilitates Bayesian analyses through the use of Hamiltonian Monte Carlo (HMC) algorithms. HMC derives solutions for posterior distributions by assigning an energy function to the system of parameters and simulating approximate Hamiltonian dynamics. Hamilton’s equations are coupled partial differential equations that can be used to find the state of minimum energy within a system from the position and momentum of each variable. In terms of HMC, the model parameters are the system variables, each with its own position and momentum, and the negative log-likelihood is the energy function. Minimising the energy using Hamilton’s equations is therefore equivalent to maximising the likelihood. The position of parameter  $\theta_j$  is equivalent to the value of  $\theta_j$ , and this is updated with most iterations of the HMC algorithm. A momentum is randomly assigned to each parameter with each iteration of the HMC algorithm. The HMC algorithms discretise Hamilton’s equations using the leapfrog method. This requires two tuning parameters, which are the number of simulation steps and the size of

those steps. Mixing rate and rapid convergence are highly dependent on the values of the HMC tuning parameters. If Hamiltonian dynamics are simulated for too few steps then parameters will not move far from their starting positions, and if there are too many steps then parameters may move as far away from their starting positions as they can before doubling back and travelling towards the starting position. To achieve good mixing rates it is important that, with each HMC iteration, the updated parameters move far away from their starting positions. This depends on both the step size and the number of steps. The step size should be tuned so that the entire posterior distribution can be explored by the algorithm: posteriors with a high degree of curvature require a small step size so that the leapfrog approximation can explore low probability regions. Choosing values for these tuning parameters can be very difficult, but is fortunately not required since STAN can do it automatically through its primary algorithm, the No U-Turn Sampler (NUTS). The NUTS algorithm is so-called because it detects when parameters simulated by Hamiltonian dynamics reach the positions furthest from their starting values and begin to travel backwards, it then chooses the step size and step number so that these u-turns are prevented and a good mixing rate is achieved — this is done during warm-up iterations (termed ‘burn-in’ for other Monte Carlo methods). Parameter values returned from the warm-up iterations are discarded and the remaining — post warm-up — iterations form Markov chains providing samples from the posterior distributions. For more information, Neal (2011) provides an excellent and thorough introduction to HMC.

### 5.3 Results

Summary statistics for each model parameter (mean values, standard deviations, and credible intervals) are given in the appendix to this chapter (section 5.5). Tables 5.2 to 5.7 give the summary statistics for cod, haddock, and whiting in area VIa, and tables 5.8 to 5.11 give the same information for Clyde haddock and whiting.

### 5.3.1 Cod: area VIa

The model fit to the landings, discards, and the numbers in the survey are plotted in fig. 5.2. The model produced a good fit to the fishery catch data, although there was a tendency for the discards to be overestimated. The numbers in the survey were poorly fitted in the first half of the time series when the model produced several large overestimates, but the model corresponded closely to the data in the second half of the time series.

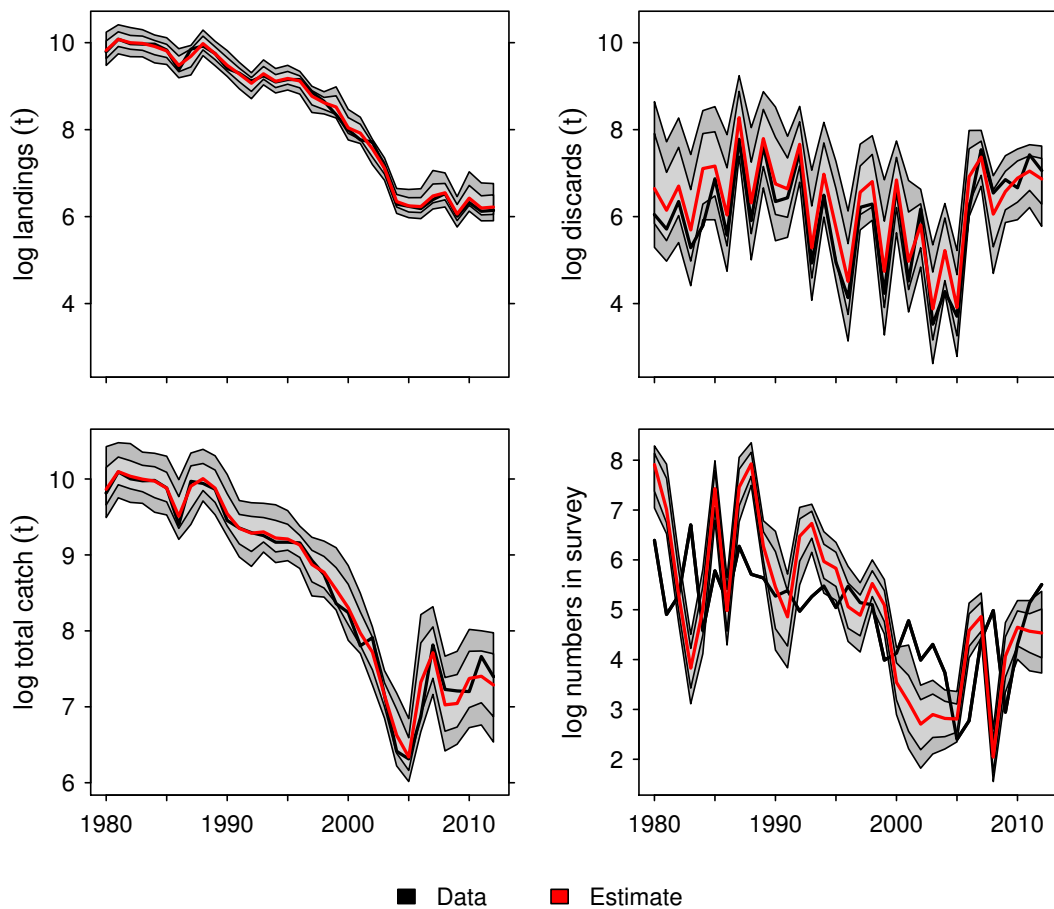


Figure 5.2: The natural logarithm of the median values of estimated landings, discards, total catch, and total numbers present in the annual survey samples, plotted against the data for cod in area VIa. The light and dark grey polygons show 75% and 95% credible intervals respectively.



The selectivity of the survey and the selectivity and retention fraction of the fishery are plotted in fig. 5.3. The survey selectivity peaked at a length in the range  $l^v = [34.1, 39.0]$  cm (table 5.2), and approached zero at large lengths greater than 80 cm. There was less precision in the estimate of fishery selectivity, as the length at 50% selection was estimated in the range  $l_{50}^f = [21.4, 39.1]$  cm (table 5.2).

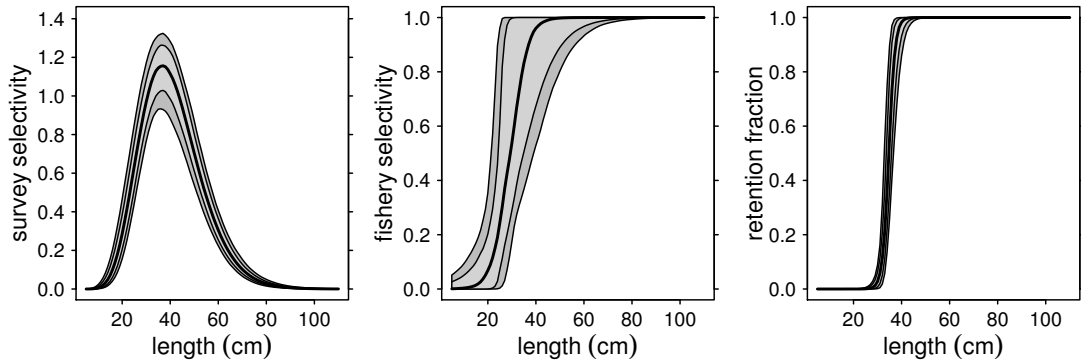


Figure 5.3: Thick lines are the median values of estimated survey selectivity, fishery selectivity,  $s_l^f$ , and retention fraction,  $s_l^d$ , for cod in area VIa. The plot of survey selectivity shows  $q s_l^v$ , the selectivity multiplied by the catchability. The light and dark grey polygons show 75% and 95% credible intervals respectively.

Figure 5.4 shows time series of estimated fishing mortality rate, total stock numbers, stock biomass, and recruited numbers compared to the estimates produced from the ICES age-based model (ICES, 2013b). The model estimated a trend of increasing fishing mortality rate. The fishing mortality rate matched the age-based estimates from the early 2000s onwards, but was considerably lower than the age-based results for most of the time series. The trends in abundance and recruitment estimated by the length- and age-based models were broadly similar. The length-based model produced recruitment estimates that were considerably lower in several years, which caused the numbers in the stock to be lower than predicted by the age-based model. The stock biomass estimated by the length- and age-based models was a closer match, although the length-based biomass was larger during the early 1980s.

The survey length distributions estimated by the model are plotted against the data in figs. 5.5 to 5.7. The fit to the survey length distributions were poor overall. In many

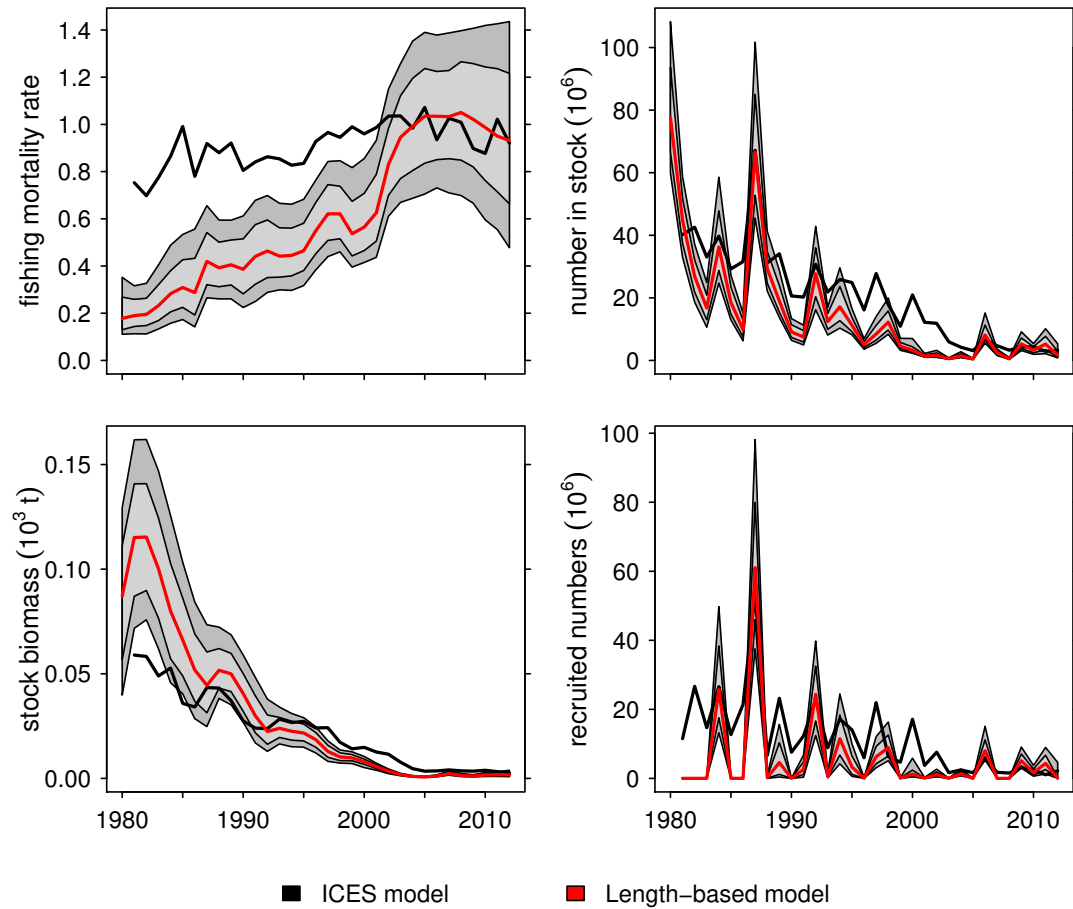


Figure 5.4: Thick red lines are the median values of the estimates of fishing mortality rate (averaged over ages 2–5 years), total numbers in the stock, total stock biomass, and number of new recruits for cod in area VIa. The light and dark grey polygons show 75% and 95% credible intervals respectively. Thick black lines are the estimates produced by the ICES age-based model.

years, the model did not account for large fish that were present in the survey data; this was most likely due to the low survey selectivity at large lengths.

Trends in  $\hat{L}_\infty$  and  $\hat{k}$ , and the resulting von Bertalanffy growth curves are shown in fig. 5.8. The model estimated a decline in  $\hat{k}$  in the second half of the time series, and a steadily increasing  $\hat{L}_\infty$ . Table 5.2 shows that neither of these trends in growth parameters were significant. The resulting growth curves show that modelled mean length-at-age changed little over time.

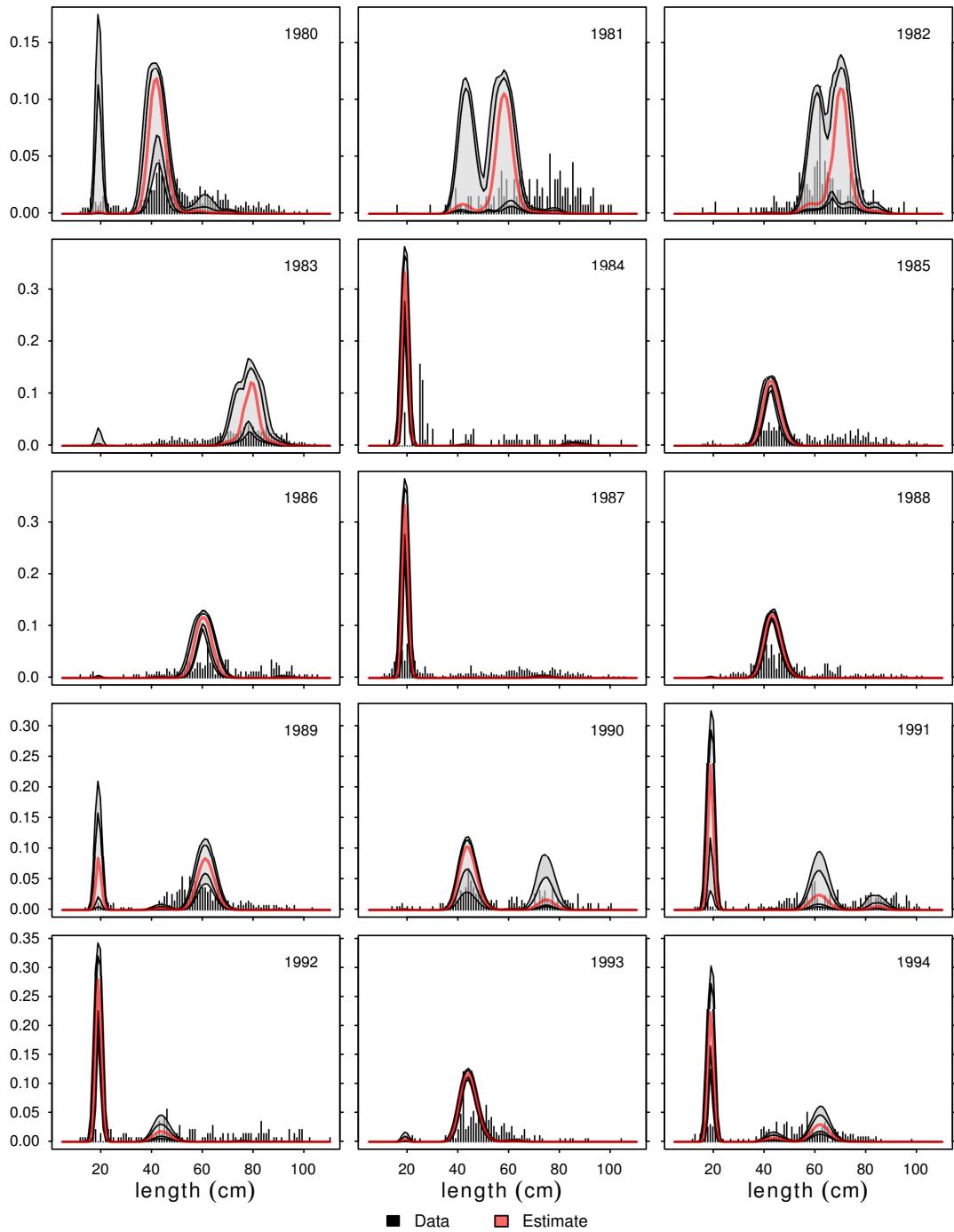


Figure 5.5: Vertical lines show the normalised length distributions from the survey data for area VIa cod. Red lines are medians of model estimates for these survey samples. The light and dark grey polygons show 75% and 95% credible intervals respectively.

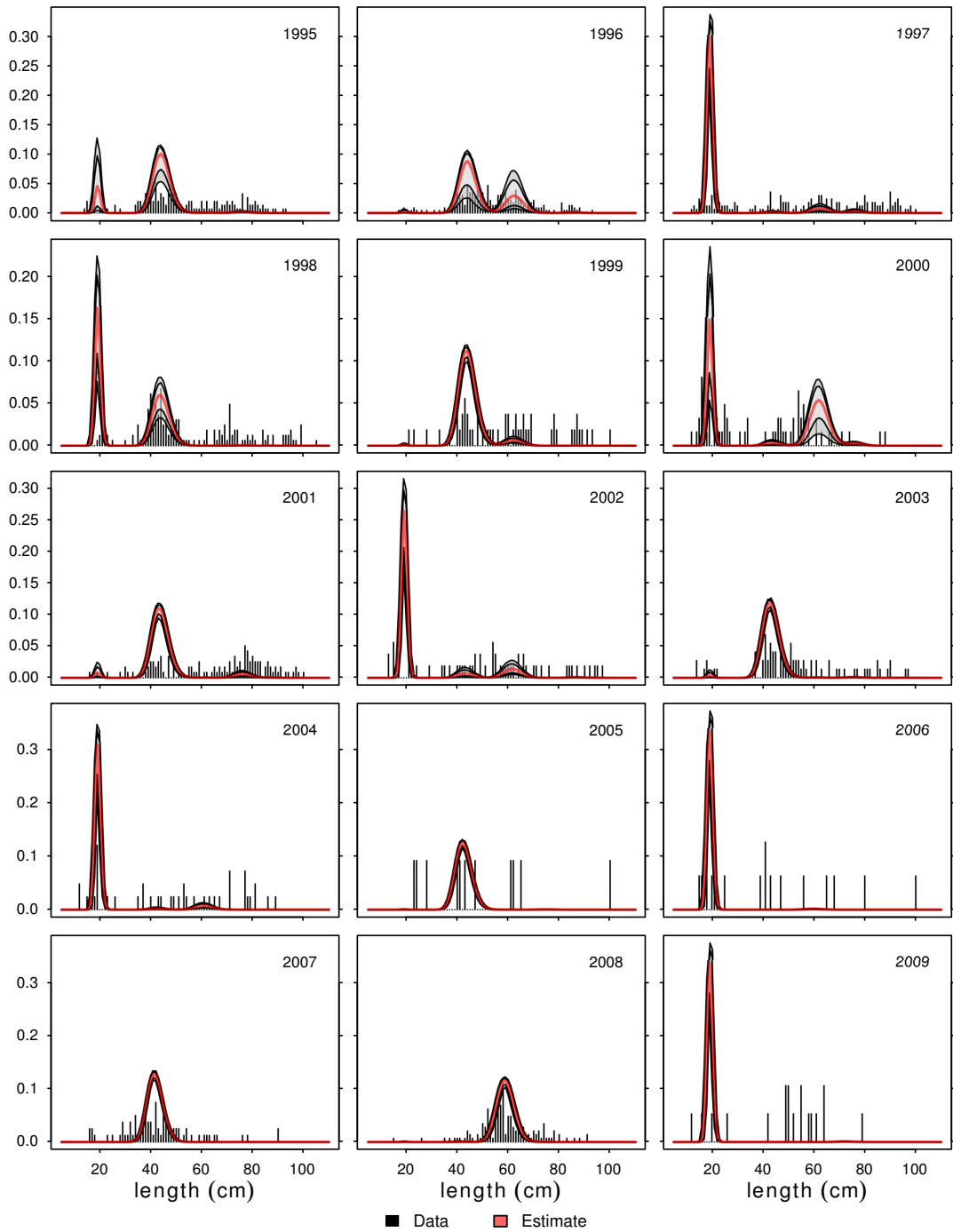


Figure 5.6: Vertical lines show the normalised length distributions from the survey data for area VIa cod. Red lines are medians of model estimates for these survey samples. The light and dark grey polygons show 75% and 95% credible intervals respectively.

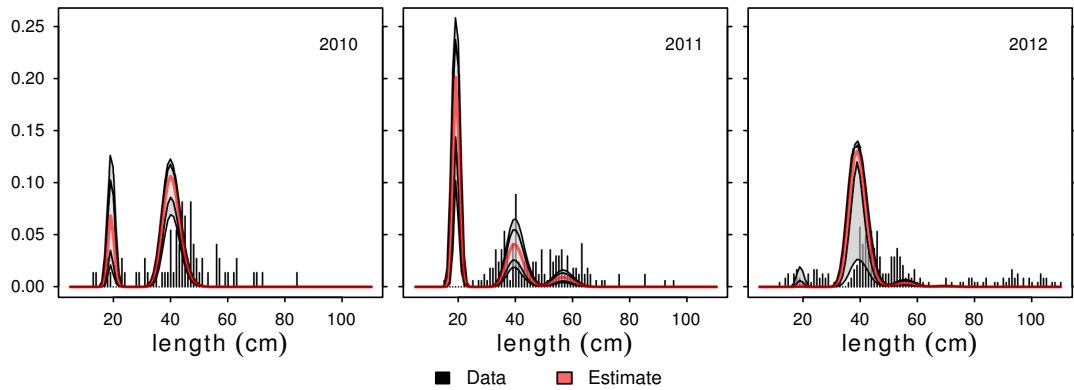


Figure 5.7: Vertical lines show the normalised length distributions from the survey data for area VIa cod. Red lines are medians of model estimates for these survey samples. The light and dark grey polygons show 75% and 95% credible intervals respectively.

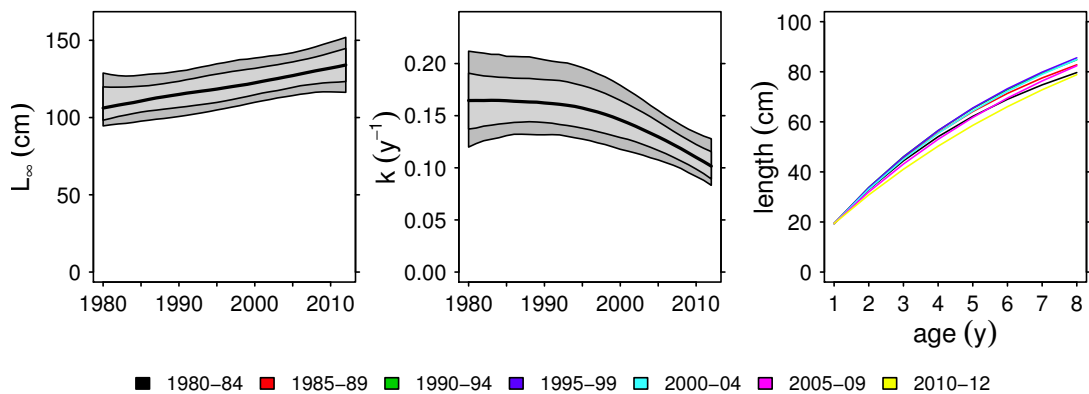


Figure 5.8: Thick black lines are the median values of the estimated growth parameters for area VIa cod. The light and dark grey polygons show 75% and 95% credible intervals respectively. The rightmost plot shows the von Bertalanffy growth curves that resulted from assuming recruits were 1 year old and averaging the growth parameters over the periods shown.

### 5.3.2 Haddock: area VIa

The model fit to the landings, discards and the numbers in the survey are plotted in fig. 5.9. The model produced a good fit to the fishery catch data, although the discards tended to be overestimated. The modelled numbers in the survey were a good match to the data from the early 1990s onwards, but the fit to data was poor in the 1980s.

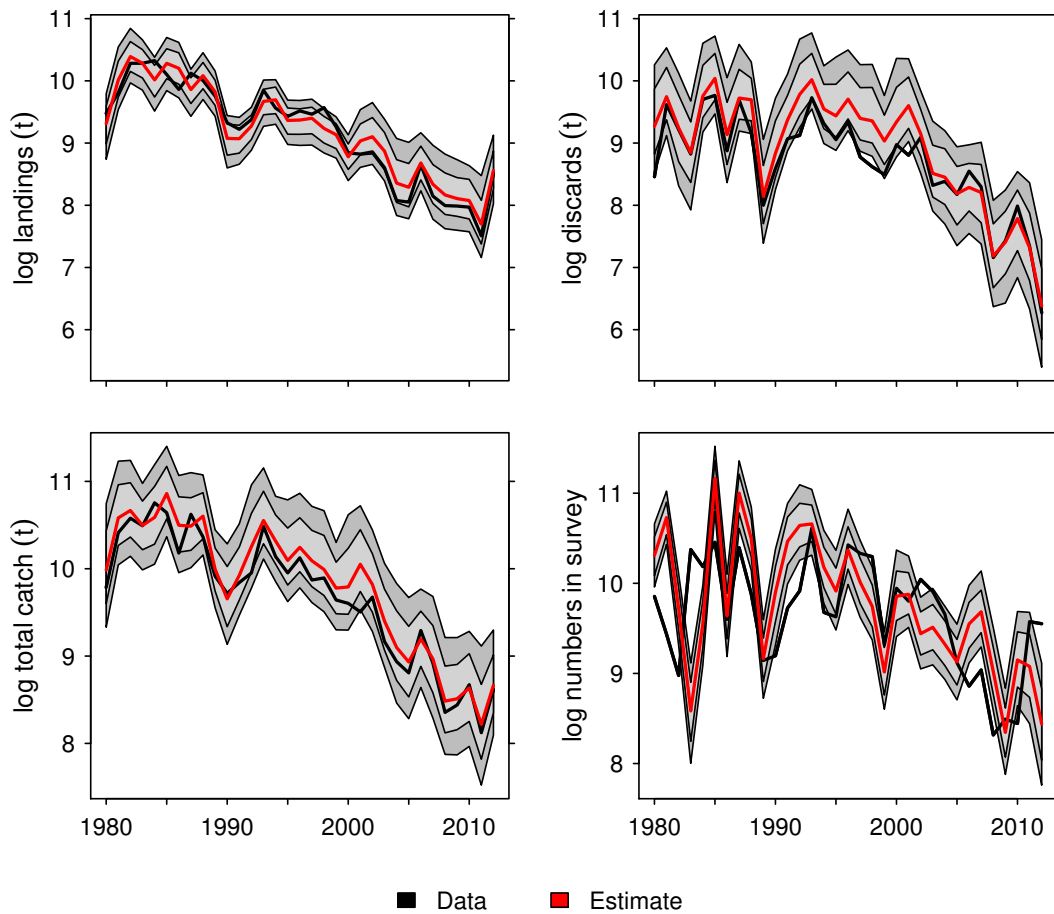


Figure 5.9: The natural logarithm of the median values of estimated landings, discards, total catch, and total numbers present in the annual survey samples, plotted against the data for haddock in area VIa. The light and dark grey polygons show 75% and 95% credible intervals respectively.

The selectivity of the survey and the selectivity and retention fraction of the fishery are plotted in fig. 5.10. The survey selectivity peaked at a length in the range  $l^v = [21.3, 24.3]$  cm (table 5.4), and approached zero at lengths greater than about 45 cm. The length at which 50% of haddock were selected by the fishery was estimated in the range  $l_{50}^f = [18.4, 25.6]$  cm (table 5.4).

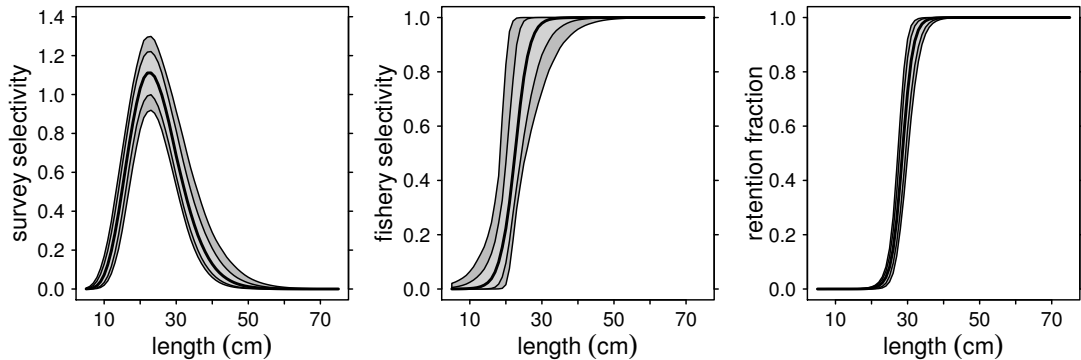


Figure 5.10: Thick lines are the median values of estimated survey selectivity, fishery selectivity,  $s_l^f$ , and retention fraction,  $s_l^d$ , for haddock in area VIa. The plot of survey selectivity shows  $q s_l^v$ , the selectivity multiplied by the catchability. The light and dark grey polygons show 75% and 95% credible intervals respectively.

Figure 5.11 shows time series of estimated fishing mortality rate, total stock numbers, stock biomass and recruited numbers compared to the estimates produced from the ICES age-based model (ICES, 2013b). The fishing mortality rate increased between 1980 and 1990, then rapidly declined from the late 1990s. The fishing mortality rate estimated by the ICES age-based model followed a similar trend and was within the 95% credible interval for most of the time series, although the age-based estimates were greater than the length-based estimates from 2004 onwards. Estimates of recruitment and numbers in the stock produced by the length- and age-based models were a close match. There was more difference between the estimated stock biomass, but both models produced similar results.

The survey length distributions estimated by the model are plotted against the data in figs. 5.12 to 5.14. The model produced a reasonable fit to the survey length distributions, although the modelled distributions did not include the largest fish present in

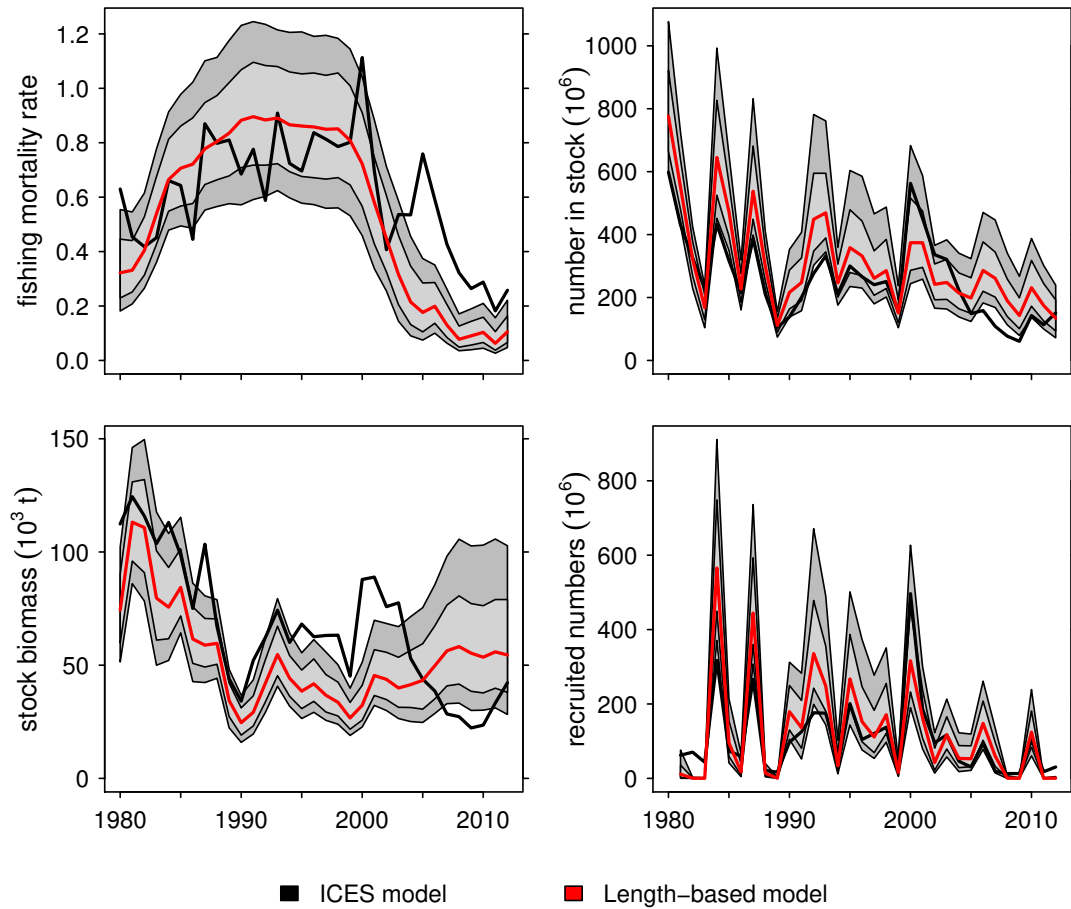


Figure 5.11: Thick red lines are the median values of the estimates of fishing mortality rate (averaged over ages 2–6 years), total numbers in the stock, total stock biomass, and number of new recruits for haddock in area VIa. The light and dark grey polygons show 75% and 95% credible intervals respectively. Thick black lines are the estimates produced by the ICES age-based model.

the data in several years.

Trends in  $\hat{L}_\infty$  and  $\hat{k}$ , and the resulting von Bertalanffy growth curves are shown in fig. 5.15. The model estimated a decline in  $\hat{L}_\infty$  and an increase in  $\hat{k}$ . Most of the change in these parameters occurred at the start of the time series, and table 5.4 indicates that the trends were statistically significant. The growth curves show that mean length-at-age was in decline for most of the time series, but started to increase from 2005 onwards.



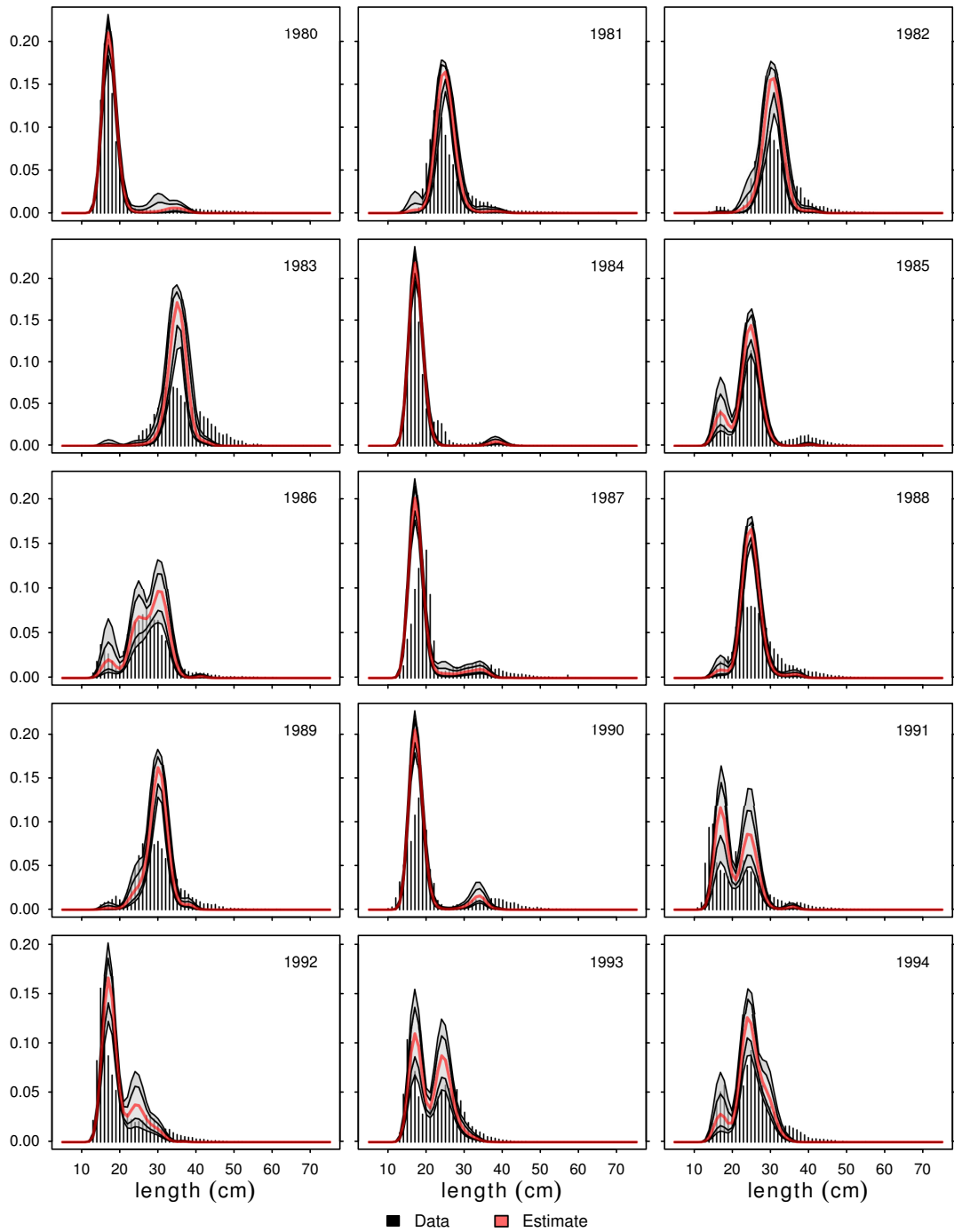


Figure 5.12: Vertical lines show the normalised length distributions from the survey data for area VIa haddock. Red lines are medians of model estimates for these survey samples. The light and dark grey polygons show 75% and 95% credible intervals respectively.

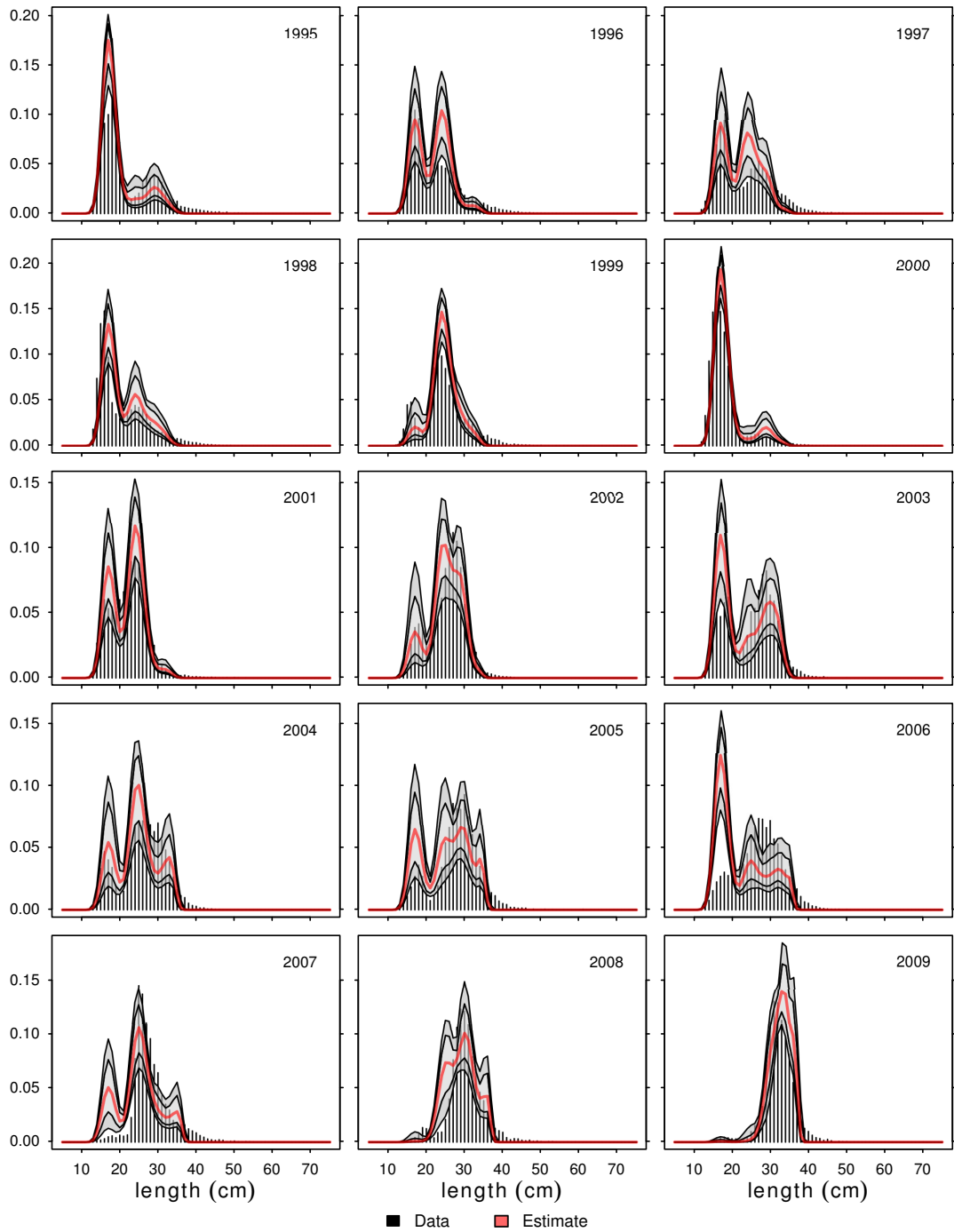


Figure 5.13: Vertical lines show the normalised length distributions from the survey data for area VIa haddock. Red lines are medians of model estimates for these survey samples. The light and dark grey polygons show 75% and 95% credible intervals respectively.

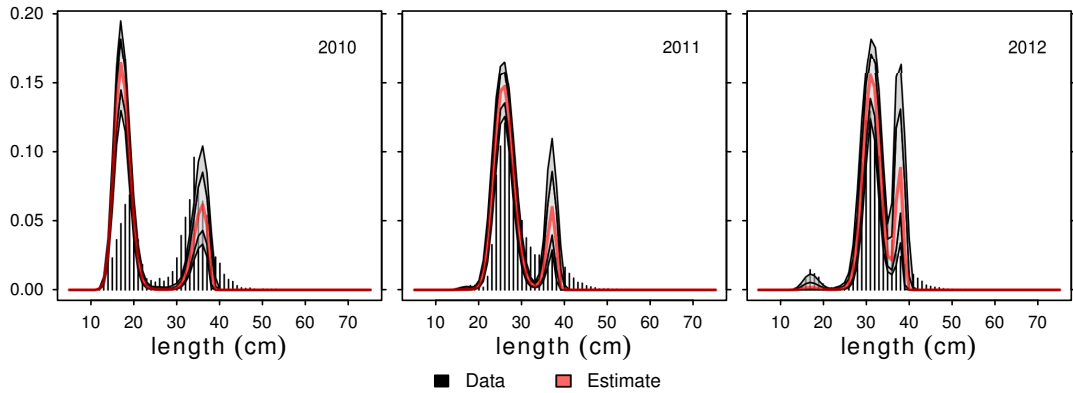


Figure 5.14: Vertical lines show the normalised length distributions from the survey data for area VIa haddock. Red lines are medians of model estimates for these survey samples. The light and dark grey polygons show 75% and 95% credible intervals respectively.

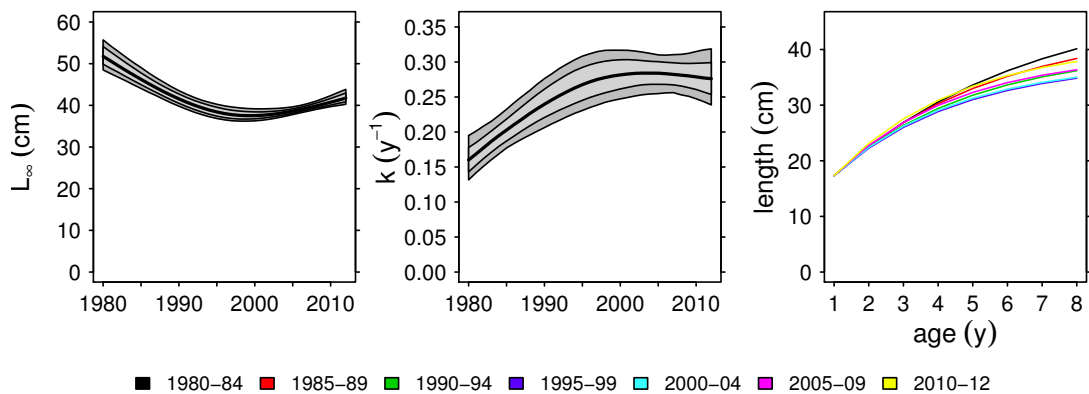


Figure 5.15: Thick black lines are the median values of the estimated growth parameters for area VIa haddock. The light and dark grey polygons show 75% and 95% credible intervals respectively. The rightmost plot shows the von Bertalanffy growth curves that resulted from assuming recruits were 1 year old and averaging the growth parameters over the periods shown.

### 5.3.3 Whiting: area VIa

The model fit to the landings, discards and the numbers in the survey are plotted in fig. 5.16. The model returned a good fit to the fishery catch data, the 75% credible intervals contained the observed landings and discards in most years. The fit to the survey sample sizes was poorer, but most of the data points were within the 95% credible interval, particularly in the second half of the time series.

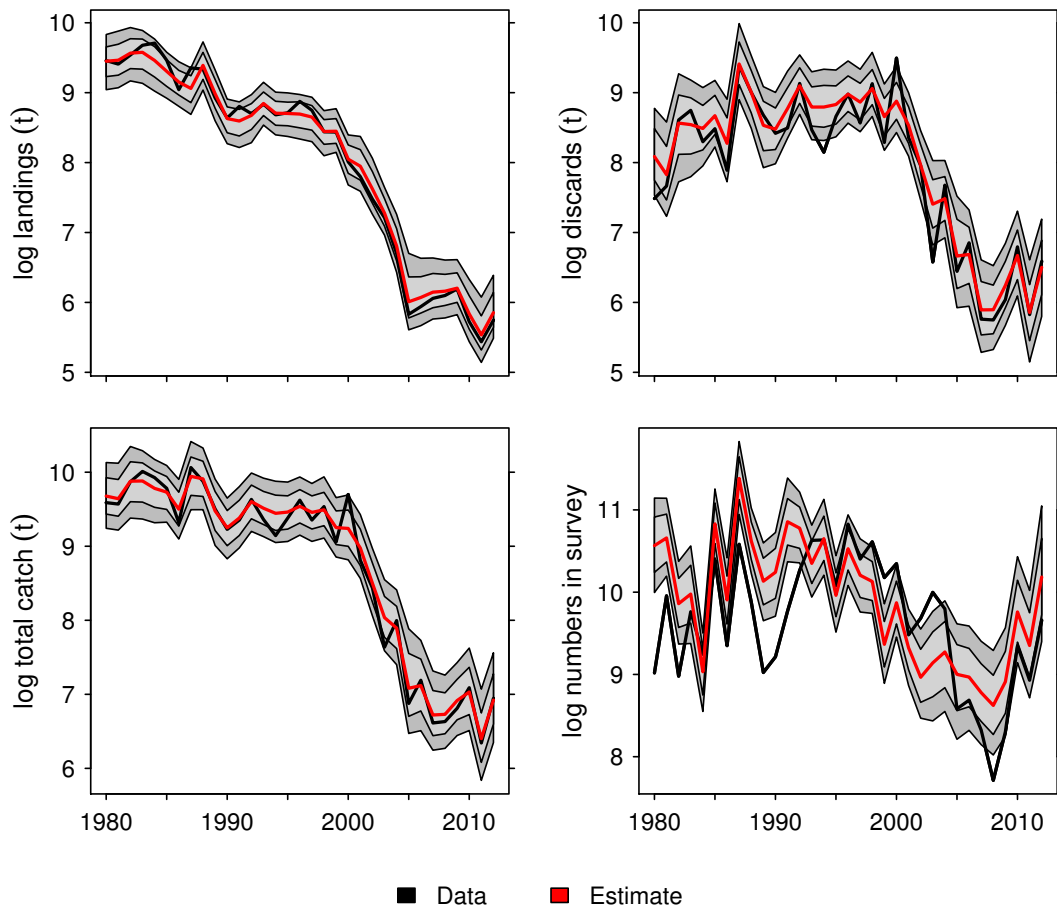


Figure 5.16: The natural logarithm of the median values of estimated landings, discards, total catch, and total numbers present in the annual survey samples, plotted against the data for whiting in area VIa. The light and dark grey polygons show 75% and 95% credible intervals respectively.

The selectivity of the survey and the selectivity and retention fraction of the fishery are plotted in fig. 5.17. The selectivity of the survey peaked at a length in the range  $l^v = [19.3, 21.7]$  cm (table 5.6), and approached zero at lengths greater than about 40 cm. The length at which 50% of whiting were selected by the fishery was estimated in the range  $l_{50}^f = [18.2, 29.7]$  cm. The relatively large selection range,  $\beta^f$ , caused the fishery selectivity curve estimated for VIa whiting to have a shallower slope than observed for cod or haddock.

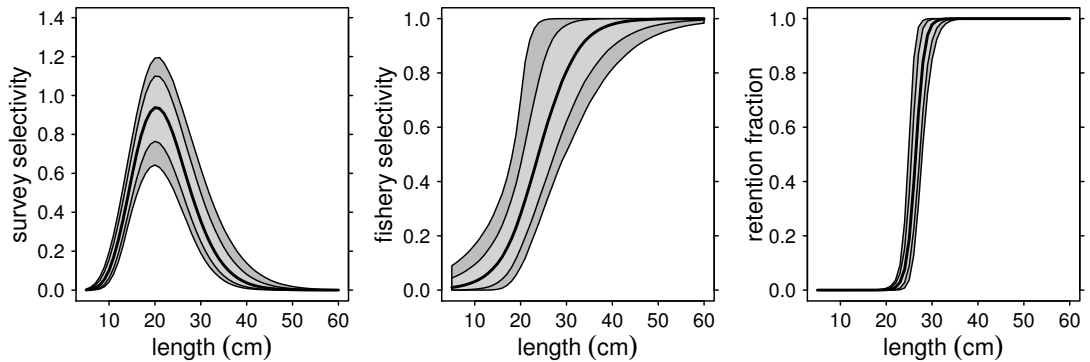


Figure 5.17: Thick lines are the median values of estimated survey selectivity, fishery selectivity,  $s_l^f$ , and retention fraction,  $s_l^d$ , for whiting in area VIa. The plot of survey selectivity shows  $q s_l^v$ , the selectivity multiplied by the catchability. The light and dark grey polygons show 75% and 95% credible intervals respectively.

Figure 5.18 shows time series of estimated fishing mortality rate, total stock numbers, stock biomass and recruited numbers compared to the estimates produced from the ICES age-based model (ICES, 2013b). The fishing mortality rate was lower than the estimates produced by the ICES age-based model, although they followed a similar trend and the age-based estimates were within the 95% credible interval in most years. The stock biomass estimates of the length- and age-based models were very similar. Estimates of stock numbers and recruitment tended to be greater than the age-based values during the second half of the time series.

The survey length distributions estimated by the models are plotted against the data in figs. 5.19 to 5.21. The model produced a good fit to the survey length distributions at small to medium lengths, but the largest fish in the samples were not well modelled

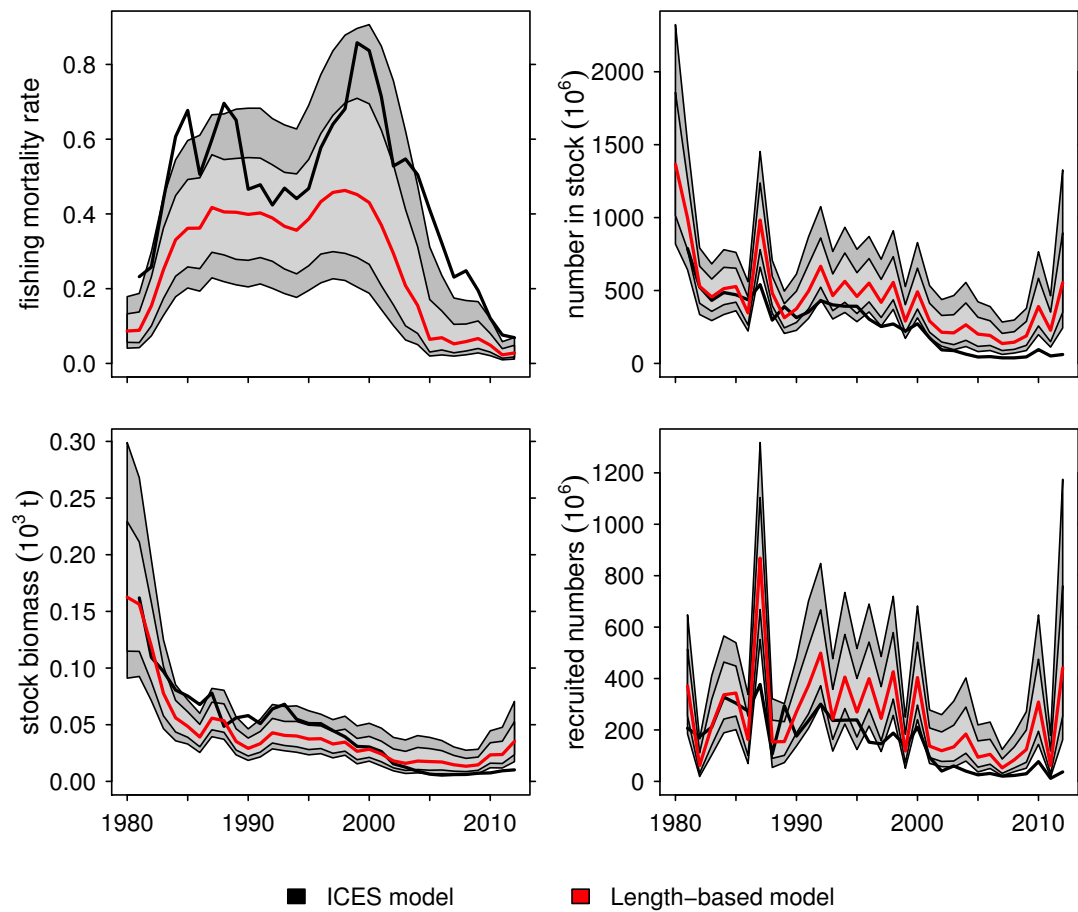


Figure 5.18: Thick red lines are the median values of the estimates of fishing mortality rate (averaged over ages 2–4 years), total numbers in the stock, total stock biomass, and number of new recruits for whiting in area VIa. The light and dark grey polygons show 75% and 95% credible intervals respectively. Thick black lines are the estimates produced by the ICES age-based model.

in several years.

Trends in  $\hat{L}_\infty$  and  $\hat{k}$ , and the resulting von Bertalanffy growth curves are shown in fig. 5.22. The  $\hat{L}_\infty$  parameter decreased significantly over time, but the decline in the mean value of  $\hat{k}$  was not significant (table 5.6). This resulted in the model estimating a steady decline in the mean length-at-age.

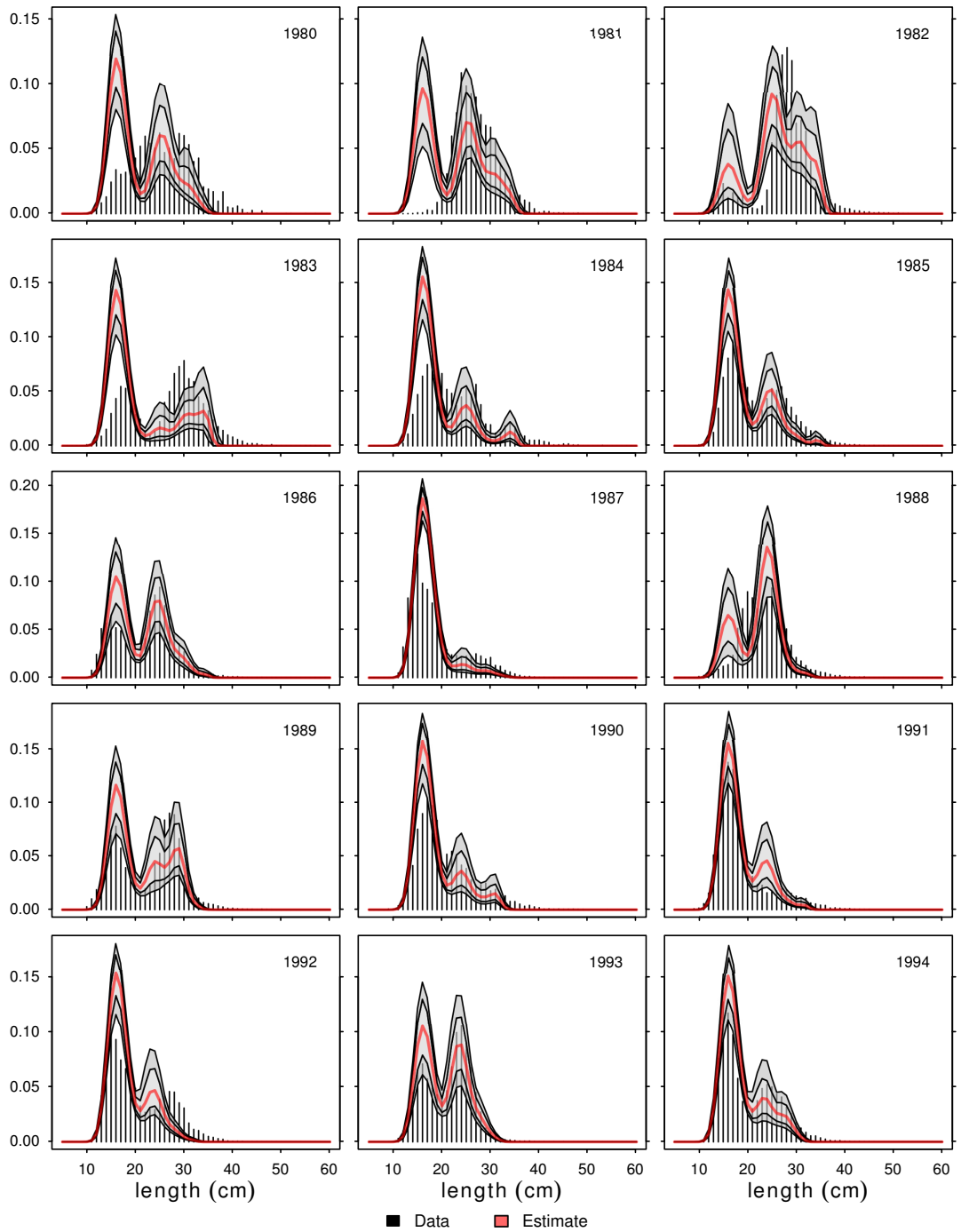


Figure 5.19: Vertical lines show the normalised length distributions from the survey data for area VIa whiting. Red lines are medians of model estimates for these survey samples. The light and dark grey polygons show 75% and 95% credible intervals respectively.

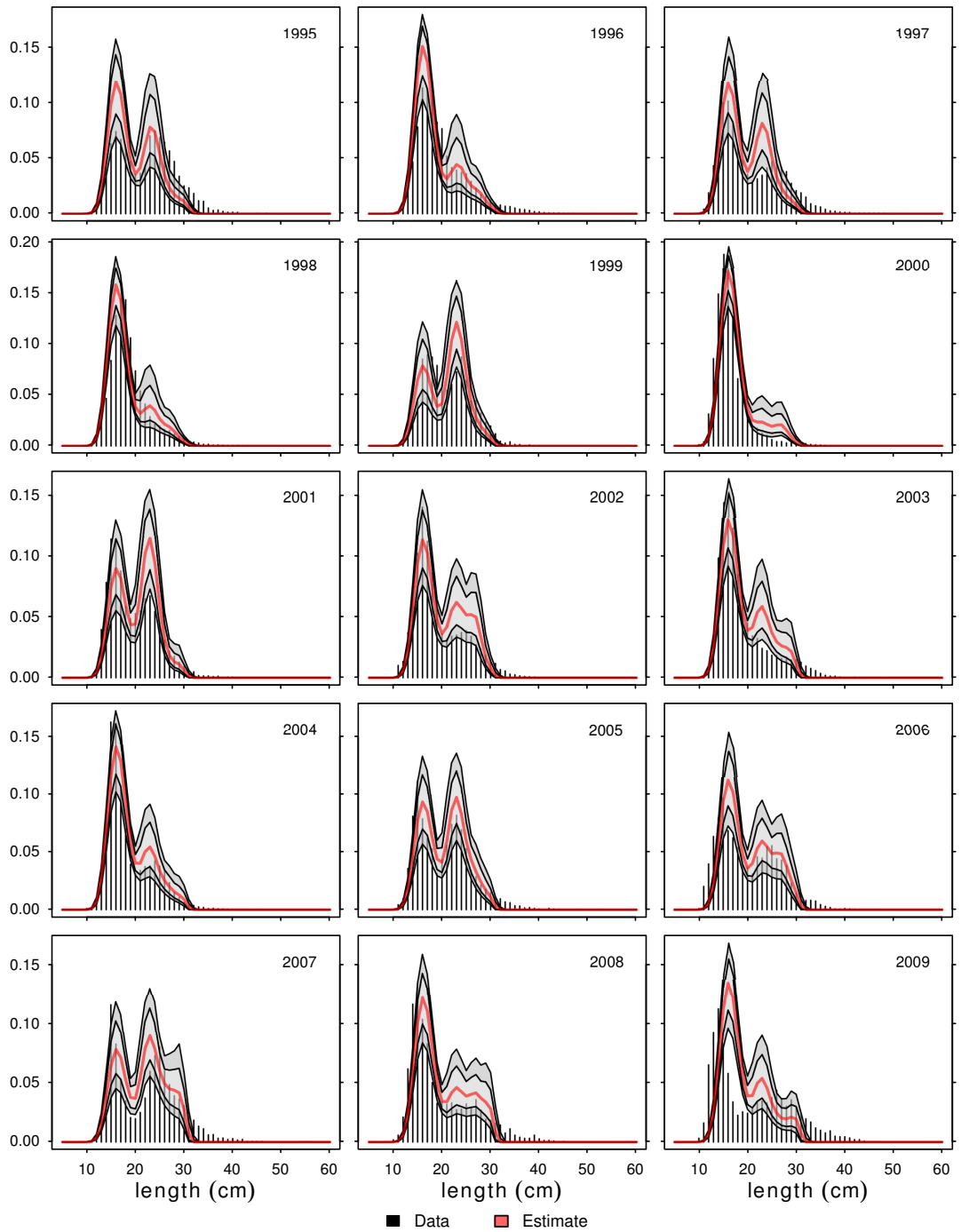


Figure 5.20: Vertical lines show the normalised length distributions from the survey data for area VIa whiting. Red lines are medians of model estimates for these survey samples. The light and dark grey polygons show 75% and 95% credible intervals respectively.



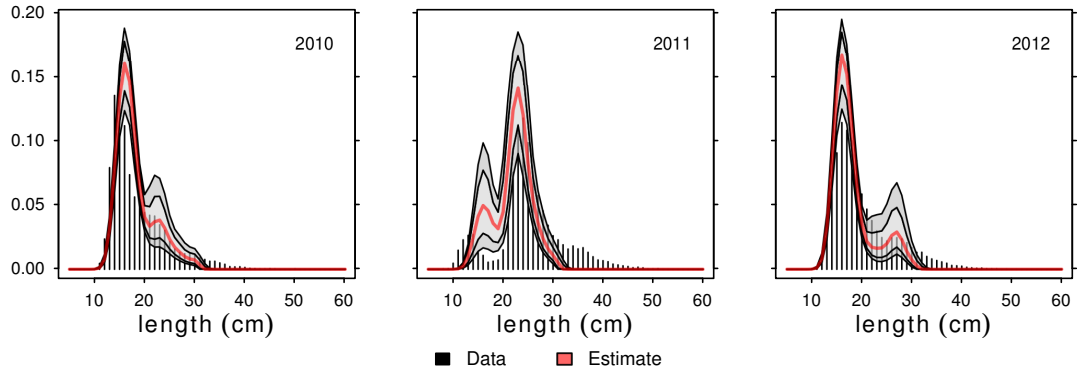


Figure 5.21: Vertical lines show the normalised length distributions from the survey data for area VIa whiting. Red lines are medians of model estimates for these survey samples. The light and dark grey polygons show 75% and 95% credible intervals respectively.

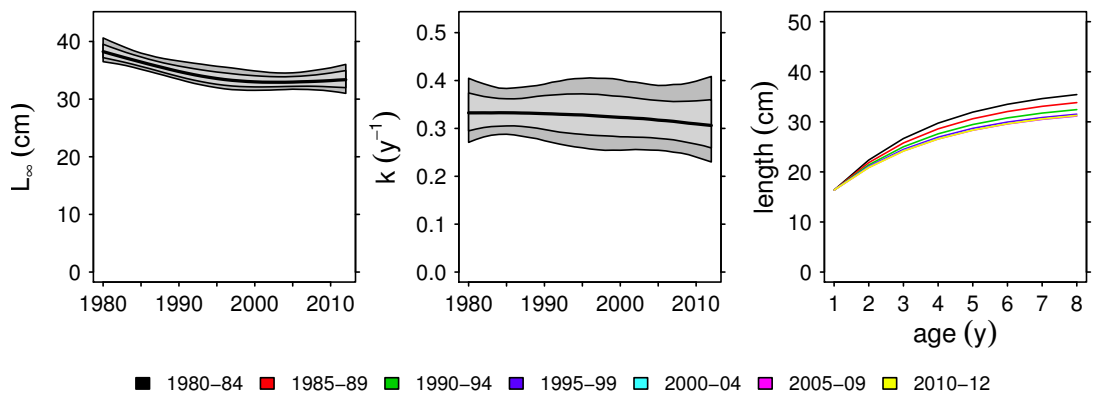


Figure 5.22: Thick black lines are the median values of the estimated growth parameters for area VIa whiting. The light and dark grey polygons show 75% and 95% credible intervals respectively. The rightmost plot shows the von Bertalanffy growth curves that resulted from assuming recruits were 1 year old and averaging the growth parameters over the periods shown.

### 5.3.4 Haddock: Clyde

The model fit to the landings, discards and the numbers in the survey are plotted in fig. 5.23. The model produced a reasonable fit to the landings data; observed landings were within the 95% credible intervals, and most data points lay within the 75% credible intervals. The discards tended to be overestimated, but almost all data points were within the 75% credible interval. The model tended to overestimate the numbers sampled by the survey, although the trend was quite well replicated and all but the first data point lay within the 95% credible interval.

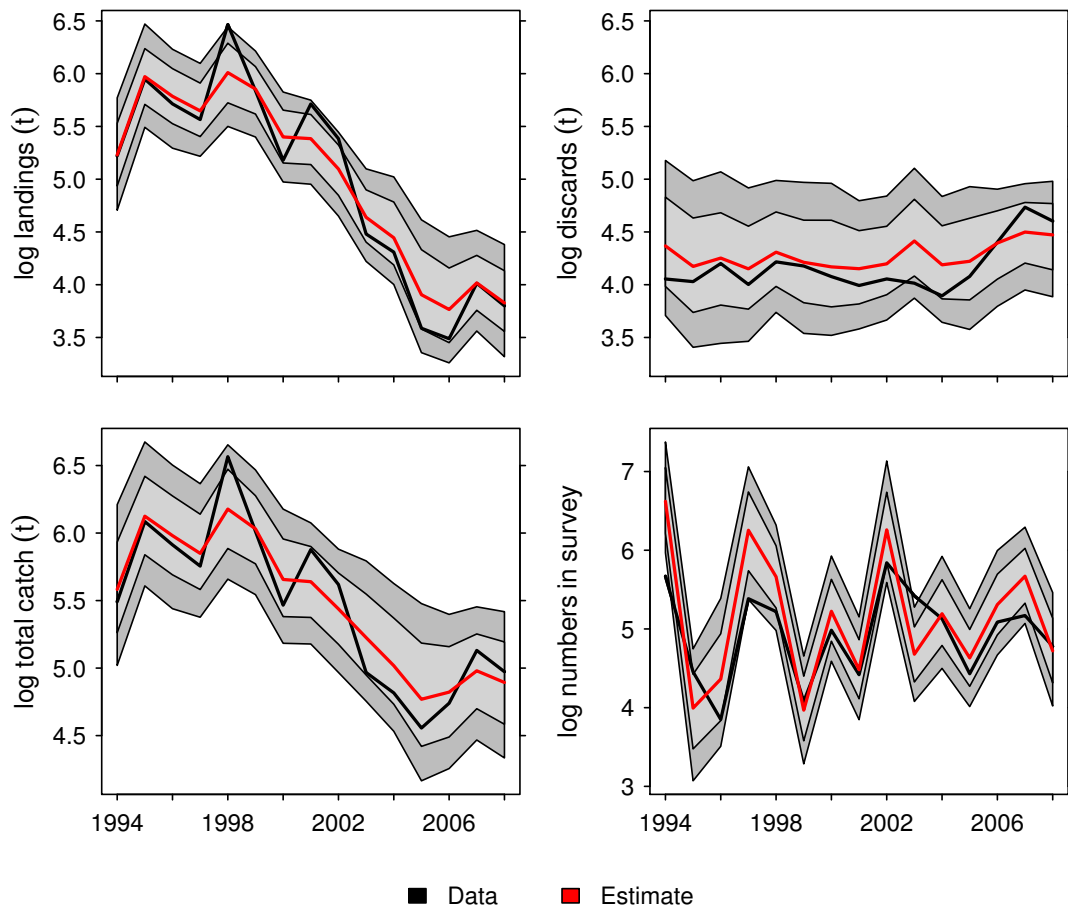


Figure 5.23: The natural logarithm of the median values of estimated landings, discards, total catch, and total numbers present in the annual survey samples, plotted against the data for Firth of Clyde haddock. The light and dark grey polygons show 75% and 95% credible intervals respectively.

The selectivity of the survey and the selectivity and retention fraction of the fishery are plotted in fig. 5.24. The survey selectivity curve for Clyde haddock differs from that estimated for the whole of area VIa because the length at peak selectivity is smaller and selectivity declines to near-zero at much smaller lengths — this is due to relatively few large fish being sampled from the Clyde. The fishery selectivity curve also differed from that produced for area VIa, it was shifted towards large length classes, suggesting that the fishery catchability of haddock in area VIa is greater than in the Clyde.

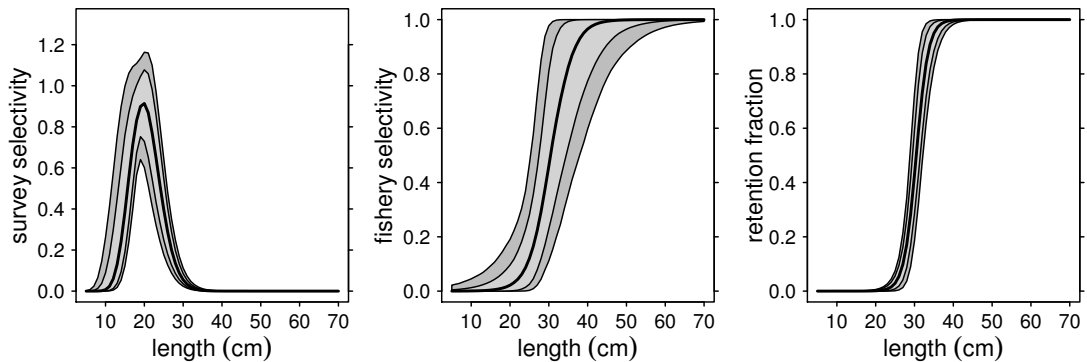


Figure 5.24: Thick lines are the median values of estimated survey selectivity, fishery selectivity,  $s_l^f$ , and retention fraction,  $s_l^d$ , for Firth of Clyde haddock. The plot of survey selectivity shows  $q s_l^v$ , the selectivity multiplied by the catchability. The light and dark grey polygons show 75% and 95% credible intervals respectively.

Figure 5.25 shows time series of estimated fishing mortality rate, total stock numbers, stock biomass and recruited numbers. Fishing mortality rate appears to have declined between 1998 and 2008, although the wide credible intervals cast doubt on this assertion. Stock biomass also appears to have declined, however, there was no indication of a decline in stock numbers or recruitment, which suggests that the proportion of small fish within the stock has increased over time.

The survey length distributions estimated by the model are plotted against the data in fig. 5.26. The model returned a reasonable fit to the bulk of the survey length distributions, although the largest fish present in the samples were not well represented by the model.

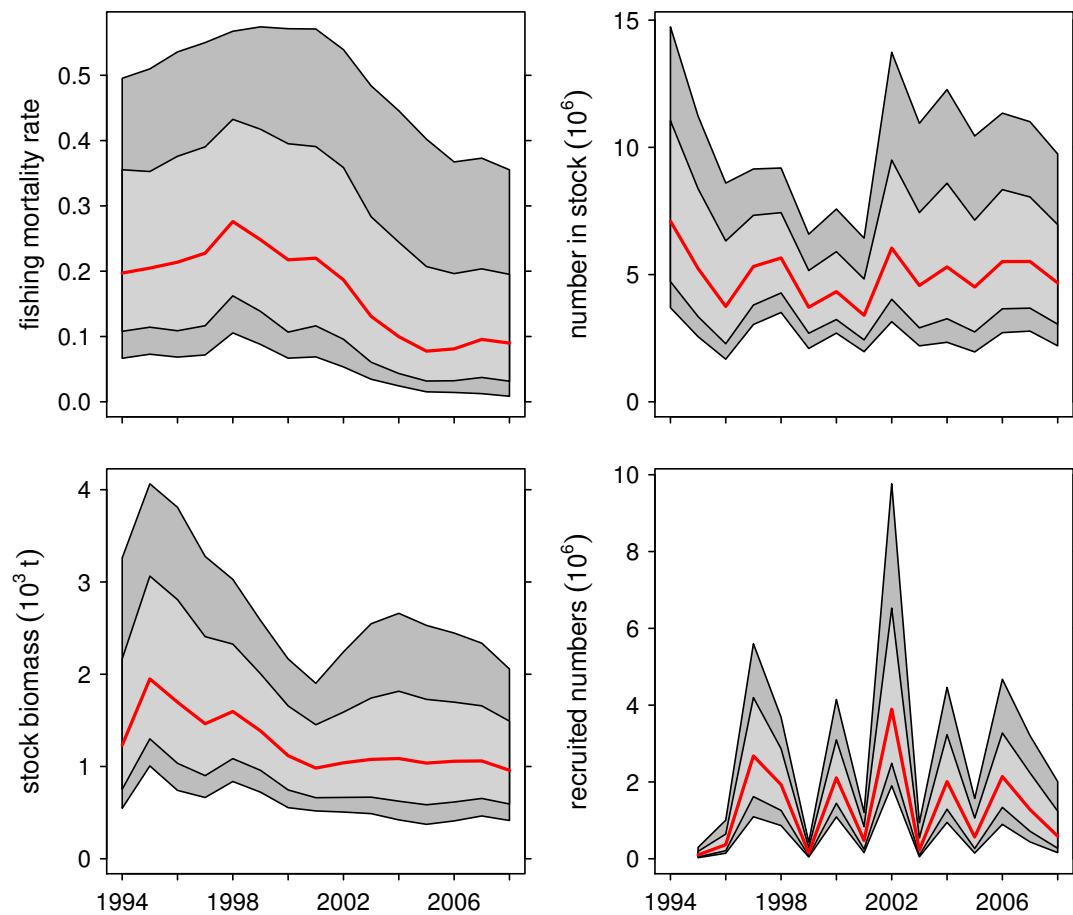


Figure 5.25: The median values of the estimates of fishing mortality rate (averaged over ages 2–6 years), total numbers in the stock, total stock biomass, and number of new recruits for Firth of Clyde haddock. The light and dark grey polygons show 75% and 95% credible intervals respectively.

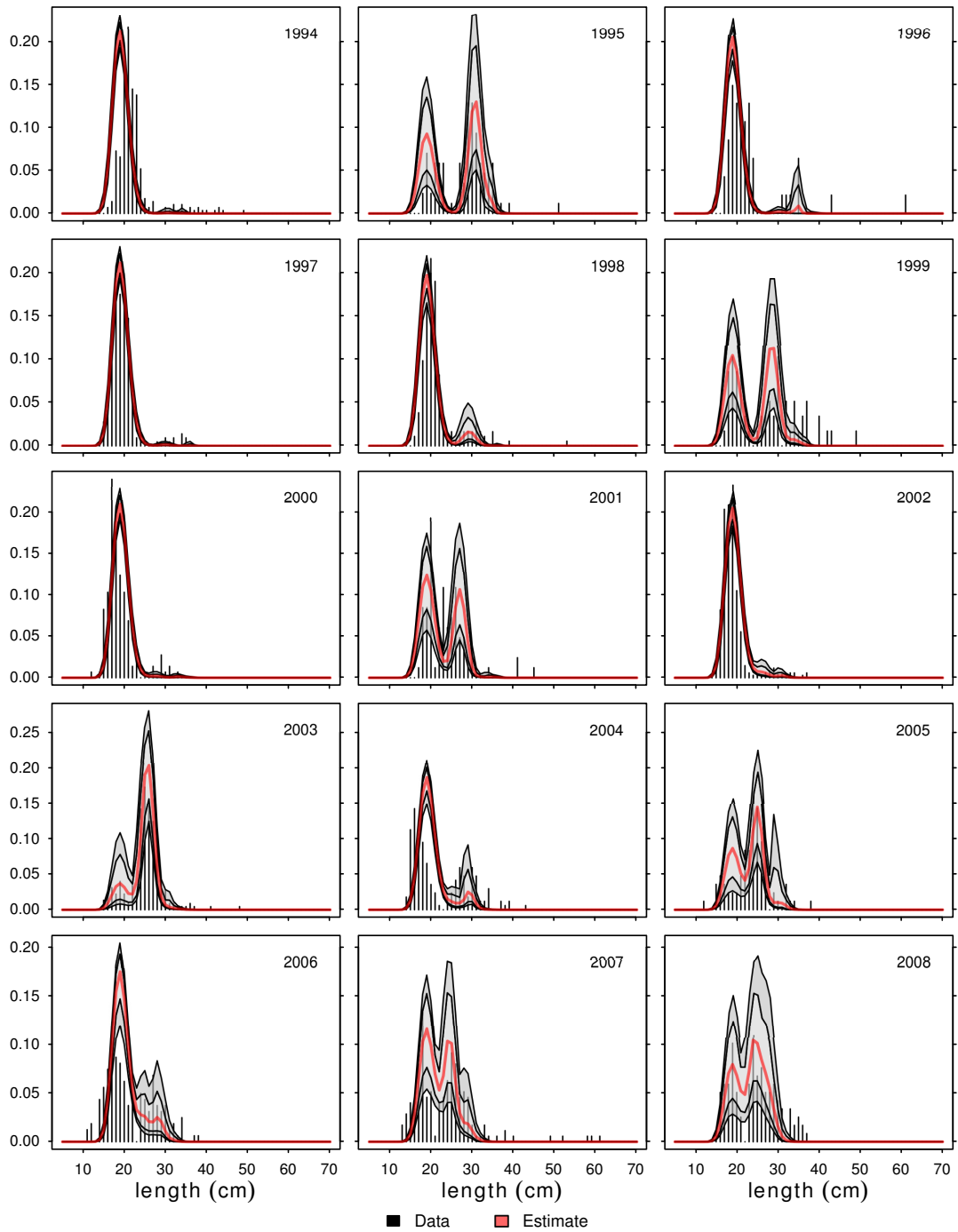


Figure 5.26: Vertical lines show the normalised length distributions from the survey data for Firth of Clyde haddock. Red lines are medians of model estimates for these survey samples. The light and dark grey polygons show 75% and 95% credible intervals respectively.

Trends in  $\hat{L}_\infty$  and  $\hat{k}$ , and the resulting von Bertalanffy growth curves are shown in fig. 5.27. The model estimated declines in the mean values of both  $\hat{L}_\infty$  and  $\hat{k}$ , but only the decline in  $\hat{L}_\infty$  was significant (table 5.8). The result of this was a substantial decline in mean length-at-age.

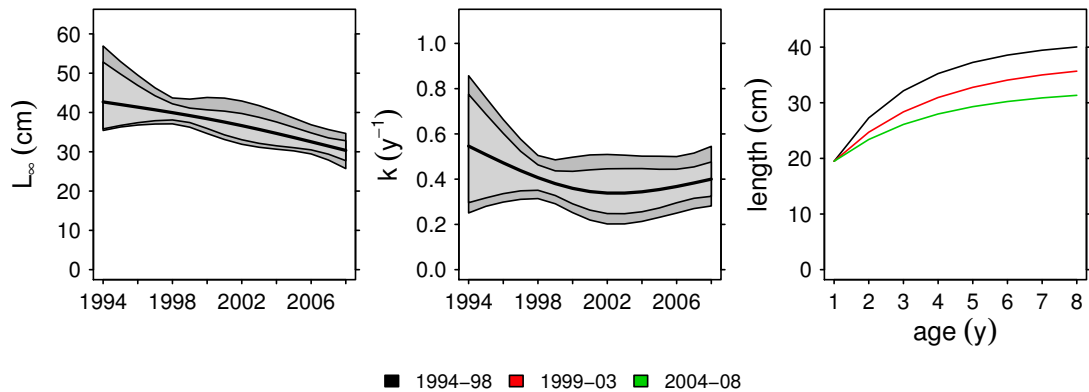


Figure 5.27: Thick black lines are the median values of the estimated growth parameters for Firth of Clyde haddock. The light and dark grey polygons show 75% and 95% credible intervals respectively. The rightmost plot shows the von Bertalanffy growth curves that resulted from assuming recruits were 1 year old and averaging the growth parameters over the periods shown.

### 5.3.5 Whiting: Clyde

The model fit to the landings, discards and the numbers in the survey are plotted in fig. 5.28. The model fit to the landings data was excellent, however, the fit to fishery catch data was poor because the discards tended to be overestimated and discards accounted for the majority of the catch. Although a few points were poorly estimated, most of the data points for total surveyed numbers were within the credible intervals of the modelled values.

The selectivity of the survey and the selectivity and retention fraction of the fishery are plotted in fig. 5.29. As happened for haddock, the survey selectivity curve for Clyde whiting declined to near-zero at smaller lengths than observed in area VIa. The fishery selectivity curve was different from that estimated for area VIa whiting as it was shifted further towards the smaller length classes, suggesting that fishery catchability

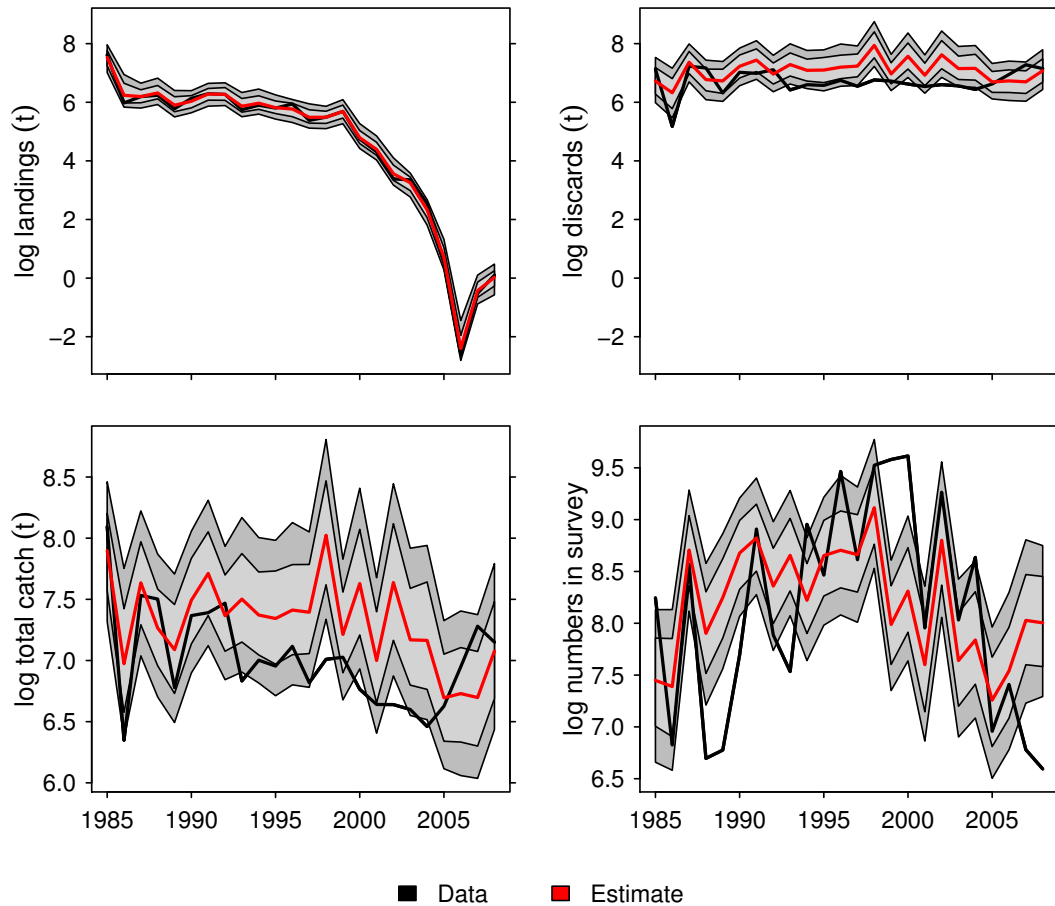


Figure 5.28: The natural logarithm of the median values of estimated landings, discards, total catch, and total numbers present in the annual survey samples, plotted against the data for Firth of Clyde whiting. The light and dark grey polygons show 75% and 95% credible intervals respectively.

of whiting is greater in the Clyde than in area VIa.

Figure 5.30 shows time series of estimated fishing mortality rate, total stock numbers, stock biomass and recruited numbers. The mean value of the fishing mortality rate slowly increased throughout the time series, but the credible intervals were very wide so the estimated trend in the mortality rate is uncertain. The estimates of recruited numbers and total numbers in the stock tended to increase over time, and were very similar to each other, indicating that the majority of the stock consists of newly recruited individuals. The estimates of stock biomass were also similar to estimates of recruitment and stock numbers, but an increase in biomass was not apparent, which

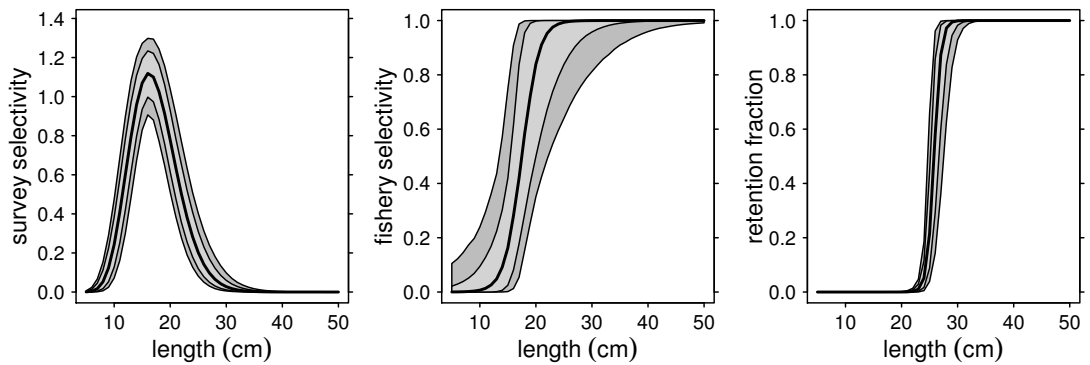


Figure 5.29: Thick lines are the median values of estimated survey selectivity, fishery selectivity,  $s_l^f$ , and retention fraction,  $s_l^d$ , for Firth of Clyde whiting. The plot of survey selectivity shows  $q s_l^v$ , the selectivity multiplied by the catchability. The light and dark grey polygons show 75% and 95% credible intervals respectively.

suggests that the proportion of the stock consisting of large fish has declined over time.

The survey length distributions estimated by the model are plotted against the data in figs. 5.31 and 5.32. The model produced a reasonable fit to the survey length distributions in most years, and it is clear from visual inspection of the data that the majority of fish present in the samples were small, i.e. new recruits.

Trends in  $\hat{L}_\infty$  and  $\hat{k}$ , and the resulting von Bertalanffy growth curves are shown in fig. 5.33. The  $\hat{L}_\infty$  parameter decreased rapidly over time, while  $\hat{k}$  was almost stationary, resulting in substantial declines in mean lengths-at-age.



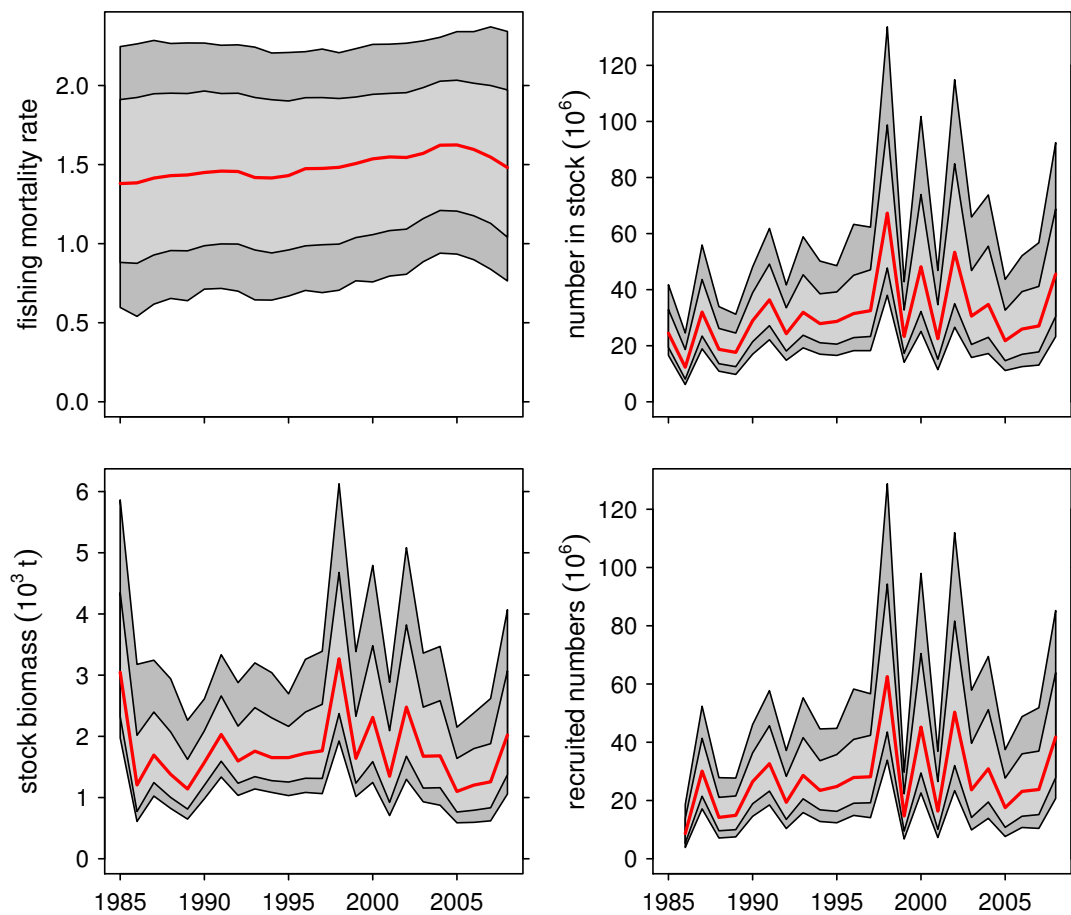


Figure 5.30: The median values of the estimates of fishing mortality rate (averaged over ages 2–4 years), total numbers in the stock, total stock biomass, and number of new recruits for Firth of Clyde whiting. The light and dark grey polygons show 75% and 95% credible intervals respectively.

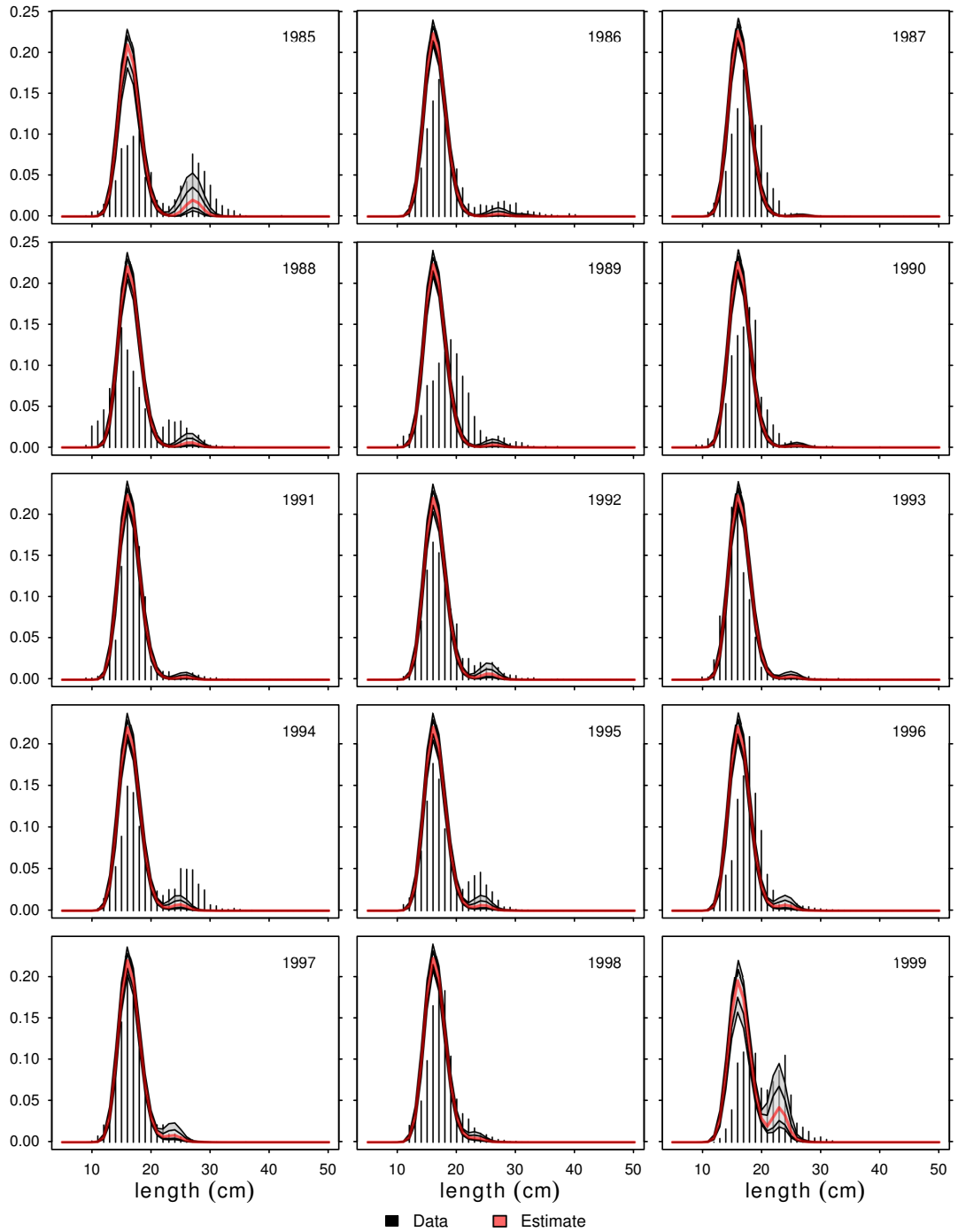


Figure 5.31: Vertical lines show the normalised length distributions from the survey data for Firth of Clyde whiting. Red lines are medians of model estimates for these survey samples. The light and dark grey polygons show 75% and 95% credible intervals respectively.

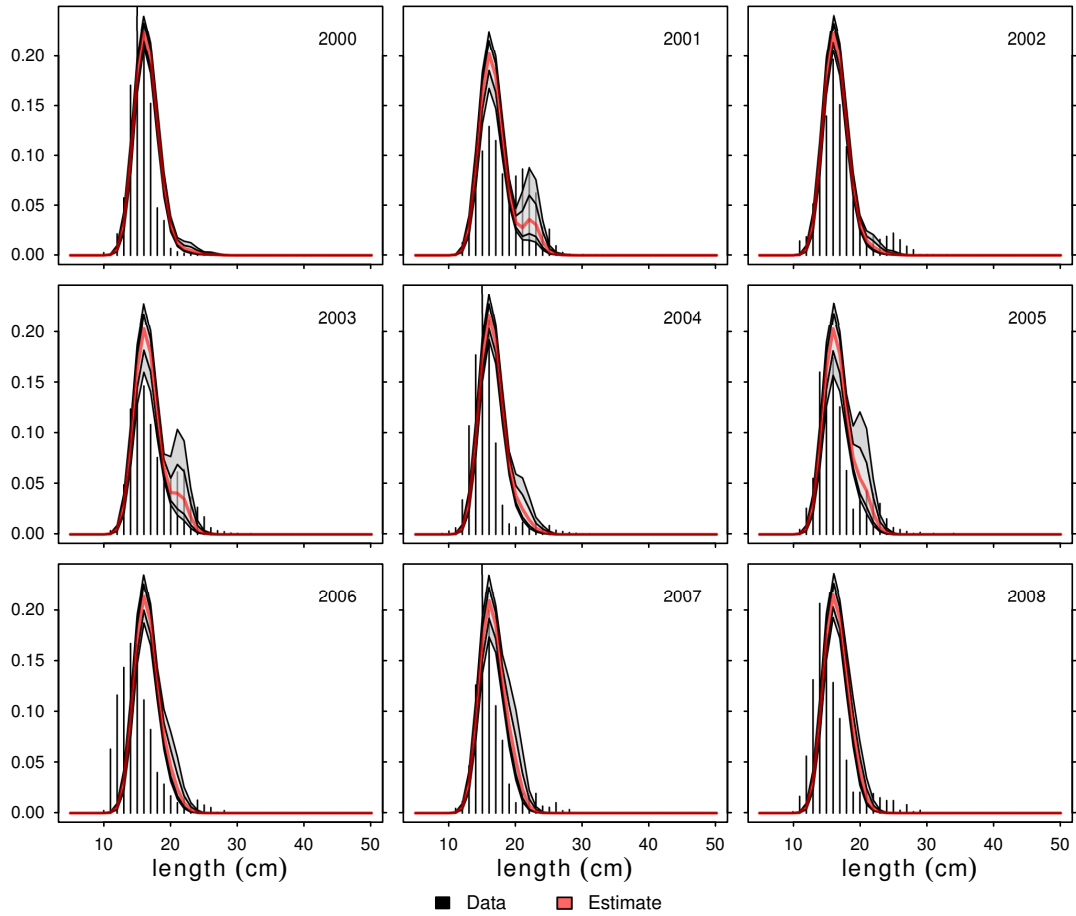


Figure 5.32: Vertical lines show the normalised length distributions from the survey data for Firth of Clyde whiting. Red lines are medians of model estimates for these survey samples. The light and dark grey polygons show 75% and 95% credible intervals respectively.

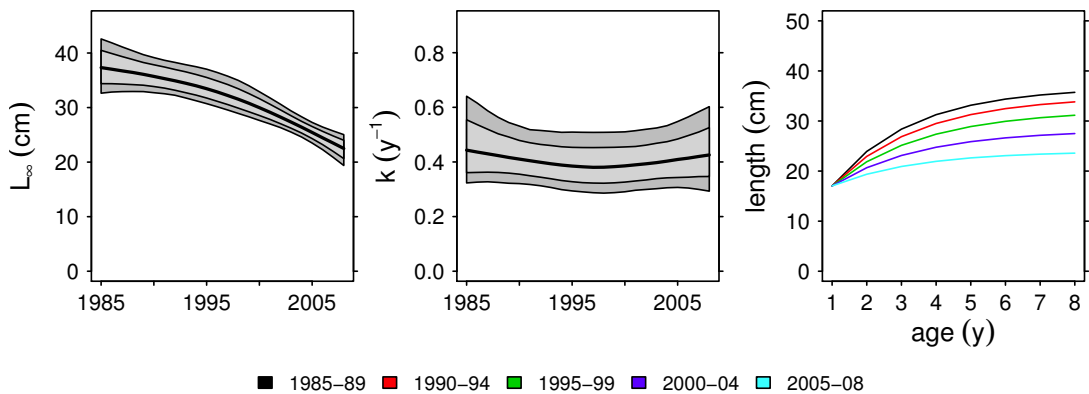


Figure 5.33: Thick black lines are the median values of the estimated growth parameters for Firth of Clyde whiting. The light and dark grey polygons show 75% and 95% credible intervals respectively. The rightmost plot shows the von Bertalanffy growth curves that resulted from assuming recruits were 1 year old and averaging the growth parameters over the periods shown.

## 5.4 Discussion

### 5.4.1 Area VIa stocks

The results of our length-based model were encouraging. Trends in the abundance of cod, haddock, and whiting from area VIa were similar to the trends estimated by the ICES age-based models (ICES, 2013b). Both the age- and length-based models returned long-term declines in the abundance of these three stocks. The length-based model estimates of recruitment and fishing mortality rate of haddock and whiting were also qualitatively similar to the age-based results. The fishing mortality rate estimated for cod was lower than the age-based estimates for most of the time series, and recruitment was frequently much lower than the age-based estimates. Thus, gauging from comparisons with the age-based model results, the length-based model appears to have performed better for haddock and whiting than for cod. The broadly similar results produced by the age- and length-based models for haddock and whiting suggest that our length-based model could potentially be used in place of the more conventional age-based models.

The model produced close fits to the landings data for all three species. No attempt was made to account for potential misreported landings, but this may be considered in future formulations of our model as landings of west of Scotland cod and whiting are suspected to be subject to significant misreporting (Patterson, 1998). The discards were fitted less precisely, and the model had a tendency to overestimate total annual discards; this was most apparent in the results for cod (fig. 5.2). The increased discards of cod from 2006 was an expected consequence of the introduction of the Registration of Fish Sellers and Buyers and Designation of Auction Sites (Scotland) Regulations in 2005. The model accounted for this by increasing the proportion of bulk discards of cod from the late 2000s (table 5.3).

The total numbers sampled by the survey, combined with the proportion of the study area swept out by the survey trawls, provides an index of relative abundance. The model produced decent fits to the numbers present in the survey, although it did

tend to return overestimates for the first half of the time series; these overestimates were most apparent in cod and whiting (figs. 5.2 and 5.16). As these overestimates were observed in multiple species we suspect some common cause. A potential explanation may be that we did not account for the duration of survey tows decreasing after 1998 — this is discussed further below. The survey length distribution data for haddock and whiting tended to be well reproduced by the model, at least for small to medium length classes (figs. 5.12 to 5.14 and 5.19 to 5.21). In general, the model returned poor fits to the length distribution data for cod (figs. 5.5 to 5.7). The largest length classes sampled by the survey were frequently not well accounted for by the model due to the survey selectivity decreasing to near-zero at large lengths (figs. 5.3, 5.10 and 5.17). This behaviour of the survey selectivity curves was possibly caused by fitting the model to every length class in the survey length distribution data, including classes with zero sampled fish. The largest fish present in the data were often separated by several length classes with zero sampled fish, so assigning equal weight to every length class causes the model to fit equally strongly to zeros at large lengths as it does to the large fish that were actually observed. It is likely that the survey selectivity at large lengths tended to zero as a result of this, which is physically unrealistic. Three potential solutions include (1) constraining the survey selectivity curve to be greater than some prespecified values at large lengths, (2) grouping large length classes together when fitting to the survey length data (Punt et al., 2013), or (3) using an indicator matrix to force the expected surveyed numbers at length to equal zero for length classes with zero sampled fish (i.e. only fit to length classes with observations). As methods (1) and (2) involve subjective decisions, method (3) could be the preferred option.

It is important to account for potential changes in growth rate within stock assessment models because trends in growth can influence estimates of stock biomass (Lorenzen, 2016). The growth parameters estimated by our model for haddock and whiting resulted in long-term declines in mean length-at-age; although the mean length-at-age of haddock was estimated to increase from the late 2000s. Modelled mean lengths-at-age for cod were relatively stationary. These model estimated changes in growth are in good agreement with the results of analyses of otolith age data (Hunter et al., 2016).

The model estimates of  $\hat{L}_\infty$  and  $\hat{k}$  were strongly correlated (figs. 5.8, 5.15 and 5.22), so future applications of the model could account for this correlation, perhaps by imposing some joint prior distribution on these parameters.

Informative prior distributions were used for all of the parameters (table 5.1). Many of the choices for the prior distributions were guided by plots of the survey data, previous estimates of growth parameters, and the value of minimum landing size. Feasible ranges for many parameters were known a priori, and parameters whose values were relatively uncertain were assigned priors with large variances so that a wider range of values were accessible to the model. Using informative prior distributions was necessary for some model parameters that were not directly informed by the data. In particular, the fishery selectivity and retention fraction parameters required informative priors; this was due to a lack of information about the length distribution of the catch and would probably not be necessary if the model were also fitted to catch-at-length data (data which is available for these VIa stocks). The influence that the choice of priors has upon the model results requires further investigation. The results would be more objective if less informative prior distributions were used, so we will try a range of priors, including non-informative uniform distributions, in future work on this model.

The survey catchability,  $\hat{q}$ , of whiting exhibited multimodality when given a less informative (higher variance) prior, so the variance of the prior for  $\hat{q}$  was reduced until this multimodal behaviour ceased. Although this multimodal behaviour was not observed when fitting to data on haddock, we used the same low-variance prior for consistency among species. On reflection, it would be better to revert back to a less informative prior for the  $\hat{q}$  of haddock. The model for cod was initially implemented after obtaining results for haddock and whiting, and the low-variance prior for  $\hat{q}$  was used for consistency, so we do not know whether  $\hat{q}$  for cod would exhibit multimodal behaviour under a less informative prior. The survey catchability was unique in displaying strong multimodal behaviour. A potential explanation is that the procedure used to collect the survey data changed in 1999, when the duration of individual survey tows decreased from 1 hour to 30 minutes. This decrease in the duration of survey tows could influence the catchability of fish in the path of the trawling gear. Adjusting

the model so that  $\hat{q}$  is estimated separately for the periods before and after 1999 (as in Wilberg and Bence, 2006) should enable the model to account for potential effects of this decrease in tow durations, hopefully resolving the issue of multimodality and enabling the successful use of less informative priors for  $\hat{q}$  in all species.

The  $R^{\text{mean}}$  and  $R^{\text{sd}}$  values, used to parameterise the hyper-priors for the mean number of recruits, were based on the recruitment estimates returned by the ICES age-based model (ICES, 2013b) because these represented our prior knowledge of recruitment.  $R^{\text{mean}}$  was derived from the mean of the age-based recruitment estimates for 1980–2012, and  $R^{\text{sd}}$  was chosen so that most of the age-based recruitment estimates were within the interquartile range of the hyper-prior distributions for the mean number of recruits,  $\mu^R$ . Even though these hyper-priors for  $\mu^R$  were given a large variance they could be made more general by using less informative distributions. Uniform hyper-priors for  $\mu^R$  should probably be used instead of the more informative log-normal distributions. Since hyper-priors tend to be less sensitive to misspecification than priors for primary model parameters, a change to uniform hyper-priors is unlikely to greatly influence the results. Uniform priors for  $\mu^R$  have already been tested for VIa and Clyde whiting, and we found very little change to the results.

The effective sample sizes that weighted the survey length distribution data were chosen to be substantially less than the actual sample sizes. Choosing low weights for the length distribution data reflects the fact that composition (length or age) data tend to be subject to substantial correlations that reduce effective sample sizes (Pennington and Vølstad, 1994; Francis, 2011). The values chosen for the weights were essentially arbitrary; the models were fitted with a range of weighting values, and the lowest weights to return reasonable fits to the length data were selected. Although choosing somewhat arbitrary effective samples sizes is not uncommon (Hulson et al., 2012), the undesirable arbitrariness could be lessened or eliminated by specifying weights using one of methods described by Francis (2011) or Hulson et al. (2012).

### 5.4.2 Firth of Clyde stocks

Given the current interest in restoring the Firth of Clyde fin-fish fisheries (McIntyre et al., 2012) there is a pressing need for assessment of these stocks. Stock assessments have not previously been conducted for Clyde fish stocks, so the results presented here represent a first attempt at doing so. These results are interesting and potentially useful, but should be treated with caution for several reasons. Firstly, the model applied to Clyde stocks is subject to all of the same criticisms discussed in the previous section for the area VIa results. Secondly, since no other stock assessments are available for comparison, it is difficult to gauge whether our results have provided realistic representations of the abundance of haddock and whiting within the Clyde. Thirdly, the values used for the observed discarded biomass in years subsequent to 1998 were crudely approximated (by assuming that discard rates presented in Stratoudakis et al., 2001, did not change after 1998) and do not constitute real data. The acquisition of accurate discard data will be critical in providing reliable assessments of Clyde fish stocks because discards from *Nephrops* vessels form such a large proportion of the total catch (McIntyre et al., 2012). Lastly, the hyper-priors used for the mean number of recruits,  $\mu^R$ , were not based on real prior knowledge, as the value of  $R^{\text{mean}}$  was guessed by dividing the estimates for the mean number of recruits in area VIa. This issue with the hyper-priors used for recruitment strengthens the case — discussed in the previous section — for replacing the log-normal distributions with uniform distributions; when stock assessments have not been previously conducted there is no basis for specifying informative hyper-priors for recruitment. Despite these issues — the need for further model refinement and acquiring recent discard data — the results were interesting and the performance of the model was encouraging.

The models returned decent fits to the data, although the discards of both haddock and whiting tended to be overestimated (figs. 5.23 and 5.28). The fishery selectivity curves suggest that haddock are less available to the fishery in the Clyde than they are in area VIa as a whole, which is probably due to Clyde fishers almost exclusively targeting *Nephrops*. The reverse was observed for whiting, as the fishery catchability was greater within the Clyde than area VIa; this is more difficult to explain, but may



be related to the high abundance of Clyde whiting and the relatively low value of this species. Analyses of survey data indicates that whiting are highly abundant within the Clyde (Heath and Speirs, 2012), so catches of whiting may be unavoidable in this region; and since whiting is not a particularly profitable species, demersal fishers in area VIa may attempt to avoid catches of whiting in favour of other species. The biomass of haddock present in the Clyde was estimated to have decreased from about 2000 t in 1995 to approximately 1000 t during 2001–2008, even though there was no trend in recruitment and despite the fishing mortality rate decreasing between 1998 and 2005. The model produced a decline in  $\hat{L}_\infty$  that substantially reduced the mean length-at-age of haddock, which explains the decrease in the biomass of the stock. Declines in mean length-at-age were also observed from analyses of survey age data (Hunter et al., 2016). There was a lot of uncertainty in the fishing mortality rate estimated for Clyde whiting, and the expected values were very high throughout the time series. This explains why the whiting stock consisted primarily of new recruits; most of the fish were caught before they could grow large. In fact, the weight of the total annual catches were estimated to be close to the biomass of the entire stock, so each year the harvestable stock comprises almost entirely of newly recruited individuals spawned by the previous year class. The large discrepancy between the fishing mortality rates estimated for Clyde haddock and whiting is unusual; it may be due to whiting being more available to the fishery, a misspecification of natural mortality, or whiting migrating out of the Clyde. The model returned a decline in  $\hat{L}_\infty$  that reduced mean lengths-at-age of whiting, but this did not cause a substantial decrease in stock biomass as stock numbers increased over time. Reductions in the mean lengths-at-age of Clyde whiting were also observed in the analyses of survey age data (Hunter et al., 2016).

### 5.4.3 Conclusions

The length-based model presented here extends the model of Sullivan et al. (1990) by eliminating the need for fishery catch-at-length data, accounting for time-varying growth rates, and using Bayesian methods to fit the model. Using survey length data to inform the model about the length structure of the assessed stocks should enable the

stage-structured assessment of a wide range of species. Using splines to model changes in the von Bertalanffy growth parameters worked well; the model successfully estimated declines in growth rates that are known to have occurred, and produced temporal trends in growth curves that were similar to those estimated using survey age data. The length-based models used here have produced results that are comparable to age-based models (ICES, 2013b) that have been relied upon to inform fishery management. Although more work is needed to improve some aspects of the model (particularly the specification of prior distributions), the results it has produced are promising, and there is potential for it to provide genuinely useful information about difficult-to-assess stocks.

## 5.5 Appendix

This appendix presents tables of the estimated values and credible intervals of each model parameter.

Table 5.2: Mean values, standard deviations and quantiles of the distributions produced for the scalar parameters by fitting the model to data on cod from ICES area VIa. The subscripts,  $_{123}$ , attached to  $L_\infty$  and  $k$  represent the three nodes of the splines corresponding to years 1980, 1996 and 2012 respectively.

Parameter	Mean	S.D.	2.5%	25%	75%	97.5%
$l_{50}^f$	29.41	4.57	21.36	25.80	32.55	39.05
$\beta^f$	8.63	6.13	0.70	2.89	14.27	19.39
$l_{50}^d$	34.72	0.96	32.77	34.07	35.31	36.62
$p^d$	$1.29 \times 10^{-3}$	$1.58 \times 10^{-3}$	$1.32 \times 10^{-6}$	$1.37 \times 10^{-4}$	$1.89 \times 10^{-3}$	$5.71 \times 10^{-3}$
$L_{\infty 1}$	108.08	9.13	94.59	101.52	113.54	128.87
$L_{\infty 2}$	119.65	7.78	105.82	114.34	124.73	135.60
$L_{\infty 3}$	134.20	9.22	116.34	128.08	140.40	152.93
$k_1$	0.164	0.023	0.120	0.148	0.180	0.212
$k_2$	0.156	0.018	0.126	0.144	0.167	0.194
$k_3$	0.102	0.011	0.083	0.094	0.109	0.128
$cv^g$	0.194	0.0089	0.177	0.188	0.200	0.212
$l^r$	19.40	0.48	18.44	19.06	19.80	20.21
$\sigma^r$	0.055	0.0046	0.050	0.051	0.058	0.066
$l^v$	36.64	1.27	34.11	35.81	37.49	39.01
$p^v$	$7.11 \times 10^{-5}$	$1.28 \times 10^{-4}$	$1.85 \times 10^{-6}$	$1.13 \times 10^{-5}$	$7.59 \times 10^{-5}$	$3.99 \times 10^{-4}$
$q$	1.16	0.10	0.94	1.09	1.23	1.33
$cv^L$	0.177	0.089	0.039	0.110	0.228	0.381
$cv^D$	0.838	0.327	0.311	0.574	1.071	1.507
$cv^N$	1.42	0.19	1.10	1.29	1.54	1.83
$\mu^R$	$1.11 \times 10^6$	$5.52 \times 10^5$	$3.91 \times 10^5$	$7.13 \times 10^5$	$1.37 \times 10^6$	$2.41 \times 10^6$
$\sigma^R$	3.31	0.36	2.67	3.05	3.54	4.11

Table 5.3: Mean values, standard deviations and quantiles of the distributions produced for the vector parameters by fitting the model to data on cod from ICES area VIa.

Year	Fishing mortality rate, $F_y$				Recruited numbers, $R_y$				Bulk discard proportion, $P_y^{\text{bulk}}$							
	Mean	S.D.	2.5%	75%	97.5%	Mean	S.D.	2.5%	75%	97.5%	Mean	S.D.	2.5%	75%	97.5%	
1980	0.211	0.065	0.122	0.166	0.241	1.48 × 10 <sup>7</sup>	2.51 × 10 <sup>7</sup>	4.42 × 10 <sup>5</sup>	1.05 × 10 <sup>6</sup>	6.08 × 10 <sup>6</sup>	0.037	0.039	0.00041	0.014	0.044	0.133
1981	0.216	0.054	0.132	0.178	0.246	1.26 × 10 <sup>4</sup>	1.75 × 10 <sup>4</sup>	1.14 × 10 <sup>2</sup>	1.80 × 10 <sup>3</sup>	1.60 × 10 <sup>4</sup>	0.026	0.025	0.00567	0.012	0.031	0.091
1982	0.220	0.057	0.131	0.182	0.250	4.27 × 10 <sup>3</sup>	5.96 × 10 <sup>3</sup>	3.90 × 10 <sup>1</sup>	7.93 × 10 <sup>2</sup>	5.36 × 10 <sup>3</sup>	0.048	0.038	0.01019	0.023	0.059	0.150
1983	0.261	0.072	0.151	0.210	0.304	3.59 × 10 <sup>4</sup>	1.75 × 10 <sup>5</sup>	5.51 × 10 <sup>1</sup>	1.16 × 10 <sup>3</sup>	1.48 × 10 <sup>4</sup>	0.019	0.019	0.00360	0.009	0.022	0.075
1984	0.316	0.086	0.180	0.255	0.365	2.73 × 10 <sup>7</sup>	9.57 × 10 <sup>6</sup>	1.32 × 10 <sup>7</sup>	2.05 × 10 <sup>7</sup>	3.26 × 10 <sup>7</sup>	0.015	0.024	0.00001	0.002	0.017	0.083
1985	0.348	0.094	0.200	0.280	0.403	2.05 × 10 <sup>4</sup>	2.97 × 10 <sup>4</sup>	1.43 × 10 <sup>2</sup>	3.00 × 10 <sup>3</sup>	2.65 × 10 <sup>4</sup>	0.082	0.054	0.01939	0.044	0.104	0.229
1986	0.330	0.115	0.159	0.245	0.399	1.83 × 10 <sup>4</sup>	3.39 × 10 <sup>4</sup>	7.37 × 10 <sup>1</sup>	1.61 × 10 <sup>3</sup>	1.90 × 10 <sup>4</sup>	0.046	0.047	0.00752	0.019	0.054	0.183
1987	0.464	0.103	0.292	0.391	0.526	6.28 × 10 <sup>7</sup>	1.56 × 10 <sup>7</sup>	3.75 × 10 <sup>7</sup>	5.17 × 10 <sup>7</sup>	7.22 × 10 <sup>7</sup>	0.038	0.050	0.00006	0.005	0.054	0.184
1988	0.434	0.091	0.292	0.368	0.486	2.73 × 10 <sup>5</sup>	2.51 × 10 <sup>5</sup>	9.94 × 10 <sup>3</sup>	1.18 × 10 <sup>5</sup>	3.45 × 10 <sup>5</sup>	0.035	0.033	0.000523	0.016	0.043	0.131
1989	0.443	0.090	0.294	0.378	0.492	5.51 × 10 <sup>6</sup>	4.12 × 10 <sup>6</sup>	3.97 × 10 <sup>5</sup>	2.29 × 10 <sup>6</sup>	7.90 × 10 <sup>6</sup>	0.124	0.073	0.01734	0.072	0.163	0.297
1990	0.423	0.108	0.245	0.345	0.488	9.33 × 10 <sup>3</sup>	1.50 × 10 <sup>4</sup>	6.15 × 10 <sup>1</sup>	1.35 × 10 <sup>3</sup>	1.13 × 10 <sup>4</sup>	0.085	0.070	0.01591	0.039	0.101	0.295
1991	0.481	0.119	0.274	0.399	0.556	2.90 × 10 <sup>6</sup>	1.67 × 10 <sup>6</sup>	3.41 × 10 <sup>5</sup>	1.71 × 10 <sup>6</sup>	3.80 × 10 <sup>6</sup>	0.065	0.052	0.00206	0.030	0.083	0.203
1992	0.508	0.119	0.315	0.421	0.576	2.47 × 10 <sup>7</sup>	7.02 × 10 <sup>6</sup>	1.24 × 10 <sup>7</sup>	2.00 × 10 <sup>7</sup>	2.89 × 10 <sup>7</sup>	0.073	0.075	0.00014	0.011	0.112	0.261
1993	0.487	0.107	0.317	0.407	0.549	6.24 × 10 <sup>5</sup>	3.87 × 10 <sup>5</sup>	1.61 × 10 <sup>5</sup>	3.58 × 10 <sup>5</sup>	7.93 × 10 <sup>5</sup>	0.022	0.027	0.00058	0.008	0.025	0.096
1994	0.490	0.106	0.326	0.411	0.549	1.22 × 10 <sup>7</sup>	5.15 × 10 <sup>6</sup>	4.26 × 10 <sup>6</sup>	8.55 × 10 <sup>6</sup>	1.51 × 10 <sup>7</sup>	0.052	0.059	0.00025	0.008	0.074	0.218
1995	0.512	0.103	0.350	0.439	0.572	3.74 × 10 <sup>6</sup>	2.46 × 10 <sup>6</sup>	5.87 × 10 <sup>5</sup>	1.89 × 10 <sup>6</sup>	5.08 × 10 <sup>6</sup>	0.018	0.028	0.00005	0.002	0.022	0.107
1996	0.598	0.101	0.423	0.531	0.658	6.94 × 10 <sup>4</sup>	7.84 × 10 <sup>4</sup>	1.22 × 10 <sup>3</sup>	2.15 × 10 <sup>4</sup>	9.03 × 10 <sup>4</sup>	0.014	0.017	0.00139	0.006	0.016	0.049
1997	0.672	0.109	0.486	0.598	0.740	6.63 × 10 <sup>6</sup>	2.34 × 10 <sup>6</sup>	3.10 × 10 <sup>6</sup>	4.94 × 10 <sup>6</sup>	7.72 × 10 <sup>6</sup>	0.041	0.050	0.00022	0.008	0.056	0.184
1998	0.675	0.105	0.495	0.601	0.738	9.38 × 10 <sup>6</sup>	2.97 × 10 <sup>6</sup>	5.12 × 10 <sup>6</sup>	7.27 × 10 <sup>6</sup>	1.09 × 10 <sup>7</sup>	0.045	0.054	0.00009	0.006	0.061	0.196
1999	0.598	0.115	0.426	0.514	0.661	6.35 × 10 <sup>4</sup>	5.48 × 10 <sup>4</sup>	6.72 × 10 <sup>3</sup>	3.07 × 10 <sup>4</sup>	7.89 × 10 <sup>4</sup>	0.037	0.047	0.00344	0.012	0.038	0.166
2000	0.628	0.121	0.457	0.540	0.692	1.60 × 10 <sup>6</sup>	1.52 × 10 <sup>6</sup>	4.11 × 10 <sup>5</sup>	8.39 × 10 <sup>5</sup>	1.85 × 10 <sup>6</sup>	0.207	0.104	0.01585	0.135	0.273	0.427
2001	0.695	0.136	0.495	0.593	0.775	7.76 × 10 <sup>4</sup>	9.60 × 10 <sup>4</sup>	7.81 × 10 <sup>3</sup>	2.91 × 10 <sup>4</sup>	9.37 × 10 <sup>4</sup>	0.072	0.070	0.01187	0.031	0.085	0.268
2002	0.907	0.126	0.701	0.821	0.979	1.21 × 10 <sup>6</sup>	6.09 × 10 <sup>5</sup>	4.31 × 10 <sup>5</sup>	7.71 × 10 <sup>5</sup>	1.50 × 10 <sup>6</sup>	0.105	0.080	0.00027	0.040	0.160	0.284
2003	1.024	0.147	0.752	0.924	1.117	2.39 × 10 <sup>4</sup>	2.24 × 10 <sup>4</sup>	1.73 × 10 <sup>3</sup>	8.96 × 10 <sup>3</sup>	3.10 × 10 <sup>4</sup>	0.047	0.036	0.00794	0.023	0.060	0.149
2004	1.080	0.170	0.771	0.965	1.198	1.41 × 10 <sup>6</sup>	4.96 × 10 <sup>5</sup>	7.33 × 10 <sup>5</sup>	1.06 × 10 <sup>6</sup>	1.63 × 10 <sup>6</sup>	0.073	0.080	0.00016	0.011	0.106	0.274
2005	1.130	0.175	0.807	1.008	1.245	2.63 × 10 <sup>3</sup>	4.14 × 10 <sup>3</sup>	2.23 × 10 <sup>1</sup>	3.97 × 10 <sup>2</sup>	3.04 × 10 <sup>3</sup>	0.104	0.064	0.02665	0.060	0.131	0.269
2006	1.133	0.177	0.821	1.009	1.245	8.53 × 10 <sup>6</sup>	2.41 × 10 <sup>6</sup>	5.38 × 10 <sup>6</sup>	6.88 × 10 <sup>6</sup>	9.44 × 10 <sup>6</sup>	0.144	0.141	0.00031	0.029	0.223	0.484
2007	1.142	0.184	0.816	1.019	1.259	3.32 × 10 <sup>3</sup>	4.24 × 10 <sup>3</sup>	2.42 × 10 <sup>1</sup>	6.66 × 10 <sup>2</sup>	4.25 × 10 <sup>3</sup>	0.691	0.083	0.49971	0.644	0.750	0.827
2008	1.165	0.198	0.793	1.032	1.288	1.48 × 10 <sup>3</sup>	3.30 × 10 <sup>3</sup>	1.20 × 10 <sup>1</sup>	2.10 × 10 <sup>2</sup>	1.67 × 10 <sup>3</sup>	0.371	0.126	0.13324	0.284	0.464	0.615
2009	1.146	0.222	0.746	0.989	1.288	5.33 × 10 <sup>6</sup>	1.61 × 10 <sup>6</sup>	2.99 × 10 <sup>6</sup>	4.21 × 10 <sup>6</sup>	6.17 × 10 <sup>6</sup>	0.227	0.171	0.00232	0.070	0.358	0.567
2010	1.111	0.244	0.657	0.937	1.262	1.79 × 10 <sup>6</sup>	8.33 × 10 <sup>5</sup>	6.27 × 10 <sup>5</sup>	1.19 × 10 <sup>6</sup>	2.23 × 10 <sup>6</sup>	0.512	0.158	0.13374	0.417	0.628	0.757
2011	1.089	0.264	0.615	0.964	1.256	4.56 × 10 <sup>6</sup>	1.91 × 10 <sup>6</sup>	1.30 × 10 <sup>6</sup>	3.25 × 10 <sup>6</sup>	5.60 × 10 <sup>6</sup>	0.536	0.155	0.14160	0.450	0.651	0.766
2012	1.067	0.286	0.537	0.874	1.241	3.77 × 10 <sup>5</sup>	1.41 × 10 <sup>6</sup>	1.43 × 10 <sup>2</sup>	5.47 × 10 <sup>3</sup>	7.58 × 10 <sup>4</sup>	0.611	0.143	0.22246	0.541	0.713	0.811

Table 5.4: Mean values, standard deviations and quantiles of the distributions produced for the scalar parameters by fitting the model to data on haddock from ICES area VIa. The subscripts,  $123$ , attached to  $L_\infty$  and  $k$  represent the three nodes of the splines corresponding to years 1980, 1996 and 2012 respectively.

Parameter	Mean	S.D.	2.5%	25%	75%	97.5%
$l_{50}^f$	22.40	1.81	18.41	21.38	23.64	25.62
$\beta^f$	4.72	2.58	0.99	2.79	6.13	10.68
$l_{50}^d$	28.60	0.72	27.30	28.10	29.06	30.07
$p^d$	$3.32 \times 10^{-3}$	$2.12 \times 10^{-3}$	$2.11 \times 10^{-4}$	$1.51 \times 10^{-3}$	$4.79 \times 10^{-3}$	$7.82 \times 10^{-3}$
$L_{\infty 1}$	51.90	1.85	48.51	50.64	53.05	55.71
$L_{\infty 2}$	38.09	0.89	36.53	37.47	38.69	39.88
$L_{\infty 3}$	41.84	0.91	40.27	41.12	42.40	43.83
$k_1$	0.161	0.016	0.132	0.150	0.171	0.195
$k_2$	0.272	0.020	0.235	0.259	0.286	0.312
$k_3$	0.277	0.020	0.239	0.263	0.290	0.319
$cv^g$	0.326	0.015	0.292	0.315	0.336	0.354
$l^r$	17.33	0.17	17.00	17.21	17.45	17.67
$\sigma^r$	0.105	0.0050	0.096	0.101	0.108	0.115
$l^v$	22.62	0.768	21.29	22.09	23.07	24.32
$p^v$	$8.75 \times 10^{-4}$	$1.15 \times 10^{-3}$	$1.34 \times 10^{-5}$	$1.35 \times 10^{-4}$	$1.13 \times 10^{-3}$	$4.34 \times 10^{-3}$
$q$	1.12	0.097	0.924	1.05	1.19	1.30
$cv^L$	0.301	0.094	0.152	0.230	0.359	0.507
$cv^D$	0.560	0.207	0.277	0.409	0.667	0.105
$cv^N$	0.729	0.107	0.557	0.650	0.792	0.972
$\mu^R$	$3.92 \times 10^7$	$1.52 \times 10^7$	$1.70 \times 10^7$	$2.79 \times 10^7$	$4.76 \times 10^7$	$7.32 \times 10^7$
$\sigma^R$	2.43	0.307	1.88	2.22	2.63	3.08

Table 5.5: Mean values, standard deviations and quantiles of the distributions produced for the vector parameters by fitting the model to data on haddock from ICES area VIa.

Year	Fishing mortality rate, $F_y$					Recruited numbers, $R_y$					Bulk discard proportion, $p_y^{\text{bulk}}$						
	Mean	S.D.	2.5%	75%	97.5%	Mean	S.D.	2.5%	75%	97.5%	Mean	S.D.	2.5%	75%	97.5%		
1980	0.383	0.104	0.216	0.308	0.444	0.618	$7.04 \times 10^8$	$1.24 \times 10^8$	$5.08 \times 10^8$	$6.22 \times 10^8$	$7.69 \times 10^8$	0.053	0.073	0.00004	0.0045	0.072	0.281
1981	0.396	0.101	0.233	0.327	0.454	0.628	$1.75 \times 10^7$	$2.03 \times 10^7$	$2.34 \times 10^5$	$4.45 \times 10^6$	$2.20 \times 10^7$	0.173	0.145	0.00065	0.0468	0.275	0.499
1982	0.477	0.107	0.303	0.401	0.544	0.711	$7.19 \times 10^5$	$8.15 \times 10^5$	$2.55 \times 10^4$	$2.13 \times 10^5$	$9.40 \times 10^5$	0.213	0.112	0.03333	0.1294	0.287	0.467
1983	0.626	0.123	0.412	0.541	0.701	0.886	$4.18 \times 10^5$	$6.54 \times 10^5$	$9.66 \times 10^3$	$7.93 \times 10^4$	$4.90 \times 10^5$	0.200	0.084	0.07039	0.1400	0.245	0.400
1984	0.772	0.130	0.535	0.684	0.854	1.050	$5.90 \times 10^8$	$1.39 \times 10^8$	$3.71 \times 10^8$	$4.93 \times 10^8$	$6.65 \times 10^8$	0.062	0.073	0.00011	0.0087	0.092	0.267
1985	0.817	0.147	0.551	0.715	0.907	1.143	$1.04 \times 10^8$	$4.41 \times 10^7$	$4.18 \times 10^7$	$7.09 \times 10^7$	$1.28 \times 10^8$	0.128	0.128	0.00031	0.0231	0.195	0.454
1986	0.840	0.161	0.533	0.727	0.942	1.175	$2.22 \times 10^7$	$1.73 \times 10^7$	$4.76 \times 10^6$	$1.08 \times 10^7$	$2.77 \times 10^7$	0.154	0.125	0.00077	0.0514	0.226	0.456
1987	0.913	0.160	0.632	0.800	1.010	1.250	$4.67 \times 10^8$	$1.14 \times 10^8$	$3.08 \times 10^8$	$3.89 \times 10^8$	$5.16 \times 10^8$	0.065	0.080	0.00008	0.0074	0.093	0.277
1988	0.943	0.161	0.665	0.827	1.042	1.294	$1.62 \times 10^7$	$1.01 \times 10^7$	$4.23 \times 10^6$	$3.32 \times 10^6$	$2.06 \times 10^7$	0.073	0.082	0.00009	0.0106	0.105	0.298
1989	0.987	0.169	0.671	0.868	1.089	1.349	$8.40 \times 10^5$	$9.16 \times 10^5$	$3.32 \times 10^4$	$2.40 \times 10^5$	$1.10 \times 10^6$	0.085	0.078	0.00073	0.0252	0.123	0.278
1990	1.043	0.179	0.709	0.919	1.163	1.418	$1.87 \times 10^8$	$5.47 \times 10^7$	$1.05 \times 10^8$	$1.49 \times 10^8$	$2.17 \times 10^8$	0.061	0.074	0.00007	0.0075	0.086	0.272
1991	1.068	0.182	0.735	0.942	1.189	1.435	$1.44 \times 10^8$	$5.84 \times 10^7$	$5.21 \times 10^7$	$1.03 \times 10^8$	$1.77 \times 10^8$	0.073	0.086	0.00010	0.0103	0.108	0.303
1992	1.067	0.181	0.747	0.940	1.190	1.442	$3.57 \times 10^8$	$1.21 \times 10^8$	$1.99 \times 10^8$	$2.75 \times 10^8$	$4.12 \times 10^8$	0.062	0.072	0.00009	0.0091	0.087	0.257
1993	1.075	0.171	0.776	0.956	1.186	1.428	$2.65 \times 10^8$	$8.99 \times 10^7$	$1.44 \times 10^8$	$2.07 \times 10^8$	$3.03 \times 10^8$	0.062	0.074	0.00011	0.0076	0.089	0.264
1994	1.053	0.174	0.722	0.935	1.163	1.399	$4.00 \times 10^7$	$2.35 \times 10^7$	$1.23 \times 10^7$	$2.43 \times 10^7$	$4.82 \times 10^7$	0.113	0.116	0.00011	0.0173	0.176	0.407
1995	1.047	0.172	0.716	0.933	1.166	1.392	$2.83 \times 10^8$	$9.23 \times 10^7$	$1.44 \times 10^8$	$2.22 \times 10^8$	$3.25 \times 10^8$	0.077	0.086	0.00021	0.0107	0.117	0.306
1996	1.048	0.168	0.736	0.932	1.155	1.392	$1.70 \times 10^8$	$7.65 \times 10^7$	$7.65 \times 10^7$	$1.19 \times 10^8$	$1.98 \times 10^8$	0.063	0.076	0.00010	0.0089	0.090	0.275
1997	1.040	0.164	0.722	0.930	1.142	1.377	$1.24 \times 10^8$	$5.77 \times 10^7$	$5.38 \times 10^7$	$8.33 \times 10^7$	$1.49 \times 10^8$	0.064	0.077	0.00037	0.0096	0.090	0.282
1998	1.042	0.161	0.737	0.933	1.145	1.378	$1.85 \times 10^8$	$6.55 \times 10^7$	$9.71 \times 10^7$	$1.40 \times 10^8$	$2.14 \times 10^8$	0.047	0.057	0.00009	0.0061	0.068	0.205
1999	0.996	0.156	0.698	0.890	1.097	1.306	$1.86 \times 10^7$	$1.17 \times 10^7$	$5.30 \times 10^6$	$1.09 \times 10^7$	$2.31 \times 10^7$	0.065	0.078	0.00014	0.0092	0.096	0.275
2000	0.889	0.154	0.607	0.784	0.985	1.206	$3.40 \times 10^8$	$1.14 \times 10^8$	$1.90 \times 10^8$	$2.63 \times 10^8$	$3.93 \times 10^8$	0.081	0.088	0.00018	0.0142	0.122	0.316
2001	0.710	0.155	0.417	0.606	0.813	1.039	$1.71 \times 10^8$	$5.93 \times 10^7$	$7.92 \times 10^7$	$1.30 \times 10^8$	$2.04 \times 10^8$	0.114	0.120	0.00021	0.0186	0.179	0.426
2002	0.556	0.144	0.304	0.453	0.650	0.862	$4.88 \times 10^7$	$2.78 \times 10^7$	$1.41 \times 10^7$	$2.91 \times 10^7$	$6.16 \times 10^7$	0.208	0.153	0.00047	0.0751	0.314	0.523
2003	0.395	0.136	0.180	0.296	0.473	0.703	$1.22 \times 10^8$	$3.87 \times 10^7$	$5.77 \times 10^7$	$9.41 \times 10^7$	$1.45 \times 10^8$	0.163	0.138	0.00056	0.0430	0.251	0.472
2004	0.276	0.114	0.107	0.192	0.337	0.550	$5.77 \times 10^7$	$2.72 \times 10^7$	$1.83 \times 10^7$	$3.73 \times 10^7$	$7.31 \times 10^7$	0.306	0.176	0.00542	0.1717	0.439	0.629
2005	0.225	0.096	0.088	0.154	0.281	0.445	$5.74 \times 10^7$	$2.56 \times 10^7$	$2.15 \times 10^7$	$3.90 \times 10^7$	$7.12 \times 10^7$	0.307	0.170	0.00773	0.1698	0.436	0.606
2006	0.243	0.080	0.118	0.187	0.287	0.418	$1.54 \times 10^8$	$4.80 \times 10^7$	$7.79 \times 10^7$	$1.22 \times 10^8$	$1.80 \times 10^8$	0.175	0.142	0.00050	0.0493	0.274	0.477
2007	0.164	0.066	0.070	0.117	0.199	0.317	$6.39 \times 10^7$	$3.03 \times 10^7$	$1.47 \times 10^7$	$4.30 \times 10^7$	$7.99 \times 10^7$	0.274	0.169	0.00365	0.1403	0.391	0.602
2008	0.099	0.043	0.041	0.068	0.199	0.317	$1.33 \times 10^6$	$1.94 \times 10^6$	$2.94 \times 10^4$	$2.32 \times 10^5$	$1.62 \times 10^6$	0.185	0.122	0.00167	0.0882	0.266	0.457
2009	0.111	0.045	0.045	0.079	0.137	0.222	$4.48 \times 10^5$	$7.95 \times 10^5$	$1.32 \times 10^4$	$1.07 \times 10^5$	$5.39 \times 10^5$	0.314	0.117	0.09451	0.2318	0.388	0.555
2010	0.127	0.051	0.051	0.090	0.158	0.249	$1.31 \times 10^8$	$4.48 \times 10^7$	$6.07 \times 10^7$	$9.92 \times 10^7$	$1.55 \times 10^8$	0.322	0.149	0.03144	0.2130	0.426	0.603
2011	0.080	0.039	0.031	0.052	0.098	0.176	$4.22 \times 10^5$	$5.50 \times 10^5$	$1.15 \times 10^4$	$1.18 \times 10^5$	$5.07 \times 10^5$	0.312	0.159	0.01139	0.1989	0.421	0.626
2012	0.128	0.053	0.055	0.090	0.155	0.258	$1.07 \times 10^6$	$1.58 \times 10^6$	$3.18 \times 10^4$	$2.81 \times 10^5$	$1.28 \times 10^6$	0.089	0.065	0.00179	0.0447	0.121	0.248

Table 5.6: Mean values, standard deviations and quantiles of the distributions produced for the scalar parameters by fitting the model to data on whiting from ICES area VIa. The subscripts,  $_{123}$ , attached to  $L_\infty$  and  $k$  represent the three nodes of the splines corresponding to years 1980, 1996 and 2012 respectively.

Parameter	Mean	S.D.	2.5%	25%	75%	97.5%
$l_{50}^f$	23.92	2.98	18.20	21.94	25.95	29.69
$\beta^f$	9.33	3.96	2.08	6.53	11.70	17.99
$l_{50}^d$	26.39	0.77	24.84	25.89	26.89	27.81
$p^d$	$1.92 \times 10^{-3}$	$1.90 \times 10^{-3}$	$5.10 \times 10^{-6}$	$3.85 \times 10^4$	$2.92 \times 10^{-3}$	$6.68 \times 10^{-3}$
$L_{\infty 1}$	38.34	1.04	36.50	37.65	38.97	40.61
$L_{\infty 2}$	33.46	0.95	31.79	32.79	34.04	35.56
$L_{\infty 3}$	33.44	1.29	31.00	32.54	34.34	36.02
$k_1$	0.334	0.034	0.271	0.310	0.357	0.405
$k_2$	0.329	0.038	0.257	0.303	0.354	0.405
$k_3$	0.309	0.046	0.230	0.276	0.338	0.408
$cv^g$	0.281	0.025	0.230	0.265	0.298	0.327
$l^r$	16.37	0.20	15.98	16.23	16.50	16.76
$\sigma^r$	0.123	0.0063	0.111	0.118	0.127	0.135
$l^v$	20.36	0.62	19.26	19.95	20.71	21.74
$p^v$	$1.38 \times 10^{-3}$	$1.44 \times 10^{-3}$	$4.52 \times 10^{-5}$	$3.40 \times 10^{-4}$	$1.95 \times 10^{-3}$	$5.54 \times 10^{-3}$
$q$	0.94	0.14	0.64	0.84	1.04	1.20
$cv^L$	0.224	0.077	0.100	0.167	0.272	0.392
$cv^D$	0.432	0.102	0.265	0.361	0.492	0.666
$cv^N$	0.762	0.145	0.514	0.658	0.852	1.088
$\mu^R$	$2.31 \times 10^8$	$4.82 \times 10^7$	$1.52 \times 10^8$	$1.97 \times 10^8$	$2.59 \times 10^8$	$3.39 \times 10^8$
$\sigma^R$	0.88	0.16	0.62	0.77	0.98	1.22

Table 5.7: Mean values, standard deviations and quantiles of the distributions produced for the vector parameters by fitting the model to data on whiting from ICES area VIa.

Year	Fishing mortality rate, $F_y$				Recruited numbers, $R_y$				Bulk discard proportion, $p_y^{\text{bulk}}$								
	Mean	S.D.	2.5%	75%	97.5%	Mean	S.D.	2.5%	75%	97.5%	Mean	S.D.	2.5%	75%	97.5%		
1980	0.145	0.046	0.075	0.112	0.171	0.256	7.31 × 10 <sup>8</sup>	2.23 × 10 <sup>8</sup>	4.01 × 10 <sup>8</sup>	5.67 × 10 <sup>8</sup>	8.49 × 10 <sup>8</sup>	0.031	0.041	0.00006	0.0037	0.041	0.149
1981	0.151	0.052	0.074	0.114	0.179	0.278	3.81 × 10 <sup>8</sup>	1.16 × 10 <sup>8</sup>	1.85 × 10 <sup>8</sup>	2.99 × 10 <sup>8</sup>	4.52 × 10 <sup>8</sup>	0.056	0.057	0.00014	0.0114	0.084	0.202
1982	0.263	0.074	0.145	0.209	0.308	0.432	6.93 × 10 <sup>7</sup>	3.78 × 10 <sup>7</sup>	1.90 × 10 <sup>7</sup>	4.22 × 10 <sup>7</sup>	8.82 × 10 <sup>7</sup>	0.235	0.092	0.06463	0.1728	0.293	0.427
1983	0.428	0.097	0.263	0.359	0.491	0.642	2.27 × 10 <sup>8</sup>	8.00 × 10 <sup>7</sup>	1.03 × 10 <sup>8</sup>	1.69 × 10 <sup>8</sup>	2.72 × 10 <sup>8</sup>	0.173	0.100	0.00571	0.0987	0.239	0.383
1984	0.561	0.113	0.366	0.480	0.632	0.808	3.47 × 10 <sup>8</sup>	9.68 × 10 <sup>7</sup>	1.89 × 10 <sup>8</sup>	2.78 × 10 <sup>8</sup>	4.05 × 10 <sup>8</sup>	0.041	0.049	0.00007	0.0056	0.059	0.177
1985	0.625	0.125	0.407	0.539	0.704	0.893	3.50 × 10 <sup>8</sup>	8.72 × 10 <sup>7</sup>	2.02 × 10 <sup>8</sup>	2.87 × 10 <sup>8</sup>	4.04 × 10 <sup>8</sup>	0.050	0.059	0.00008	0.0061	0.073	0.215
1986	0.635	0.142	0.385	0.534	0.729	0.938	1.73 × 10 <sup>8</sup>	6.86 × 10 <sup>7</sup>	6.96 × 10 <sup>7</sup>	1.23 × 10 <sup>8</sup>	2.12 × 10 <sup>8</sup>	0.064	0.075	0.00006	0.0071	0.097	0.264
1987	0.732	0.141	0.474	0.633	0.822	1.038	8.82 × 10 <sup>8</sup>	1.93 × 10 <sup>8</sup>	5.53 × 10 <sup>8</sup>	7.45 × 10 <sup>8</sup>	9.95 × 10 <sup>8</sup>	0.046	0.059	0.00005	0.0053	0.063	0.206
1988	0.728	0.154	0.451	0.620	0.826	1.046	1.63 × 10 <sup>8</sup>	6.77 × 10 <sup>7</sup>	5.44 × 10 <sup>7</sup>	1.14 × 10 <sup>8</sup>	2.00 × 10 <sup>8</sup>	0.129	0.111	0.00058	0.0336	0.201	0.391
1989	0.734	0.162	0.451	0.618	0.834	1.072	1.63 × 10 <sup>8</sup>	5.85 × 10 <sup>7</sup>	7.30 × 10 <sup>7</sup>	1.21 × 10 <sup>8</sup>	1.96 × 10 <sup>8</sup>	0.196	0.130	0.00100	0.0836	0.291	0.462
1990	0.739	0.167	0.445	0.618	0.840	1.102	2.81 × 10 <sup>8</sup>	8.78 × 10 <sup>7</sup>	1.38 × 10 <sup>8</sup>	2.20 × 10 <sup>8</sup>	3.31 × 10 <sup>8</sup>	0.088	0.094	0.00013	0.0129	0.138	0.327
1991	0.756	0.166	0.471	0.640	0.854	1.134	3.93 × 10 <sup>8</sup>	1.27 × 10 <sup>8</sup>	2.07 × 10 <sup>8</sup>	3.04 × 10 <sup>8</sup>	4.59 × 10 <sup>8</sup>	0.046	0.059	0.00005	0.0050	0.065	0.198
1992	0.740	0.171	0.443	0.616	0.845	1.119	5.17 × 10 <sup>8</sup>	1.37 × 10 <sup>8</sup>	2.98 × 10 <sup>8</sup>	4.23 × 10 <sup>8</sup>	5.93 × 10 <sup>8</sup>	0.090	0.099	0.00012	0.0121	0.135	0.358
1993	0.709	0.173	0.413	0.586	0.818	1.083	2.57 × 10 <sup>8</sup>	9.01 × 10 <sup>7</sup>	1.18 × 10 <sup>8</sup>	1.93 × 10 <sup>8</sup>	3.06 × 10 <sup>8</sup>	0.070	0.082	0.00011	0.0087	0.103	0.291
1994	0.700	0.176	0.398	0.578	0.806	1.090	4.23 × 10 <sup>8</sup>	1.30 × 10 <sup>8</sup>	2.23 × 10 <sup>8</sup>	3.29 × 10 <sup>8</sup>	4.98 × 10 <sup>8</sup>	0.063	0.074	0.00013	0.0079	0.091	0.265
1995	0.764	0.170	0.467	0.646	0.870	1.125	2.82 × 10 <sup>8</sup>	1.02 × 10 <sup>8</sup>	1.24 × 10 <sup>8</sup>	2.07 × 10 <sup>8</sup>	3.41 × 10 <sup>8</sup>	0.082	0.089	0.00016	0.0118	0.127	0.308
1996	0.857	0.157	0.580	0.748	0.957	1.191	4.10 × 10 <sup>8</sup>	1.18 × 10 <sup>8</sup>	2.16 × 10 <sup>8</sup>	3.28 × 10 <sup>8</sup>	4.76 × 10 <sup>8</sup>	0.057	0.066	0.00012	0.0076	0.082	0.238
1997	0.907	0.156	0.620	0.800	1.004	1.241	2.60 × 10 <sup>8</sup>	9.78 × 10 <sup>7</sup>	1.16 × 10 <sup>8</sup>	1.91 × 10 <sup>8</sup>	3.11 × 10 <sup>8</sup>	0.058	0.070	0.00006	0.0066	0.083	0.247
1998	0.930	0.158	0.631	0.820	1.030	1.252	4.45 × 10 <sup>8</sup>	1.20 × 10 <sup>8</sup>	2.57 × 10 <sup>8</sup>	3.62 × 10 <sup>8</sup>	5.12 × 10 <sup>8</sup>	0.097	0.101	0.00023	0.0153	0.151	0.346
1999	0.918	0.167	0.596	0.807	1.026	1.265	1.26 × 10 <sup>8</sup>	5.15 × 10 <sup>7</sup>	5.07 × 10 <sup>7</sup>	8.94 × 10 <sup>7</sup>	1.54 × 10 <sup>8</sup>	0.073	0.081	0.00009	0.0107	0.109	0.287
2000	0.888	0.170	0.568	0.769	0.996	1.240	4.17 × 10 <sup>8</sup>	1.15 × 10 <sup>8</sup>	2.40 × 10 <sup>8</sup>	3.39 × 10 <sup>8</sup>	4.79 × 10 <sup>8</sup>	0.169	0.147	0.00016	0.0330	0.276	0.494
2001	0.763	0.181	0.433	0.636	0.876	1.148	1.47 × 10 <sup>8</sup>	5.39 × 10 <sup>7</sup>	6.99 × 10 <sup>7</sup>	1.09 × 10 <sup>8</sup>	1.73 × 10 <sup>8</sup>	0.164	0.138	0.00048	0.0412	0.257	0.475
2002	0.621	0.183	0.290	0.488	0.738	1.013	1.30 × 10 <sup>8</sup>	5.39 × 10 <sup>7</sup>	5.72 × 10 <sup>7</sup>	9.28 × 10 <sup>7</sup>	1.56 × 10 <sup>8</sup>	0.204	0.149	0.00041	0.0738	0.312	0.509
2003	0.452	0.173	0.181	0.323	0.558	0.854	1.46 × 10 <sup>8</sup>	6.66 × 10 <sup>7</sup>	5.60 × 10 <sup>7</sup>	9.92 × 10 <sup>7</sup>	1.79 × 10 <sup>8</sup>	0.068	0.082	0.00013	0.0080	0.102	0.290
2004	0.347	0.137	0.149	0.245	0.422	0.689	1.97 × 10 <sup>8</sup>	8.40 × 10 <sup>7</sup>	7.91 × 10 <sup>7</sup>	1.37 × 10 <sup>8</sup>	2.41 × 10 <sup>8</sup>	0.208	0.158	0.00105	0.0665	0.319	0.537
2005	0.167	0.109	0.053	0.094	0.205	0.463	1.03 × 10 <sup>8</sup>	4.82 × 10 <sup>7</sup>	3.65 × 10 <sup>7</sup>	6.89 × 10 <sup>7</sup>	1.27 × 10 <sup>8</sup>	0.305	0.193	0.00259	0.1434	0.454	0.668
2006	0.159	0.077	0.063	0.109	0.192	0.375	1.13 × 10 <sup>8</sup>	4.55 × 10 <sup>7</sup>	5.02 × 10 <sup>7</sup>	8.06 × 10 <sup>7</sup>	1.35 × 10 <sup>8</sup>	0.364	0.181	0.00739	0.2403	0.500	0.673
2007	0.121	0.057	0.050	0.082	0.144	0.272	5.78 × 10 <sup>7</sup>	2.67 × 10 <sup>7</sup>	2.16 × 10 <sup>7</sup>	3.91 × 10 <sup>7</sup>	7.09 × 10 <sup>7</sup>	0.120	0.115	0.00035	0.0246	0.182	0.394
2008	0.131	0.054	0.059	0.094	0.156	0.273	9.10 × 10 <sup>7</sup>	3.84 × 10 <sup>7</sup>	3.76 × 10 <sup>7</sup>	6.33 × 10 <sup>7</sup>	1.09 × 10 <sup>8</sup>	0.105	0.104	0.00022	0.0199	0.159	0.363
2009	0.149	0.056	0.067	0.109	0.180	0.278	1.34 × 10 <sup>8</sup>	5.68 × 10 <sup>7</sup>	5.13 × 10 <sup>7</sup>	9.32 × 10 <sup>7</sup>	1.64 × 10 <sup>8</sup>	0.087	0.093	0.00020	0.0137	0.131	0.337
2010	0.111	0.048	0.043	0.077	0.136	0.226	3.31 × 10 <sup>8</sup>	1.34 × 10 <sup>8</sup>	1.45 × 10 <sup>8</sup>	2.34 × 10 <sup>8</sup>	4.01 × 10 <sup>8</sup>	0.196	0.168	0.00049	0.0460	0.314	0.572
2011	0.054	0.029	0.019	0.034	0.067	0.127	7.10 × 10 <sup>7</sup>	4.28 × 10 <sup>7</sup>	1.68 × 10 <sup>7</sup>	4.02 × 10 <sup>7</sup>	9.12 × 10 <sup>7</sup>	0.191	0.162	0.00077	0.0491	0.303	0.561
2012	0.067	0.035	0.022	0.042	0.082	0.153	4.96 × 10 <sup>8</sup>	2.59 × 10 <sup>8</sup>	1.62 × 10 <sup>8</sup>	3.21 × 10 <sup>8</sup>	6.09 × 10 <sup>8</sup>	0.230	0.180	0.00090	0.0648	0.368	0.605



Table 5.8: Mean values, standard deviations and quantiles of the distributions produced for the scalar parameters by fitting the model to data on haddock from the Firth of Clyde. The subscripts,  $_{123}$ , attached to  $L_\infty$  and  $k$  represent the three nodes of the splines corresponding to years 1994, 2001 and 2008.

Parameter	Mean	S.D.	2.5%	25%	75%	97.5%
$l_{50}^f$	30.78	3.13	25.29	28.64	32.65	37.91
$\beta^f$	6.78	3.62	1.43	4.08	8.90	15.57
$l_{50}^d$	30.46	0.85	28.83	29.89	31.04	32.16
$p^d$	$1.70 \times 10^{-3}$	$1.70 \times 10^{-3}$	$3.70 \times 10^{-6}$	$3.66 \times 10^{-4}$	$2.56 \times 10^{-3}$	$5.96 \times 10^{-3}$
$L_{\infty 1}$	42.68	7.46	35.43	36.14	49.76	56.92
$L_{\infty 2}$	37.57	2.70	33.12	35.27	39.24	43.66
$L_{\infty 3}$	30.35	2.24	25.73	29.03	31.81	34.67
$k_1$	0.546	0.202	0.251	0.337	0.725	0.857
$k_2$	0.345	0.077	0.220	0.286	0.400	0.507
$k_3$	0.400	0.066	0.282	0.355	0.442	0.545
$cv^g$	0.183	0.031	0.126	0.162	0.204	0.244
$l^r$	19.49	0.49	18.54	19.14	19.83	20.40
$\sigma^r$	0.110	0.0083	0.096	0.104	0.115	0.128
$l^v$	19.32	1.37	16.03	18.53	20.36	21.19
$p^v$	$1.20 \times 10^{-4}$	$5.34 \times 10^{-4}$	$1.87 \times 10^{-12}$	$1.05 \times 10^{-9}$	$4.93 \times 10^{-6}$	$1.42 \times 10^{-3}$
$q$	0.96	0.13	0.70	0.87	1.05	1.20
$cv^L$	0.310	0.108	0.108	0.235	0.377	0.542
$cv^D$	0.436	0.148	0.189	0.334	0.523	0.780
$cv^N$	0.643	0.177	0.361	0.514	0.748	1.047
$\mu^R$	$9.44 \times 10^5$	$3.54 \times 10^5$	$4.42 \times 10^5$	$6.95 \times 10^5$	$1.14 \times 10^6$	$1.82 \times 10^6$
$\sigma^R$	1.28	0.26	0.86	1.10	1.43	1.85

Table 5.9: Mean values, standard deviations and quantiles of the distributions produced for the vector parameters by fitting the model to data on Firth of Clyde haddock.

Year	Fishing mortality rate, $F_y$				Recruited numbers, $R_y$				Bulk discard proportion, $p_y^{\text{bulk}}$									
	Mean	S.D.	2.5%	75%	97.5%	Mean	S.D.	2.5%	75%	97.5%	Mean	S.D.	2.5%	75%	97.5%			
1994	0.341	0.164	0.134	0.228	0.417	0.761	$5.32 \times 10^6$	$1.96 \times 10^6$	$2.72 \times 10^6$	$3.96 \times 10^6$	$6.26 \times 10^6$	$1.03 \times 10^7$	0.067	0.076	0.00012	0.0086	0.102	0.271
1995	0.356	0.167	0.134	0.239	0.433	0.771	$1.15 \times 10^5$	$7.07 \times 10^4$	$2.70 \times 10^4$	$6.49 \times 10^4$	$1.48 \times 10^5$	$2.97 \times 10^5$	0.085	0.068	0.00023	0.0276	0.125	0.239
1996	0.381	0.183	0.127	0.252	0.474	0.823	$4.20 \times 10^5$	$2.33 \times 10^5$	$1.44 \times 10^5$	$2.63 \times 10^5$	$5.16 \times 10^5$	$1.00 \times 10^6$	0.153	0.082	0.01179	0.0974	0.199	0.345
1997	0.420	0.192	0.138	0.288	0.516	0.886	$2.85 \times 10^6$	$1.15 \times 10^6$	$1.10 \times 10^6$	$2.00 \times 10^6$	$3.54 \times 10^6$	$5.60 \times 10^6$	0.081	0.076	0.00020	0.0197	0.121	0.271
1998	0.524	0.174	0.274	0.406	0.606	0.931	$2.02 \times 10^6$	$7.35 \times 10^5$	$8.66 \times 10^5$	$1.50 \times 10^6$	$2.41 \times 10^6$	$3.69 \times 10^6$	0.043	0.050	0.00013	0.0060	0.062	0.181
1999	0.524	0.193	0.240	0.389	0.624	0.985	$1.73 \times 10^5$	$1.04 \times 10^5$	$4.56 \times 10^4$	$9.90 \times 10^4$	$2.24 \times 10^5$	$4.31 \times 10^5$	0.088	0.074	0.00015	0.0274	0.128	0.269
2000	0.518	0.211	0.195	0.368	0.632	1.005	$2.23 \times 10^6$	$7.78 \times 10^5$	$1.09 \times 10^6$	$1.67 \times 10^6$	$2.63 \times 10^6$	$4.15 \times 10^6$	0.138	0.100	0.00222	0.0597	0.195	0.386
2001	0.581	0.194	0.305	0.445	0.679	1.061	$5.29 \times 10^5$	$2.83 \times 10^5$	$1.63 \times 10^5$	$3.23 \times 10^5$	$6.64 \times 10^5$	$1.21 \times 10^6$	0.442	0.057	0.00006	0.0053	0.062	0.187
2002	0.573	0.204	0.284	0.433	0.680	1.086	$4.40 \times 10^6$	$2.12 \times 10^6$	$1.90 \times 10^6$	$2.96 \times 10^6$	$5.24 \times 10^6$	$9.76 \times 10^6$	0.050	0.064	0.00007	0.0058	0.070	0.236
2003	0.472	0.228	0.175	0.307	0.584	1.057	$2.98 \times 10^5$	$2.33 \times 10^5$	$5.05 \times 10^4$	$1.38 \times 10^5$	$3.82 \times 10^5$	$9.39 \times 10^5$	0.089	0.103	0.00013	0.0125	0.129	0.377
2004	0.417	0.236	0.134	0.245	0.524	1.033	$2.20 \times 10^6$	$9.24 \times 10^5$	$9.46 \times 10^5$	$1.55 \times 10^6$	$2.63 \times 10^6$	$4.46 \times 10^6$	0.093	0.102	0.00010	0.0136	0.137	0.365
2005	0.376	0.243	0.099	0.201	0.483	1.033	$6.41 \times 10^5$	$3.84 \times 10^5$	$1.48 \times 10^5$	$3.66 \times 10^5$	$8.25 \times 10^5$	$1.57 \times 10^6$	0.246	0.183	0.00139	0.0834	0.382	0.622
2006	0.413	0.239	0.123	0.243	0.521	1.043	$2.30 \times 10^6$	$9.79 \times 10^5$	$8.97 \times 10^5$	$1.63 \times 10^6$	$2.79 \times 10^6$	$4.67 \times 10^6$	0.294	0.188	0.00211	0.1330	0.438	0.644
2007	0.499	0.228	0.190	0.341	0.609	1.074	$1.42 \times 10^6$	$7.34 \times 10^5$	$4.46 \times 10^5$	$9.24 \times 10^5$	$1.76 \times 10^6$	$3.20 \times 10^6$	0.131	0.132	0.00036	0.0217	0.200	0.461
2008	0.532	0.237	0.196	0.367	0.653	1.110	$7.20 \times 10^5$	$4.92 \times 10^5$	$1.59 \times 10^5$	$3.75 \times 10^5$	$9.33 \times 10^5$	$2.01 \times 10^6$	0.128	0.135	0.00015	0.0205	0.197	0.470

Table 5.10: Mean values, standard deviations and quantiles of the distributions produced for the scalar parameters by fitting the model to data on whiting from the Firth of Clyde. The subscripts,  $123$ , attached to  $L_\infty$  and  $k$  represent the three nodes of the splines corresponding to years 1985, 1997 and 2008.

Parameter	Mean	S.D.	2.5%	25%	75%	97.5%
$l_{50}^f$	17.63	2.17	13.46	16.28	18.97	22.19
$\beta^f$	4.20	3.27	0.71	1.89	5.49	13.59
$l_{50}^d$	25.88	0.70	24.72	25.40	26.26	27.51
$p^d$	$2.70 \times 10^{-4}$	$4.62 \times 10^{-4}$	$5.81 \times 10^{-8}$	$1.26 \times 10^{-5}$	$3.30 \times 10^{-4}$	$1.53 \times 10^{-3}$
$L_{\infty 1}$	37.41	2.61	32.64	35.57	39.20	42.58
$L_{\infty 2}$	32.34	1.59	29.55	31.17	33.37	35.76
$L_{\infty 3}$	22.39	1.48	19.39	21.44	23.40	25.04
$k_1$	0.454	0.085	0.323	0.392	0.506	0.641
$k_2$	0.386	0.057	0.287	0.346	0.422	0.508
$k_3$	0.433	0.080	0.294	0.375	0.481	0.602
$cv^g$	0.152	0.035	0.083	0.128	0.176	0.220
$l^r$	17.04	0.20	16.63	16.91	17.17	17.43
$\sigma^r$	0.116	0.0050	0.107	0.113	0.120	0.127
$l^v$	16.20	0.74	14.72	15.67	16.71	17.62
$p^v$	$1.15 \times 10^{-3}$	$1.45 \times 10^{-3}$	$7.50 \times 10^{-6}$	$1.60 \times 10^{-4}$	$1.56 \times 10^{-3}$	$5.38 \times 10^{-3}$
$q$	1.13	0.10	0.93	1.07	1.21	1.32
$cv^L$	0.258	0.114	0.076	0.171	0.330	0.515
$cv^D$	0.735	0.199	0.406	0.593	0.856	1.187
$cv^N$	0.973	0.166	0.685	0.855	1.072	1.340
$\mu^R$	$2.56 \times 10^7$	$4.89 \times 10^6$	$1.80 \times 10^7$	$2.22 \times 10^7$	$2.85 \times 10^7$	$3.71 \times 10^7$
$\sigma^R$	0.664	0.136	0.429	0.570	0.748	0.971

Table 5.11: Mean values, standard deviations and quantiles of the distributions produced for the vector parameters by fitting the model to data on Firth of Clyde whiting.

Year	Fishing mortality rate, $F_y$				Recruited numbers, $R_y$				Bulk discard proportion, $p_y^{\text{bulk}}$									
	Mean	S.D.	2.5%	75%	97.5%	Mean	S.D.	2.5%	75%	97.5%	Mean	S.D.	2.5%	75%	97.5%			
1985	1.460	0.523	0.601	1.092	1.780	2.664	$1.16 \times 10^7$	$4.53 \times 10^6$	$4.55 \times 10^6$	$8.46 \times 10^6$	$1.40 \times 10^7$	$2.23 \times 10^7$	0.127	0.120	0.00020	0.0269	0.200	0.421
1986	1.467	0.533	0.551	1.097	1.795	2.707	$9.32 \times 10^6$	$3.93 \times 10^6$	$3.88 \times 10^6$	$6.42 \times 10^6$	$1.14 \times 10^7$	$1.86 \times 10^7$	0.179	0.163	0.00045	0.0345	0.293	0.548
1987	1.503	0.527	0.620	1.131	1.821	2.732	$3.12 \times 10^7$	$9.21 \times 10^6$	$1.71 \times 10^7$	$2.46 \times 10^7$	$3.63 \times 10^7$	$5.24 \times 10^7$	0.102	0.114	0.00012	0.0139	0.155	0.411
1988	1.525	0.521	0.659	1.155	1.836	2.713	$1.51 \times 10^7$	$5.35 \times 10^6$	$7.14 \times 10^6$	$1.14 \times 10^7$	$1.81 \times 10^7$	$2.78 \times 10^7$	0.167	0.154	0.00045	0.0336	0.265	0.525
1989	1.531	0.525	0.644	1.157	1.840	2.730	$1.56 \times 10^7$	$5.34 \times 10^6$	$7.52 \times 10^6$	$1.19 \times 10^7$	$1.87 \times 10^7$	$2.77 \times 10^7$	0.146	0.144	0.00019	0.0253	0.236	0.487
1990	1.557	0.519	0.720	1.187	1.859	2.804	$32.74 \times 10^7$	$7.98 \times 10^6$	$1.46 \times 10^7$	$2.16 \times 10^7$	$3.22 \times 10^7$	$4.61 \times 10^7$	0.073	0.088	0.00008	0.0091	0.105	0.316
1991	1.566	0.518	0.726	1.194	1.866	2.783	$3.40 \times 10^7$	$1.03 \times 10^7$	$1.85 \times 10^7$	$2.67 \times 10^7$	$3.95 \times 10^7$	$5.77 \times 10^7$	0.093	0.105	0.00012	0.0126	0.141	0.379
1992	1.568	0.522	0.710	1.194	1.870	2.828	$2.06 \times 10^7$	$6.86 \times 10^6$	$1.05 \times 10^7$	$1.59 \times 10^7$	$2.43 \times 10^7$	$3.72 \times 10^7$	0.105	0.116	0.00018	0.0148	0.160	0.414
1993	1.540	0.534	0.657	1.165	1.853	2.778	$3.05 \times 10^7$	$9.98 \times 10^6$	$1.59 \times 10^7$	$2.35 \times 10^7$	$3.57 \times 10^7$	$5.53 \times 10^7$	0.138	0.135	0.00026	0.0237	0.217	0.468
1994	1.538	0.537	0.652	1.166	1.842	2.757	$2.48 \times 10^7$	$8.16 \times 10^6$	$1.28 \times 10^7$	$1.92 \times 10^7$	$2.89 \times 10^7$	$4.46 \times 10^7$	0.127	0.130	0.00025	0.0208	0.195	0.460
1995	1.560	0.536	0.683	1.187	1.872	2.773	$2.57 \times 10^7$	$8.56 \times 10^6$	$1.24 \times 10^7$	$1.94 \times 10^7$	$3.08 \times 10^7$	$4.48 \times 10^7$	0.101	0.110	0.00028	0.0167	0.148	0.401
1996	1.605	0.536	0.721	1.231	1.916	2.827	$2.99 \times 10^7$	$1.16 \times 10^7$	$1.49 \times 10^7$	$2.21 \times 10^7$	$3.46 \times 10^7$	$5.83 \times 10^7$	0.062	0.075	0.00009	0.0081	0.091	0.275
1997	1.619	0.546	0.705	1.240	1.939	2.822	$3.02 \times 10^7$	$1.08 \times 10^7$	$1.41 \times 10^7$	$2.26 \times 10^7$	$3.59 \times 10^7$	$5.67 \times 10^7$	0.152	0.147	0.00029	0.0297	0.233	0.511
1998	1.635	0.547	0.719	1.252	1.954	2.846	$6.75 \times 10^7$	$2.45 \times 10^7$	$3.39 \times 10^7$	$5.04 \times 10^7$	$7.92 \times 10^7$	$1.29 \times 10^8$	0.092	0.104	0.00017	0.0129	0.137	0.362
1999	1.682	0.541	0.785	1.314	2.001	2.901	$1.57 \times 10^7$	$5.96 \times 10^6$	$6.79 \times 10^6$	$1.15 \times 10^7$	$1.88 \times 10^7$	$2.97 \times 10^7$	0.104	0.113	0.00011	0.0165	0.156	0.396
2000	1.719	0.552	0.791	1.338	2.031	2.982	$4.90 \times 10^7$	$2.01 \times 10^7$	$2.26 \times 10^7$	$3.52 \times 10^7$	$5.83 \times 10^7$	$9.80 \times 10^7$	0.106	0.118	0.00015	0.0148	0.166	0.426
2001	1.754	0.553	0.835	1.378	2.060	3.018	$1.79 \times 10^7$	$7.84 \times 10^6$	$7.28 \times 10^6$	$1.25 \times 10^7$	$2.18 \times 10^7$	$3.69 \times 10^7$	0.141	0.140	0.00030	0.0264	0.218	0.498
2002	1.778	0.550	0.872	1.406	2.085	3.034	$5.52 \times 10^7$	$2.34 \times 10^7$	$2.34 \times 10^7$	$3.86 \times 10^7$	$6.69 \times 10^7$	$1.12 \times 10^8$	0.208	0.169	0.00056	0.0538	0.333	0.564
2003	1.850	0.535	0.959	1.494	2.142	3.113	$2.62 \times 10^7$	$1.27 \times 10^7$	$9.90 \times 10^6$	$1.77 \times 10^7$	$3.20 \times 10^7$	$5.79 \times 10^7$	0.075	0.088	0.00025	0.0106	0.109	0.313
2004	1.935	0.530	1.053	1.567	2.233	3.188	$3.41 \times 10^7$	$1.52 \times 10^7$	$1.39 \times 10^7$	$2.38 \times 10^7$	$4.11 \times 10^7$	$6.94 \times 10^7$	0.058	0.072	0.00005	0.0071	0.080	0.267
2005	1.975	0.531	1.091	1.606	2.278	3.187	$1.88 \times 10^7$	$7.76 \times 10^6$	$7.65 \times 10^6$	$1.32 \times 10^7$	$2.29 \times 10^7$	$3.75 \times 10^7$	0.297	0.206	0.00072	0.1036	0.644	0.679
2006	2.003	0.531	1.100	1.640	2.301	3.272	$2.49 \times 10^7$	$1.01 \times 10^7$	$1.08 \times 10^7$	$1.78 \times 10^7$	$3.00 \times 10^7$	$4.88 \times 10^7$	0.909	0.058	0.75599	0.8935	0.965	0.968
2007	2.024	0.536	1.108	1.661	2.326	3.268	$2.56 \times 10^7$	$1.04 \times 10^7$	$1.04 \times 10^7$	$1.84 \times 10^7$	$3.08 \times 10^7$	$5.19 \times 10^7$	0.166	0.166	0.00017	0.0261	0.268	0.578
2008	2.034	0.543	1.090	1.667	2.349	3.280	$4.48 \times 10^7$	$1.69 \times 10^7$	$2.08 \times 10^7$	$3.26 \times 10^7$	$5.40 \times 10^7$	$8.52 \times 10^7$	0.085	0.102	0.00014	0.0107	0.125	0.366

## Chapter 6

# Conclusions

### 6.1 Growth and maturation of demersal fish

The analyses of Heath and Speirs (2012), which used the International Bottom Trawl Survey (IBTS) length samples to demonstrate that large fish were no-longer abundant within the Firth of Clyde, motivated the research of chapters 2 and 3 of this thesis. The aim of chapter 2 was to determine whether the absence of large demersal fish in the Clyde was partially due to declines in species-specific growth rates, and the aim of chapter 3 was to investigate whether the lengths- and ages-at-maturation of some of these demersal fish populations had changed over time. This research required combining the IBTS length samples with complementary IBTS age and maturity data. It was found that the growth rates of haddock, whiting and Norway pout had indeed declined since the 1980s, contributing to the decrease in the abundance of large fish in the Clyde. When the analyses of growth were repeated for the entire Scottish western shelf sea, excluding the Clyde, it was found that the growth rates of haddock, whiting and saithe had declined, but that the growth rate of Norway pout had actually increased over time. The results of the maturation analyses demonstrated that haddock, whiting and cod have been maturing at progressively smaller lengths since the 1980s, both in the Firth of Clyde and in the wider western shelf sea. It was also found that west of Scotland cod and haddock reach maturity at relatively young ages, compared with several other populations (e.g. Taylor and Stefánsson, 1999; Olsen et al., 2005; Pardoe

et al., 2009; Neuheimer and Taggart, 2010; Pérez-Rodríguez et al., 2013).

Commercially important demersal fish species found to the west of Scotland have been getting smaller since at least the 1980s. Not only is the reduced size of fish detrimental to fisheries due to the diminishing value of each individual, but changes in the size structure of fish populations can also influence the functioning of the ecosystem by altering inter- and intra-species interactions (Pope et al., 1994; Audzijonyte et al., 2013). As fish stocks have been observed to mature at increasingly early ages and small lengths in the years prior to stock collapse, expediting maturation and investing heavily in reproduction at the expense of growth may be an indicator of population stress (Trippel, 1995). The declines in the growth rates and lengths-at-maturation of the demersal fish populations considered in chapters 2 and 3 were not surprising given the similar findings of several studies of other distinct fish populations (e.g. Bianchi et al., 2000; Sharpe and Hendry, 2009), and it is becoming increasingly apparent that many fish stocks around the world are gradually becoming smaller and maturing earlier. Since the ‘shrinking’ fish phenomenon is so widespread it is reasonable to assume some pervasive cause: globally rising temperatures and industrial trawl fishing are the two prime candidates (Conover and Munch, 2002; Daufresne et al., 2009). There is an extensive literature assessing whether declines in the size of fish can be ascribed to rising temperatures or fishing practises, and it has been found that both of these factors can cause decreases in the growth rates of fish (Swain et al., 2007; Cheung et al., 2012). Similarly, there is a wealth of research demonstrating that temperature and fishing practises can influence maturation scheduling (e.g. Dunlop et al., 2009; Kuparinen et al., 2011). Regressions indicated that rising temperature did not strongly influence the growth or maturation of demersal fish in the west of Scotland. Instead, it appears that fishing has been largely responsible for the declines in growth rates and lengths-at-maturation. This is challenging to prove, and it was not proven conclusively here, but it seems highly probable for the following reasons. The Firth of Clyde is a semi-enclosed region home to resident fish populations; fishing effort density is substantially greater in the Clyde than in the rest of the Scottish western shelf sea; the use of small mesh *Nephrops* trawling gears is much more prevalent in the Clyde than western shelf;

and growth rates and lengths-at-maturation declined much more rapidly in populations from the Clyde than western shelf. Thus, it seems highly probable that size-selective trawl fishing has contributed to, and may be the main cause of, declines in the growth rates and lengths-at-maturation of west of Scotland fish.

Global average temperatures are forecast to continue rising throughout the 21<sup>st</sup> century (IPCC, 2014), so it is likely that the shrinking fish phenomenon will persist and become more widespread (Cheung et al., 2012). On a local level, however, it should be possible to mitigate the impacts of current deleterious fishing practises by improving fisheries management (Caddy and Cochrane, 2001; Caddy and Seijo, 2005). Innovative fishing strategies such as balanced harvesting are hypothesised to limit fishing-induced damage to ecosystems and may help to restore the length structure of exploited fish communities (see Jacobsen et al., 2014; Froese et al., 2015; Breen et al., 2016, for modelling studies and critiques of this particular strategy). A region such as the Firth of Clyde, which is fairly typical of an overexploited coastal ecosystem, offers an ideal testing ground for innovative management strategies as it is geographically small and thus relatively easy to regulate. Chapters 2 and 3 of this thesis demonstrated that lengths-at-age and lengths-at-maturation of Clyde demersal fish declined over the time during which the mixed fishery collapsed. We therefore stress the importance of reversing those changes, as this will surely be necessary for restoring the fishery. Future fisheries regulations introduced to the Clyde should be designed to help protect large fish so that the size structure of the demersal community may recover.

## 6.2 Growth and maturation of pelagic fish

Long term trends in the growth and maturation of pelagic species — herring, sprat, and mackerel — were investigated in chapter 4 using analyses similar to those discussed above for demersal fish. North Sea and west of Scotland populations were considered. Herring, sprat, and mackerel were the only pelagic species for which age or maturity data were collected as part of the IBTS. We used these data to investigate changes in growth and maturation even though pelagic stocks, spread throughout the water column, would not be fully represented. The results of chapter 4 should therefore be

treated with caution, as they are based on data that is biased toward the portion of the stocks found near the sea floor. More reliable assessments of trends in the growth and maturation of pelagic stocks would use acoustic and mid-water trawl survey data, but long time series of such data were not available. We found that growth rates of herring and mackerel declined in the North Sea and west of Scotland populations. Declines in the growth rates of Firth of Clyde herring were much more severe than the declines observed in the rest of the Scottish western shelf sea. Changes in the growth rates of sprat were more variable: the growth rates of northern North Sea sprat increased over time whereas the growth rates of sprat from the southern North Sea declined; growth rates of Clyde sprat declined whereas growth rates of sprat from the western shelf sea increased over time. There were relatively few significant trends in typical lengths-at-maturation, although since the 1980s, herring from the west coast of Scotland and southern North Sea have been maturing at increasingly large lengths, and the lengths-at-maturation of male North Sea mackerel have been in decline.

Compared to commercially important demersal species, the literature on long term changes to the growth rates and maturation scheduling of herring, sprat, and mackerel is relatively sparse, so it is not known whether similar widespread declines in growth rates and maturation lengths have occurred in these species (see Engelhard and Heino, 2004; Wheeler et al., 2009, for notable exceptions demonstrating long term changes in these life history traits in herring from Norwegian and Newfoundland waters respectively). Since these pelagic fish species tend to be smaller and have shorter reproductive timescales than most of the demersal fish considered here (Froese and Pauly, 2015), size-selective fishing is likely to have less of a direct impact upon growth rates or maturation scheduling. Variations in abundance, temperature, and predation rates are likely to have greater influence upon the growth and maturation of these pelagic fish (Cardinale et al., 2002; de Roos and Persson, 2002; Brunel and Dickey-Collas, 2010; Madin et al., 2010; Jansen and Gislason, 2011; Casini et al., 2014; Langård et al., 2014). Temperature and abundance appeared to influence the growth and maturation of the pelagic stocks more than the demersal stocks considered in the previous chapters, but these variables nonetheless often failed to account for the observed trends in growth



and lengths-at-maturation. Assessing how temperature and abundance affected growth was difficult because of correlation between the von Bertalanffy growth parameters. It may therefore be useful to consider an alternative growth index, such as the growth performance (Pauly, 1991), in future work. It seems that although rising temperature and variations in abundance have influenced the growth and maturation of these pelagic fish, there are other important factors that were not accounted for. Perhaps size-selective fishing influenced growth and maturation through reducing the abundance and average size of predators, or by altering food availability through disproportionate harvest of competing species. The results of chapter 4 show the manner in which the growth and maturation of herring, sprat, and mackerel stocks has changed over time, but determining precisely what has caused these changes will require further study. Results from this chapter may be of use for further modelling studies, although they should be treated with caution as they are based on bottom trawl samples that cannot represent the stocks in their entirety.

### **6.3 The length-based stock assessment model**

The stock assessment model presented in chapter 5 extends the length-based model of Sullivan et al. (1990) in three important respects: by utilising different data types, by accounting for time-varying growth, and by using Bayesian fitting methods. Our length-based model does not rely upon any age data or fishery catch-at-length data. Instead, the model is fitted to data on the total fishery landings and discards, and fitted to survey data which provides an abundance index and information about the length structure of the stock. As these data are available for many different species in many locations, our length-based model should be widely applicable. This is in contrast to the original model of Sullivan et al. (1990) that was fitted to catch-at-length data usually collected only for the most commercially valuable species. Our model should be useful for assessing the abundance of stocks for which fishery catch composition data or age data are not collected. As these types of data are often aggregated over large geographical areas, our model should also be useful for assessing stocks within relatively small regions. Our model will therefore hopefully be used to assess several of

the Firth of Clyde fish stocks.

Our stock assessment model successfully accounted for temporally variable growth rates, as it estimated declines in length-at-age that generally agreed with the results produced in the analyses of survey age data in chapter 2. The ability to account for varying growth is an important feature of stock assessment models (Lorenzen, 2016), as trends in growth can influence abundance estimates. The method of using splines to model variation in the growth parameters is flexible and could be easily adapted — through the choice of the number and positioning of the spline node points — if the model were applied to other data sets. Although the spline method was successful, the choice of the number and positioning of the node points is subjective, and it may prove useful to test alternative methods of modelling time-varying growth. For example, modelling the growth parameters using random walks would involve fewer subjective decisions (see Wilberg and Bence, 2006, for a stock assessment modelling time-varying catchability as a random walk).

Our model was fitted using Bayesian methods. The main practical benefit of this is that measures of uncertainty can be simply derived for each parameter and modelled quantity by drawing samples from the posterior distribution. Another practical benefit is that the model may be constrained through the choice of prior distribution used for each parameter. We have made liberal use of informative priors, which lessens the objectivity of our results as other modellers may have decided to use substantially different priors. It still remains to thoroughly assess the choice of prior distributions and the influence that these priors have upon the results. I am confident, however, that most of the priors have been sensibly chosen. The prior for the survey catchability is the only one that troubles me, as it was set with a low variance despite a lack of prior knowledge for this parameter. As discussed in chapter 5, this prior was chosen to be precise in order to prevent the multimodal behaviour of catchability in whiting. It is likely that this multimodal behaviour was a consequence of the change in the duration of the survey tows in 1999. Accounting for this change in survey tow durations by estimating two catchability values (Wilberg and Bence, 2006) will hopefully solve the problem of multimodality and allow the model to be implemented with a less precise prior on

catchability. Although our stock assessment model requires some further work, the results presented in chapter 5 are promising and indicate that work will be worthwhile. We hope to apply our model to difficult-to-assess stocks in the near future.

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