Spatial and Long-term Variability in Demersal Fish Species of the Western North Sea

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Abstract

This thesis explores historical and contemporary patterns of spatial and temporal change in demersal fish species of the western North Sea. Comparing trawl data from over a century ago with those from contemporary trawl surveys are challenged by biases associated with differences in gear types and methods of operation. To compare contemporary data with rare 1892-1913 data from Northumberland Sea Fisheries Committee surveys on the Northumberland coast (UK), an attempt was made to replicate the original trawl gear and methods used by drawing on the literature, historical photographs and expertise of the trawl industry. The replica gear, comprising a 6.7 m beam connecting two Brixham-style wrought-iron trawl heads with a triangular-shaped trawl net and rounded ground-rope, was trialled in August 2018 and March 2019, and catches were compared with a modern otter trawl. In the first trial period, the otter and replica beam trawl had similar efficiencies in catching flatfish, whereas catches made by the replica gear in March were either very low or zero. As a result, the otter trawl was employed in place of the replica gear in all subsequent resurveys and catches were standardised for comparison with historical surveys. Catches revealed substantial declines in the abundance of the overall inshore fish assemblage and among individual species between 1899-1913 and 2018-2019. Elasmobranchs and historically dominant species such as grey gurnard *Eutrigla gurnardus* were either completely absent or rare in the 2018-2019 surveys. Abundance-size spectra also exhibited significant differences between periods, declining more steeply in contemporary trawls. Analysis of demersal fish stomach contents data revealed large shifts in diet composition over the period spanning 1896-2015. Bivalves dominated plaice *Pleuronectes platessa*, dab *Limanda limanda* and haddock *Melanogrammus aeglefinus* diets in the early and mid-20th century but declined substantially in subsequent decades. Conversely, polychaetes increased in importance by number and mass overtime and were the main prey resource for plaice in the 1970s and 2000s. These diet shifts point to likely changes in the benthic prey base of the North Sea, linked to increased beam trawling in the 1960s-1970s, eutrophication, and climatic processes. Finally, contemporary stomach contents and bulk stable isotope data were used as complementary techniques to assess temporal and spatial variation in the diet within and between two sympatric flatfishes, plaice and dab, in four coastal bays off the Northumberland coast. Stomach data indicated similar diets and significant dietary overlap at short temporal scales, yet dorsal muscle and liver tissue $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ data revealed substantial inter- and intra-specific variation in resource use among sites and lower levels of niche overlap at longer time scales. Sandeels *Ammodytes tobianus* were highly abundant in flatfish stomachs, whereas Bayesian isotope mixing models indicated that squid were the important contributors to both predators. Dorsal and liver isotope data also indicated that bivalves and ophiuroids were major contributors to plaice and dab diet, respectively, across sites. These findings provide evidence of profound change in demersal fish species and their trophic ecology, further underpinning the value of using historical and contemporary data to elucidate broad-scale temporal and spatial patterns of change.

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1.1. The development of Britain's fishing industry

1.1.1. *UK fisheries*

Sea fishing has occurred in European coastal waters for centuries (Barrett et al. 2004), and has been subject to unprecedented changes in fishing effort, gear, and target fish species (Engelhard, 2008). Today, fisheries are largely dependent on the bottom trawl, the main gear for catching demersal fish species, despite the fact that little is known about its origin (Collins, 1889; Graham, 1956). The earliest historical reference to a trawl dates as far back as the 14th century, when Edward III prohibited the use of the "wondyrchoun", an instrument that was already described by fishers as being destructive to vast amounts of immature fish and shellfish (primarily mussels and oysters) (Collins, 1889; Graham, 1956). However, until the mid-19th century, bottom trawling was limited to a few places along the south coast of England (Thurstan et al. 2014). Early bottom trawls were towed across the seabed by sail-powered fishing smacks close to shore (Alward, 1932), and comprised of a wooden beam (approximately 3 m long) that held open a bag-shaped net (Robinson, 1996). The development of railways in the late 1820s promoted the rapid growth of trawling (Thurstan et al. 2014), and opened up markets for selling fresh and cheap fish in inland towns and cities (Robinson, 1996). In response to increased demand and improved transport links, the size of the English trawl fleet expanded from 130 to over 800 boats between 1840 and 1860, respectively (Roberts, 2007). Moreover, with the introduction of ice for preserving fish, trawlers extended their range northwards as far as Aberdeen, and by the mid-1870s, most of the shallower parts of the North Sea were exploited (Fig 1.1) (Graham, 1956).

Trawling by sail reached its peak in the North Sea by the 1870s (Engelhard, 2008) and conventional sail smacks were soon displaced by steam-powered vessels (Alward, 1932; Robinson, 1996). At the time, several attempts were made to apply steam power to fishing vessels in the form of paddle tugs (Engelhard, 2008), and the first successful trawlers were worked out of North Shields in the north-east of England (Robinson, 1996). The commercial success of steam trawling prompted the arrival of purpose-built screw trawlers in east coast ports (Grimsby and Scarborough), and subsequently in all other major fishing ports in the UK (Engelhard, 2008). By the 1880s, the advent of steam power revolutionised the fishing industry and promoted further growth of the trawl fleet (Thurstan et al. 2014). In parallel, steam-powered trawlers were subject to various modifications, including the size, storage capacity, speed, and tonnage of the vessel (Garstang, 1900).

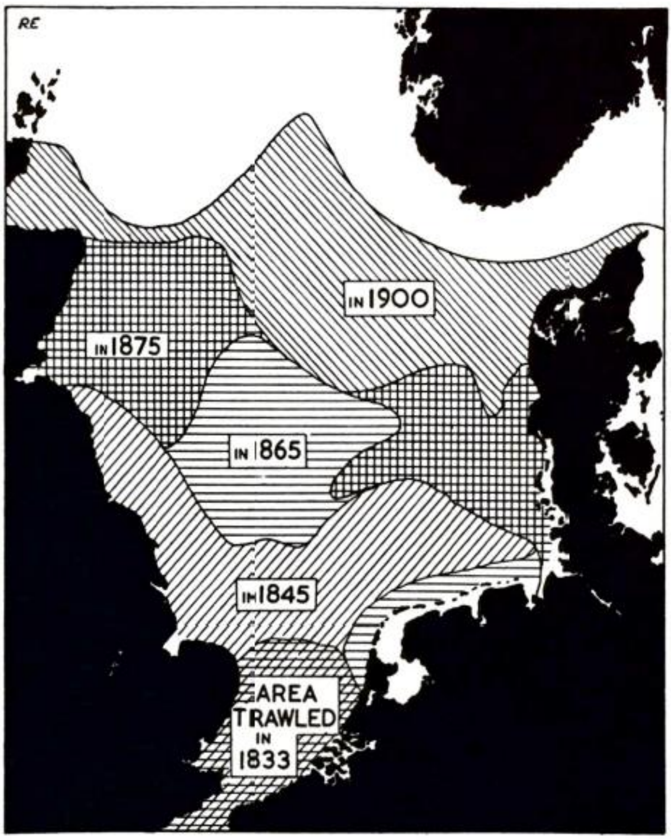


Figure 1.1. Expansion of English trawl fisheries in the mid-19th century (Graham, 1956).

Steam power enabled vessels to tow much larger trawl nets than by sail, and fish for longer durations, further offshore, and at considerably deeper depths (Robinson, 1996; Engelhard 2008). By 1900, steam-powered fishing vessels were five times more efficient at catching marketable fish species (e.g., plaice *Pleuronectes platessa* and cod *Gadus morhua*) than sail smacks (Garstang, 1990). Beam trawls were initially towed by sail and early steam trawlers; however, despite enhanced power from steam, beam trawls soon reached their workable limit as the prescribed length of the beam prevented increasing the net size further (Heape, 1887; Edwards, 1909). In a short space of time, a new type of trawl gear patented by Mr Scott of Granton in 1895, the otter trawl, bypassed the need for a beam (Cunningham, 1896; Kyle, 1903). Instead, an unwieldy wooden beam was replaced by two 'otterboards' or doors that functioned as underwater kites, one on either side to keep the mouth of the net open (Cunningham, 1896). Compared to beam trawls, otter trawls could rise higher off the seafloor to catch a greater diversity of species (Edwards; 1909) and were far more capable of being towed with greater fishing power (37% more efficient; Garstang, 1900). Improved catch rates soon led to the widespread use of otter trawls throughout Britain's fishing ports, and with the addition of bobbins, a series of rollers, and tickler chains designed to stir up flatfish within the seabed, steam trawlers were able to work grounds that were previously too rough (Graham, 1956). In the early 1920s, the efficiency of otter trawls were further improved through the adoption of Vigneron-Dahl gear, which comprised lengths of steel cable extensions between each otter board and the net to increase the overall spread of the net (Graham, 1956). This modification increased the width of the net while minimising its resistance and drag, thereby facilitating the capture of more fish over a greater expanse of sea floor (Graham, 1956).

The quantity of demersal fish landed into England and Wales dramatically increased in line with technological improvement, development of the fishing fleet, and expansion into new fishing grounds by the mid-20th century (Thurstan et al. 2010). However, landings were disrupted by an abrupt halt in fishing effort during both World Wars (Fig 1.2; Kerby et al. 2012) as vessels were requisitioned for war service; particularly for deployment as mine sweepers (Beare et al. 2010). Britain dominated North Sea demersal fisheries for most of the first half of the century; however, the fleet declined by 97% between 1938 and 1941 (Engelhard, 2008). This remarkable dip in effort enabled fish populations to recover temporarily (Beare et al. 2010), but this was short-lived as landings fell to pre-war levels within a couple of years and went into long-term term decline thereafter (Roberts, 2007).

The British sailing trawl fleet was reduced to relatively shallow parts of the southern North Sea in the early 20th century (Fig 1.2), where it primarily operated out of Lowestoft (Engelhard, 2008). For a short period, the last sailing-powered fishing vessels competed with steam trawlers in the early 20th century, targeting commercially important flatfish (Engelhard, 2008). However, this did not prevent the collapse of the British sailing trawl fleet, which was accelerated by both World Wars (Engelhard, 2008). In the period after the 2nd World War, North Sea fishing grounds also declined in importance as steam trawlers fuelled by coal increased their distant-water trips (Robinson, 1996; Kerby et al. 2012). Declines in inshore stocks together with a growing demand for food promoted the expansion of British distant-water fleets, which targeted new fishing grounds in the Arctic and Western Africa (Thurstan et al. 2010; Kerby et al. 2012). Meanwhile, purpose-built motor trawlers fuelled by diesel were introduced and outcompeted steam trawlers in terms of total landings by the 1960s (Fig 1.2). Between 1956 and the early 1980s, catches of demersal fish landed by British trawlers declined dramatically as distant-water stocks became fully exploited (Roberts, 2007; Thurstan et al. 2010). This, coupled with increased competition in international waters, led to disputes over which countries should have access to productive fishing grounds (Robinson, 1998; Roberts, 2007). By the mid-1970s, many countries extended their territorial waters to 200 nautical miles from the shore (Pauly et al. 2005).

Over the course of 20th century, landings of North Sea fish had risen from under 1 million in 1900 to 3.5 million tonnes in 1970 (Christensen et al. 2003). Catches were only sustained by increasing fishing power, trawling at greater distances, in deeper waters, and switching to less favourable species (e.g., monkfish *Lophius piscatorius*) (Roberts, 2007). Together, these trends have masked local depletion and disappearance of principal target species (Roberts, 2007). Technological advancements have also enabled fishers to catch more at cheaper costs; for example, echo sounders and transducers used for fish detection has made the catching process more accurate and efficient (Kerby et al. 2012). As catches have fallen over time, fishers have responded by fishing more intensively. While some nations benefited from the 'gadoid outburst' in the 1960s (Kerby et al. 2012), landings continued to decline up to the 1990s, remaining relatively constant for about a decade, before declining again at the turn of the 21st century (Fig 1.2).

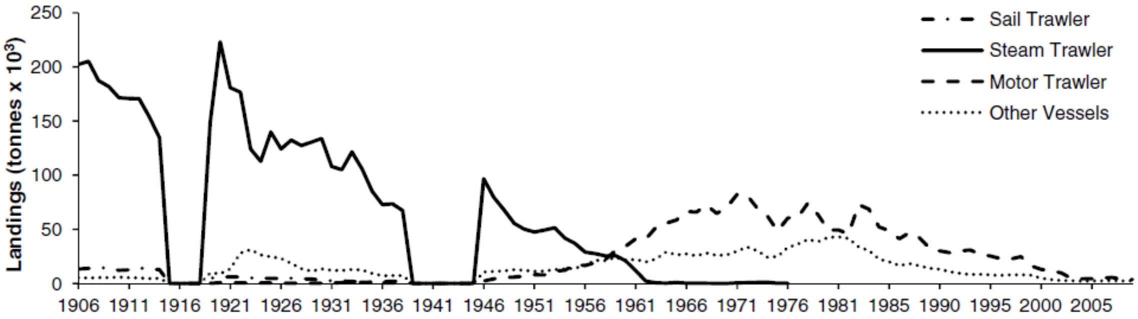


Figure 1.2. Total demersal landings by sail, steam, and motor trawlers, and other vessel types (steam and motor seiners; sail, steam and motor liners; other vessels) from the North Sea into England and Wales (Kerby et al. 2012).

In recent years, a significant reduction in fishing effort has caused a subsequent decline in the number of fishing vessels and led to the implementation of strict management measures such as quotas, total allowable catches (TACs) and surveillance activities (Moussis, 2008). To date, the North Sea has recouped some importance in terms of landings by UK fisheries (Kerby et al. 2012). However, the fishing industry can no longer support the domestic market from its own reduced catching capacity and share of the European Community's resources (Symes, 1992; Kerby et al. 2012). Until now, EU coastal states have had 'equal access' to marine resources within the UK's Exclusive Economic Zone (EEZ), however Brexit poses a major challenge to the stability of European fisheries management as responsibility is now divided between Europe and the UK (Phillipson and Symes, 2018). A 'taking back control' approach of UK fisheries within the EEZ will destabilise longstanding relations, potentially slowing down an ecosystem-based management based approached to fisheries and thus risk the recent recovery and future sustainability of fish stocks (Phillipson and Symes, 2018).

1.1.2. *Northumberland coast fisheries*

The Northumberland coast is located on the northeast coast of England and borders the North Sea (Fig 1.3). It consists of a sequence of wide bays that are separated by rocky stretches of cliffs and supports a wide range of ecologically important habitats and species (Bennett and Foster-Smith, 1998). The coastal zone has supported juvenile and adult populations of numerous commercially and ecologically important species such as plaice *Pleuronectes platessa* and dab *Limanda limanda*, for centuries (Meek, 1896), but has been subject to various human pressures during this time, including pollution (Eagle et al. 1979), dredging (Norman, 1863; M'Intosh, 1872) and fishing (Walmsley and Pawson, 2007; Thurstan et al. 2014). Fishing has traditionally been an important part of the economy since fishing villages were firmly established along the coast from the late 18th century (Muirhead, 1992; Marshall, 1997). From this time, inshore fishers worked from a small open boat referred to as 'coble' ranging from ca. 7 – 8 m in length (Muirhead, 1992). The coble's small size and lightness meant that it was easy to handle and its design varied in response to local conditions and fisher preference. Fishers primarily used short and long lines; however, a small number of cobles were used in the inshore trawl fishery to target flatfish (e.g., plaice, sole *Solea solea*, and turbot *Scophthalmus maximus*) (Muirhead, 1992). Before the introduction of steam power, near-shore static and drift fishing gears, including crab and lobster pots, drift nets for herring *Clupea harengus*, and long-lines for species such as cod *Gadus morhua*, ling *Molva molva*, and haddock *Melanogrammus aeglefinus*, were widely used by fishers throughout the region (Meek, 1896). However, trawlers in the form of paddle tugs were already widespread at large ports (primarily North Shields; Fig 1.3), which prospered at the expense of traditional fishing villages (Thurstan et al. 2014). Consequently, these areas declined in importance as the quantity of fish increased at ports along the coast.

Figure 1.3. Map of the main fishing ports on the Northumberland coast (Walmsley and Pawson, 2007).

Steam trawling became a highly contentious issue along the entire British coast. Local fishers using static gears competed with steam trawlers for fish (Robinson, 1996), and perceived trawling as a wasteful and damaging mode of fishing (Roberts, 2007). This outcry led to two Royal Commissions of Enquiry in 1863 and 1885, respectively, which aimed to address persistent complaints of local depletion of inshore fish stocks and damage to the seabed as a result of trawling (Report of the Commissioners, 1866; Report of the Commissioners, 1885). The Commissioners of the enquiry compiled evidence by documenting the testimonies of people who were closely linked to fishing industry during the early days of trawling (Thurstan et al. 2014). Most notably, declines were more commonly perceived from witness testimonies on the north-east coast, where 85% of witnesses who gave quantitative accounts perceived a decline in the catch rates of whitefish (Thurstan et al. 2014). Despite the scale of objection to trawling documented throughout both enquiries, the testimonies put forward were hindered by a lack of fisheries data, an expanding fishing industry, and conflicting views among different classes of fishers, which precluded any firm conclusions (Thurstan et al. 2014). However, recommendations from both enquiries promoted the collection of national fisheries statistics from all major ports in England and Wales from the late 1880s onwards (Report of the Commissioners, 1885). By 1891, Local Sea Fisheries Committees were established in England and Wales and inshore trawling was soon prohibited due the introduction of a three-mile territorial limit (Allen, 1897).

Further offshore, the early 1880s saw a rapid growth in steam long-liners engaged in fishing for cod, ling, hake *Merluccius merluccius* and Atlantic halibut *Hippoglossus hippoglossus*, with the number of steam liners more than doubling at North Shields from 18 to 42 between 1880-1885 (Muirhead, 1992). Landings of whitefish by trawl and long-liners from North Shields increased from the 1870s to the early 1900s (Fig 1.4), coinciding with a growth in the number of vessels registered at North Shields and adoption of the otter trawl throughout the region (Muirhead, 1992). At the turn of the 20th century, the number of steam liners operating out of North Shields declined, falling from 44 in 1895 to 17 in 1905, and catches of target species were landed from areas beyond the North Sea (Muirhead, 1992). Thus, liners in the region faced the familiar cycle of falling catches and rising costs of prime fish, which was not enough to offset dwindling stocks and longer fishing trips. By comparison, steam trawlers registered at North Shields continued to fish on grounds relatively close to port (Muirhead, 1992). This tendency was reinforced by the development of the Norway lobster *Nephrops norvegicus* and herring fishery in the early 20th century (Muirhead, 1992). *Nephrops* were targeted in inshore grounds that extended from Coquet Island to Hartlepool, whereas herring were landed at greater distances from port (Muirhead, 1992). By 1913, 31 steam trawlers targeted herring from North Shields, and comprised ~12% of the total landings (Muirhead, 1992). In the same year, 60% of all fish, excluding shellfish, landed in the region came ashore at North Shields (Muirhead, 1992), reinforcing North Shield’s position as the region’s most important fishing port.

Today, North Shields is the only port within the district that has an official designated fish market, with vessels often targeting species within a daily steaming distance (Walmsley and Pawson, 2007). Since the 1970s, the demand for *Nephrops* has increased as white fish landings have declined in line with quota allocations (Walmsley and Pawson, 2007). *Nephrops* are typically caught using otter trawls, while whitefish are landed as bycatch in the *Nephrops* fishery (Walmsley and Pawson, 2007). Potting, which includes using traditional creels and parlour pots targeting European lobster *Homarus gammarus*, brown crab *Cancer pagurus*, and to a lesser extent, velvet crab *Necora puber*, is now the most widespread fishing practice off the coast (Stephenson et al. 2018), with some vessels using drift nets to capture salmon and a smaller number of vessels using towed gears (Garside et al. 2003).

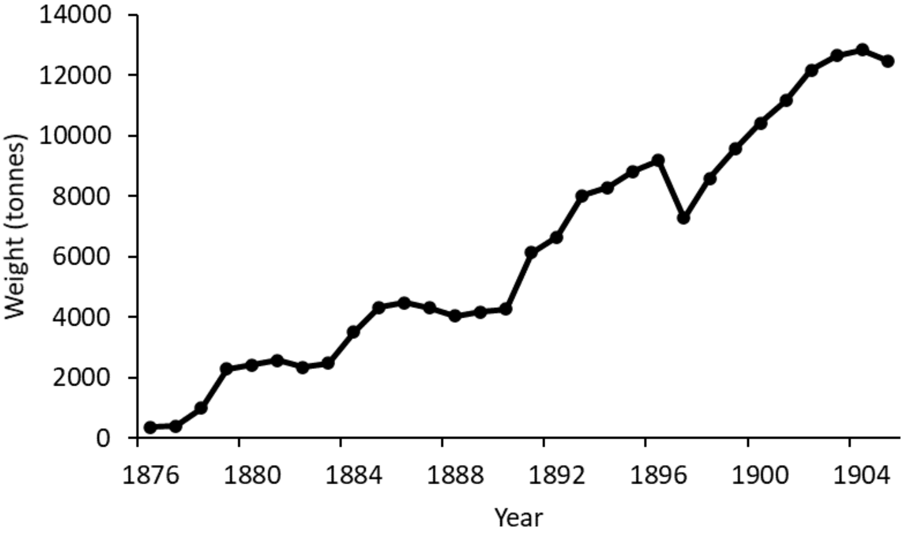


Figure 1.4. Landings of whitefish into North Shields between 1876 and 1905 (Meek, 1905).

In England, fishing activities are monitored by regional conservation groups called 'Inshore and Conservation Authorities' (IFCAs) (Clarke et al. 2016; Soldant, 2020). Since, 2011, inshore fisheries of the Northumberland coast are managed by the Northumberland Inshore Fisheries Conservation and Authority (NIFCA), whose district extents out to 6 nautical miles from the shore, from the Scottish border in the North to the River Tyne in the south (Fig. 1.3). Under the Marine and Coastal Access Act of 2009, NIFCA play an important role in ensuring that marine resources are exploited sustainably in the district through monitoring and enforcing fishing activities. This also includes monitoring of several important European Marine Sites (EMS) such as the Berwickshire and Northumberland Coast Special Areas Conservations (BNNC SAC) and Coquet to St. Mary's Island Marine Conservation Zone (CSM MCZ), which aim to protect the quality of its marine habitats and associated species (Natural England, 2020). Local management aims to ensure that these EMS continues to be an areas of international importance, yet several fishing activities including potting, drift netting, and bottom trawling, are still permitted in these protected areas (e.g., in the BNNC SAC; AONB Partnership and EMS Management Group, 2009). The 'baseline' condition of these protected areas are 'set' at the time of designation and conservation objectives fail to consider restoration of fish communities, with features (e.g., mud and sandflats) being maintained in 'favourable condition' based on recent baseline information. As much of the Northumberland coast was commercially fished centuries before EMS designation, the actual 'baseline' condition is unclear as the environment has already changed by human activities (Bennet and Foster-Smith, 1998). There are 355 designated Marine Protected Areas (MPAs) in UK waters (Solandt, 2018), and there is a pressing need to shift consideration of recent ecological 'baselines' as a 'normative state' to an awareness of human impacts prior to designation. Management measures often fail to account for long-term impacts and MPAs have conservation objectives that vastly underestimates the recovery potential of an ecosystem (e.g., Plumeridge and Roberts, 2017), and in turn encourage management measures that are insufficient to attain improvement in condition of marine resources.

1.2. Understanding long-term change

1.2.1. *Shifting baselines*

Humans have impacted the marine environment for millennia and there are very few pristine ecosystems anywhere on the planet (Myers and Worm, 2003). Consequently, anthropogenic influences such as commercial fishing and pollution, have accentuated the rate and scale of change in marine systems overtime, altering their structure and functioning overtime (Jackson et al. 2001; Lotze and Milewski, 2004). Understanding the full extent and magnitude of these changes requires information on the 'virgin' state of a population or ecosystem (Pinnegar and Engelhard, 2008), however this is difficult as we are unaware of what ecosystems looked like prior to the onset of large-scale anthropogenic disturbance (Lotze and Milewski, 2004). The baseline of "natural" conditions has shifted human perceptions of biological systems due to loss of experience about past conditions (Papworth et al. 2009). In 1995, Pauly termed the concept the 'shifting baseline syndrome' (SBS), where new generations fail to fully appreciate the gradual changes that have degraded habitats and reduced marine populations over relatively short space of time.

There is an increasing body of empirical evidence that underpins the existence of SBS, the majority of which comes from fisheries science. For example, Braulik et al. (2020) revealed precipitous declines in sawfish abundance in Tanzania, inferred from age-related declines in local ecological knowledge of their existence; fishers between 70-80 years old were familiar sawfishes, whereas only 10 % of younger fishers interviewed (less than 20 years old) had heard of their existence. Bender et al. (2014) drew similar conclusions in the southwest Atlantic, whereby younger and less experienced artisanal fishers recognised fewer species that were considered overexploited compared to older and more experienced fishers. Likewise in the Raja Ampat archipelago in Eastern Indonesia, a region that has experienced dramatic declines in biodiversity in recent decades, younger fishers have been observed to recall fewer marine species than older ones, thereby noting a lower degree of population decline (Ainsworth et al. 2008). These studies illustrate the need for baselines in order to measure change against, otherwise our understanding of what was natural will only continue to shift, and we risk becoming complacent about the rarity of species (Pauly, 1995).

Jackson et al. (2001) highlighted that impacts of overfishing on large marine animals and shellfish was the first major anthropogenic disturbance in coastal ecosystems. Unfortunately, these impacts can only be interpreted through historical analysis as they precede scientific investigations (Jackson et al. 2001). Around the British Isles, 19th century witness testimonies have provided early evidence of the dramatic transformations that occurred as a result of intensive trawling practices (Thurstan and Roberts, 2010; Jones et al. 2016). As early as 1863, the UK government led the first Royal Commission of Enquiry in response to fears of overfishing around the British coast (Report of the Commissioners, 1866). However, even at this point in time, these memories will have been affected by shifting baselines as fisheries around the UK were exploited for many generations previously. In addition, the industrialisation of fisheries has further masked declines in fish populations due to improved fishing technologies and catching capacities. For example, the adoption of steam power to fishing vessels in the 1880s enabled trawlers to fish further offshore and exploit 'virgin' fishing grounds in the North Sea. Subsequently, declines in inshore stocks were obscured as demersal landings peaked (Garstang 1900), thereby masking real declines in inshore fish communities.

SBS is viewed as a form of generational amnesia, whereby older generations fail to pass on their own experience to younger generations, or as personal amnesia, when experiences and baselines are forgotten and modified over the course of an individual's life (Kahn, 2002; Papworth et al. 2009). Forgetting former states of changing biological systems is caused by problems generated by autobiographical memory, for example, when older individuals inaccurately recall past conditions and change when were was none, or transmission between individuals of different age cohorts (Papworth et al. 2009; Rost, 2018). To demonstrate SBS conclusively, data must be available on an individual's perception of change and consistently used in conjunction with independent biological data (Papworth et al. 2009). Evidence from accounts of early explorers examined by Sáenz-Arroyo et al. (2006) revealed declines in abundance and biodiversity of marine species in the Gulf of California, but did not demonstrate SBS in the human population. By contrast, Saenz-Arroyo et al. (2005) noted inter-generational shifts within three generations of fishers in the same region, eluding to possible generation amnesia in the population studied. Older fishers recalled productive nearshore fishing grounds and the presence of larger fish, whereas younger fishers did not appreciate the former prevalence of larger species (Sáenz-Arroyo et al. 2005). Ainsworth et al. (2008) characterised SBS as shifting cognitive baselines and revealed age-related differences in fisher experience after comparing perceptions of biological change with catch per unit effort data in Raja Ampat. These studies highlight the importance of ensuring that differences in human perceptions of change are consistent with the biological data in question. Particular aspects of intergenerational and personal memory, in combination with biological change, should therefore be considered when interpreting SBS in the environment.

1.2.2. *Value of historical data*

Although commercial sea fishing has taken place for centuries, modern research often fails to account for the effects of long-term human exploitation (Jackson et al. 2001). Until recently, most fisheries management and conservation efforts focus on the past few decades, long after the start of intensive human activities (Lotze and Worm 2009). Studies that have accounted for short-term impacts have provided some insight into the disturbance and recovery of fish communities and their associated habitats (Rice and Gislason, 1996; Kaiser and Spencer, 1996). However, researchers are turning to history to better understand past ecosystem states (Jackson et al. 2001). Studies that incorporate historical data into assessments of change, which are based on a long time-series of data, frequently reveal far greater declines in comparison to using short-term data alone (McClenachan et al. 2012). A long-term perspective is thus valuable in a) providing us with a clearer understanding of the magnitude of alteration and decline of marine populations, b) identifying underlying causes of such changes, and c) providing a benchmark against which the ecological state of marine ecosystems can be assessed and set achievable goals for their management.

In the field of marine historical ecology, an extensive range of data sources (e.g. anecdotal evidence, fishery statistics, research survey data) have been amalgamated to facilitate our understanding on past fish abundances (Pinnegar and Engelhard, 2008). When compared to contemporary data, historical sources have indicated that the magnitude of change is far greater over long time periods. For example, on Canada's Scotian Shelf, the total biomass of cod from recent stock assessments was found to be ~4% of the historic adult biomass (1852), as revealed by catch and effort data during the mid-19th century (Rosenberg et al. 2005). Similarly in the Adriatic Sea, a multidisciplinary approach showed that 98% of traditional marine resources have been exhausted to less than 50% of former abundances (Lotze et al. 2011). These examples underpin the value of historical data in contrast to depending on contemporary sources alone. Data that predates anthropogenic disturbance, particularly modern industrial fishing, can provide realistic baselines or reference points for managing fish and their associated environments more effectively (Plumeridge and Roberts, 2017).

Shifting baselines have direct consequences in the way marine species are managed due to an intergenerational loss of information and reliance on recent data (McClenachan et al. 2012), which in turn can have major implications for fisheries management and recovery target setting (Thurstan et al. 2015). If policy makers and resource managers omit relevant historical information from assessments, false perceptions of past ecological conditions may follow, and thus result in lower recovery targets and higher fishing quotas (McClenachan et al. 2012). This has been the case for the Dogger Bank in the south-central North Sea, which is now a candidate Special Area of Conservation under the European Habitats Directive (Plumeridge and Roberts, 2017). Although the region has been subject to prolonged declines in fish abundances due to centuries of intensive trawling, as revealed by historical records, current conservation targets for the Dogger Bank are based on present day data only. This has substantially underestimated the recovery potential for the Dogger Bank ecosystem, and in turn promotes unambitious recovery objectives. Plumeridge and Roberts (2017) highlight the value of historical data as an essential component for conservation decision making.

1.2.3. *Data limitations*

There are relatively few quantitative fishery records that exist prior to the onset of industrial fishing, and the majority of abundance information spans the last 50 years (e.g. Heessen and Daan, 1996; Rogers and Millner, 1996), and data from the 18th and 19th centuries are largely underutilised (Rogers and Ellis, 2000). It was only until the end of the 19th century that systematic data was collected (Roberts, 2007). Fish catch records (e.g., numbers and sizes of fish landed) can be traced back to the early 20th century for a few species, whereas estimates of population sizes of target species are only available as far back as the 1950s or 1960s (Roberts, 2007). This poses a challenge when estimating historical fish abundances; hence, our awareness of how humans have exacerbated fish abundance over many decades is also very limited.

Assessment of long-term change is difficult due to the complex nature of marine systems and the paucity of time-series data (Rijnsdorp et al. 1996). In the UK, national catch statistics are only available from 1886 onwards (Thurstan et al. 2014), but large-scale fishing occurred much earlier than this (Barrett et al. 2004; Jones, 2018). Indeed, the most severe impacts on fishery resources around the UK occurred are likely to have taken place in mid-19th century, several decades prior to the collection of systematic fishery statistics (Thurstan, 2013). Further, long-term catch or effort data is biased towards commercially-important species, which were regularly and extensively monitored (Rijnsdorp et al. 1996). It is even more difficult to assess abundance changes for non-target species as long-term data is sparse (Sguotti et al. 2016). This hinders the evaluation of the effects of long-term impact as complex biological processes and human activities interact.

Despite recent developments in long-term data collection and analysis, incorporating different historical records, such as narrative and catch data, into standardised fisheries management protocols poses a challenge due to disparate or incomplete data (Alexander et al. 2011; McClenachan et al. 2012). Similarly, contemporary assessments of fisheries for integrated decision-making frameworks may not be set up to accommodate the use of historical information (Thurstan et al. 2014). Interpretation of long-term fisheries-dependent and independent data requires a degree of caution as differences in sampling methods may bias analyses (Sguotti et al. 2016). For example, the design and operation of different fishing gears may affect the selectivity of individual species, particularly in relation to their size and shape (Dealteris et al. 1989). Consequently, it is important to standardise trawl gear and methods in research surveys for reliable comparisons. Studies that contrast trawl records from different periods and trawl gears are thus faced with the challenge of accounting for the potential bias of varying selectivity among different fishing gears (Rijnsdorp et al. 1996; Greenstreet et al. 1999; Rogers and Ellis, 2000; Cardinale et al. 2009; Sguotti et al. 2016).

1.3. Long-term changes in marine food webs

1.3.1. *Fishery-induced changes*

Since the beginning of the 20th century, catch data on fish communities in the North Sea have been recorded during irregular research surveys (Garstang, 1905). Between 1906-1909 and 1990-1995, contrasting beam and otter trawl surveys revealed reduced abundances of the total demersal fish community and within individual groups in the south-eastern North Sea, as well as a shift towards smaller-sized fish (Rijnsdorp et al. 1996). Similarly, in the north-western North Sea, Greenstreet and Hall (1996) documented lower diversity and greater species dominance when contrasting trawl records between the periods of 1929-1953 and 1980-1993. These authors noted that these differences were mostly driven by subtle changes in the abundances of less-common taxa. These conclusions were further supported by a follow-up study conducted by Greenstreet et al. (1999) using a temporally (1925-1996) and spatially (addition of the central North Sea) expanded dataset. This study highlighted that species diversity amongst the entire groundfish assemblage declined in areas where fishing pressure was high. In coastal areas of the British Isles, comparison of demersal fish catches collected from research surveys between historical (1901-1907) and contemporary (1989-1997) revealed declines in the abundance of larger-bodied species, particularly skates and rays, while smaller, non-target species (e.g., dragonet) increased in abundance (Rogers and Ellis, 2000). These observations were consistent with findings from other North Sea studies (Greenstreet and Hall, 1996; Rice and Gislason, 1996; Jennings et al. 1999). Collectively, studies suggest that the selective removal of larger-bodied target species by commercial fishing are more vulnerable to exploitation than their smaller-bodied counterparts (Pinnegar and Engelhard, 2008).

Abundance diversity indices (e.g., species richness, evenness) are often used as a method of measuring biodiversity in terrestrial and marine systems. Using an array of diversity indicators, Heath and Speirs (2012) documented changes in the demersal fish community in the Firth of Clyde, southwest coast of Scotland, following the repeal of a trawl ban in 1962 that had been implemented since 1889. Once trawling recommenced, biomass of smaller-sized fish increased and comprised of one predominant species (whiting *Merlandgius merlangus*), whereas biomass was previously distributed across a range of functionally-different species, including larger-bodied individuals. As trawling pressure ceased due to declines in catches, the recovering system was deficient in both large fish and individuals of species that were able to exceed maximum lengths of 40 cm (Heath and Speirs, 2012).

In the Kattegat-Skagerrak region, north-eastern North Sea, several studies have demonstrated the usefulness of historical data in piecing together past population dynamics of exploited fish species, including plaice, cod, and turbot (e.g. Cardinale et al. 2009; Cardinale et al. 2010). In this region, historical trends in fish abundance and distributions are critical to the assessment of recent fishery resources (Cardinale et al. 2009). For example, Cardinale et al. (2009) reconstructed the past dynamics of turbot and their analyses showed that turbot biomass had declined by 86% between 1925 and 2007, maximum body sizes had truncated by 20 cm, and the northern stock had virtually disappeared in the Kattegat-Skagerrak. Moreover, Cardinale et al. (2009) highlighted that a time-series beginning only three decades ago would have provided inaccurate values for measuring baseline levels of turbot stock status. Between 1901 and 2007, a longer-term analysis (1901-2007) of plaice population dynamics in the region revealed that contemporary biomass was approximately 40% of the maximum length observed at the start of century (Cardinale et al. 2010). Although mean annual maximum sizes of plaice recovered between WWII and the mid-1980s, the total decline in size over the 107 year period was about 10 cm. Bartolino et al. (2012) used a spatially-explicit historical dataset to reconstruct the long-term dynamics of Atlantic cod and identified a northern and southern aggregation within the Kattegat-Skagerrak region. Following a peak in fishery landings in the 1960s-1970s, their study highlighted the widespread loss of both aggregations as cod stocks collapsed in the study area. Lund et al. (2011) utilised historical data (1905) of cod from early scientific investigations with local fishers employing traditional cod traps in shallow areas of the Søndeled fjord, southern Norway, and compared historical age and length distributions with recent (2006) data from resurveys of same areas using similar traps. Contrary to the aforementioned studies, Lund et al. (2011) revealed that age and length distributions were directed towards older and larger cod sampled in 2006 compared to a century prior, with fish reaching 50% maturity at smaller lengths and younger ages in the historical period.

Historical trends of abundance, size structure and distribution are fundamental components for understanding the response of biological systems to exploitation by fishing (Cardinale et al. 2009). Detailed information on the stock status prior to and during the expansion of industrial fishing (end of the 19th and beginning of the 20th centuries) is key to elucidating the effects of exploitation from the natural dynamics of the system (Cardinale et al. 2010). In this respect, such data will provide a baseline for estimating reference points for the restoration and long-term management of fish populations (Jackson et al. 2001). During the first years of industrial fishing, low fishing effort can have a disproportionately large impact on the most vulnerable species, particularly large-bodied predatory marine species (Pinnegar and Engelhard, 2008). These species tend to exhibit low intrinsic growth rates, longer life spans and late maturities (Jennings et al. 1999). As a consequence of these life-history traits commercial target species can be the most susceptible to fishing pressure, and thus decline more rapidly than their smaller and faster-growing counterparts (Jennings and Kaiser, 1998). This has been the case for many elasmobranch species across the world, where the expiration and decline of some species has been well documented (Baum and Myers 2004; Ferretti et al. 2013). In the Gulf of Mexico, Baum and Myers (2004) compared catch rates of pelagic sharks caught in commercial longlines between the 1950s and late-1990s. They revealed alarming declines in ocean white *Charcharhinus longimanus* and silky sharks *Carcharhinus falciformis* between the two periods, declining by more than 99% and 90%, respectively. In another example, Ferretti et al. (2013) used standardised catch data from trawl surveys conducted from 1948-2005 to investigate trends in abundance of an elasmobranch community in the Adriatic Sea. Since 1948, catch rates fell by > 94% with strong declines overtime in most of the 33 species identified in trawl surveys, and 11 species vanishing over the study period (Ferretti et al. 2013). Similar dramatic declines in elasmobranch abundance have also been detected around coastal areas of the British Isles (Rogers and Ellis, 2000; McHugh et al. 2011). In inshore waters of the English Channel, McHugh et al. (2011) reported dramatic changes within the elasmobranchs, characterised by the apparent disappearance of the angel shark *Squatina squatina*, reduction in the abundance of all (Rajidae) skates, along with significant declines in the overall size distributions of elasmobranchs.

1.3.2. *Climate-induced changes*

In addition to the pronounced effects of fishing, climatic variability has also been implicated as a major driver of altering fish abundance and diversity in both demersal and pelagic communities (Genner et al. 2004; Hiddink and ter Hofstede, 2008). The impacts of anthropogenic climate change are due to an array of direct and indirect effects of a number physical and chemical factors, including temperature, pH, mixing events, nutrients, salinity, among others, that operate at different temporal and spatial scales (Brander 2010). Such effects will have direct implications on the recruitment, distribution, and behaviour of fish populations, as well as indirectly via ambient ecological processes (Harley et al. 2006; Brander, 2010). The synergistic interactions of climate change and other anthropogenic factors, particularly fishing, make it increasingly difficult to unravel the effects of these drivers as they act simultaneously (Ter Hofstede and Rijnsdorp 2011).

Elucidating climatic responses on fish populations is done best using long-term time-series data (McHugh et al. 2011). Between 1902 and 2008, Ter Hofstede and Rijnsdorp (2011) contrasted changes in species richness and mean body sizes of fish at varying levels of fishing pressure and climate (water temperature) in the North Sea. Based on standardised mean catch rates from swept area correction factors, the study revealed a substantially higher species richness for warm-favouring species, and a smaller mean body size during periods of warmer sea temperatures irrespective of fishing pressure. Using catch per unit effort data of 72 taxa collated from otter trawls between 1913-2002, Genner et al. (2004) found that dominant species within a fish assemblage in the English Channel was significantly associated with sea surface temperature (SST). This association was driven by an increase in abundances with periods of warming. In the same region, Genner et al. (2010) later revealed that size-dependent fluctuations of smaller species was linked to climate-driven regime changes over a 97 year period (1911-2007), whereas persistent declines in the sizes and abundances of larger species were consistent cumulative effects of commercial fishing.

In temperate regions such as the North Sea, individual fish species have responded to rising sea temperatures by shifting their latitudinal (Perry et al. 2005) and depth range (Dulvy et al. 2008). Sea temperatures have increased more rapidly in the North Sea than in adjacent seas over the past century, and is thus considered a ‘hotspot’ for marine climate change (Brander 2010; Sguotti et al. 2016). In the last three decades, a prominent warming trend in the North Sea has deepened the demersal fish community by ~3.6 m per decade (Dulvy et al. 2008) and has concurred with a northward shift in the distribution of several fish species (Beare et al. 2004; Perry et al. 2005). For example, plaice have responded to climate change over the last nine decades by moving their distribution northwards, with the centre of gravity of latitude and longitude shifting by ~1°-2°, and their range deepening by ~20 m (Engelhard et al. 2011). Engelhard et al. (2014) used a similar dataset to ascertain long-term distribution shifts in cod over the period 1913-2012. Most notably, cod appear to be distributed in deeper waters of the northern and north-eastern parts of the North Sea, whereas historically, they were concentrated in the west, off England and Scotland. These conclusions are in line with Perry et al. (2005) and Dulvy et al. (2008), and with the general assumption that climate change dictates a poleward, deepening shift (Rijnsdorp et al. 2009).

1.3.3. *'Bottom up' changes*

In the mid-19th century, fishermen argued that bottom trawling enhanced food availability and sustained benthic fish production by 'ploughing' the seafloor (Thurstan et al. 2014). In more recent years, there is an ongoing debate in the literature as to whether trawling increases food availability for demersal, benthivorous fish species (De Veen, 1976; Jennings et al. 2001; Hiddink et al. 2008). Driving this debate, there have reports of increased growth rates of flatfish such as sole and plaice, which has coincided with higher trawling pressure and increases in food availability (Rijnsdorp et al. 1996; Rijnsdorp and Vingerhoed, 2001). By contrast, others have revealed widespread declines in the biomass, productivity and species richness of benthic epifauna (Hinz et al. 2009; Hiddink et al. 2011).

The direct impact of physical disturbance of mobile bottom-fishing on benthic communities is well understood (e.g. Jennings et al. 2001), however less is known about broader, ecosystem-level effects. Short-term, experimental investigations of the benthos have been shown to have immediate ecological impacts, including displacement of physical habitats, direct mortality of benthic fauna (Jones, 1992; Freese, 2001), and increased scavenging by demersal fish and invertebrates (Kaiser and Spencer, 1996). By comparison, longer-term effects of trawling have led to changes in species composition and substantial reductions in benthic biodiversity and abundance (Callaway et al. 2007; Hinz et al. 2009). The frequency and magnitude of these impacts are highly species-dependent (Van Denderen et al. 2013). For example, smaller, soft-bodied organisms (e.g. polychaetes) with short generation times are less susceptible to physical disturbance in contrast to large and hard-bodied benthic invertebrates (e.g. bivalve molluscs and crustaceans) (Kaiser et al. 2006), and tend to dominate benthic communities in areas of high fishing pressure, either through life-history adaptations or an ability to regenerate body tissues (Van Denderen et al. 2013).

In the south-eastern North Sea, Bergman and Van Santbrink (2000) found that a single pass of a commercial trawl resulted in the direct removal of several benthic invertebrate groups. For example, mortality ranged from 5-40 % of initial densities for gastropods, starfishes, annelid worms, and small crustaceans, whereas observed mortality was much higher in bivalves from a single trawl pass (up to 65%; Bergman and Van Santbrink, 2000). Similar rates of removal have been detected by Sainsbury et al. (1992) and Freese (2001) who revealed that a single trawl pass was capable of removing 90% and 67% of large sponges, respectively. Successive trawling of an area may favour smaller-bodied species, which may compensate for the loss of production among larger organisms (Jennings et al. 2001). Several long-term studies also support these findings, and have speculated that changes in composition are related to intensive trawling (e.g Kröncke, 1988; Callaway et al. 2007; Strain et al. 2012). Using historical and contemporary records, Callaway et al. (2007) revealed that several slow-growing and long-lived species (mainly bivalves) had declined throughout the 20th century, most notably, in the southern and central North Sea, which in turn coincided with high fishing intensity.

Benthic invertebrates form an important prey base for a large component of the demersal, benthivorous fish community in the North Sea (Frid et al. 1999), and trawling-induced changes in prey availability may have substantial implications on the overall carrying capacity for demersal fish (Smith et al. 2013). Several studies have revealed that generalist predators, which feed on broad spectra of prey, are less affected by the indirect effects of trawling in contrast to specialised feeders as they are more capable of predating on less vulnerable prey, which may be more abundant following a single trawl pass (Shephard et al. 2010; Smith et al. 2013). While these short-term impacts are well documented, few studies have examined the indirect, longer-term effects of bottom trawling on fish diet. Time-series data of benthic community biomass and composition are uncommon, and changes in benthic production are incredibly difficult to link to long-term shifts in fish production (Link, 2004). For certain benthic predators, however, several authors have noted a change in diet in the North Sea throughout the 20th century (Frid et al. 1999; Rijnsdorp and Vingerhoed, 2001). Rijnsdorp and Vingeroed. (2001) revealed a major change in diet composition in two commercially important flatfish, plaice and sole, whereby the dominance of bivalves as a key prey resource shifted to polychaetes during the 20th century. In recent decades, the increased importance of polychaetes as a key prey resource for plaice and sole concurred with an increase in their growth rate (Millner and Whiting, 1996), which in turn coincided with an increase in beam trawl activity in the 1960s and 1970s (Rijnsdorp and Vingerhoed, 2001; Sell and Kröncke, 2013).

Clearly, physical habitats and benthic invertebrates play an important role in the production and sustainability of demersal fish species. The loss of benthic prey by trawling may indirectly decrease the carrying capacity of the entire demersal ecosystem (Hiddink et al. 2011), which in turn may reduce the production of key commercial species, and thus prohibit the rebuilding of fish stocks to historic levels. Associated short and long-term changes in predator-prey relationships and shifts in allocations of energy among benthic and pelagic communities (Choi et al. 2004) could further affect the stability of marine food webs subject to ‘top down’ and ‘bottom up’ impacts of fishing. It is, therefore, vital to understand how the broader ecosystem effects of commercial fishing is affects the long-term sustainability of target and non-target populations, and underlines the need for an ecosystem approach to fisheries management.

1.4. Approaches to studying food-webs

1.4.1. *Traditional methods of dietary analysis*

Maximum sustainable yields (MSY) of fish stocks have traditionally been based on conventional single-species assessments. Not all fish stocks, however, can be simultaneously maintained at MSY levels due to the complex nature of predator-prey interactions in marine systems (Mackinson et al. 2009). The is a growing demand for information on “who eats whom” in food webs (Pinnegar et al. 2014) and ecological interactions are increasingly being considered as part of an ecosystem-based approach to fisheries management, which explicitly accounts for the broader, ecosystem effects of fishing activities (Jennings and Kaiser, 1998). An ecosystem approach will require accurate information on a specie’s diet composition and feeding habits as it provides a basis for understanding nutrition and energy flow, termed trophodynamics, among organisms (Pinnegar and Polunin, 1999). Understanding these trophic relationships will also enable us to deduce how changes one area of the ecosystem may have consequences in another part (Pinnegar et al. 2014).

Diet is an essential component to the life history of a fish and information about its diet composition is useful in defining predator-prey relationships (Mohanraj and Prabhu, 2012). Importantly, this type of knowledge may provide a preliminary estimate of trophic level, and thus contribute to a deeper understanding of (Stergiou and Karpouzi, 2002). While a compilation of prey items consumed by a predator will result in identification of food preferences, information on fish diet is widely used as a source of information for strategic ecosystem-based management (Bax, 1998). Trends in diet can characterise many ecological components of the life history of an organism including energy intake, habitat use, behaviour, and inter- and intra-specific interactions (Chipps and Garvey 2007).

Traditionally, food webs have been investigated through faecal and stomach content analysis, or by direct observation of food intake in the laboratory and field (Hyslop 1980; Bowen, 1996; Pauly and Trites 1998; Lukoschek and McCormick 2001; Iverson et al. 2007). Stomach content analysis (SCA) is the most widely used technique for generalising about an organism's diet composition (Hyslop 1980), and is valuable for establishing new dietary linkages and understanding the occurrence and strength of predator-prey interactions (Deb, 1997). For fish, SCA emphasises what is present in the gut at the time of capture; hence sampling location, time of year, season, and prey availability are important considerations for food web studies (Chipps and Garvey, 2007). Historically, methods for quantifying diet composition in fish have centred on individual behaviours of predators and their prey (Lima and Dill, 1990) and the taxonomic identification of diet composition (Bowen, 1996). A number of methods employed in the collection of fish stomach samples includes the non-lethal gastric lavage technique, which involves flushing the gut contents using a pressured stream of water (Waters et al. 2004) or euthanising the fish and directly preserving dietary material to prevent the further loss of taxonomic resolution (Garvey and Chipps, 2012). However, choosing the proper technique and indices for dietary analyses ultimately depend on the hypothesis in question, desired taxonomic resolution, and available resources (Chipps and Garvey, 2007).

SCA provides a high degree of taxonomic accuracy and a 'snapshot' of the diet from the ~24 hours of predation, yet diet can vary seasonally, and some predatory fish species are highly opportunistic feeders (Wainright et al. 1993). The process of collecting comprehensive fish stomach content data can be laborious, expensive, and often intrusive (Chipps and Garvey, 2007). Other limitations include the loss of dietary material through regurgitation upon capture (e.g. from active or passive fishing gears) (Bowen, 1996), underestimation of specific prey material in the gut (Hyslop, 1980), including important component of marine food webs such as gelatinous zooplankton and detritus (Jennings et al. 2001), grinding of particular body parts (e.g. pharyngeal organs) (Chipps and Garvey, 2012), and assimilation of prey, which may further preclude identification (Michener and Schell, 1994).

Contemporary efforts are hindered by a lack of historical data available for deducing historical fishery-induced changes in marine food webs (Frid et al. 1999). Although diet data is undoubtedly biased, several studies have used fish stomachs as a proxy for estimating prey abundance (e.g. Lilly et al. 2000; Fahrig et al. 1993), however there are surprisingly few that have used stomach samples to infer long-term changes in benthic food webs (Frid et al. 1999;

Link, 2004). Since demersal predators have been closely correlated with densities of benthic invertebrates (Knust, 1996; Sell and Kröncke 2013), it seems reasonable that historical and contemporary stomach records can be utilised as an indirect method for inferring long-term change. Link et al. (2004) evaluated this approach and affirmed the use of fish stomachs as samplers of the benthos at broad spatial and temporal scales. Thus, the inclusion of long-term time-series diet data can help facilitate our understanding of fishing-induced changes in benthic systems as well as guide management efforts aimed at improving fish production.

1.4.2. *Stable isotope analysis*

While SCA provides a short-term view of a predator's diet, stable isotope analysis (SIA) can provide a more time-integrated picture of diet and energy flow in marine food webs (Peterson and Fry 1987). Stable isotopes in the tissues of marine animals provide an indication of prey assimilated by predators (Hesslein et al. 1993). SIA has become a widely applied tool for investigating food web structure and elucidating important feeding interactions that may otherwise go undetected by traditional dietary techniques (Chipps and Garvey, 2007). It has provided new insights into many aspects of marine ecology such as inter-and intra-specific dietary variation and overlap in fish feeding habits (Vander Zanden and Rasmussen, 2002; Skinner et al. 2019); migration (Hansson et al. 1997); estimating benthic-pelagic pathways (Kopp et al. 2015; Duffill-Telsnig et al. 2019); and tracking spatial and temporal changes in trophic food webs (Jennings et al. 1997).

Carbon and nitrogen are the two primary elements used in SIA, and their isotopic delta (δ) values, $\delta^{13}C$ and $\delta^{15}N$, respectively, have been widely used to describe food web structure (Daleurm and Angerbjorn, 2005). This is conducted by analysing differences in the relative abundances of carbon and nitrogen isotopic ratios of an organism and its diet, which is termed trophic fractionation, enrichment, or discrimination factor (Caut et al. 2009). In food webs, fractionation is caused by enzymatic selection, whereby the heavier isotope increased in abundance with each assimilation step compared with lighter isotopes (^{12}C and ^{14}N) (Mintenbeck et al. 2007). For $\delta^{13}C$ (^{13}C: ^{12}C), the trophic fractionation of is small (0.4 ± 1.4 ‰; Post, 2002) and is weakly enriched as trophic level increases (Pinnegar and Polunin, 1999). This makes ^{13}C a useful tracer of differentiating between different sources of production from benthic and pelagic pathways (Kopp et al. 2015; Dufill-Telsnig et al. 2019). This distinction is possible because animals that consume pelagic phytoplankton tend to exhibit relatively low (highly negative) $\delta^{13}C$ values compared to those feeding on benthic algae, which are more enriched (less negative $\delta^{13}C$) in ^{13}C (Ramsvatn and Pedersen, 2012). By contrast, the abundance of $\delta^{15}N$ in the tissues of predators is generally enriched by ~3 ‰ relative to their prey and has thus been used to estimate trophic levels (Post, 2002; Malek et al. 2016).

The conservative transfer of $\delta^{13}C$ from prey to consumer is a particularly useful tracer of primary carbon sources where there are large differences in their isotope values, such as between C3 and C4 plants, nearshore versus offshore systems, and terrestrial and marine systems (Michener and Kaufman, 2007). Some marine consumers are not reliant on pelagic or benthic algae for their carbon as they tend to eat sedimentary detritus (Cole et al. 2006). Because the isotope signatures of these two carbon sources can overlap, their $\delta^{13}C$ values may fail to accurately discriminate between sources of production (Croisetiere et al. 2009). Additional tracers such as sulphur isotopes ($\delta^{34}S$) can assist with resolving these differences, which may not be otherwise detected using a dual approach (Peterson et al. 1986; Barnes and Jennings, 2007). $\delta^{34}S$ can improve resolution in food web structure and help to identify source materials because the isotopic signatures of consumers are within 4 ‰ of their sulphur sources (Connolly et al. 2004) and there is little or no fractionation across trophic levels (0-1 %; McCutchan et al. 2003; Barnes and Jennings, 2007). The are only two sulphur-containing amino acids (cysteine and methionine) that are essential constituents to animals (Hesslein et al. 1991) and so there is minimal fractionation associated with the incorporation of these amino acids into animal tissues (Barnes and Jennings, 2007). However, fractionation can be considerably more variable when organic sulphur is oxidised and during other metabolic processes (Barnes and Jennings, 2007).

Dual isotope bi-plots between $\delta^{13}C$ and $\delta^{34}S$ are considered more informative than $\delta^{13}C$ versus $\delta^{15}N$ plots (Kwak and Zedlar, 1997). This is largely due to small levels of assimilated fractionation per trophic transfer as well as high ratios of among-to within-producer isotope ratio variation (Barnes and Jennings, 2007). Differences in $\delta^{34}S$ values among marine consumers are described by differences in isotope values between sedimentary sulphur (benthic species) and water-column sulphate (planktonic primary producers) (Peterson, 1999). Sedimentary sulphides are depleted in $\delta^{34}S$ by up to -10 ‰ during reduction of sulphur to hydrogen sulphide in anaerobic sediments by bacteria (Canfield, 2001), whereas seawater sulphate has a consistent mean $\delta^{34}S$ value of 21 ‰, likely a consequence of biogeochemical cycling of sulphur (Böttcher et al. 2006; Barros et al. 2010). These broad-scale differences make

$\delta^{34}S$ a valuable tracer in differentiating between benthic versus pelagic producers with little fractionation in complex systems such as inland and coastal environments (Carr et al. 2017).

Fractionation of $\delta^{13}C$ and $\delta^{15}N$ varies when propagating up the food web and the origin of such variability is not fully understood (Michener and Kaufman, 2007). Apart from fractionation, other factors such as feeding behaviours, baseline isotope values, turnover time among different tissues, prey quality, lipid and amino acid composition are also responsible for spatial and temporal isotopic variation in food webs (Michener and Kaufman, 2007). Without accurate temporal and spatial baseline estimates it is not possible to determine whether a variation in $\delta^{13}C$ and $\delta^{15}N$ of an organism is due to a change in the baseline, or variations in carbon flow or food web structure (Post, 2002). In many cases, suspension feeders (e.g. mussels) and algal grazers are used to estimate $\delta^{15}N$ at the base of the food web (Post, 2002).

Lipids are often removed as variation in lipid content can substantially influence the $\delta^{13}C$ of a consumer, thereby influencing food web interpretation (Sweeting et al. 2006). Lipids tend to be ~6-8% depleted in $\delta^{13}C$ relative to other tissues, and $\delta^{13}C$ values are more negative when normalised (Sweeting et al. 2006). To compensate for the potential influence on $\delta^{13}C$ values, some researchers have employed a chemical liquid extraction technique, or standardising lipid content by using mathematic correction techniques (Post et al. 2007). They are advantageous as they remove most lipids, generating uniform $\delta^{13}C$ values for comparison; however, these techniques are laborious and they may cause fractionation in $\delta^{15}N$ (Pinnegar and Poluninn, 1999).

SIA can reflect days, months, or sometimes years of consumer's diet into a single estimate, depending on the tissue turnover time of the body tissue analysed (Dalerum and Angerbjörn, 2005). For fish, white dorsal tissue have isotopic turnover rates ranging from a few months to over a year (Hesslein et al. 1993; MacNeil et al. 2005). Thus, the isotopic values of small, fast growing fish (e.g. herring) reflects a diet over a few months, whereas the isotopic turnover time of large, slow growing elasmobranchs is much longer (11-14 months) (Malek et al. 2016). Different types of body tissues provides an insight in to an organism's resource use over a range of different temporal scales (Dalerum and Angerbjörn, 2005). For example, the turnover time of a tissue is related to metabolic rate, and some tissues, such as liver and plasma, exhibit high turnover rates, and their isotopic signatures reflect recent dietary inputs. Others, such as muscle tissue, have slower turnover rates, and integrates average dietary inputs over a few months (Martínez Del Rio et al. 2009). However, any dietary shifts will not be apparent instantaneously in the isotopic composition of a consumer's tissues, particularly in tissues with slow turnover rates, and is lagged over a period of time until equilibrium is achieved (Hobson and Clark, 1992). Consequently, the isotopic values of an organism could be influenced by both previous and recent dietary inputs (Sweeting et al. 2005).

By investigating differences between the isotope signatures of consumers and their average diet, it is possible to model isotope mixing and infer the relative importance of prey sources to the consumer (Inger and Bearhop, 2008). Trophic discrimination factors (TDF, Δ) are often used in isotope mixing models to account for variation that may arise from physiological processes during the incorporation of dietary protein into consumer tissue (Bond and Diamond, 2011). To derive TDFs, researchers have applied quantitative estimates of dietary contributions from taxonomically and/or functionally similar species, often from means of other studies (Caut et al. 2009). However, TDFs are subject to uncertainty because discrimination may vary, and hence their estimation can be confounded, depending on nutritional status, tissue type, diet quality, lipid extraction, physiology and diet composition (Vanderklift and Ponsard, 2003; Caut et al., 2009), thus small differences in TDF values may result in important differences in the output of mixing models (Ben-David and Schell, 2001).

Isotope ecologists often describe the isotopic composition of an animal's tissue in multivariate space (Newsome et al. 2007). This "δ-space", in which axes are the isotopic values for different elements (i.e., δ^{13}C versus δ^{15}N), is reflective of the trophic niche in *n*-dimensional space because an animal's chemical composition is directly affected by its diet and the environment in which it inhabits (Newsome et al. 2007). Variation in the isotopic assimilation within an animal's tissues thus enables ecological inference of the relative contribution of inter-and intra-specific variation to a predator's isotopic niche. By comparing among isotopic compositions of tissues with different turnover rates, it is possible to elucidate individuals that shift their trophic niches over time as well as individuals that exhibit relatively constant diets (Martinez del Rio et al. 2009).

The ecological niche is an abstract *n*-dimensional hypervolume (Hutchinson, 1957) composed of individuals within a population defined by temporal, spatial and trophic axes (Schoener, 1974). Overlap in the ecological niches of co-existing species and their conspecifics implies inter- and intra-specific competition of resources, which could lead to competitive exclusion and subsequent niche shifts as individuals partition their resources along several axes of the niche hypervolume (Ratcliffe et al. 2013). This niche partitioning may result in co-existing species and conspecifics segregating their trophic niches and/or contract on to a narrower range of prey (Costa-Pereira et al. 2019). A population with a narrow niche may be consist of individuals with narrow and specialised niches (Amundsen, 1995). Conversely, population niche expansion can occur when individuals either diversify their diet (i.e., vary in resource use between individuals), comprising specialised individuals with little or no overlap in resource use, and/or when individuals of a population become more generalist (i.e., each individual varies in its own resource use) (Amundsen, 1995). This specialisation may occur as individuals alter their diet to incorporate underutilised and less favourable resources when competition is high (Bolnick et al. 2003; Start, 2018).

Ecological niche theory suggests that the co-occurrence of sympatric predators may cause individuals to segregate their trophic niches and/or contract on to a narrower range of prey in order to optimise resource intake and avoid competition (Costa-Pereira et al. 2019). Individuals may rank resources differently according to their energy gain per unit time, but this largely depends on resource availability and an individual's phenotypic ability to capture and handle prey (Bolnick et al. 2003; Araújo et al. 2011). With abundant resources, predators can afford to be selective and specialise on particularly prey types (Amundsen, 1995), but will expand their niche by incorporating underutilised prey types when preferred resources are scarce (Bolnick et al. 2003; Start, 2018). Such specialisations are thought to be more common where densities of competing predators are higher (Araújo et al. 2011), which makes coastal environments a prime location for co-occurring individuals to exhibit differing foraging behaviours.

1.5. Thesis outline and objectives

The overarching aim of this thesis is to examine historical and contemporary patterns of spatial and long-term change in demersal fish species of the western North Sea. This PhD was inspired by an amalgamation of unique and valuable datasets that sampled trawl-caught fish species from as early as the late 19th and early 20th century. These datasets provide an unprecedented opportunity to repeat surveys of the same sites facilitating the collection of contemporary counterparts in order to elucidate spatial and temporal patterns of change in commercially important fish species. This thesis intends to provide a useful benchmark for improving ecosystem status and provide appropriate baselines against which realistic recovery targets can be made for rebuilding fish stocks.

Chapter 2 aims to document the details of the design and methods for the historical trawl gear used during scientific trawling experiments conducted by the Northumberland Sea Fisheries Committee (NSFC) in inshore waters of the Northumberland coast in 1892 – 1913. This chapter collated relevant information from the literature, gleaned historical photographs, and acquired expertise from the fishing industry in an attempt to describe the evolution, design and functioning of late 19th century beam trawls used around the British Isles. This research enabled the modern reconstruction of the original trawl gear employed by the NSFC using currently available materials. The trawl design, materials, methods of operation is reviewed in context of the literature and the reconstruction of each gear component is discussed. A series of gear trials were conducted in 2018 and 2019 to test the performance and catchability of the replica gear by comparing catch rates and size distributions of the main species with modern trawl gear. Given that beam trawls originated in European waters and were the first major development of the commercial trawl industry, this work provides an invaluable repository for researchers interested in trawl technology and survey designs.

Chapter 3 utilised historical catch data collated by the NSFC (1899 – 1913) and resurveyed the same sites a 120 years later (2018 – 2019) to quantify and describe long-term changes in an inshore fish assemblage in the western North Sea. Here, the study aims to provide an insight into long-term change within a potentially important habitat in inshore North Sea waters. It further strives to reveal baseline changes to an inshore fish assemblage in order to enhance our ability to assess and better manage changing coastal ecosystems. Catch rates were carefully standardised to enable robust comparisons of the abundance and size distribution of species between historical and contemporary surveys, and were analysed using multivariate techniques and community diversity measures. Discrepancies between trawl gears are evaluated and changes in key taxa are interpreted in light of potential long-term drivers of change.

Chapter 4 investigates multi-decadal trends in the diet composition of six demersal and benthivorous fish predators in the western North Sea. This chapter utilises unique stomach content data spanning 1896 – 2015, digitised from Cefas' DAPSTOM database and ICES 'Year of the Stomach' dataset, to identify shifts in the importance of particular benthic prey across the 20th century as well as compare dietary differences in diet with predator size. Results are interpreted in context of human pressures, predominantly fisheries, climate change and eutrophication. This work underlines the value of historical diet data to elucidate broad-scale and long-term changes on continental shelves.

Greater understanding of inter- and intra-specific variation in predator resource use can help predict how species will respond to fluctuations in prey availability as coastal environments change. Chapter 5 uses contemporary stomach content and bulk stable isotope data of fast and slow tissues, collected as part of this thesis, to assess temporal and spatial variability in the diet of two commercially important flatfish, European plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*), across multiple locations on the Northumberland coast. A new tri-isotope ellipsoid approach was applied to examine isotopic niches and determine the degree of dietary overlap between predators, while Bayesian mixing models were used to ascertain the main source contributions to predator diet.

Finally, Chapter 6 synthesises the key findings of this research and expands on their contributions and implications to fisheries science and management. Knowledge gaps, limitations, and caveats to the interpretation of results are provided, and fruitful avenues of future research are discussed in detail.

Chapter 2: Replicating a Late 19th Century Beam Trawl for Inshore Scientific Trawling

2.1. Introduction

Scientific bottom trawl surveys have been used worldwide to assess the status of marine ecosystems. Fishery-independent data obtained from these surveys is highly valuable because it provides one of the most robust sources of evidence of long-term change in fish populations (McHugh et al. 2011). Comparisons of historical and contemporary trawl catches can yield insight into past ecosystem status (Pinnegar and Engelhard, 2008) and reveal major changes in fish abundances, body sizes and distributions over long periods (e.g. Greenstreet and Hall, 1996; McHugh et al. 2011; Heath and Speirs, 2011), sometimes providing a rare opportunity to examine change during the early phase of commercial exploitation.

Investigations of long-term change, however, are often faced with many biases relating to differences in sampling gears and methods of operation employed across different surveys (Rijnsdorp et al. 1996). Any observed changes between different trawl catches may therefore reflect gear effects as well as real temporal changes in relative fish abundance and size (Rogers Ellis, 2000). For example, the general design and functioning of a trawl can influence the selectivity and quantity of the species caught, particularly in relation to an individual species' size and shape (Millar, 1992). Importantly, the size and configuration of the mesh will strongly influence the selectivity of a trawl net, especially in the rear portion of the net where most fish are retained (MacLennan, 1992). Here, the chance for a fish of a given size to escape is largely determined by the degree of opening of the codend meshes (Jones, 1963), but also by the twine material (Tokac et al. 2004) and thickness used (Sala et al. 2007). The species and size composition of the catch will also be controlled by the geometry of the trawl mouth (Jennings et al. 2001), which can vary substantially among different trawl gears (Engås and Godø, 1986). For instance, a constant net opening is maintained in beam trawls by a fixed width (Gunderson and Ellis, 1986), whereas the size of the mouth opening of conventional otter trawls changes with towing speed, bottom conditions and depth (West, 1982).

Understanding how trawl geometry can influence selectivity is essential for standardising comparisons between catch rates in time and space. Modern scientific surveys are often very prescriptive about trawl durations, towing speeds and gear types in order to yield consistent and comparable catch rates (Jennings et al. 2001). However, studies that attempt to contrast trawl catches over longer time frames should account for developments in fishing power and technology over the past century (Engelhard, 2008). This is often achieved by standardising catch rates by applying a constant fishing power or swept-area correction factors (Rijnsdorp et al. 1996). Alternatively, it is possible to resurvey historical sites and imitate original fishing practices to quantify long-term change in fish populations; albeit these types of studies are not routinely performed due to logistical factors and high costs associated with trawl surveys (Currie et al. 2018). In southwest England, McHugh et al. (2011) resurveyed historical sites using a similar otter trawl and mesh sizes to reveal significant differences in assemblage composition between 1913-1922 and 2008-2009. In the Skagerrak, Lund et al. (2011) used traditional traps of similar design to directly compare present life history parameters of cod (*Gadua morhua*) with those in 1905. However, these authors did not correct for potential differences in gear as historical photographs and preserved historical traps revealed that their basic design had not changed substantially overtime. Similarly, Currie (2017) resurveyed inshore areas of the Agulhas Bank, South Africa, which were originally surveyed in 1897-1904, by reconstructing the gear and imitating methods used in the late 19th century. They rebuilt an original 'Granton' otter trawl net based on historical plans, dimensions, and materials, and replicated fishing practices, to accurately investigate long-term ecological change (Currie et al. 2018).

Around the British coast, bottom trawls were initially towed close to port by sail-powered fishing vessels in the early 19th century (Thurstan et al. 2010). Early trawls consisted of a wooden beam, varying in size (6-12 m) depending on the size and power of the vessel that towed it (Collins, 1889; Alward, 1932; March, 1953). The beam held open a triangular bag-shaped net ~1.1 m above the seafloor, secured at either side by two metal 'trawl heads' (Alward, 1932). Sailing smacks typically worked beam trawls that were ~6 m in length, but the addition of steam power in the late 1880s enabled vessels to tow much larger beams up to 12-15 m (Alward, 1932). From this point onwards, steam-driven trawlers displaced sail smacks as they were not limited by a reliance on the wind and tide for propulsion (Edwards, 1909).

Despite enhanced fishing power and easier access to deeper fishing grounds, beam trawls reached their workable limit as the manageable length (and weight) of the beam prevented an expansion to the size of the net (Heaper, 1887; Edwards, 1909). By the end of the 19th century, a further increase in fishing power led to the widespread use of a new type of trawl gear, the Granton otter trawl (Kyle 1903; Engelhard, 2008). On steam trawlers, beams were soon replaced by a pair of otter boards (Fulton, 1902), which act as underwater kites to keep the mouth of the net open (Holdsworth, 1874; Cunningham 1896). As a result, the use of beam trawls were reduced to the shallow, southern part of the North Sea, where the last sailing trawlers targeted plaice (*Pleuronectes platessa*), sole (*Solea solea*), brill (*Scophthalmus rhombus*), and turbot (*Psetta maxima*) (Engelhard, 2008). Unlike unwieldy beams, otter boards could be conveniently stowed aboard the vessel and increased the spread of the net for catching a greater diversity of species (Kyle, 1903). The headline of an otter trawl could rise higher off the seabed in contrast to cumbersome beam trawls, and the width of the net could expand to a much larger volume (Kyle, 1903), thereby increasing the number and diversity of fish caught. By 1898, Garstang (1900) estimated that the total fishing power of one steam otter trawler was equivalent to eight sail-powered beam trawlers, or two steam-powered beam trawlers from 1884. Improved catch rates soon led to the widespread use of otter trawls throughout Britain’s fishing ports.

Among the earliest fishery-independent surveys in inshore waters of the British Isles were those undertaken by the Northumberland Sea Fisheries Committee (NSFC) and the Dove Marine Laboratory, Cullercoats, in north-east England between 1892 to 1913 (Meek, 1895-1913). These surveys were undertaken to examine the status of inshore fish stocks after the implementation of a trawl ban in 1891, which prohibited all sail and steam trawlers from fishing within three miles from the shoreline (Meek, 1895). The trawl ban aimed to protect a range of commercially and ecologically important fish species, such as plaice, sole, turbot, dab (*Limanda limanda*) and grey gurnard (*Eutrigla gurnardus*), which utilised inshore areas of the coastline during their juvenile and adult life stages (Meek, 1895). Aboard two steam paddle tugs, the *Livingstone* and *Stanley,* naturalists of the NSRC collected extensive information on abundance and size for the entire inshore fish community between June – September in five coastal bays (see Chapter 3). Availability of these early data provides a unique opportunity to resurvey these bays and examine long-term change in the inshore fish community. While studies indicate that the greatest change in fish communities occurred in the late 19th and early 20th century (Thurstan et al. 2010; McHugh et al. 2011), fishery managers and fishers expressed their concern for the demise of inshore stocks long before the addition of steam power to trawlers (Thurstan et al. 2013). Although it is thus not possible to determine accurately how the inshore community would have been structured prior to the initiation of fishing, the data collected in historical and contemporary surveys can be used to identify potential benchmarks for improving ecosystem status.

Consequently, the aim here was to directly compare trawl catches between historical and contemporary time periods by designing and reconstructing a comparable trawl gear. The specific objectives were to (1) collate information from the literature that described what a late 19th century beam trawl looked like, and (2) using materials currently available, describe design elements for gear that would be similar in functioning to the beam trawl used in historical surveys. Finally, (3) conduct a series of comparative gear trials to test the efficiency of the replica beam trawl with a modern otter trawl by comparing catch rates and length-frequency distributions.

2.2. Methods

2.2.1. *Gear review and reconstruction*

To recreate a comparable late 19th century beam trawl, information on historical trawling practices were collated by extensively reviewing relevant literature sources. Firstly, gear-specific and survey information was acquired from NSFC reports, accessed online via the Biodiversity Heritage Library (www.biodiversitylibrary.org). Survey-specific information was also attained from local newspaper articles from the British Newspaper Archive (www.britishnewspaperarchive.co.uk). Where details were lacking in NSFC reports, information on early beam trawl design plans, gear components and materials was collated from other sources, including the wider literature, photographs, newspaper articles, and direct correspondence with the fishing industry (Table 2.1). Literature searches were conducted using a combination of key word search terms, such as early beam trawls; 19th century trawl gears; net plans; wooden beam; historical net plans; mesh sizes; and net materials. Historical photographs illustrating the original gear, research vessel and deck scenes were sourced and scanned from one article written by Alexander Meek in the Windsor Magazine (1899). Additional vessel-specific information and images for estimating dimensions were obtained from the website 'Tyne Tugs and Tug Builders' (http://www.tynetugs.co.uk).

We attempted to distil the information that was thought to be relevant for a possible reconstruction of a late 19th century beam trawl. Dimensions of the original gear were not specified in NFSC reports. Instead, dimensions discernible in historical photographs were scaled and approximately estimated using Image J software (version 1.52). Firstly, the known width of the paddle tug *Livingstone* was used to scale and measure the depth of the vessel's gunwale (Fig B1), as it was a common feature present in photographs. Secondly, the estimated depth of the gunwale was used to scale the trawl heads and beam diameter using the measuring tool in Image J. Without knowing precise dimensions of objects within the images, it was difficult to verify this procedure. However, other features (e.g., average height of a man in the 1890s) were used to support whether the vessel and gear were approximately and realistically scaled. Data recorded in NSFC reports, such as site-specific tow durations and distances, were utilised for calculation of historical trawl speeds.

For the gear reconstruction, many historical materials (e.g., hemp twine) were no longer available due to technological changes in the construction of trawl nets. Instead, we found matches by sourcing alternative materials and components that were thought to have similar functional properties (e.g., weight and density) to the original gear (see Results for details).

Table 2.1. Summary of historical sources separated out by type of information collated.

Type of information	**Historical source**
Gear and survey-specific information	NSFC reports (Meek, 1892 – 1913); Windsor magazine (Meek, 1899)
Early net plan designs	Holdsworth, 1874; Collins, 1889; Garstang, 1905; Davies, 1937
Net materials	Collins, 1889; Wood, 1911; Davies, 1927; Alward, 1932; March, 1953
Mesh sizes	Holdsworth, 1874; Alward, 1932; Schofield, 1948; Davis, 1958.
Trawl heads	Windsor magazine (Meek, 1899); Holdsworth, 1874; Collins, 1889; Wood, 1911; March, 1953
Beam	Windsor magazine (Meek, 1899); Holdsworth, 1874; Collins, 1889; Afalo, 1904; Edwards, 1904; Wood, 1911; Davis, 1927
Methods of operation	Windsor magazine (Meek, 1899); Holdsworth, 1874; Collins, 1889; March, 1953; David, 1958,

2.2.2. *Gear trials*

To examine the catchability and efficiency of the reconstructed beam trawl, we conducted comparative trawls with a modern otter trawl in August 2018 and March 2019. Gear trials were conducted in the same shallow (<20 m) coastal bays that were previously surveyed by the NSFC 120 years ago (see Fig 3.1 in Chapter 3). The August trials were conducted in five coastal bays, namely Blyth Bay, Cambois Bay, Alnmouth Bay, Druridge Bay and Skate Roads, whereas March surveys were carried out at the former two sites only (see Table A.1 for individual location details). All trawls were conducted in the daytime at similar depths in the same substrate type (coarse sandy habitat), with a standard one hour haul duration on board Newcastle University's Research Vessel *The Princess Royal*. The same trawl tracks were not repeatedly trawled over in a single day of surveys. The polypropylene otter trawl had a headline length of 8.2 m, total length of 12.8 m and bridle length of 73.1 m. Each net panel consisted of a 80 mm stretched inside mesh. We estimated the net and wing-end spread at 26.5m and 4.1m, respectively. The otter trawl was towed at ~1.29 ms^{-1} and beam trawl at ~1.03 ms^{-1} to imitate historical towing speeds.

After each haul, the contents of the cod-end(s) were sorted by species, identified, and all fish were counted and total length (cm) measured. For the main species caught by both gears, catch rates were expressed per unit area (numbers of fish per 1000 m^2) per hour swept of the seabed to enable us to test whether the catch efficiency of gears differed, irrespective of the differences in towing speed. Swept area was calculated based on the wing-end spread (horizontal net opening) of the otter trawl (4.1 m) and fixed width of the beam trawl (6.7 m), in conjunction with distance trawled. As all catch data were not normally distributed, non-parametric Wilcoxon Mann-Whitney *U*-tests were applied to statistically compare catch rates of the main species caught by the replica beam trawl and otter trawl. To avoid potential confounding effects of mesh selectivity in comparisons, we only included fish > 15 cm in analyses.

Length-frequency distributions of plaice and dab (*Limanda limanda*) from August gear trials were examined based on sufficient data availability for comparisons between the replica beam and otter trawl. Two-sample Student and Welch *t*-tests were used to assess differences in the mean lengths (cm) of plaice and dab, respectively. Dab length data was log transformed to ensure approximate fit to a normal distribution. Additionally, Kolmogorov-Smirnov two-sample tests were conducted on plaice and dab separately, comparing the maximum absolute differences between the cumulative length-frequency distribution of the two trawl gears. Length-frequency distributions in March gear trials were not statistically compared for these species due to insufficient sample sizes obtained by the replica gear in this period.

2.3. Results

2.3.1. *19th century beam trawl net designs*

Review

The design of trawl nets can vary according to the species targeted, type of substrate trawled and fishing power of the vessel towing the gear, however the various components of a trawl are proportionate to its size (Nair, 1969). For beam trawls, the net configuration is determined by the prescribed length of the beam, height of the trawl heads and ground-rope length.

Unlike the variable net opening of an otter trawl, the horizontal mouth width of a beam trawl is fixed, and its geometry is subject to less variability as a constant width is maintained (Kuipers, 1975). However, the dimensions of the different portions of the net, including the materials and thickness of the twine, and method of connecting the net panels, will ultimately affect the behaviour and shape of the trawl net (Currie et al. 2018).

In principle, a beam trawl net in the mid to late 19th century comprised an elongated, triangular-shaped net (Fig 2.1a; Collins, 1889; Edwards, 1909; March, 1953). Although this same basic shape was adopted by beam trawlers all around the British coast, the precise length and dimensions of the net were adapted depending on the size and power of the vessel that towed it as well as the characteristics of the seabed where the vessel was operating (Holdsworth, 1874). The total length of the net was approximately twice the beam length, while the upper part or "square" made up half the size of the entire net length (Holdsworth, 1874; Collins, 1889; March, 1953). The square was fastened to the beam in sections by rubber grommets (Fig 2.1b; Collins, 1889) and typically raised 0.9- 1.2 m above the seafloor in large beam trawls (Wood, 1911; Alward, 1932; Butcher, 1980). The underneath section or "belly", extending from one trawl head to the other, was cut away to form a sweeping semi-circle located close the ground (Fig 2.1b; Collins, 1889, Wood, 1911). Here, the "bosom" or centre of the curve was typically set at a depth equal to the length of the beam (Holdsworth, 1874). The two corresponding narrow sides of the net, termed "wings", extended from the trawl heads to the bosom (Davies, 1927). The wings were made from individual pieces of netting and inserted after the trawl was laced together (Holdsworth, 1874).

Cod-ends were approximately one-seventh the size of the entire length and fastened together at one end by a 'cod-line' (Fig 2.1b; Holdsworth, 1874; Collins, 1889), which retained and prevented the escape of fish. Like modern trawl nets, the underside of the cod-end was protected from chafing as it was dragged over the seabed with the addition of 'rubbing pieces' or 'false bellies', old pieces of netting, which were fitted in overlapping sections (Holdsworth, 1874; Davies, 1927). As per the original net, late 19th century nets were fitted with pockets laced between the belly and back, one on either side (Fig 2.1b; Holdsworth, 1874; Wood, 1911; Davies, 1927), creating a funnel-shaped passage ahead of the cod-end for fish to enter (Graham, 1956). At the entrance of the cod-end, a loose piece of netting knowns as a 'flapper' was laced to the upper surface and functioned as a trap to prevent fish from escaping after entering the codend (Holdsworth, 1874; March 1970). Although they do not feature in modern trawl nets, pockets and flappers continued to serve their purpose for several decades into the 20th century (Davies, 1927; Currie et al. 2018).

In reference to the original ‘22-foot beam trawl’ employed in NSFC scientific surveys, Meek (1899) stated that ‘The large net is conical in shape. The upper part of the broad end is fastened to the beam and the lower half is weighted, usually with a thick, heavy rope… The net is provided with pockets…”. Beyond this description, there was no specific design plan of the original beam trawl documented by the NSFC. Alternatively, we compiled various net plans and descriptions that provided detailed information on the construction of late 19th century beam trawl nets. The most comprehensive drawings and descriptions we found from this era were by Holdsworth (1874) and Collins (1889). These plans detailed key net features and provided an account of general net parameters relative to a trawl’s size and methods of construction. To further support these descriptions, we examined various examples of different sizes of 19th century and early 20th century beam trawl nets and their specific dimensions (Collins 1889; Garstang, 1905; Davies, 1927). It is worth noting that these refer to large commercial nets employed at various locations around the British coast; specific details on smaller beam trawls were not readily available. We also reviewed net plans of a 13.7 m 1880’s replica beam trawl used during fishing trials conducted onboard a restored Lowestoft sail trawler the *SS Excelsior* (Millner et al. 1997; John Wylson, personal communication 2018).

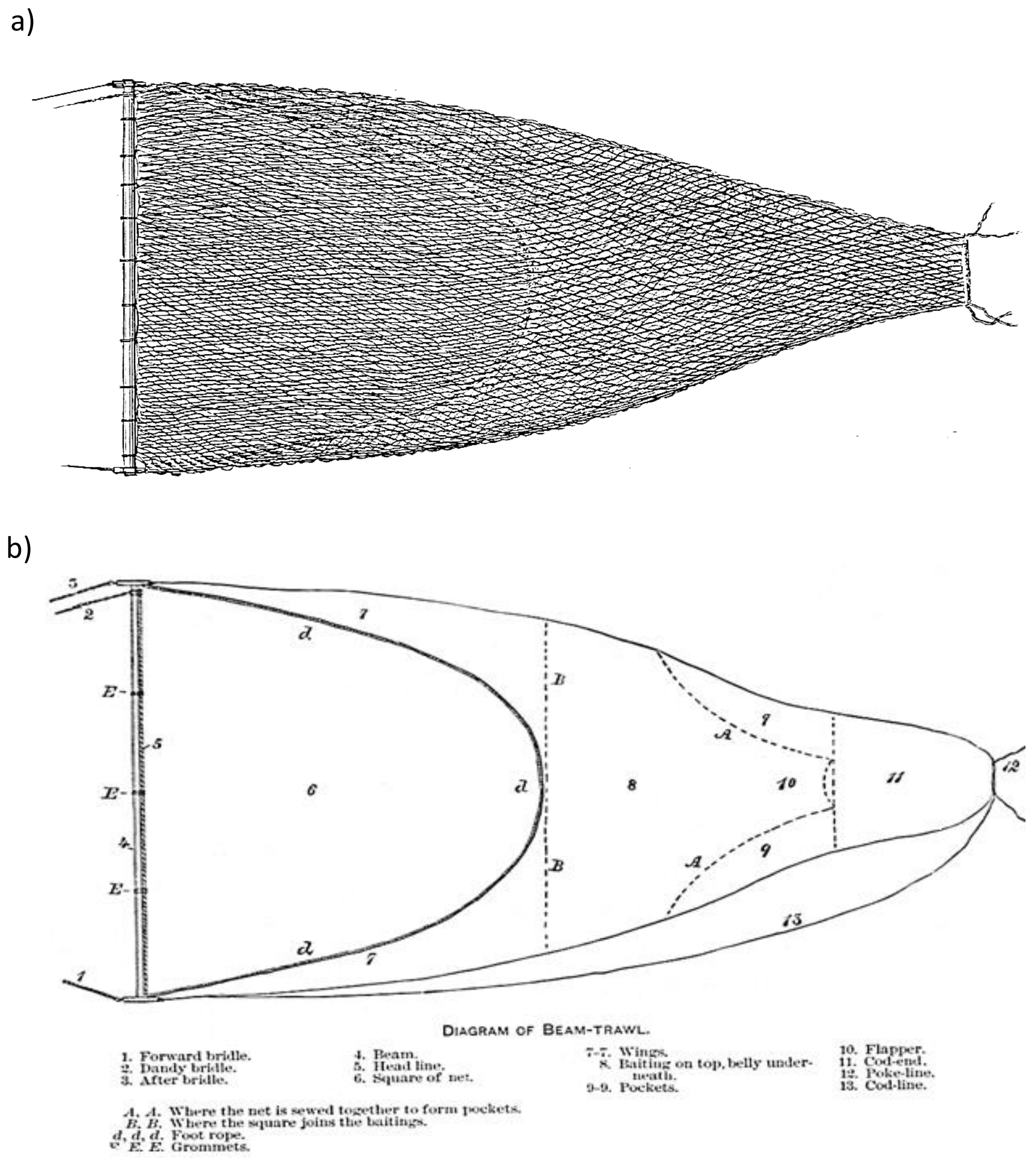


Figure 2.1. Plan view of a late 19th century beam trawl net, illustrating a) a triangular-shaped net with an unopened codend and b) a detailed net plan with labelled features (adapted from Collins, 1889).

Reconstruction

For our replica beam trawl, we designed a net to fit a 6.7 m beam based on the aforementioned design plans and collective descriptions obtained from multiple sources. Our net design was similar to the dimensions and methods of construction of trawl nets reported in the literature (based on 12 to 15 m beam trawls), but we adjusted the dimensions and number of meshes of each net panel accordingly to fit a 6.7 m beam trawl. On this basis, the total size of the replica net was downscaled to 13.3 m (Fig 2.2). The square of the net was 7.3 m and the cod-end was scaled to be approximately one-seventh the length of the net (2.1 m).

The number of meshes were determined by the height and lengths of the various net panels, twine thickness and mesh size (these are discussed in separate sections below). Based on the literature, pockets were laced to the baitings and belly and separated by the flapper at the codend entrance (Fig 2.2). As in historical trawl nets, the flapper was connected to the upper surface of the codend.

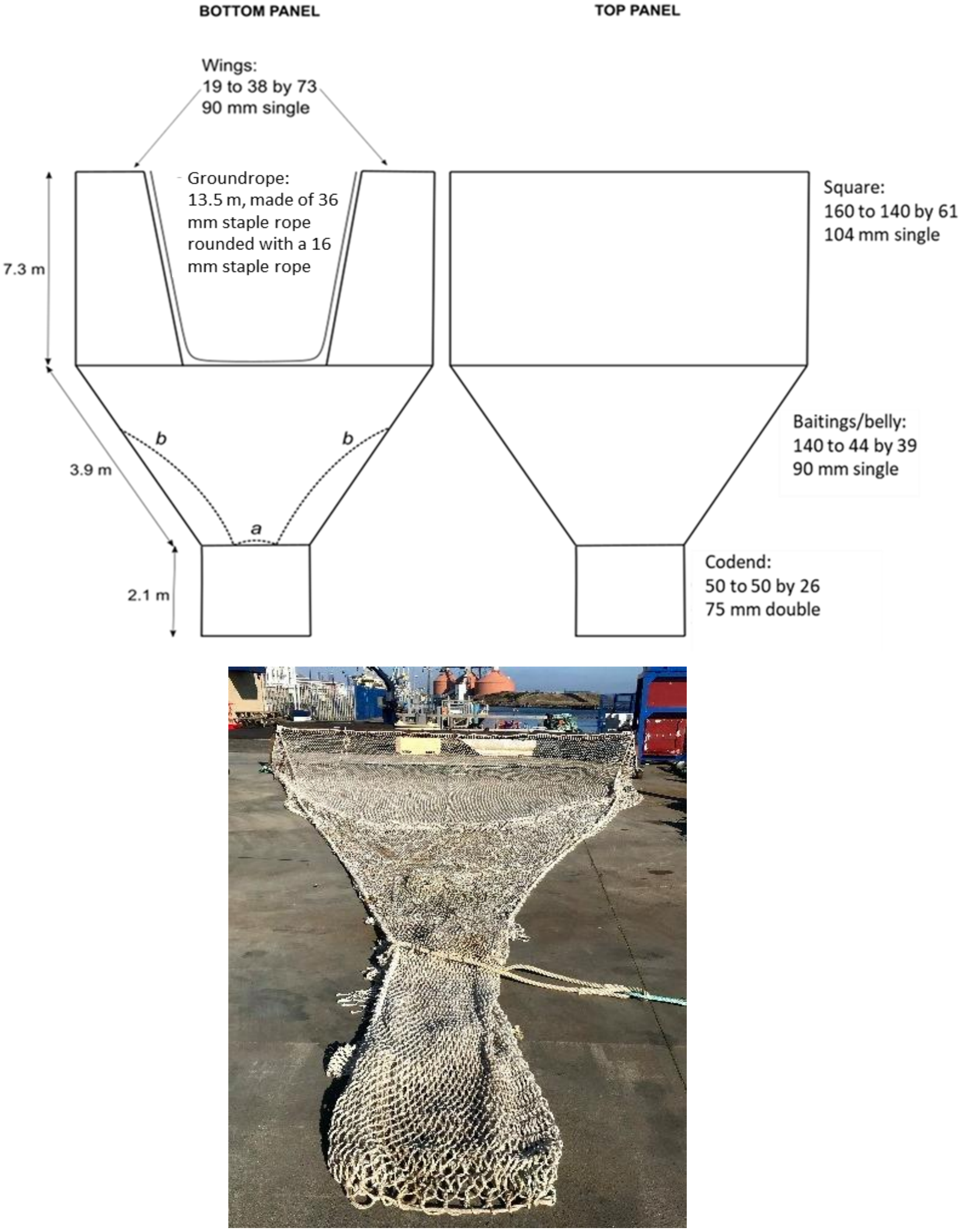


Figure 2.2. Detailed plan and photograph of the replica trawl net used to simulate the original net employed by the NSFC in the late 19th century. Mesh numbers of individual panels are listed as 'front-width to back-width by depth'. Stretched inside meshes are given in mm. The codend was comprised of 3 mm double twine and remaining net panels of 4 mm single twine (*a* = flapper; *b* = pockets).

2.3.2. *Net materials*

Review

The majority of selectivity occurs in the cod-end of a trawl net. Apart from the overall trawl design, there are a number of other gear parameters that can influence cod-end selectivity. For example, the properties of different twines (e.g., specific gravity, flexibility, thickness) used to construct a net can affect fishing performance (Table 2.2; Holden, 1971; Ferro & O'Neill, 1994; Lowry & Robertson, 1996). A cod-end composed of thin and relatively flexible twine will allow more fish to escape compared to one made of stiffer and thicker material (Boerema, 1956; Isakensen et al. 1990). Thicker twines may thus decrease cod-end selectivity by increasing the resistance of the mesh openings (Lowry and Robertson, 1996). Moreover, different twines possess varying specific gravities (Table 2.2). Twines with lower specific gravities such as synthetic fibres are more buoyant than natural fibres, which will ultimately influence the form and behaviour of the net when towed (Radhalekshmy and Gopalan Nayar, 1973; Currie et al. 2018).

Around the British coast, hemp (*Cannabis sativa*) was largely used in the construction of trawl nets until the 1860s (Edwards, 1909). However, hemp was substituted for Manila hemp (*Musa textilis*) in subsequent decades due to claims of increased strength (Collins, 1889; Wood, 1911). This pre-dates the first use of synthetic fibres in trawl nets by a substantial margin, as these only became widespread in the late 1950s and early 1960s (Davis, 1958). Natural twines soon became a redundant component in the construction of trawl nets as synthetic twines possessed greater durability and strength (Davis, 1958; Radhalekshmy and Gopalan Nayar, 1973). These advantages further removed the need to constantly treat nets with dressings and preservatives (Davis, 1958). Historically, hemp or Manilla nets were soaked in coal tar to increase stiffness and longevity of the fibres as well as to reduce water absorption (Atkins & Warren, 1953). Synthetic twines do not undergo this process as they have a higher resistance to rot and mildew (Table 2.2).

Historically, trawl nets were braided by hand as machine-made nets could not be adapted to the shape and taper required for fishing (Alward, 1932; March, 1953). In the early days of trawling, nets were typically made at sea by the smacksmen operating the trawl vessel, but were later hand-woven by women ashore (March, 1953). Following increased demand for trawl nets in the late 19th century, twines were knotted around pieces of hardwood or rounded ‘spools’, which were shaped into sets to standardise the sizes required (Alward, 1932; Davis, 1958). Today, machine-made synthetic trawl nets are set in looms based on the desired twine material, thickness and mesh size, and mass produced in sheets for commercial use (Darren Edwards, Brixham Trawl Makers Limited, personal communication, 2018).

Table 2.2. Physical properties of natural and synthetic fibres that have been used in the manufacture of trawl nets. Information sourced from Fangueiro (2011) and G.P Johnson and Associates, Inc. (n.d; Florida).

Net material	Specific gravity	Breaking tenacity (g/denier)	Water absorption of fibres	Elongation at break (%)	Resistance to rot and mildew	Moisture regain (%)
Hemp	1.50	5.8-6.8	High	2-4	Poor	12
Manila	1.38	5.0-6.0	High	10-12	Poor	12
Polyester	1.38	7.0-9.5	Very low	12-15	Excellent	0.1-0.4
Nylon	1.14	7.8-10.4	Very low	15-28	Excellent	4-4.5
Polyethylene	0.95	6.0	None	20-24	Excellent	0

Reconstruction

Materials used in the original gear were not specified in NSFC reports; however, it is likely that the net was composed of Manila hemp based on its widespread use around the British coast in the late 19th century. As natural twines have now almost completely been replaced by synthetic netting, Manila hemp was not readily available in sufficient quantities for the reconstructed net. We therefore chose white nylon as the next best alternative based on a twine that was logistically available to us and recommendations by a British net manufacturer (Darren Edwards, Brixham Trawl Makers Limited, personal communication, 2018). Like Manila hemp, nylon fibres produce a relatively stiff rope but possess a slightly lower specific gravity (1.14), whereas polyester has the same density (1.38) and has softer fibres relative to Manila (Table 2.2). In contrast, polyethylene nets float in water and have a much lower specific gravity (0.95) than Manila.

For our replica trawl, we used machine-made netting due to the high costs and difficulties associated with obtaining hand braided net panels. For the construction of modern trawls nets, the standard procedure is to order large quantities of netting (sheets) in a given mesh size (Darren Edwards, Brixham Trawl Makers Limited, personal communication, 2018). Fortunately, we found a netting supplier (Swan Net Gundry Ltd) who could provide exact quantities of netting required for each net panel (based on our design plan) and reset their looms to our desired mesh sizes (see *Mesh sizes* for details). Unlike natural twines, our replica net was not treated with any coatings or preservatives.

2.3.3. *Mesh sizes*

Review

There is no universal protocol for describing a trawl net mesh size, but they have been described in a number of different ways since the 19th century. Mesh size nomenclature was originally based on “finger-widths” of trawlermen at sea, starting with four to five finger-widths in the square of the net and decreasing to two in the cod-end (Alward, 1932). Meshes were later hand braided ashore and wooden ‘spools’ were used to standardise their size (Davis, 1958). Today, the mesh size of a modern trawl net is often described by the longitudinal distance of two opposing knots when fully extended. This tends to refer to the distance within the mesh excluding the knots (Currie et al. 2018).

While most authors are explicit in the way they refer to a mesh size, misinterpretation can arise due to the range of ways they are described. For instance, a mesh of 2 inches was often described as 2-inch ‘bar’ or ‘square’, both of which could refer to a measure along one side of a mesh, or denote the distance between two opposing knots of one mesh when fully stretched (i.e., 4 inches extended longitudinally), or it could be the sum of all four sides (Fig A.1; Schofield, 1948; Davis, 1958). In large commercial trawl nets (beam and otter), mesh sizes in the upper part of the net (“square”) typically ranged from 15.2-20.3 cm fully stretched (3-4-inch ‘bar’), grading down in size through to the baitings and codend (Holdsworth, 1874). On the other hand, cod-end meshes were typically much smaller at ~7.6 cm fully stretched (1.5-inch ‘bar’; Table A.2). A cod-end was frequently braided with double twine and the rest of net was typically constructed using single twine (Holdsworth, 1874).

Reconstruction

Mesh sizes were not estimated from historical photographs due to the lack of resolution. Combining evidence reported in the historical literature, the minimum size of fish species recorded during NSFC trawl surveys (~10 cm), and mesh availability, we chose a 3 mm double twine with a 75 mm mesh size (inside mesh) as being appropriate for the cod-end. For the square, 104 mm mesh (inside mesh) with a 4 mm single twine was used, whereas the remainder of the net was made of 90 mm meshes (inside mesh) with a 4 mm single twine.

2.3.4. *Trawl heads*

Review

The trawl heads, or head irons, were large, metal frames that functioned as runners to raise the beam off the seafloor, approximately 91-121 cm in large beam trawls ground (Collins, 1889; Wood, 1911; March, 1953), and to keep the mouth of the net open to allow fish to enter (Fig 2.3a; Collins, 1889). In late 19th century beam trawls, trawl heads were stirrup-shaped, however their design varied at different ports along the British coast (Holdsworth, 1874; Collins, 1889). The most common frames, used by trawlers from Grimsby, Hull and other major fishing ports on the eastern coast, were those illustrated in Fig 2.3a. In this design, beams were squared off at the end and fixed into sockets above the top part of the trawl head (Holdsworth, 1874; March, 1953). In less common designs, either the sockets or the iron loop through which the ground-rope passes (or both) were constructed on the inside of the frame (Fig 2.3b; Holdsworth, 1874). The latter was often used by smaller vessels that trawled inshore at ports such as Lowestoft and Ramsgate, whereas a more semi-circle design with sockets fixed on the inside of the upper part of the trawl head, known as the ‘Barking pattern’ (Fig 2.3b), was frequently adopted by trawlers in the Thames and Yarmouth (Holdsworth, 1874; Collins, 1889).

The size and weight of trawl heads employed in the late 19th century varied according to the size of the net and beam and depth of water worked in (Collins, 1889; March, 1953). Unlike otter boards, exact dimensions and weights of different sizes of trawl heads used in the late 19th century were rarely reported in the literature. Instead, the general weight of a pair of large trawl heads were described. The most commonly referenced (minimum) weight for a pair of trawl heads used in a beam trawl of about 14 m was ~101 kg (Holdsworth, 1874; Collins, 1889; Davies, 1927; Alward, 1932; Butcher, 1980). However, on large North Sea sail trawlers the weights of the trawl heads were much larger, ranging from 160 to 181 kg (Collins, 1889).

Constructed from wrought-iron, the frame of the trawl heads were the same thickness, except the trawl ‘shoes’ at the bottom were twice as thick in order to compensate for the abrasive action of the seabed (Collins, 1889; March, 1953; Butcher, 1980).

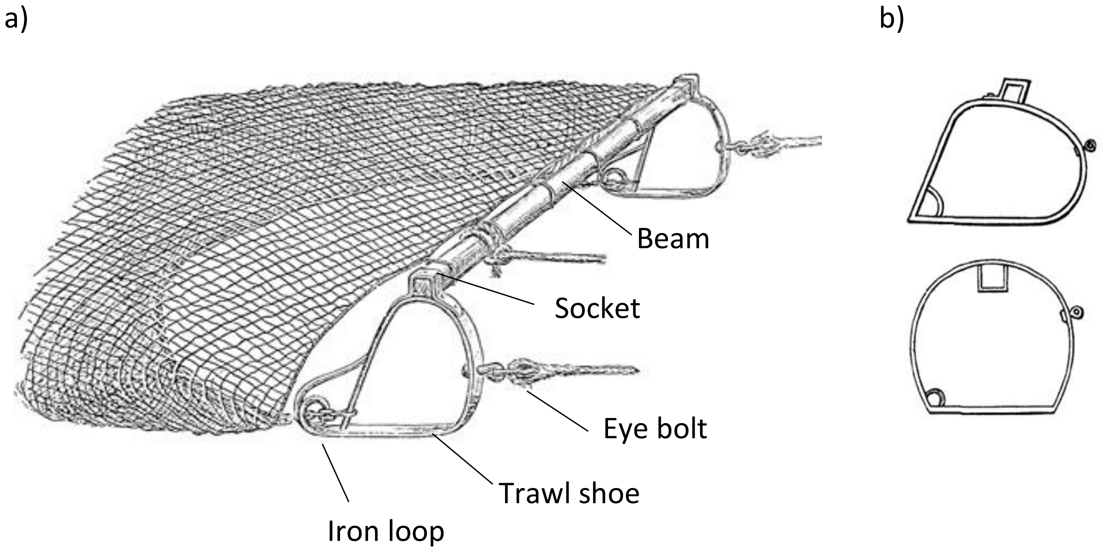


Figure 2.3. Photograph of the original 6.7 m beam trawl being hauled by members of the NSFC on the starboard side of the paddle tug *Livingstone* (Meek, 1899).

Reconstruction

Based on materials available, we reconstructed the trawl heads using black steel, which has a similar specific gravity to wrought iron (~7.8; Reade International Corporation, 2018). The weight of the two trawl heads were approximately 100 kg; similar to the minimum weights reported in the literature (Holdsworth, 1874; Collins, 1889; Davies, 1927; Alward 1932; Butcher 1980). Fortunately, one of the trawl heads used on board the *Livingstone* is clearly visible in a photograph of the crew hauling in the net (Fig 2.4), and resembles the most common trawl head design employed in eastern British ports (Fig 2.3). After measuring and scaling the dimensions from the image, we estimated the trawl heads to have a height of 68.6 cm, which is about a third smaller than the heights reported in the literature. The depth and length of the trawl shoes were assumed to be 1.3 and 115.8 cm, respectively.

For the reconstructed trawl heads, we used a similar square socket to the one visible in Fig 2.4. The socket was bolted to the main frame using 12 mm bolts at *d* to provide a flat union between the socket and the main frame *a*, and bolted in the centre at *c* (Fig 2.5). The trawl shoes were stitch-welded to the base of the frames and secured at the heel of trawl head (*b*), resulting in a total depth of 2.6 cm (twice the thickness relative to the main frame). For attachment of the bridles, a 16 mm eyebolt was shackled into the front of each trawl head (Fig 2.5). The positioning of the eyebolt is an important setting for the effectiveness and efficiency of the trawl heads as the gear is it towed over seabed (Nigel Gray, personal communication, 2018).

Figure 2.4. Photograph of the original 6.7 m beam trawl being hauled by members of the NSFC on the starboard side of the paddle tug *Livingstone* (Meek, 1899).

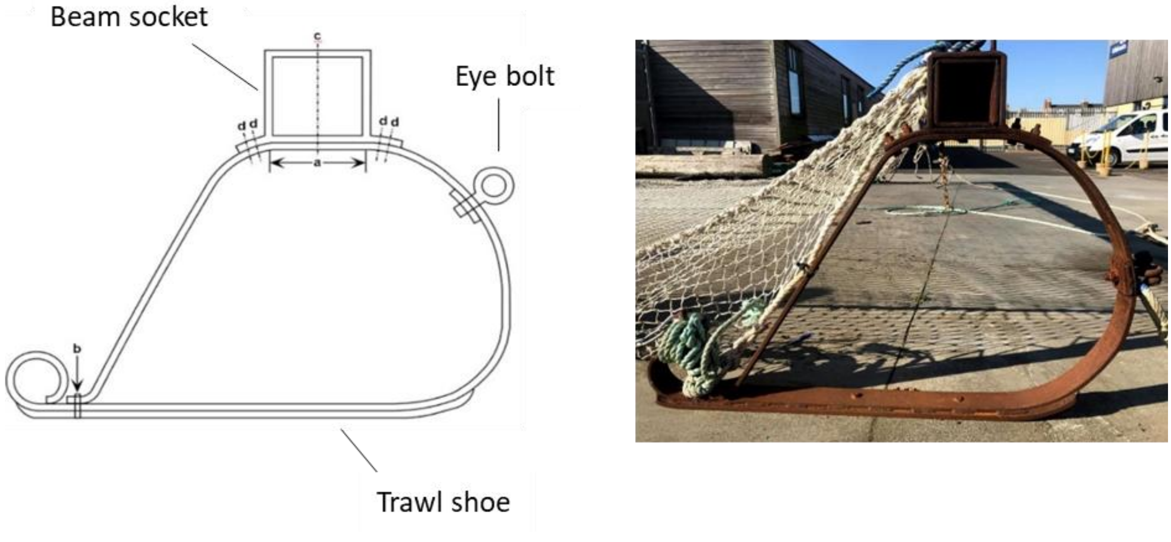


Figure 2.5. Side plan and photograph of the reconstructed trawl heads based on the original design employed by the NSFC in the late 19th century. *a* = main frame; *b* = trawl heel; *c* = socket bolt; and *d* = 12 mm bolts securing socket into main frame.

2.3.5. *Ground rope*

Review

Running along the lower edge of the wings and bosom in the centre, a ground-rope, consisting of an old piece of ‘towing hawser’ rounded with a smaller Manilla or hemp rope (Fig. A2), served to disturb the sediment and entice bottom fish into the net (Holdsworth, 1874; Collins, 1889; Wood, 1911). In large beam trawls, Collins (1889) reported that these ropes were approximately 60 mm diameter (7.5 inches in circumference) and 16-20 mm in diameter (2-2.5 inches in circumference), respectively. Other authors noted that ground-ropes had a central core of wire that was covered with old netting and rounded in the same way (Kyle, 1903; Wood, 1911; Davis, 1927). The smaller rope was “rounded” from end to end to increase the overall weight of the ground-rope and to prevent it from chafing during contact with the seabed (Fig. A2; Holdsworth, 1874; Collins, 1889). Ground-ropes were attached to the meshes net via a ‘bolsh’ or ‘balch’ line (Fig A.2b; Collins, 1889), while a short piece chain connected either end of the ground-rope to the back of each trawl head (Collins, 1889). Bolsh lines were approximately 1 cm in diameter (1.25 inch diameter), and set at 30 cm increments along the wings and at smaller distances along the bosom (Fig A.2b; Collins, 1889; Kyle, 1903; Davis, 1927).

As in modern nets, historical ground-ropes varied in length and diameter depending on location, target species, net size, and habitat over which it was worked (Davis, 1927). In 14-15 m beam trawls, ground-ropes were typically 28-29 m in length (Collins, 1889; March, 1953). Moreover, it was common practice for trawlers in the late 19th century, particularly beam trawlers targeting flatfishes such as sole (*Solea* solea), to further weight their ground-ropes with heavy lengths of chain to increase contact with the seabed (Collins, 1889; Kyle, 1903). The arrangement of these ranged from a piece of chain (4.5-6 m in length) or leaded weights attached the middle of the ground-rope (Holdsworth, 1874; Collins, 1889; March 1970) to a series of metal rings spaced in equal increments around the ground-rope, each linked by an iron chain (Fig A.2a; Kyle, 1903).

Reconstruction

The ground-rope used by the NSFC during scientific trawl surveys is visible in photographs of the crew hauling in the beam trawl (Fig 2.4), which appears to be consistent with the aforementioned description. After scaling the photograph, we estimated the ground-rope to be ~70 mm in diameter. This estimate was smaller than the ground-rope diameters reported for larger beam trawls. For our replica ground-rope, we used a 36 mm diameter braided staple rope rounded with a 16 mm diameter rope (Fig 2.6), which resulted in total diameter of ~68 mm. The chain used to connect the ground-rope to the trawl-heads and part of the bolsh line is clearly visible in Fig 2.4, albeit the chain appears to continue along the underside of the ground-rope. This implies that a chain was either used around the entire length or placed in sections of the ground-rope, instead of just in the bosom area as reported in the historical literature.

For the reconstructed ground-rope, we attached short pieces of chain in sections on the underside of the ground-rope. As per 2.4, a short piece of iron chain was used to attach either end of the ground-rope to the trawl-heads through the iron loop (Fig 2.6a). To connect the ground-rope to the meshes, we used a bolsh line that was set in larger increments along the wings and smaller in the bosom (Fig 2.6b). Following initial gear trials in June 2018, we extended the ground-rope by 1 m either side of the wings to compensate for slack in the bolsh line, resulting in a total length of 14.5 m.

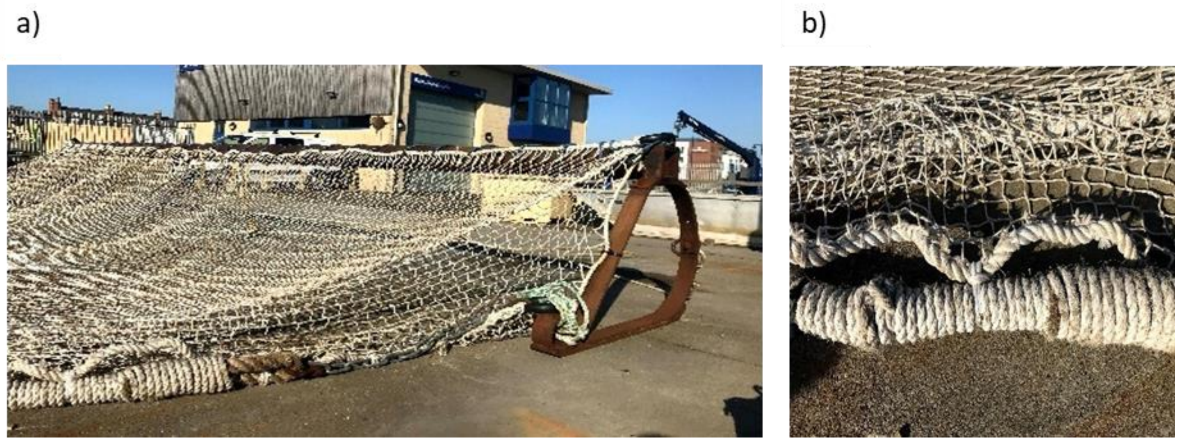


Figure 2.6. Photographs showing a) the reconstructed ground-rope attached to back of the trawl head via a short piece of chain, and b) rounded ground-rope attached to meshes via the bolsh line.

2.3.6. *Beam*

Review

The size of a beam was largely determined by the length and power of the fishing vessel that towed it (Holdsworth, 1874; Collins, 1889; Alwards, 1932), but also by the vessel's capacity to adequately stow the beam (Holdsworth, 1874). In the late 19th century, inshore trawlers worked small beams from 3 m upwards (Collins, 1889), whereas large vessels, generally for deep-sea trawling, could tow beams up to 14-15 m in length (Butcher 1980). The diameter of a beam ranged from 20-22 cm (Butcher, 1980). Historically, beams were made of wood, typically ash, beech, oak or elm; the latter being the most common (Holdsworth, 1874, Collins, 1889; Aflalo, 1904; Edwards, 1909; Wood, 1911). A single piece of wood was usually employed in beams up to about 10 m, however beyond this size, two or sometimes three pieces of wood were scarfed together and reinforced with iron bands to form a long splice (Collins, 1889). This method was used to increase the strength and durability of larger beams (Davis, 1927).

Reconstruction

For our replica gear, we initially tried to mimic the historical beam as closely as possible to match the length (6.7 m) using a single piece of timber. The beam was shaped into a 14 cm^2 square socket at end of each trawl head, as estimated from Fig 2.4. Due to the lack of beam specification, we compared the densities of currently available timber with the densities of timber known to be used historically, to suitably select a material for our reconstructed beam. We chose Douglas fir, largely because it has a relatively similar density (530 kg/m^3) to English elm (550-600 kg/m^3). Upon testing the gear during initial gear trials in June 2018, buoyancy issues arose as the wooden beam prevented the net from settling on the seafloor. Collins (1889) suggested that spare beams were sometimes soaked in water for several hours before use in trawl ports. Other than this, there is no evidence to suggest that beams were sunk prior to trawling (or for how long). Unlike the net, the materials used to construct the beam is unlikely to influence fishing performance (Neil Armstrong, Blyth Marine Station personal communication, 2018). To counter the buoyance issues, we subsequently used a 6.7 m steel beam with a diameter of 15.2 cm in place of the wooden beam.

2.3.7. *Methods of operation and towing speeds*

Review

In the late 19th century, smooth fishing grounds and a favourable tide were essential factors for sail smacks and paddle tugs. The shooting and hauling of a 14-15 m beam trawl in the late 19th century was a laborious task and manoeuvring it into the correction position required careful skill (Wood, 1911). Beam trawls were towed over the seafloor by a single trawl warp, consisting of a hemp or Manilla rope, attached at one end to two smaller ropes, the bridles, which were fastened to the front of each trawl head via swivel eyebolts (Holdsworth, 1874;

Collins, 1889). Firstly, the cod-end was thrown over the port side of the vessel, followed by the rest of the net, until the net was cleared of the vessel and trailing from the beam (Holdsworth, 1874). The beam was then lowered over the side, carefully maintained in its upright position, and net streamed away from the vessel at sea surface. The fore-bridle was slackened to allow the fore trawl-head to 'square away' at a 90° angle to the stern of the vessel, while the other trawl head remained in place by the dandy bridle, which was secured to the trawl warp at one end and the aft end of the beam (Holdsworth, 1874). The bridles and warp were then 'paid out' until the trawl settled on the bottom at a distance astern and windward of the vessel (March, 1953). Once the required length of warp was reached, the warp was secured through a stopper and towing post, which helped control the rate at which the warp was paid out (Davis, 1958).

On the windward side of the vessel, trawl nets were hauled in using the motive power of steam-powered capstans and winches, which lightened the load of the crew hauling in the catch (Collins, 1889; Butcher, 1980). At the junction between the warp and bridles, the dandle bridle was cast off the trawl warp and later attached to a dandy winch, which was used to heave the after end of the beam towards the stern (Collins, 1889; Davis, 1958; Butcher, 1980). The after bridle was heaved in first and secured to the taff-rail, followed by the fore-bridle, which was bought in via a forward winch (Collins, 1889). As both trawl-heads swung in line with the port side, they were lowered and secured on deck, while the remainder of the net and ground-rope were hauled in by hand (Collins, 1889; Davis, 1958). Next, the 'cod-line', extending from the forward end of the beam to the cod-end (Fig 2.1b), was used to haul in and suspend a heavily weighted cod-end over the deck via the capstan. This was to relieve the strain of the rest of the net before the 'poke line' was untied to release the contents of the net (Collins, 1889).

From the various scenes captured of the crew hauling in the original beam trawl onboard the paddle tug *Livingstone* in 1889 (Fig 2.7), it appears that the gear was hauled in entirely by hand on the starboard side. A photograph of the *Livingstone* is shown in Fig A.3a, with a view from the stern. There was no evidence of any mechanical winches or a capstan on the *Livingstone* to aid with retrieving the net. Instead, a third bridle, attached in the centre of the beam, was used in addition to the fore-and-after bridles to haul in the net (Fig 2.7). A larger, more powerful paddle tug, *Stanley*, was later (from 1901) employed by the NSFC for scientific trawl surveys, which was 33 m in length, 5.7 m wide, and 3 m draft (Meek, 1901). Meek (1901) mentioned that a ‘powerful steam winch and davits’ were used, which made hauling in the trawl lighter work for the crew.

Between the 19th century and today, the process of shooting and hauling a trawl net became more mechanised and efficient, which vastly enhanced the fishing performance of trawlers over time (Engelhard, 2008). Steam trawlers were less powerful and slower compared to modern vessels (Currie et al. 2018), varying among different classes of trawlers and gears. Trawl speeds were not systematically documented in historical reports by the NSFC, however Meek (1901) reported that ‘Unless otherwise stated, the steamer was trawling at the time the net was being used, and the speed would therefore be about 2 knots.’ This speed is supported by similar towing speeds reported in the literature from the same era. For example, Garstang (1905) obtained 2.1 knots on average during trawl investigations conducted on the *SS Huxley* in the early 20th century. Kyle (1903) reported that steam-driven beam trawls were towed at 2 knots, while M’Intosh (1895) reported that the average towing speed was ~2.5 knots. Moreover, a sail smack could reach speeds of 8-9 knots, but this was offset by 6-7 knots due to the drag of the net (Holdsworth, 1874).

Reconstruction

For our repeat surveys, the reconstructed beam trawl was deployed from the stern of a 18.9 m catamaran *The Princess Royal* (Fig A.3b). The vessel has an overall width of 7.3 m and draft of 1.6 m. In modern trawlers, it is common practice for trawl nets to be operated from the stern to enable faster shooting and hauling of the net, further reducing time between trawls as the codend is emptied and reassembled while the vessel is repositioned for the next trawl (Currie et al. 2018). We shot and hauled in our replica gear using a single cable warp attached to two cable bridles at one end, which were in turn connected to the front of each trawl head via an eyebolt. The length of warp used for trawling was controlled by a central trawl winch via a hydraulic A-frame at the stern of the vessel.

During gear trials, we maintained a towing speed of 2 knots (1.03 m/s^{-1}). This was based on trawl speeds reported in the literature and speeds calculated from tow durations and approximate distances trawled during historical trawl surveys. The mean towing speed calculated was estimated to be 1.8 knots (0.93 m/s^{-1}) in historical NSFC trawl surveys.

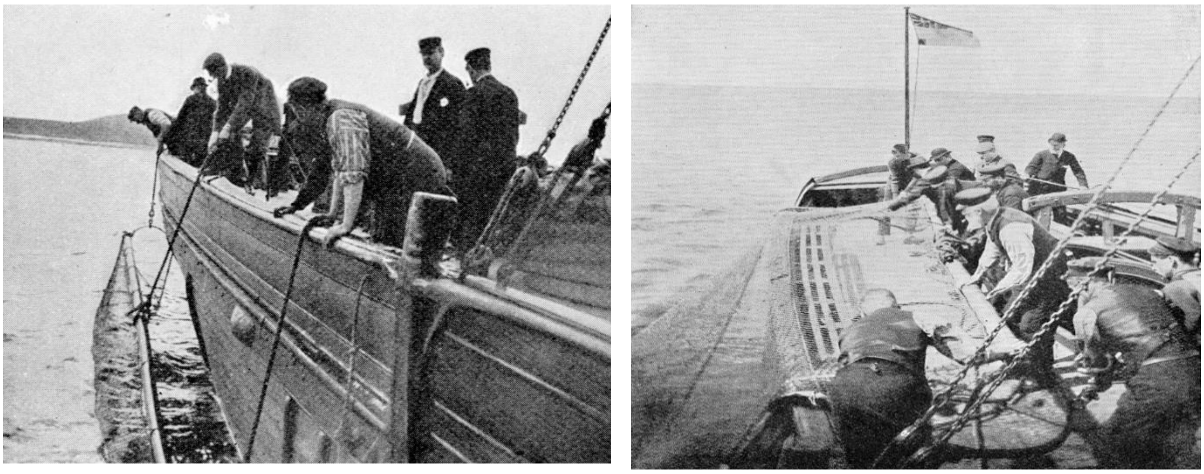


Figure 2.7. Photographs of NSFC crew hauling the beam on the starboard side of the *Livingstone* by hand via a central bridle and the fore-and-after bridles (Meek, 1889).

2.3.8. *Gear trials*

In all, a total of 20 hauls were made using the replica beam trawl and 8 with the otter trawl in August 2018 (see Table A.1). In March 2019, we conducted a further 6 trials using the replica beam and 4 with the otter trawl. Of the 6 trawls made by the replica beam trawl in March, three hauls yielded no fish whatsoever. Fig 2.8 shows the median catch rates of the main species per unit area (1000 m^2) swept for each gear type and trial period (including the zero-catch tows in March). In August, similar median catch rates were observed in dab, plaice and flounder (*Platichthys flesus*) between the two gears, albeit medians were slightly higher for the latter two species caught by the otter trawl (Fig 2.8a). In comparison, the median catch rate of European lobster (*Homarus gammarus*) was substantially higher for the otter trawl than the beam trawl. By contrast, median catch rates of all fish species landed by the beam trawl in March trials were either 0 or marginal, whereas substantially more dab and plaice were landed by the otter trawl in this period (Fig 2.8b), although still much lower in August. Wilcoxon Mann-Whitney *U*-tests detected significant differences in flounder and lobster catches between gears in August trials ($P < 0.01$ and $P < 0.05$, respectively), but not for flounder ($P = 0.065$). Conversely, Mann-Whitney *U*-tests revealed significant differences in dab and plaice catches ($P < 0.05$) but not for flounder ($P = 0.236$) between the two trawl gears in March.

In August trials, the mean lengths were significantly smaller in the replica gear for plaice (Student's *t*-test, $P < 0.001$) and dab (Welch's *t*-test, $P < 0.001$) compared to the otter trawl (Fig 2.9a). Similarly, the mean lengths of these two species were smaller in March gear trials

(Fig 2.9b), but were not tested statistically due to low sample sizes in the replica gear for this period. A Kolmogorov-Smirnov test also revealed a significant difference in the length-frequency distribution of plaice between gears ($D = 0.39$, $P < 0.001$) but not for dab ($D = 0.39$, $P = 0.131$).

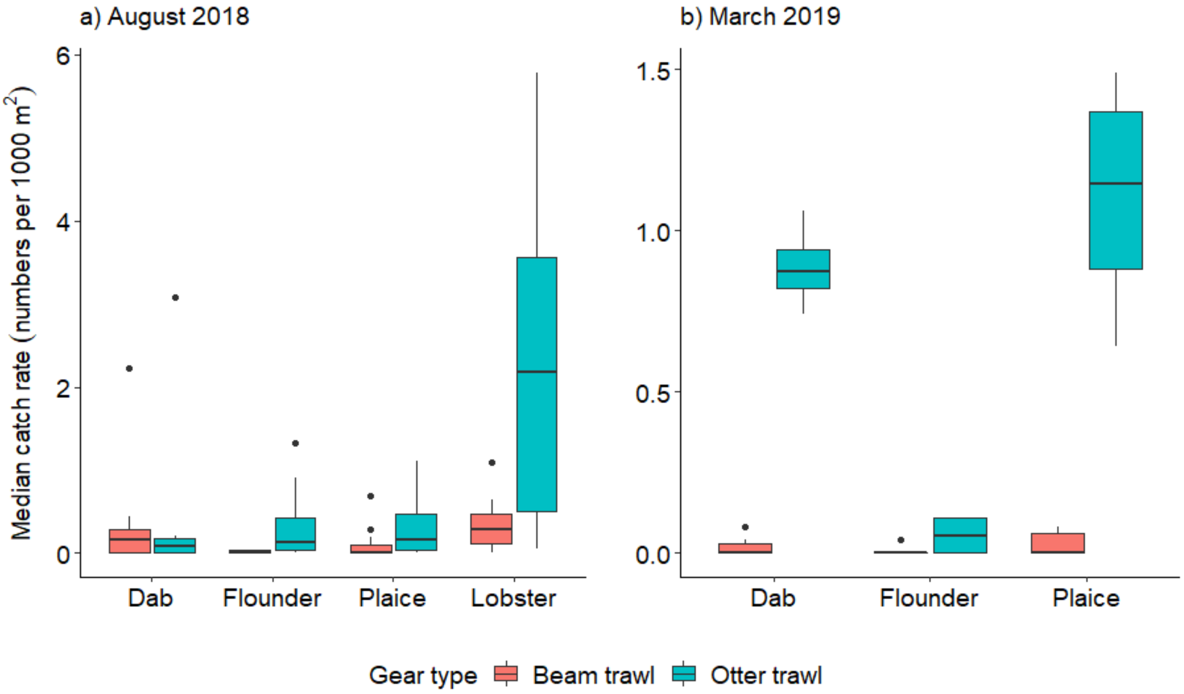


Figure 2.8. Median catch rate (numbers per 1000m^2) with confidence intervals of the main species landed during gear trials in a) August 2018 and b) March 2019.

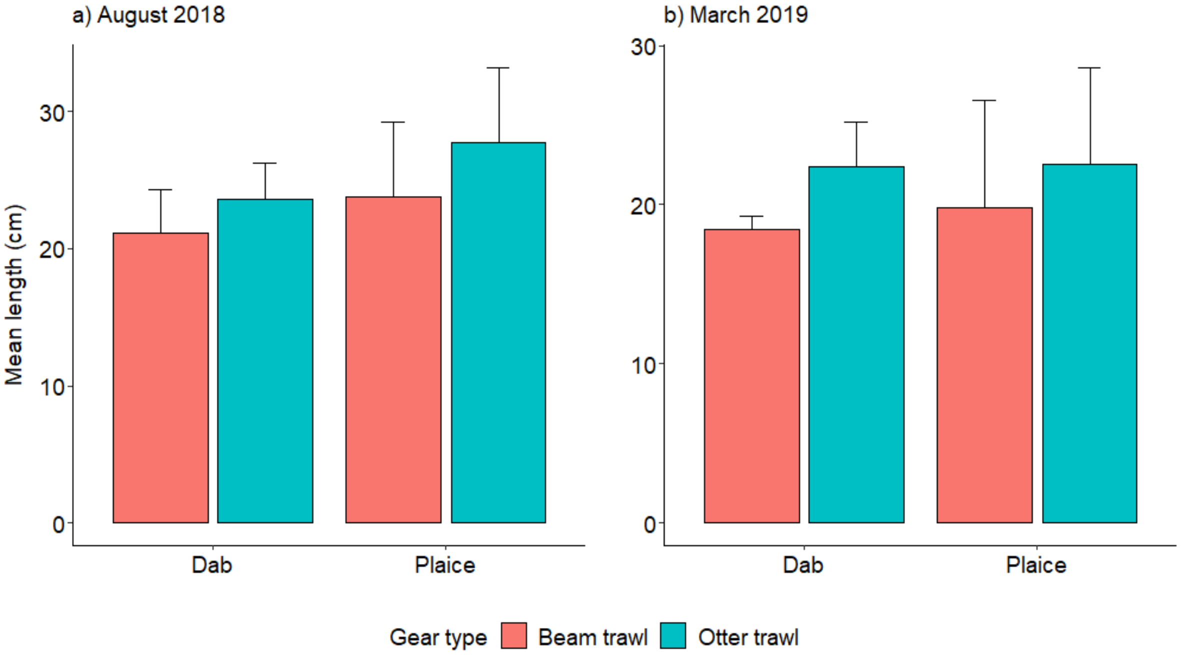


Figure 2.9. Mean lengths (± standard deviation) of plaice and dab (>15 cm) caught by the replica beam and otter trawl during gear trials in a) August 2018 and b) March 2019. In total, 181 and 121 plaice and dab were landed by the replica beam and otter trawl in August, respectively, whereas the beam only landed 6 plaice and dab in total and the otter 149 in the March trials.

2.4. Discussion

This study provides an important repository of knowledge for understanding the design, technology and operation of beam trawls used in the late 19th century. Information was compiled from a wide range of historical sources, including reports, literature, photographs, and newspaper articles, as well as input and advice from numerous stakeholders within the modern trawl industry, demonstrating the feasibility of reconstructing a beam trawl that was first used in scientific trawling experiments over 120 years ago. On this basis, we provide a detailed design plan, incorporating features and dimensions that were carefully scaled to fit a 6.7 m beam, which aimed to functionally replicate a historical beam trawl using contemporary materials (summarised in Table 2.3).

Following construction, we tested the performance and catchability of the replica beam trawl by conducting a series of comparative trawls (with a modern otter trawl) in August 2018 and March 2019. The otter trawl and replica beam trawl exhibited broadly similar efficiencies in catching flatfish during the August trials, albeit the otter trawl caught a higher proportion of lobsters. In March however, the otter trawl was more efficient at catching flatfish (albeit still much lower than in August) in comparison to the replica gear. We also observed systematic differences in the mean lengths of plaice and dab between the two gears, which were consistently smaller in the replica beam trawl. Comparison of standardised length-frequency distributions between gears revealed significant differences for plaice but not for dab.

A complete picture of the dimensions and how the original gear was constructed was not possible, thereby requiring a number of assumptions to be made and uncertainties to be addressed. For example, there was a lack of detailed information on late 19th century beam trawl plans that were similar in size to the one used by the NSFC. Instead, the reconstructed net based was on plans and descriptions of large commercial trawls with ~14-15 m beams towed by sail and steam-powered vessels in the mid to late 19th century (Holdsworth, 1874; Collins, 1889), but scaled-down to the appropriate size. The paucity of information is surprising considering that primitive beams were ~3-4 m in length and were in widespread use around the British coast from the mid-18th century onwards (Robinson, 1996; Jones, 2018). Moreover, it is likely that variations in gear design were minimal as significant modifications were not adopted until the invention of the otter trawl in 1894 (Cunningham, 1896; Kerby et al. 2012).

Table 2.3. Summary of historical options and sources by gear component, and final decisions made for the reconstruction of the replica 19th century beam trawl. A brief description of gear modifications following June 2018 gear trials are also provided for each component.

Gear component	Historical materials (options)	Historical descriptions/ dimensions	Key references	Final decision for replica gear reconstruction	Modifications following June 2018 gear trials
19th century trawl net designs		Square: Half the length of the entire net Cod-end: one-seventh the length of entire net Total length: approximately double the length of the beam Features: pockets and flapper	Holdsworth, 1874; Collins, 1889; Wood, 1911; Davies, 1927	Square: 7.3 m Cod-end: 2.1 m Total length: 13.3 m Fitted with pockets and a flapper	
Net materials	Manilla hemp or hemp		Holdsworth, 1874; Collins, 1889	White nylon	
Mesh sizes		Square: 15.2-20.3 cm fully stretched (single twine) Cod-end: ~7.6 cm fully stretched (double twine)	Holdsworth, 1874; Collins, 1889	Square: 104 mm (inside) with 4 mm single twine Cod-end: 75 mm (inside) with 3 mm double twine Other net panels: 90 mm (inside) with 4 mm single twine	
Trawl heads	Wrought iron	Height: 91 – 121 cm*	Collins, 1889; Wood, 1911; March, 1953	Black steel Height: 68.6 cm	Repositioning of the eye-bolt

		Weight: ~101 – 181 kg	Holdsworth, 1874; Collins, 1889; Davies, 1927; Alward, 1932; Butcher, 1980	Weight: 100 kg	
Ground rope	Old 'towing hawser' or central wire core Manilla or hemp rope rounded around central rope or core	60 mm diameter* 16-22 mm diameter*	Collins, 1889 Collins, 1889	36 mm (diameter) braided staple rope with a 16 mm diameter rope. Total length of 12.5 m	Extended by 1 m either side, resulting in total length of 14.5 m
Beam	Elm, ash, beech, or elm	Original beam was 6.7 m in length Length of inshore beams started from ~3 m upwards 14-15 m in length for large beam trawls; 20-22 cm^2 diameter	Meek, 1889 Holdsworth, 1874; Collins, 1889 Wood, 1911; Butcher, 1980	Douglas fir with a length of 6.7 m and diameter of 14 cm^2	6.7 m steel beam with a 15.2^2 diameter

*Refers to the dimensions documented for large beam trawls (14- 15 m length)

Where historical materials were not available, we also faced some difficulties with sourcing appropriate contemporary materials for the reconstructed net. Compared to historically hand-braided nets made of natural fibre twine, modern trawl nets are machine-made and consist of synthetic fibres due to their superior quality (e.g., greater breaking strength and durability; Davis, 1958; Kerby et al. 2012) and cheaper production costs. Today, it is standard practice to supply netting in bulk in a given mesh size (Darren Edwards, Brixham Trawl Makers Limited, personal communication, 2018). Compromises were therefore made during our attempt to reconstruct replica trawl net. Differences in the physical properties of the twine material used to construct the original (manilla hemp or hemp) and replica (white nylon) trawl net are likely to have resulted in varying selectivity factors and may have thus yielded slightly different catches. Properties such as flexibility, specific gravity and elongation at break can influence the potential escape of fish as a function of their size and shape (Isakensen et al. 1990; Lowry and Robertson, 1996). Compared to the stiff, natural fibres employed in the original net, fewer fish are likely to have been retained by the synthetic replica net as nylon is more flexible and exhibits a greater elongation at break (10 – 12% versus 15-28%, respectively; Table 2.2). Several studies have shown that trawl nets made of nylon landed fewer fish (10-15 % less) compared with meshes of the same size and nets made of Manilla twine (Clark, 1956; Clark and Jensen, 1963). Instead of white nylon, Currie et al. (2018) used a combination of polyester and polyethylene material for the reconstruction of a late 19th century 'Granton' otter trawl net in South Africa. They used polyester as it has the same specific gravity in water as Manilla (1.38) and polyethylene to stimulate a similar stiffness, to produce a rope that, together, created similar properties to the natural fibre twine used in the original Granton net. In a second attempt to trial an 1880's replica beam trawl on board the *SS Excelsior,* in November 1998, fishery scientists and members of the Excelsior trust also used white nylon based on materials available that most matched the appearance and density of natural fibre twines (John Wylson, personal communication 2018).

The reconstructed beam trawl underwent various modifications following initial testing in June 2018 (summarised in table 2.3) and prior to comparing the catch efficiency of both modern and historical trawl gears. Firstly, the wooden beam was replaced with a steel beam due to buoyancy issues, which prevented the trawl from settling on the seafloor (see *Beam* section in Results). Secondly, we reduced the number of meshes in the front-width of square of the trawl net from 180 to 160 (see Fig 2.2) and lengthened the ground-rope by 1 m either side of the wings. Prior to this second adjustment, the gear did not trawl for fish effectively and we subsequently ‘streamed’ the net alongside of the vessel whilst moving to visually assess the behaviour of the net at the sea’s surface. It became apparent that there was excess netting in the upper portion of the net that caused the net to “balloon” as it was being towed at the surface. Consequently, we addressed this issue by reducing the size of the square and extending the ground-rope to compensate for slack in the bolsh-line.

Although the replica beam trawl had a similar catch efficiency to the otter trawl (for flatfish) in August 2018 after being adjusted, catches made by the replica gear in March 2019 were negligible. In fact, three out of six hauls made by the replica gear had zero catches. Consequently, the beam trawl was deemed to not be functioning efficiently in this period. The gear therefore was not used for its intended purpose of resurveying inshore grounds in order to compare historical and contemporary catches (Chapter 3). We were unable to investigate and resolve these issues further due to practical and logistical constraints. It also important to note that differences in trawl catches from the gear trials may be attributed to differences in catchabilities between the replica beam and otter trawl. For example, the trawl geometry, variable for the otter trawl and fixed for the beam, as well as the degree of contact between the ground-rope and seabed, will have considerable influence on its selectivity for fish composition and size (Jennings, 2001). The horizontal net opening is an important element in the standardisation of trawl catch rates (Rogers and Ellis, 2000), and such changes in trawl geometry were accounted for by applying a swept area model to both gears.

Although the exact dimensions of original beam trawl net could not be fully resolved, we remain convinced that the replica gear is of value to those interested in reconstructing historical trawl gear, providing an important foundation to rebuild trawl gear that will closely imitate the behaviour and selectivity of a late 19th century beam trawl. To our knowledge, this is one of only two studies (Currie et al. 2018) that has set about to replicate like-for-like trawl gear to accurately compare historical and contemporary fish catches. Although in April 1998, an initial attempt was made to investigate the fishing power of the sail trawler, the *SS Excelsior*, using an 1880’s replica beam trawl, which was historically capable of landing vast quantities of fish in the southern North Sea. However, the authors of this study failed to land any fish despite their considerable efforts to imitate historical practices (Millner et al. 1997; Engelhard, 2008). In their second attempt at reconstructing a 1880’s beam trawl, the gear was trialled twice for ca. 45 minutes off the coast of Lowestoft in November 1998, and was successful in catching a small number of fish species, primarily sole (*Solea solea*) (John Wylson, personal communication 2018). Catches from our replica beam trawl were also either relatively low or virtually zero across the two trial periods, especially when compared to our otter trawl catches in March gear trials. There could be a number of reasons at play to explain these findings. Beam trawls in the late 19th century were carefully handled by experienced and skilled crew without the aid of a steam winch to haul in the catch (Collins, 1889). Although the same experienced skippers were consistently employed in the handling of the replica gear, we used a mechanical winch at the stern of the vessel to deploy and retrieve the catch. It is a very challenging task to accurately replicate the methods of handling historical trawl gear when we do not possess the skills as the NSFC did in the late 19th century. Engelhard (2008) suggested that the zero catches attained by the 1880s replica beam trawl of the *SS Excelsior* could have been attributed to the lack of fishing power and/or skills in handling the gear. Could our findings therefore be in part due to our minimal experience in working a late 19th century beam trawl, or could it be due to a substantially diminished fish stock compared to a 120 years ago? Or is it because even relatively primitive beam trawls were capable of catching fish effectively but not now? It is notable that the otter trawl also caught fewer fish and lobsters in March compared to in August and so another important factor could be the seasonal migration of juvenile fish (and lobsters) away from the coast during spring, which could greatly affect the apparent ‘catchability’ of the net, thus reflecting a very real disappearance of the fishing during this season.

Given that beam trawls originated in European waters and were the first major development of the commercial trawl industry (Alward, 1932; Visel, 1980), this work provides an invaluable repository for researchers interested in trawl technology and survey design, as used in other parts of the British coast (Fulton, 1895; Garstang, 1905) and wider North Sea (Garstang, 1905; Todd, 1911). This research demonstrates the feasibility of such gear reconstructions, and building on this repository, repeat trawl surveys using replica gear could be credibly developed in other parts of the world, enabling more robust comparisons to assess the long-term status of fish populations.

Chapter 3: Long-term Change in an Inshore Fish Assemblage of the Western North Sea

3.1. Introduction

For centuries, commercial fishing practices have intensified and undergone rapid changes in gear technology and target species (Engelhard, 2008), while once productive ecosystems have experienced widespread changes in biodiversity and local extirpations (Christensen et al. 2003; Roberts, 2007). Since the late 19th century, fishers have shifted their catch by targeting less-fished species, which are typically smaller and feed at lower trophic levels (Pauly et al. 1998). The addition of steam power to fishing vessels led to increases in fishing power and effort from the late 1800s, and increased access to new and previously unfished grounds, and hence concerns for long-term impact on fish populations (Engelhard, 2008; Thurstan et al. 2014). However, it is highly likely that fish stocks were impacted by pre-industrial fisheries long before the late 19th century (Pinnegar and Engelhard, 2008; Thurstan et al. 2014). It is now recognised that marine habitats and communities are rapidly declining as they are continually degraded through fishing (Myers and Worm, 2003).

Bottom trawling is often blamed for declines in the diversity and abundance of target fish populations (Rijnsdorp et al. 1996; Roger and Ellis, 2000; Genner et al. 2010; Novaglio et al. 2020), as indicated by long-term monitoring and contemporary resurveys for which historical datasets are available (Jennings and Kaiser, 1998; Currie et al. 2020). It is often larger and late-maturing species that are removed first and decline more rapidly in response to sustained fishing in comparison to their smaller counterparts (Jennings et al. 1999; Piet et al. 2009). This has resulted in widespread changes in target species (Thurstan and Roberts, 2010; Heath and Speirs, 2012), with a shift by inshore fisheries to species at lower trophic levels (Thurstan et al. 2015). For example, the Firth of Clyde once sustained abundant and diverse fisheries for species including cod *Gadus morhua*, turbot *Scophthalmus maximus* and flounder *Platichthys flesus* in the early 19th century, whereas invertebrates such as Norway lobster *Nephrops norvegicus* and scallops *Pecten maximus* are the only target species in the region today (Thurstan and Roberts, 2010). Similarly, in the Gulf of Maine, the removal of large predatory ground fishes such as cod and haddock *Melanogrammus aeglefinus* has effectively resulted in a monoculture of American lobsters (*Homarus americanus*) as a consequence of centuries of overfishing (Steneck et al. 2011).

Larger fish are more vulnerable to fishing and have less capacity to sustain high levels of mortality (Myers and Worm, 2005). Many studies have documented notable reductions in the sizes of large fish (e.g., Pope et al. 1988; Cardinale et al. 2012; Turner, 2017) as well as increasing abundances of smaller fish (e.g., Rijnsdorp et al. 1996; McHugh et al. 2011). Comparisons of British trawl catches between the early and late 20th century reveal increases in relative abundances of several non-target species (e.g., dragonet *Callionymus* sp.) as well as declines in some elasmobranchs and the sizes of large fishes (Rogers and Ellis, 2000). More recently, Fortibuoni et al. (2017) used fishery landings and a suite of ecological indicators such as the large species indicator and elasmobranch-bony fish ratio to examine long-term changes (1945-2014) in the northern Adriatic sea fish community. Negative trends for these indicators showed drastic declines in elasmobranchs and large-sized species following World War II, but also revealed a shift towards smaller species over the time-series due to "predator release" as their predators are depleted (Fortibuoni et al. 2017). Although such studies are based on information collected long after commercial exploitation started altering them (Lotze and Worm, 2009), they strengthen our understanding of long-term change at a species and ecosystem level (Greenstreet and Rogers, 2006).

Coupled with fishing, climatic shifts have also been implicated as major causes of fluctuations in fish populations (Rutterford et al. 2015). The North Atlantic and British coastal areas have warmed more rapidly than adjacent seas (MacKenzie and Schiedek, 2007), with a 1.3°C increase in North Sea annual sea surface temperature over the past 30 years (Sherman and Hempel, 2009). Analyses of North Sea fish trawl surveys have revealed redistributional shifts of fish to higher latitudes (Beare et al. 2004; Drinkwater and Kristiansen, 2018) and deeper waters (Dulvy et al. 2008), northerly range expansions of warm-water species (Perry et al. 2004), and long-term changes in local abundance, recruitment and growth associated with warming (Rijnsdorp et al. 2009; Capuzzo et al. 2018). Increasing temperatures may disrupt the timing and locations of spawning events of fish and invertebrates, with implications for the entire ecosystem (Beaugrand et al. 2003; Genner et al. 2010). Given predictions of increasing temperatures over the next century (Sheppard, 2004), together with the cumulative effects of fishing, there is an urgent need to understand the timescales and magnitude of these changes in marine populations.

Modern conservation frameworks often fail to consider the effects of long-term anthropogenic disturbance and are often based on data spanning the last few decades

(Mackinson, 2002; Engelhard, 2008), thus encompassing populations that are far from pristine. Historical reference points can provide useful benchmarks for recovery by providing valuable context to current ecological states (Thurstan et al. 2015) as well as unravel the mechanisms that have driven these changes (Pickett, 1989). However, the systematic collection of national fisheries statistics did not begin until the 1880s when trawling was already widespread (Russell and Edser, 1925; Thurstan et al. 2014), thus preceding the onset of large-scale impacts. Although these records do not include the earliest years of industrial fishing, it is rare for researchers to unearth detailed historical fishery records that allow comparison with contemporary data (Rijnsdorp et al. 1996; Thurstan et al. 2010; Currie et al. 2020). Such information provides stakeholders with a historical perspective for effectively rebuilding fish stocks and realistic benchmarks for their potential long-term recovery.

The Northumberland coastline, north-east England, is a sequence of wide bays separated by rocky stretches of cliffs and supports a wide range of ecologically important habitats and species (Bennett and Foster-Smith, 1998). The coastal zone has supported juvenile and adult populations of numerous commercially and ecologically important species such as plaice *Pleuronectes platessa* and dab *Limanda limanda*, for centuries (Meek, 1896), but has been subject to various human pressures during this time, including pollution (Eagle et al. 1979), dredging (Norman, 1863; M'Intosh, 1872) and fishing (Walmsley and Pawson, 2007; Thurstan et al. 2014). Fishing has traditionally been important to the economy, but the industry has declined in recent decades (Frid et al. 1991). Before the introduction of steam trawling in the late 19th century, fishers used near-shore static gears for crabs and lobsters, drift nets for herring *Clupea harengus*, and long-lines for plaice, cod, haddock, turbot, ling *Molva molva*, whiting *Merlangius merlangus*, among other species (Meek, 1896). At the turn of the century, these fish species were landed in much larger quantities by steam trawlers, and a new fishery developed for the Norway lobster (Meek, 1900).

Today, *Nephrops*, typically caught using otter trawls, has assumed greater importance while whitefish landings have declined, often being bycatch in the *Nephrops* fishery (Walmsley & Pawson, 2007). Potting, which includes using traditional creels and parlour pots targeting European lobster, brown crab *Cancer pagurus*, and to a lesser extent, velvet crab *Necora puber*, is now the most widespread fishing practice off the Northumberland coast (Stephenson et al. 2018), with some vessels using drift nets to capture salmon and a smaller number of vessels using towed gears (Garside et al. 2003). Herring were also historically caught in vast quantities using drift nets (Meek, 1896); since this fishery re-opened in 1984, fishing effort has been minimal as local stocks have failed to recover (Frid et al. 1998; Walmsley & Pawson, 2007).

In the late 1880s, local Sea Fisheries Committees were established in England and Wales, and a three-mile territorial limit was established around the coastline in an attempt to address a widespread outcry by fishers on the destructive impacts of trawling on inshore fish stocks (Allen, 1897). In Northumberland, the ban came into effect in 1891 and prohibited all sail and steam trawlers from fishing within the three-mile limit (Fig 3.1a; Meek, 1895). In subsequent decades, a series of scientific trawling investigations were established by the Northumberland Sea Fisheries Committee (NSFC) and Dove Marine Laboratory, Cullercoats, to examine whether the ban had benefited inshore fish stocks (Meek, 1895). These investigations, among the earliest fisheries-independent trawl surveys undertaken in European waters, focussed on sampling fish species in inshore fishing grounds between 1892 and 1913 (Meek, 1895-1913). Despite their ecological importance and proximity to shore, only a few long-term surveys have been conducted in inshore waters compared with the number of offshore surveys (e.g., Tulp et al. 2008; Thurstan and Roberts, 2010; McHugh et al. 2011). Availability of data from several inshore sites thus provides an unprecedented opportunity to resurvey historical inshore areas and identify potential reference points against which recovery targets might be made. In this paper, trawl catch data documented by the NSFC from the late 19th century was utilised and the same sites were resurveyed in 2018 and 2019 to quantify and describe changes in the demersal fish community between the two periods. Specifically, the aim was to a) compare catch rates and identify changes in community structure between historical and contemporary periods, and b) examine differences in body length distributions between these periods. Changes in key taxa were identified to reveal whether they are consistent with those observed in offshore areas, and findings are interpreted in light of long-term anthropogenic pressures.

3.2. Methods

3.2.1. *Study sites*

Historically, five inshore sandy bays, namely Skate Roads, Alnmouth, Druridge, Cambois and Blyth bays, were surveyed off the Northumberland coast (Fig 3.1b). The sites are shallow inlets located within 1 km of the shoreline, and comprise soft, sandy sediments that are fringed by adjacent rocky habitats in water depths of <20 m (Frid et al. 1998).

Since 2011, there has been limited trawling activity in all five locations as current Northumberland Inshore Fisheries and Conservation Authority (NIFCA) byelaws restrict the size of vessels trawling to <12 m 0-6 nautical miles from the shore (NIFCA, 2021). These byelaws set out catch prohibitions and restrictions such as minimum landing sizes for fish and crustaceans to minimise impacts on the benthos (NIFCA, 2021). The most northerly site in the district, Skate roads, resides within the Berwickshire and North Northumberland Coast European Marine Site (AONB Partnership and EMS Management Group, 2009), whereas the other four sites are located in the Coquet to St. Mary's Marine Conservation Zone (Natural England, 2020). In recent decades, trawl effort has been limited in these conservation areas (Walmsley and Pawson, 2007), largely because byelaws prohibit the use of mobile fishing gear, including all trawls and dredges (NIFCA, 2021). Historically, the bays were protected as productive nursery grounds for many fish species (Meek, 1895), however today, they are protected on the basis of being ecologically important areas for seabirds, seals and invertebrates (Natural England, 2020).

3.2.2. *Historical surveys*

Records derived from NSFC logbooks were digitised and held in the Centre for Environment, Fisheries and Aquaculture Science's (Cefas) Fishing Survey System. Historical logbooks provide anecdotal accounts of the environmental conditions and sea state of each trawl survey, albeit do not include specific details on start and end locations of individual hauls. The original trawls were conducted from May to September on board two steam paddle tugs, initially on the *Livingstone* between 1892 – 1900, and on the *Stanley*, in the latter part of the 1900 season until 1913. Trawls recommenced after World War I in 1920 for one more season on board the tug *Sentinette*. A 6.7 m wooden beam trawl was employed, albeit information on specific gear details is lacking. Mesh sizes were not specified; however, the minimum size fish recorded was either four inches or 10 cm. This implies a stretched mesh of ~80 – 90 mm (Neil Armstrong, personal communication 2017), which approximates the most commonly referenced cod-end mesh of ~75 mm used in British beam trawls in the late 19th century (see Chapter 2).

Between 1892 – 1899, numbers of fish were reported but specific details on haul durations were lacking. From 1899 onwards, logbooks contain information on the location, duration of each haul, and the abundance and total length of all fish species collected. Prior to 1904, fish were measured to the nearest inch and to the nearest centimetre thereafter. Individual positions, depths, times of day, and trawl speeds were not routinely specified; however, in one case, Meek (1901) mentioned the trawl speed to be ‘about 2 knots’. This is congruent with towing speeds reported for late 19th and early 20th century beam trawls (M’Intosh, 1895; Kyle, 1903). On this basis, the towing speed was assumed to be ~1.03 m s^{-1} (2 knots).

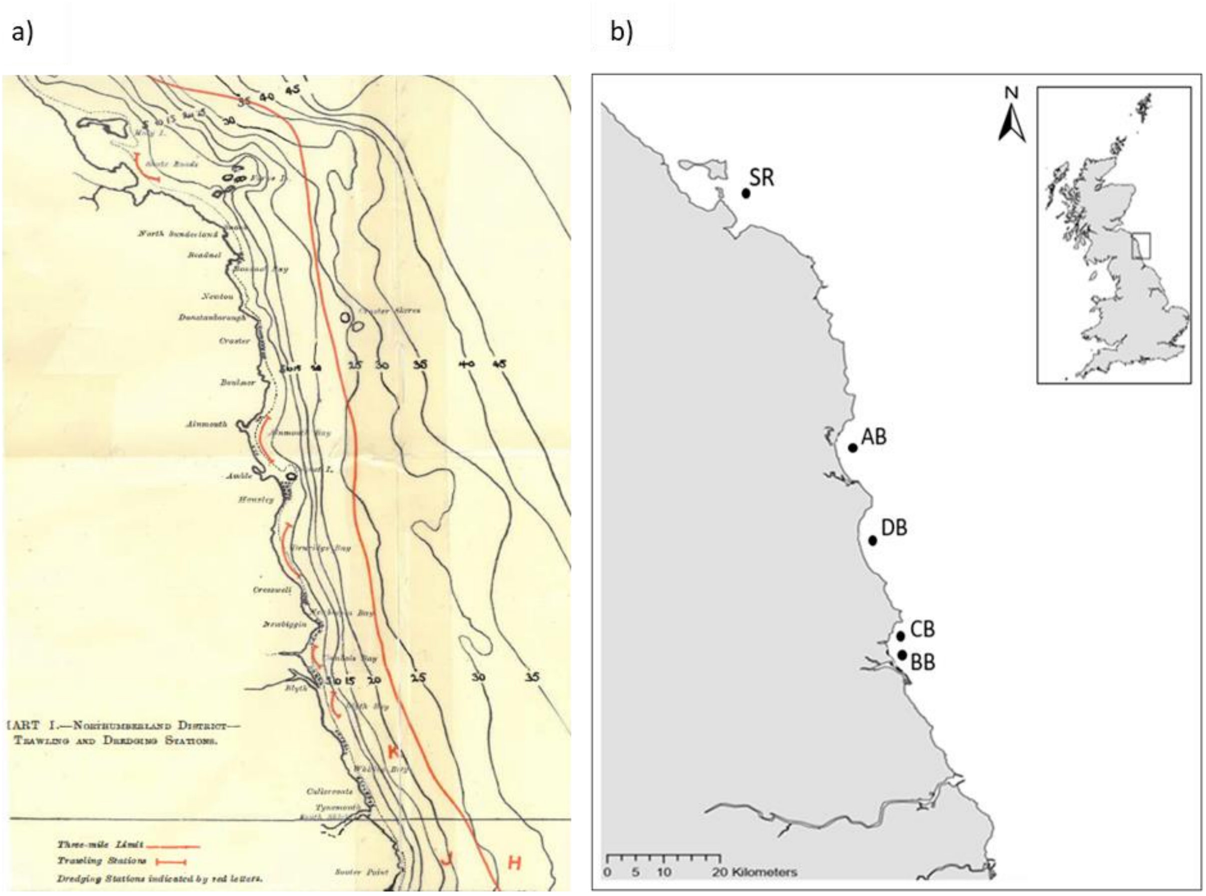


Figure 3.1. Maps of the Northumberland coast showing a) historical trawl tracks of original sampling stations with the three-mile territorial limit boundary marked in red (NSFC, 1902), and b) sampling locations of historical and contemporary surveys (SR, Skate Roads; AB, Alnmouth Bay; DB, Druridge Bay; CB, Cambois Bay; BB, Blyth Bay).

3.2.3. *Contemporary resurveys*

Repeat trawl surveys were undertaken on Newcastle University’s research vessel *The Princess Royal*, a 18.9 m catamaran. Despite uncertainties relating to precise locations of historical trawls and to minimise potential biases in comparisons between periods, contemporary resurveys were conducted within 1 km of the shore and in the same depth ranges that are sporadically mentioned in NSFC reports (e.g., Meek, 1905). Individual trawls had a duration of 60 minutes, and although trawls were conducted consecutively at each site (2-4 times) during daylight hours, the same tracks were not trawled over repeatedly in a given day. The trawl gear used was an otter trawl with a 8.2 m headline and 80 mm (tight) meshed cod-end. The otter trawl was towed at ~1.29 ms^{-1} (2.5 knots) for all hauls. The contents of the net were sorted and identified to species level and the total length (cm) of all fish species were measured to the nearest centimetre. Start and end positions and average depth were recorded for every haul. Additional environmental variables were measured at every site (salinity, sea surface temperature, average depth) using a handheld CTD probe which was attached to a rope and lowered over the side of the vessel.

3.2.4. *Data selected for comparison*

Data were only included in analyses if haul durations were recorded for each trawl because this information is required for standardising trawl catches for comparisons with other surveys (Rijnsdorp et al. 1996). We therefore restricted comparisons of fish catches and community structure to 1899 – 1913 and 2018 – 2019 (Table 3.1). A total of 175 and 59 trawls were included in analyses for historical and contemporary periods, respectively. For all years combined, mean trawl durations varied between sites in historical surveys: 71.5 min for Druridge Bay; 69.5 min for Alnmouth Bay; 62.2 for Cambois Bay; 68.5 mins for Skate Roads; and 61.9 mins for Blyth Bay (Table 3.1). For body size comparisons, fish measured in inches were removed in the years prior to 1904 as directly converting fish measured to the nearest inch to centimetres could skew analyses and thus confound interpretation of the data.

Table 3.1. Details of all historical and contemporary trawls used in analyses by site; Druridge Bay (DB); Alnmouth Bay (AB); Cambois Bay (CB); Skate Roads (SR); Blyth Bay (BB).

Year	Number of trawls					Mean haul duration (range) in minutes				
	DB	AB	CB	SR	BB	DB	AB	CB	SR	BB
1899	3	2	2	2	-	90(90-90)	83 (75-90)	75(75-75)	75(75-75)	-
1900	4	3	1	2	2	64(55-70)	73 (70-80)	90	60(60-60)	50(30-50)
1901	4	2	3	4	1	71(60-85)	60(60-60)	70(60-90)	73(60-75)	50
1902	2	3	3	3	1	60(60-60)	63(60-70)	60(60-60)	53(40-60)	50
1903	3	2	2	3	2	62(60-65)	60(60-60)	60(60-60)	72(60-85)	50(40-60)
1904	3	2	3	1	3	63(60-65)	60(60-60)	67(60-75)	60	60(55-70)
1905	3	2	4	2	2	60(60-60)	67(60-75)	63(60-70)	55(50-60)	39(30-48)
1906	3	2	2	3	4	66(60-75)	60(60-60)	60(60-60)	60(60-60)	55(45-60)
1907	3	1	1	7	8	90(60-120)	60	15	78(50-120)	106(60-165)
1908	3	-	-	3	3	90(90-90)	-	-	90(90-90)	90(90-90)
1909	3	3	-	3	2	75(45-90)	103(90-120)	-	90(60-150)	83(75-90)
1910	1	1	-	-	1	90	90	-	-	60
1913	4	9	-	4	5	60(60-60)	65(60-75)	-	65(60-70)	67(60-75)
2018	1	2	2	2	-	60(60-60)	60(60-60)	60(60-60)	60(60-60)	60(60-60)
2019	14	13	10	5	10	60(60-60)	60(60-60)	60(60-60)	60(60-60)	60(60-60)

Comparisons of catch data collated from different vessels, trawl gears and mesh sizes may be biased due to differences in the size at full selectivity (Rijnsdorp et al. 1996; Harley and Myers, 2001). In this study, there was a marked discrepancy between the modal lengths of fish in historical and contemporary surveys, with a larger proportion of smaller fish observed in historical periods (Fig 3.2). The modal lengths of all fish caught in historical surveys ranged from 16 – 18 cm and 20 – 22 cm in contemporary surveys (Fig 3.2a). For flatfishes, modal lengths ranged from 19 – 21 cm and 21 – 23 cm in historical and contemporary surveys (Fig 3.2b), respectively. Although this could be potentially due to a larger proportion of smaller individuals present in historical trawls, these discrepancies are likely to reflect differences in the mesh selectivity of the two trawl gears. Consequently, we adopted a conservative approach by only including individuals larger than 20 cm (total length) in all analyses. Removing fish below this size thus reduces inconsistencies relating to gear selectivity and provides an adequate compromise between the need for robust comparisons and the lack of complete information on historical mesh sizes. This cut off is further supported by other studies that have adopted similar conservative approaches in an attempt to minimise the effect of gear selectivity on catch per unit effort comparisons (e.g., removing fish <25 cm; Cardinale et al. 2009; Cardinale et al. 2010).

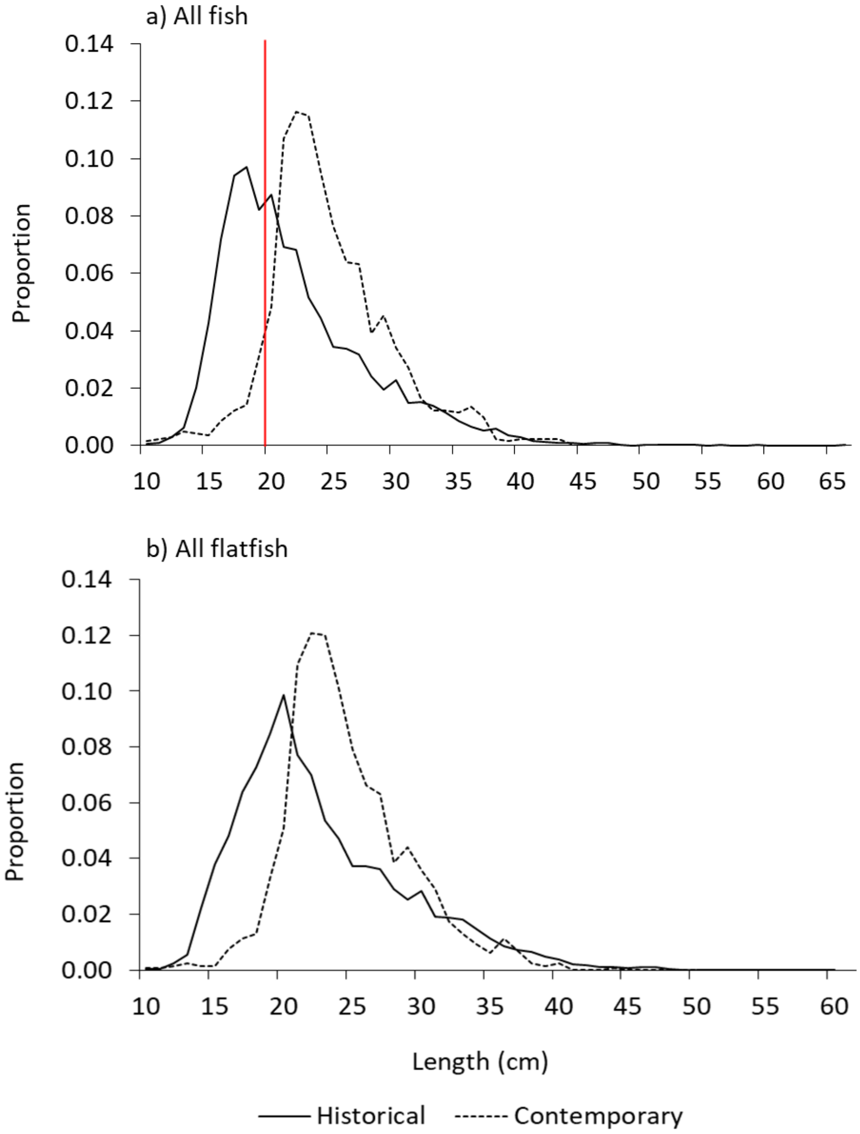


Figure 3.2. Length-frequency distribution (cm) of a) all fish and b) flatfish caught in historical (1904-1913) and contemporary surveys (2018-2019). The red line indicates the minimum size cut off for all fish included in analyses.

3.2.5. *Data standardisation*

Trawl catches were standardised to help account for differences between gears and methods of operation. Differences in trawl speed are thought to have little influence on the catch efficiency of most demersal fish species (Rogers and Ellis, 2000). For otter trawls, a towing speed of 1.02 m s^{-1} (2 knots) and 1.29 m s^{-1} is considered sufficient to catch the largest and fastest swimming demersal species (Greenstreet and Hall, 1996).

Swept area estimates are widely regarded as an important way to account for differences in trawl gear and standardise trawl catch comparisons (Rijnsdorp et al. 1996; Ragnarsson and Steingrimsson, 2003). The size of the area swept largely depends on towing speeds (or distance towed per hour) and width of the net opening (Rijnsdorp et al. 1996). For beam trawls, the net opening is fixed by length of the beam, whereas the size of the opening of otter trawls can vary substantially with the depth and speed at which the gear is being towed over the seafloor (Rijnsdorp et al. 1996). The door spread tends to increase with depth due to changes in trawl geometry (Ragnarsson and Steingrimsson, 2003); however, errors in the swept area calculations are unlikely because all hauls were conducted at depths of <20 m. Some authors have assumed the net opening to be two-thirds the length of the headline for historical gears (Rogers and Ellis, 2000), while others have used net or wing-end spread as a measure of the horizontal net opening (e.g. Trenkel et al. 2004; Broadhurst et al. 2012). In the resurveys, swept area was defined as the net wing-end spread (4.07 m) multiplied by the distanced trawled (based on a towing speed of 1.29 m s^{-1} and trawl duration). The estimated swept area per hour of trawling for the otter trawl was 18,800 m^2. For the historical beam trawl, the swept area per hour of trawling was larger, estimated at 24,800 m^2 based on a towing speed of ~1.03 ms^{-1} and beam width of 6.7 m.

3.2.6. *Data analysis*

At each site and for both historical and contemporary time periods, mean catch rates (numbers per hour standardised for swept area) of individual species were calculated and used to generate cumulative frequency curves (k-dominance plots):

$$C_{sw} = \frac{C}{a}$$

where C_{sw} is the swept area standardised catch; C is the count for the specified taxon; a is the area of seafloor swept by the trawl (1000 m^2/h). Community diversity metrics, Shannon-Weiner (H’), Simpson index of Diversity (D), and index of evenness (Pielou, 1969) were calculated at each sampling site and period.

Changes in fish community structure (based on standardised catch rates) between the two time periods at each site were analysed using ordination and a two-way permutational multivariate analysis of variance (PERMANOVA; Anderson, 2005) based on Bray-Curtis resemblance matrices and fixed factors year and site. The “adonis” procedure in the vegan package in R version 4.0.2 was applied (R Core Team, 2020) to the PERMANOVA analysis. Ordinations were plotted with non-metric Multidimensional Scaling (nMDS) to provide a two-dimensional visualisation of dissimilarities in community structure. SIMPER analysis was employed to identify the percent contributions of the most typifying species in each time period and site, and discriminate species between periods using Bray-Curtis dissimilarities in R (Clarke, 1993).

To investigate differences in size distributions, data were pooled from all sites within each survey period and were analysed for all fish, flatfish, and plaice and dab separately, where sufficient data were available. The lack of detailed length-frequency data in contemporary surveys precluded such analyses for roundfish and other individual fish species. For each group (all fish, flatfish, dab and plaice), four generalised linear models (GLM-ANCOVAs) were ran to further investigate potential differences in the slopes of log catch numbers against size between historical and contemporary periods.

3.3. Results

3.3.1. *Changes in fish abundance and community composition*

The mean catch rates of individual fish species varied between sampling periods and sites (Table 3.2); contemporary catch rates of all species present in historical surveys were considerably lower. Overall, flatfish, predominantly dab and plaice, dominated historical and contemporary catches; however, roundfishes were rarely observed in 2018-2019 surveys. Grey gurnard *Eutrigla gurnardus* was the third most abundant species historically but was absent in contemporary trawls. Of the other roundfish, only haddock and monkfish *Lophius piscatorius* were present in both time periods. By comparison, mackerel *Scomer scombrus* was the only species absent in historic trawls but present in the resurveys. Elasmobranchs (thornback ray *Raja clavata,* starry ray *Amblyraja radiata* and sandy ray *Raja circularis* and unidentified rays and skates) were present in low abundances in historical surveys, but they were completely absent from recent trawls across all sites (Table 3.2).

Table 3.2. Mean (± S.E.) catch rates (numbers of fish per 1000 m^2) standardised for area swept in historical (H) and contemporary (C) surveys in Skate Roads, Alnmouth, Druridge, Cambois and Blyth Bays.

	Skate Roads		Alnmouth Bay		Druridge Bay		Cambois Bay		Blyth Bay	
	H	C	H	C	H	C	H	C	H	C
Flatfish										
Limanda limanda	0.30 ± 0.04	0.14 ± 0.05	1.22 ± 0.12	0.48 ± 0.17	1.62 ± 0.22	0.79 ± 0.22	1.20 ± 0.16	1.03 ± 0.29	0.83 ± 0.12	0.16 ± 0.12
Platichthys flesus	0.24 ± 0.04	0.14 ± 0.4	0.35 ± 0.06	0.27 ± 0.10	0.04 ± 0.01	0.09 ± 0.02	0.11 ± 0.04	0.05 ± 0.01	0.14 ± .03	0.11 ± 0.03
Hippoglossoides platessoides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01 ± 0.01	0.00
Pleuronectes platessa	2.46 ± 0.30	0.01 ± 0.01	1.19 ± 0.11	0.05 ± 0.02	1.14 ± 0.16	0.14 ± 0.04	0.93 ± 0.15	0.85 ± 0.13	1.23 ± 0.16	0.46 ± 0.14
Solea solea	0.01 ± <0.01	0.00	0.08 ± 0.02	0.00	0.10 ± 0.02	0.00	0.20 ± 0.04	0.00	0.08 ± 0.02	0.03 ± 0.01
Microstomus kitt	0.00	0.00	0.00	0.00	<0.01 ± <0.01	0.00	0.20 ± 0.04	0.00	<0.01 ± <0.01	0.00
Scophthalmus maximus	0.08 ± 0.02	0.00	0.04 ± 0.01	0.00	0.05 ± 0.01	0.00	0.02 ± 0.01	0.00	0.03 ± 0.01	0.00
Scophthalmus rhombus	0.01 ± <0.01	0.00	<0.01 ± <0.01	0.00	<0.01 ± <0.01	0.00	<0.01 ± <0.01	0.00	<0.01 ± <0.01	0.00
Roundfish										
Gadus morhua	0.00	0.00	<0.01 ± <0.01	0.00	<0.01 ± <0.01	0.00	<0.01 ± <0.01	0.00	0.01 ± <0.01.	0.00
Melanogrammus aeglefinus	0.00	0.00	<0.01 ± <0.01	0.00	<0.01 ± <0.01	0.00	0.00	0.00	<0.01 ± <0.01	0.00
Merlangius merlangus	0.00	0.00	0.02 ± 0.01	0.00	<0.01 ± <0.01	0.01 ± <0.01	0.01 ± 0.01	<0.01 ± <0.01	<0.01 ± <0.01	0.00
Eutrigla gurnardus	0.14 ± 0.04	0.00	1.59 ± 0.50	0.00	1.11 ± 0.19	0.00	0.34 ± 0.12	0.00	0.41 ± 0.11	0.00
Chelidonichthys lucerna	<0.01 ± <0.01	0.00	0.00	0.00	<0.01 ± <0.01	0.00	0.00	0.00	<0.01 ± <0.01	0.00
Clupea harengus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	<0.01 ± <0.01	0.00
Scomer scombrus	0.00	0.00	0.00	0.01 ± <0.01	0.00	<0.01 ± <0.01	0.00	0.00	0.00	0.00
Lophius piscatorius	0.10 ± 0.05	0.00	0.13 ± 0.03	0.05 ± 0.02	0.16 ± 0.03	0.02 ± 0.01	0.15 ± 0.05	0.04 ± 0.01	0.19 ± 0.06	0.04 ± 0.02
Callionymidae	0.00	0.00	0.00	0.00	<0.01 ± <0.01	0.00	0.00	0.00	<0.01 ± <0.01	0.00
Pollachius pollachius	0.00	0.00	0.00	0.00	0.00	0.00	<0.01 ± <0.01	0.00	0.00	0.00
Anarhichas spp.	<0.01 ± <0.01	0.00	<0.01 ± <0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Elasmobranchs										
Amblyraja radiata	<0.01 ± <0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Raja clavata	<0.01 ± <0.01	0.00	0.00	0.00	<0.01 ± <0.01	0.00	0.00	0.00	0.00	0.00
Raja circularis	<0.01 ± <0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Unidentified skates and rays	<0.01 ± <0.01	0.00	<0.01 ± <0.01	0.00	<0.01 ± <0.01	0.00	<0.01 ± <0.01	0.00	0.00	0.00

The Shannon-Weiner Index (H’) indicates a more diverse inshore fish assemblage in the late 19th and early 20th century than now (Table 3.3); however, the distribution of individuals of different species was more equitable in the contemporary community. For all sites, except at Skate Roads, Simpson Diversity (D) values were slightly higher in historical periods (Table 3.3), reflecting that particular species tended to dominate the community more at that time. Historically, the fish community at Skate Roads was less evenly distributed and was dominated by a single species (plaice), which comprised 73% of the catch (Table 3.2). The *k*-dominance curves are steeper and more elevated, indicating that the contemporary assemblage is dominated by fewer species (Fig 3.3). This was particularly notable at Skate Roads, where only two out of three species present in contemporary surveys were equally dominant at this site (Fig 3.3e). Hence, the cumulative frequencies of mean abundances against species rank were much steeper in contemporary surveys (Fig 3.3).

Table 3.3. Species richness and diversity metrics of the demersal fish community in historical (H) and contemporary (C) trawls at each site.

	Skate Roads		Alnmouth Bay		Druridge Bay		Cambois Bay		Blyth Bay	
	H	C	H	C	H	C	H	C	H	C
Species richness	13	3	13	5	15	7	12	5	16	5
Shannon-Weiner Index (H')	1.02	0.81	1.47	1.06	1.41	0.81	1.50	0.89	1.54	1.12
Simpson Diversity (D)	0.44	0.53	0.73	0.58	0.71	0.41	0.72	0.54	0.80	0.61
Evenness	0.40	0.74	0.57	0.66	0.52	0.42	0.61	0.55	0.56	0.70

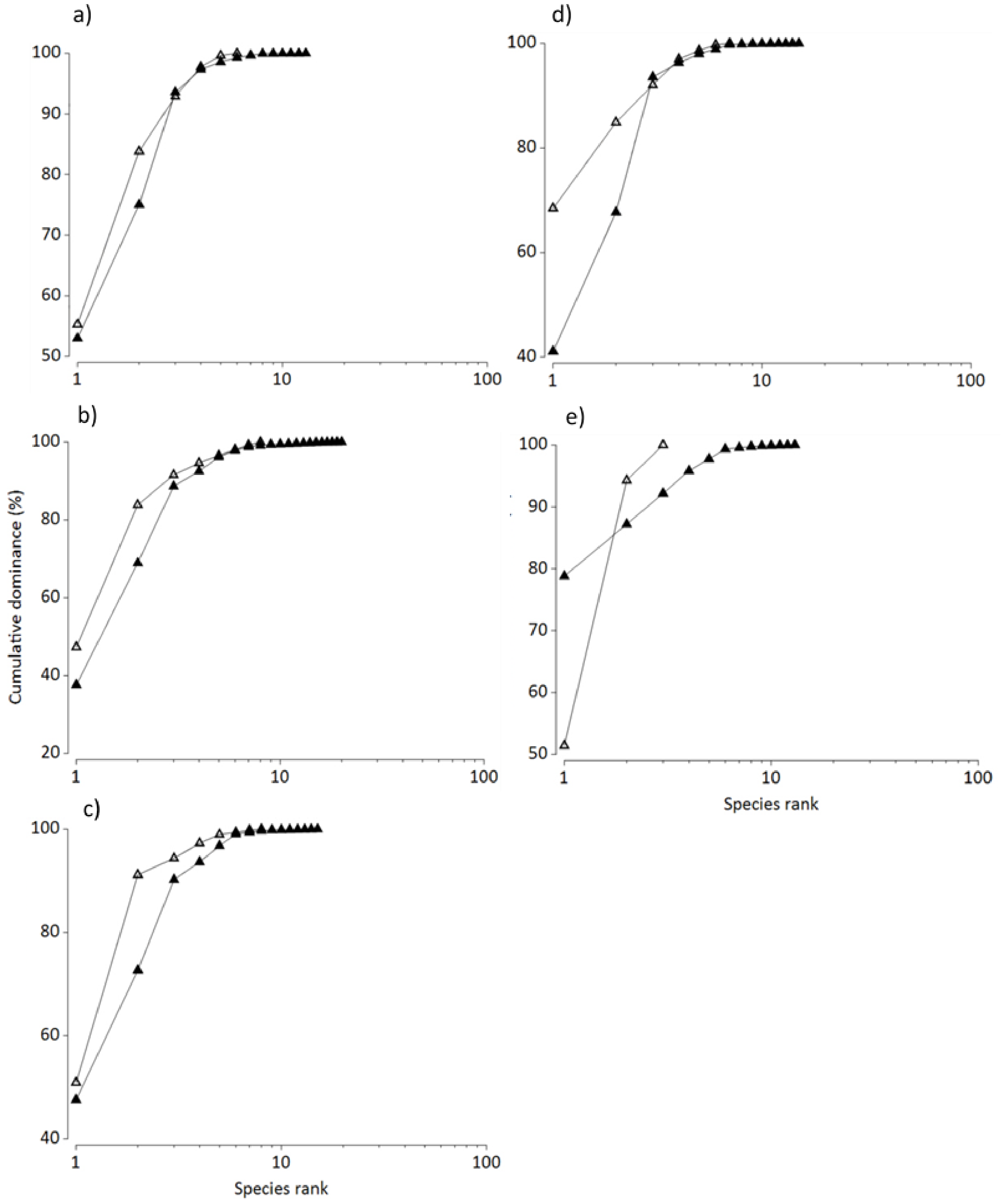


Figure 3.3. k- dominance plots based on the cumulative frequency of numerical abundances of species sampled by historical (▲) and contemporary (△) surveys in a) Alnmouth Bay, b) Blyth Bay, c) Cambois Bay, d) Druridge Bay and e) Skate Roads.

The nMDS plots of fish abundances showed an almost complete separation of all species combined and flatfish between historical and contemporary surveys (Figs 3.4a and b); this was most apparent at Skate Roads and Alnmouth Bay. These distinctions were confirmed by PERMANOVA analyses, which yielded highly significant differences in assemblage structure for all species and flatfish among sampling locations and between periods (Table 3.4; $P < 0.001$).

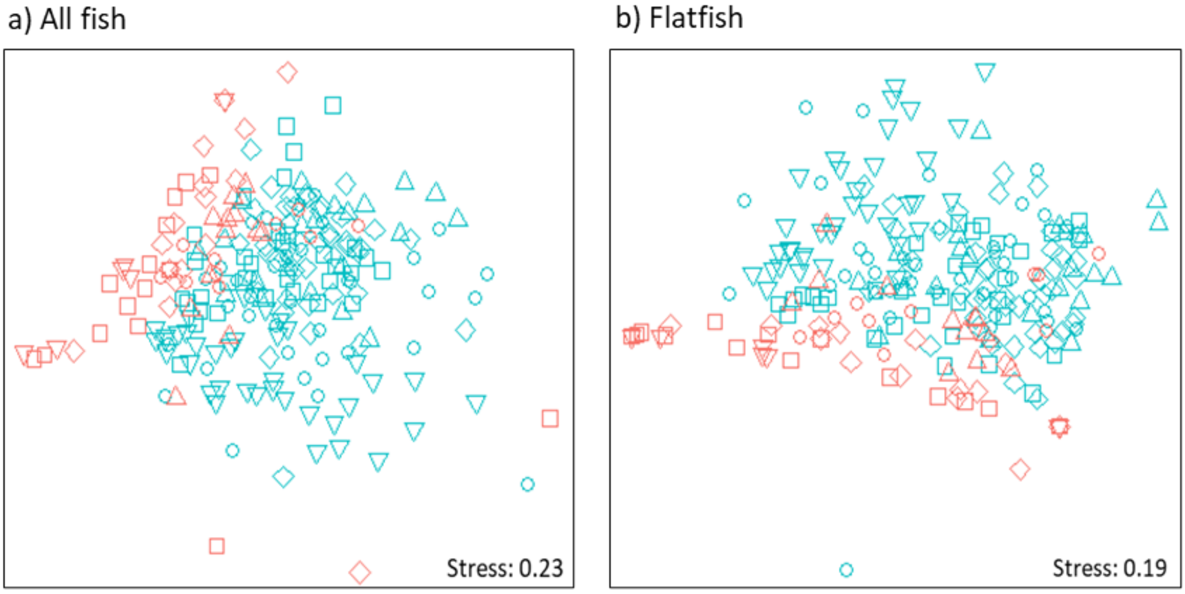


Figure 3.4. Non-metric Multi-dimensional scaling (nMDS) ordination plots of community dissimilarity (Bray-Curtis matrix) between historic (▽ Skate roads, ◇ Druridge Bay, □ Alnmouth Bay, △ Cambois Bay, ○ Blyth Bay) and contemporary trawls (▽ Skate roads, ◇ Druridge Bay, □ Alnmouth Bay, △ Cambois Bay, ○ Blyth Bay) for a) the entire fish assemblage and b) flatfish.

Table 3.4. Results of PERMANOVA comparisons of abundances between periods (historical and contemporary) and locations for all species and flatfish (df = degrees of freedom, *SS = sum of squares*).

Taxa	Source	df	SS	Pseudo-*F*	*P*
All fish	Period	1	6.83	48.5	<0.001
	Site	4	5.67	9.35	<0.001
	Period * Site	4	2.69	4.78	<0.001
	Residuals	221	31.13		
Flatfish	Period	1	5.84	47.83	<0.001
	Site	4	1.17	9.6	<0.001
	Period * Site	4	0.63	5.14	<0.001
	Residuals	221	27.02		

SIMPER analyses revealed that the historical and contemporary assemblage were characterised by plaice and dab across sites (Table 3.5). However, grey gurnard only typified historical surveys whereas flounder were more dominant in contemporary trawls. Skate Roads was historically typified by plaice (85.1%) and exhibited the largest between-period dissimilarity (87.3%) compared to all other sites (Table 3.6). By contrast, Cambois and Blyth Bay showed the lowest between-period dissimilarity (51.2% and 55.9%, respectively). Although absent at particular sites, monkfish and sole were also typifying species and contributed <5% of the dissimilarity (along with turbot) between periods (Table 3.6).

Table 3.5. Percentage contributions of typifying species (>1%) to within-period Bray-Curtis similarity in historic and contemporary surveys using SIMPER analysis.

	Skate roads		Alnmouth Bay		Druridge Bay		Cambois Bay		Blyth Bay	
	H	C	H	C	H	C	H	C	H	C
Plaice	85.1		35.5	12.7	34.0	20.4	30.4	52.7	52.5	36.5
Dab	8.7	55.2	36.3	42.0	41.6	68.6	54.6	41.3	33.4	53.3
Grey gurnard	1.3		22.3		19.4		8.8		7.6	
Flounder	3.4	44.8	3.3	36.1		9.4	1.3	3.9	2.9	5.9
Monkfish	1.0		1.2	7.8	2.2		1.1	1.9	1.6	2.2
Sole			1.0		1.5		3.5		1.5	1.2
Average within survey similarity	63.6	41.0	45.1	34.8	52.2	40.3	52.6	50.3	51.5	52.1

Table 3.6. Results of SIMPER analysis showing percent contributions of fish species to average within-period dissimilarity at each site.

	Skate roads	Druridge Bay	Alnmouth Bay	Cambois Bay	Blyth Bay
Plaice	64.5	19.7	23.8	13.4	20.1
Dab	7.3	24.7	20.5	20.5	14.7
Grey gurnard	3.4	18.3	20.4	6.4	8.3
Flounder	5.9	2.1	7.0	4.5	4.1
Monkfish	2.0	3.2	3.2	3.1	3.9
Sole		2.0	2.0	4.5	1.8
Turbot	3.1	1.0			
Average between survey dissimiliarity	87.3	71.2	78.0	51.2	55.9

3.3.2. *Changes in fish size distribution*

The abundance size-spectra of all fish combined, all flatfish, and dab, decreased more steeply with length in contemporary than in historical periods (Table 3.7; Fig 3.5), reflecting higher relative abundances of larger fish in historical surveys (Fig 3.5). Conversely, the slope of the regression for plaice declined more steeply in historical than in contemporary periods. Differences in the slopes of the declining limb of log abundance against size revealed highly significant differences between historical and contemporary periods for all fish (GLM-ANCOVA, $F_{1,62} = 7.903$; $P < 0.01$) and dab (GLM-ANCOVA, $F_{1,27} = 18.091$; $P < 0.001$), and to a lesser extent for flatfish (GLM-ANCOVA, $F_{1,50} = 5.053$; $P < 0.05$) and plaice (GLM-ANCOVA, $F_{1,48} = 4.883$; $P = < 0.05$).

Table 3.7. Slopes of the regression of the log numbers against size for all fish, flatfish, dab and plaice. H = Historical; C = Contemporary.

	Period	Slope	S.E.	r^2	Size-range (cm)
All fish	H	-0.070	0.168	0.89	22-87
	C	-0.099	0.144	0.94	22-44
Flatfish	H	-0.090	0.172	0.97	22-60
	C	-0.110	0.150	0.96	22-44
Dab	H	-0.140	0.185	0.97	22-40
	C	-0.210	0.229	0.93	22-33
Plaice	H	-0.085	0.181	0.89	22-63
	C	-0.055	0.094	0.65	22-44

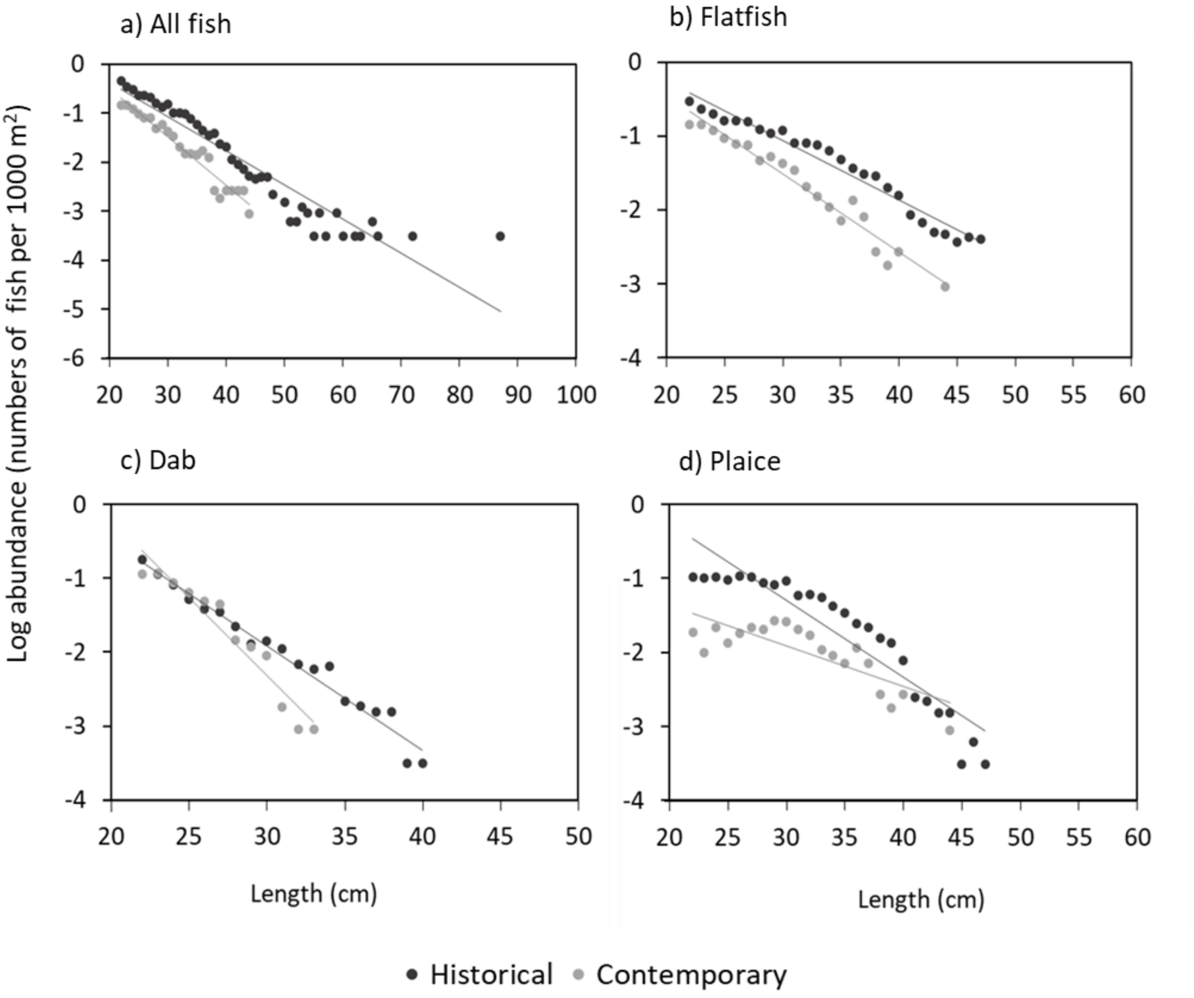


Figure 3.5. Log abundance-size spectra for a) all fish, b) flatfish, c) dab and d) plaice for historical and contemporary time periods. Trend lines represent the slope of the regression of the log abundance against size.

3.4. Discussion

It is evident that there has been a substantial decline in the numerical abundance of the overall fish assemblage, which has decreased by 70.1%, between 1899 – 1913 and 2018 – 2019. Species that historically dominated trawl catches, namely plaice, dab and grey gurnard, were 36.5%, 78.9%, and 100% less abundant, in recent surveys, respectively. The results show that the inshore fish assemblage is also now significantly less diverse compared to the historical assemblage. Although present in relatively low abundances historically, all elasmobranchs and other demersal fish species such as cod, haddock, dragonets, turbot *Scophthalmus maximus,* and brill *Scophthalmus rhombus*, were completely absent from recent trawls. Other species including flounder and monkfish, were frequent species in historical surveys, but have evidently declined in abundance, albeit flounder was the third most abundant species in contemporary surveys. Our results also showed significant changes in the abundance size-spectra slopes of the whole assemblage, among all flatfish, and dab, between periods. Here, slopes decreased more steeply in contemporary periods, which implies a decline in the number of larger individuals that were present in the past.

It is generally accepted that comparison of trawl catches from different gears and surveys will result in biases relating to varying selectivity and catchabilities (Rijnsdorp et al. 1996; Rogers and Ellis, 2000; Currie et al. 2020). There was considerable variation in the number of trawls conducted between historical and contemporary periods (e.g., 7 historical versus 37 contemporary trawls at Skate Roads). These differences were attributed to the fact that the resurveys were conducted over two years (2018 – 2019) as opposed to 14 consecutive years (1899 – 1913). The study did not account for the potential effect of increasing sample sizes on multivariate precision, such as by applying power analyses (e.g., see Currie et al. 2020), largely due to logistical and time constraints during the resurveys. Nevertheless, we attempted to minimise such biases by resurveying the same sites, time of day and in the same season as well as standardise trawl catches by employing swept area correction factors. However, this does not fully resolve differences between trawl gears because they have a catchability that is specific to their design and the way they are operated varies in relation to a particular species (Rijnsdorp et al. 1996). Because a towing speed of ca. 1.02 m s^{-1} (2 knots) is thought to retain most larger-bodied demersal species (Greenstreet and Hall, 1996; Rogers and Ellis, 2000), differences in towing speeds are unlikely to have impacted the catch efficiency of the demersal fish assemblage. Details of mesh sizes were not specified in historical logbooks; the higher proportion of smaller fish documented in historical surveys suggests that the beam trawl likely had a finer mesh than the contemporary otter trawl. In an effort to compensate for any overestimation in changes in abundance, the present analyses were confined to individuals > 20m. Although a substantial amount of resolution was lost by removing smaller fish, notable changes in fish abundance and diversity were still detected between historical and contemporary surveys. On balance, the present results suggest that most demersal fish species are now considerably less abundant while other species are completely absent in Northumberland's inshore waters.

Shifts in the abundance and diversity of the inshore fish assemblage demonstrated here may partly reflect commercial fishing at a regional scale. Increasing empirical evidence suggests that overfishing can lead to major changes in fish community structure (Hutchings and Reynolds, 2004), by driving declines in abundance (Hutchings and Baum, 2005) and truncating the size structure (Genner et al. 2010; Heath and Speirs, 2012). Additional drivers may have also played a role, which could include climate change, dredging and nearshore pollution (Eagle et al. 1979; Walmsley and Pawson, 2007). Besides evolving fishery regulations, the three-mile limit on trawling in the bays from 1891 as well as implementation of new MPAs in recent years may have mitigated some of these impacts. Disentangling various drivers would require substantial data that are unavailable. It is only possible to speculate about factors that might explain why species have declined, following 120 years of mostly increasing fishing pressure.

Large, slow growing predators, with low intrinsic population growth potential are typically more susceptible to fishing pressure (Myers and Worm, 2003). Many elasmobranch species fall into this description due to their slow growth, late maturation, and low fecundity (Walker and Heessen, 1996; Ferretti et al. 2010; McHugh et al. 2011). This vulnerability may help explain the demise of elasmobranchs in inshore waters and this is congruent with previous reports of localised extirpations and declines in other parts of the British coast (Roger and Ellis, 2000; McHugh et al. 2011). Importantly, the formerly abundant grey gurnard was absent in the contemporary resurveys, supporting evidence of their decline in coastal waters over the 20th century (Greenstreet and Hall, 1996; Rogers and Ellis, 2000). In the Firth of Clyde, Heath and Speirs (2012) revealed that grey gurnard was the fourth most dominant species in 1920 – 1969, accounting for 7.9% of the total demersal biomass, but was completely absent in subsequent periods (1960 – 2009). Surveys in 2008 – 2009 off the Plymouth coast also demonstrated that grey gurnard >15 cm had either declined or were absent at certain sites but had been highly abundant in 1913– 1922 (McHugh et al. 2011). Declines of other target species in Northumberland waters also corroborates with other long-term studies (e.g. Thurstan and Roberts, 2010), but apparent declines in certain non-target taxa (e.g. dragonets) contrast with increases in their relative abundance in other coastal regions (Rogers and Ellis, 2000; McHugh et al. 2011).

Increased trawling, especially mechanised beam trawling, over the 20th century (Engelhard, 2008) has also caused long-term shifts in the structure and composition of benthic fauna (Callaway et al. 2007; Frid et al. 1999; Fock et al. 2014). Trawling reduces biomass and production in the benthos (Kaiser et al. 2000) and shifts community structure from high-biomass fauna to smaller-bodied infauna (Jennings et al. 2001; Shepard et al. 2010). This can have consequences for demersal fish populations, the quantity and quality of the benthic prey of which is reduced (Choi et al. 2004; Smith et al. 2013; Johnson et al. 2015). In this scenario, reductions in benthic biomass over the 20th century may have contributed towards a decrease in the overall abundance and diversity of the inshore fish assemblage, thus decreasing the overall carrying capacity of species through possible reduced prey availability. However, the dominance of dab in particular in the contemporary assemblage (albeit in smaller abundances compared to historical trawls) may also reflect their ability to maintain food intake when the composition and quality of their food supply is changed by bottom trawling. Dab are widely distributed throughout the North Sea and exhibit high levels of exploitation and bycatch mortality (Kaiser and Spencer, 1995), but tend to have large and stable populations (Heessen and Daan, 1998; Rogers et al. 1998). The resistance to exploitation of dab may in part be due to their foraging strategy as they readily adapt their diet to trawling-induced disturbance.

Shallow coastal waters are particularly sensitive to rising sea temperatures, and long-term shifts in climate variability can significantly alter local species abundances via changes in their distribution (Engelhard et al. 2011) and migration phenology (Teal et al. 2012). Understanding species' responses to climate change is best achieved using time-series data; however, the present study focuses solely on two distinct time periods, with a 105 year time interval in-between. Nevertheless, observed differences in the data between these intervals corroborate other long-term studies that have attributed changes to climatic shifts. In the North Sea, Engelhard et al. (2011) interpreted climate as the main driver of shifts in plaice distribution, with individuals responding to increasing sea temperatures by shifting their depth distribution (Dulvy et al. 2008) and latitudinal range northwards (Perry et al. 2005; Hiddink and ter Hofstede, 2008; Engelhard et al. 2011). Juvenile plaice typically inhabit coastal zones and gradually move offshore as they increase in size. In the Wadden Sea, formerly abundant 1-group plaice have undergone a gradual offshore shift and have been rare in shallow coastal waters since the late 1990s, attributed to a long-term climatic shift in their distribution (van Keekan et al. 2007). Other studies have reported increases in smaller fish species in line with sustained climate change (van Hal et al. 2010). In Northumberland, no increases in the abundance of particular fish species were observed in the resurveys, in contrast to long-term surveys conducted at similar depths around the UK coast (Rogers and Ellis, 200; McHugh et al. 2011) and further offshore (Greenstreet and Hall, 1996).

Other drivers such as habitat modification, pollution, and changes in food availability and/or overall ecosystem productivity, may have also contributed to declines in the inshore assemblage. The Northumberland coast was historically an important nursery ground for many demersal species (Meek, 1896), but numerous anthropogenic changes have substantially altered this. Fishing, by removal of large predatory fish, may have resulted in lowering the predation risk and/or intra- or inter-specific competition in deeper waters (van Keekan et al. 2007), enabling younger individuals to disperse over a wider area. Overtime, larger individuals may have also shifted their distribution offshore in response to a reduced number of predators and competitors in inshore waters, as predicted for large plaice (20-39 cm) on the Dutch and Danish coasts (van Keekan et al. 2007). On the other hand, flatfish are also exposed to a higher predation risk in coastal waters due to an expanding seal population (Thompson and Duck, 2010). In the mid-19th and early 20th century, the grey seal (*Halichoerus grypus*) population size of the Farne Islands off the Northumberland coast, was estimated to at around 100 individuals (Lambert, 2002), but this has now increased to more than 4000 (Berwickshire & Northumberland Marine Nature Partnership, 2021). The grey seals forage predominantly on sandeels, but are also dependent on some gadoid and flatfish species (Thompson and Duck, 2010). Therefore, an increase in their abundance may be reflected in the very low abundances of fish species in contemporary surveys, particularly at Skate Roads, which is located within 3 miles of the Farne Islands.

This study replicated some of the earliest quantitative surveys of inshore fisheries in British waters, but it is unlikely that during 1896-1913 the inshore fish assemblage was representative of near-pristine conditions. This is largely because the surveys were conducted after the advent of steam trawling in the 1880s (Engelhard, 2008), and concerns for the depletion of inshore stocks were expressed early on, especially with respect to juvenile fish populations (Garstang, 1900). Threats to local fish stocks were considered great enough to establish a number of closed areas, including a three-mile nautical mile closure to bottom trawling in 1891 along the Northumberland coast (Meek, 1895). Inshore trawl fisheries for flatfish and gadoids operated out of North Shields from the mid-19th century (Meek, 1900), and near-shore static gear has been operating on a commercial scale for far longer. Given the long history of inshore fisheries, it is therefore not possible to accurately determine what the assemblage would have looked like prior to the onset of commercial fishing, but it offers a useful reference point from a period when anthropogenic stressors were far lower. The present study could constitute a benchmark for rebuilding inshore fish stocks and improving ecosystem status, rather than a baseline on which to base recovery to pristine conditions.

3.5. Conclusion

This study provides evidence from little studied inshore sites of dramatic change in the abundance of commercially and ecologically important fish species between the late 19th century and the present. Over a century of trawling is expected to have reduced benthic diversity in the region (Engel and Kvitek, 1998; Auster and Langton, 1999), resulting in a habitat that now supports low macrofaunal diversity and favouring species that inhabit ‘soft grounds’ over those that prefer heterogenous environments. In this altered state, shellfish species such as *Nephrops*, European lobsters and brown crabs will flourish as they are adapted to simplified environmental conditions and subject to reduced predation pressure (Thurstan and Roberts, 2010). Today, the potting fishery for lobsters and crabs is of great importance for Northumberland fishers (Stephenson et al. 2018), along with the otter trawl fishery for *Nephrops* (Walmsley & Pawson, 2007). In combination, habitat altering properties of these fisheries and bycatch of juvenile fish associated with *Nephrops* trawls may continue to preclude the recovery of demersal fish species. This low diversity ecosystem could be further at risk of parasitism, invasive species, and susceptibility to changes in environmental conditions in the future (Worm et al. 2006), with consequences for current fishing practices. Failing to prevent a collapse of a population will thus have negative implications for the local ecosystem (Hutchings and Reynolds, 2004). With more focus being placed on the value of historical data as important components of understanding past ecosystem states, it is perhaps timely to link this information with current conservation and management plans to assess the status of resources in human-dominated ecosystems.

Chapter 4: Long-term Trends in the Diet of Six Predatory Fish in the Western North Sea

4.1. Introduction

Although a considerable amount is known about “who eats whom” in marine food webs to understand how changes in one part of the ecosystem may influence another (Pinnegar et al. 2015), much less is understood about how marine predators respond to changes in prey availability (Greenstreet et al. 1998). Many commercially important fishes, such as flatfish and gadoids, are opportunistic and generalist predators that consume a broad spectra of benthic invertebrates for part of or all of their life history (Hiddink et al. 2011), with capabilities of switching between prey types in response to variations in local prey availability, whether this be on a seasonal, spatial, or inter-annual basis (Pinnegar et al. 2006). Demersal fish predators may indiscriminately forage on the most abundant prey in their immediate environment or select particular prey types due to differences in behaviour, ontogeny, prey morphology and energetic costs (Hinz et al. 2005; Timmerman et al. 2020). Optimal foraging theory suggests that predators preferentially select prey that optimise net energy intake per time spend feeding (Weber et al. 2010). However, the trade-offs associated with ontogenetic dietary shifts largely depends on the balance between mortality risk by predation and energetic benefits of their prey (Sánchez-Hernández et al. 2019). Other intrinsic factors, such as predator body size and/or gape size that are positively correlated with prey selection, promote these ontogenetic change, which will thus have important consequences for population and ecosystem functioning and stability (Scharf et al. 2000; Timmerman et al. 2020).

The combined effects of resource overexploitation, habitat destruction and pollution have led to widespread changes in benthic prey base of demersal fish predators (Jackson et al. 2001; Lotze and Milewski, 2004). Physical disturbance from bottom trawling has been found to decrease benthic biomass and alter community production levels (Queirós et al. 2006; Collie et al. 2017). Meanwhile, anthropogenic nutrient enrichment (eutrophication) from terrestrial inputs has increased primary productivity in coastal areas (Pihl, 1991), enhancing microbial respiration rates and depleting oxygen levels, with consequences that may persist for long enough to either remove or increase benthic invertebrates abundance (Powers et al. 2005). Together, trawling and eutrophication may therefore have widespread consequences for demersal fish species, either negatively via the reduction of specific prey for specialist predators with implications on their carrying capacity (Hiddink et al. 2011), or positively, through enhanced food production for opportunistic species (Jennings et al. 2002; Juan et al. 2007). Trawling may also induce a shift in benthic community structure from large, sessile fauna to smaller, highly-productive opportunistic species (de Groot, 1984; Rijnsdorp and Vingerhoed, 2001). In the North Sea, increased growth rates in the flatfishes, European plaice *Pleuronectes platessa* and sole *Solea solea*, have coincided with an increase in eutrophication and beam trawl effort in the 1960s and 1970s (Rijnsdorp and Van Leeuwen, 1996; Millner and Whiting, 1996), which be manifested through a shift of productivity towards smaller-bodied benthic species such as polychaetes (Rijnsdorp and Vingerhoed, 2001). By contrast, other studies suggest that the removal of certain benthic invertebrates by trawling has led to temporal declines in the body condition of demersal fish species (Choi et al. 2004). Alterations in allocation of energy among species and functional groups in the ecosystem may further affect the stability of benthic food webs, decreasing functional diversity and spatial heterogeneity (Shephard et al. 2010).

Short-term effects of human-induced disturbance revealed by immediate changes in fish abundance and behaviour are well known (Kaiser and Ramsay, 1997; Collie et al. 2000), however the longer-term implications of altered predator-prey dynamics are poorly understood (Frid et al. 1999). Recently, fish stomach content data has been incorporated into multi-species models to better understand ecosystem functioning, and to facilitate a move towards ecosystem-based approaches to fisheries management (Rault et al. 2017). A number of co-ordinated fish stomach databases have been used to address this agenda in the North Sea (e.g. Daan, 1989; Hislop et al. 1997), but these tend to only encompass a small number of predators and are limited in temporal coverage, typically the most recent three decades (Pinnegar et al. 2015). In a small number of localities however, historical data are available, and hence fish stomach contents may provide useful insights in to how fish diet has changed over a long time period as well as in response to changes in prey availability (Frid and Hall, 1999; Rijnsdorp and Vingerhoed, 2001).

To date, most studies of long-term change have focused on the reanalysis of fish abundance and epibenthic data collected from trawl surveys and grab samples (e.g. Rogers and Ellis, 2000; Callaway et al. 2007). However, others have used fish stomach content data to track temporal and spatial changes in the benthos (Link, 2004; Lilly et al. 2000; Dwyer et al. 2010). For example, Frid and Hall (1999) used dab *Limanda limanda* stomachs to infer changes in North Sea benthos between the middle and late 20th century. Long-term studies of Atlantic cod *Gadus morhua* diet have shown declines in euphausiids and increases in herring in the north-western Atlantic (Hanson and Chouinard, 2002). Moreover, the diet of several bottom-feeding fish have been used collectively to infer temporal changes in benthic community dynamics (Link, 2004).

In the present chapter, we use historical stomach data spanning more than 100 years to investigate long-term trends in the western North Sea for six demersal and benthivorous fishes, namely European plaice, dab, cod, whiting *Merlangius merlangus*, haddock *Melanogrammus aeglefinnus* and grey gurnard *Eutrigla gurnardus*. Specifically, this paper aims to 1) compare multi-decadal trends in predatory fish diet and identify shifts in the importance of particular prey items, and 2) compare differences in predator diet with size.

4.2. Methods

4.2.1. *Study area and stomach datasets*

Stomach content data were downloaded from the Cefas DAPSTOM database (Pinnegar, 2014a; Pinnegar, 2014b) and the International Council for the Exploration of the Sea 'Year of the Stomach' (ICES YOS) database (Daan, 1989; Hislop et al. 1997). The study area focussed on fish stomachs collected from sampling stations surveyed between 1896-2015 in the western North Sea, within ICES area sub-division IVb, a region encompassing the Dogger Bank and the north-east coast of England (Fig 4.1).

The latest version of the DAPSTOM dataset contains 256,354 stomach records from 9,445 distinct research cruises, covering the period 1836-2016 (Pinnegar, 2019). The vast majority of DAPSTOM records contain information on the feeding preferences of fish species throughout the Northeast Atlantic, with over half (52% of stomachs) relating to the North Sea. The DAPSTOM data portal has been made widely available online via Cefas' data hub website (https://www.cefas.co.uk/cefas-data-hub/fish-stomach-records/). In this study, the choice of predators was governed by data availability within the study area, allowing sufficient sample sizes for temporal analyses for all six predators. Stomach samples were originally collected during different sampling campaigns employing a wide variety of fishing gears, and Cefas' research vessels (*Huxley, Cirolana, Clione, Corystes, Corella, Platessa, Tellina, Ernest Holt, Sir*

Lancelot and *Cefas Endeavour*). Additional samples were also obtained from other fishing vessels chartered for scientific research purposes (with data uploaded to the DAPSTOM portal). For the 'historical' period, stomach samples were primarily collected from the UK government vessel *RV Huxley* between 1902-1907 (Todd, 1905; Todd, 1907) as well as scientific trawling experiments conducted by the Northumberland Sea Fisheries Committee (NSFC), using the steam vessels *Livingstone* and *Stanley* during 1896-1907 (Meek, 1900-1906). The aim of the NSFC surveys was to investigate the 'food of fishes' off the north-east coast of England during the summer months every year, while *RV Huxley* surveys were conducted at unstratified stations throughout the North Sea across all seasons (Fig 4.2). In 1923, a large number of adult cod stomachs were collected in the study area, however details on the number of full or empty stomachs were not provided (Graham, 1923). In contemporary surveys from the DAPSTOM database (2000-2015), predator stomachs were mostly acquired from distinct survey campaigns funded by the UK department for Environment Food and Rural Affairs (Defra), across a systematic grid and using standardised gear and protocols (Fig 4.2). Additionally, whiting stomachs were acquired through a Fishery-Science Partnership project in 2006, which examined the diet of whiting off the coast of northeast England (Stafford et al. 2006).

The ICES YOS dataset provides diet information on 35 species, albeit detailed data is only available for 9 roundfish species, collected during quarterly International Bottom Trawl Surveys (IBTS) of the North Sea in 1981 and 1991, using nine research vessels. Additional samples were also collected opportunistically during other research surveys and on commercial vessels, and in intervening years for cod and whiting (Hislop et al. 1997). Stomach samples were stratified by ICES statistical rectangles, measuring approximately 30 x 30 nautical miles (one-degree x 0.5 degree latitude) and collected in each quarter of the year using a Grande Ouverture Verticale (GOV) trawl (ICES, 2012). A detailed description of both sampling campaigns is given in the respective reports and manuals for the ICES North Sea sampling projects in 1981 (Daan, 1989) and 1991 (Hislop et al. 1997). In the present study, YOS data were only available for cod, whiting, haddock, and grey gurnard.

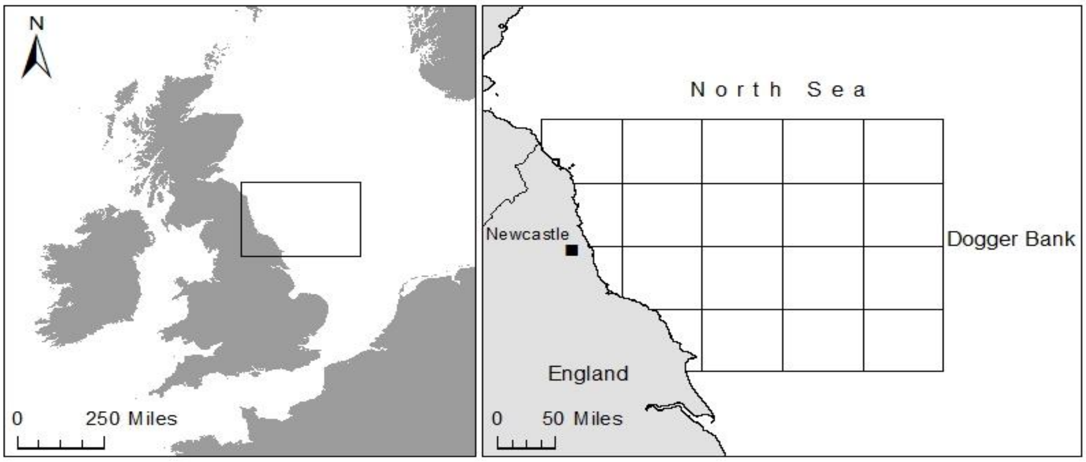


Figure 4.1. Location of study area in the western North Sea by ICES area.

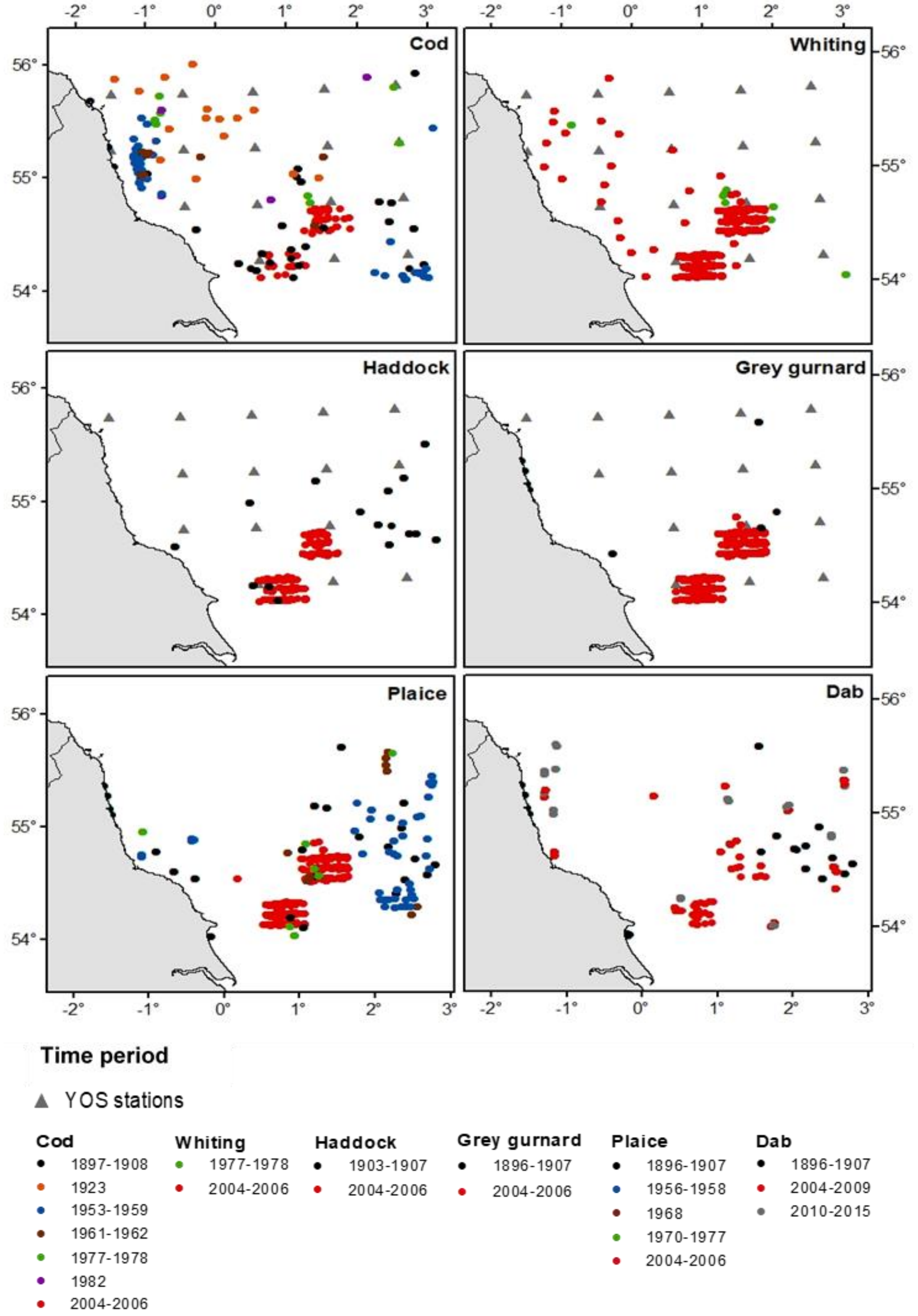


Figure 4.2. Map of fishing stations for six predatory fish by year group in the study area. Each colour corresponds to a period of time: circles represent locations from the DAPSTOM dataset and triangles from the 'Year of the Stomach' data.

4.2.2. *Data preparation*

In the DAPSTOM and ICES YOS datasets, a sufficient number of stomachs were collected in quarters two (April – June) and three (July – September) compared to the rest of the year (Table A.3), thus analyses were restricted to these two periods to minimise possible seasonal effects of dietary changes. Both datasets comprise a mixture of pooled samples from multiple pooled fish stomachs with data collected at the level of the individual fish (Pinnegar, 2014a). Sometimes only information on the number of stomachs containing a particular prey item was available (i.e., frequency of occurrence), rather than the exact number of a particular prey item. Hence, data extractions were interpreted with care and all outputs were viewed as the 'minimum number' of prey items consumed. In the YOS data, some unrealistically high numbers of smaller prey items (e.g., euphausiids) were documented in cod, gurnard, whiting and haddock stomachs. As a way of standardising temporal comparisons across the two datasets, stomach records containing on average more than 50 individual items per stomach were subsequently removed from analyses (see Table A.4). We adopted this pragmatic approach to reduce bias in comparing stomachs with exact versus unspecified prey numbers. It was not possible to compare proportions of empty stomachs or vacuity levels among decades as they were not consistently documented (see Table 4.1).

In the DAPSTOM database, predator size information (measured to the nearest cm) were available for individual fish whereas pooled samples were categorised into varying size classes depending on the survey (e.g., 5 and 10 cm bins). No individual stomach records were available in the ICES YOS dataset; instead, pooled stomach were grouped into pre-determined predator and prey size classes. There was also a lack of temporal coverage of smaller fish and analyses were therefore only concerned with fish > 20 cm to maintain consistency in comparisons of diet between datasets.

4.2.3. *Dietary analyses*

All dietary analyses were performed on individual and pooled stomach data (Table 4.1). Prey items were categorised into relatively broad taxonomic groups; different classification levels were used for flatfish and roundfish to highlight specific dietary trends. Completely unrecognisable prey items that were omitted; however, any 'unidentified fish' or 'unidentified invertebrates', for example, were redistributed proportionally among their respective identifiable counterparts.

For both pooled and individual stomachs from the DAPSTOM database, we expressed the 'minimum number' of individual prey items consumed in each category relative to the number of full stomachs in a particular decade, by percent (%) number (Hyslop, 1980). In the absence of raw prey mass data, robust 'fresh mass' (g) estimates of invertebrate and fish prey encountered in fish stomachs have been made available in version 5.5 of the DAPSTOM database (Pinnegar, 2019). For invertebrates, average prey masses were calculated based on a number of observed individual masses of a given species acquired from benthic surveys and other literature sources. In other cases, masses of individuals actually observed in predator stomachs from the DAPSTOM database were used to supplement the paucity of relevant information available for species. For all fish and cephalopods observed as prey, theoretical prey lengths (TPL), based on the observed relationship between predator and prey lengths in Pinnegar et al. (2003) and Scharf et al. (2000), were averaged, to create the relationship:

Prey length = (0.2057x predator length) + 1.618

In conjunction with TPL, weight-length exponents for fish (Silva et al. 2013) and cephalopods (Merella et al. 1997; Emam et al. 2014) were used to calculate wet weights in the DAPSTOM database. For the YOS data, this approach wasn't applied; instead, actual mean prey mass, which were averaged by prey size classes, were used since all predator stomachs were pooled. Calculated prey masses for individual fish and invertebrates were multiplied by the 'minimum number' of prey, and also expressed as percent mass (Hyslop, 1980). To maintain consistency between the two datasets, this same approach was applied to the YOS data using known prey numbers and masses. The number and masses of each prey category were subsequently adjusted by redistributing unidentified prey components among the various identified components, taking in to account the taxonomic level of identification.

A total of 15,875 stomachs (pooled and individual) from the DAPSTOM and YOS database were used to examine decadal trends (% number and weight) in spring and summer between 1896 and 2015 (Table 4.1). For all predators, the vast majority of stomachs were collated from either the earliest time period (1896 – 1907) or from the 1980s onwards, whereas stomach records were lacking intervening decades for dab, grey gurnard, haddock and whiting. By comparison, sufficient sample sizes collected at the individual level for plaice and dab enabled statistical comparisons of multi-decadal trends in diet (Table 4.1).

Table 4.1. Numbers of full and empty fish predator stomachs in each sampling period used for temporal comparisons of diet composition (separated into pooled and individual stomachs). Fish stomachs were sourced from the DAPSTOM database unless stated as 'Year of the Stomach' (YOS) data in the 'Source' column.

Predator	Source	Sampling period	Pooled		Individual	
			Nfood	Nempty	Nfood	Nempty
Plaice		1896-1907	284	17	188	83
		1956-1958	-	-	490	23
		1961-1968	-	-	131	9
		1970-1977	-	-	145	40
		2002-2006	-	-	602	305
Dab		1896-1908	222	6	169	77
		2002-2009	-	-	591	181
		2010-2015	-	-	857	247
Cod		1897-1908	165	6	119	16
		1923	-	-	899	-
		1953-1959	-	-	229	61
		1961-1963	-	-	290	63
		1977-1978	-	-	78	14
	YOS	1981-1989	2147	317	80	13
		1982-1984	-	-	-	-
		1990-1994	-	-	-	-
	YOS	1991	236	11	-	-
		2002-2006	-	-	99	13
Grey gurnard		1896-1908	58	-	100	34
	YOS	1991	482	62	-	-
		2002-2006	-	-	1277	727
Haddock		1902-1908	510	9	14	1
	YOS	1981	314	35	-	-
	YOS	1991	390	24	-	-
		2002-2006	-	-	456	142
Whiting	YOS	1981-1987	1258	611	-	-
	YOS	1991	861	238	-	-
		2002-2006	-	-	1794	3303

4.2.4. *Statistical analyses*

All pooled stomach records were omitted from statistical analyses due to the loss of data resolution. Instead, only individual plaice and dab stomach data were modelled to examine decadal and size-based trends in their diet composition. In order to statistically determine the most important variables for explaining predator diet, the 'minimum number' of prey items were treated as presence data (i.e., 0 or 1). Generalised Linear Models (GLMs) were conducted in statistical software *R* version 3.5.2 (R Core Team, 2018), to determine the relationship between several potential predictor (presence of prey) and dependent variables (decade and predator size). A negative binomial distribution family and log-link function was used in all GLMs. Canonical Correspondence Analysis (CCA) was performed to evaluate which factors explained the observed variability in diet composition. Permutation tests were used to test the statistical significance (at the 5% level) between diet composition and explanatory variables. The arrows of the explanatory variables indicate the direction of maximum change. CCA analyses were performed using the vegan package in R (Oksanen et al. 2013).

4.2.5. *Decadal changes in fish diet*

4.2.5.1. Flatfishes

Over the period 1896-2015, there were substantial changes in the diet composition of prey consumed by all six predators >20 cm between April-September. For plaice, bivalves (mostly Mactridae sp., *Ensis* sp.*, Spisula subtruncata* and *Tellina tenuis*) were major prey in the early to mid-20th century, dominating the diet in the 1950s in terms of number and mass (Fig 4.3a-b, 80% and 86.7%, respectively). However, bivalves declined in subsequent decades and polychaetes became more prominent in plaice diet from the 1960s onwards. Polychaetes were the most important prey resource by number for plaice in the 1970s and 2000s, comprising 38.9% and 32.3% of their diet, respectively. Bivalves also declined in importance by number in dab diet from 35.8% to 12.4% between the 1900s and 2010s (Fig 4.3c). In all time periods, bivalves only comprised <15% of dab diet by mass while polychaetes represented <7% of the total diet by number and mass. By comparison, crustaceans (mainly the hermit crab *Eupagurus bernhardus*) remained a stable part of the dab diet across all time periods and represented the largest proportion of the diet by mass in the 1900s (73.7%), 2000s (32%) and 2010s (44.4%, Fig 4.3d).

The proportion of echinoderms in flatfish diets increased in importance from the early 1900s to 2000s (Fig 4.3). From the 1960s onwards, the echinoderms most commonly eaten by plaice were *Ophiura* sp., while these were consistently consumed by dab in all time periods. By contrast, sea urchins, particularly *Echnocyamus pusillus*, were the most important echinoderm species observed in dab diet in recent years, while they were relatively absent in the 1900s. Of the fish, sandeels (*Ammodytes* sp) were the most frequently consumed category in both flatfishes (Fig 4.3). In plaice, the proportion of sandeels increased by mass from 13.5% in the 1900s to 52.7% in the 2000s. Meanwhile, sandeels increased in importance by 12% in dab diet between historical and contemporary periods whereas, the prey category "other fish", represented <3% of the total diet.

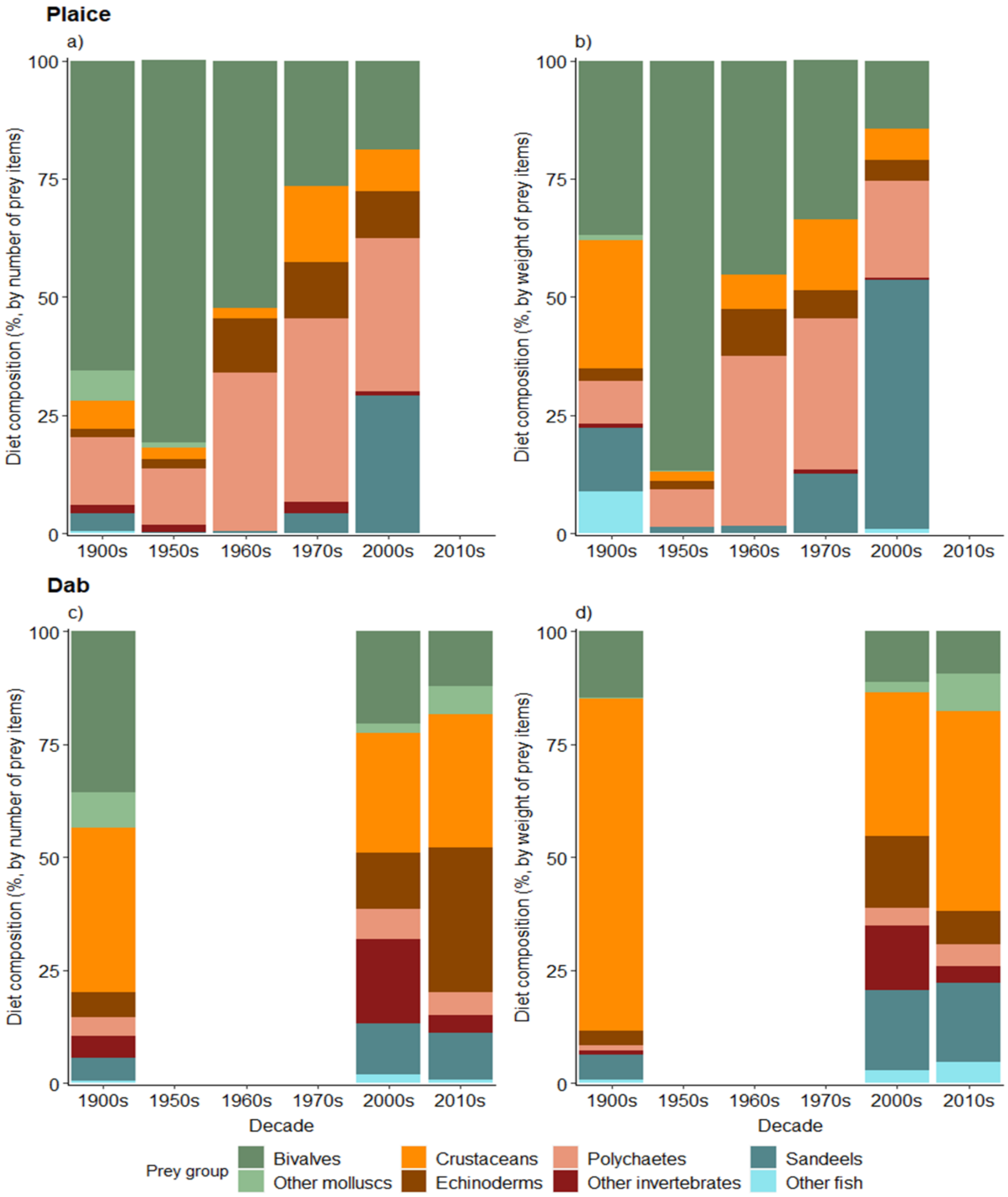


Figure 4.3. Diet composition of (a-b) plaice and (c-d) dab > 20 cm based on the number and weight of prey items consumed between April and September.

4.2.5.2. Roundfishes

Crustaceans and fish were both important constituents of cod diet across all decades, however fish consistently represented >60% of the total mass (Fig 4.4a-b). Among the crustaceans, crabs and hermits were consistently eaten by cod, and were major prey in the 1900s (59.7%) and 2000s (49.1%; Fig 4.4a). Of the crabs and hermits, *Pagurus bernhardus,* masked crab *Corystes cassivelaunus*, *Portunus* sp. and *Hyas coarctatus* were the most numerous species in cod diet, increasing in prevalence in the earlier and later half of the 20th century compared to intervening decades. Euphausids represented 30.6% and 19.6% of cod diet by number in the 1970 and 1980s, respectively, but were absent in the decades prior and occurred in very low quantities (<2%) from the 1990s onwards. Flatfishes and gadoids were generally important fish prey by mass across the time series, except in the 2000s, where sandeels and other fish dominated (Fig 4.4b). Cannibalism in cod only occurred in small amounts in the 1920s, 1980s and 1990s, accounting on average for 1.7% of prey mass. Meanwhile, clupeoids (primarily herring *Clupea harengus*) represented a highly variable portion of cod diet between the decades and were the most important prey taxon by mass in the 1990s, comprising 35.8% of the total diet. In the 'other fish' category, the dragonet *Callionymus lyra* was relatively abundant in cod diet across the time-series, while Atlantic mackerel (*Scomber scomber*) was only consumed in the 1920s.

The dietary importance of bivalves also declined in haddock between the early 20th century and recent time periods (Fig 4.4). Bivalves (primarily *Solen* sp.) dominated haddock diet in the 1900s, constituting 41.7% by number and 34.8% by mass; however, they decreased substantially from the 1980s onwards (Fig 4.4c-d). Polychaetes typically comprised <11% of haddock diet; however, in the 1990s, 32% of their total diet by mass consisted primarily of the polychaete *Aphrodita aculeata*. Haddock consumed increasingly more echinoderms in recent decades compared to the 1900s, becoming the most important prey resource in the 1980s (47%) and 2000s (38.4%). The brittle star *Amphiura filiformis* was often consumed by haddock in the 1900s, while *Echinocyamus pusillus* was consistently consumed in high numbers in the 1900s, 1980s and 1990s. By comparison, sandeels were considerably more important in terms of mass in the 1980s and 1990s, representing 71.8% and 27.7 % of the total biomass. However, sandeels declined substantially between the 1980s and 2000s, while crabs and hermits became a more prominent component of haddock diet by mass (52%) in the 2000s (Fig 4.4d).

In terms of mass, fish were highly important prey, particularly cluepoids and sandeels, to whiting and gurnard diet across the time series (Fig 4.4e-h). In the 2000s, ‘other fish’ made up 57.9% of the total diet by mass, which mainly comprised larval fish and dragonets. In the 1990s, amphipods were major prey for whiting, making up just over half of the total diet by number (51.3%), and were overwhelmingly dominant in gurnard diet (71.5%; Fig 3g). By contrast, 79.1% of prey mass in gurnard diet were sandeels, while clupeoids (mainly European sprat *Sprattus sprattus*) and sandeels (*Ammodytes* sp.) were relatively equal constituents in whiting diet in the 1990s, accounting for 43% and 39.6%, respectively, of the total mass (Fig 4.4f). In gurnard diet, sandeels contributed a great portion to the diet by number in the early 20th century in contrast to the 1990s, however they were vastly more important in terms of mass in this decade. Moreover, invertebrates were also more important prey to gurnards in the early 20th century by mass and number. In particular, relatively few cephalopods were consumed in the 1900s, but represented the most important item in terms of mass (35.6%). Other crustaceans (mainly the mysid *Gastrosaccus spinifer*) and shrimps (*Crangon* sp.) were equally important prey by number in the early 20th century, while echinoderms were absent from gurnard diet.

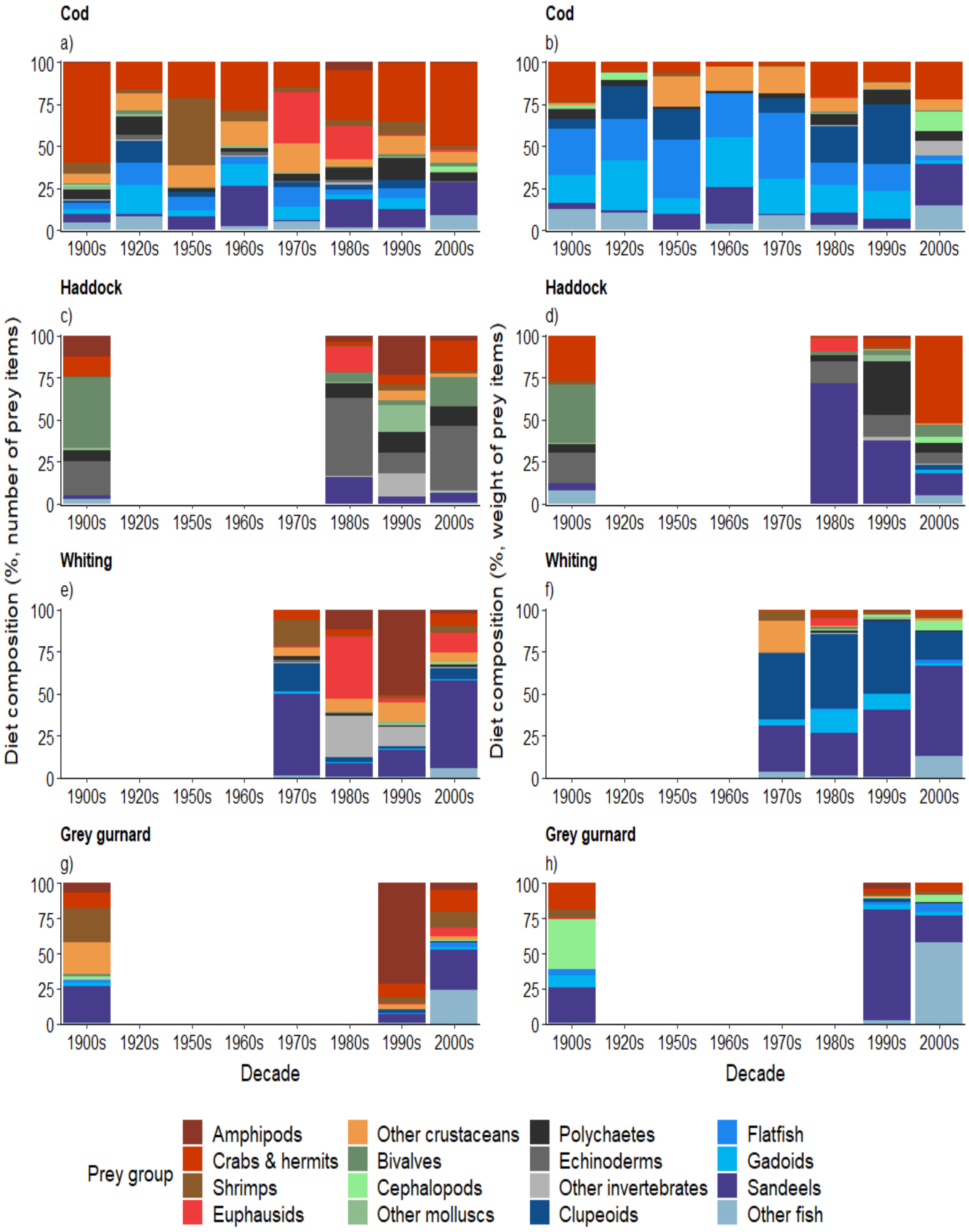


Figure 4.4. Diet composition of > 20 cm (a-b) cod, (b-c) haddock, (d-e) whiting, and (f-g) grey gurnard expressed as percent number and mass of prey consumed in quarters two and three by decade.

4.2.6. *Trends with body size in individual plaice and cod diets*

For the individual plaice data, length and decade had significant effects on diet composition for all prey groups in the GLMs (Table 4.2). As their relative importance declined overtime, the presence of bivalves had a strong significant relationship ($P < 0.001$) with increasing plaice length. Conversely, model outputs indicate that polychaetes had a significantly negative relationship with plaice size. Decade and length had no significant effect on the prey category 'Other fish'. The presence of crustaceans and echinoderms steadily declined with increasing plaice size, however their presence increased significantly with size in all decades except in the 2000s and in the 1960s for crustaceans. In the 1960s and 1970s, no relationship was detected between presence of sandeels and plaice size, however there was a highly significant positive trend in the 2000s with size ($P < 0.0001$; Table 4.2). There was a marginally non-significant positive relationship between plaice length and incidence of 'Other fish'. However, it should be noted that in certain decades, some of the less common prey were rare or completely absent.

For cod, changes in the relative contributions of different prey items were observed across the range of cod length (20-120 cm). Incidence of fish prey was statistically significantly related to cod length (Table 4.3); their presence increased in larger fish. Of the fish prey, clupeoids, gadoids and sandeels became more important in cod diet overtime and were consumed to a lesser extent in the 1900s. The contribution of crustaceans to diet generally decreased with cod size; other crustaceans and shrimps were the only crustaceans that were significantly related to cod size ($P < 0.0001$). Among the decades, crabs and hermits exhibited a strong negative relationship with cod size in the decades 1950s-1970s and 1990s-2000s (Table 4.3). Unlike plaice, the presence of polychaetes increased significantly with cod length ($P < 0.0001$), whereas there were no detectable relationships between the presence of bivalves with cod size or decade.

The CCA explained 8.7% of the total variation in plaice diet and the first two canonical axes accounted for 74.2% and 17% of the constrained (explained) variation, respectively. Permutation tests revealed that diet was significantly associated with decade and predator size. The decade 2000s was the most important explanatory variable, with sandeels and other fish prey being mostly associated with this decade (Fig 4.5a). Of all the prey groups, bivalves were closely associated with plaice length, while echinoderms, crustaceans and particularly polychaetes, were mainly consumed in the 1960s and 1970s. By comparison, the CCA plot in Fig 4b explained only 6.4% of the total variation in cod diet and the first two canonical axes accounted for 40.5% and 25.4% of the constrained variation. Cod diet was significantly associated with decade and length ($P < 0.001$), as revealed by permutation tests. In Fig 4.5b, the 1960s and 1970s were important determinants of cod diet, and thirdly, predator size. Sandeels, echinoderms and other invertebrates were important in the 1960s, while shrimps were closely associated with the 1950s. Meanwhile, flatfishes and other fishes, and to a lesser extent clupeoids, were more associated with the 1980s and 1990s. In contrast, the 2000s appeared to be the least important explanatory variable for plaice.

Table 4.2. Summary results from GLMs examining the relationships between the presence of prey in plaice diet with explanatory variables decade and predator length.

Prey category	Model	Estimate	S.E.	*Z*	*P* - value
Bivalves	Intercept	0.465	0.432	1.075	0.282
	1960s	-1.24	0.25	-4.951	<0.0001*
	1970s	-2.505	0.239	-10.451	<0.0001*
	2000s	-2.963	0.329	-7.592	<0.0001*
	Length	0.044	0.207	-14.308	<0.0001*
		AIC: 1294	adR^2= 0.365	Deviance explained = 29.6%	
Polychaetes	Intercept	-0.233	-0.625	0.532	<0.0001*
	1960s	1.144	0.217	5.261	<0.0001*
	1970s	1.509	0.213	7.058	0.006
	2000s	0.483	0.177	2.719	0.001*
	Length	-0.031	0.009	-3.36	0.0007*
		AIC: 1595.7	adR^2= 0.05	Deviance explained = 4.9%	
Crustaceans	Intercept	-2.927	0.63	-4.642	<0.0001*
	1960s	-0.692	0.632	-1.094	0.2742
	1970s	1.82	0.318	5.711	<0.0001*
	2000s	0.795	0.321	2.478	0.0132*
	Length	-0.003	0.015	-0.245	0.8068
		AIC: 740.38	adR^2= 0.03	Deviance explained = 5.8%	
Sandeels	Intercept	-10.338	1.118	-9.245	<0.0001*
	1960s	1.066	1.242	0.858	0.391
	1970s	1.632	1.018	1.604	0.109
	2000s	5.645	0.794	7.104	<0.0001*
	Length	0.116	0.017	6.511	<0.0001*
		AIC: 1096.5	adR^2= 0.16	Deviance explained = 24.2%	
Echinoderms	Intercept	-4.493	0.751	-5.981	<0.0001*
	1960s	2.507	0.48	5.223	<0.0001*
	1970s	2.665	0.471	5.653	<0.0001*
	2000s	2.136	0.468	4.565	0.111
	Length	0.007	0.016	0.471	0.637
		AIC: 741.1	adR^2= 0.03	Deviance explained = 7.4%	
Other fish	Intercept	-22.423	870.952	-0.026	0.9795
	1960s	0.161	1771.78	0	0.9999
	1970s	0.162	1733.65	0	0.9999
	2000s	18.529	870.95231	0.021	0.983
	Length	0.04673	0.02717	1.72	0.0854
		AIC: 332.91	adR^2= 0.03	Deviance explained = 17.6%	
Other molluscs	Intercept	-7.043	1.691	-4.165	<0.0001*
	1960s	-17.31	2524.66907	-0.007	0.9945
	1970s	-17.327	2442.13	-0.007	0.9943
	2000s	-1.594	1.191	-1.338	0.1809
	Length	0.0759	0.037	2.038	0.415
		AIC: 99.53	adR^2= 0.02	Deviance explained = 16.8%	

Table 4.3. Summary results from GLMs examining the relationships between the presence of prey in cod diet with explanatory variables decade and predator length.

Prey category	Model	Estimate	S.E.	*Z*	*P* - value
Crab and hermits	Intercept	1.267	0.311	4.072	<0.0001
	1950s	-1.727	0.252	-6.845	<0.0001
	1960s	-1.57	0.242	-6.468	<0.0001
	1970s	-2.054	0.331	-6.2	<0.0001
	1980s	-0.257	0.32	-0.803	0.4217
	1990s	-0.576	0.29	-1.987	0.0469
	2000s	-0.945	0.313	-3.01	0.0026
	Length	-0.004	0.0041	-1.032	0.3022
		AIC: 1308.7	adR^2= 0.09	Deviance explained = 8.8%	
Shrimp	Intercept	0.0917	0.43	0.213	0.8313
	1950s	1.568	0.322	4.855	<0.0001
	1960s	-0.614	0.366	-1.676	0.0937
	1970s	-0.936	0.55	-1.702	0.0887
	1980s	-0.268	0.501	-0.535	0.5926
	1990s	0.043	0.376	0.116	0.9079
	2000s	-2.418	0.664	-3.64	0.0002
	Length	-0.042	0.007	-5.568	<0.0001
		AIC: 752.5	adR^2= 0.14	Deviance explained = 17.2%	
Other crustaceans	Intercept	-0.832	0.375	-2.215	0.0267
	1950s	0.732	0.304	2.406	0.0161
	1960s	0.187	0.307	0.612	0.5406
	1970s	1.428	0.352	4.056	0.0887
	1980s	0.28	0.407	0.688	0.4915
	1990s	-0.469	0.394	-1.19	0.2342
	2000s	-2.122	0.654	-3.243	0.0011
	Length	-0.018	0.005	-3.362	<0.0001
		AIC: 921.35	adR^2= 0.06	Deviance explained = 7.3%	
Bivalves	Intercept	-2.259	0.831	-2.717	0.0065
	1950s	-2.081	1.1253	-1.849	0.0644
	1960s	-17.222	1036.25	-0.017	0.9867
	1970s	-17.286	1988.311	-0.009	0.993
	1980s	0.542	0.727	0.745	0.456
	1990s	0.316	0.658	0.48	0.631
	2000s	-0.306	0.772	-0.397	0.691
	Length	-0.021	0.014	-1.529	0.1263
		AIC: 921.35	adR^2= 0.02	Deviance explained = 16.8%	
Polychaetes	Intercept	-2.999	0.439	-6.832	<0.0001
	1950s	-0.955	0.378	-2.523	0.0117
	1960s	-1.801	0.441	-4.076	<0.0001
	1970s	-0.929	0.531	-1.75	0.0802
	1980s	0.061	0.391	0.157	0.8749
	1990s	0.827	0.356	2.324	0.0201
	2000s	-0.065	0.489	-0.134	0.893
	Length	0.023	0.005	3.998	<0.0001
		AIC: 584.62	adR^2= 0.09	Deviance explained = 11.6%	

Clupeoids	Intercept	-6.083	7.586	-8.02	<0.0001
	1950s	0.12	0.584	0.206	0.8365
	1960s	-17.16	1008	-0.017	0.9864
	1970s	-0.425	0.851	-0.5	0.6168
	1980s	0.809	0.561	1.44	0.1498
	1990s	2.243	0.563	3.982	<0.0001
	2000s	1.553	0.713	2.013	0.0441
	Length	4.908	0.84	5.84	<0.0001
		AIC: 318.54	adR^2= 0.16	Deviance explained = 26.1%	
Flatfishes	Intercept	-3.718	0.475	-7.817	<0.0001
	1950s	-0.753	0.402	-1.87	0.0615
	1960s	-1.027	0.4	-2.566	0.0103
	1970s	-0.928	0.588	-1.577	0.1148
	1980s	0.984	0.379	2.599	0.0093
	1990s	0.533	0.406	1.31	0.19
	2000s	-1.73	1.064	-1.625	0.1041
	Length	0.031	0.006	5.222	<0.0001
		AIC:525.95	adR^2= 0.12	Deviance explained = 16.6%	
Gadoids	Intercept	-3.657	0.4904	-7.458	<0.0001
	1950s	-0.845	0.521	-1.621	0.105
	1960s	0.836	0.39	2.142	0.0321
	1970s	-0.32	0.623	-0.514	0.6069
	1980s	1.527	0.432	3.536	0.0004
	1990s	1.576	0.429	3.667	0.0002
	2000s	-1.469	1.08	-1.36	0.1739
	Length	0.02	0.005	3.612	0.0003
		AIC:635.36	adR^2= 0.08	Deviance explained = 13%	
Sandeels	Intercept	-4.171	0.634	-6.572	<0.0001
	1950s	0.696	0.581	1.197	0.2313
	1960s	2.485	0.528	4.699	<0.0001
	1970s	-14.131	445.062	-0.032	0.974
	1980s	1.237	0.619	1.999	0.045
	1990s	1.308	0.61	2.142	0.0321
	2000s	2.067	0.617	3.35	0.0008
	Length	0.014	0.006	2.292	0.0218
		AIC: 711.96	adR^2= 0.09	Deviance explained = 12.4%	
Other fish	Intercept	-2.461	0.513	-4.795	<0.0001
	1950s	-17.598	710.044	-0.025	0.9802
	1960s	-1.892	0.498	-3.797	<0.0001
	1970s	-0.946	0.584	-1.619	0.1055
	1980s	-0.249	0.461	-0.541	0.5884
	1990s	-1.278	0.591	-2.162	0.0321
	2000s	-0.366	0.5302	-0.691	0.0008
	Length	0.009	0.007	1.273	0.2028
		AIC: 711.96	adR^2= 0.09	Deviance explained = 12.4%	

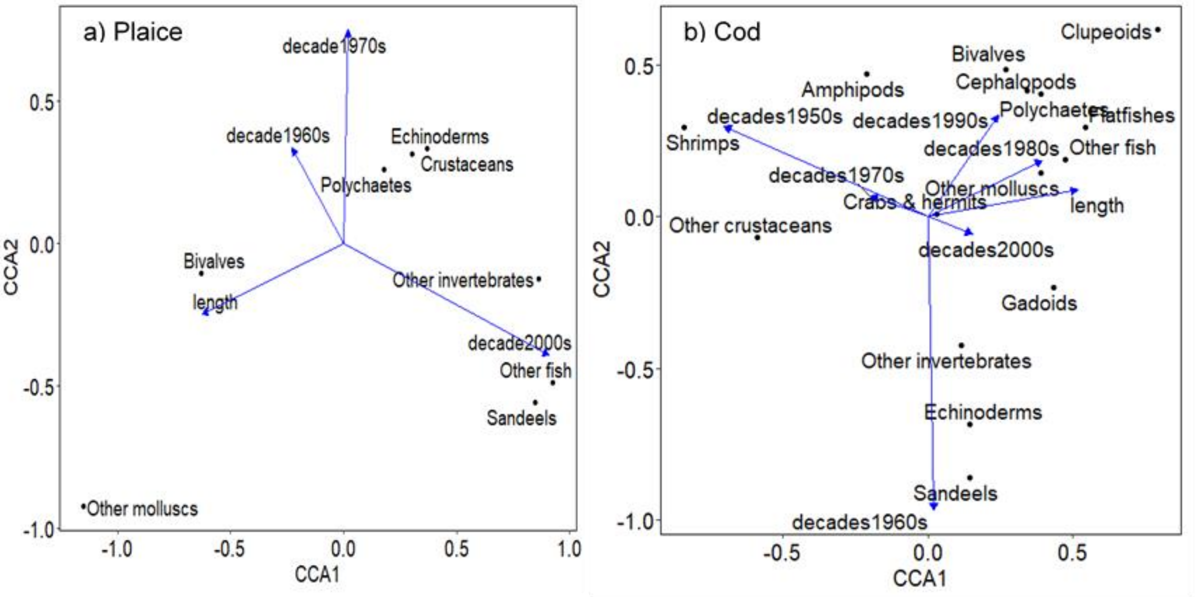


Figure 4.5. CCA ordination diagrams for a) plaice and b) cod. The arrow indicate significant explanatory variables, with the arrowheads indicating an increase in gradient. Data points indicate CCA scores of prey categories in ordination space.

4.3. Discussion

The diet of the six demersal predatory fish species in the western North Sea was highly variable over long periods of time, with some clear shifts in the importance of major prey taxa in three out of the six species. In general, the main prey of cod and grey gurnard has not changed considerably in the region over the past 100 years. Since the late 19th century, fish and crustaceans have dominated cod diet, however fish were more important in terms of mass. Crustaceans decreased and fish increased in importance with increasing cod size. Similar dietary patterns have been observed historically in the region and adjacent waters (Todd, 1907; Jones, 1954), and in the wider North Sea (Daan, 1973; Pihl, 1994) and Celtic Sea (Pinnegar et al. 2003). In this study, fish were also the most important prey by mass for whiting and gurnard, while invertebrates dominated gurnard diet historically. For the other predators, plaice, dab and haddock, major shifts in dietary composition were detected between the historical and contemporary decades. Bivalves were the predominant food source consumed by these predators in the first part of the 20th century, while their importance drastically declined in the latter half and in the 2000s. Meanwhile, polychaetes, echinoderms and sandeels increased in importance as prey resources in recent periods. Bivalves and other molluscs were found to increase in importance with plaice size, whereas the contribution of all other prey groups decreased.

Although major temporal changes in predator diet were observed in the present study, it is important to recognise the caveats and limitations associated with stomach content data, especially when analysing such data from multiple sources. Importantly, we used a mixture of ‘pooled’ information and stomach data collected from individual fish, and the way prey items were recorded varied considerably between sampling regimes. For example, information on the presence or number of stomachs containing a specific prey item (i.e., ‘frequency of occurrence’) were typically reported in historical surveys (e.g., Meek, 1900; Todd, 1905; Todd, 1907), rather than the actual number of a given prey item. Conversely, the ICES YOS data methodically details prey numbers and masses in pooled size categories (Daan, 1989; Hislop et al. 1997). Thus, the number of observations of a predator eating the specified prey needs to be interpreted with care. While the ‘minimum number’ of prey consumed does not give a true indication of absolute quantities, it does give an overall impression of the most important prey items taken as a key food resource. This should have little impact on benthic predator species that feed on large prey items, however numbers could drastically underestimate total prey numbers in plankton-feeding species such as mackerel and herring (Pinnegar, 2019), not considered in the present study. A standardised approach was adopted here by removing suspiciously high numbers of prey items observed in a small number of stomachs, which were likely to skew data comparisons, especially by % number. In particular, hyperiid amphipods, calanoid copepods, and euphausiids were among the prey items that were removed from the YOS data (see Table A.3 in Appendix 2); the high prey numbers still showed that these were dominant taxa in certain decades.

There are a range of dietary measures have been used to quantify the gut contents of fishes, from simple presence/absence or frequency of occurrence of different prey categories (e.g., Abrantes et al. 2011) to estimates of nutritional value of ingested prey (e.g., Hartman and Brandt, 1995). In addition to the ‘minimum number’ of prey items, we applied individual gravimetric (mass-balanced) estimates to invertebrates and fish prey, which offered a considerably different impression to predator diet than by number. Although the findings were largely indicative and sensitive to the assumed average size of an individual prey item, using both number and weight provides a more balanced representation of dietary importance (Pinkas et al. 1971; Liao et al. 2001). Together, these indices also reduces the bias of the particular emphasis of individual metrics of diet composition (Hart et al. 2002).

4.3.1. *Dietary changes in flatfish diet*

The long-term shift in plaice diet observed in this study is consistent with other flatfish dietary studies conducted in other parts of the North Sea (Pihl, 1994; Frid and Hall, 1999; Rijnsdorp and Vingerhoed, 2001), and other investigations that have examined changes in benthic assemblages throughout the 20th century (Callaway et al. 2007; Kröncke, 2011). In the southern and eastern North Sea, Rijnsdorp and Vingerhoed (2001), reported that molluscs were the most important prey in both areas (occurring in 91% of stomachs) in the early 1900s, shifting to a dominance of polychaetes at the end of the century (occurring in 85% and 88%, respectively). On the Dogger Bank, Kröncke (2011) observed large changes in the occurrence of the bivalves *Mactra* and *Spisula* species, which existed in extensive patches across the Bank in the first part of the 20th century, occurring in very high numbers in plaice stomachs (Kröncke, 2011), but almost completely disappeared in the latter part of the century. Similarly, we observed very high numbers of *Mactra* sp. in plaice stomachs in the 1900s and 1950s, declining in subsequent decades.

From the 1960s, the increased importance of polychaetes as a major prey resource for plaice corresponds with observed changes in the benthos. In the latter half of the 20th century, benthic macrofaunal biomass increased along with abundances of opportunistic, short-lived taxa in the central and southern North Sea. Since the 1970s, several authors have reported an increase in prevalence of polychaetes and echinoderms off northeast coast of England, while others have found similar trends further offshore on the Dogger Bank and wider North Sea. Lindley et al. (1995) reported increases in echinoderm larvae in the study area from the 1960s, which may explain why plaice consumed more echinoderms in, predominantly ophiuroids, in later decades in the present study. These findings are also consistent with *a priori* predictions presented by Frid and Hall (1999) in the Moray Firth, whereby dab consumed more echinoderms in the mid-1990s than the 1950s, corresponding with an increase in fishing intensity.

4.3.2. *Dietary changes in roundfish diet*

Investigations from other areas of the North Sea at the beginning of the 20th century showed that echinoderms were major prey (59% of the diet) of dab along the Dutch coast between April and October, while crustaceans occurred in only 18% of dab stomachs (Todd, 1907). By comparison, in the eastern North Sea, molluscs and polychaetes were selected almost equally by dab, while echinoderms only accounted for 8% of the total diet historically (Todd, 1907). In the Kattegat, echinoderms and crustaceans were selected equally (35% of biomass consumed) by dab (Blegvad, 1916), but the relative importance of echinoderms increased, dominating the diet in the 1980s (April – September), while epibenthic crustaceans declined in the same period (Pihl, 1994). Of the echinoderms, *Amphiura filifrmormis* dominated dab diet historically in this study and were consumed in high numbers elsewhere (Todd, 1907), however they were rarely consumed in contemporary time periods unlike in other regions.

Sandeels, particularly *Ammodytes* sp., have formed an important component of predator diet in this study, particularly in recent decades. No studies have quantified long-term trends on sandeel availability in predator diet due to the paucity of data available to analyse such trends. However, other studies have shown that sandeels are a major prey resource to demersal fish (Pinnegar et al. 2006) and tend to be consumed in areas where they are locally abundant (Engelhard et al. 2013). On the Dogger Bank, Macer (1966) found that cod and whiting consumed sandeels in large numbers in the early 1960s, while in other areas of the Bank they were much less important as a prey resource, suggesting that predators were relatively opportunistic. Engelhard et al. (2013) linked sandeel availability to the body condition of predatory fish, and found that plaice, whiting, haddock and grey gurnard body condition were all linked to higher sandeel abundances on the Dogger Bank. This suggests that these predators may benefit from sandeels where and whenever they are available in the environment without depending on them as a food source. In this study, we found that sandeels only comprised a relatively small proportion of haddock diet by number, whereas studies off Scotland revealed that they feed extensively on sandeels (Greenstreet et al. 1998; Temming et al. 2004), implying that the reliance of haddock on sandeels may differ widely between areas of the North Sea.

Sandeels made up a considerable proportion of whiting diet (>20 cm) by mass from the 1970s onwards, however euphausids dominated their diet in the 1980s, while shrimps were also consumed in high abundances in the 1990s. Whiting is typically a highly selective feeder from ~ca. 25 cm on, when it is very largely piscivorous (Hislop et al. 1991). Additionally, whiting tends to rely on a few fish species as prey, such as Norway pout (*Trisopterus esmarkii*), *Ammodytes* sp. sandeels, herring, and sprat (Knijn et al. 1993; Temming et al. 2004; Lauerburg et al. 2018). Thus, changes in the availability of such important prey to whiting are likely to influence their growth rates, as demonstrated at a local scale (Engelhard et al. 2013) and in the wider North Sea (Lauerberg et al. 2018). On the other hand, haddock are considered highly opportunistic predators, and tend to consume benthic invertebrates regardless of their availability (Engelhard et al. 2008; Schückel et al. 2010; Smith et al. 2013). In our study, haddock fed almost exclusively on invertebrates, predominantly bivalves, in the early 20th century, but sandeels became more important in contemporary decades, albeit consumed to a lesser extent. In other areas, haddock have been found to consume extensively sandeels (Greenstreet et al. 1998; Temming et al. 2004). In trawl-disturbed areas with fewer epi-benthic species available, Smith et al. (2013) found that haddock consumed more sandeels, implying that haddock readily adapt their diet based on prey availability due to benthic disturbance. Hence, that the reliance of demersal predators on particular prey types varies widely in the North Sea, however it seems to compensate for the lack of key prey resources without experiencing a significant decline as a consequence (Rijnsdorp and Millner, 1996), clearly demonstrating their potential flexibility in the face of changes to their prey base.

Euphausiids, a prominent prey of cod in the 1970s and 1980s, were consumed in low numbers in all other decades. Similar findings have been observed in other regions such as the Gulf of Lawrence, whereby euphausiids were prominent prey in cod from 1959 to 1987 but disappeared from the diet in the 1990s to 2000s (Hanson and Chouinard, 2002). Elsewhere, when euphausiids are present in the ecosystem, they comprise an important component of cod diet (e.g., Powles, 1958; Greenstreet, 1995). Cod, however, are generalist predators and are able to change their diet to include prey that are most abundant in the immediate environment (Hanson and Chouinard, 2002). Hence, the reduced importance of these prey can be offset by consuming other prey. Moreover, the loss of certain prey types such as euphausiids in cod diet in the more recent decades may represent a loss of high nutritional value or increased availability of more easily caught foods (e.g., sandeels); euphausids can contain 50-70% lipid dry mass (Falk-Petersen et al. 2000). Thus, this may have a negative effect on cod growth if their energy intake cannot be compensated for by decreased foraging costs from alternate prey.

4.3.3. *Anthropogenic influences on predator diet*

It is often difficult to elucidate effects of trawling from other factors in the North Sea such as eutrophication or climate change; all impacts increased in the latter part of the 20th century (Callaway et al. 2007). The drastic long-term changes in diet observed in this study could be attributed to the marked changes observed in the availability of certain prey types (and documented by authors such as Kröncke, 2011) over the last 120 years, predominantly as a result of expanding trawling pressure but also anthropogenic processes such as eutrophication and climate change. However, evidence from our study suggests that trawling, i.e., the long-term abrasion and removal of slow-growing organisms, is the most probable cause for changes in fish diet because of (1) timings of changes in benthic communities and (2) the nature of the species subject to declining importance in predator diet.

Generally, bottom trawling may affect prey availability either negatively or positively depending on the preferred diet of the particular fish and cumulative effects of trawling (Hiddink et al. 2016). The biomass of benthic invertebrates, particularly large invertebrates, tend to decrease strongly with increased trawling (Jennings et al. 2002), thus reducing the total amount of prey available to many benthivorous fish species. In this study, the reduced presence of bivalves in predator diet coincides with a dramatic increase in beam trawl effort for flatfish species in the central and southern North Sea, particularly since the 1960s, with the advent of heavy twin beam-trawlers (De Veen, 1976; Rijnsdorp and Van Beek, 1991; Millner & Whiting, 1996; Engelhard, 2008). By contrast, beam trawling causes a proliferation of short-lived prey such as many polychaetes, because they tend to suffer low mortality and have high intrinsic rates of population increase (Brey, 1988). Their abundances are therefore promoted in fishing areas as they are relatively resilient to fishing and may escape the direct impact of trawl gear (Bergman and Hup, 1992; Kaiser et al. 2000).

In the North Sea, observed increases in overall benthic biomass, particularly in the abundance of the type of prey selected by plaice and sole, have been correlated with increases in their growth rates in the past half-century (Rijnsdorp and Van Beek, 1991). Coupled with fishing, increased growth rates in these species have also been attributed to enhanced primary production since the 1960s, which, together, may have had synergistic effects on demersal fishes and their prey. The widespread use of fertilisers in the North Sea has led to increased nutrient loading in the run-off of major European rivers from the 1950s to the 1980s (Capuzzo et al. 2015). In coastal areas where eutrophication is more pronounced, some demersal feeders may have benefited from secondary production as a result of enhanced food availability (Powers et al. 2005). Consumers of small macrofaunal invertebrates may thus be exposed to higher densities of prey following hypoxic events because of colonisation by numerous small opportunists (Pihl, 1994; Peterson et al. 2000). By contrast, declines in favourable prey species due to low oxygen may have serious population consequences for some predators via reductions in the nutritional value of particular prey items. In the Kattegat, Pihl (1994) documented reduced consumption of epibenthic crustaceans, which are sensitive to low oxygen levels, and increases in echinoderms, particularly in abundances of *Amphiura filiformis*, in dab and long rough dab (*Hippoglossoides platessoides*) diets during hypoxia in the 1980s. The energetic value of echinoderms is approximately half of that of crustaceans and bivalves per unit biomass (Brey et al. 1988). If these predators cannot compensate for the reduction in energy intake with an increased consumption, their growth may be negatively impacted.

In addition to fishing and eutrophication, benthic communities in the North Sea have been influenced by progressive climate driven changes since the beginning of the 20th century. Generally, climatic changes are expected to substantially affect the distribution of benthic communities. Planktonic larvae are likely to be influenced by temperature changes (Beaugrand, 2004), and in the late 1970s and 1980s, there may have been an ecosystem regime shift in the North Sea, which caused changes in plankton and benthic communities as well as in fish stocks (Reid et al. 2001; Weijerman et al. 2005). Increased temperatures tend to result in increased benthic biomass and declines in other species (Neumann et al. 2009; Collie et al. 2017), which will ultimately influence the prey available for demersal predators. Overall, although we consider that sustained high trawling effort has significantly affected the diet composition of demersal fish predators over the past 120 years the most, eutrophication and climate change may have influenced the benthic system in the western North Sea to a lesser extent.

4.4. Conclusion

Assessing food habits in fishes, particularly in opportunistic feeders, can give insight into prey species distributions that are otherwise difficult to survey (Link, 2004; Cook and Bundy, 2012). This study adds further evidence of significant long-term trends in the diet of several key predatory fish species, but also provides a general assessment of changes to their benthic prey base in the western North Sea, and has identified important temporal links between prey resources and their predators. This is supported by other studies that have used fish stomach content data as trackers of prey abundance (Link, 2004; Mills et al. 2007; Buchheister and Latour, 2016) and indicators of change in the marine environment (Dwyer et al. 2010). Such links are seldom considered in management decisions; however, the complexity and interconnectivity of benthic food webs are now becoming better appreciated in sustainable fisheries management, and descriptors of healthy food webs (D4) and sea floor integrity (D6) are an important consideration to achieve ‘Good Environmental Status’ under EU Marine Strategy Framework Directive (MSFD; European Commission, 2020). This emphasises the need for ecosystem-level management that will improve the resilience and long-term viability of demersal fish species and their prey resources on continental shelves.

Chapter 5: Inter- and Intra-specific Variation in the Diet of Two Sympatric Flatfish Species

5.1. Introduction

Coastal environments are essential habitats for many fish species at different stages in their life history, from nursery areas for juveniles to sustaining adult populations (Costanza et al. 1997). Trophic interactions among fish species are a key regulator of population dynamics and ecosystem functioning in these areas (Gibson, 1994; Peterson et al. 2000), which are driven by resource availability, physical traits and prey preferences of the predator species (Scharf et al. 2000). Ecologically similar species that occupy the same habitat at the same time are expected to partition their food resources to reduce inter- and intra-specific competition and facilitate co-existence (Schoener 1974), including among sympatric fishes that inhabit highly productive coastal systems (Russo et al. 2008).

Diet variation is often linked to ontogeny or body size (Werner and Gilliam, 1984), which itself can be linked to factors such as gape size (Scharf et al. 2000). However, it is becoming increasingly apparent that individuals within a population of a given age and size can differ considerably in their resource use (Araújo et al. 2011; Ingram et al. 2018). At the population-level, highly mobile dietary generalists may couple spatially distinct food chains as they feed on a diverse suite of prey taxa (Quevedo et al. 2009; Araújo et al. 2011), which can enhance food web stability and alter energy flows (McCann et al. 2005). However, individual-level trophic specialisation may arise when resources are scare and/or when inter- and intra-specific competition is high at differing spatial and temporal scales (Araújo et al. 2011), maintaining separation of trophic pathways from discrete food webs (Matich et al. 2011). The role of predatory species in food web connectivity has largely focused on treating populations as homogenous units (Quevedo et al. 2009), often disregarding the potential effects of intra-specific variations in resource use in population-level assessments. This may be misleading because dietary specialisation has been reported in a wide range of taxa, including predatory fish (Bolnick et al. 2003; Hammerschlag-Peyer and Layman, 2010).

The study of trophic niches represents a valuable tool for describing trophic pathways and elucidating foraging behaviours of predators in coastal regions (Kostecki et al. 2012; Cicala et al. 2019). Dietary studies have typically used stomach content analyses to quantify trophic interactions in closely-related species (e.g., Carter et al. 1991; Amara et al. 2001; Vinagre et al. 2011), providing a high degree of taxonomic resolution in their dietary habits. However, stomach data reflect temporally limited snapshots of a predator's diet only up to a few hours before capture, and therefore reflect recent encounters rather than long-term resource use if prey are patchily distributed, abundances vary in space and time, or contain only a few items at one time (Araújo et al. 2007), then stomach data can incorporate heavy bias when inferring diet. By comparison, bulk stable isotope analyses are not subject to the same sampling biases as stomach data, and provide greater temporal consistency due to their slow turnover, albeit at the cost of reduced dietary resolution (Araújo et al. 2011). Carbon ($\delta^{13}C$) stable isotope ratios is a useful indicator of source production in food webs (DeNiro and Epstein, 1978; Pinnegar and Polunin, 1999), while nitrogen ($\delta^{15}N$) provides an indication of trophic position (Connolly et al. 2004). By comparison, sulphur isotopes ($\delta^{34}S$) are less widely used in dietary studies (Barnes and Jennings, 2007), but are increasingly being used as a third element to discriminate between potential food sources that may not separate by $\delta^{13}C$ and $\delta^{15}N$ (Connolly et al. 2004). Sulphur also has the advantage that there appears to be little to no diet-tissue fractionation in $\delta^{34}S$ in fish (0-1 ‰, Peterson and Fry, 1987; Barnes & Jennings 2007) as errors in assumptions about fractionation from prey to consumer will be smaller than $\delta^{13}C$, which has a diet-tissue fractionation of 1-2 ‰ (Sweeting et al. 2007).

Different animal tissues can assimilate dietary isotope signatures over a scale of weeks to months (e.g., liver 10-20 days, white muscle 49-107 days; Buchheister and Latour, 2010), thereby offering inferences into resource use at medium and longer-term time scales. Consequently, predators that consistently forage on the same resource over time (i.e., are more specialist) should have similar isotope values in different tissues despite the stochastic nature of feeding events, whereas species that change resources overtime (e.g. seasonally) will show disparity between fast and slow tissues (Martinez del Rio et al. 2009; Araújo et al. 2011). Fast tissues such as liver can thus help to clarify recent variations in predator diet between sites at a regional scale (Gaston and Suthers, 2004), especially for migratory species that exhibit high spatiotemporal heterogeneity in their resource use (Buccheister and Latour, 2010). However, the lack of resolution provided by slow tissues (e.g., muscle) will compound dietary variability from seasonal and regional movements as dietary habits will be reflected over several months (Buccheister and Latour, 2010). Nonetheless, muscle isotope signatures can be used to infer more temporal consistency in predator resource use (Araújo et al. 2007; Carter et al. 2019).

Despite its potential importance for population stability and ultimately management (Bolnick et al. 2003), there is often little appreciation of dietary variation and specialisation among co-occurring fish predators (Knickle and Rose, 2014), especially in coastal environments. This is despite the fact that coastal systems support a high density of ecologically-similar flatfishes (Amara et al. 2001; Vinagre et al. 2011), including European plaice *Pleuronectes platessa* and dab *Limanda limanda*, and are thus likely to compete for shared resources where they co-exist (Schoener, 1974). Although considered dietary generalists, dab are believed to opportunistically forage on a wider range of prey on the seabed (e.g., ophiuroids, crustaceans) (Hinz et al. 2005) compared to plaice, which predominantly target infaunal prey such as bivalves and polychaetes (Basimi and Grove, 1985; Rijnsdorp and Vingerhoed, 2001). Despite these differences, plaice and dab are likely to optimise their feeding strategies and compete for the same resources where they co-exist in times when focal resources are not accessible (Pinnegar et al. 2003). Greater understanding of inter- and intra-specific variation in predator resource use could thus help predict how species will respond to fluctuations in prey availability as coastal environments change (Gulka et al. 2017).

To date, most studies have either focused on a single species or on several species of interest but sampled from a single locality (e.g., Svanbäck et al. 2008; Knickle et al 2014; Cobain et al. 2019). Such approaches neglect either the importance of inter-and intra-specific competition in shaping individual trophic behaviour, or are limited in their generality due to sampling at a single location. In this study, stable isotope analysis and contemporary stomach content analyses were used to investigate spatial and temporal variation in the diet of two sympatric flatfish across multiple sites on the Northumberland coast, UK. Specifically, the objectives of the study were to a) examine inter-specific dietary variation in dab and plaice between and within four coastal sites, b) compare intra-specific diet variation among individuals using multiple measures across short, medium, and long-term time scales, and c) investigate the strength of inter-and intra-specific nice overlap in dietary resources. Stable isotope analysis of fast and slow tissues determining $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$, paired with stomach content data, has rarely ever been used together to study resource portioning in sympatric predators. These methods combined offer an unprecedented opportunity to provide a more complete representation of their dietary patterns and how they may respond to localised environmental change.

5.2. Methods

5.2.1. *Study site and sampling*

The study took place in four bays (<20 m) on the Northumberland Coast (UK); Alnmouth Bay, Druridge Bay, Blyth Bay and Cambois Bay (Fig 5.1). These shallow bays primarily comprise sandy substrate and are fringed by adjacent rocky reefs (Frid et al. 1991), with relatively limited freshwater input and estuarine influence (Bennett and Foster-Smith, 1998). However, the Rivers Aln and Coquet flow in to the north and south of Alnmouth Bay, respectively, and River Blyth into Blyth Bay and River Wansbeck into Cambois Bay (Fig 5.1). These bays have long been considered essential habitats for juvenile and adult of fish species including plaice, dab and flounder *Platichthys flesus* (Meek, 1895; Davis and Dunn, 1982; Walker, 1984) as well as other commercially important species such as European lobster (*Homarus gammarus*) (Chapter 2).

Sampling was conducted over a four month period between May and September 2019 during the daytime using an otter trawl (75 mm tight mesh, 26.7 m net spread) on board Newcastle University's research vessel *The Princess Royal*. A total of 47 trawls were carried out at approximately 2.5 knots for one hour. For each haul, catches were sorted, identified to species level, counted and the total length (cm) of all fish measured. All plaice and dab were retained for dietary analysis and immediately frozen on board at -20°C to prevent further decomposition of their gut contents. For stable isotope analysis, common prey types of plaice and dab (e.g., bivalves, polychaetes, ophiuroids) were also collected using a Van Veen grab to supplement samples retained from predator stomachs. Three repeat grabs were conducted per site and during each sampling day. Key prey groups were identified, sorted and immediately frozen on board until further analysis.

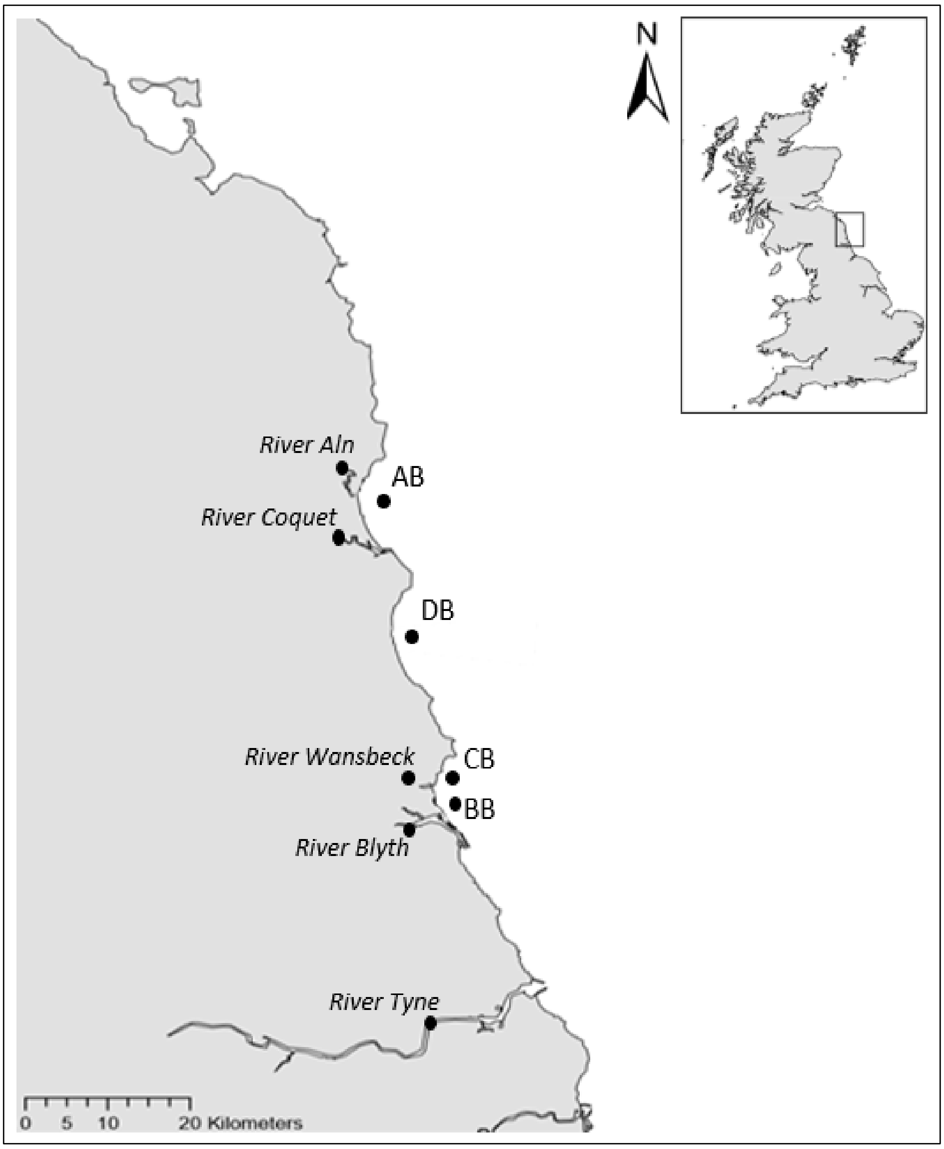


Figure 5.1. Location of sampling areas on the Northumberland coast (AB, Alnmouth Bay; BB, Blyth Bay; CB, Cambois Bay; BB, Blyth Bay.

5.2.2. *Stomach content analysis*

5.2.2.1. Sample preparation

In the laboratory, individual plaice and dab were defrosted, total length (cm) re-measured, and stomachs excised and weighed before and after prey items were removed. For each stomach, prey items were identified to species level where possible and sorted into relatively broad categories under a binocular microscope. For each prey category, items were counted, and volume estimated (mm^3) using methods described by Hellawell and Abel (1971). Intact and non-digested prey were rinsed thoroughly with Milli-Q water and subsequently refrozen for stable isotope analysis.

Stomach contents of 308 plaice and 595 dab collected between May and September were pooled for dietary analyses (Table 5.1). The vast majority of stomachs were sampled in the earlier part of the season between May – July (n = 731), whereas fewer were obtained between August – September (n = 172). We initially explored potential size-based differences in diet using two size classes for each flatfish species: 15-24 cm and 25-41 cm. For each predator, multivariate analyses of similarities (ANOSIMs) indicated that there were no statistically significant differences in diet composition between the two size classes at each site ($P > 0.05$), therefore all stomachs were pooled and analysed across their entre size range at each site.

Table 5.1. Summary of the total number of flatfish stomachs (NS) and size ranges (total length, cm) pooled for stomach content analysis between May and September.

Site	Plaice		Dab	
	Size range (cm)	N_S	Size range (cm)	N_S
Alnmouth Bay	18-36	14	17-30	141
Druridge Bay	15-41	47	16-31	191
Cambois Bay	17-39	138	18-38	140
Blyth Bay	16-39	109	16-33	123

5.2.2.2. Dietary analyses

Two dietary indices were used to express the relative importance of prey taxa in plaice and dab diet at each site. We applied the index of relative importance I_{RI} (Pineas et al. 1971), which balances the proportional frequency of occurrence for each prey category p_N, proportional frequency p_F and proportional volume p_V:

$$I_{RI} = p_F \times (p_N + p_V)$$

$$I_{MF} = \sqrt{\left(\frac{p_V \times (p_N + p_F)}{2}\right)}$$

We also applied the main food index, I_{MF}, originally described by Zander (1982), however wet volume was used instead of dry weight (Cobain et al. 2019). Values for each prey group of both indices were normalised to their total for comparisons between sites and predators. To compare dietary overlap between the two predators, Schoener’s proportional similarity index PS, was used (Schoener, 1968):

$$PS_{ij} = 1 - \frac{1}{2}\sum_{k}\left|p_{ik} - p_{jk}\right|$$

where p_{ik} and p_{jk} represents the proportion of prey category k consumed by predators i and j, respectively. This index ranges from 0, when no food is shared, to 1, when there is exactly the same proportional use of prey resources. Dietary overlap is typically considered biologically significant when values are greater than 0.6 (Wallace and Ramsey, 1983). The number of empty stomachs was counted, and the vacuity index, I_V, was calculated as the proportion of empty stomachs for each predator by site. One-way ANOSIMs were used to statistically test for differences between predator diets at each site.

To estimate levels of individual specialisation, taken as the average pair-wise dietary overlap among individuals of the same species and within sites, we calculated the E index, following Araújo et al. (2008):

$$E = 1 - \frac{\sum_{pairs} PS_{ij}}{n(n-1)}$$

where, E ranges from 0, when all individuals consume the same resources in similar proportions, to 1, when all individuals are specialising on completely different resources (Araújo et al. 2008). A smaller number of prey items per individual may artificially inflate estimates of individual specialisation. However, this can be tested using Monte Carlo resampling methods, allowing testing of whether the observed diet variation exceeds the mean null value based on stochastic sampling of the population mean diet (Bolnick et al. 2002; Araújo et al. 2008). The observed E index was therefore adjusted to account for this bias (Zaccarelli et al. 2013):

$$E_{adj} = 1 - \frac{\sum E_{obs}\, E_{null}}{1 - E_{null}}$$

Dietary analyses were conducted in RStudio version 1.3.1093 (R Core Team, 2020). Individual specialisation metrics were performed using the package “RInSp” v1.2 (Zaccarelli et al. 2013).

5.2.3. *Stable isotope analysis*

5.2.3.1. Sample preparation

For stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$), individual plaice and dab representative of their size distribution were pseudo-randomly selected from the total catch in July. Individual fish were selected during this month based on sufficient availability of samples across sites. To examine potential variation in predator diet among different months, individual plaice were also pseudo-randomly chosen from in May, July, August and September from Cambois Bay (based on sufficient availability of samples across the season). Based on their representative size distribution, dab between 19 – 30 cm and plaice between 19 – 41 total length were processed to minimise possible ontogenetic changes in diet (Table 5.4). Length at first maturity for female and male plaice is about 34 cm and 22 cm, respectively (Rijnsdorp et al. 1989), whereas female and male dab tend to mature at smaller sizes at 14 cm and 11 cm, respectively (Rijnsdorp et al. 1992). Separate samples of dorsal muscle and liver tissue (~1 cm^3) were excised from each fish, rinsed in Milli-Q water to wash away excess skin and blood, stored in Eppendorf tubes and immediately refrozen.

For intact benthic prey (either extracted from predator stomachs or sediment grabs), plugs of soft muscle tissue were taken from the abdomen of squid and shrimps, claw and thorax samples from crabs, adductor and foot samples from bivalves, fillets of white musculature from sandeels, and whole polychaetes, were used for stable isotope analysis. All prey samples were rinsed thoroughly with Milli-Q water to remove excess digestive material and to prevent contamination by sediment carbonates (Kharlamenko et al. 2001) before being refrozen in Eppendorf tubes. All fish and prey tissues were freeze-dried for 48h and ground to a homogenous powder. For smaller prey, some samples were pooled across multiple individuals (e.g. bivalves and ophiuroids) collected from the same site and month, and homogenised together to obtain enough material for analysis. Ophiuroids were treated with 1 M of hydrochloric acid to remove any traces of inorganic carbonates, rinsed with distilled water, and freeze-dried for another 24h.

Approximately 2.5 mg of homogenised fish white dorsal muscle and liver tissue and benthic prey were weighed into 3 x 5 mm tin capsules and analysed for C/N/S stable isotopes using a PyroCube elemental analyser (Elementar) coupled to an Elementar VisION Mass Spectrometer at the NERC Life Sciences Mass Spectrometry Facility, East Kilbride, UK. Stable isotope ratios are reported using the delta (δ) notation with measured values given in parts per mil (‰), expressed by:

$$\delta = \left[\frac{R_{sample}}{R_{standard}} - 1\right] \times 1000$$

where *R* is the ratio of heavy to light isotope (e.g. ^{15}N:^{14}N). All isotope values are reported relative to their respective international standards (Vienna Pee Dee Belemnite for carbon, atmospheric air for nitrogen, and Vienna Cãnon Diablo Troilite for sulphur). Multiple internal standards were analysed at the start and end of each C/N/S run for calibration and to correct for accuracy and drift. For international standard USGS40 (glutamic acid), analytical precision (sd) for δ^{13}C and δ^{15}N was 0.04 and 0.12, respectively, and for IAEA-S1, IAEA-S2 and IAEA-S3, it was 0.33, 0.38 and 0.82 for δ34S, respectively. For internal standards, analytical precision (sd) of materials MSAG2 (methanesulfonamide, gelatin and water solution), M2 (methionine, glycine, gelatin, ^{15}N-alanine, and water), and ANR (dorsal muscle of *Antimora rostrata*) was 0.18, 0.19, 0.09 for δ^{15}N, 0.06, 0.08, and 0.03 for δ^{13}C, and 1.12, 0.46, and 0.26 for δ^{34}S, respectively. Internal reference materials were run between every ten samples.

5.2.3.2. Lipid correction

High-lipid tissues can potentially skew carbon isotope data interpretations as some tissues may be enriched or depleted in ^{13}C relative to diet (Pinnegar and Polunin, 1999; Sweeting et al. 2006; Post et al. 2007). C:N ratios are used as a proxy measurement for lipids in sample tissues (Post et al. 2007), with values of >3.5 assumed to have enriched lipid concentrations enough to deplete δ^{13}C values. Therefore, δ^{13}C values of predator liver tissues (>3.5) were mathematically corrected using the Kiljunen-Post model from Skinner et al. (2016):

$$L = -20.54 + 7.24 \times C{:}N$$

$$\delta^{13}\mathrm{C}' = \delta^{13}\mathrm{C}' + D \times \left(\mathrm{I} + \frac{3.90}{1 + 2.87/L}\right)$$

where, *L* is the percent of lipid (Post et al. 2007), δ^{13}C’ is the lipid-free δ value (Kiljunen et al. 2006); *D* is 7.018, differences in δ^{13}C between protein and lipid; and I is the constant 0.048. All dorsal muscles values had C:N ratios <3.5 and therefore mathematical correction was deemed unnecessary.

5.2.3.3. Ellipsoid metrics

All statistical analyses were conducted in RStudio version 1.3.1093 (R Core Team, 2020). The "SIBER" package in R (Jackson et al. 2011) has been widely used to analyse bivariate stable isotope data. This was applied to a three-dimensional case following extensions described by Skinner et al. (2019) in order to calculate ellipsoid volumes and niche overlap of liver and muscle trivariate isotope data. Firstly, Bayesian estimates were calculated based on sample means and covariance matrices assuming a three-dimensional multivariate normal distribution (three chains of 15,000 iterations with a burn in of 1000 and thinned by a factor of 25) using the R package RJAGS (Plummer, 2018). Secondly, ellipsoid volumes were calculated from each posterior draw, fitted to 75% of the data, providing a posterior distribution of ellipsoid volumes (EV_B). EV_B estimates were determined for each predator and tissue type by site and expressed as the median volume with interquartile range of the posterior (25-75%). Additionally, Bayesian posterior means and standard deviations were estimated for plaice liver and muscle to statistically examine monthly variations in diet at Cambois Bay.

Finally, a Bayesian approach was applied to estimate the degree of niche overlap between predators based on functions described by Skinner et al. (2019) using R packages "rgl" (Adler et al. 2018) and "geometry" (Habel et al. 2019), which numerically estimate the overlap as the volume of the intersection between three-dimensional meshes that approximate predator niches. Posterior overlaps between predators at each site were calculated from 7,500 iterations with a burn in of 5,000 and a mesh subdivision value of 4. The degree of overlap was given as median percentage with 95% credible intervals to show the uncertainty in the overlap estimates between predators at each site. A median percentage overlap of 0% between two ellipsoids indicates completely distinct niches whereas a 100% indicates entirely overlapping ellipsoids. We considered a median overlap to be significant when two overlapping niches were ≥60%, the same criteria applied in Schoener's PS index (Schoener, 1968).

5.2.3.4. Isotope mixing models

To elucidate the main source contributions to predator diet by site, Bayesian stable isotope mixing models were run using the MixSIAR package in R (Stock and Semmens, 2017) Mixing models using $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ data were run separately for each predator and tissue type with site and individuals nested within site as random effects. Models were also run with two error terms (residual * process), where the residual error accounts for potential unexplained variation among predators (e.g., metabolic rate, digestibility) and the process error refers to variation from sampling predator isotope distributions (see Stock and Semmens, 2016). Model convergence was evaluated using the Gelman-Rubin diagnostic tests. The initial model using all three isotopes for dab liver did not converge as consumer δ^{13}C values were outside the source mixing polygon. A second model using only δ^{15}N and δ^{34}S was then run on dab liver, and when plotted, consumer data were inside the source mixing polygon.

Benthic prey extracted from predator stomachs and grabs between May – July were only used in the mixing models to ensure temporal consistency with predator isotope data collected in July. Mixing models can yield biased results if there are too many source contribution estimates (Ward et al. 2011). A standard method of reducing the number of sources is to a) logically combine a priori if source values are isotopically and biologically similar (e.g., trophic guild), or b) if source isotope values are isotopically distinct and proportional contributions are aggregated a posteriori (Phillips et al. 2005). However, source isotope values may be statistically distinct but still exhibit similar isotope signatures. Mean isotope values and standard deviations were calculated for prey taxa to represent different sources contributions in the mixing models. Stable isotope values of crabs, shrimps and polychaetes for all sites were compared using and ANOVAs and Kruskal-Wallis tests, which revealed no significant differences for δ^{13}C (ANOVA, $F = 1.7$, $P > 0.05$), but significant differences were detected for δ^{15}N (Kruskal-Wallis, $\chi^2 = 28.8$, $P < 0.001$) and δ^{34}S (ANOVA, $F = 14.5$, $P < 0.001$). Despite these differences, crabs, shrimps and polychaetes were pooled ainto one source group (‘benthic omnivores’) because differences in their means values were small (~1 ‰). Other prey taxa (bivalves, sandeels, squid, and ophiuroids) were treated as separate source groups in mixing models.

Trophic discrimination factors (TDF, Δ), the difference between the isotope signatures of consumers and their average diet, for δ^{13}C and δ^{15}N, were selected based on fish dorsal muscle and liver tissue reviews from Caut et al. (2009). We applied TDFs that accounted for potential variability such as diet quality, a predator’s nutritional status, lipid correction, size and tissue type rather than using fixed TDFs (e.g., Post, 2002). In this way, TDF values for dorsal muscle tissue was dependent on mean prey values: $\Delta\delta^{13}$C = $-0.248 \times \delta^{13}C - 3.477$ and $\Delta\delta^{15}$N = $-0.281 \times \delta^{15}N + 5.879$. For liver tissue, the TDF was 0.77 for $\Delta\delta^{13}$C and 1.6 for $\Delta\delta^{15}$N (Caut et al. 2009). The $\Delta\delta^{34}$S for consumers is thought to be negligible (~0 ‰) despite the lack of published data (Peterson and Fry, 1987; Hobson, 2008). Barnes and Jennings (2007) revealed that $\Delta\delta^{34}S$ of European seabass *Dicentrarchus labrax*, relative to its diet, was -0.53 ‰. However, other laboratory feeding studies have documented a $\Delta\delta^{34}S$ of 1.4 ‰ in brook trout *Salvelinus fontinalis* (Peterson et al. 1985) and 1.5 ‰ in broad whitefish *Coregonus nasus* (Hesslein et al. 1993). We therefore applied a $\Delta\delta^{34}S$ of 0 ‰. For all TDFs, we applied a standard deviation of 1 to conservatively account for uncertainty and natural variability in individual TDFs. Mixing models were run with 3 chains for 1,000,000 iterations, with a burnin of 500,000, and a thinning factor of 500.

5.3. Results

5.3.1. *Stomach content data*

There was broad agreement between I_{RI} and I_{MF} values (Table 5.2). According to both indices, sandeels (*Ammodytes tobianus*) were a highly important prey resource to both plaice and dab across all bays between May and September. At Alnmouth Bay, sandeels were highly prevalent in plaice diet (I_{RI} = 0.98) unlike in dab (I_{RI} = 0.43), where ophiuroids (I_{RI} = 0.18; *Ophiura ophiura* and *Ophiura affinis*), crabs (I_{RI} = 0.18; mainly *Corystes cassivelaunus*) and shrimps (I_{RI} = 0.1; *Crangon crangon*) were also important prey. By comparison, bivalves (*Abra* sp. and *Ensis ensis*) were an important prey resource for both predators at Druridge Bay. Bivalves also contributed to plaice diet at Blyth and Cambois Bays, but were less important to dab diet at these sites. Crabs were rarely consumed by plaice across sites; however, they were relatively important to dab everywhere except at Blyth Bay. Other prey groups (most notably squid) made only minor contributions to plaice and dab diet (Table 5.2). Low levels of vacuity were also observed in plaice and dab stomachs across all four bays, with the highest proportion of empty stomachs occurring in plaice at Alnmouth Bay (38%; Table 5.2). There were no significant differences in diet composition based on proportion numerical abundances between predators at Blyth Bay (ANOSIM, R = 0.009, P = 0.141) and Druridge Bay (ANOSIM, R = -0.036, P = 0.882); however, there was a small significant difference between diets at Cambois Bay (ANOSIM, R = 0.021, P < 0.05).

There was generally a high degree of dietary overlap between plaice and dab across all four bays (Table 5.3); Blyth, Cambois and Druridge Bays had >60% overlap although Alnmouth Bay had a moderate similarity index of 0.4 (albeit with a much smaller sample size for plaice). The E_{adj} metric also detected significant levels of individual specialisation except for plaice at

Alnmouth Bay. Specialisation was relatively low within species across the bays, but slightly higher among individual plaice. Compared to the other bays, both predators were specialising most at Druridge Bay with minimal levels of specialisation among dab and plaice at Alnmouth Bay (Table 5.3).

Table 5.2. Index of Relative importance (I_{RI}) and Main Food Index (I_{MF}) in parentheses based on stomach contents of plaice and dab sampled between May and September. N is the number of stomachs sampled and I_v is the Vacuity Index. D_{ij} represents Schoener's Index of similarity between predators at each site. Values of 0.1 or greater (major prey components) are highlighted in bold.

	Dab				Plaice			
	Druridge Bay	Alnmouth Bay	Blyth Bay	Cambois Bay	Druridge Bay	Alnmouth Bay	Blyth Bay	Cambois Bay
N	191	141	123	140	47	14	109	138
I_v	0.26	0.14	0.19	0.26	0.31	0.38	0.15	0.18
Prey	I_{RI} (I_{MF})							
Algae	<0.01(0.02)	<0.01(0.01)	<0.01(0.01)	<0.01(0.01)	0(0)	0(0)	0(0)	<0.01(<0.01)
Amphipods	<0.01(<0.01)	<0.01(0.02)	0(0)	<0.01(<0.01)	<0.01(0.02)	0(0)	<0.01(0.02)	<0.01(<0.01)
Bivalves	**0.11(0.12)**	0.05(0.07)	0.03(0.09)	0.01(0.05)	**0.26(0.26)**	0.01(0.03)	0.07**(0.12)**	0.08**(0.16)**
Brittle stars	0.06(0.08)	**0.18(0.15)**	0.02(0.06)	0.05**(0.11)**	<0.01(0.02)	0(0)	<0.01(0.03)	<0.01(0.04)
Crabs	**0.15(0.17)**	**0.18(0.16)**	0.02(0.07)	0.04**(0.11)**	0.01(0.05)	0(0)	<0.01(0.02)	<0.01(0.02)
Cumacean	<0.01(<0.01)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	<0.01(<0.01)
Crustacean remains	<0.01(0.01)	0(0)	<0.01(0.02)	<0.01(<0.01)	0(0)	0(0)	0(0)	0(0)
Gastropod	<0.01(<0.01)	<0.01(0.01)	<0.01(0.01)	<0.01(<0.01)	<0.01(0.01)	0(0)	0.01(0.05)	<0.01(<0.01)
Nemertea	0(0)	0(0)	<0.01(<0.01)	0(0)	0(0)	0(0)	<0.01(0.02)	0(0)
Isopod	<0.01(<0.01)	0(0)	0(0)	<0.01(<0.01)	0(0)	0(0)	0(0)	0(0)
Mysids	0(0)	<0.01(0.01)	0(0)	<0.01(<0.01)	0(0)	0(0)	0(0)	0(0)
Other crustaceans	0(0)	<0.01(0.01)	0(0)	<0.01(<0.01)	0(0)	0(0)	0(0)	0(0)
Other echinoderms	0.01(0.03)	<0.01(0.01)	<0.01(0.02)	<0.01(<0.01)	<0.01(0.01)	0(0)	<0.01(0.01)	<0.01(0.02)
Other fish	<0.01(0.01)	<0.01(0.02)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
Peanut worms	<0.01(0.01)	0(0)	<0.01(0.01)	0(0)	0.02(0.06)	0(0)	0.03(0.09)	<0.01(0.01)
Polychaetes	<0.01(0.03)	0.03(0.06)	<0.01(0.01)	<0.01(0.02)	0.03(0.09)	0(0)	<0.01(0.02)	0.04**(0.12)**
Sandeels	**0.62(0.36)**	**0.43(0.24)**	**0.92(0.58)**	**0.87(0.54)**	**0.68(0.48)**	**0.98(0.89)**	**0.87(0.53)**	**0.87(0.62)**
Shrimps	0.02(0.06)	**0.1(0.13)**	0.01(0.06)	0.01(0.04)	0(0)	0.01(0.08)	0.01(0.06)	<0.01(0.01)
Squid	<0.01(0.01)	<0.01(0.01)	0(0)	<0.01(0.02)	0(0)	0(0)	0(0)	0(0)
Unidentified fish	<0.01(0.01)	<0.01(0.02)	0(0)	0(0)	0(0)	0(0)	0(0)	<0.01(<0.01)
Unidentified invertebrates	0.03(0.08)	0.01(0.04)	0.01(0.04)	0.01(0.05)	<0.01(0.01)	0(0)	0(0)	<0.01(<0.01)
Unidentified material	0(0)	<0.01(0.02)	0(0)	<0.01(0.03)	0(0)	0(0)	<0.01(0.03)	0(0)

Table 5.3. Dietary overlap and individual specialisation metrics based on plaice and dab stomach contents data between May and September. E_{adj} is the pair-wise individual dietary overlap adjusted based on the mean null value of Monte-Carlo resampling methods. D_{ij} represents Schoener's Index of similarity between predators at each site. Level of significance are indicated by asterisks (***$P < 0.001$, *$P < 0.05$).

	Plaice			Dab			
Site	Non-empty stomachs	E_{adj}	Stomachs with only one prey item	Non-empty stomachs	E_{adj}	Stomachs with only one prey item	D_{ij}
Alnmouth Bay	12	0.017	9	87	0.159*	56	0.4
Blyth Bay	88	0.282***	62	104	0.188***	74	0.82
Cambois Bay	101	0.217***	58	115	0.25***	70	0.74
Druridge Bay	35	0.303***	18	130	0.281***	75	0.62

5.3.2. *Stable isotope data*

5.3.2.1. Trophic niches

There was substantial differences in muscle and liver isotope values between predators and among sites (Table 5.4). For dab, δ^{13}C values ranged from -18.85 to -17.71 ‰ for muscle and -19.05 to -13.98 ‰ for liver tissue, δ^{15}N ranged from 12.25 to 14.58 ‰ for muscle and 11.28 and 13.65 ‰ for liver, and δ^{34}S from 14.71 to 20.56 ‰ for muscle and 15.24 and 19.90 ‰ for liver. For plaice, δ^{13}C values ranged from -18.83 to -16.84 ‰ for muscle and -19.35 to -12.16 ‰ for liver tissue, δ^{15}N ranged from 11.71 to 13.93 ‰ for muscle and 10.85 and 13.63 ‰ for liver, and δ^{34}S from 13.88 to 20.67 ‰ for muscle and 15.35 to 20.55 ‰ for liver.

For liver, dab exhibited greater variance in isotopic space compared to plaice, with considerably larger trophic niches (Fig 5.2). In three-dimensional space, the 75% median niche volumes of dab liver were almost twice and three times larger than that of plaice at Cambois (Fig. 5.2h; 20.63 and 12.51, respectively) and Druridge Bays (Fig 5.2l; 8.23 and 2.75, respectively), respectively. There were cases of complete niche separation between predators based on the liver data, but the muscle data indicate considerable niche overlap across sites (Fig 5.3). Plaice exhibited greater variance in isotopic space based on muscle data, and had considerably larger niches (Fig 5.3). The median niche volumes of plaice muscle were twice as large as the niches of dab at Blyth (Fig 5.3d; 7.30 and 3.76, respectively) and Cambois

Bays (Fig 5.3h; 7.55 and 3.58, respectively). Trophic niches represented by 75% ellipsoid volumes in three-dimensional space are shown in Figs A.4 and A.5 (Appendix 3).

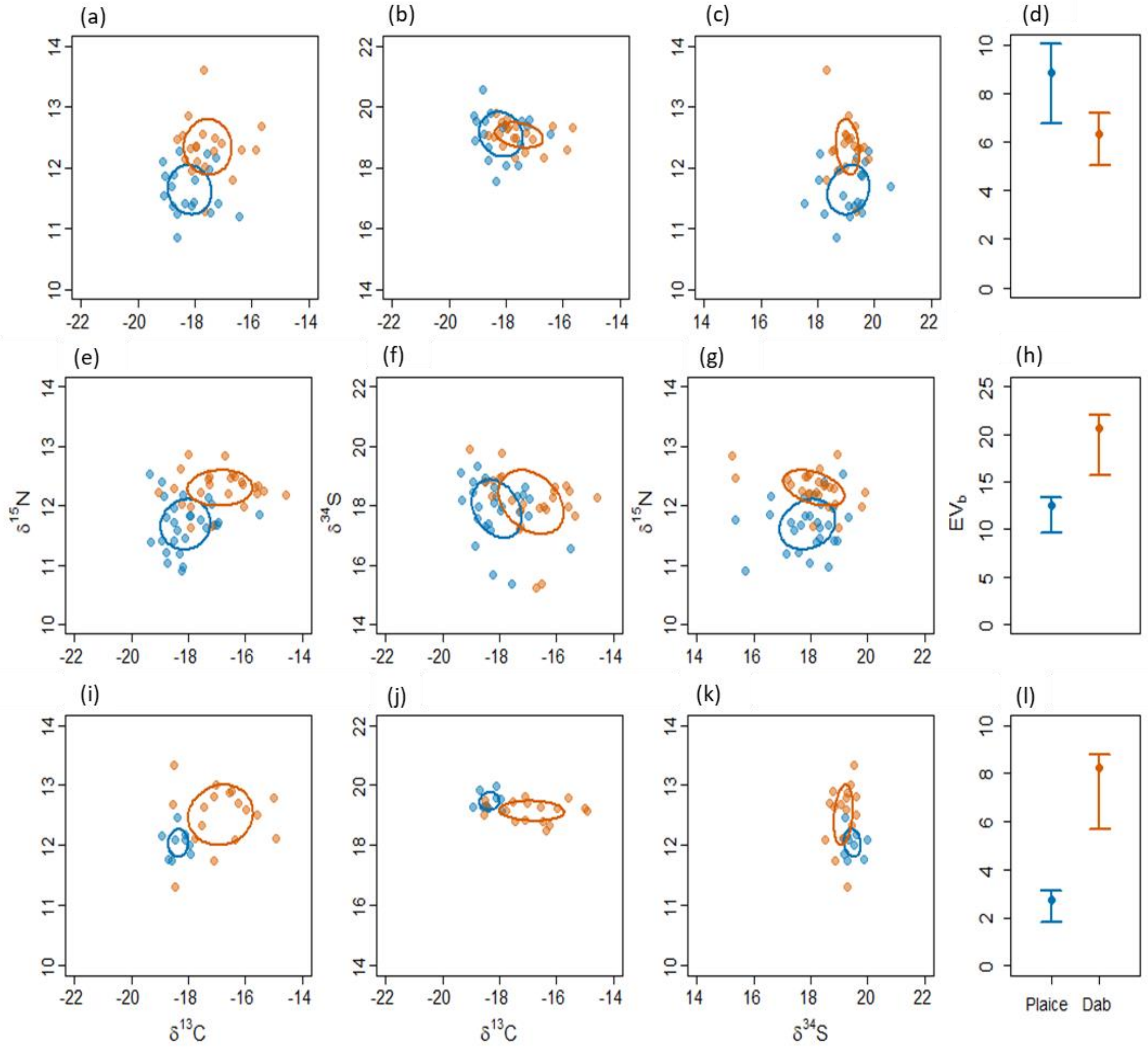


Figure 5.2. Trophic niches of plaice (blue) and dab (orange) represented by Standard Ellipse Areas (SEAs) and Bayesian 75% ellipsoid volume (EV$_b$) estimates of liver δ^{13}C, δ^{15}N and δ^{34}S data at (a-d) Blyth Bay, Cambois Bay (e-h) and Druridge Bay (i-l). SEAs represent 40% of the data. EV$_b$ estimates are presented as the median with interquartile range (IQR, 25th and 75th percentile).

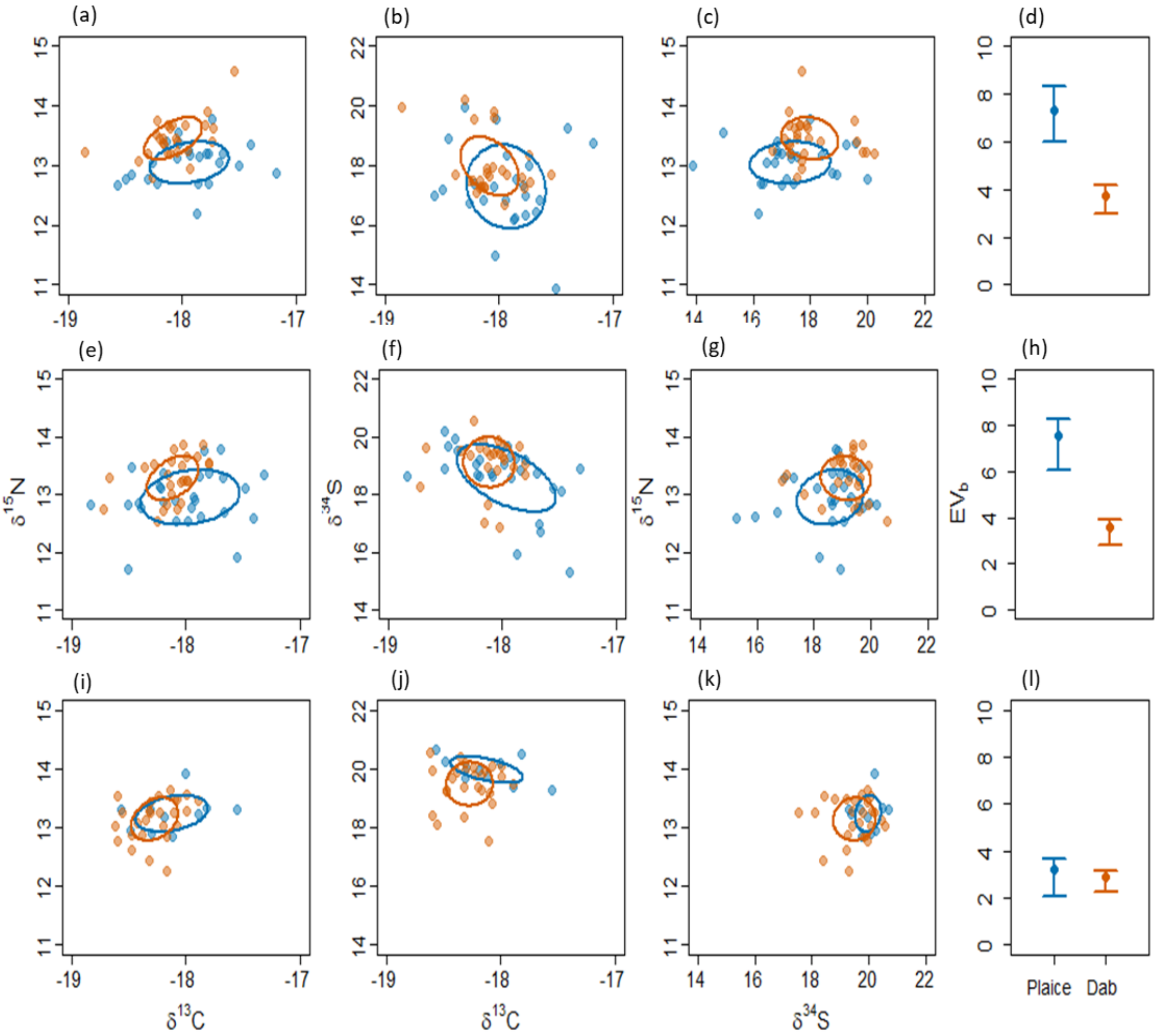


Figure 5.3. Trophic niches of plaice (blue) and dab (orange) represented by Standard Ellipse Areas (SEAs) and Bayesian 75% ellipsoid volume (EV_b) estimates of muscle $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ data at (a-d) Blyth Bay, Cambois Bay (e-h) and Druridge Bay (i-l). SEAs represent 40% of the data. EV_b estimates are presented as the median with interquartile range (IQR, 25th and 75th percentile).

Table 5.4. Mean $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ (‰) values (± standard error) of plaice and dab sampled in July by site for muscle and liver tissue.

Species	Site	Size range (cm)	Muscle				Liver			
			n	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$	*n*	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$
Plaice	Alnmouth Bay	-	-	-	-	-	-	-	-	-
	Druridge Bay	19-41	10	-18.13 ± 0.10	13.24 ± 0.10	19.97 ± 0.14	9	-18.35 ± 0.12	12.04 ± 0.08	19.47 ± 0.10
	Blyth Bay	19-33	25	-17.94 ± 0.07	13.05 ± 0.07	17.29 ± 0.28	19	-18.18 ± 0.17	11.63 ± 0.09	19.09 ± 0.17
	Cambois Bay	19-33	28	-17.96 ± 0.08	12.95 ± 0.09	18.56 ± 0.22	27	-18.10 ± 0.17	11.68 ± 0.08	17.89 ± 0.19
Dab	Alnmouth Bay	19-28	25	-17.78 ± 0.30	13.63 ± 0.04	19.93 ± 0.30	21	-17.54 ± 0.19	12.34 ± 0.10	19.06 ± 0.09
	Druridge Bay	20-30	26	-18.27 ± 0.04	13.14 ± 0.07	19.49 ± 0.14	17	-16.86 ± 0.27	12.51 ± 0.12	19.15 ± 0.08
	Blyth Bay	19-30	26	-18.08 ± 0.19	13.45 ± 0.07	17.98 ± 0.19	20	-15.95 ± 0.09	12.56 ± 0.30	18.63 ± 0.12
	Cambois Bay	19-30	25	-18.12 ± 0.04	13.28 ± 0.08	19.11 ± 0.17	26	-16.87 ± 0.22	12.28 ± 0.06	17.87 ± 0.32

5.3.2.2. Niche overlap

The degree of ellipsoid overlap was generally moderate between predators for both muscle and liver tissue across all sites (Table 5.4). The median niches of dab muscle significantly overlapped with plaice at both Blyth (61%) and Cambois Bays (76%). By contrast, only 32% and 36% of plaice muscle ellipsoids overlapped with dab at these sites, respectively. The degree of overlap among predators was moderate for muscle at Druridge Bay. For liver tissue, niche overlap was relatively low at Cambois and Druridge Bays, where dab had a niche that overlapped with plaice by only 22% and 13%, respectively (Table 5.4). Conversely, the niche of plaice overlapped with dab by 36% and 29% at these site, respectively.

Table 5.5. Median % overlap in 75% Bayesian ellipsoid volumes (based on $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ data) with 95% credible intervals showing the uncertainty in the overlap estimates between plaice and dab by site. Significant overlap (≥60%) is highlighted in bold. The table should be read as, for example, in Blyth Bay, 61% of the dab muscle ellipsoid overlapped with the plaice muscle ellipsoid, and 32% of the plaice ellipsoid overlapped with dab ellipsoid.

	Muscle		Liver	
	Dab	Plaice	Dab	Plaice
Blyth Bay	**61 (36-88)**	32 (16-51)	38 (18-66)	28 (11-50)
Cambois Bay	**76 (54-100)**	36 (21-55)	22 (1-40)	36 (17-59)
Druridge Bay	51 (26-78)	46 (15-66)	13 (0-27)	39 (1-77)

5.3.2.3. Monthly variations in plaice diet

The Bayesian posterior means and standard deviations (with 95% confidence intervals) for plaice $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$ muscle and liver isotope signatures between May and September at Cambois Bay are given in Table A.4 (Appendix 3). There were minimal differences among months in the posterior means of the three muscle isotope signatures of plaice; however, mean liver $\delta^{13}C$ and $\delta^{34}S$ values were more variable among months. Mean muscle isotope signatures (± *S.D.*) were marginally more ^{13}C-depleted in August (-18.17 ± 0.45 ‰) and September (-18.09 ± 0.26) than in preceding months (Table A.4). In September, liver was considerably more variable and depleted in ^{13}C (-16.98 ± 1.69). By contrast, mean muscle became more ^{34}S-depleted across the season and exhibited greater variability, whereas liver $\delta^{34}S$ values were significantly more enriched in August (19.13 ± 0.56) and September (19.45 ±

0.58). Minimal differences were observed in mean δ^{15}N values of muscle and liver, albeit muscle values were consistently more ^{15}N-enriched (Table A.4). The isotopic niches indicated by plaice muscle and liver tissue generally overlapped across the survey period (Fig 5.4). However, plaice exhibited highly variable and isotopically distinct niches in July and September, but had considerably narrower niches in May (Fig 5.4).

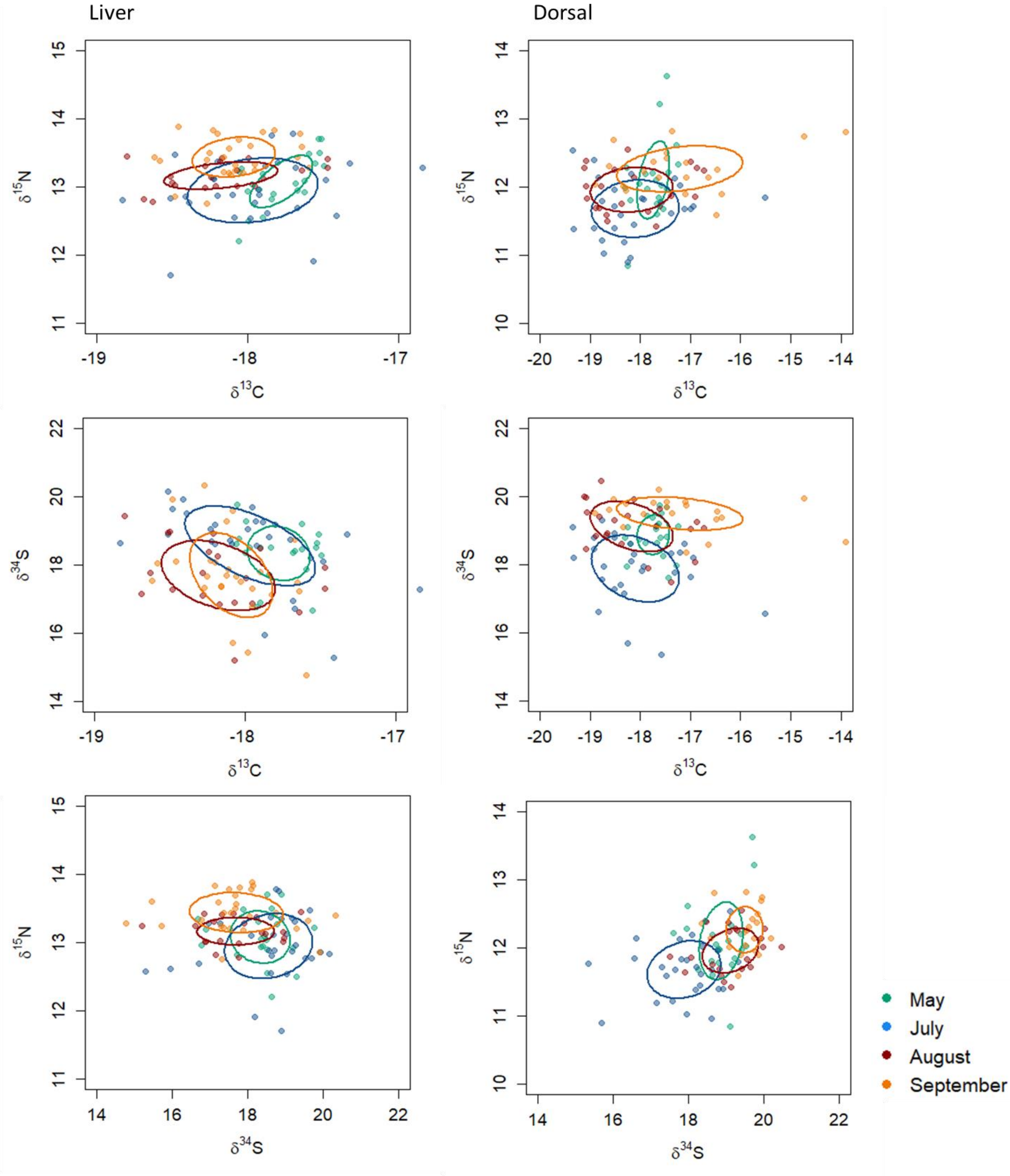


Figure 5.4. Trophic niches of plaice at Cambois Bay by month based on liver (left) dorsal muscle (right), represented by Standard Ellipse Areas (SEAs).

5.3.2.4. Prey signatures and source contributions to predator diet

Prey groups exhibited substantial differences in their stable isotope signatures (Fig 5.5 and Table A.5), apart from crabs (*Corystes cassivelaunus* and Portunidae sp.), shrimps (*Crangon crangon*) and polychaetes (*Nereis* sp. and *Nephtys* sp.), which had relatively similar isotope values. Compared to other prey groups, bivalves (*Abra sp.* and *Ensis ensis*) were the most ^{15}N-depleted, while sandeels (*Ammodytes tobianus*) were depleted in ^{13}C and relatively enriched in ^{34}S (Fig 5.4). By contrast, ophiuroids (*Ophirua ophiura* and *Ophiura albida*) were highly variable and depleted in ^{34}S compared to other prey groups, while squid (*Loligo sp.*) were highly variable and enriched in ^{34}S (albeit only represented by 4 individuals; Table A.5).

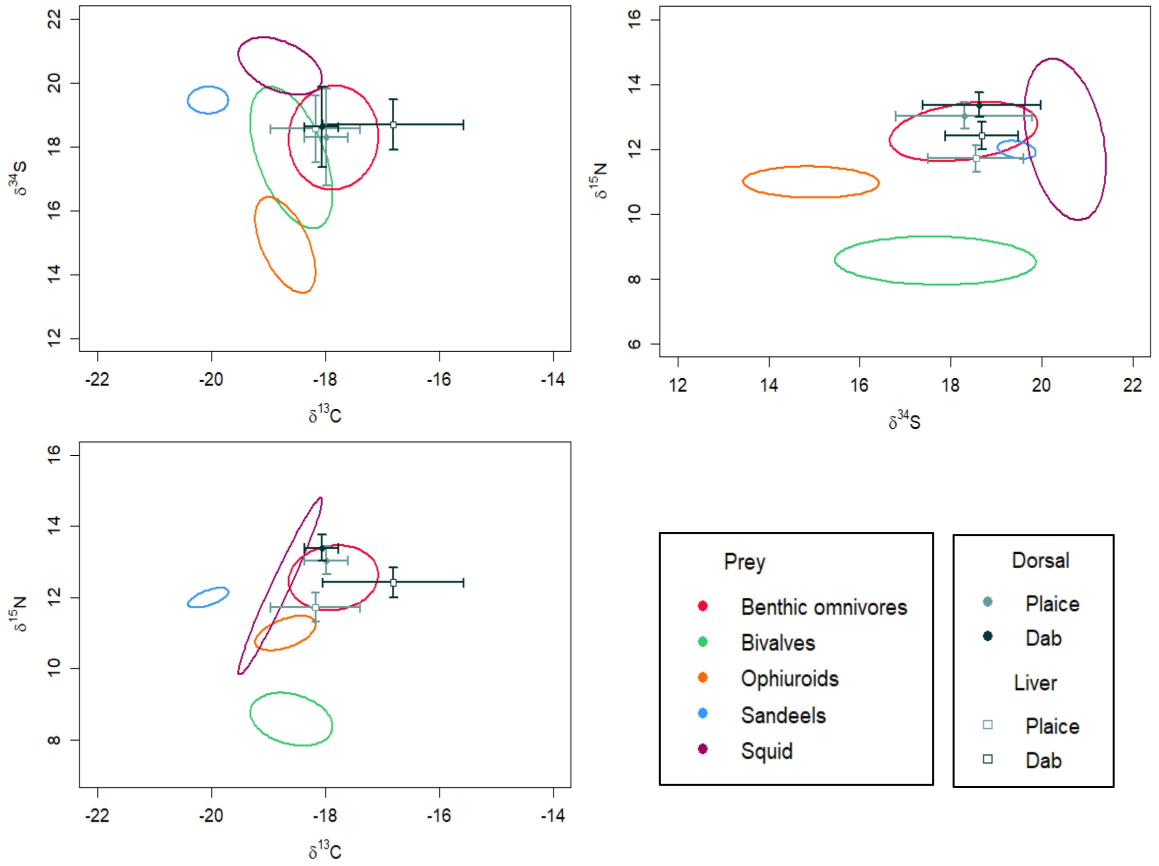
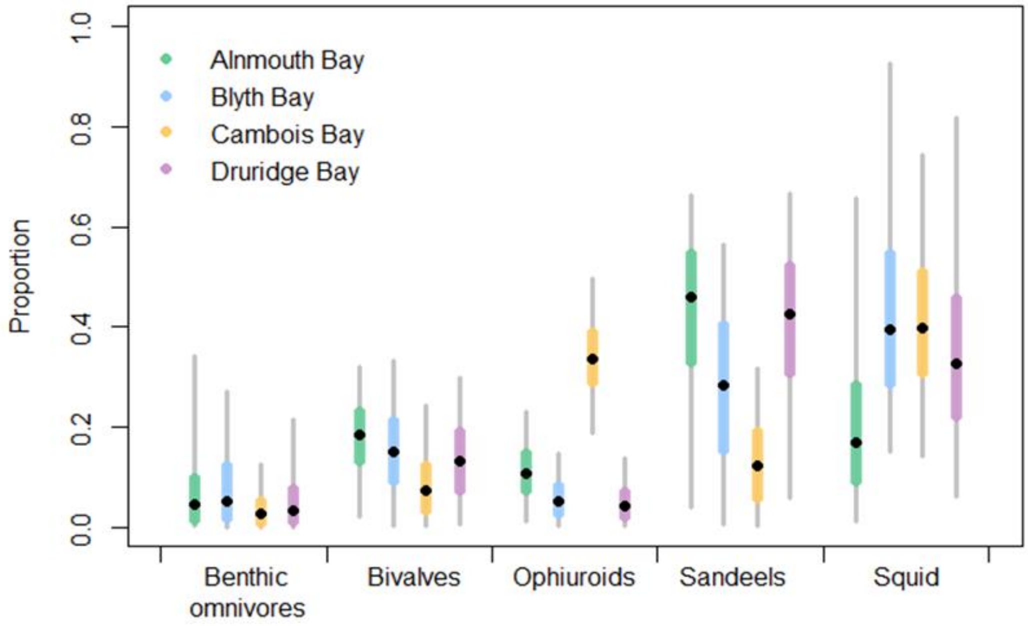


Figure 5.5. Standard Ellipse Areas (SEAs) representing major prey items of plaice and dab collected between May – July (combined for all sites). Biplots also illustrate the means (points) and standard deviations (lines) of plaice and dab fo liver and dorsal muscle tissue collected in July across all sites.

For muscle and liver, isotope mixing models revealed considerable variation in prey source contributions between predators and among sites (Figs 5.6 and 5.7). Mixing model isospace plots for each predator and tissue type with sources are shown in Figs A.7 – A.11 (Appendix 3). Of the prey sources, liver mixing models indicated that dab had a higher reliance on sandeels, whereas plaice showed a marked preference for bivalves across sites (Fig 5.6). Ophiuroids were also important contributors to both plaice and dab at Cambois Bay based on the liver data (18% and 34%, respectively; Fig 5.6). Plaice muscle also showed a marked preference for bivalves in the long-term, especially at Blyth (42%) and Cambois Bays (38%), whereas their contribution to dab diet was low at these sites (Fig 5.7). At Alnmouth Bay, ophiuroids were the most important contributors to plaice diet with a median reliance of 43%, while both plaice and dab were almost equally reliant on ophiuroids at Blyth Bay (30% and 35%, respectively). After squid, sandeels were of secondary importance to both predators at Druridge Bay, with a median reliance of 28% and 13%, respectively (Fig 5.7). Squid also appeared to be major contributors of plaice and dab diet based on both liver and muscle data. The proportional contribution of prey sources based on the dab liver mixing model for all three isotopes did not yield any conclusive results (Fig A.6).

a) dab



b) plaice

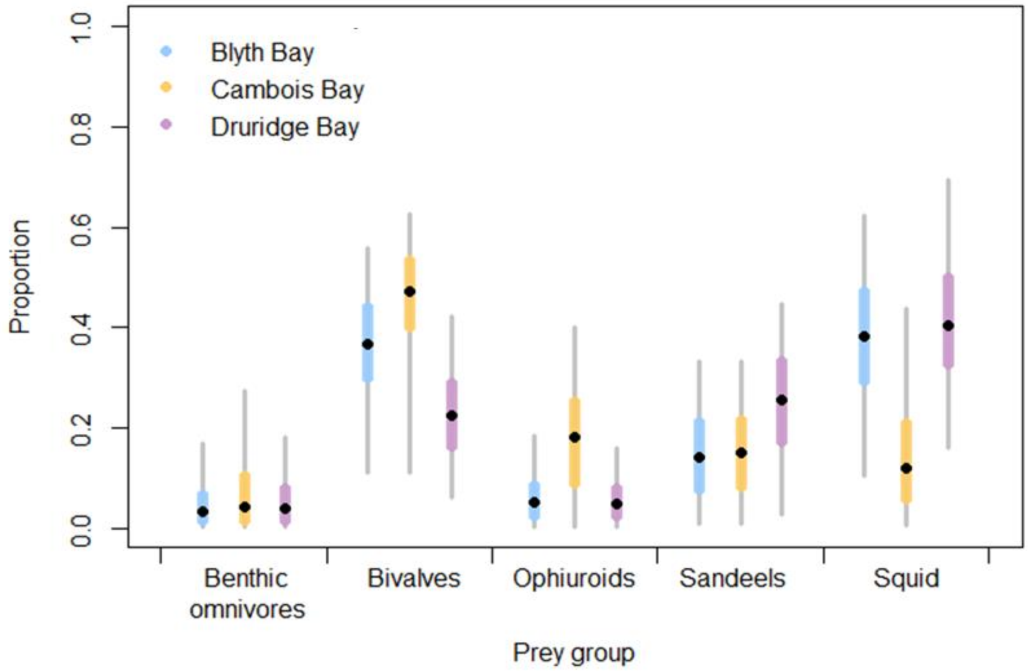


Figure 5.6. Proportional contribution of five prey resources based on mixing model estimates and trophic discrimination factors for a) plaice and b) dab liver by site. Thin grey bars represent 2.5%-97.5% credible intervals and thick bars represent 25%-75% around the modal contribution of each prey resource. Black dots represent the median (50%).

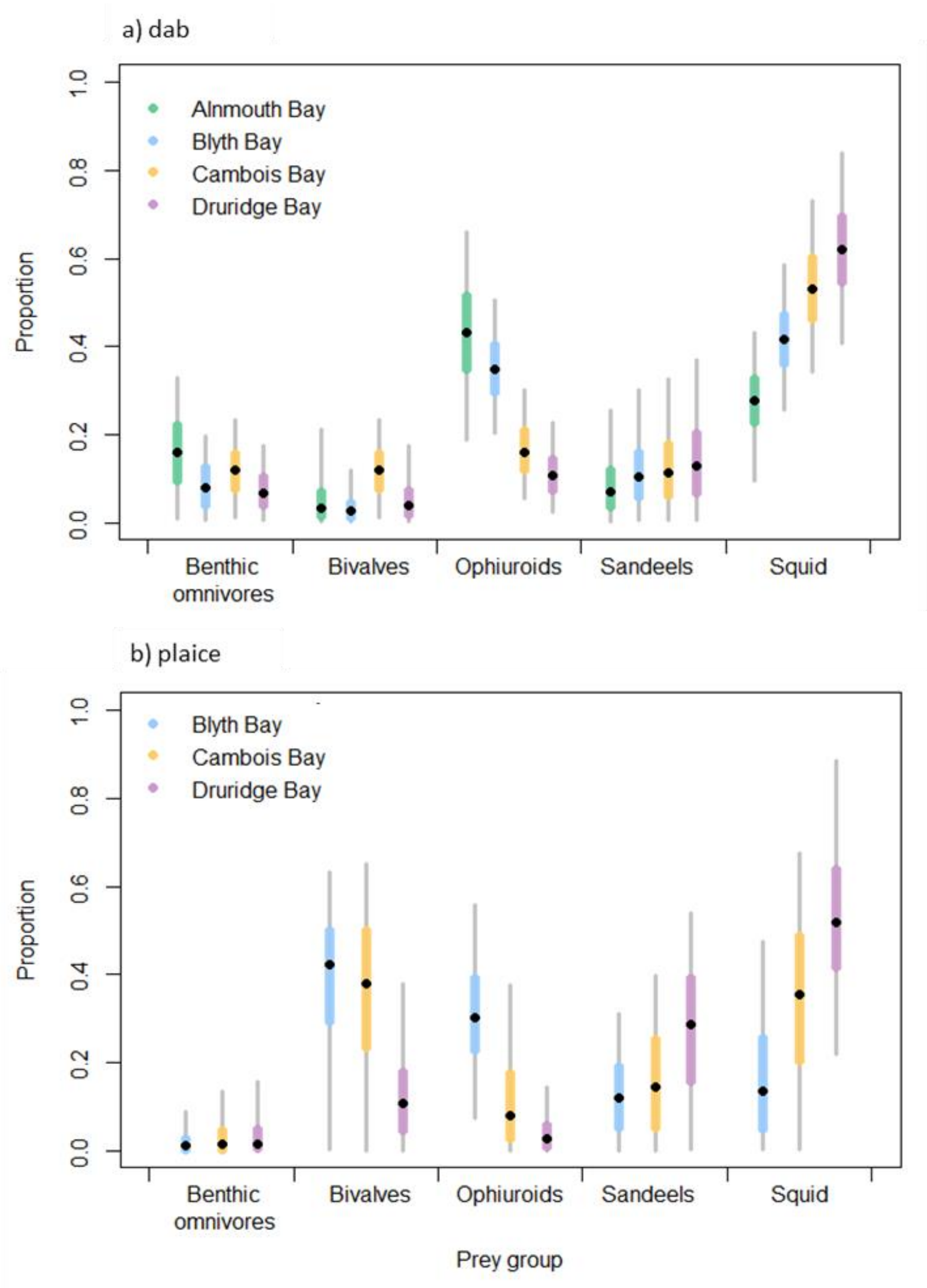


Figure 5.7. Proportional contribution of five prey resources based on mixing model estimates and trophic discrimination factors for a) plaice and b) dab muscle by site. Thin grey bars represent 2.5%-97.5% credible intervals and thick bars represent 25%-75% around the modal contribution of each prey resource. Black dots represent the median (50%)

5.4. Discussion

To the best of our knowledge, this is the first study to examine inter- and intra-specific variation in diet of two sympatric flatfish species using trophic tracers integrated at three time scales (i.e., short, medium, and long-term) replicated across multiple sites. This study investigated the trophic ecology of two sympatric flatfish predators, plaice and dab, and provided new insights into their spatiotemporal feed strategies and interactions across four ecologically-important coastal areas of the Northumberland coast using two complementary sources: stomach content data and stable isotope analyses. This study further highlights how the incorporation of multiple dietary data sources across different timescales provides greater ecological insight compared to either stomach contents or stable isotope analysis of a single tissue type alone.

5.4.1. *Inter- and intra-specific spatial variation in diet*

Stomach content data revealed high similarities between the diet of plaice and dab across all four sites, which was characterised by an overwhelming prevalence of sandeels in their stomachs. This could result from either opportunistic utilisation or high preferential selection of this lipid-rich prey resource. Dab is typically considered an opportunistic benthic feeder, with its diet having been linked to prey densities in the environment (Hinz et al. 2005; Eggleton et al. 2018). Conversely, plaice is commonly regarded as a benthivorous species that feeds on polychaetes and bivalves (e.g., Rijnsdorp and Vingerhoed, 2001) rather than as a sandeel predator. Preferential selection of bivalves by plaice was also reflected in the stomach data in low proportions, although the increased importance of this prey item to both predators at Druridge Bay implies that their diet varied in relation to regional differences in the availability of potential prey. In contrast to plaice, dab diets were typically more varied as they consumed a wider range of prey across sites. This in part could be attributed to the lower number of plaice stomachs sampled, but corroborates the opportunistic feeding behaviours previously demonstrated in this species (e.g., Duineveld and Van Noort, 1986; Hinz et al. 2005; Johnson et al. 2015).

The short-term reliance on sandeels observed here coincides with their peak abundance in the summer when they tend to aggregate at benthic resting sites (Reay, 1970; Engelhard et al. 2008); both predators may simply benefit from sandeels where and when they are available in the immediate environment. In the wider western North Sea, sandeels also form a significant part of plaice diet between April and September (accounting for >50% of their total diet), but were far less important to co-occurring dab, contributing to less than 25% of stomachs by number across the same period (Chapter 4). Other studies have revealed systematic differences in the stomach contents of large plaice and dab (separated by less than 28 km) on the Dogger Bank (Pinnegar et al. 2006; Engelhard et al. 2008), which is not consistent with dietary patterns observed at similar spatial scales here (four sites separated by less than 35 km). At one site, plaice diet was characterised by an increased availability of sandeels in spring, however they were far less apparent at the other site where molluscs dominated the diet during the same period (Pinnegar et al. 2006). Sandeels were also only present in 29% of dab stomachs at the first site but absent from the second (Engelhard et al. 2013). Both sites comprise similar substrates, predominantly fine sand and mud (Kröncke and Knust, 1995), to the four coastal bays sampled in the present study, thus discrepancies in feeding patterns between sites on the Dogger Bank are likely driven by differences in prey availability rather than bottom habitat.

While offering highly detailed taxonomic description of the diet, stomach content analyses provide only a snapshot of recently consumed prey in the order of hours (Hyslop, 1980; Marshall and Elliot, 1997). In the present study, this method may have underrepresented particular prey types (i.e., small prey such as amphipods) at particular sites due to differences in prey digestibility, evacuation rates and periodicity in prey availability (Hyslop, 1980). Stable isotope analysis of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ data help to reduce such biases and provide a more time-integrated dietary picture of predator diet on a scale of weeks to months (MacNeil et al. 2006; Buccheister and Latour, 2010). Here, the liver and muscle data indicated considerable variation in diets among sites at medium and long time scales, despite similarities observed among predator stomachs. Because liver stable isotope values tend to reflect consumer diet over 1-3 weeks (Gaston and Suthers, 2004; Buchheister and Latour, 2010), these data corroborate with the stomach data in suggesting the diets of both predators (most notably dab) are focused on sandeels when these highly available during the summer period (Engelhard et al. 2008). Dab continued to exhibit a strong preference for sandeels at all sites in the medium-term except at Cambois Bay (where they were more dependent on ophiuroids, Fig 5.6). By comparison, plaice exhibited an increasing reliance on benthic prey types (primarily bivalves) at Blyth and Cambois Bays, but still exhibited considerable on reliance on sandeels compared with bivalves at Druridge Bay (Fig 5.6). Because plaice widely select bivalves when they tend to be more available in the spring and summer (Basimi and Grove, 1985; Rijnsdorp and Vingerhoed, 2001; Tulp et al. 2010), it may be that across the Northumberland sites, plaice and dab take advantage of the high nutritional value of sandeels when focal prey are neither as relatively abundant nor easily accessible in order to satisfy their nutrition and energy requirements (Pinnegar et al. 2003).

As fish muscle tissue turns over more slowly than liver (Buchheister and Latour, 2010), the muscle isotope values in predators sampled during July reflect integrated prey consumption that occurred potentially as far back as the late winter and/or early spring. These data revealed that plaice also exhibit a similar reliance on sandeels in the longer-term as to that revealed by liver tissue, however, dab were far less reliant on sandeels across all four sites (Fig 5.7). Sandeels exhibit strong seasonal patterns and tend to bury themselves in the sediment over the autumn and winter (Winslade, 1974; Holland et al. 2005), when they are likely to be less accessible to predators. Dab exhibited a longer-term reliance on ophiuroids at Alnmouth and Blyth Bays and were overall more important prey to dab than to plaice (Fig 5.7). Duineveld and Van Noort (1986) have highlighted the importance of ophiuroids to dab diet, suggesting that the annual consumption of *Amphiura* arms by dab was of the order of 0.85 g wet weight per m^2 in the North Sea. Similarly, other studies have revealed that ophiuroids (e.g. *Ophiura albida*) become prominent prey to dab diet in winter while other prey groups are less important (Knust, 1996; Hinz et al. 2005). Off the Dutch coast, Hinz et al. (2005) showed that prey consumption was significantly influenced by densities of prey in the immediate environment, regardless of other factors such as prey palatability and mobility; implying dab that have similar dietary preference for prey species spanning many taxonomic groups. High densities of ophiuroids on the seabed likely allow dab to opportunistically derive a higher rate of food intake with relatively minimal effort in spite of their low nutritional content(Hinz et al. 2005).

It is worth noting that prey stable isotope compositions incorporated into mixing models were mostly derived from individuals sampled from predator stomachs (complemented by grab samples). Therefore, their isotope values may not necessarily reflect site-specific signatures if predators are moving and acquiring resources beyond the sites at which they were captured. This potentially confounds the interpretation of the level of variability in predator resource use spatially if predator mobility is high. Further, it was not possible to define site-specific prey isotope composition due to logistical constraints. Despite this, dietary differences demonstrated here suggests that both predators are capable of adapting their diet in response to likely seasonal variations in prey availability. While plaice continued to exhibit a strong preference for bivalves in the long-term (Fig 5.7), other studies have shown a gradual seasonal shift in the diet of large plaice from summer to winter, where polychaetes tend to become more important than bivalves (Basimi and Grove, 1985; Pinnegar et al. 2006; Rault et al. 2017). In the present study, polychaete isotope signatures were indistinct from other prey groups (i.e., crabs and shrimps), which limits the ability of mixing models to differentiate certain diet components. Here, the liver and dorsal muscle mixing models also revealed a surprisingly strong link with squid by both predators despite their rare occurrence in predator stomachs. Although the use of the three isotopes ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) rather than two ($\delta^{13}C$ and $\delta^{15}N$) allows for much better 'triangulation' of diet composition proportions (Phillips et al. 2005), it is possible that undefined prey types with similar isotope signatures to squid were influencing predator isotope values. Alternatively, the high proportional contributions of squid in both predators could be a real reflection of their importance as a primary prey resource. Abundances of squid (*Loligo* sp.) have increased significantly in the North Sea in recent years (van der Kooij et al. 2016), although they tend to be available mainly in the summer and autumn (Bellido-Millan et al. 2001; Pierce and Boyle, 2003).

Stable isotope mixing models should be interpreted with care as they can be sensitive to variation in TDF values, which can impact model outputs and estimates of prey contributions (Wilson et al. 2009; Bond and Diamond, 2011). To account for this variability, regression equations were applied based on meta-analysis from Caut et al. (2009) for muscle tissue $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$, which demonstrated linear trends observed in TDF with prey stable isotope ratios for fishes. However, the same study suggests the use of a mean $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$ for liver tissues as differences in predator-prey isotope ratios were not significantly correlated with corresponding prey isotope compositions (Caut et al. 2009).

The initial liver isotope mixing model using all three isotopes for dab liver did not converge due to the large spread in $\delta^{13}C$ values relative to prey, which fell outside the source mixing polygon. Although lipids were accounted for by mathematically applying a correction factor to $\delta^{13}C$ liver values (Skinner et al. 2016), faster turnover tissues such as liver are inherently more variable than muscle even after lipid correction (Pinnegar and Polunin, 1999), and are more reactive to differences in isotopic enrichment through various physiological and metabolic processes (Sweeting et al. 2005). The vast majority of fish processed for stable isotope analysis were mature females, thus the large variability in dab $\delta^{13}C$ liver values could be influenced by the mobilisation of lipids that are synthesised in greater quantities in the liver during bouts of spawning (Gallagher et al. 1991; Saborowski and Buchholz, 1997). Dab spawn annually between January and September with a broad peak from February to April (van der Land, 1991; Rijnsdorp et al. 1992), and although the $\delta^{13}C$ liver values did not reflect dietary patterns after peak spawning, lipids will be continually mobilised by the liver throughout the entire spawning period (Jonsson et al. 1997). By comparison, plaice spawn from December to March with a peak in February (Hunter et al. 2003), and their less variable $\delta^{13}C$ values are therefore not likely subject to the same metabolic influences as dab because lipid stores are expected to be depleted following spawning (Gallagher et al. 1991). The dab liver mixing model was therefore based on $\delta^{34}S$ and $\delta^{15}N$ values only, which yielded considerable separation among prey groups and sites (Fig 5.6a). Although large variability in liver isotope values should thus be interpreted with care when investigating trophic interactions among different species and sexes, the faster turnover of liver relative to muscle can further help reduce bias resulting from dietary variability by responding more rapidly to consumed material (Buchheister and Latour, 2010).

In fish, there appears to be little to no difference in $\delta^{34}S$ from prey to consumer (0-1‰, Peterson and Fry, 1987; Barnes & Jennings 2007), thus reducing the influence on estimated contributions of different sources in isotope mixing models (e.g. Parnell et al. 2010). However, there are very few published studies on $\Delta\delta^{34}S$ compared to $\delta^{13}C$ and $\delta^{15}N$ despite the increasing use of $\delta^{34}S$ as a third tracer for source differentiation in food web studies (Connolly et al. 2004; Barnes and Jennings, 2007). The addition of $\delta^{34}S$ is valuable in discriminating between primary producers in coupled marine benthic-pelagic systems where rates of sulphate reduction greatly differ (Duffill-Telsnig et al. 2019), as is the case for seawater (no reduction resulting in higher $\delta^{34}S$) and benthic sediment (anoxic reduction resulting in lower $\delta^{34}S$) (Michener and Lajtha, 2008). Interestingly, high pelagic $\delta^{34}S$ values (>21.5 ‰) predicted for the western North Sea (Glew et al. 2019) could help explain the relatively high $\delta^{34}S$ predator and prey values in the present study compared with areas of higher freshwater influence or sedimentary mixing (e.g. lower $\delta^{34}S$ in coastal and estuarine fishes in the Thames estuary and adjacent areas; Leakey et al. 2008). Additionally, the substantially larger muscle $\delta^{34}S$ ranges (3.01 – 6.09 ‰) compared to the $\delta^{13}C$ and $\delta^{15}N$ ranges in both predators could have facilitated better discrimination in the mixing models (Barnes and Jennings, 2007). This likely arose from different types of production sources consumed by their prey (which also had large δ^{34}S ranges); both organic and inorganic sulphur contribute towards the total sulphur pool and stable isotope ratios of the predators (Barnes and Jennings, 2007). Plaice and dab may thus reflect a diet that more closely integrates the average local input from both pelagic and benthic sources.

5.4.2. *Trophic niche width and overlap*

Sympatric predators that co-exist are typically expected to consume slightly different prey to reduce trophic niche overlap (Schoener 1974). However, the high level of significant niche overlap observed between plaice and dab based on the stomach data was largely attributed to the consumption of the same dominant prey type (sandeels). Since both predators exhibit plasticity in their feeding habits (Hinz et al. 2005; Pinnegar et al. 2006), they can readily overlap in their resource use in the short-term with limited competitive hinderance, particularly when food sources like sandeels tend be periodically overabundant (Engelhard et al. 2008). This may have resulted in a possible absence of competition between predators, but overlapping niches does not necessarily result in increased competition for resources (Cabral et al. 2002; Layman et al. 2012), perhaps because they are focused on resources that are periodically and highly available. By contrast, the degree of dietary overlap was low to moderate based on the liver and muscle stable isotope data; there were only two occurrences of significant overlap at Blyth and Cambois Bays (Table 5.5). This potentially reflects limited direct competition between these predators as they consume a greater and differing diversity of prey and partition resources by moving over varying spatiotemporal scales (Papastamatiou et al. 2006; Russo et al. 2008). Alternatively, predators foraging on ecologically different prey may display similar isotope values due to their incorporation into tissue overtime (Skinner et al. 2019), potentially blurring the degree of competition that exists between predators as interpreted by the isotopic niche.

Compared to the muscle isotope data, the degree of ellipsoid isotopic niche overlap was lower between predators based on the liver data, with cases of complete niche separation in isotopic space at Cambois and Druridge Bays (Fig 5.2). This is suggestive of ecological divergence between the two species in the medium-term in order to maintain co-occurrence; despite muscle tissue isotopic niches being suggestive of more average ecological similarity in the long-term. This medium-term separation could be a response to a decreased food supply (or diversity) at these sites and consequential increase in inter-specific competition between predators. The comparatively lager isotopic niches for dab can largely be attributed to the over dispersed dab liver $\delta^{13}C$ values, which as mentioned previously, is likely driven by metabolic differences in dab and plaice relative to spawning periods. By contrast, the isotopic niches of plaice muscle tissue were considerably larger compared to those of dab at Blyth and Cambois Bays (Fig 5.3), suggesting that plaice populations exhibited wider foraging plasticity and greater intra-specific variability in their diet at these sites. Such specialisation is thought to be strongly linked to ecological opportunity and may be more apparent where prey diversity and density of competing individuals is higher (Araújo et al. 2011). Plaice and dab are more abundant in Blyth and Cambois Bays than at Druridge Bay (Chapter 4), thus the degree of resource partitioning and specialisation may be higher at these sites, prompting plaice to select a wider range of prey.

Inter-specific variations in predator diets here may be explained by the level of site fidelity exhibited by plaice and dab as well as by the magnitude of their migratory patterns. While juvenile flatfish tend to exhibit strong site fidelity (Burrows et al. 2004), subadult and adults are highly mobile and tend to exhibit lower habitat specificity as they forage over much broader area (Gibson et al. 2014). For plaice in particular, local differences in diet are perhaps unexpected given their known dispersive abilities and large-scale migrations offshore to winter spawning grounds in the North Sea (Hunter et al. 2004; Van Keeken et al. 2007). However, the longer-term, broader niches of plaice compared to dab, as revealed by the muscle isotope data (Fig 5.3), may be explained by their greater mobility as they move over a larger potential prey base to satisfy their energy demand. There is very little published data on the movements of dab in the North Sea specifically; they are thought to remain in localised areas for longer periods (Saborowski and Buchholz, 1997), but tagging studies suggest that dab undertake seasonal migrations over considerable distances between spawning and feeding grounds (DeClerck, 1984; Rijnsdorp et al. 1992). In spite of these long-distance movements, feeding strategies were not ubiquitous across sites and small-scale variations in diet are also likely to reflect local feeding patterns and site-specific availability of prey resources (Lancaster and Waldron, 2001).

The stomach data yielded significant but relatively low levels of specialisation among individual plaice and dab (Table 5.3). The degree of specialisation measured by the *E* index is compounded by the widespread dominance of sandeels across stomachs, whereas significance levels are inflated by low numbers of prey observed in predator stomachs as well as the likely patchy distribution of prey and therefore none-independence feeding events (Araújo et al. 2008). By contrast, other studies have not been influenced by these factors as similar levels of individual specialisation, as measured by the *E* index, did not yield significant results, whereas higher levels of individual trophic specialisation are matched with statistical significance (e.g., values approaching 0.6 in estuarine seabass; Cobain et al. 2019).

The trophic niches of dab muscle were relatively narrow across sites, which could be indicative of specialised or generalist foraging if dab are exposed to a uniform food supply (Bearhop et al. 2004; Sweeting et al. 2005). Alternatively, reductions in prey diversity across sites may have directly contributed to smaller niche widths as individual dab forage optimally on a few, energetically-favourable prey types (Bearhop et al. 2004). As such, there is less scope for either chance (e.g., patchily distributed prey) or specialisation (Bolnick et al. 2003) within populations that target different subsets of available prey taxa, thereby reducing the level of intra-specific niche variation. Yet this is in contrast to plaice, which exhibited considerable intra-specific variation in isotopic niches among sites, as revealed by the muscle data, with greater dispersion in isotopic space at Blyth and Cambois Bays compared to Druridge Bay (Fig 5.3) that are presumably exposed to the same prey resources as co-occurring dab. Plaice populations may have expanded their isotopic niche widths by individuals specialising on differing prey to reduce intra-specific competition at these sites, especially when favoured prey are scarce (e.g., bivalves) and as individuals switch to forage on previously underutilised resources (Amundsen, 1995; Araújo et al. 2011), and matches with the expected behaviour of increased opportunistic feeding behaviours noted in dab compared to plaice.

At Cambois Bay, where sampling was such that isotopic niches could be constructed throughout the season, the trophic niches of plaice overlapped considerably (Fig 5.4). However, the liver isotopic data revealed more subtle intra-specific differences in their diet than the muscle data, which is more likely to be detected in the medium-term versus the long-term tissue type. For example, liver $\delta^{34}S$ values were statistically more separated between months; plaice exhibited more benthic feeding in July (^{34}S-depleted) and shifted towards pelagic feeding in September (^{34}S-enriched). This separation was also mirrored by the $\delta^{15}N$ values, but was less evident in $\delta^{13}C$ due to the large overall variation exhibited in the isotope ratios. A shift towards more pelagic feeding later in the season is likely linked to changes in ecological opportunity due to the seasonal dynamics of prey becoming more accessible (Araújo et al. 2011), notably the availability of sandeels as demonstrated in the stomach data and mixing model outputs. Assessing dietary variation across the season only based on δ^{13}C and δ^{15}N alone may have masked this pattern (Connolly et al. 2004; Barnes and Jennings, 2007). This further underpins the value of δ^{34}S to elucidate intricate variation in trophic niches and dietary behaviour (Peterson et al. 1986). As expected, differences in monthly dietary patterns were more evident in liver than muscle due to its faster turnover, thus highlighting it ability to better track monthly dietary changes than muscle.

5.5. Conclusions

Sympatric flatfish are thought to be dietary generalists, but the results reported here show considerable differences in resource utilisation throughout the year and across sites, highlighting how trophic resource use can vary between ecologically-similar species at a scale of tens of kilometres. Stomach data revealed similar diets and significant dietary overlap at short temporal scales, whereas liver and dorsal muscle showed substantial inter- and intra-specific differences in diet spatially as well as low to moderate levels of niche overlap at medium and longer-term time scales. These results suggest that plaice and dab are able to facilitate co-existence in coastal bays by trophic versatility, switching between a portfolio of prey types in response to variations in local prey availability, whether this be on a seasonal, spatial, or inter-annual basis. Previous studies have demonstrated that plaice and dab have both undergone dramatic changes in their diet in coastal areas of the North Sea over the past century (see Chapter 4; Frid & Hall 1999; Le Quesne and Pinnegar, 2012), largely attributed to a marked shift in the availability of certain prey types as a consequence of human-induced activities such as intensive beam trawling pressure, eutrophication, and climatic processes. Plaice and dab have experienced declines across the study sites since the late 19th century (see Chapter 3), yet these predators still persist and co-occur in relatively high numbers, attributed in part maybe to their inherent adaptability to changes in prey availability.

The present study further highlights how stable isotopes in conjunction with other diet techniques help to contrast trophic interactions of sympatric predators at different spatiotemporal scales (Cloern et al. 2002; Fry, 2006). Stable isotope data alone may fail to reveal important food web components and track energy flows in coastal systems (Guzzo et al. 2013), whereas stomach data in isolation may mask adaptive trophic behaviours that facilitate co-occurrence when dealing with opportunistic diet habits. Pairing stable isotope analyses with stomach contents data provides a more integrative assessment of consumer feeding ecology than either method alone, providing both taxonomic specificity and measures of time integration in what is actually assimilated. Not enough studies have used liver as an additional dietary tracer in food web studies, yet with faster tissue turnover it can address prey utilisation at medium-term scales (Perga and Gerdeaux, 2005; Buccheister and Latour, 2010), and reduce bias resulting from long-range fish movements or isotopic heterogeneity of prey, despite potential metabolic influences in data. Together, these methods characterised the trophic behaviour of plaice and dab more comprehensively, and can thus be of great benefit in predicting how predatory fish will respond to changes in resource availability as coastal environments change.

Chapter 6: General Discussion

6.1. Summary

This thesis set out to examine patterns of change in demersal fish species at differing temporal and spatial scales in the western North Sea. Multiple approaches, fisheries-independent trawl surveys, stomach content and stable isotope data, were employed, and have provided a rare historical and contemporary snapshot into the status and trophic ecology of demersal fish species. This chapter provides an overview of the thesis, highlighting key findings and resulting contributions to knowledge. Limitations are reviewed and caveats to the interpretation of the results provided. The work is placed within the wider context of fisheries management and implications for their application are discussed.

6.2. Main findings and contributions to knowledge

Chapter 2 collated extensive information on the evolution, design and functioning of late 19th century beam trawls to facilitate the construction of original custom-built gear used in the NSFC historical trawl surveys. Using contemporary alternatives where required, the replica trawl gear was carefully imitated in its design, materials and function, and the resultant fishing power and catchability are assumed to be closely related to those of the original gear. In Chapter 3, analysis of historical (1899 – 1913) and contemporary (2018 – 2019) catches demonstrates the extent to which a demersal inshore fish assemblage has been altered over the past 120 years. Striking declines in key taxa point to considerable modifications of the benthic ecosystem during the 20th century. Changes included the complete absence of formerly abundant species (e.g., grey gurnard) and elasmobranchs. All other species have experienced declines in their abundance since the late 19th century; the inshore fish assemblage is now substantially less diverse and dominated by plaice and dab. Investigation of stomach contents data from this period provided new quantitative evidence of long-term change in the diet of demersal predators in the western North Sea. Multi-decadal trends in predator diet showed that bivalves declined after the mid-20th century whereas polychaetes, sandeels and echinoderms became a more important prey in recent periods. These diet shifts were attributed to changes in the benthic prey base over the 20th century, linked to increased beam trawling in the 1960s-1970s (the abrasive removal of slow-growing invertebrates), eutrophication, and climatic processes. Taking a more contemporary approach, Chapter 5 uses stomach contents and stable isotope data of fast and slow tissues, to reveal new insights into the spatiotemporal feeding strategies and interactions of two sympatric flatfish species, which now dominate coastal areas of the Northumberland coast at a scale of tens of kilometres. Evidence of inter- and intra-specific differences in resource use by plaice and dab demonstrate their trophic versatility in relation to their co-existence in coastal areas. Results here also imply that this may be attributed in part to their inherent adaptability to respond to changes in prey availability.

Although it was not possible to use the replica gear to accurately resurvey historical sites, Chapter 2 provides an internationally relevant overview of beam trawl technology used in early commercial and scientific surveys, for example, in other parts of the UK and wider North Sea (e.g., Fulton, 1895; SS Huxley, Garstang, 1905; Todd, 1911), Ireland (e.g., SS Helga; Holt, 1910), and United States (e.g., Collins, 1889; Smith, 1894; Jensen, 1967). Given that beam trawls were the first major development of the commercial trawl industry in the 19th century and originated in European waters (Collins, 1889), this work offers a repository of information for researchers and the trawl industry interested in similar historical comparisons of trawl technology and survey designs. By building upon the information collated in Chapter 2, repeat trawl surveys using replica gear could credibly be developed in other regions, enabling more confident comparisons to be made of the historical and contemporary states of fish populations.

Chapter 3 provides further evidence of systematic declines in a demersal fish assemblage from previously understudied inshore sites and will contribute towards assessments of ecosystem status for the region (e.g., Walmsley and Pawson, 2007). Given that some of the most drastic impacts on inshore fish populations likely occurred from the mid-19th century (Meek, 1900; Thurstan et al. 2014), it was not possible to describe what the assemblage looked like immediately prior to the initiation of intensive beam-trawl fishing. Results from this chapter should thus not be used as a baseline on which to base recovery to pristine conditions as so much else has changed, but rather as a reference point for rebuilding fish stocks and improving ecosystem status. Current European inshore fisheries management is tending towards decentralisation and increased regional responsibility for monitoring of fish stocks (Phillipson and Symes, 2010; Jentoft and Knol, 2014). In UK inshore waters, this change was established under the Marine and Coastal Access Act (2009) through the establishment of regional Inshore Fisheries and Conservation Authorities (IFCAs) in 2011, with a vision to '*manage a sustainable* *marine environment and inshore fisheries, by successfully securing the right balance between social, environmental and economic benefits to ensure healthy seas, sustainable fisheries and a viable industry'*. This trend towards devolved management is likely to continue, and with more emphasis being placed on the value of historical data to understand long-term change, there is an increasing need for regionally specific data. Prior to this thesis, no fishery-independent studies of long-term change in coastal fish species in Northumberland waters had been conducted. Relatively few long-term studies have examined inshore waters in general compared with the number conducted offshore (e.g., Rogers and Millner, 1996; De Désauany et al. 2006; Tulp et al. 2008; McHugh et al. 2011). NSFC surveys were conducted in areas that were not previously sampled by government surveys (e.g., Rijnsdorp et al. 1996), despite the importance of these areas as nursery grounds for a range of taxa. The novel achievements of this chapter thus lie in the rare insights provided by the comparisons between some of the earliest quantitative trawl surveys and contemporary resurveys conducted in inshore waters. The present findings are directly relevant to the Northumberland IFCA, which now manages coastal waters out to six nautical miles; this management is concerned with fisheries sustainability but has been increasingly tasked with biodiversity and habitat conservation, including the new Coquet to St. Mary's Marine Conservation Zone.

Diverse fish assemblages are essential for ecosystem stability and functioning in coastal waters and they need to be retained, even for the most abundant and widespread species (Gaston and Fuller, 2007). Failing to prevent the collapse of a population is likely to have far-reaching implications for the local ecosystem (Hutchings and Reynolds, 2004), thus some of the species documented in Chapter 3 clearly require more effective management interventions to enable their recovery or persistence. Currently, fisheries management of the Northumberland coast is focused on shellfish, predominantly European lobster, brown crab, and *Nephrops*, as these species have assumed greater economic importance (Stephenson et al. 2018) and fin-fish landings have fallen in line with quota allocations (Walmsley and Pawson, 2009). The Northumberland coast represents a case study in the problems of shifting baselines that can lead to low conservation ambition and inadequate management. The 'baseline' conditions of MPAs in British and European waters have typically been 'set' at the time of designation and the majority can still be legally trawled in (Solandt et al. 2020). On the Northumberland coast, MPA conservation objectives fail to consider restoration of fish communities, with features (e.g., mud and sand flats) being maintained in 'favourable condition' based on recent baseline information. It is clear from evidence in Chapter 3 that a far greater decline has occurred on the Northumberland coast than has been considered in initial habitat assessments. Data that do not account for long-term change thus produce a baseline that substantially underestimates the recovery potential of marine resources conducive to inadequate management measures that fail to reach any improvement in condition. The historical context provided by Chapter 3 should be considered by decision-makers such as the NIFCA to inform appropriate reference points and help facilitate conservation priorities at the local-level.

Chapter 4 highlights the value of using alternative data sources to understand long-term change in demersal fish predators. Long-term high quality stomach contents data with good spatiotemporal coverage are scarce because of the considerable effort and resources required to collect and analyse such data at this scale. It is even rarer to utilise and analyse fish stomach data that were collected from a period when anthropogenic stressors were lower in the late 19th and early 20th century. This chapter also provides an indirect indication of likely changes in the benthic prey base and can be used to identify temporal links between predators and their resources. This is on the basis that the diets of these relatively opportunistic species are somewhat driven by prey availability. Temporal changes in diet offer some insights about the changes in the benthic communities (e.g., Frid and Hall, 1999; Link, 2004; Dwyer et al. 2010); however, progress on this knowledge would requires further research, for example, investigation of how closely fish diets can track prey availability over varying spatiotemporal scales.

The novelty of chapter 4 also lies in the application of individual gravimetric (mass-based) estimates of invertebrate and fish prey (from the latest version 5.5 of the DAPSTOM database; Pinnegar, 2019) to provide insight into the past nourishment of fish predators. Although these findings are sensitive to the assumed average size of an individual prey item, the data could inform multi-species food web models to better understand ecosystem functioning and how this has changed over the multiple decades. Europe has a legal obligation to 'restore stocks to levels that can produce the Maximum Sustainable Yield (MSY)' and maintain 'Good Environmental Status' under the EU Marine Strategy Framework Directive (MSFD; European Commission, 2020), or whatever might replace it in UK waters. However, modelling studies suggest that fish populations cannot be maintained at precautionary MSY reference levels simultaneously because fisheries interact, and individual species consume each other

(Mackinson et al. 2009). Consequently, “Stomach data are of vital importance” and the intention is to transition to the provision of multi-species advice on fisheries (ICES, 2013). Until recently, the use of historical data in multi-species models has been limited by the need for complete spatial coverage of stomach data in a given year. Yet model developments have made it conceivable to incorporate regional diet data into multi-species ecosystem models (Huwer et al. 2014). The added evidence provided by Chapter 4 could thus be used to estimate multi-species interactions at a much lower cost than that incurred by sampling new stomachs. The longevity of the data series could also be used to test the long-term stability of regional models.

Chapter 5 provides a more comprehensive understanding of spatiotemporal feeding dynamics and could be valuable for predicting how predatory fish respond to fluctuations in prey availability as coastal environments change. The presence of intra-specific variability among sympatric predators will have important implications for management as it suggests that behavioural differences among individuals may influence the persistence of the populations (Bolnick et al. 2003; Cobain et al. 2019). Management measures should ultimately improve the capture of the range of individual behaviours exhibited within populations to effectively conserve a population and its intrinsic diversity (Bolnick et al. 2003). Such information is essential to generate realistic species and/or ecosystem models to advise policy decisions (Cobain et al. 2019). The novel achievements of Chapter 5 lie in pairing stomach content and stable isotope analyses of liver and muscle to contrast trophic interactions at differing spatiotemporal scales. Taken together, these methods have captured the trophic behaviour of plaice and dab more comprehensively than using stomach data and/or a single tissue type in isolation.

6.3. Study limitations and directions for future research

Sampling artefacts are an unavoidable problem of all data. It is important to address these limitations if data from multiple sources (especially historical sources) are used as ecological tools to track spatiotemporal changes in species and ecosystems. Although limitations and caveats specific to each dataset are addressed accordingly in each chapter, general limitations and recommendations for future research are discussed below.

A combination of factors, including poor weather, vessel availability, issues with the replica gear, and interactions with other sea users impacted fieldwork and data collection over the course of this thesis. Financial and logistical constraints precluded further refinement of the replica trawl gear (discussed in more detail in Chapter 2). Consequently, utilisation of modern trawl gear in place of the replica gear facilitated contemporary resurveys and data collected from these surveys enabled comparison with historical data in Chapter 3. The lengths undertaken to recreate the original gear employed by the NSFC to accurately compare contemporary with historical catch data reiterates the innate uncertainties of such comparisons. These biases are heightened in Chapter 3 because of the differences associated with the different designs of the two gear types (Rogers and Ellis, 2000), which will ultimately influence the volume, size and species composition of the catch (Currie et al. 2018). For example, beam trawls specifically target species buried in the first few cm of the seabed (primarily flatfish), whereas the geometry of otter trawls allows for capture of these species but also selects for pelagic species (such as Atlantic mackerel) (Jennings et al. 2009). Despite these uncertainties, a thorough attempt was made to account for these factors as much as possible. Time of day, season, and geographical locations were standardised, and swept area correction factors were applied to standardise differences in trawl speeds, tow duration and gear size for comparisons of catches between periods. Moreover, a conservative cut off removing fish < 20 cm (total length) was applied to analyses in Chapter 3 to ensure that both trawl gears were fully selective by the largest mesh size.

Numerous sources of variability can influence fish abundance over relatively short time scales, including inter-annual natural and human-induced changes, seasonal fluctuations due to foraging strategies and/or spawning, and catchability variation due to changing oceanographical conditions (Arreguín-Sánchez, 1996; Currie et al. 2020). Unfortunately, it was not possible to undertake multi-year comparisons in Chapter 3; however, sampling at five geographically distinct sites at similar depths and confining comparisons to between May and September will have considerably reduced any potential short-term biases. Chapter 3 would have benefited from converting numerical abundances into biomass data based on length-weight relationships (e.g., Silva et al. 2013). Biomass data can provide a more ecologically meaningful metric as a direct measure of resource use and energy flow in fish assemblages (Henderson and Magurran, 2010). Ecological modellers may thus benefit from further research that can apply a suitable conversion factor to historical data. However, this may require sourcing additional weight or length information from relevant time periods to improve the degree of certainty in conversion factors. Additionally, calculation of the maximum observed length or L_{max} is less affected by trawl standardisation procedures and could be applied to the historical data as a potentially robust measure for evaluating baselines for the inshore assemblage. This is because L_{max} assumes that size reduction is due to increased exploitation that removes older and larger individuals (Piet and Jennings, 2005; Cardinale et al. 2009).

Spatial and temporal variability in fish stomach contents data is often combined in such a way (i.e. averaged among years or across broad geographic areas) that real dietary signals may be lost (Deroba, 2018). Stomach data provide ‘snapshots’ of diet sampled at particular points in space and time (Pinnegar et al. 2003) and are strongly linked to environmental variables such as habitat type, temperature and depth (Eggleton et al. 2018). In Chapter 4, stomach data were not systematically recorded in each year (particularly in historical time periods) and several years were thus combined for multi-decadal comparisons. Further, stomach data were pooled and analysed at a regional spatial scale, which was dictated by sufficient sample sizes to validate comparisons between decades. Combining data in this way will have masked fine-scale variations in predator diet and should therefore be viewed with considerable caution. Still, Chapter 4 provides evidence of broad-scale change in the diet of demersal fish and corroborates with other studies of long-term change in the benthos in the North Sea across the 20th century, for example loss of bivalves and increase in polychaetes (Frid et al. 1999; Rijnsdorp and Vingerhoed, 2001; Callaway et al. 2007; Kröncke, 2011).

The strength of results provided by the stomach contents data could be bolstered if they were related to benthic fauna collected by grabs and epibenthic trawls in the same localities and time periods. Although such data are incredibly rare for the early 20th century, some datasets are available for the Dogger Bank (e.g. Callaway et al. 2007; Kröncke, 2011). Utilising these data would be challenging but together they could facilitate valuable links between fish diet and prey availability. As no single indicator used in isolation is perfect, fish diets could be used in conjunction with other indices to provide a more complete picture of the magnitude of long-term change in benthic food webs. With further effort, this would greatly benefit the progression towards an ecosystem-based approach to fisheries management (EBFM). To achieve this, EBFM needs to be applied in a way that addresses the wider interactions between human-induced activities and the whole ecosystem based on the best scientific information available (Garcia and Cochrane, 2005). The knowledge gained in Chapters 3 and 4 can be used in combination with commercial fisheries data to facilitate this as well as improve confidence in the interpretation of long-term change.

Chapter 5 advanced understanding of inter- and intra- specific trophic interactions between large sympatric flatfish across multiple temporal and spatial scales. However, it would be advantageous to compare trophic affiliations between juveniles and adult populations, especially as coastal areas have long been recognised as important nursery areas for juveniles (e.g. Cabral et al. 2002). Examination of dietary variations across the full size range of species would provide a better understanding of how individuals partition their resources to reduce competition and facilitate co-existence in regions of high density – few studies have explored patterns in inter-specific trophic competition across broad ontogenetic ranges for fishes. Chapter 5 demonstrates the value but highlights the understudied caveats associated with using liver stable isotope data as a medium-term dietary tracer in trophic ecology studies. Highly variable $\delta^{13}C$ liver isotope values for dab skewed interpretation of the liver data to the point where the mixing model did not converge nor produce accurate proportional estimates of prey contributions to diet. It was not possible to account for overdispersion in the $\delta^{13}C$ liver values for dab after lipid correction that was attributed to inherent reactivity to isotopic enrichments through multiple physiological and metabolic processes associated with this organ (Sweeting et al. 2005). Isotopic sampling only spanned one season (May – September), while this facilitated comparisons within the same environmental season, asynchrony in the spawning season of these two species resulted in physiological mismatch. Thus, confidence in the use of liver isotope values would be improved if they were collected monthly across the whole year. This would allow the investigator to capture variability in isotope ratios across the whole spawning period from oocyte development and release through to physiological recovery. A second limitation stems from the use of TDFs from the literature and the uncertainty of their confident application to a particular system of interest beyond the scope of Chapter 5. While the use of TDFs stemming from meta-analysis of data presumably improve generality, it still could be beneficial to conduct sensitivity analyses to reveal the potential effects that borrowed parameters may have on the conclusions drawn (Buccheister and Latour, 2010). However, TDF values for fish liver are scarce for $\delta^{13}C$ and $\delta^{15}N$, and even more so for $\delta^{34}S$ regardless of tissue type. In combination with an understanding of an animal's ecology and behaviour, future work should conduct sensitivity analyses using a range of TDFs to increase the robustness of parameter estimates in liver (and muscle) stable isotope mixing models. Moreover, further experimental trophic discrimination studies will be required to expand the use of TDFs with greater confidence across less well studies systems and taxa.

Beyond Chapter 5, it is my intention to take analyses a step further by expanding the quantification of metrics for individual specialisation to include not only stomach contents, but also stable isotope data. This can be demonstrated, for example, by using a method to accurately quantify a standard index of individual specialisation (Bolnick et al. 2002) that can be compared among populations and to those derived from gut contents. If individual predators have different diets, and their prey also differs isotopically, then their isotope signatures will also differ (Araújo et al. 2011). Hence, isotope variance within populations may be used as a more reliable way to measure intra-population diet variation when it is 'normalised' relative to the isotopic variability observed in their prey (Sweeting et al. 2004). Importantly, variation in isotope values among individual predators and their prey can complement gut content measures (Araújo et al. 2007), and can thus be used to assess the validity of gut contents.

6.4. Conclusions

The research presented in this thesis has demonstrated that the recovery of underutilised historical data can help to understand the past and certainly has the potential to guide reference points for rebuilding fish populations. This thesis has advanced the knowledge of historical reference points and subsequent change in the western North Sea. Unique historical data were analysed to document the status of demersal fish species between the late 19th century and present day, while contemporary data facilitated understanding of trophic interactions of commercially important species that persist in coastal areas of the Northumberland coast today. These datasets have been made possible by the collaboration and efforts in digitising a wealth of historical data housed at Cefas collected by naturalists, fishermen, and scientists of bygone eras.

Results from thesis and continued analysis of historical and contemporary data from multiple sources will contribute to the growing body of studies that provide strong evidence of long-term change in marine ecosystems. Similar narratives have been replayed across the world (e.g., Jackson et al. 2001; Pinnegar and Engelhard, 2008), and points to human impacts on the oceans on a vast scale. Research into the past can unravel the magnitude of change that has occurred as well as the extent to which marine resources have been transformed in individual regions. Without historical and contemporary data, on-going impacts, management measures and recovery targets cannot be properly evaluated if ecosystem baselines continue to shift. These data are of vital importance for the recovery of our oceans from centuries of exploitation and from the synergistic effects of human impacts we face in the coming decades.

Appendices

Appendix 1

Table A.1. Summary of the locations, sampling dates and depths of the gear trials conducted in August 2018 and March 2019.

Augut 2018	**Gear**	**Date**	**Location**	**Depth (m)**	**Lat/long shot**		**Lat/long haul**	
	Replica beam	15/08/2018	Alnmouth	8.6	55.34	-1.57	55.39	-1.57
		22/08/2018	Alnmouth	10.5	55.34	-0.15	55.39	-1.56
		22/08/2018	Alnmouth	8.4	55.4	-1.55	55.35	-1.56
	Otter	28/08/2018	Alnmouth	9.5	55.34	-1.56	55.4	-1.56
		28/08/2018	Alnmouth	10.1	55.4	-1.54	55.34	-1.55
	Replica beam	14/08/2018	Blyth	5.7	55.11	-1.48	55.09	-1.46
		14/08/2018	Blyth	7.4	55.11	-1.46	55.09	-1.43
		14/08/2018	Blyth	7.5	55.11	-1.47	55.09	-1.42
		23/08/2018	Blyth	17.6	55.11	-1.46	55.09	-1.43
		23/08/2018	Blyth	11.1	55.11	-1.45	55.09	-1.43
	Replica beam	14/08/2018	Cambois	7.3	55.14	-1.5	55.16	-1.51
		14/08/2018	Cambois	6.8	55.14	-1.5	55.16	-1.5
		22/08/2018	Cambois	16.2	55.14	-1.48	55.16	-1.49
		23/08/2018	Cambois	21.2	55.14	-1.46	55.17	-1.46
		23/08/2018	Cambois	10.5	55.14	-1.48	55.17	-1.49
	Otter	29/08/2018	Cambois	5.4	55.14	-1.49	55.17	-1.5
		29/08/2018	Cambois	9.5	55.14	-1.47	55.17	-1.51
	Replica beam	15/08/2018	Druridge	4	55.24	-1.53	55.3	-1.55
		15/08/2018	Druridge	9.2	55.24	-1.51	55.3	-1.58
		15/08/2018	Druridge	8.6	55.24	-1.52	55.3	-1.53
		21/08/2018	Druridge	19.5	55.24	-1.151	55.3	-1.53
		22/08/2018	Druridge	19.5	55.3	-1.5	55.24	-1.48
	Otter	29/08/2018	Druridge	5.4	55.25	-1.53	55.32	-1.53
		29/08/2018	Druridge	6.1	55.31	-1.51	55.24	-1.5
	Replica beam	21/08/2018	Skate Roads	5.3	55.62	-1.71	55.65	-1.73
		21/08/2018	Skate Roads	5.7	55.66	-1.75	55.62	-1.72
	Otter	28/08/2018	Skate Roads	5.3	55.62	-1.7	55.66	-1.76
		28/08/2018	Skate Roads	12.5	55.66	-1.76	55.6	-1.7
Mach 2019	Replica beam	28/03/2019	Blyth*	8	55.11	-1.48	55.09	-1.46
		28/03/2019	Blyth*	7.1	55.11	-1.47	55.09	-1.45
		28/03/2019	Blyth	9.5	55.11	-1.46	55.09	-1.43
	Otter	28/03/2019	Blyth	8.1	55.11	-1.48	55.09	-1.44
		28/03/2019	Blyth	7.2	55.11	-1.47	55.09	-1.45
	Replica beam	29/03/2019	Cambois*	7.3	55.14	-1.5	55.16	-1.5
		29/03/2019	Cambois	6.5	55.14	-1.48	55.16	-1.49
		29/03/2019	Cambois	9.1	55.14	-1.47	55.17	-1.49
	Otter	28/03/2019	Cambois	7.9	55.14	-1.47	55.17	-1.5
		28/03/2019	Cambois	10	55.14	-1.47	55.17	-1.49

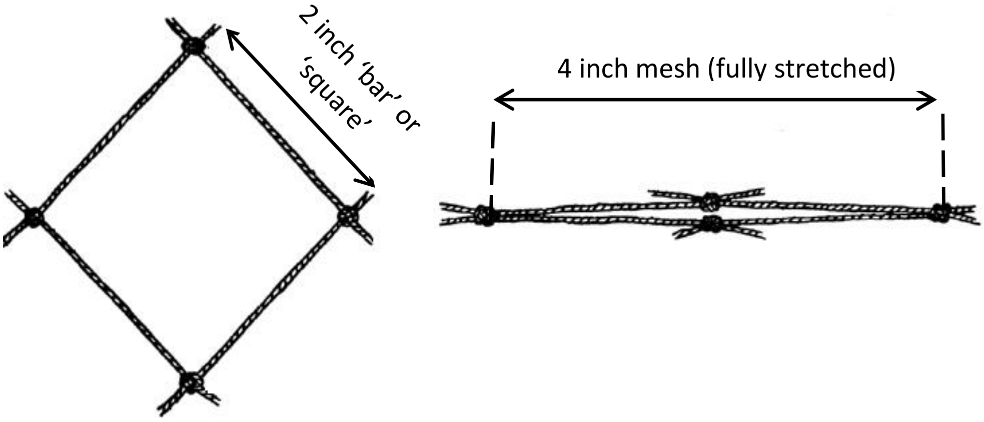


Figure A.1. A two-inch mesh size, open and fully stretched (modified from Schofield, 1948).

Table A.2. Cod-end mesh sizes of large trawl nets commonly used around the British Isles in the late 19th and early 20th century.

Codend mesh sizes	Source
1.5 inch 'square'	Holdsworth,1895
1.5 inch	Collins, 1889
0.75-1.5 inch 'square'	Holt, 1895
1.5 inch 'knot to knot'	Kyle, 1903
1.5 inch	Aflalo, 1904
1.2 inch	Garstang, 1905
1.5 inch 'square'	Wood, 1911
1.5-1.25 inch 'bar'	Davis, 1923
1.5-2.5 inch 'bar'	Alward, 1932

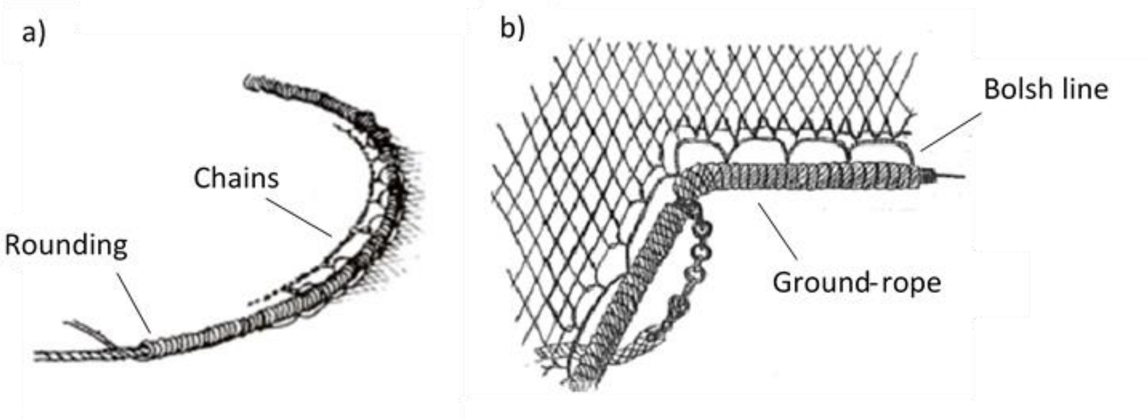


Figure A.2. Drawings of how late 19th century ground-ropes a) were rounded and tickler chains attached (adapted from Butcher, 1980), and b) were set to the net meshes via the bolsh line (adapted from Davis, 1927).

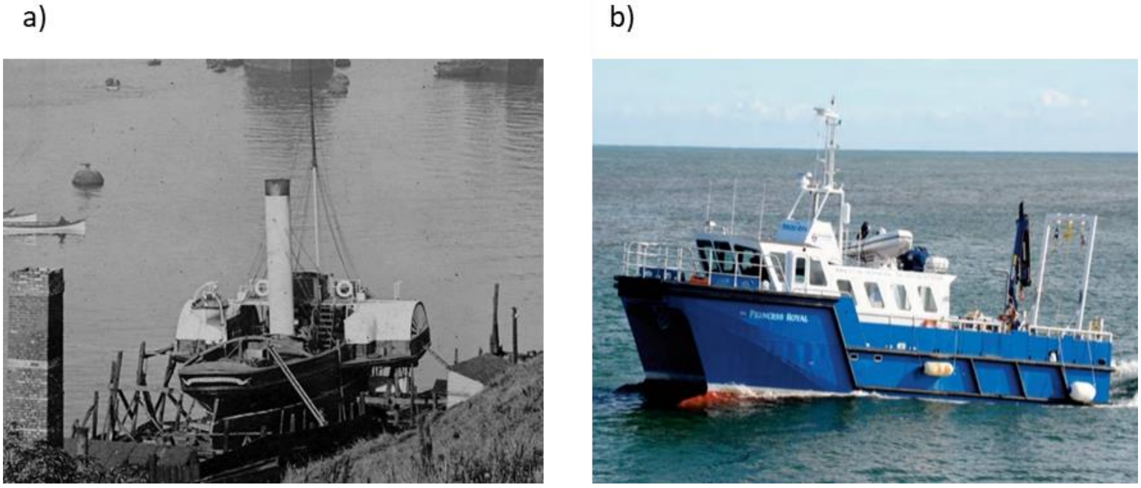


Figure A.3. Photographs of a) the paddle tug *Livingstone* employed by the NSFC for scientific trawling experiments, and b) the RV *The Princess Royal* employed by Newcastle University for 2018-2019 gear trials. The date of the photo is unknown; however, the photograph was taken at Harrison's Yard at Bill Quay on the River Tyne (Tyne Tugs and Tug Builders, n.d.)

Appendix 2

Table A.3. Number of fish with food (Nfood) and the number of empty stomachs (Nempty) separated by quarter and by sampling year. The fish stomach data is derived from the DAPSTOM database unless stated otherwise by the YOS dataset.

Predator	Source	Sampling years	Quarter							
			1		2		3		4	
			Nfood	Nempty	Nfood	Nempty	Nfood	Nempty	Nfood	Nempty
Plaice		1896-1907	213	49	266	22	206	78	81	9
		1956-1958	-	-	490	23	-	-	-	-
		1961-1968	-	-	131	9	1	2	-	-
		1970-1977	-	-	108	37	23	17	-	-
		2002-2006	-	-	351	178	251	127	192	115
Dab		1896-1908	-	-	233	12	158	71	-	-
		2002-2009	-	-	290	99	301	82	55	47
		2010-2015	-	-	383	125	474	122	-	-
Cod		1897-1908	137	32	273	19	11	3	24	1
		1923	-	-	360	-	539	-	-	-
		1953-1959	-	-	195	59	34	2	-	-
		1961-1963	23	4	-	-	290	63	-	-
		1977-1978	-	-	-	-	154	22	-	-
	YOS	1981-1989	1201	214	238	16	1909	301	102	13
		1982-1984	-	-	-	-	-	-	47	1
		1990-1994	1461	18	-	-	-	-	-	-
	YOS	1991	158	36	106	6	130	5	40	-
		2002-2006	-	-	63	8	36	5	152	14
Grey gurnard		1896-1908	19	5	74	-	103	39	-	-
	YOS	1991	59	91	285	37	197	25	103	85
		2002-2006	-	-	701	575	576	152	563	393
Haddock		1902-1908	124	-	442	10	82	-	53	-
	YOS	1981	114	15	173	13	141	22	123	39
		1990-1994	399	91	-	-	-	-	-	-
	YOS	1991	39	18	171	11	219	13	83	28
		2002-2006	-	-	356	110	100	32	103	59
Whiting		1977-1978	-	-	-	-	69	47	-	-
	YOS	1981-1987	521	467	213	38	1045	573	114	105
		1990-1994	887	243	492	137	369	101	200	67
	YOS	1991	67	139	492	137	369	101	200	67
		2002-2006	-	-	1010	991	784	2312	874	2353

Table A.4. Summary of high prey numbers (>50 prey items per stomach on average) recorded in the DAPSTOM and YOS dataset within the study area. These data were excluded from analyses.

Predator	Year	Stomach ID	Nfood	Prey name	Prey category	Prey Number	Average no. of prey per stomach
Grey gurnard	1991	11189	1	Hyperiidae	Amphipods	250	250
		11192	2	Hyperiidae	Amphipods	350	175
		10271	3	Hyperiidae	Amphipods	480	160
		10307	1	Hyperiidae	Amphipods	120	120
		9606	1	Hyperiidae	Amphipods	120	120
		11213	2	Hyperiidae	Amphipods	200	100
		11213	2	Hyperiidae	Amphipods	200	100
		9596	2	Hyperiidae	Amphipods	180	90
		10173	1	Hyperiidae	Amphipods	84	84
		11238	2	Hyperiidae	Amphipods	150	75
		11218	4	Hyperiidae	Amphipods	300	75
		11150	2	Hyperiidae	Amphipods	150	75
		10198	2	Hyperiidae	Amphipods	150	75
		10141	2	Hyperiidae	Amphipods	150	75
		9295	10	Hyperiidae	Amphipods	750	75
		11193	6	Hyperiidae	Amphipods	430	72
		10320	3	Hyperiidae	Amphipods	210	70
		10258	1	Hyperiidae	Amphipods	70	70
		9327	4	Hyperiidae	Amphipods	250	63
		9330	10	Hyperiidae	Amphipods	660	66
		11159	10	Hyperiidae	Amphipods	570	57
		9291	10	Hyperiidae	Amphipods	550	55
		10279	3	Hyperiidae	Amphipods	160	53
		10823	1	Euphausia	Euphausids	50	50
		10258	1	Euphausia	Euphausids	50	50

		9598	4	Dromiacea	Crabs & hermits	200	50
		9606	1	Crustacea	Unidentified crustaceans	50	50
		9596	2	Crustacea	Unidentified crustaceans	160	80
		9597	6	Crustacea	Unidentified crustaceans	400	67
		10269	1	Crustacea	Unidentified crustaceans	60	60
	2005, 2006	END07-05-100\GUG-7	1	Hyperiids	Amphipod	100	100
		END07-05-100\GUG-12	1	Hyperiids	Amphipod	70	70
		END17-06-13\GUG-4	1	Mysids	Other crustaceans	80	80
Cod	1981	945	27	Euphausiidae	Euphausids	13317	493
		1228	11	Euphausiidae	Euphausids	1100	100
		1109	18	Euphausiidae	Euphausids	1710	95
		1067	3	Euphausiidae	Euphausids	250	83
		822	18	Euphausiidae	Euphausids	1135	63
		883	4	Euphausiidae	Euphausids	540	135
		5442	1	Calanoida	Other crustaceans	200	200
		4233	1	*Buccinum undatum*	Other molluscs	150	150
		774	10	*Myoxocephalus scorpius*	Other fish	3660	366
		979	1	Ammodytidae	Sandeels	120	120
Whiting	1981, 1985, 1986	30551	12	Parathemisto	Amphipods	4572	381
		29585	10	Hyperiidea	Amphipods	2600	260
		29584	9	Hyperiidae	Amphipods	1844	205
		30464	14	Parathemisto	Amphipods	1000	71
		29779	1	Hyperiidae	Amphipods	70	70
		29679	9	Hyperiidea	Amphipods	475	53
		29680	8	Hyperiidae	Amphipods	421	53
		30550	11	*Thysanoessa* sp.	Euphausids	1140	104
		30463	11	*Thysanoessa raschi*	Euphausids	990	90
		28080	10	*Meganyctiphanes norvegica*	Euphausids	775	78
		28115	10	*Meganyctiphanes norvegica*	Euphausids	700	70
		28674	10	Calanoida	Other crustaceans	2024	202
		28765	9	Calanoida	Other crustaceans	1260	140

	28719	7	Calanoida	Other crustaceans	680	97
	31360	1	Cumacea	Other crustaceans	83	83
	28771	5	Chaetognatha	Other invertebrates	350	70
	30464	14	Chaetognatha	Other invertebrates	900	64
	30447	20	Oikopleura	Other invertebrates	1000	50
	30455	6	Crustacea	Unidentified crustaceans	486	81
1991	35992	4	Parathemisto	Amphipods	2252	563
	35992	6	Parathemisto	Amphipods	3112	519
	35992	9	Parathemisto	Amphipods	2432	270
	35992	8	Parathemisto	Amphipods	1970	246
	35946	9	Parathemisto	Amphipods	1647	183
	34544	10	Parathemisto	Amphipods	1741	174
	34544	5	Parathemisto	Amphipods	853	171
	34596	1	Parathemisto	Amphipods	156	156
	34596	5	Parathemisto	Amphipods	742	148
	36003	9	Parathemisto	Amphipods	764	85
	34645	3	Parathemisto	Amphipods	244	81
	35500	6	Parathemisto	Amphipods	422	70
	34941	5	Parathemisto	Amphipods	348	70
	34952	4	Parathemisto	Amphipods	278	70
	34887	5	Parathemisto	Amphipods	337	67
	35292	7	Parathemisto	Amphipods	456	65
	35509	5	Parathemisto	Amphipods	296	59
	35391	4	Parathemisto	Amphipods	207	52
	34596	8	Euphausiidae	Euphausids	798	100
	32226	5	Thysanoessa	Euphausids	436	87
	35924	7	Euphausiidae	Euphausids	600	86
	32232	8	Euphausiidae	Euphausids	523	65
	32232	8	Euphausiidae	Euphausids	523	65
	34919	9	Euphausiidae	Euphausids	550	61
	34930	7	Euphausiidae	Euphausids	357	51

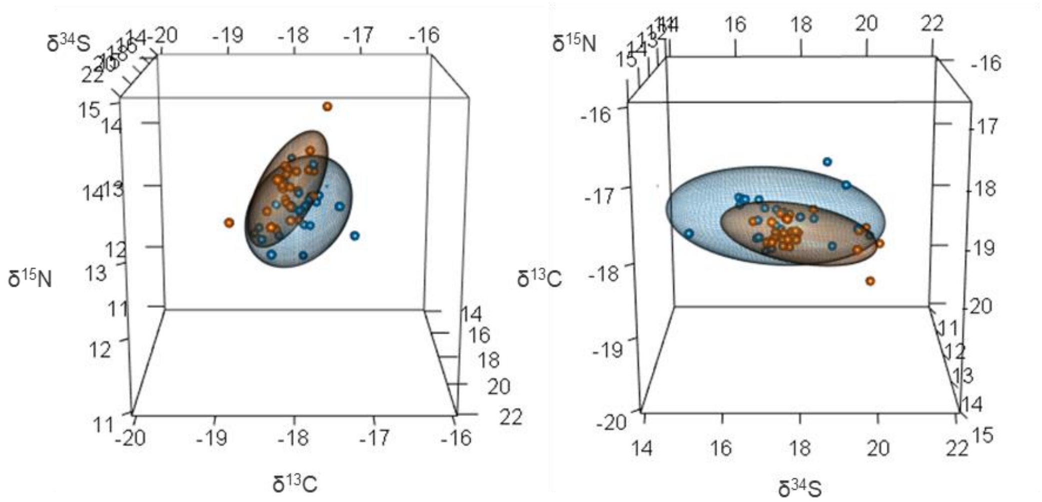
32231	10	*Thysanoessa inermis*	Euphausids	551	55
35513	4	Calanoida	Other crustaceans	4319	1080
34543	10	Calanoida	Other crustaceans	4816	482
35992	7	Calanoida	Other crustaceans	1883	269
35344	10	Calanoida	Other crustaceans	2113	211
35946	6	Calanoida	Other crustaceans	1141	190
34596	2	Calanoida	Other crustaceans	210	105
34596	4	Decapoda	Other crustaceans	469	117
34596	5	Decapoda	Other crustaceans	491	98
35296	5	Decapoda	Other crustaceans	340	68
34887	5	Decapoda	Other crustaceans	255	51
34543	11	Oikopleura	Other invertebrates	53000	4818
34543	7	Oikopleura	Other invertebrates	26000	3714
35513	9	Oikopleura	Other invertebrates	17000	1889
35992	10	Oikopleura	Other invertebrates	6408	641
34596	4	Oikopleura	Other invertebrates	600	150
35944	10	Chaetognatha	Other invertebrates	820	82
34645	3	Chaetognatha	Other invertebrates	211	70
34543	9	*Spiratella retroversa*	Other molluscs	18560	2062
35513	4	*Spiratella retroversa*	Other molluscs	7850	1963
35992	9	*Spiratella retroversa*	Other molluscs	3850	428
35992	6	*Spiratella retroversa*	Other molluscs	1690	282
35344	3	*Spiratella retroversa*	Other molluscs	610	203
35344	10	*Spiratella retroversa*	Other molluscs	1960	196
34544	10	*Spiratella retroversa*	Other molluscs	1595	160
35924	10	*Spiratella retroversa*	Other molluscs	800	80
35391	4	*Spiratella retroversa*	Other molluscs	300	75
31860	6	*Spiratella retroversa*	Other molluscs	415	69
31859	4	*Spiratella retroversa*	Other molluscs	270	68
34887	11	*Spiratella retroversa*	Other molluscs	740	67
35348	4	*Spiratella retroversa*	Other molluscs	233	58

	2006	END11-06-90\WHG-5	1	Larval sandeel	Sandeels	85	85
Haddock	1981	11863	7	Hyperiidae	Amphipods	3000	429
		12345	1	Amphiuridae	Echinoderms	200	200
		12130	1	Euphausiidae	Euphausids	128	128
		12251	1	*Meganyctiphanes norvegica*	Euphausids	95	95
		12253	10	*Meganyctiphanes norvegica*	Euphausids	943	94
		12170	7	*Meganyctiphanes norvegica*	Euphausids	621	89
		12095	2	*Meganyctiphanes norvegica*	Euphausids	163	82
		11920	2	Calanoida	Other crustaceans	3900	1950
		11863	7	Calanoida	Other crustaceans	9700	1386
		11850	3	Calanoida	Other crustaceans	4000	1333
		11782	3	Calanoida	Other crustaceans	2800	933
		11794	9	Calanoida	Other crustaceans	6000	667
		11730	10	Calanoida	Other crustaceans	3400	340
		11907	4	*Ammodytes tobianus*	Sandeels	234	59
	1991	16750	1	Parathemisto	Amphipods	750	750
		16750	1	Parathemisto	Amphipods	420	420
		16750	1	Parathemisto	Amphipods	370	370
		16750	1	Parathemisto	Amphipods	322	322
		16750	5	Parathemisto	Amphipods	1440	288
		16750	5	Parathemisto	Amphipods	1400	280
		16750	1	Parathemisto	Amphipods	210	210
		16697	4	Parathemisto	Amphipods	720	180
		16697	1	Parathemisto	Amphipods	156	156
		16697	5	Parathemisto	Amphipods	700	140
		16697	4	Parathemisto	Amphipods	560	140
		16697	1	Parathemisto	Amphipods	130	130
		16697	1	Parathemisto	Amphipods	111	111
		15544	5	Parathemisto	Amphipods	550	110
		16727	1	Parathemisto	Amphipods	98	98
		16729	1	Parathemisto	Amphipods	93	93

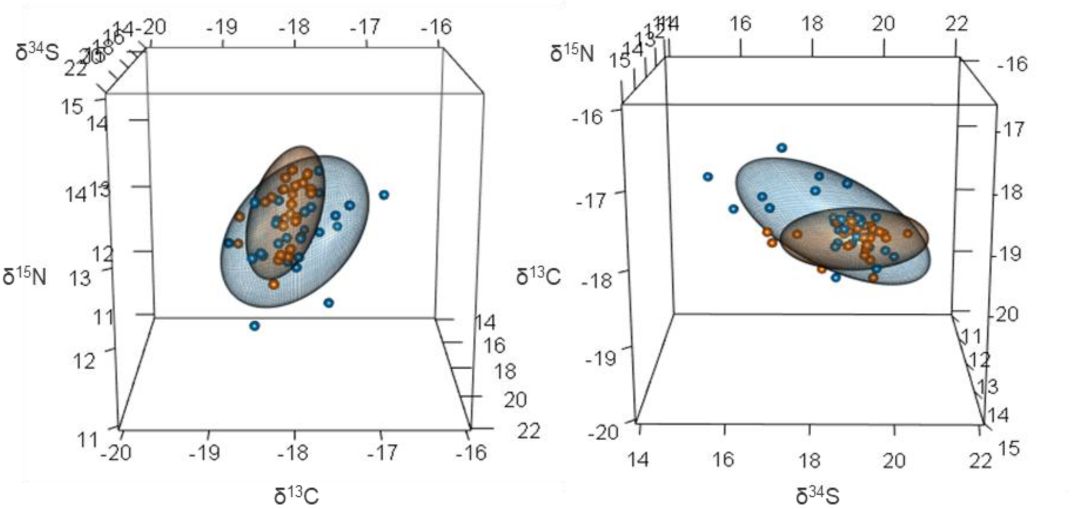
	16705	1	Parathemisto	Amphipods	74	74
	16750	1	*Parathemisto compressa*	Amphipods	500	500
	16750	1	Calanoida	Other crustaceans	1840	1840
	16750	3	Calanoida	Other crustaceans	1750	583
	16750	5	Calanoida	Other crustaceans	2600	520
	16750	1	Calanoida	Other crustaceans	440	440
	16750	3	Calanoida	Other crustaceans	1200	400
	16750	1	Calanoida	Other crustaceans	250	250
	16750	2	Calanoida	Other crustaceans	470	235
	16750	3	Calanoida	Other crustaceans	560	187
	16698	3	Calanoida	Other crustaceans	205	68
	16750	1	Hydrobia	Other molluscs	250	250
	16812	1	Hydrobia	Other molluscs	86	86
2004	CORY09-04-123\HAD-8	1	Crab	Crabs &hermits	750	750
	CORY09-04-123\HAD-5	1	Larval crab	Crabs &hermits	200	200
	CORY09-04-123\HAD-5	1	Aphrodite	Polychaetes	1	1

Appendix 3

a) Blyth Bay



b) Cambois Bay



c) Druridge Bay

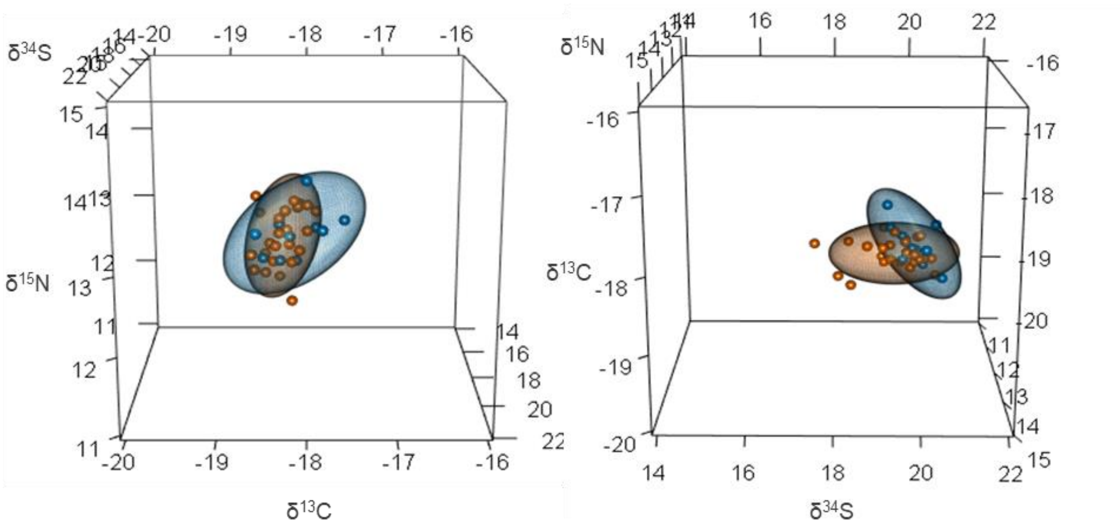
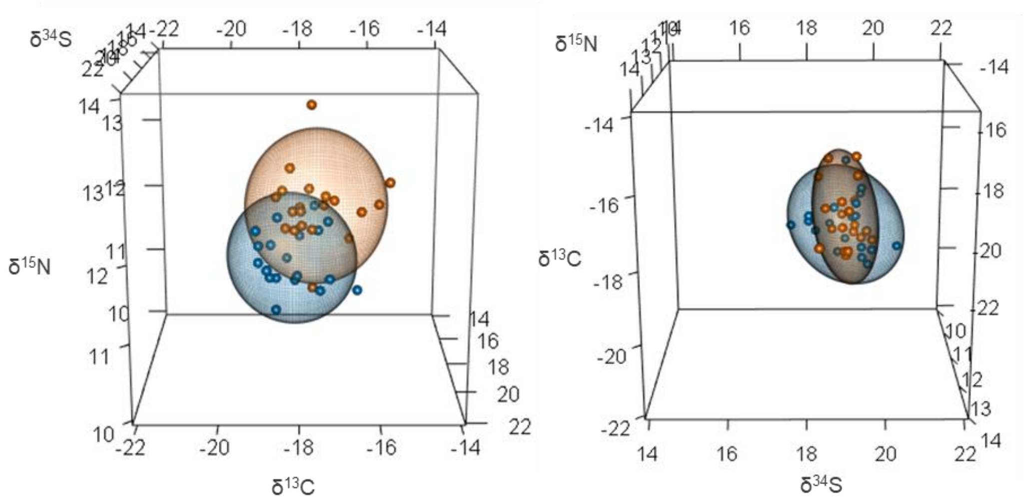
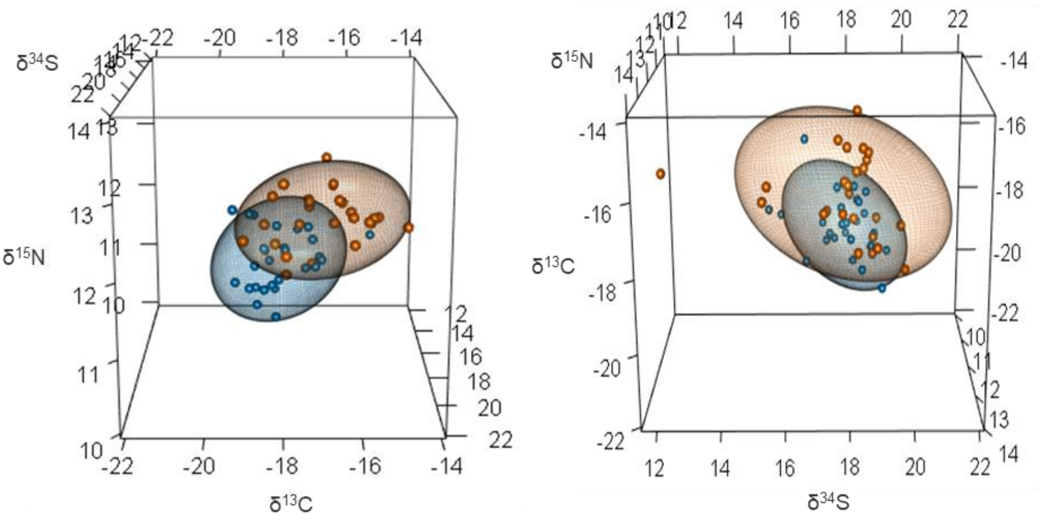


Figure A.4. 75% ellipsoids using δ^{13}C, δ^{15}N and δ^{34}S (‰) stable isotope data for plaice (blue) and dab (orange) dorsal muscle at a) Blyth Bay, b) Cambois Bay and c) Druridge Bay.

a) Blyth Bay



b) Cambois Bay



c) Druridge Bay

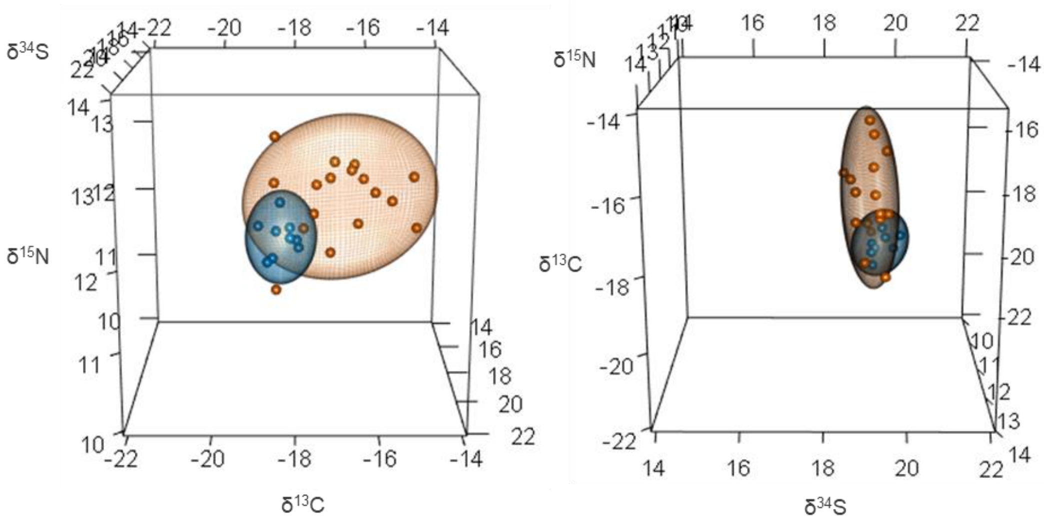


Figure A.5. 75% ellipsoids using $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ (‰) stable isotope data for dab (blue) and dab (orange) liver tissue at a) Blyth Bay, b) Cambois Bay and c) Druridge Bay.

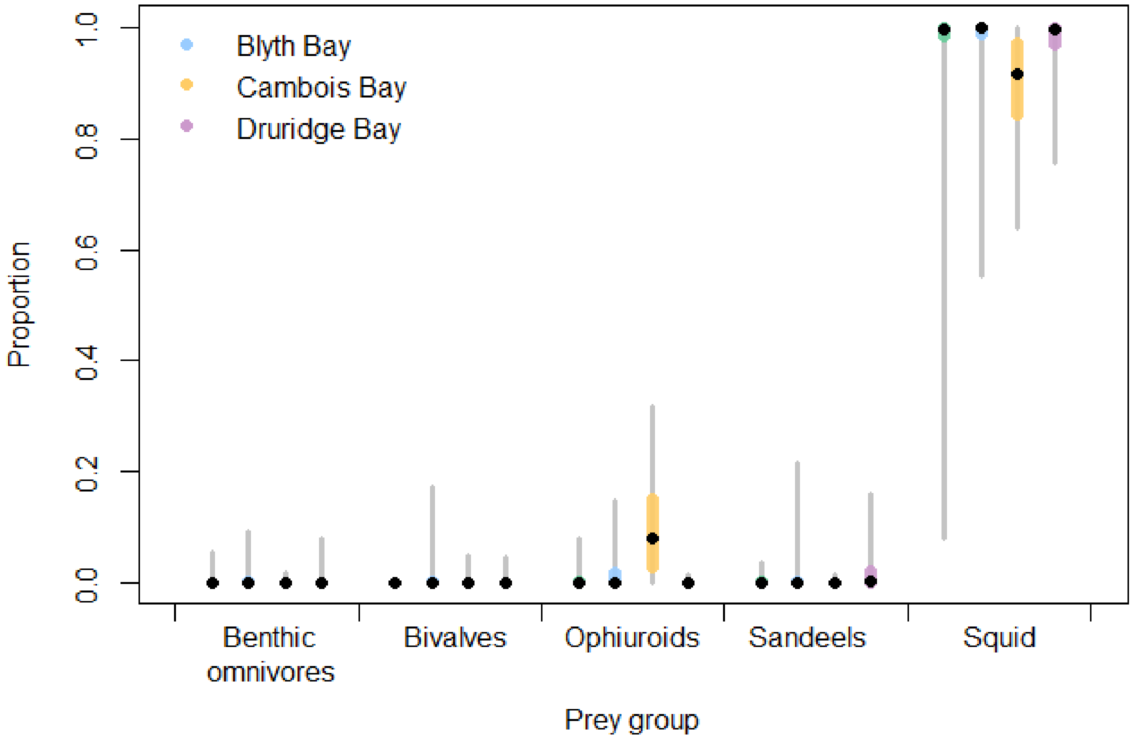


Figure A.6. Proportional contribution of five prey resources based on δ^{13}C, δ^{15}N and δ^{34}S mixing model estimates and trophic discrimination factors for dab liver. Thin grey bars represent 2.5%-97.5% credible intervals and thick bars represent 25%-75% around the modal contribution of each prey resource. Black dots represent the median (50%).

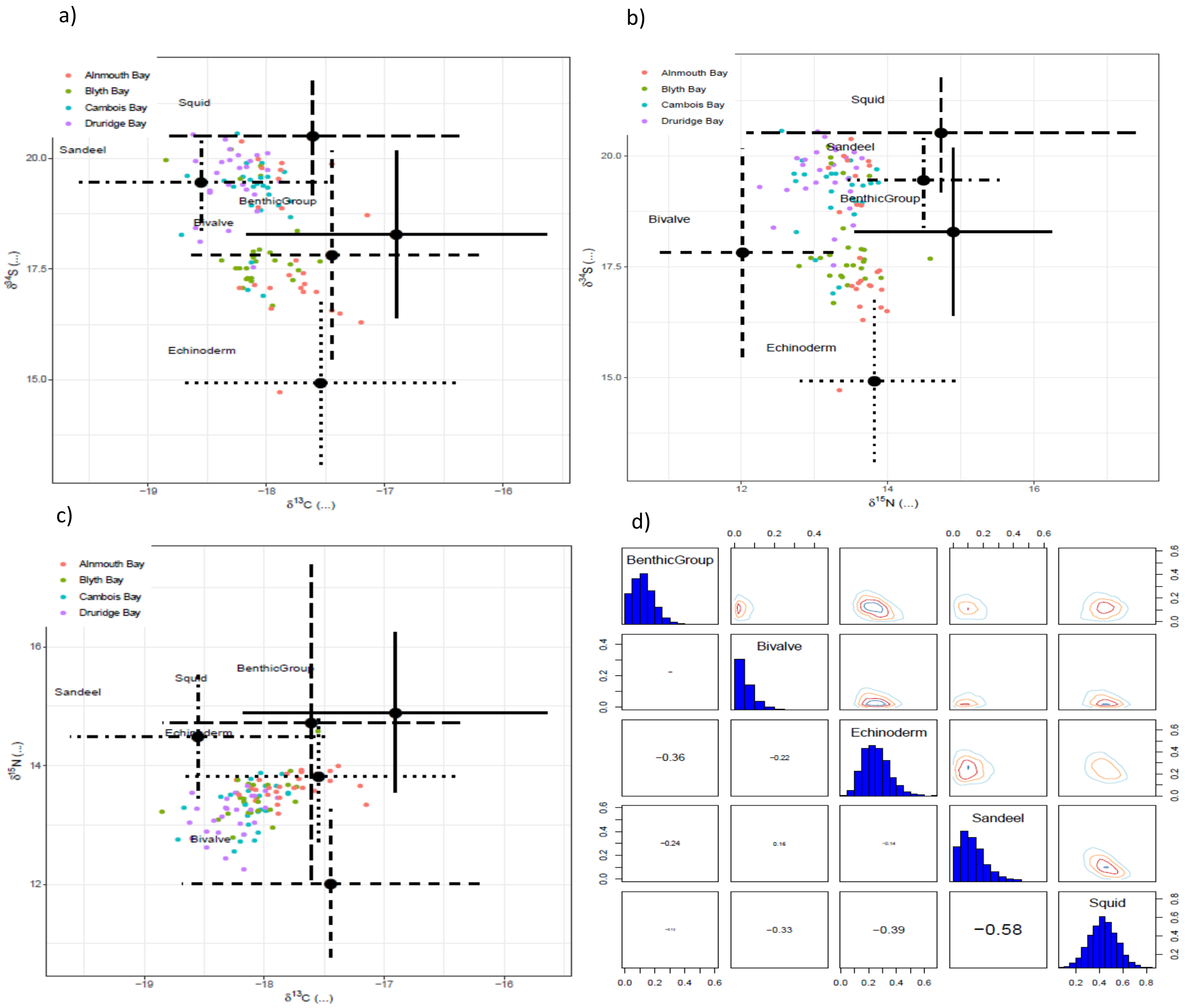


Figure A.7. Mixing model (a-c) isospace plots of δ^{13}C, δ^{15}N and δ^{34}S (‰) for dab dorsal muscle with their prey and (d) pair plots showing correlations between each prey pair.

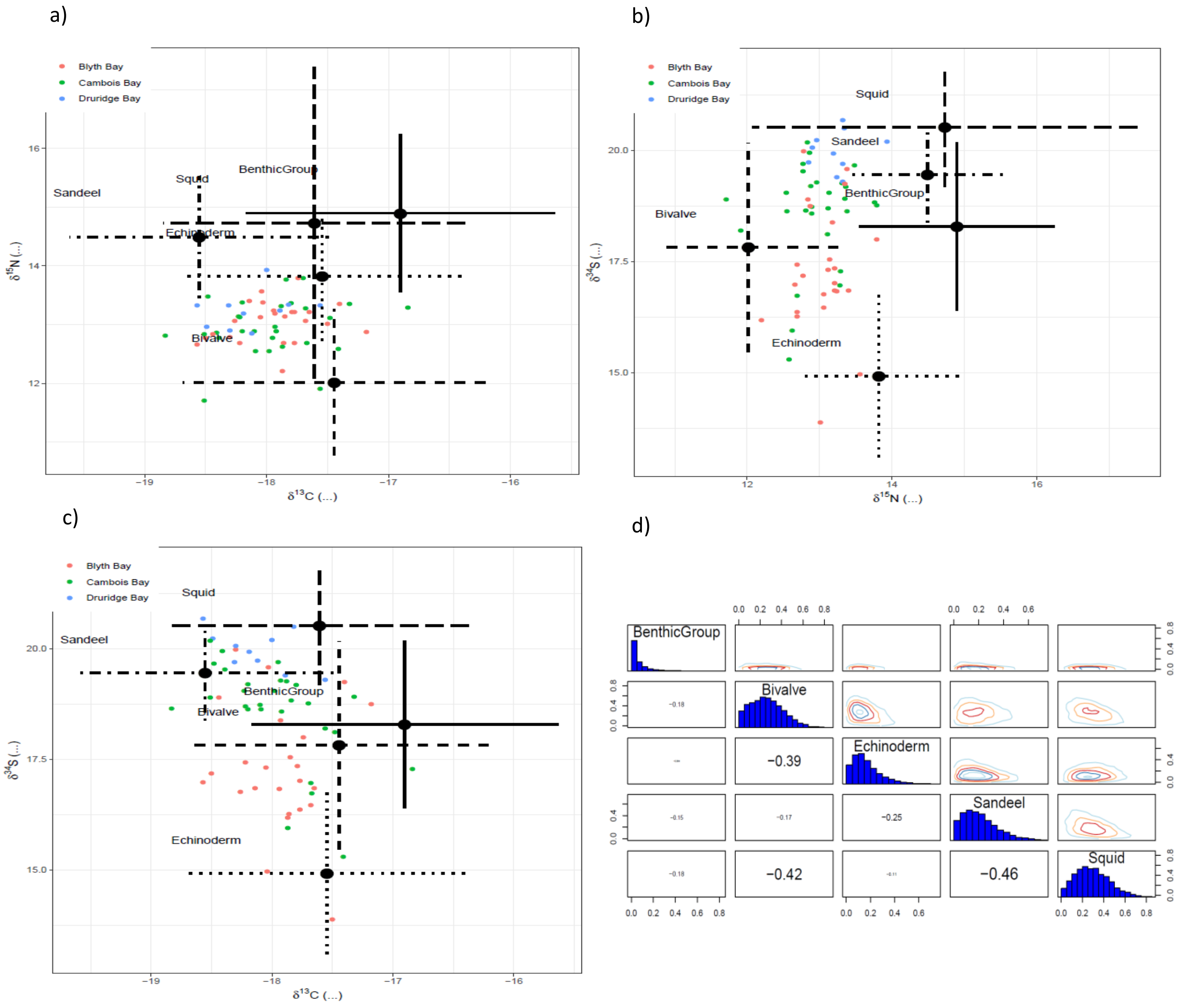


Figure A.8. Mixing model (a-c) isospace plots of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ (‰) for plaice dorsal muscle with their prey and (d) pair plots showing correlations between each prey pair.

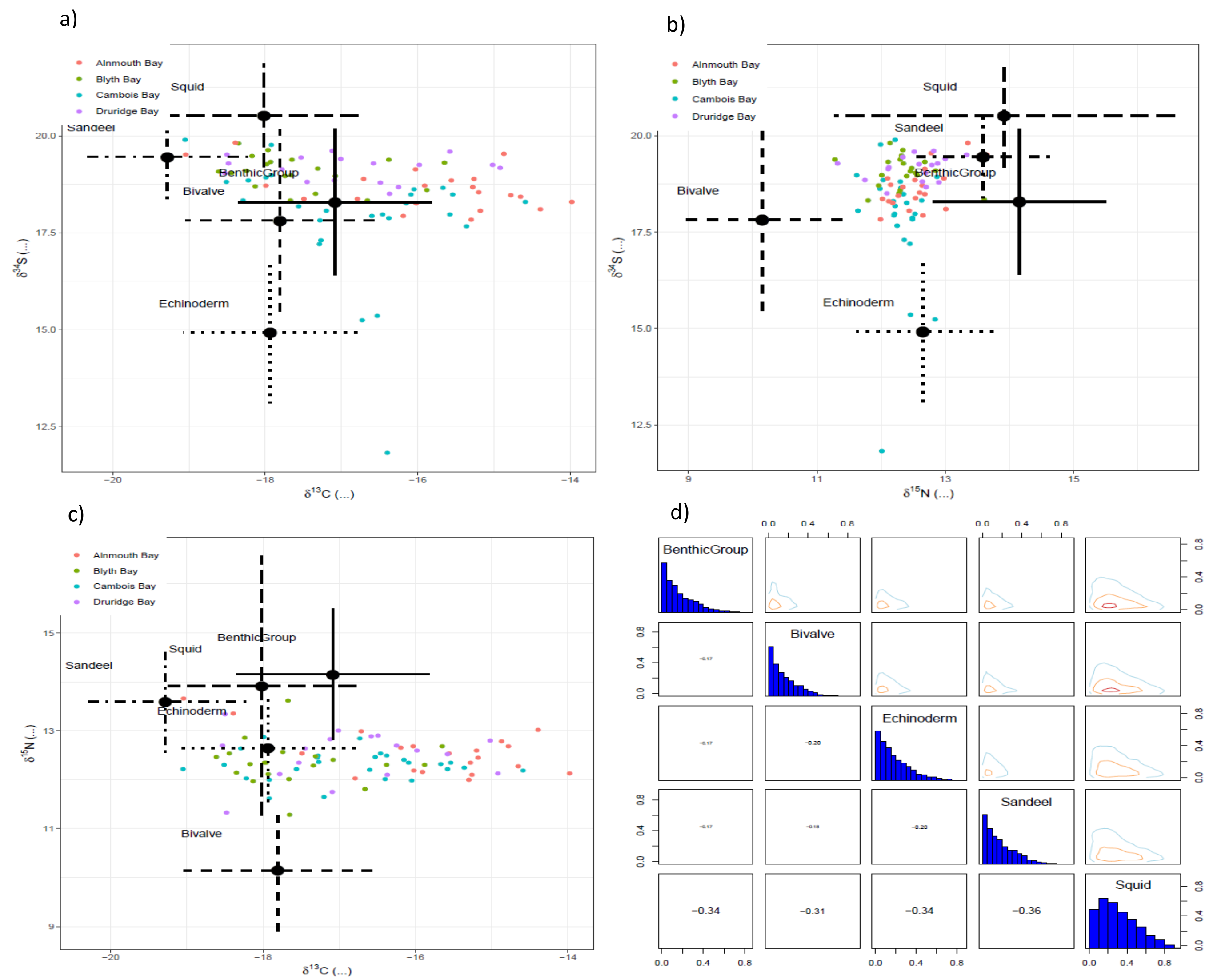


Figure A 9. Mixing model (a-c) isospace plots of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ (‰) for dab liver with their prey and (d) pair plots showing correlations between each prey pair.

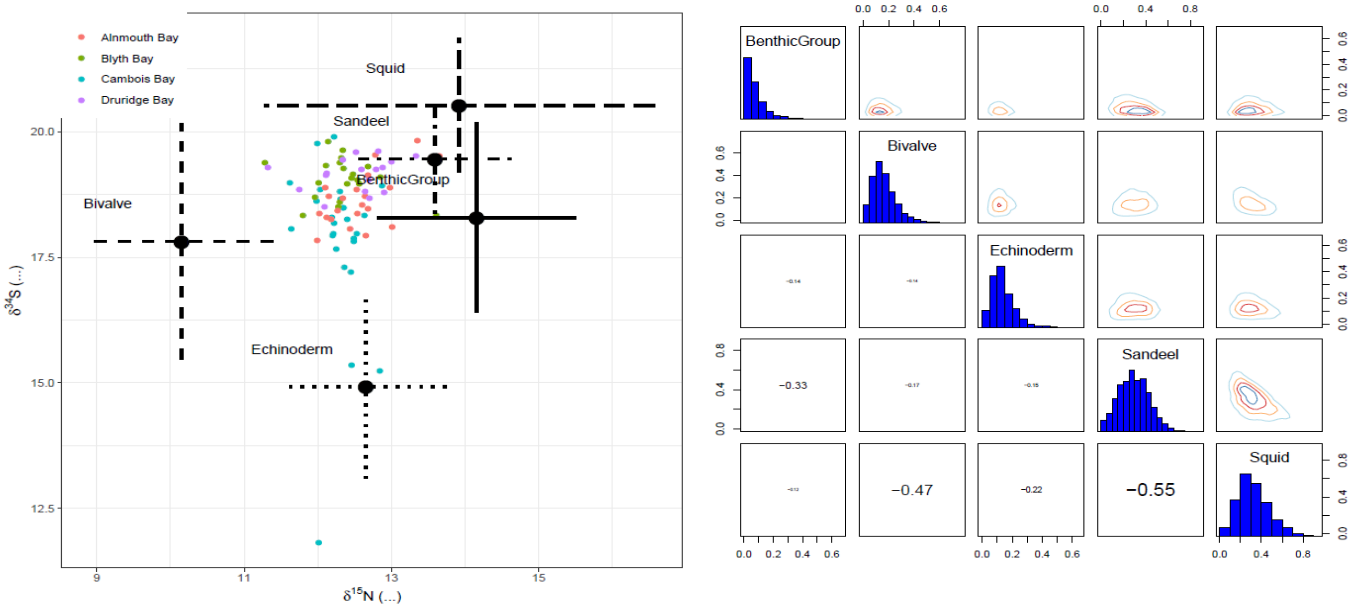


Figure A.10. Mixing model (a-c) isospace plots of δ15N and δ34S (‰) for dab liver with their prey and (d) pair plots showing correlations between each prey pair.

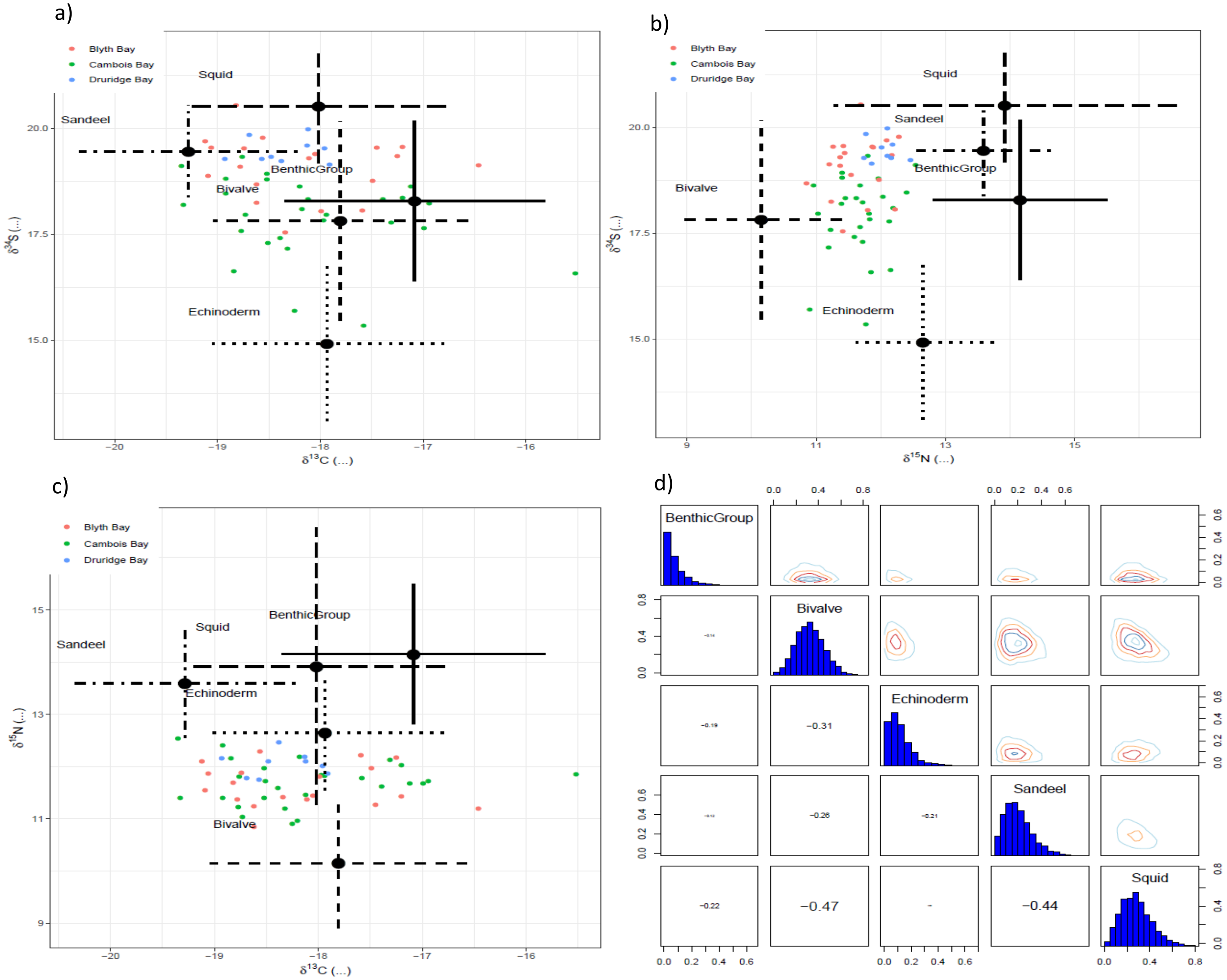


Figure A.11. Mixing model (a-c) isospace plots of δ^{13}C, δ^{15}N and δ^{34}S (‰) for plaice liver with their prey and (d) pair plots showing correlations between each prey pair.

Table A.5. Bayesian mean posteriors and standard deviations of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ isotopes for plaice dorsal muscle and liver tissue at Cambois Bay by month. 95% confidence intervals (CI) are given in parentheses.

Tissue	Month	$\delta^{13}C$		$\delta^{15}N$		$\delta^{34}S$	
		Mean (CI)	S.D	Mean (CI)	S.D	Mean (CI)	S.D
Dorsal	May	-17.76(-17.82, -17.73)	0.31(0.25, 0.32)	13.08(13.01, 13.14)	0.45(0.37, 0.46)	18.33(18.20, 18.43)	0.84(0.67, 0.84)
	July	-17.96(-18.02, -17.90)	0.48(0.41, 0.49)	12.95(12.89, 13.02)	0.51(0.43, 0.53)	18.57(18.45, 18.74)	1.19(1.04, 1.23)
	August	-18.17(-18.24, -18.11)	0.45(0.35, 0.45)	13.17(13.13, 13.22)	0.31(0.25, 0.31)	17.69(17.52, 17.83)	1.07(0.87, 1.09)
	September	-18.09(-18.14, -18.05)	0.26(0.29, 0.35)	13.44(13.39, 13.48)	0.36(0.30, 0.36)	17.70(17.58, 17.89)	1.28(1.08, 1.31)
Liver	May	-17.74(-17.80, -17.69)	0.40(0.33, 0.41)	12.11(12.00, 12.18)	0.62(0.52, 0.64)	18.88(18.81, 18.99)	0.63(0.51, 0.64)
	July	-18.09(-18.21, -17.99)	0.90(0.75, 0.91)	11.68(11.61, 11.73)	0.47(0.40, 0.48)	17.88(17.79, 18.02)	1.01(0.87, 1.05)
	August	-18.16(-18.26, -18.02)	0.86(0.72, 0.89)	11.96(11.91, 12.03)	0.41(0.33, 0.41)	19.13(19.02, 19.23)	0.56(0.67, 0.82)
	September	-16.98(-17.20, -16.73)	1.69(1.36, 01.70)	12.26(12.21, 12.33)	0.41(0.33, 0.41)	19.45(19.37, 19.54)	0.58(0.48, 0.59)

Table A.6. Mean δ^{13}C, δ^{15}N and δ^{34}S (‰) values (± standard error) of prey groups sampled at each site between May and July.

Prey group		Druridge Bay				Alnmouth Bay		
	n	δ^{13}C	δ^{15}N	δ^{34}S	*n*	δ^{13}C	δ^{15}N	δ^{34}S
Bivalves	6	-18.60 ± 0.45	8.64 ± 0.45	18.47 ± 0.23	6	-18.19 ± 0.37	8.58 ± 0.37	17.28 ± 0.85
Crabs	11	-17.80 ± 0.26	12.60 ± 0.08	19.62 ± 0.38	4	-18.63 ± 0.28	13.40 ± 0.38	19.20 ± 0.75
Ophiuroids	4	-18.69 ± 0.21	11.12 ± 0.17	14.16 ± 0.92	6	-19.19 ± 0.15	10.58 ± 0.16	15.82 ± 0.42
Polychaetes	5	-17.44 ± 0.25	12.18 ± 0.25	17.53 ± 0.38	5	-17.05 ± 0.12	11.54 ± 0.13	18.03 ± 0.32
Sandeels	5	-20.17 ± 0.16	11.92 ± 0.11	19.30 ± 0.20	7	-19.78 ± 0.09	12.21 ± 0.07	19.37 ± 0.19
Shrimps	5	-17.96 ±0.40	12.58 ± 0.53	17.52 ± 0.55	5	-17.38 ± 0.19	13.03 ± 0.17	17.92 ± 0.22
Squid	2	-18.36 ± 0.70	13.57 ± 1.98	20.29 ± 0.88	1	-18.91	11.81	21.6

Prey group		Cambois Bay				Blyth Bay		
	n	δ^{13}C	δ^{15}N	δ^{34}S	*n*	δ^{13}C	δ^{15}N	δ^{34}S
Bivalves	7	-18.93 ± 0.13	8.41 ± 0.17	18.55 ± 0.21	3	-18.32 ± 0.39	8.85 ± 0.39	14.37 ± 2.55
Crabs	6	-17.99 ± 0.13	12.64 ± 0.18	18.28 ± 0.18	6	-18.20 ± 0.33	13.27 ± 0.16	20.07 ± 0.90
Ophiuroids	2	-18.04 ± 0.39	11.31 ± 0.06	12.84 ± 0.52	3	-18.34 ± 0.16	11.40 ± 0.24	15.18 ± 0.13
Polychaetes	4	-17.64 ± 0.28	12.49 ± 0.22	17.31 ± 0.69	5	-17.94 ±0.15	11.90 ± 0.11	17.00 ± 0.27
Sandeels	4	-20.43 ± 0.15	11.58 ± 0.06	19.86 ± 0.12	6	-20.03 ± 0.11	12.03 ± 0.05	19.41 ± 0.11
Shrimps	4	-17.92 ± 0.22	13.64 ± 0.72	18.16 ± 0.61	5	-18.37 ± 0.67	11.43 ± 0.60	16.83 ± 1.07
Squid	2	-19.15 ± 0.49	11.30 ± 2.33	20.20 ± 0.24	-	-	-	-

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