Long-term change in a North Sea inshore fish assemblage between 1899–1913 and 2018–2019

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ABSTRACT: Marine communities have been impacted by human activities for centuries, yet historical data are rarely incorporated into modern conservation efforts and restoration targets. For inshore waters, survey data sets are typically lacking because they extend back by only a few decades, despite their ecological significance as nursery grounds for many fish species. We investigated long-term change in a demersal fish assemblage from inshore waters of the Northumberland coast (UK). We collated unique historical data (1899–1913) that were sampled using a wooden beam trawl during scientific trawling investigations, shortly after the onset of widespread mechanised trawling in the North Sea. Twelve decades later (2018–2019), we re-surveyed the same bays using a modern otter trawl. The results revealed marked declines in the abundance and diversity of the entire fish and flatfish assemblage as well as among individual species. Elasmobranchs and formerly abundant species such as grey gurnard *Eutrigla gurnardus* were completely absent in contemporary surveys, while dab *Limanda limanda* and plaice *Pleuronectes platessa* were the most dominant species in both periods. Changes were also detected in the size distributions of the entire fish and flatfish assemblages, with proportionally fewer large individuals recorded in contemporary surveys. These findings suggest that over a century of trawling and climate change, combined with pollution, habitat alteration and increased predation risk are likely contributors to changes in the inshore fish assemblage. This work provides further evidence of long-term decline in North Sea inshore waters and offers an invaluable benchmark for improving coastal ecosystem status.

KEY WORDS: Inshore fisheries · Long-term change · Demersal fish · Historical trawl surveys

1. INTRODUCTION

Commercial fishing practices have undergone rapid changes in trawl gear technology, effort and target species over the last 2 centuries in European waters (Engelhard 2008). Early trawls were towed across the seabed by sail-powered fishing smacks close to shore until the mid-19th century (Alward 1932). They were soon displaced by steam-powered fishing vessels in the 1880s, which marked the rapid growth of trawling effort across the North Sea (Robinson 1996, Engelhard 2008). The addition of steam power enabled vessels to fish for longer durations, work previously unfished grounds further offshore at deeper depths and tow much larger trawl nets (Thurstan et al. 2010). Over the 20th century, fishers responded to falling catches by trawling more intensively and switching to less favourable fish species (Pauly et al. 1998), which in turn has

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masked local depletions and disappearances of target species (Roberts 2007).

Trawling is often associated with declines in the abundances of demersal populations or assemblages (Rijnsdorp et al. 1996, Novaglio et al. 2020, Currie et al. 2020) as well as reduced diversity and increasing dominance of particular species (Greenstreet & Hall 1996, Heath & Speirs 2012). It is often larger, long-lived and late-maturing species that are more vulnerable to sustained trawling, whereas smaller species that mature faster tend to be more resilient and rebound faster (Jennings et al. 1999). Long-term studies have revealed gradual shifts in target and by-catch species towards lower trophic species in some localities (Pauly et al. 1998, Thurstan et al. 2015), accelerated by habitat modification and depletion of their predators due to trawling (Brown & Trebilco 2014). For example, the Firth of Clyde in Scotland once sustained diverse fisheries for species including cod *Gadus morhua*, turbot *Scophthalmus maximus* and flounder *Platichthys flesus* in the early 19th century, whereas invertebrates such as the Norway lobster *Nephrops norvegicus* and scallops *Pecten maximus* are the only commercial fisheries that remain today (Thurstan & Roberts 2010). Similarly, in the Gulf of Maine, removal of large predatory species such as Atlantic cod and haddock *Melanogrammus aeglefinus* by fishing has left American lobsters *Homarus americanus* as the principal resource (Steneck et al. 2011). Such studies are often based on information collected long after fisheries started impacting marine populations (Lotze & Worm 2009), yet they strengthen understanding of past ecosystem states at community and species levels (Greenstreet & Rogers 2006).

Climate change has also caused major fluctuations in the abundance and distribution of fish populations. Sea surface temperatures of the North Atlantic and coastal waters of the British Isles have increased more rapidly than adjacent seas over the last century (MacKenzie & Schiedek 2007). Consequently, marked changes in North Sea fish assemblages, including distributional shifts in mean latitudes and/or depths (Perry et al. 2005, Dulvy et al. 2008) and increasing abundances of southern species and those with smaller body sizes (Rijnsdorp et al. 2009, Engelhard et al. 2011a), have been attributed to warming, as have synchronous, long-term shifts in growth (Baudron et al. 2014) and recruitment dynamics (Capuzzo et al. 2018). Increasing temperatures can indirectly disrupt the timings and locations of key spawning events of fish and invertebrates (Beaugrand et al. 2003), leading to potential trophic

mismatch in the timings between prey availability and predators (Régnier et al. 2019). Given predictions of rising temperatures over the next century (Sheppard 2004), together with the long-lasting 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 longer-term effects of anthropogenic disturbance on marine systems, and are based on data spanning the last few decades (Mackinson 2002, Pinnegar & Engelhard 2008), thus encompassing populations that are far from pristine. Historical reference points can provide useful benchmarks for recovery by providing valuable context on current ecological states (Pinnegar & Engelhard 2008, Thurstan et al. 2015) as well as help to unravel the mechanisms behind these changes (Pickett 1989). However, the systematic collection of national fisheries statistics did not begin until the 1880s when trawling was already widespread (Russell & Edser 1925, Thurstan et al. 2014), thus well after the onset of large-scale impacts. It is rare for researchers to unearth detailed historical fishery records that allow comparison with contemporary data (Rijnsdorp et al. 1996, Currie et al. 2020). Such information provides stakeholders with a historical perspective for biodiversity restoration and rebuilding fish stocks for their potential long-term recovery.

The Northumberland coastline, north-east England, consists of a sequence of wide bays separated by rocky stretches of cliffs and supports a wide range of ecologically important habitats and species (Bennett & Foster-Smith 1998). The coastal zone has supported juvenile and adult populations of commercially and ecologically important species such as European plaice *Pleuronectes platessa* and common dab *Limanda limanda* for centuries (Meek 1895, 1896), but has been subject to various human pressures during this time, including pollution (Eagle et al. 1979), dredging (Norman 1863) and fishing (Walmsley & Pawson 2007, Thurstan et al. 2014). Fishing has traditionally been an important part of the economy since fishing villages were established along the Northumberland coast from the late 18th century (Muirhead 1992), but the industry has declined in recent decades (Frid et al. 1991). In the late 19th century, fishers used nearshore static gears for crabs (e.g. edible crab *Cancer pagurus*) and European lobster *Homarus gammarus*, drift nets for Atlantic herring *Clupea harengus* and long-lines for plaice, cod, haddock, turbot, ling *Molva molva* and Atlantic whiting *Merlangius mer-*

langus, among other species (Meek 1896). At the turn of the 20th 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 in deeper, muddier waters, has assumed greater importance while whitefish landings have declined, although are often landed as bycatch in the *Nephrops* fishery (Walmsley & Pawson 2007). Potting, which includes using traditional creels and parlour pots targeting lobster, edible crab and to a lesser extent velvet crab *Necora puber*, is now the most important fishing practice off the Northumberland coast, with highest effort occurring in the summer months (Stephenson et al. 2018).

In the late 1880s, local Sea Fisheries Committees were established in England and Wales, and a 3 mile (~4.8 km) territorial limit was established around the coastline to prohibit trawling and protect inshore nursery and spawning grounds (Allen 1897). On the Northumberland coast, the ban came into effect in 1891 (Meek 1895, 1899a). In subsequent years (1892−1913), this legislation prompted naturalists of the Northumberland Sea Fisheries Committee (NSFC) and the Dove Marine Laboratory, Cullercoats, to set up a series of scientific trawling investigations and collect information on species composition, size distributions and 'food of fishes' in inshore waters (Meek 1895−1913, 1899a,b). To our knowledge, these investigations represent one of the earliest fisheries-independent trawl surveys conducted in temperate inshore waters. Despite their proximity to shore and ecological importance as nursery grounds, only a few long-term trawl surveys exist in shallow (<40 m depth) inshore waters (e.g. Rogers & Ellis 2000, McHugh et al. 2011, Heath & Speirs 2012). In the North Sea, investigations of long-term change in trawled fish communities have largely focused on deeper waters over vast spatial areas (e.g. Rijnsdorp et al. 1996, Sguotti et al. 2016). These early inshore trawl surveys thus provide a rare opportunity to compare historical records with contemporary survey data by revisiting inshore waters more than a century later.

In this study, we contrast historical records from NSFC trawl surveys (1899−1913) with data collected in contemporary surveys (2018−2019) to elucidate long-term change in the community structure of an inshore fish assemblage. Given the known transformative effects of fishing on marine communities, we expected that trawling caused a reduction in the abundance, diversity and size distribution of commercial and non-target species (Hypothesis 1). With marked increases in temperature in the North Sea over the past century, we also expected that climate change induced a shift in fish distribution patterns, contributing to the overall restructuring of the inshore fish assemblage (Hypothesis 2). Results are discussed in light of trawling, regional climate change and other possible drivers. We address the challenge of comparing historical and contemporary fisheries data due to differences in gear technology and methods over time (Currie et al. 2020). This work reinforces the value of using historical and contemporary data to provide a baseline for ecosystem recovery in inshore waters.

2. MATERIALS AND METHODS

2.1. Study area

Five inshore bays, namely Skate Roads, Alnmouth, Druridge, Cambois and Blyth Bays (Fig. 1), were originally surveyed by the NSFC between 1892 and 1913. The bays are shallow inlets consisting of soft, sandy sediments fringed by adjacent rocky habitats in water depths of <20 m. Contemporary surveys were also conducted in all 5 bays between May and September 2018 and 2019 (Fig. 1). All 5 bays now reside in a number of marine protected areas (MPAs) that have been designated to protect marine biodiversity, including the Berwick to St. Mary's Marine Conservation Zone (MCZ) (https://www.gov.uk/government/publications/marine-conservation-zones-berwick-to-st-marys). The most northerly bay, Skate Roads, also resides within the Berwickshire and North Northumberland Coast Special Area of Conservation (BNNC SAC; https://www.xbordercurrents.co.uk/mpas/bnnc-sac/), whereas the other 4 bays are located within the Coquet to St. Mary's MCZ (https://www.gov.uk/government/publications/marine-conservation-zone-coquet-to-st-marys). Commercial fishing in the bays is managed by the Northumberland Inshore Fisheries and Conservation Authority (NIFCA) (Fig. 1b), and, following a review of their byelaws in 2015 and 2018, a permit is required to trawl within their jurisdictional area (0−6 nautical miles, n miles). NIFCA restricts the size of fishing vessels to <12 m within 0−3 n miles of the district, sets catch restrictions (e.g. minimum landing sizes) for fish and crustaceans and limits the use of mobile gear in the MPAs, including a complete ban on heavy trawls and dredges in the BNNC SAC (NIFCA 2021). Since 2018, NIFCA has also limited the use of mobile fishing gears to light otter trawls in the Coquet to St Mary's MCZ (NIFCA 2021).
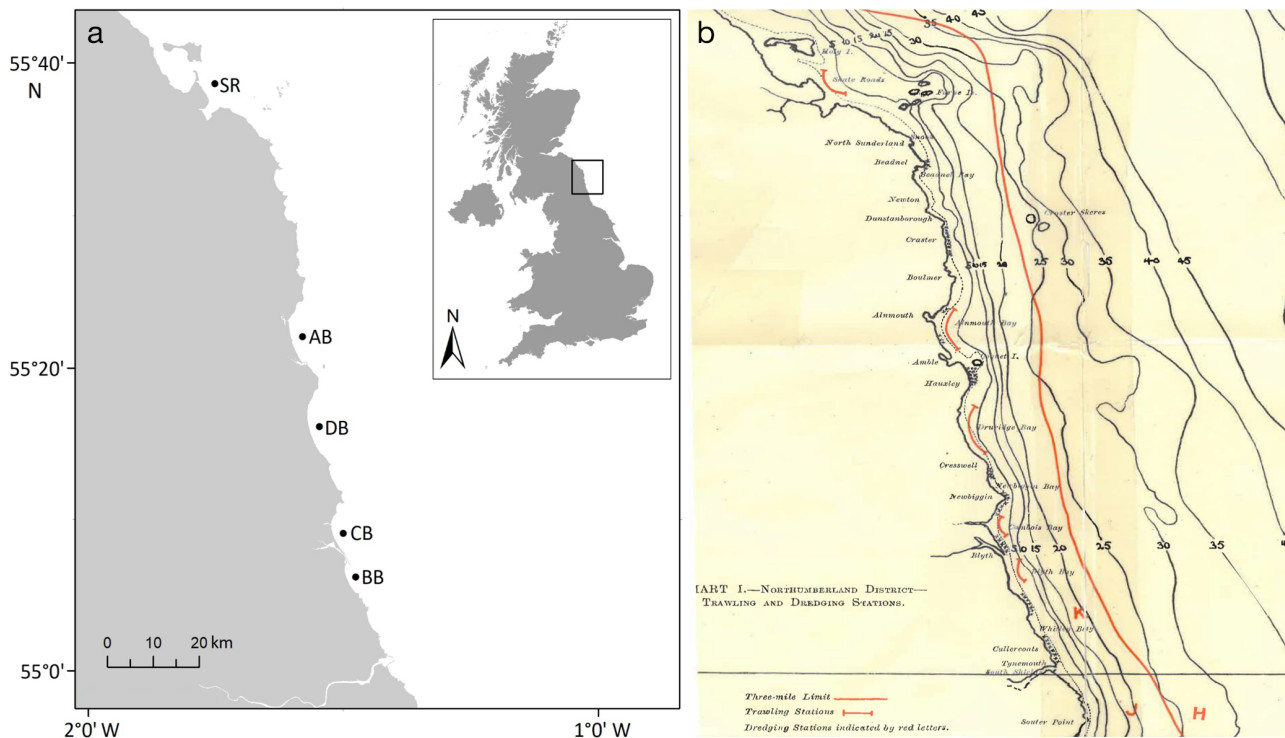
Fig. 1. Northumberland coast (UK), showing (a) sampling locations of historical and contemporary surveys (SR: Skate Roads; AB: Alnmouth Bay; DB: Druridge Bay; CB: Cambois Bay; BB: Blyth Bay) and (b) historical trawl tracks of Northumberland Sea Fisheries Committee (NSFC) sampling stations (short red curves) with the 3 mile (~4.8 km) territorial limit boundary (continuous red line) (adapted from Meek 1902, which is in the public domain)

2.2. Historical surveys

Records were digitised from NSFC logbooks held in the Centre for Environment, Fisheries and Aquaculture Science's (Cefas) Fishing Survey System. Historical logbooks provide anecdotal accounts of the environmental conditions, sea state and a general overview of combined trawls conducted per day in each location. Between 1892 and 1900, trawls were conducted from May to September during daylight hours onboard 2 steam-powered paddle tugs, initially the 'Livingstone', and later the 'Stanley' from the latter part of the 1900 season until 1913. Logbooks refer to a 6.7 m wooden beam trawl, which was consistently employed by the NSFC across the entire sampling period. Beyond this description, there was no reference to net dimensions or mesh sizes. However, the minimum size of fish reported in logbooks was 10 cm. This implies a stretched mesh of ~80–90 mm (N. Armstrong pers. comm.), which also aligns with commonly referenced cod-end mesh sizes (~76 mm) used in British beam trawls during the late 19th and early 20th centuries (Holdsworth 1874, Collins 1889, Aflalo 1904). During the 1892–1899 surveys, numbers of fish were recorded in logbooks, but details on haul

durations were lacking. From 1899 onwards, logbooks contain information on the location (although specific details on the start and end points of each haul are not given), duration of individual hauls (ranging from 15 to 165 min; Table 1) and the numbers and sizes (total length) of all fish species landed. Prior to 1904, fish were measured to the nearest inch, and to the nearest centimetre thereafter. Individual positions, depths and trawl speeds were not routinely documented; however, Meek (1901) stated the trawl speed was 'about 2 knots'. This is consistent 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).

2.3. Contemporary surveys

Repeat trawls were undertaken in 2018 and 2019 onboard Newcastle University's RV 'The Princess Royal', an 18.9 m catamaran, during the same months (May–September) as historical surveys. An attempt was made to rebuild the original NSFC beam trawl for use in the surveys to account for biases that arise when comparing catches from different trawl gears

Table 1. Summary information of historical and contemporary trawls at the 5 study sites: Skate Roads (SR), Alnmouth Bay (AB), Druridge Bay (DB), Cambois Bay (CB) and Blyth Bay (BB)

Year	Number of trawls					Mean haul duration (range) in minutes				
	SR	AB	DB	CB	BB	SR	AB	DB	CB	BB
1899	2	2	3	2	—	75(75—75)	83 (75—90)	90(90—90)	75(75—75)	—
1900	2	3	4	1	2	60(60—60)	73 (70—80)	64(55—70)	90	50(30—50)
1901	4	2	4	3	1	73(60—75)	60(60—60)	71(60—85)	70(60—90)	50
1902	3	3	2	3	1	53(40—60)	63(60—70)	60(60—60)	60(60—60)	50
1903	3	2	3	2	2	72(60—85)	60(60—60)	62(60—65)	60(60—60)	50(40—60)
1904	1	2	2	3	3	60	60(60—60)	63(60—65)	67(60—75)	60(55—70)
1905	2	2	3	4	2	55(50—60)	67(60—75)	60(60—60)	63(60—70)	39(30—48)
1906	3	1	3	2	5	60(60—60)	60(60—60)	66(60—75)	60(60—60)	55(45—60)
1907	7	1	5	1	8	78(50—120)	60	90(60—120)	15	106(60—165)
1908	3	—	3	—	3	90(90—90)	—	90(90—90)	—	90(90—90)
1909	3	4	4	—	3	90(60—150)	103(90—120)	75(45—90)	—	83(75—90)
1910	—	1	1	—	1	—	90	90	—	60
1913	4	10	7	—	6	65(60—70)	65(60—75)	60(60—60)	—	67(60—75)
2018	1	2	2	2	—	60(60—60)	60(60—60)	60(60—60)	60(60—60)	60(60—60)
2019	6	13	14	10	10	60(60—60)	60(60—60)	60(60—60)	60(60—60)	60(60—60)

and methods employed (Hunt 2022). In the same locations, we conducted gear trials in August 2018 using the replica gear and an otter trawl, with an 8.2 m headline and 80 mm (tight) meshed cod-end, to contrast their relative (standardised) catch rates. The species composition of both trawl gears was the same; catch rates were broadly similar for flatfish, and no roundfish were landed (see Hunt 2022). In the current study, the otter trawl was used in place of the replica gear for the surveys due to technical and logistical constraints following further gear trials conducted in March 2019. This decision was further supported by the observed similarities in catch rates between the 2 gears during August 2018 trials.

Although individual start/end positions and tracks of historical trawls were not known, contemporary surveys were conducted in close proximity to original fishing stations (identified in Fig. 1) and at depths sporadically reported in NSFC reports (e.g. <10 m; Meek 1905). Individual trawls had a haul duration of 60 min, and although trawls were conducted consecutively at each bay (2—4 times) during daylight hours, the same tracks were not trawled over repeatedly in a given day. The towing speed was ~1.29 m s^{-1} (2.5 knots). The contents of the net were sorted and identified to species level, and the total length of all fish species was measured to the nearest centimetre. Start and end positions and mean depth were recorded for every haul. Sampling was approved by Newcastle University's Animal Welfare and Ethical Review Board (Project ID No: 564) and carried out in accordance with the UK Home Office Scientific Procedures (Animals) Act requirements.

2.4. Data preparation

Data were only included in analyses if haul durations were recorded for individual trawls. We therefore restricted comparisons of fish catches and community structure between 1899—1913 and 2018—2019. A total of 172 and 60 trawls were included in analyses for historical and contemporary periods, respectively (Table 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 is likely to skew analyses.

Comparisons of catch data collected from different vessels, trawl gears and mesh sizes can be biased by differences in the relative selectivity of fish landed due to their size, shape and behaviour (Currie et al. 2019) In this study, there were marked discrepancies between the modal lengths of fish in historical and contemporary surveys, with a larger proportion of small fish recorded in historical periods (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m733p079_supp.pdf). For the entire fish assemblage, modal length ranges were 16—18 cm in historical surveys and 20—22 cm in contemporary surveys. For flatfish, modal lengths were 19—21 and 21—23 cm in historical and contemporary surveys, respectively. Although this could potentially be due to an increased prevalence of smaller individuals observed in historical trawls, these discrepancies may also reflect differences in the selectivity of mesh sizes between the 2 trawl gears. However, to reduce potential gear selectivity as much as possible, we omitted individuals smaller than 20 cm (total length) across all

analyses. This conservative approach, which has similarly been adopted in other studies (e.g. Rogers & Ellis 2000, Cardinale et al. 2009), provides a compromise between the need for robust comparisons and the lack of complete information on historical mesh sizes.

2.5. Swept area calculations

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 & Steingrímsson 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 the 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 & Steingrímsson 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 & 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 contemporary surveys, swept area was defined as the net wing-end spread (4.07 m) multiplied by the distance trawled (based on trawl duration and a towing speed of 1.29 m s^{-1}). The estimated swept area per hour of trawling for the otter trawl was 18800 m^2. For the historical beam trawl, the swept area per hour of trawling was larger, estimated at 24800 m^2 based on a towing speed of ~1.03 m s^{-1} and beam width of 6.7 m.

2.6. Comparisons of historical and contemporary catches

For both periods, mean catch rates (±SE), expressed as numbers per hour standardised for area swept, were calculated in each bay per species:

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

where C_{sw} is the swept area of standardised catch; C is the count for the specified taxon; and a is the area of seafloor swept by the trawl (1000 m^2 h^{-1}).

It was considered appropriate here to account for differences in sampling effort between historical and contemporary surveys, as this could have potentially influenced comparisons of community diversity between the 2 periods. These differences were (1) the historical period was sampled over more years (13 yr) than the contemporary period (2 yr); (2) mean trawl durations were longer historically; and (3) a higher number of hauls were undertaken historically (n = 172) compared to the contemporary period (n = 60). For (1), we assumed that change in the historical fish assemblage was minimal across the 13 yr. For (2), overall mean trawl durations for historical and contemporary periods were 71.2 and 60 min, respectively. Longer trawl durations in the historical surveys could potentially increase estimates of diversity, as it is a function of effort for many community parameters (e.g. number of species). However, because differences in mean trawl durations were relatively small, we assumed that this would only have a minimal effect on diversity indices between the 2 periods. Thus, our main effort in standardising sampling effort between historical and contemporary periods was on (3), the number of trawls.

The number of species sampled will increase with the number of hauls undertaken, and differences in sampling effort could thus bias estimates of species richness, as well as transfer to other diversity indices if these are a function of species richness (Barry et al. 2013). To account for the large difference in hauls between historical and contemporary periods, we conducted a randomised procedure to allow for trawl-standardised comparisons on the community diversity metrics. To achieve this, 60 hauls from the historical data set were randomly selected for further analysis, while ensuring that the number of hauls in each bay was the same as in the contemporary data set. Species richness, the Shannon-Wiener index (H'), Simpson diversity (D) and evenness (Pielou 1969) were then calculated to examine changes in community diversity between the randomised historical data set and contemporary data set. We repeated the random selection procedure 1000 times over possible historical sampling designs. The medians and their 95% ranges of standardised values were calculated for each of the diversity indices for the standardised historical data set.

To further quantify changes in fish community structure between the 2 periods, all other analyses were conducted on the original historical and contemporary data sets (based on C_{sw}) without random selection. k-dominance curves were calculated by

ranking species abundances and plotting the cumulative proportion of individuals against their rank order. Ordination and a 2-way permutational multivariate analysis of variance (PERMANOVA 'adonis' function; Anderson 2005) were performed using Bray-Curtis resemblance matrices and fixed factors 'year' and 'bay'. Ordinations were plotted with non-metric multidimensional scaling (nMDS) to provide a 2-dimensional visualisation of dissimilarities in community structure. Similarity percentage (SIMPER) analysis was then used to pinpoint the species responsible for the greatest dissimilarity between periods within each bay, and then identify those species that characterised or typified historical and contemporary catches based on their contribution percentages (Clarke 1993). These methods are not as affected by differences in sampling effort in comparison to the community diversity metrics. This is because they use dissimilarity matrices or ordination scores based on individual trawls, rather than aggregate the data across all the trawls in the same way that the diversity metrics do. All statistical analyses were conducted in R version 4.2.0 (R Core Team 2022). nMDS, PERMANOVA ('adonis') and SIMPER were performed using the 'vegan' package in R (Oksanen et al. 2020).

To compare differences in size distributions between historical and contemporary periods, data were pooled from all bays within each survey period for all fish, flatfish and plaice and dab separately, where sufficient data were available. Standardised abundances (numbers per 1000 m^2) were log transformed and plotted against their respective size distributions. Generalised linear models (GLMs) with analysis of covariance (ANCOVA) were then applied in R to test for differences in the slopes of the abundance size spectra between periods.

3. RESULTS

3.1. Changes in assemblage structure

Community diversity metrics revealed differences in the fish assemblage structure between historical and contemporary periods, with lower median species richness and diversity observed in the contemporary surveys (Table 2). The median Simpson diversity (D) values were lower in the contemporary surveys, except in Skate Roads, where a single species (plaice) dominated the historical assemblage. By comparison, the distribution of species was overall more even in contemporary periods, except in Druridge and Cambois Bays (Table 2). The slopes of the k-dominance curves for the contemporary period were initially higher across the bays except in Skate Roads (Fig. S2). The steeper curve for the contemporary assemblage in Skate Roads reflected equal dominance by 2 out of 3 species (dab and flounder). However, the higher evenness value (0.74) compared to the historical period (0.44) represented a more balanced distribution (Table 2).

For the entire fish and flatfish assemblage, the nMDS ordination plots showed a clear separation in community structure between historical and contemporary periods, which was most apparent in Skate Roads and Alnmouth Bay (Fig. 2). These distinctions were confirmed by PERMANOVAs, where statistically significant differences in standardised abundances were detected among the bays and periods for both assemblages (Table 3; p < 0.001). Compared to the historical period, consistently lower abundances were observed for almost all fish species in contemporary surveys (Table 4). Flatfish dominated the inshore assemblage in both periods, but roundfish were rarely observed in the contemporary period (only Atlantic

Table 2. Community diversity metrics of the whole fish assemblage based on historical (H) and contemporary (C) trawls in each bay. The medians and their 95% ranges of standardised values were calculated for each diversity metric based on the randomised historical data set

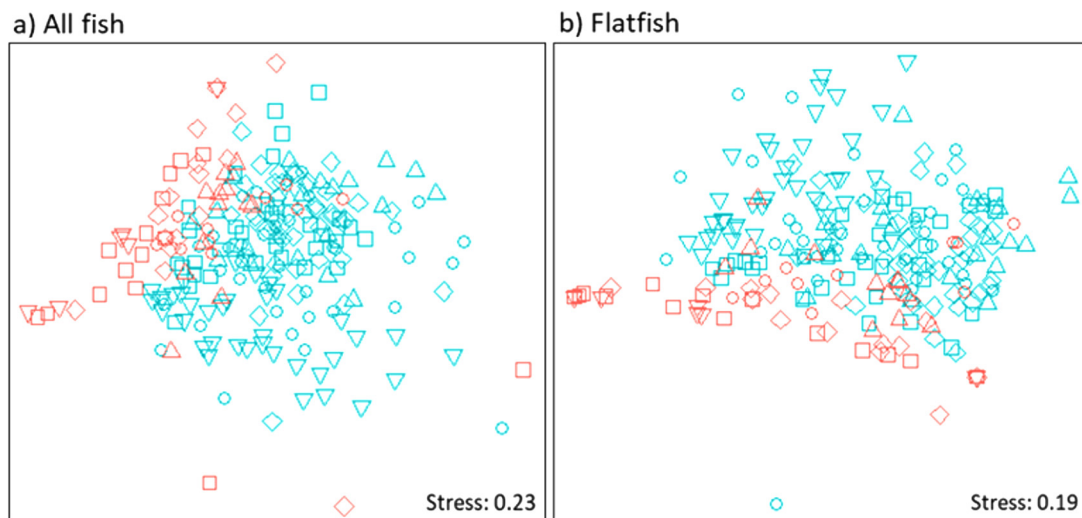|	Skate Roads H	C	Alnmouth Bay H	C	Druridge Bay H	C	Cambois Bay H	C	Blyth Bay H	C
Species richness	9 (7—11)	3	10 (8—12)	5	11 (8—13)	7	11 (8—12)	5	10 (8—14)	5
Shannon-Wiener Index (H')	0.98 (0.74—1.27)	0.8	1.46 (1.34—1.56)	1.08	1.4 (1.33—1.48)	0.82	1.49 (1.39—1.57)	0.88	1.5 (1.33—1.69)	1.12
Simpson diversity (D)	0.44 (0.32—0.58)	0.53	0.73 (0.68—0.76)	0.58	0.71 (0.68—0.73)	0.41	0.71 (0.68—0.74)	0.54	0.72 (0.65—0.76)	0.61
Evenness	0.44 (0.33—0.58)	0.74	0.63 (0.56—0.71)	0.66	0.59 (0.53—0.66)	0.42	0.63 (0.57—0.71)	0.55	0.63 (0.56—0.72)	0.7

Fig. 2. Non-metric multi-dimensional scaling (nMDS) ordination plots of community dissimilarity (Bray-Curtis matrix) between historical (blue) and contemporary (red) trawls (∇ Skate roads, □ Alnmouth Bay, ◇ Druridge Bay, △ Cambois Bay, ◯ Blyth Bay) for (a) the entire fish assemblage and (b) flatfish

Table 3. Results of permutational ANOVA (PERMANOVA) comparisons of abundances between periods (historical and contemporary) and bays for all species and flatfish

Group	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		

mackerel *Scomber scombrus* and monkfish *Lophius piscatorius*). Among the most notable changes was the absence of grey gurnard *Eutrigla gurnardus* from contemporary surveys, while they were the third most abundant species historically across all the bays (ranging from 0.14 ± 0.04 to 1.59 ± 0.50 per 1000 m^2). Elasmobranchs were also entirely absent from the contemporary period but were historically present in low abundances (Table 4). SIMPER analyses indicated that in the historical period, the assemblage was typified by plaice, dab, and grey gurnard across the bays, whereas the former 2 species and flounder typified the contemporary assemblage (Table S1). Plaice and dab were also primary contributors to the observed dissimilarity between periods, with average community dissimilarity ranging from 55.9 to 87.3% across the bays (Table S2).

3.2. Changes in size distribution

For all species combined and for the flatfish assemblage, relative abundances at size had steeper slopes in the contemporary period, indicating a higher proportion of larger fish present in historical surveys (Table S3; Fig. 3a,b). Statistically significant differences in the slopes were detected between historical and contemporary periods for the entire fish assemblage (GLM, ANCOVA; $F_{1,62} = 7.903$; p < 0.001) and flatfish assemblage (GLM, ANCOVA; $F_{1,50} = 5.053$; p = 0.031). For dab, statistically significant differences were also evident between the 2 periods (GLM, ANCOVA; $F_{1,27} = 18.091$; p < 0.001), with proportionally fewer larger individuals observed in contemporary surveys (Fig. 3c). For plaice, a smaller yet statistically significant change in slopes was also evident between periods (GLM, ANCOVA: $F_{1,48} = 4.883$; p = 0.024); the abundance size spectrum was steeper in the historical period (Fig. 3d).

4. DISCUSSION

This study revealed marked changes in the community structure of a North Sea inshore fish assemblage over the past 120 yr. Our results show that demersal fish species in the contemporary period have now become less abundant and diverse compared to late 19th and early 20th century. Although plaice and dab were the most dominant species in both periods across the bays, declines in standardised catches were

Table 4. Mean (±SE) catch rates (numbers of fish per 1000 m^2) standardised for area swept in historical (H) and contemporary (C) surveys in Skate Roads, and Alnmouth, Druridge, Cambois and Blyth Bays

|	Skate Roads		Alnmouth Bay		Druridge Bay		Cambois Bay		Blyth Bay		Overall mean catch rate	
	H	C	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	1.04 ± 0.08	0.65 ± 0.1
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 ± 0.03	0.11 ± 0.03	0.15 ± 0.02	0.13 ± 0.03
Hippoglossoides platessoides	0	0	0	0	0	0	0	0	0.01 ± 0.01	0	<0.01 ± <0.01	0
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	1.42 ± 0.1	0.3 ± 0.05
Solea solea	0.01 ± <0.01	0	0.08 ± 0.02	0	0.10 ± 0.02	<0.01 ± <0.01	0.20 ± 0.04	0	0.08 ± 0.02	0.03 ± 0.01	0.08 ± 0.01	<0.01 ± <0.01
Microstomus kitt	0	0	0	0	<0.01 ± <0.01	0	0.20 ± 0.04	0	<0.01 ± <0.01	0	<0.01 ± <0.01	0
Scophthalmus maximus	0.08 ± 0.02	0	0.04 ± 0.01	0	0.05 ± 0.01	0	0.02 ± 0.01	0	0.03 ± 0.01	0	0.05 ± 0.01	0
Scophthalmus rhombus	0.01 ± <0.01	0	<0.01 ± <0.01	0	<0.01 ± <0.01	0	<0.01 ± <0.01	0	<0.01 ± <0.01	0	<0.01 ± <0.01	0
Roundfish												
Gadus morhua	0	0	<0.01 ± <0.01	0	<0.01 ± <0.01	0	<0.01 ± <0.01	0	0.01 ± <0.01.	0	<0.01 ± <0.01	0
Melanogrammus aeglefinus	0	0	<0.01 ± <0.01	0	<0.01 ± <0.01	0	0	0	<0.01 ± <0.01	0	<0.01 ± <0.01	0
Merlangius merlangus	0	0	0.02 ± 0.01	0	<0.01 ± <0.01	0.01 ± <0.01	0.01 ± 0.01	<0.01 ± <0.01	<0.01 ± <0.01	0	<0.01 ± <0.01	0
Eutrigla gurnardus	0.14 ± 0.04	0	1.59 ± 0.50	0	1.11 ± 0.19	0	0.34 ± 0.12	0	0.41 ± 0.11	0	0.75 ± 0.12	0
Chelidonichthys lucerna	<0.01 ± <0.01	0	0	0	<0.01 ± <0.01	0	0	0	<0.01 ± <0.01	0	<0.01 ± <0.01	0
Clupea harengus	0	0	0	0	0	0	0	0	<0.01 ± <0.01	0	<0.01 ± <0.01	0
Scomber scombrus	0	0	0	0.01 ± <0.01	0	<0.01 ± <0.01	0	0	0	0	0	<0.01 ± <0.01
Lophius piscatorius	0.10 ± 0.05	0	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	0.15 ± 0.02	0.03 ± 0.01
Callionymidae	0	0	0	0	<0.01 ± <0.01	0	0	0	<0.01 ± <0.01	0	<0.01 ± <0.01	0
Pollachius pollachius	0	0	0	0	0	0	<0.01 ± <0.01	0	0	0	<0.01 ± <0.01	0
Anarhichas spp.	<0.01 ± <0.01	0	<0.01 ± <0.01	0	0	0	0	0	0	0	<0.01 ± <0.01	0
Elasmobranchs												
Amblyraja radiata	<0.01 ± <0.01	0	0	0	0	0	0	0	0	0	<0.01 ± <0.01	0
Raja clavata	<0.01 ± <0.01	0	0	0	<0.01 ± <0.01	0	0	0	0	0	<0.01 ± <0.01	0
Raja circularis	<0.01 ± <0.01	0	0	0	0	0	0	0	0	0	<0.01 ± <0.01	0
Unidentified skates and rays	<0.01 ± <0.01	0	<0.01 ± <0.01	0	<0.01 ± <0.01	0	<0.01 ± <0.01	0	0	0	<0.01 ± <0.01	0
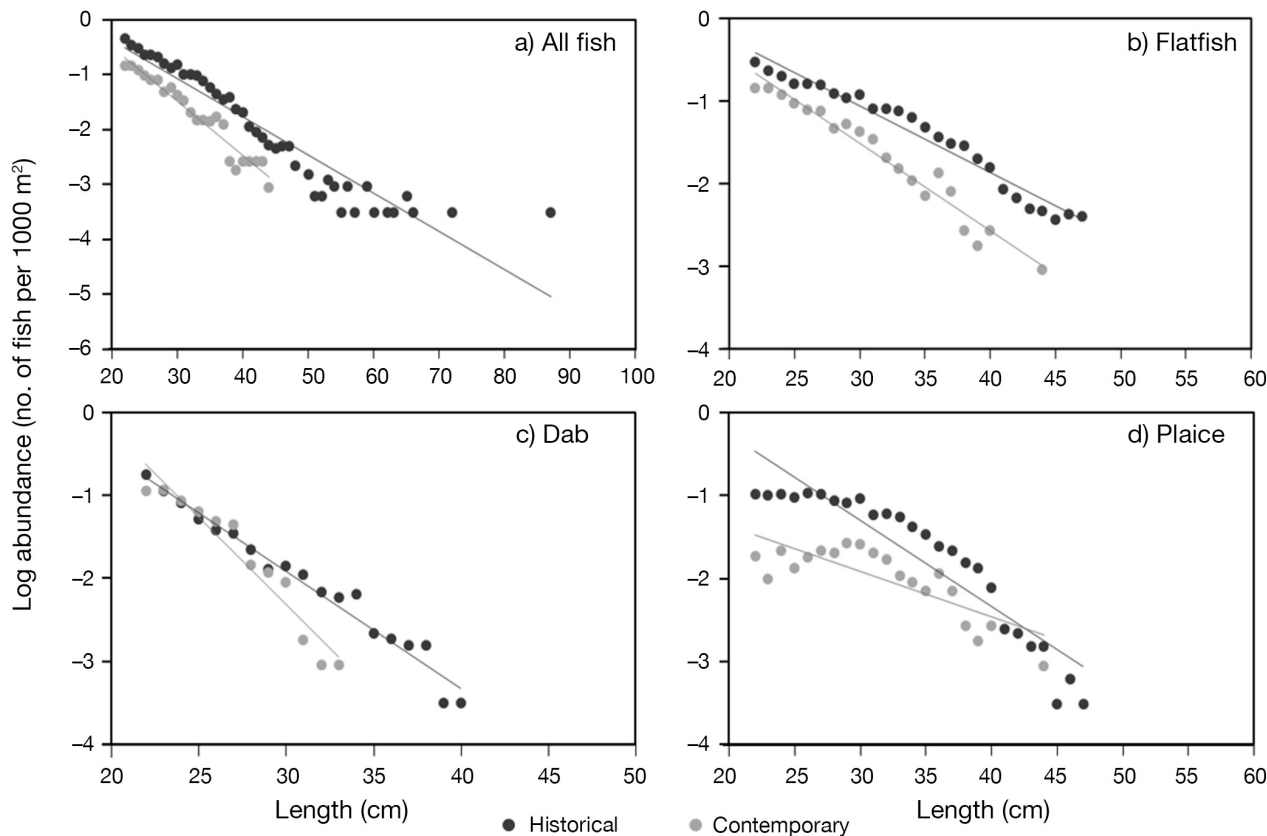
Fig. 3. Length-frequency distributions for (a) all fish, (b) flatfish, (c) dab and (d) plaice for historical and contemporary time periods. Trend lines represent the slope of the regression of log abundance against size

driven by previously abundant species that were either absent or rare in the contemporary surveys. We also detected statistically significant shifts in the relative abundances at size for the entire fish and flatfish assemblage, with proportionally fewer large fish observed in the contemporary period.

There are several factors, primarily differences in sampling gears and methods of operation, which can bias comparisons between historical and contemporary surveys. Factors such as geographic location, season, time of day and differences between trawl gears were standardised and accounted for as far as possible. However, these do not fully resolve all biases because fishing gears have an efficiency specific to their design that can vary among fish species (Rogers & Ellis 2000). In this study, it is therefore possible that observed changes between the historical and contemporary period may partly reflect differences in the catchabilities of the 2 trawl gears, rather than genuine changes in relative abundance and size (Rogers & Ellis 2000). Trawl geometry, variable in otter trawls and fixed in beams, as well as the degree of contact between the ground-rope and seabed, will

have considerable influence on catchability (Jennings et al. 2001). In beam trawls, catchability is generally higher for flatfish than roundfish, whereas the opposite is true in otter trawls (Fraser et al. 2009). However, during comparative gear trials in August 2018, the same otter trawl and a replica late-19th century beam trawl had broadly similar catch rates and no roundfish were caught (see Hunt 2022). After standardisation, these results supported the applicability of using the 2 trawl gears to contrast historical and contemporary trawl catches.

There are many challenges that researchers grapple with when analysing historical data, particularly when there is a lack of complete information on survey gears and methods, as highlighted in this study and elsewhere (McClenachan et al. 2012, Novaglio et al. 2020). An explanation of changes in relative abundance at size may be due to variability in mesh sizes of both trawl gears. It is likely the historical beam trawl had a smaller mesh size because it retained a larger proportion of smaller (<20 cm) individuals. However, by restricting our analyses to fish >20 cm (in line with Cardinale et al. 2009), inconsistencies relating to gear

selectivity at the lower size range were substantially reduced. There was also some uncertainty around trawl speeds attained during historical NSFC surveys. Trawl speeds are pivotal to swept area calculations, and inaccurate assumptions about them may thus bias comparisons of catch rates (Currie et al. 2020). Following examination of the wider literature, we assumed a tow speed of 1.03 m s^{-1} (2 knots) was deemed sufficient to effectively catch most larger-sized flatfish species (Greenstreet & Hall 1996, Rijnsdorp et al. 1996). Of major importance in this study was the need to standardise the number of trawls between contemporary and historical periods. This allowed us to acquire a more unbiased picture of differences in community composition and diversity characteristics between the 2 periods. Despite the inevitable differences in the catchability of the 2 trawl gears, we argue that a possible gear effect is insufficient to account for the fundamental changes observed.

Trawling is a likely contributor to the observed declines in abundance and diversity of this fish assemblage (Hypothesis 1), facilitating the removal of commercial and non-target species and leading to habitat modification (Jennings et al. 1999). The most susceptible to trawling tend to be larger-sized species with low fecundity and late maturity (Myers & Worm 2003); many elasmobranchs fall into this description (Walker & Heessen 1996). Thus, fishing impacts might explain their absence from contemporary surveys in this study. Grey gurnard were historically dominant across the 5 bays but were likewise absent from the contemporary surveys; this is consistent with long-term investigations in several other inshore waters, which highlighted fishing impacts. In the Firth of Clyde, grey gurnard was the fourth most dominant species in 1920−1969 but absent from catches thereafter (Heath & Speirs 2012). Off the Plymouth coast, medium- or larger-sized gurnards (>15 cm) were highly abundant in the early 20th century but had either declined or were absent from surveys carried out in 2008−2009 (McHugh et al. 2011). By comparison, the dominance of plaice and dab in recent surveys (albeit in smaller abundances compared to 120 yr ago) likely reflects their ability to maintain relatively constant levels of food intake irrespective of reduction or other shifts in prey availability (Johnson et al. 2015). Dab, in particular, are widely distributed throughout the North Sea, and although subject to high bycatch mortality (Kaiser & Spencer 1995), they nevertheless tend to have large and stable populations (Heessen & Daan 1996). Apparent resilience of dab to trawling disturbance may hence be attributed to their ability to readily adapt their diet to invertebrate species inhabiting soft seabed without reduced feeding capacity (Johnson et al. 2015).

For some species, declines in abundance observed here, as well as changes in the size spectra of the entire fish and flatfish assemblage, may also be explained by a long-term response to climate variability via changes in their distribution (Engelhard et al. 2011b) and migration phenology (Teal et al. 2012) (Hypothesis 2). Since the 1980s, rising temperatures in the North Sea have caused flatfish species to shift their distribution range northwards and offshore into cooler, deeper waters (Dulvy et al. 2008, Teal et al. 2012), although some species (e.g. sole *Solea solea*) have migrated south to shallower waters (Engelhard et al. 2011b). Shallow coastal areas warm up faster than deeper waters in summer (van der Veer & Bergman 1986), which may have caused some species in our study to abandon inshore areas earlier in the season. In the south-eastern North Sea, van Keeken et al. (2007) showed that juvenile plaice exhibited an offshore shift in their distribution in the 1990s, attributed to the potential avoidance of increased temperatures in inshore waters. Similarly, van Hal et al. (2016) revealed that adult plaice and dab have also shifted to deeper and cooler waters, implying that they too avoid higher temperatures and do not migrate back to areas when temperatures fall after the peak of summer. While this may explain the observed declines in abundance observed in this study, it could also reflect why proportionally fewer larger fish (especially dab) were recorded in contemporary surveys. Interestingly, a higher proportion of smaller plaice as well as other species <20 cm (not included in final analyses) were present in historical surveys. The bays historically served as important nursery grounds to a range of juvenile fish species (Meek 1895, 1899a), but their habitat suitability in recent decades may have been reduced due to the combined effects of rising temperatures and trawling. Apart from the rare occurrence of Atlantic mackerel *Scomber scombrus* in contemporary surveys, we found no systematic increases in any other species. This contrasts with other studies that report notable increases in the abundance of smaller-bodied Lusitanian fish species (e.g. dragonet *Callionymus lyra*; solnette *Buglossidium luteum*) around the British coast (Rogers & Ellis 2000, McHugh et al. 2011) and in other parts of the North Sea (van Hal et al. 2010, 2016).

In addition to climate change and fishing, other factors may have also contributed to observed changes in community structure over the last 120 yr. These include habitat modification, increased nutrient load-

ing, pollution and changes in prey availability and/or ecosystem productivity. Four decades (1956—1992) of continuous, large-scale disposal of fly-ash has altered the local environment, particularly at its source near Cambois and Blyth Bays, via permanent changes to sediment dynamics and reduced macrobenthic cover (Herrando-Perez & Frid 1998). Declines in the abundance of larger fish inshore could have promoted an offshore shift to deeper waters by lowering predation risk and/or inter- or intra-specific competition, as was predicted for large plaice (>20 cm) along the Dutch and Danish coasts (van Keeken et al. 2007). The contemporary fish assemblage is also exposed to higher predation pressure due to an expanding grey seal *Halichoerus grypus* population on the Farne Islands off the Northumberland coast (Thompson & Duck 2010). In the mid-19th and early 20th century, the Farne Islands grey seal population was estimated to be around 100 individuals (Lambert 2002), whereas recent numbers of pups born annually are estimated at approximately 3200 (Russell et al. 2019). Grey seals predominantly forage on flatfish, several gadoid species and sandeels (Thompson & Duck 2010), and increased predation may thus have contributed to a reduced inshore fish assemblage, most notably in Skate Roads, which is located within 3 miles (~4.8 km) of the Farne Islands.

Besides evolving fishery regulations, the 3 mile limit ban on trawling in 1891 as well as the implementation of new MPAs in recent years may have alleviated some of these impacts. Disentangling multiple stressors on the inshore fish assemblage is best achieved using detailed time-series data, much of which are unavailable for inshore waters. In this study, it is unlikely that the historical demersal fish assemblage was representative of near-pristine conditions, largely because the NSFC surveys started more than a decade after the onset of steam trawling in the 1880s (Engelhard 2008). Further, it is important to reiterate that observed changes in community structure may to some extent reflect differences in the catchability of the 2 trawl gears as well as true changes in relative abundance and size. Concerns for the demise of juvenile fish in inshore waters were expressed by fishers early on, which ultimately resulted in the 3 mile trawl ban on the Northumberland coast (Meek 1895, 1899a, Thurstan et al. 2014). Inshore trawl fisheries have operated out of North Shields since the mid-19th century (Meek 1900), and nearshore static gears have operated on a commercial scale for much longer. It is hence not possible to capture what the system looked like prior to the onset of trawling in this area. Instead, this work offers a his-torical reference point from a period when human-induced disturbance was far lower than now, albeit not absent, providing a useful benchmark for improving coastal ecosystem status in the future.

Over a century of trawling, regional climate change and other pressures are expected to have reduced benthic diversity in the region (Engel & Kvitek 1998), resulting in an environment that now supports lower diversity and favours lower trophic species that inhabit 'soft grounds' over those that prefer heterogeneous environments. Elsewhere in inshore waters, studies reported that in this altered state, shellfish species such as *Nephrops* and other lobsters will flourish as they are adapted to simplified environmental conditions (Thurstan & Roberts 2010). In Northumberland waters, the potting fishery has assumed greater importance in recent years (Stephenson et al. 2018), along with the otter trawl fishery for *Nephrops* further offshore (Walmsley & Pawson 2007). Habitat-altering properties of these fisheries and bycatch of fish associated with the *Nephrops* fishery may continue to preclude the recovery potential of demersal fish species in inshore waters. A less diverse ecosystem could be at further risk of parasitism and invasive species, and may become more susceptible to changes in environmental conditions in the future (Worm et al. 2006). With more focus being placed on the value of historical data to unravel past ecosystem states, integration of this work is essential for rebuilding inshore fish stocks and setting realistic management targets.

LITERATURE CITED

Aflalo FG (1904) The sea-fishing industry of England and Wales: a popular account of the sea fisheries and fishing ports of those countries. Edward Stanford, London

Allen EJ (1897) The regulations of the local sea fisheries committees in England and Wales. J Mar Biol Assoc UK 4:386—395

Alward GL (1932) The sea fisheries of Great Britain and Ireland. A record of the development of the fishing industry and its world-wide ramifications. Albert Gait, Grimsby

Anderson MJ (2005) Permutational multivariate analysis of

variance. Department of Statistics, University of Auckland, Auckland

Barry J, Birchenough S, Norris B, Ware S (2013) On the use of sample indices to reflect changes in benthic fauna biodiversity. Ecol Indic 26:154−162

Baudron AR, Needle CL, Rijnsdorp AD, Marshall TC (2014) Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. Glob Change Biol 20:1023−1031

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426:661−664

Bennett TL, Foster-Smith JL (1998) South-east Scotland and north-east England (Dunbar to Bridlington) (MNCR Sector 5). In: Hiscock K (ed) Marine nature conservation review: benthic Ecosystems of Great Britain and the North-east Atlantic. JNCC, Peterborough, p 155−176

Broadhurst MK, Sterling DJ, Cullis BR (2012) Effects of otter boards on catches of an Australian penaeid trawl. Fish Sci 131:67−75

Brown CJ, Trebilco R (2014) Unintended cultivation, shifting baselines, and conflict between objectives for fisheries and conservation. Conserv Biol 28:677−688

Capuzzo E, Lynam CP, Barry J, Stephens D and others (2018) A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment. Glob Change Biol 24: e352−e364

Cardinale M, Linder M, Bartolino V, Maiorano L, Casini M (2009) Conservation value of historical data: reconstructing stock dynamics of turbot during the last century in the Kattegat-Skagerrak. Mar Ecol Prog Ser 386:197−206

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Austral Ecol 18: 117−143

Collins JW (1889) The beam trawl fishery of Great Britain with notes on beam trawling in other European countries. Government Printing Office, Washington, DC

Currie JC, Sink KJ, Attwood CG, Atkinson LJ, Engelhard GH (2019) Reconstructing the past: design and function of Granton otter trawl gear at the turn of the twentieth century, as used in South Africa's first trawl surveys (1897−1904). Marit Stud 18:1−16

Currie JC, Atkinson LJ, Sink KJ, Attwood CG (2020) Long-term change of demersal fish assemblages on the inshore Agulhas Bank between 1904 and 2015. Front Mar Sci 7: 355

Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. J Appl Ecol 45:1029−1039

Eagle RA, Hardiman PA, Norton MG, Nunny RS, Rolfe MS (1979) The field assessment of effects of dumping wastes at sea. The disposal of solid wastes off the north-east coast of England. Fish Res Tech Rep 51. Directorate of Fisheries Research, Ministry of Agriculture, Fisheries and Food, Lowestoft, p 51−34

Engel J, Kvitek R (1998) Effects of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary. Conserv Biol 12:1204−1214

Engelhard GH (2008) One hundred and twenty years of change in fishing power of English North Sea trawlers. In: Payne A, Cotter J, Potter T (eds) Advances in fisheries science: 50 years on from Beverton and Holt. Blackwell Publishing, Oxford, p 1−26

Engelhard GH, Ellis JR, Payne MR, Ter Hofstede R, Pinnegar JK (2011a) Ecotypes as a concept for exploring responses to climate change in fish assemblages. ICES J Mar Sci 68: 580−591

Engelhard GH, Pinnegar JK, Kell LT, Rijnsdorp AD (2011b) Nine decades of North Sea sole and plaice distribution. ICES J Mar Sci 68:1090−1104

Fraser HM, Greenstreet SP, Piet GJ (2009) Selecting MPAs to conserve groundfish biodiversity: the consequences of failing to account for catchability in survey trawls. ICES J Mar Sci 66:82−89

Frid CLJ, Evans SM, Clark RB (1991) North east coast of England environmental appraisal. Shell Exploration and Production UK, Aberdeen

Greenstreet SPR, Hall SJ (1996) Fishing and the ground-fish assemblage structure in the north-western North Sea: an analysis of long-term and spatial trends. J Anim Ecol 65: 577−598

Greenstreet SPR, Rogers SI (2006) Indicators of the health of the North Sea fish community: identifying reference levels for an ecosystem approach to management. ICES J Mar Sci 63:573−593

Heath MR, Speirs DC (2012) Changes in species diversity and size composition in the Firth of Clyde demersal fish community (1927−2009). Proc R Soc B 279:543−552

Heessen HJL, Daan N (1996) Long-term trends in ten non-target North Sea fish species. ICES J Mar Sci 53: 1063−1078

Herrando-Perez S, Frid CLJ (1998) The cessation of long-term fly-ash dumping: effects on macrobenthos and sediments. Mar Pollut Bull 36:780−790

Holdsworth EWH (1874) Deep-sea fishing and fishing boats: an account of the practical working of the various fisheries around the British Islands. With illustrations and descriptions of the boats, nets, and other gear in use. Edward Stanford, London

Hunt GL (2022) Spatial and long-term variability in demersal fish species of the western North Sea. PhD dissertation, Newcastle University, Newcastle upon Tyne

Jennings S, Greenstreet SPR, Reynolds JD (1999) Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. J Anim Ecol 68:617−627

Jennings S, Kaiser MJ, Reynolds JD (2001) Marine fisheries ecology. Blackwell Science, London

Johnson AF, Gorelli G, Jenkins SR, Hiddink JG, Hinz H (2015) Effects of bottom trawling on fish foraging and feeding. Proc R Soc B 282:20142336

Kaiser MJ, Spencer BE (1995) Survival of by-catch from a beam trawl. Mar Ecol Prog Ser 126:31−38

Kyle HM (1903) Fishing nets, with special reference to the otter-trawl. J Mar Biol Assoc UK 6:562−586

Lambert RA (2002) The grey seal in Britain: a twentieth century history of a nature conservation success. Environ Hist 8:449−474

Lotze HK, Worm B (2009) Historical baselines for large marine animals. Trends Ecol Evol 24:254−262

M'Intosh WC (1895) Remarks on trawling. J Mar Biol Assoc UK 3:307−334

MacKenzie BR, Schiedek D (2007) Daily ocean monitoring since the 1860s shows record warming of northern European seas. Glob Change Biol 13:1335−1347

Mackinson S (2002) Simulating management options for the North Sea in the 1880s. In: Pitcher T, Cochrane K (eds) The use of ecosystem models to investigate multispecies

management strategies for capture fisheries. Res Rep 10. Fisheries Centre, University of British Columbia, Vancouver, p 73—82

McClenachan L, Ferretti F, Baum JK (2012) From archives to conservation: why historical data are needed to set baselines for marine animals and ecosystems. Conserv Lett 5: 349—359

McHugh M, Sims DW, Partridge JC, Genner MJ (2011) A century later: long-term change of an inshore temperate marine fish assemblage. J Sea Res 65:187—194

Meek A (1895) Report on the scientific investigations for the year 1892—1895. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1896) Report on the scientific investigations for the year 1896. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1897) Report on the scientific investigations for the year 1897. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1898) Report on the scientific investigations for the year 1898. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1899a) Trawling for scientific purposes. In Hutchison A (ed): The Windsor magazine: an illustrated monthly for men and women, Vol. 10. Ward Lock & Co., London, p 533—537

Meek A (1899b) Report on the scientific investigations for the year 1899. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1900) Report on the scientific investigations for the year 1900. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1901) Report on the scientific investigations for the year 1901. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1902) Report on the scientific investigations for the year 1902. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1903) Report on the scientific investigations for the year 1903. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1904) Report on the scientific investigations for the year 1904. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1905) Report on the scientific investigations for the year 1905. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1906) Report on the scientific investigations for the year 1906. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1907) Report on the scientific investigations for the year 1907. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1908) Report on the scientific investigations for the year 1908. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1909) Report on the scientific investigations for the year 1909. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1910) Report on the scientific investigations for the year 1910. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1911) Report on the scientific investigations for the year 1911. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1912) Report on the scientific investigations for the year 1912. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Meek A (1913) Report on the scientific investigations for the year 1913. Northumberland Sea Fisheries Committee, Newcastle-upon-Tyne

Muirhead G (1992) The fishing industry of Northumberland and Durham 1780—1914. PhD dissertation, Newcastle University, Newcastle-upon-Tyne

Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423:280—283

NIFCA (Northumberland Inshore Fisheries Conservation Authority) (2021) Northumberland Inshore Fisheries Conservation Authority byelaws booklet. NIFCA, Blyth

Norman AM (1863) Report on the Crustacea of the dredging expedition to the Dogger Bank and the coasts of Northumberland. Trans Tyneside Nat Field Club 5:263—267

Novaglio C, Smith AD, Frusher S, Ferretti F (2020) Identifying historical baseline at the onset of exploitation to improve understanding of fishing impacts. Aquat Conserv 30:475—485

Oksanen AJ, Blanchet FG, Friendly M, Kindt R, Legendre P, Mcglinn D, Szoecs E (2020) Vegan: community ecology package. R Package Version 2(5—7), https://cran.r-project.org/web/packages/vegan/index.html

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1998) Fishing down marine food webs. Science 279: 860—863

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308:1912—1915

Pickett STA (1989) Space-for-time substitution as an alternative to long-term studies. In: Likens GE (ed) Long-term studies in ecology: approaches and alternatives. Springer-Verlag, New York, NY, p 110—135

Pielou EC (1969) An introduction to mathematical ecology. Wiley, New York, NY

Pinnegar JK, Engelhard GH (2008) The 'shifting baseline' phenomenon: a global perspective. Rev Fish Biol Fish 18: 1—16

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Ragnarsson SÁ, Steingrímsson SA (2003) Spatial distribution of otter trawl effort in Icelandic waters: comparison of measures of effort and implications for benthic community effects of trawling activities. ICES J Mar Sci 60: 1200—1215

Régnier T, Gibb FM, Wright PJ (2019) Understanding temperature effects on recruitment in the context of trophic mismatch. Sci Rep 9:15179

Rijnsdorp AD, van Leeuwen PI, Daan N, Heessen HJ (1996) Changes in abundance of demersal fish species in the North Sea between 1906—1909 and 1990—1995. ICES J Mar Sci 53:1054—1062

Rijnsdorp AD, Peck MA, Engelhard GH, Möllmann C, Pinnegar JK (2009) Resolving the effect of climate change on fish populations. ICES J Mar Sci 66:1570—1583

Roberts CM (2007) The unnatural history of the sea. Island Press, Washington, DC

Robinson R (1996) Trawling: the rise and fall of the British trawl fishery. University of Exeter Press, Exeter

Rogers SI, Ellis JR (2000) Changes in the demersal fish assemblages of British coastal waters during the 20th century. ICES J Mar Sci 57:866—881

Russell DJ, Morris CD, Duck CD, Thompson D, Hiby L (2019) Monitoring long-term changes in UK grey seal pup production. Aquat Conserv 29:24−39

Russell ES, Edser T (1925) The fishery statistics of England and Wales. J R Stat Soc 88:221−259

Sguotti C, Lynam CP, García-Carreras B, Ellis JR, Engelhard GH (2016) Distribution of skates and sharks in the North Sea: 112 years of change. Glob Change Biol 22:2729−2743

Sheppard C (2004) Sea surface temperature 1871−2099 in 14 cells around the United Kingdom. Mar Pollut Bull 49: 12−16

Steneck RS, Hughes TP, Cinner JE, Adger WN and others (2011) Creation of a gilded trap by the high economic value of the Maine lobster fishery. Conserv Biol 25: 904−912

Stephenson F, Mill AC, Scott CL, Stewart GB, Grainger MJ, Polunin NV, Fitzsimmons C (2018) Socio-economic, technological and environmental drivers of spatio-temporal changes in fishing pressure. Mar Policy 88:189−203

Teal LR, van Hal R, van Kooten T, Ruardij P, Rijnsdorp AD (2012) Bio-energetics underpins the spatial response of North Sea plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.) to climate change. Glob Change Biol 18: 3291−3305

Thompson D, Duck C (2010) Berwickshire and North Northumberland Coast European Marine Site: grey seal population status. Report to Natural England, 20100902-RFQ

Thurstan RH, Roberts CM (2010) Ecological meltdown in the Firth of Clyde, Scotland: two centuries of change in a coastal marine ecosystem. PLOS ONE 5:e11767

Thurstan RH, Brockington S, Roberts CM, (2010) The effects of 118 years of industrial fishing on UK bottom trawl fisheries. Nat Commun 1:15

Thurstan RH, Hawkins JP, Roberts CM (2014) Origins of the bottom trawling controversy in the British Isles: 19th century witness testimonies reveal evidence of early fishery declines. Fish Fish 15:506−522

Thurstan RH, McClenachan L, Crowder LB, Drew JA and others (2015) Filling historical data gaps to foster solutions in marine conservation. Ocean Coast Manag 115:31−40

Trenkel VM, Pinnegar JK, Rochet MJ, Rackham BD (2004) Different surveys provide similar pictures of trends in a marine fish community but not of individual fish populations. ICES J Mar Sci 61:351−362

van der Veer HW, Bergman MJN (1986) Development of tidally related behaviour of a newly settled 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. Mar Ecol Prog Ser 31:121−129

van Hal R, Smits K, Rijnsdorp AD (2010) How climate warming impacts the distribution and abundance of two small flatfish species in the North Sea. J Sea Res 64:76−84

van Hal R, van Kooten T, Rijnsdorp AD (2016) Temperature induced changes in size dependent distributions of two boreal and three Lusitanian flatfish species: a comparative study. J Sea Res 107:14−22

van Keeken OA, van Hoppe M, Grift RE, Rijnsdorp AD (2007) Changes in the spatial distribution of North Sea plaice (*Pleuronectes platessa*) and implications for fisheries management. J Sea Res 57:187−197

Walker PA, Heessen HJL (1996) Long-term changes in ray populations in the North Sea. ICES J Mar Sci 53: 1085−1093

Walmsley SA, Pawson MG (2007) The coastal fisheries of England and Wales, V. A review of their status 2005−6. Sci Ser Tech Rep 140. Cefas, Lowestoft

Worm B, Barbier EB, Beaumont N, Duffy JE and others (2006) Impacts of biodiversity loss on ocean ecosystem services. Science 314:787−790