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Changes in the demersal fish assemblages of British coastal waters during the 20th century

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Catches of demersal fish from research vessel surveys in three areas around the British Isles from 1901 to 1907 were compared with survey catches in the same areas from 1989 to 1997. Mesh size and other characteristics of the trawls used suggested that some of these data were comparable, and could be used to describe changes in demersal fish assemblages over the last 80 years. In Start Bay (NW English Channel) and the Irish Sea, species diversity was the same in both periods, although the most abundant species in each period were not the same. In English coastal regions of the southern North Sea, fish populations became more diverse, as plaice *Pleuronectes platessa* and whiting *Merlangius merlangus* became less abundant, and the relative abundance of several non-target species such as dragonet *Callionymus* spp., bib *Trisopterus luscus*, and bull-rout *Myoxocephalus scorpius* increased. The proportion in the catch of small fish species (maximum body length <30 cm), which would be least vulnerable to capture by commercial trawls, increased between the two survey periods in Start Bay and the southern North Sea. None of these small species was commercially exploited. The proportions of larger teleosts (maximum body length >30 cm) in catches decreased in all regions during the time period, except in the Irish Sea where plaice replaced grey gurnard *Eutrigla gurnardus* as a dominant species. There was a decline in abundance of large sharks, skates and rays, including the common skate, *Raja batis*, white skate *R. alba* and the angel shark *Squatina squatina*. During historic surveys, 60% of the elasmobranch fauna consisted of thornback ray *Raja clavata*, whereas in contemporary surveys the lesser spotted dogfish *Scyliorhinus canicula* was the most abundant elasmobranch. Changes in length-frequency distribution of fish in both target and non-target categories, and other observed changes, were thought to be a response to commercial exploitation, and corresponded to similar observations recorded elsewhere.

Key words: species composition, diversity, vulnerability, elasmobranch, temporal change.

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Introduction

It is now widely accepted that, since the late 19th century, commercial fisheries have reduced the abundance of target populations, affected life-history parameters such as growth rate and age at maturity and, in extreme circumstances, resulted in the local extirpation of species (Brander, 1981; Casey and Myers, 1998; Jennings and Kaiser, 1998; Pauly *et al.*, 1998). Fishing effort around the British Isles increased rapidly in the 1890s with the advent of steam-powered trawlers, and seasonal closed areas were soon introduced to protect juvenile flatfish (Garstang, 1903b; Holt, 1910). With the exception of the war years, fishing effort has remained high (Wood, 1956; Greenstreet and Hall, 1996; Pope and Macer, 1996; Rijnsdorp and Millner, 1996). Although recent research into the short-term impacts of trawl gears has provided some understanding of the disturbance and recovery of seabed faunas, and the survivorship of non-target species caught during fishing (Duplisea and Kerr, 1995; Kaiser and Spencer, 1995; Pope, 1989; Rice and Gislason, 1996p; Collie *et al.*, 1997; Kaiser & Spencer, 1996), it has proved difficult to quantify changes in community structure that may have been caused by fishing (Rogers *et al.*, 1999). This is largely because there are no quantitative records of fish

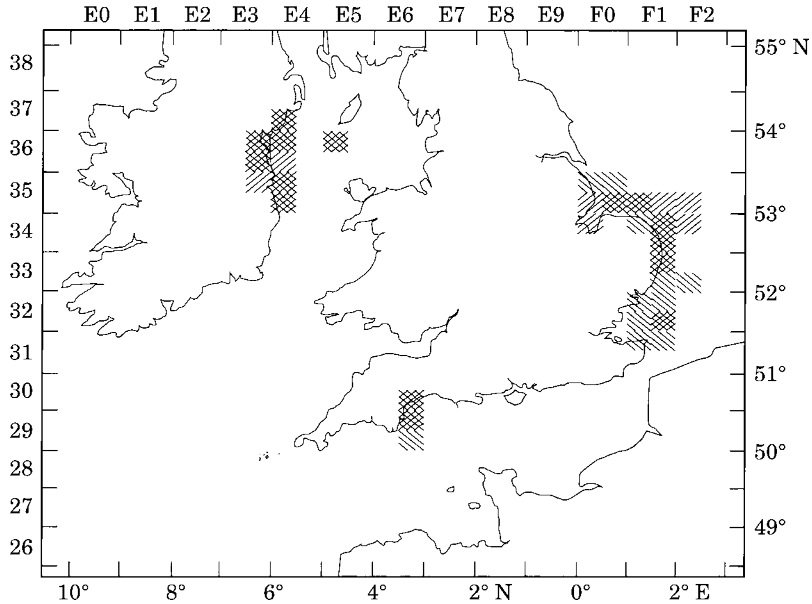

Figure 1. Map of the study area showing the quarter ICES rectangles that were sampled by Holt (1910) and Garstang (1903a, 1905) (shading slopes right to left), and those sampled by contemporary CEFAS groundfish surveys (shading slopes left to right).

community structure in European waters from the period before commercial fisheries became established. Most fish abundance data cover only the past 50 years (Heessen & Daan, 1996; Rogers & Millner, 1996; Tiews, 1990; Vooys and Meer, 1998). Some researchers have identified data sets which predate the 1920s (Greenstreet & Hall, 1996; Johannessen & Sollie 1994; Quero & Cendrero, 1996; Ruud, 1968), but very few have access to data from the 18th or 19th centuries (Quero, 1998).

We examined data from research surveys in the coastal waters of the British Isles from 1901–1907, and from 1989–1997. Our purpose was to compare catch rates of demersal species from these two periods, and to identify changes in the demersal fish fauna, including non-target species, that may have occurred during the 20th century. In addition to analyses of fish catch rates and length–frequency distribution, we investigated changes in community structure using the relative vulnerability of different species to fishing, based on the size of the species and its reproductive mode. Throughout the analysis, particular attention was paid to the potential effects of different gear catchabilities and sampling protocols.

Materials and methods

Historic and contemporary data from research vessel surveys in three areas around the British Isles were compared. These surveys caught demersal fish using otter or beam trawls from 1901 to 1907, and using beam trawls between 1989 and 1997 (Garstang, 1903b, 1905; Holt, 1910; Rogers *et al.*, 1999, 1998).

Historic data

Northwest Irish Sea

From November 1901 to October 1907, the SS "Helga" sampled demersal fish in the coastal waters of the east coast of Ireland (Holt, 1910) (Fig. 1). The beam trawl normally used was 12.8 m wide with a cod-end of 32 mm mesh (Table 1). The trawl was covered with a fine mesh bag of an undisclosed mesh size but described as "sprat mesh" or "mosquito muslin". The catch (number/hour) of all fish from the trawl and the trawl cover was analysed for 39 hauls, at 30 sites, taken during March and the period 15 August to 15 October (Table 1). At four stations, a 9.1 m beam trawl was used with the same mesh and cover as for the larger gear. The mean duration of the hauls was 1.5 h, with a total duration of 56.8 h (Table 1). Commercially important fish were measured to the nearest cm total length, or disc width in the case of batoids.

Start Bay, Devon

Between 1901 and 1902, experimental trawling in and around Start Bay, Tor Bay and Teignmouth Bay was undertaken by the steamer SS "Oithona", towing an otter trawl described by Kyle (1903) and Garstang (1903b). The trawl had a headline length of 19.5 m and a cod-end mesh size of 25–38 mm (Table 1). Trawling

Table 1. Summary details of the historic (H) and contemporary (C) surveys used in the comparison of demersal fish populations. Details marked by N/A were not appropriate to the gear. Mesh size data are shown for stretched mesh. Catch efficiency of gears is shown relative to the 4 m beam trawl.

	Northwest Irish Sea		Start Bay		North Sea	
	H	C	H	C	H	C
Length of beam (m)	12.8	4	N/A	4	13.1	4
Head line length (m)	N/A	N/A	19.5	N/A	N/A	N/A
Length of ground rope (m)	~13–15	9.4	27.4	9.4	24.4	9.4
Wings and square	N/A	120–125	63	120–125	106–129	120–125
Cod-end (mm)	32	75	25–38	75	63	75
Cover	Sprat mesh/mosquito muslin	N/A	N/A	N/A	N/A	N/A
Cod-end liner (mm)	N/A	40	N/A	40	N/A	40
Tow speed (knots)	~2.5	4	2.5	4	~2	4
Swept area (1000 m^2/h)	59.2	29.6	60.1	29.6	48.5	29.6
Relative catch efficiency	2	1	2.03	1	1.63	1
Survey vessel	SS Helga	RV Corystes	SS Oithona	FV Carhelmar	SS Huxley	RV Corystes
Survey dates	1902–1907	1989–1997	1901–1902	1989–1997	1903	1989–1997
Reference	Holt (1910)	Symonds and Rogers (1995)	Garstang (1903)	Rogers *et al.* (1998)	Garstang (1905)	Rogers *et al.* (1998)
Trawl period	Mar. and Sept./Oct.	Mar. and Sept./Oct.	Aug. 1901–Oct. 1902	Oct.	Jun.–Nov.	Aug.
Total hauls	39	91	111	64	14	66
Mean tow duration	1 h 30 min	31 min	1 h 30 min	48 min	2 h	30 min
Total tow duration	56 h 48 min	47 h 48 min	208 h	52 h 24 min	37 h 18 min	30 h 18 min

was undertaken monthly during a 14 month sampling period. Hauls in which fish were only given a qualitative estimate of abundance (e.g. "many"), or were not accurately identified to species level (e.g. "ray species") have been omitted from the analysis. The abundance (n/h^{-1}) of all fish captured was recorded at 111 trawl stations, from 10 sites (Table 1). A total of 208 h of trawling records were available (Table 1).

Fish lengths were not systematically recorded for all species, but at most stations the abundance greater and less than 20.3 cm was recorded for dab, *Limanda limanda*, flounder, *Pleuronectes flesus*, sole, *Solea solea*, plaice, *Pleuronectes platessa*, whiting, *merlangius merlangus*, grey gurnard, *Eutrigla gurnardus*, John Dory, *Zeus faber* and red mullet *Mullus surmuletus*, and abundance greater and less than 25.4 cm was recorded for turbot, *Scophthalmus maximus* and brill, *S. rhombus*. For ray species, a width of 30.5 cm across the wings was used to distinguish small and large individuals.

Southern North Sea

Between June and November 1903, the SS "Huxley" sampled demersal fish populations at 14 fishing stations in the southern North Sea, using a 13.1 m beam trawl with a 63 mm cod-end mesh (Garstang, 1905) (Table 1; Fig. 1). Hauls whose total duration exceeded 3 h were excluded from the analysis; a total of 37.3 h trawling records were subsequently available (Table 1). Although the abundance of all commercial and many non-target species was recorded, the presence of some non-target fish, possibly the least abundant, was described in anecdotal observations of the benthos bycatch. In common with the trawling exercise in Start Bay, fish lengths were not recorded systematically, or at all stations, but the abundance of some species were given in 10 cm length groups.

Contemporary data

Irish Sea, Western Channel and southern North Sea

Surveys in the Irish Sea and southern North Sea have been undertaken at fixed station positions by RV "Corystes" during September or October 1989–1997, and during March 1993–1994 and 1996–1997. The beam trawl was 4 m wide, with a 40 mm mesh cod-end liner, and a chain mat and flip-up ropes to prevent large rocks entering the net (Symonds and Rogers, 1995; Rogers *et al*., 1998) (Table 1). Surveys in the Western Channel during September or October 1989–1997 were undertaken by a chartered commercial beam trawler MFV "Carhelmar", using the same gear (Rogers *et al*., 1998) (Fig. 1). Haul duration was normally 30 min, and over 130 h of trawling in these three areas were available for analysis (Table 1). The catch rate (n/h^{-1}) and total length of all fish caught was recorded.

Table 2. Pelagic and small demersal species recorded and enumerated during the surveys but excluded from the analysis.

Pelagic	
Herring	*Clupea harengus*
Sprat	*Sprattus sprattus*
Lesser silver smelt	*Argentina sphyraena*
Argentines	Argentinidae
Norway pout	*Trisopterus esmarki*
Horse mackerel	*Trachurus trachurus*
Sandeels	Ammodytidae
Mackerel	*Scomber scombrus*
Small demersal	
Fries goby	*Lesuerigobius friesii*
Sand gobies	*Pomatoschistus* spp
Jeffrey's goby	*Buenia jeffreysii*

Data standardization

The fish catches were standardized to compensate for the differences between gears and their methods of operation. First, it is assumed that differences in trawl speed have little effect on the catch efficiency of most demersal fish. A towing speed for otter trawls of 2–2.5 knots is thought to be fast enough to catch all but the largest and fastest swimming demersal species (Greenstreet and Hall, 1996). Towing speed during all surveys was approximately 2–4 knots (Table 1). Although the mesh sizes in the cod-ends ranged from 32–75 mm, with the smallest being used during the historic surveys, these differences will mostly affect the selectivity of the gear for small fish. To standardize gear selectivity as much as possible, some small bodied species were removed from the dataset (Table 2). Pelagic species were also excluded from the datasets (Table 2).

To standardize the catch rates of the different gears, the swept area of each trawl was estimated using the width of the net opening and the distance towed per hour. For beam trawls the width is equal to the length of the beam, and for the otter trawl used by SS "Oithona", the trawl width was assumed to be two thirds of the headline length (Rijnsdorp *et al*., 1996). The swept area was lowest for the 4 m beam trawl used in contemporary surveys (29 600 m^2/h^{-1}) and highest for the 12.8 m beam trawl towed by SS "Helga" (59 200 k m^2/h^{-1}) and the otter trawl of SS "Oithona" (60 100 m^2/h^{-1}) (Table 1).

Data analysis

In each region and for both historic and contemporary surveys, the mean standardized catch numbers per hour of each species were calculated and used to generate cumulative frequency curves (k-dominance plots). For

Table 3. Description of the factors used to allocate each fish species to a category of vulnerability. Maximum body lengths used are based on length typically achieved by adults rather than the maximum recorded species length (Wheeler, 1978).

Code	Description of fish characteristics
A	Small teleosts (<29.9 cm maximum total length) with pelagic eggs
B	Large teleosts (≥30 cm maximum total length) with pelagic eggs
C	Small teleosts (<14.9 cm maximum total length) laying or carrying demersal eggs
D	Large teleosts (≥15 cm maximum total length) laying or carrying demersal eggs
E	Oviparous or viviparous species (<84.9 cm maximum total length)
F	Oviparous or viviparous species (≥85 cm maximum total length)

Table 4. Regression equations describing the relationship between total length (L) and disc width (D) of seven ray species.

	cm		
Raja batis	D=0.694 L+2.514	n=6	r^2=0.99
Raja brachyura	D=0.735 L − 1.079	n=89	r^2=0.99
Raja montagui	D=0.666 L+0.172	n=648	r^2=0.98
Raja naevus	D=0.586 L − 1.103	n=386	r^2=0.99
Raja fullonica	D=0.630 L − 2.926	n=10	r^2=0.99
	mm		
Raja clavata	D=0.694 L − 1.610	n=168	r^2=0.99
Raja microocellata	D=0.739 L − 14.585	n=308	r^2=0.99

this analysis in the North Sea, all species which had not been counted in the historic survey were removed from contemporary data sets, to standardize the comparison between periods. Exceptions included four species (eel-pout, *Zoarces viviparus*, five-bearded rockling, *Ciliata mustela*, poor cod, *Trisopterus minutus* and undulate ray, *Raja undulata*) which had already been recorded in the southern North Sea and elsewhere during earlier surveys by Garstang (1903b, 1905). It was thought that these species would have been counted if caught.

Ordination and clustering techniques were used to illustrate the degree of similarity in the species composition of catches from the different regions and time periods. All multivariate analyses, using the PRIMER analytical package (Clarke, 1993), used the percentage of species in the catch (Warwick and Clarke, 1993). Cluster analyses were performed on all historic and contemporary data from each region, using the Bray-Curtis index of similarity and the group-average method of linkage on root–root transformed data, to reduce the influence of abundant species. These relationships were further investigated using multi-dimensional scaling

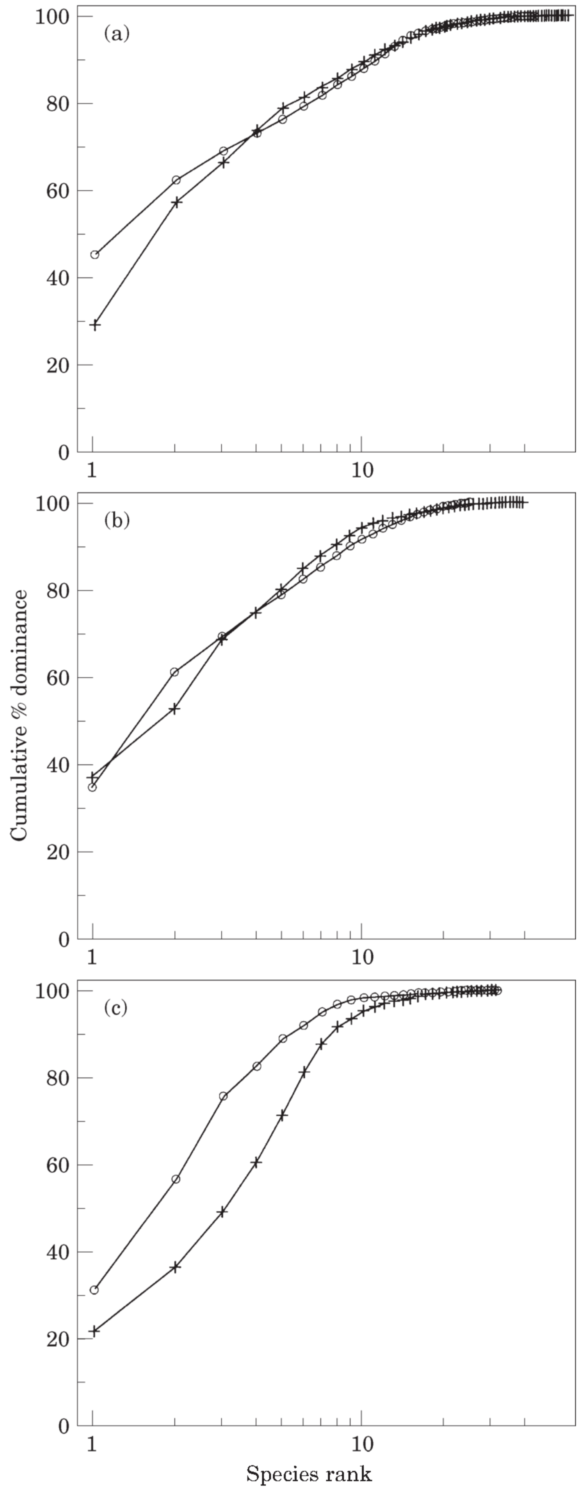

Figure 2. The cumulative frequency of abundance (or k-dominance plots) of species sampled by historic (open circle) and contemporary (cross) surveys in the Irish Sea (a), Start Bay (b) and the southern North Sea (c).

(MDS) to produce a two-dimensional representation of the relationships between samples. Partly to avoid high levels of stress (>0.23) in the 2-D representation of samples from all three regions (Warwick and Clarke, 1993), surveys undertaken in the Irish Sea and Start Bay were compared separately from the historic and contemporary North Sea data sets. Analysis of similarity tests (ANOSIM) were used to test the significance of observed differences between survey data sets.

Similarity of percentages (SIMPER) analysis identified those species which typified historic and contemporary catches in the southern North Sea and in the combined data set from the Irish Sea and Start Bay, and also identified those species which discriminated between them (Clarke, 1993).

Each species was allocated to one of six categories of potential vulnerability to commercial exploitation, to assess whether temporal changes in species relative abundance were related to fishing effects. Teleosts which release eggs into the water column were categorized as small or large (< or >30 cm) based on the maximum length of the species as reported by Wheeler (1978). Teleosts which carry eggs or deposit them onto the seabed (e.g. pipefish, *Syngnathus* spp., blennies *Blennius* spp), and hence may intuitively be more vulnerable to towed gears than those which release pelagic eggs, were similarly allocated to length categories of less than or greater than 15 cm. All oviparous and viviparous species (including all elasmobranchs and eelpout *Zoarces viviparus*) were categorized according to whether the normally observed maximum length was less than or greater than 85 cm (Table 3).

The standardized catch rates of species in 4 cm length classes (Irish Sea) and in 10 cm length classes (North Sea), were compared to monitor changes in length-frequency between hirostic and contemporary surveys. The disc widths of all rays from historic samples were converted to total lengths using relationships determined from wild samples (Table 4).

Results

Changes in fish catch data

The k-dominance plots of catches from the Irish Sea and Start Bay surveys indicated that species diversity was similar in the two time periods (Fig. 2a, b). It would, however, be misleading to assume that the assemblages had undergone little change. In the Irish Sea, approximately 60% of the historic catch consisted of dab and grey gurnard, while contemporary surveys recorded approximately the same proportion of dab and plaice (Table 5). In Start Bay, dab and plaice dominated catches at the turn of the century, while recent surveys found that dragonets *Callionymus* spp. and poor cod were the two most abundant taxa (Table 5). In contrast, the k-dominance curve for contemporary southern North Sea catch data was below that for historic data (Fig. 2c), indicating an increase in species diversity. The historic catches were dominated by only a few species, principally whiting, plaice and dab (Table 5).

An MDS ordination plot of all Irish Sea and Start Bay data (Fig. 3) had a 2-D stress value of 0.2, which was sufficiently low to provide a useful representation of the distribution of this large number of samples in two dimensions (Clarke and Warwick, 1994). This 2-D MDS ordination of combined data appeared to separate the historic Irish Sea and Start Bay survey data sets from contemporary samples (Fig. 3). These differences were confirmed by one-way ANOSIM analyses which showed that, in each region, the time-period samples were significantly different ($p<0.01$ for both between time-period comparisons). MDS analysis of southern North Sea data (Fig. 4) also showed clear separation between time-period data, and these differences were also found to be significant (ANOSIM $p<0.01$ for between time-period comparison).

The results of SIMPER analysis of the fish catch data for combined historic surveys in the Irish Sea and Start Bay showed that they were typified by dab, plaice, grey gurnard, thornback ray *Raja clavata* and whiting (Table 6). Contemporary surveys in these two regions showed that although all of these species, except thornback ray, were still relatively abundant, additional species such as dragonets, poor cod, sole and pogge *Agonus cataphractus* also typified the catches (Table 6). Species which contributed most to the discrimination between time periods were dragonnet, poor cod, solenette *Buglossidium luteum*, dab, whiting and plaice (Table 7).

Mean standardized catch rates of each species, also expressed as a proportion of the total catch (Table 5), showed why these patterns emerged. Species which were important typifying species in the Irish Sea and Start Bay (dab, grey gurnard and thornback ray) declined in relative abundance. Non-target species (dragonet, solenette, poor cod and pogge), which contributed to the dissimilarity between historic and contemporary surveys, have consistently higher catch rates and relative abundances in contemporary catches (Table 5).

Historic southern North Sea catches were typified by whiting, plaice, dab, grey gurnard and sole (Table 6). All these species, except grey gurnard, also typified the fauna in contemporary North Sea catches, although non-target species such as bib *Trisopterus luscus* and poor cod also became important typifying and consistent discriminating species (Table 6; Table 7). Dragonet, bull-rout and pogge, which were not quantified during the historic North Sea survey and hence were not included in the SIMPER analysis, comprised approximately 33% of the catch of contemporary surveys (Table 5). The relative abundance of dab and grey gurnard decreased in the North Sea to mirror changes in the Irish

Table 5. Catch rates (numbers per hour standardised for area swept) and proportions of demersal species caught in surveys during 1901–1907 (H) and 1989–1997 (C). In the SS "Huxley" survey of the North Sea, those species which were not counted are shown by "+". The category of vulnerability applied to each species is marked. See Table 3 and text for an explanation of these codes.

			Irish Sea				Start Bay				North Sea			
		Vulnerability	H		C		H		C		H		C	
Spurdog	*Squalus acanthias*	F	1.8	2	0.1	<1	0.2	<1	0.2	<1	0.1	<1	—	—
Angel shark	*Squatina squatina*	F	<0.1	<1	—	—	0.8	2	—	—	—	—	—	—
Blackmouthed dogfish	*Galeus melastomus*	E	—	—	—	—	—	—	—	—	—	—	—	—
Lesser spotted dogfish	*Scyliorhinus canicula*	E	2.1	3	13.7	2	0.3	<1	1.6	<1	<0.1	<1	10.1	2
Nurse hound	*Scyliorhinus stellaris*	F	—	—	0.1	<1	—	—	—	—	—	—	—	—
Tope shark	*Galeorhinus galeus*	F	0.1	<1	<0.1	<1	—	—	—	—	<0.1	<1	<0.1	<1
Starry smooth hound	*Mustelus asterias*	F	0.3	<1	0.1	<1	—	—	—	—	—	—	1.3	<1
White skate	*Raja alba*	F	—	—	—	—	<0.1	<1	—	—	—	—	—	—
Common skate	*Raja batis*	F	0.1	<1	—	—	—	—	—	—	—	—	—	—
Blonde ray	*Raja brachyura*	F	<0.1	<1	1.4	<1	1.3	2	0.4	<1	<0.1	<1	0.2	<1
Thornback ray	*Raja clavata*	F	2.2	3	0.7	<1	4.3	8	1.9	<1	0.7	<1	2.3	<1
Small-eyed ray	*Raja microocellata*	E	—	—	—	—	0.1	<1	0.2	<1	—	—	—	—
Spotted ray	*Raja montagui*	E	0.4	1	2.5	<1	0.2	<1	1.6	<1	<0.1	<1	1.6	<1
Cuckoo ray	*Raja naevus*	E	—	—	3.6	<1	—	—	—	—	—	—	—	—
Undulate ray	*Raja undulata*	E	—	—	—	—	—	—	—	—	—	—	0.4	<1
Eel	*Anguilla anguilla*	B	—	—	—	—	0.0	<1	0.1	<1	—	—	0.1	<1
Conger eel	*Conger conger*	B	0.1	<1	0.1	<1	<0.1	<1	—	—	<0.1	<1	—	—
Cod	*Gadus morhua*	B	1.3	2	8.9	1	<0.1	<1	—	—	5.5	3	4.4	1
Haddock	*Melanogrammus aeglefinus*	B	0.8	1	18.9	2	—	—	—	—	11.0	6	—	—
Whiting	*Merlangius merlangus*	B	1.8	2	81.7	9	1.5	3	10.2	2.1	56.7	31	28.6	7
Pollack	*Pollachius pollachius*	B	0.1	<1	—	—	—	—	—	—	—	—	—	—
Saithe	*Pollachius virens*	B	0.1	<1	—	—	—	—	—	—	—	—	—	—
Bib	*Trisopterus luscus*	B	1.2	2	0.7	<1	1.9	4	1.7	<1	0.2	<1	38.3	9
Poor cod	*Trisopterus minutus*	A	1.2	2	44.1	5	<0.1	<1	78.8	15.9	—	—	30.6	7
Five-bearded rockling	*Ciliata mustela*	A	—	—	0.2	<1	—	—	—	—	—	—	1.6	<1
Northern rockling	*Ciliata septentrionalis*	A	—	—	0.1	<1	—	—	—	—	—	—	—	—
Four-bearded rockling	*Enchelyopus cimbrius*	A	0.1	<1	0.1	<1	—	—	0.1	<1	—	—	0.7	<1
Common ling	*Molva molva*	B	—	—	0.3	<1	—	—	—	—	<0.1	<1	—	—
Hake	*Merluccius merluccius*	B	—	—	0.4	<1	—	—	0.2	<1	—	—	—	—
Angler	*Lophius piscatorius*	B	0.2	<1	3.0	<1	—	—	0.2	<1	0.1	<1	—	—
Clingfish family	*Gobiesocidae*	C	<0.1	<1	0.2	<1	—	—	—	—	—	—	—	—
John dory	*Zeus faber*	B	0.2	<1	0.4	<1	0.5	<1	1.0	<1	<0.1	<1	—	—
Snake pipefish	*Entelurus aequoreus*	D	<0.1	<1	—	—	—	—	—	—	—	—	—	—
Greater pipefish	*Syngnathus acus*	D	<0.1	<1	0.8	<1	—	—	0.7	<1	—	—	—	—
Nilsson's pipefish	*Syngnathus rostellatus*	D	—	—	0.1	<1	—	—	—	—	+	—	0.6	<1
Red gurnard	*Aspitrigla cuculus*	B	0.1	<1	0.2	<1	0.2	<1	2.7	<1	0.3	0	—	—
Grey gurnard	*Eutrigla gurnardus*	A	12.5	17	22.2	2	2.9	5	5.7	1.2	12.5	7	2.3	<1
Tub gurnard	*Trigla lucerna*	B	—	—	0.3	<1	0.7	1	1.2	<1	0.4	<1	0.1	<1
Streaked gurnard	*Trigloporus lastoviza*	B	—	—	—	—	<0.1	<1	—	—	—	—	—	—
Bull-rout	*Myoxocephalus scorpius*	D	—	—	7.7	<1	—	—	—	—	+	—	39.8	9
Sea scorpion	*Taurulus bubalis*	D	—	—	—	—	—	—	—	—	+	—	9.2	2

Table 5. *(Continued)*.

			Irish Sea				Start Bay				North Sea			
		Vulnerability	H		C		H		C		H		C	
Pogge	*Agonus cataphractus*	C	<0.1	<1	19.0	2	0.1	<1	8.0	1.6	+	—	65.2	15
Lump sucker	*Cyclopterus lumpus*	D	—	—	0.1	<1	—	—	—	—	—	—	—	—
Sea snail	*Liparis liparis*	C	—	—	0.3	<1	—	—	—	—	+	—	0.2	<1
Montagu's seasnail	*Liparis montagui*	C	—	—	—	—	—	—	—	—	+	—	0.1	<1
Sea bass	*Dicentrarchus labrax*	B	—	—	—	—	—	—	0.4	<1	—	—	—	—
Black sea-bream	*Spondyliosoma cantharus*	D	—	—	—	—	—	—	<0.1	<1	—	—	—	—
Red mullet	*Mullus surmuletus*	B	—	—	0.1	<1	0.1	<1	2.5	<1	<0.1	<1	0.3	<1
Red bandfish	*Cepola rubescens*	B	—	—	—	—	—	—	0.3	<1	—	—	—	—
Goldsinny	*Ctenolabrus rupestris*	A	—	—	0.4	<1	—	—	—	—	—	—	—	—
Cuckoo wrasse	*Labrus mixtus*	D	—	—	0.1	<1	—	—	—	—	—	—	—	—
Eelpout	*Zoarces viviparus*	E	—	—	—	—	—	—	—	—	—	—	0.5	<1
Snake blenny	*Lumpenus lampretaeformis*	B	0.1	<1	—	—	<0.1	<1	—	—	—	—	—	—
Butterfish	*Pholis gunnellus*	D	0.1	<1	2.7	<1	—	—	—	—	+	—	4.7	1
Lesser weever	*Echiichthys vipera*	A	—	—	2.2	<1	—	—	1.4	<1	+	—	2.1	<1
Greater weever	*Trachinus draco*	B	—	—	—	—	0.2	<1	—	—	0.3	<1	—	—
Butterfly blenny	*Blennius ocellaris*	D	—	—	1.7	<1	—	—	<0.1	<1	—	—	—	—
Dragonet family	*Callionymiidae*	A	1.2	2	66.7	7	2.1	4	78.7	15.9	+	—	37.4	9
Goby family	*Gobiidae*	A	—	—	7.3	<1	—	—	2.3	<1	—	—	—	—
Megrim	*Lepidorhombus whiffiagonis*	B	0.1	<1	0.2	<1	—	—	—	—	—	—	—	—
Norwegian topknot	*Phrynorhombus norvegicus*	A	—	—	1.1	<1	—	—	0.7	<1	—	—	—	—
Turbot	*Scophthalmus maximus*	B	0.1	<1	0.3	<1	<0.1	<1	0.1	<1	0.1	<1	0.1	<1
Brill	*Scophthalmus rhombus*	B	0.1	<1	0.6	<1	0.3	<1	0.7	<1	0.3	<1	0.5	<1
Topknot	*Zeugopterus punctatus*	A	—	—	0.1	<1	—	—	—	—	—	—	—	—
Scaldfish	*Arnoglossus laterna*	A	0.1	<1	1.1	<1	1.2	2	25.3	5.1	0.4	0	—	—
Witch	*Glyptocephalus cynoglossus*	B	0.3	<1	7.9	<1	—	—	—	—	0.3	<1	—	—
Long rough dab	*Hippoglossoides platessoides*	A	3.0	4	11.1	1	—	—	—	—	5.9	3	—	—
Dab	*Limanda limanda*	A	32.5	45	260.6	29	18.5	35	29.5	6.0	34.6	19	34.5	8
Lemon sole	*Microstomus kitt*	B	1.3	2	7.2	<1	<0.1	<1	0.3	<1	3.0	2	26.6	6
Flounder	*Platichthys flesus*	B	0.2	<1	1.1	<1	0.4	<1	0.7	<1	<0.1	<1	5.3	1
Plaice	*Pleuronectes platessa*	B	4.8	7	254.3	28	13.9	26	24.1	4.9	47.0	26	17.3	4
Solenette	*Buglossidium luteum*	A	1.1	1	15.0	2	0.6	1	183.5	37.1	0.2	<1	0.4	<1
Thick back sole	*Microchirus variegatus*	B	<0.1	<1	19.6	2	<0.1	<1	13.4	2.7	—	—	0.1	<1
Sand sole	*Solea lascaris*	B	—	—	—	—	0.1	<1	—	—	—	—	0.1	<1
Sole	*Solea solea*	B	0.4	1	4.5	<1	0.5	<1	13.8	2.8	2.1	1	58.2	14

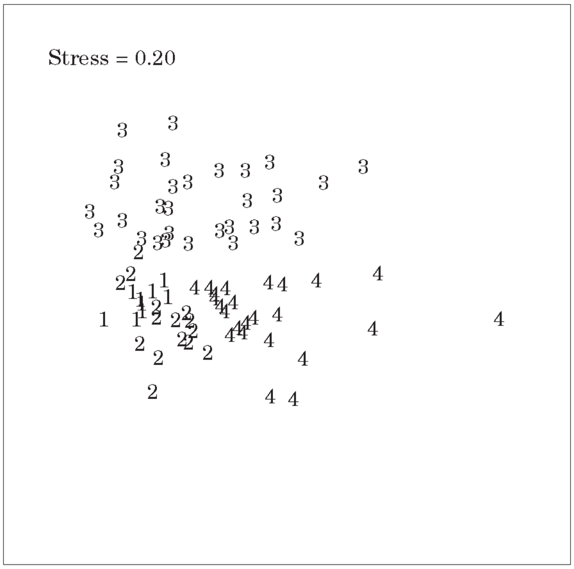

Figure 3. Multi-dimensional scaling ordination plots for historic (1) and contemporary (2) surveys in Start Bay, and for historic (3) and contemporary (4) surveys in the Irish Sea.

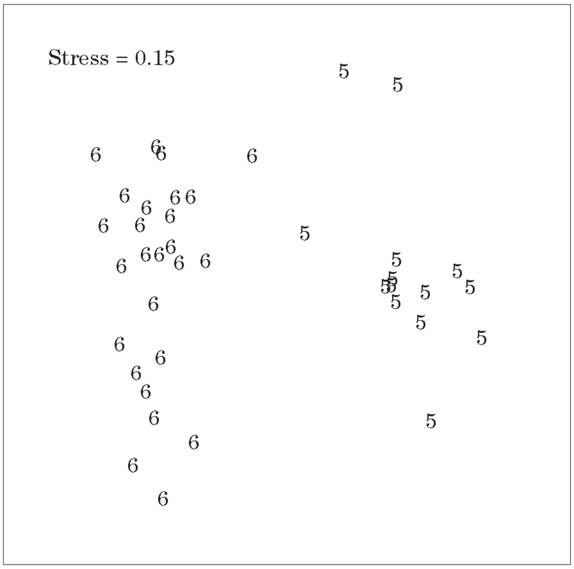

Figure 4. Multi-dimensional scaling ordination plots for historic (5) and contemporary (6) surveys in the southern North Sea.

Sea and Start Bay, and catches of thornback ray were consistently low.

Changes in vulnerability

One possible explanation for the apparent increase in abundance of non-target species is the different degree of vulnerability of fish taxa to the effects of commercial exploitation. The proportion of small bodied teleosts in the catch (vulnerability categories A & C in Table 3) increased in the North Sea and Start Bay between the two survey periods (Fig. 5). None of the species in this category is commercially exploited. Surprisingly, these teleosts, which either carry eggs or lay them on the seabed, also increased as a proportion of catches, particularly in the North Sea. The proportion of larger bodied teleosts with pelagic eggs (category B) decreased in the southern North Sea and Start Bay, but not the Irish Sea, where plaice has replaced grey gurnard as a dominant species. There was also a decline in the abundance of large and small oviparous and viviparous fish in westerly regions. When trends in elasmobranch abundance were examined in detail (Fig. 6), it was clear that large bodied skates and sharks, including the common and white skate (*R. batis* and *R. alba*) and the angel shark *S. squatina*, which formed a small proportion of catches, had decreased as a proportion of the total elasmobranch catch. Rays of intermediate body size showed marked declines in relative abundance, especially the blonde ray *R. brachyura* and the thornback ray *R. clavata*. Consequently, the contemporary elasmobranch catches comprised mainly smaller species such as the spotted ray *R. montangui*, cuckoo ray *R. naevus* and lesser spotted dogfish *Scyliorhinus canicula* (Fig. 6).

Changes in fish size distribution

Consistent changes in length-frequency distribution of target species, non-target species, and rays, in favour of smaller individuals, occurred during the 80 yr interval between sampling in the Irish Sea and North Sea (Fig. 7). In the Irish Sea, the recent increase in abundance of lesser spotted dogfish, which has replaced the thornback ray as a dominant elasmobranch, resulted in an increase in mean length of all combined elasmobranchs (Fig. 7e). In Start Bay, where the lack of detailed length-frequency data precluded such analyses, these changes were not evident using the proportions of ten species less than and greater than 20 cm total length (Fig. 8).

Discussion

The apparent increases in abundance of non-target fish in all regions studied, and the consistent changes in length-frequency distribution of target species from the Irish Sea and southern North Sea in favour of smaller fish, strongly suggests the influence of commercial fisheries. It is possible, however, that these temporal differences between surveys result from the different catch efficiencies of the gears employed, rather than genuine changes in fish relative size and abundance. There are published observations and some theoretical predictions which can help to explain why these changes may have

Table 6. The average percentage occurrence of fish in historic and contemporary samples from North Sea and combined westerly surveys, from SIMPER analysis. Those species which contributed >5% to the Bray-Curtis similarity of each group are shown. Species which consistently typify the community (mean/s.d.>2) are shown by *. Some species (1) were not quantified in the historic North Sea data set.

	Start Bay+Irish Sea		North Sea	
	Historic	Contemporary	Historic	Contemporary
Plaice	8.0	12.8	14.7*	5.4
Sole		3.6	8.6*	22.2*
Dab	14.7	11.5	14.7	5.0
Lemon sole			5.4	4.0
Dragonet spp. (1)		9.9		
Pogge (1)		2.0		
Whiting	1.1	8.9	35.9	5.7
Poor cod		8.2		5.3
Bib				11.9
Grey gurnard	5.3	3.2	8.7	
Thornback ray	3.4			
Average within survey similarity	41.2	45.4	57.9	58.0

Table 7. Percentage contributions (>3.5%) of demersal species to the average between-survey dissimilarity, using SIMPER analysis (Clark, 1993). Those species marked by * are consistent in discriminating between surveys (mean/s.d.>1.5). Some species (1) were not quantified in the historic North Sea data set.

	Between historic and contemporary surveys	
	Irish Sea+Start Bay	North Sea
Solenette	4.8	
Plaice	4.3	5.1
Dab	4.5	5.1
Sole		5.4
Lemon sole		5.2
Flounder		4.2
Bib		8.3*
Whiting	4.4	7.7
Poor cod	4.8	6.8*
Cod		4.4
Dragonet family (1)	5.0	
Pogge (1)	3.6	
Grey gurnard		7.7*
Lesser spotted dogfish	3.5	4.0
Thornback ray		4.2
Goby family		5.7
Average between survey dissimilarity	63.9	56.0

occurred as a direct response to commercial exploitation. But first we must consider the influence on these observations of the different trawls used.

All fishing gears have a catchability and efficiency which is specific to their design and the way they are operated in relation to particular species. Thus, changes in fish assemblage structure observed using the catches of different trawls will incorporate both gear effects as well as genuine spatial and/or temporal changes. The relative efficiencies of different trawls can be estimated using comparative fishing exercises, but these are expensive, logistically complex and are not routinely undertaken (Groeneveld & Rijnsdorp, 1990; ICES, 1993; Knijn *et al.*, 1993; Sangster & Breen, 1998). These comparisons provide raising factors for the most important or abundant fish, but these are often specific to individual species and cannot easily be applied to others. Estimating the efficiencies of historic gears is hampered by the absence of trawls made of correct materials and to the necessary specification, and the steam powered vessels to tow them. We can, therefore, only use our best judgement of the likely catchability of these historic trawls, based on the information to hand.

Details of net mesh sizes, and evidence from the size structure of demersal fish catches, suggests that the mesh selectivity using historic and contemporary gears was similar. Omitting the smallest members of the fish assemblage, such as gobies, from the analyses may have helped to standardize the catch of fish at the lower end of the size range. For larger fish, a tow speed of approximately 2 knots is thought likely to retain most of the larger bodied flatfish (Greenstreet and Hall, 1996; Rjinsdorp *et al.*, 1996). Little is known about the different effects of the tickler chains attached to these gears, but they will disturb fish (e.g. sole) living on the seabed, and increase their rate of capture in the net (Creutzberg *et al.*, 1987). It was common practice for demersal trawls at the turn of the century to incorporate heavy lengths of chain on the ground rope to increase contact with the seabed (Kyle, 1903). With increases in vessel power, and hence towing speed, the modern beam trawl is now fitted with a number of chains and the 4 m beam trawl incorporates a heavy chain mat. Although this configuration is designed for use over rough ground,

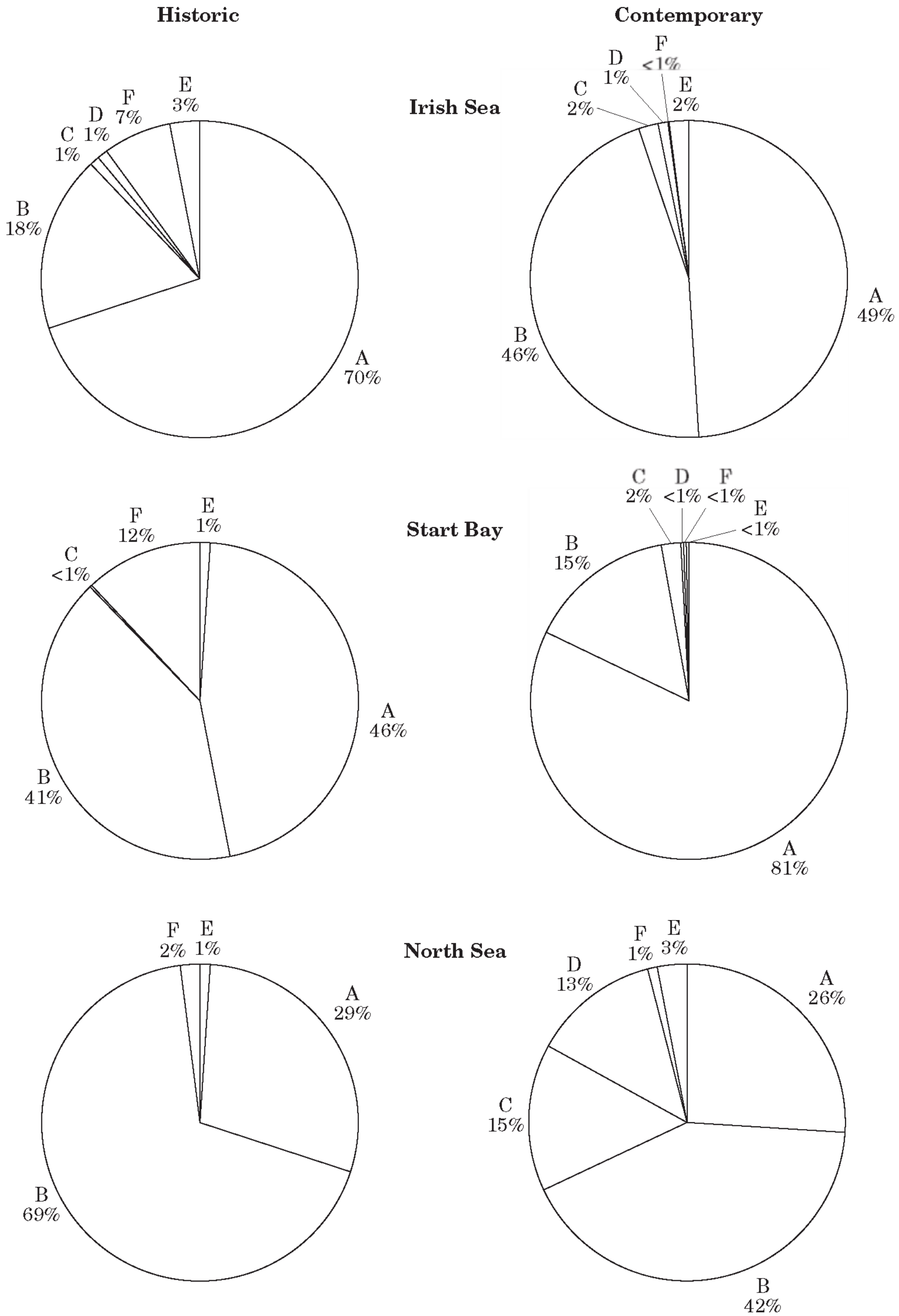

Figure 5. Between area and between time-period variation in the proportions of fish allocated to six categories, based on their potential vulnerability. Categories are: all small bodied species with pelagic eggs (a), large bodied species with pelagic eggs (b), small species laying demersal eggs (c), large species laying demersal eggs (d), and small (e) and large (f) oviparous and viviparous species. See text and Table 3 for more details of this categorization.

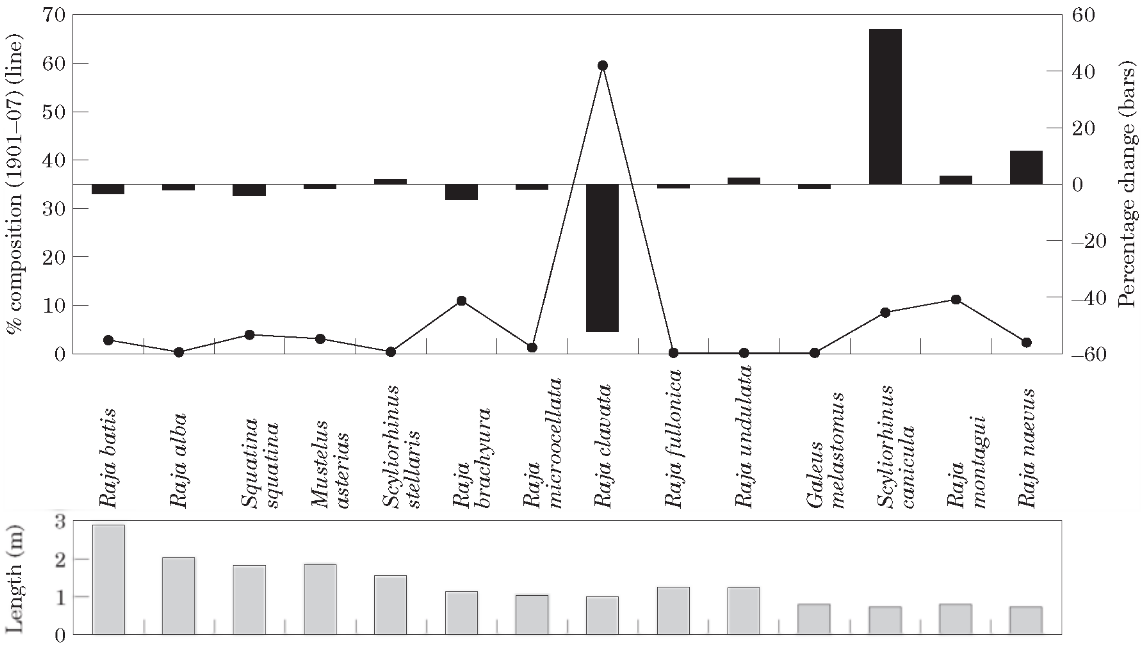

Figure 6. Percentage composition of the elasmobrach fauna from historic survey data (line), and the change in the percentage composition when compared to contemporary samples (% in contemporary data minus % in historic data) (bars). The approximate maximum length of each species (m) is shown by bars below each species name. Redrawn from Greenstreet and Rogers (2000).

it is particularly effective for catching flatfish. It is possible that the relatively high catch rates of sole in contemporary Start Bay surveys is a function of their greater vulnerability to the modern beam trawl, compared to the otter trawl used in 1901–1902 (Kyle, 1903).

The traditional mixed demersal fisheries of the late 19th and early 20th century are thought to have caught large numbers of small fish. Mesh sizes in use at that time were in the range 4–7 cm, and small fish were either discarded or landed for the fish meal industry (Rijnsdorp and Millner, 1996). Concern for this depletion of juvenile populations was expressed at an early stage (Garstang, 1903a) and the threat to local populations was considered great enough to establish a number of closed areas (Garstang, 1903b). By the 1930s, the total UK landings of demersal species from the North Sea had exceeded 200 000 t per year, while the equivalent landings from the English Channel and Irish Sea were approximately 20 000 t (Wood, 1956). Thus, the survey data analysed in this paper do not allow a comparison between populations before and after the influence of commercial fisheries. They can only identify differences that may have resulted from continuous and increasing fishing mortality.

The increased abundance of smaller bodies species, and lower catch rates of larger fish, are consistent with results from other studies in the North Sea (Greenstreet and Hall, 1996; Rice and Gislason, 1996; Rijnsdorp *et al.*, 1996; Jennings *et al.*, 1999) and Northwest Atlantic (Duplisea and Kerr, 1995; Pope and Knights, 1982). These authors suggest that the selective removal of larger bodied target species by commercial fisheries is responsible for these patterns. Effects of fishing on species diversity, however, do not appear to be consistent. For example, in the English coastal region of the southern North Sea, a marked increase in diversity was observed in this study between the historic catches, dominated by whiting and plaice, and contemporary catches in which a range of non-target species were present. This conflicts with other published information from the central North Sea, which also included SS "Huxley" data (Rijnsdorp *et al.*, 1996), and which identified a decrease in diversity caused largely by the recent increase in the population of dab. In the north-west North Sea, a similar long-term decrease in diversity was thought to be caused by a recent increase in abundance of the target species Norway pout (Greenstreet and Hall, 1996). Ecological theory suggests that there could be a unimodal relationship between diversity and habitat productivity. As productivity (resulting from a disturbance such as fishing activity) rises to moderate levels, diversity begins to increase but then declines with further increases in productivity (Rosenzweig, 1995; Tilman, 1996). It is possible that the different stages of dominance recorded here and in the literature represent different points along this unimodal relationship. However in both the Irish Sea and Start

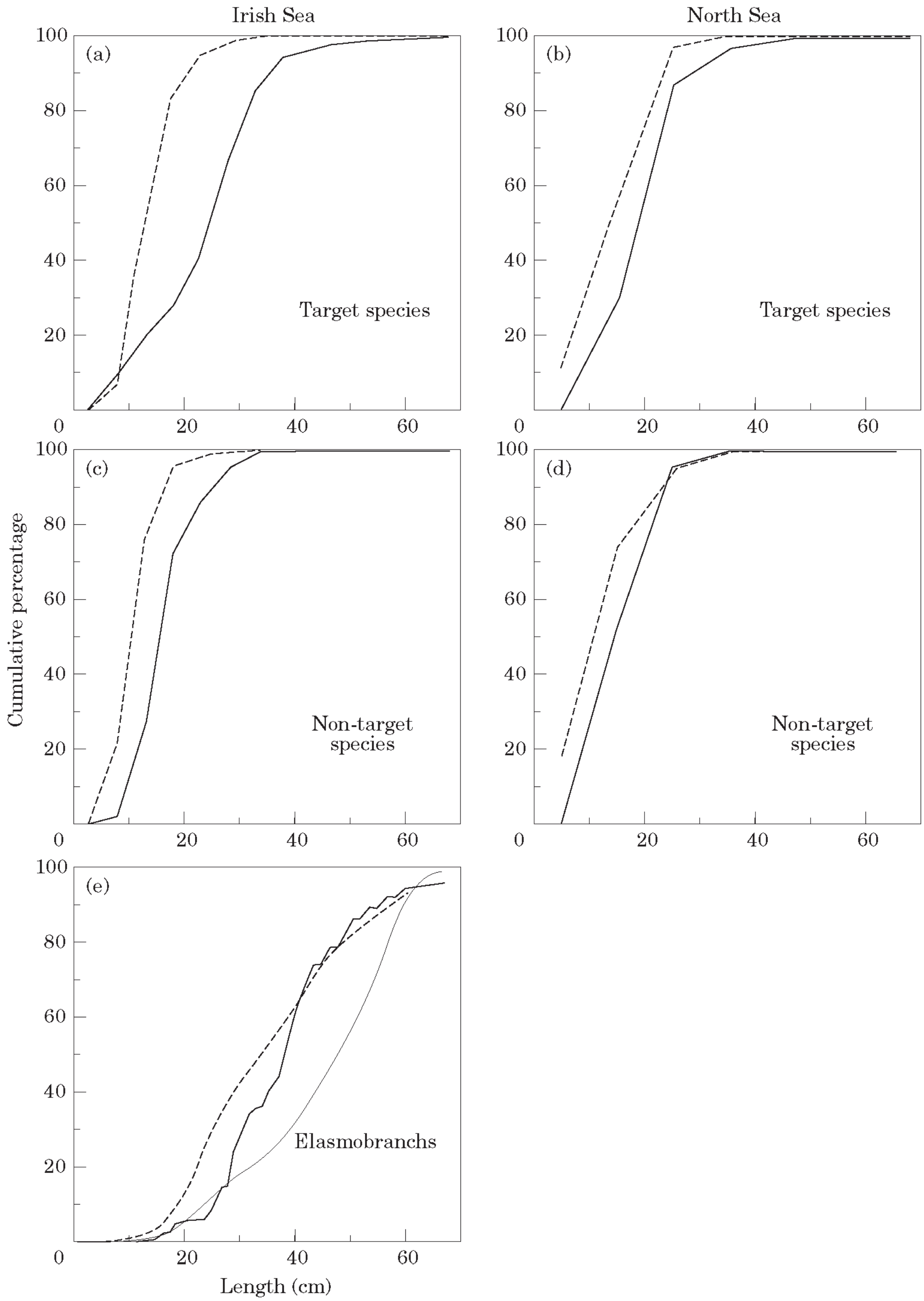

Figure 7. The proportion of individuals in length classes of target (a, b) and non-target species (c, d) from historic (bold line) and contemporary (broken line) samples from the Irish Sea and North Sea. The length distribution of all Irish Sea elasmobranchs (e) from historic samples (bold line), is shown with the length distribution of contemporary samples of ray species only (broken line) and of all elasmobranch species combined (fine continuous line). Disc widths of rays from historic Irish Sea surveys were raised to total length. The limited numbers of elasmobranchs in contemporary North Sea samples precluded analysis.

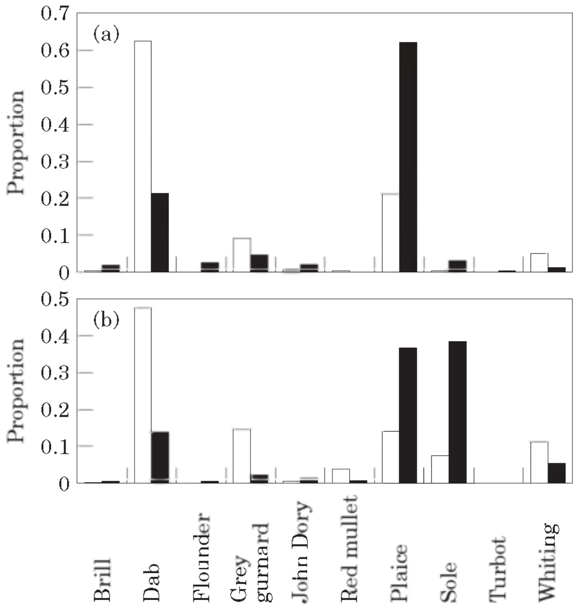

Figure 8. The proportions of ten species less than and greater than 20 cm total length recorded during historic (a) and contemporary (b) surveys of Start Bay.

Bay, despite a long history of fishing activity, there were no clear changes in fish species diversity between historic and contemporary surveys. This suggests that there may be other factors which influence the response of fish populations to fishing. So, to fully explain these temporal changes in diversity, it may also be necessary to consider information on the life-history characteristics of those species which occupy the region, and the physical factors which describe the habitat. This approach will identify species with high growth rates and high reproductive potential, and which are able to respond rapidly to changes in population sturcture when they occur. It will also provide information on the structure and complexity of the habitat, which would suggest whether it was suitable, and sufficiently extensive, for these species to become dominant members of the fish community.

Elasmobranchs are vulnerable to exploitation because of their generally slow growth rate, late maturation and lower potential rates of population increase (Hoenig and Gruber, 1990; Jennings *et al.*, 1998). The angel shark *S. squatina* was relatively abundant in Start Bay during surveys in 1901–1902, and Day (1880) reported that they were also common in the North Sea and along the south coast of England, including Devon and Cornwall. Recent surveys throughout the continental shelf rarely encounter this species (MAFF, unpublished data). *S. squatina* is a warm water species with its northern limit at the British Isles, so its abundance in the southwest in the early 1900s may be partly attributed to warmer temperature regimes at the time, which resulted in increased catches of the common octopus *Octopus vulgaris* (Garstang, 1901). Its absence from other contemporary surveys south of the British Isles, however (Sanchez *et al.*, 1995; Quero and Cendrero, 1996; Quero, 1998), cannot be attributed exclusively to temperature effects. The decreased abundance of commercially exploited elasmobranchs, as a response to directed exploitation, has been observed for several species, notably the basking shark *Cetorhinus maximus* and the porbeagle *Lamna nasus* in the North Atlantic, and the tope shark *Galeorhinus galeus* off California (Anderson, 1990). Catches of demersal elasmobranchs caught as a by-catch of mixed fisheries have also declined, for example the common skate in the Irish Sea (Brander, 1981) and the barndoor skate *R. laevis* in the north-western Atlantic (Casey and Myers, 1998).

Almost 70% of the fish fauna of the British Isles is comprised of species which are widely distributed and do not belong exclusively to either a northern of southern fauna (Rogers, 1991), so it is unlikely that long-term climatic changes in the north-east Atlantic (Lynagh, 1997) have greatly influenced the underlying structure of the inshore fish assemblage.

The historic datasets described here represent some of the earliest, and most comprehensive, published descriptions of demersal fish faunas. When compared with contemporary data sets, they show that large bodied species have declined in abundance, while smaller, non-target species, have become more abundant. Length-frequency distributions for target species, non-target species and elasmobranchs show consistent declines in favour of smaller individuals. Large bodied skates and sharks are now rare or absent from catches, rays of intermediate size have declined, and smaller species such as the lesser spotted dogfish, spotted ray and cuckoo ray are now the dominant elasmobranch species. It is suggested that the most likely cause of these changes in fish assemblage structure is the long-term effect of commercial fisheries.

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