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The inshore demersal fish community on the Swedish Skagerrak coast: regulation by recruitment from offshore sources

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To elucidate the species composition, size structure and abundance of inshore demersal fish community on the Swedish Skagerrak coast relative to the offshore community, a series of seven trawl surveys have been made in 2000–2001 and the results have been compared with scattered information from historic sources. The results show that abundance of fish >30 cm is presently extremely low for most long-lived species compared to historical records from the 1920s to 1970s. Cod, haddock, whiting, plaice, dab, long rough dab all showed a marked shift of the size spectra to the smaller sizes. Flounder was a notable exception: the size distribution had even widened and included more smaller as well as larger fish than in the historical records. Because flounder is the only long-lived species that is coast-bound and stationary, local fishing activity is apparently not responsible for the observed shift in the less stationary species. Also, fishing in the coastal zone has presumably been reduced because of the absence of the size range suitable for consumption. Overall, the demersal fish catches were dominated by immature fish that disappear when they grow older and most likely migrate offshore. The persistently high abundance of juvenile fish and the absence of adult fish suggest that the inshore demersal fish populations are presently regulated by recruitment from offshore sources, while historical information indicate that spawning aggregations of several of these species were common in these areas. It was hence hypothesized that a major change of the inshore demersal community has taken place during the last twenty years: local (sub-)populations of demersal fish have been eradicated, and the inshore area has become more and more dependent on transport of recruits from offshore spawning areas.

Keywords: abundance, cod, demersal fish, *Gadus morhua*, size distribution.

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Introduction

During the last twenty years, little attention has been paid to the abundance and structure of the inshore demersal fish assemblages of the Swedish west coast, i.e. inside the trawling limit (2 nm off the coastal base line, unless transferred closer to the coast). Partly in response to public concern regarding declining catches of cod (*Gadus morhua* L.) in particular, a study was initiated with the aim of verifying whether significant changes have taken place in the demersal fish community. Analyses of existing log-book records for offshore areas have revealed a persistent and almost simultaneous decline in the abundance of large cod in the Skagerrak and Kattegat since the beginning of the 1980s, while informal statistics such as records of sport fishing clubs and notes made by coastal fishermen indicated that the catches of inshore cod declined at the end of the 1970s before the offshore catches declined (Svedäng and Bardon, 2003). However, in the absence of systematic trawl surveys in inshore areas during the last 20 years, the scattered information available did not allow an evaluation of the present status of the demersal fish stocks in inshore areas. Here I describe the results of recent surveys aimed at estimating abundance and the size distribution of the inshore demersal fish community, and try to relate these to historical records.

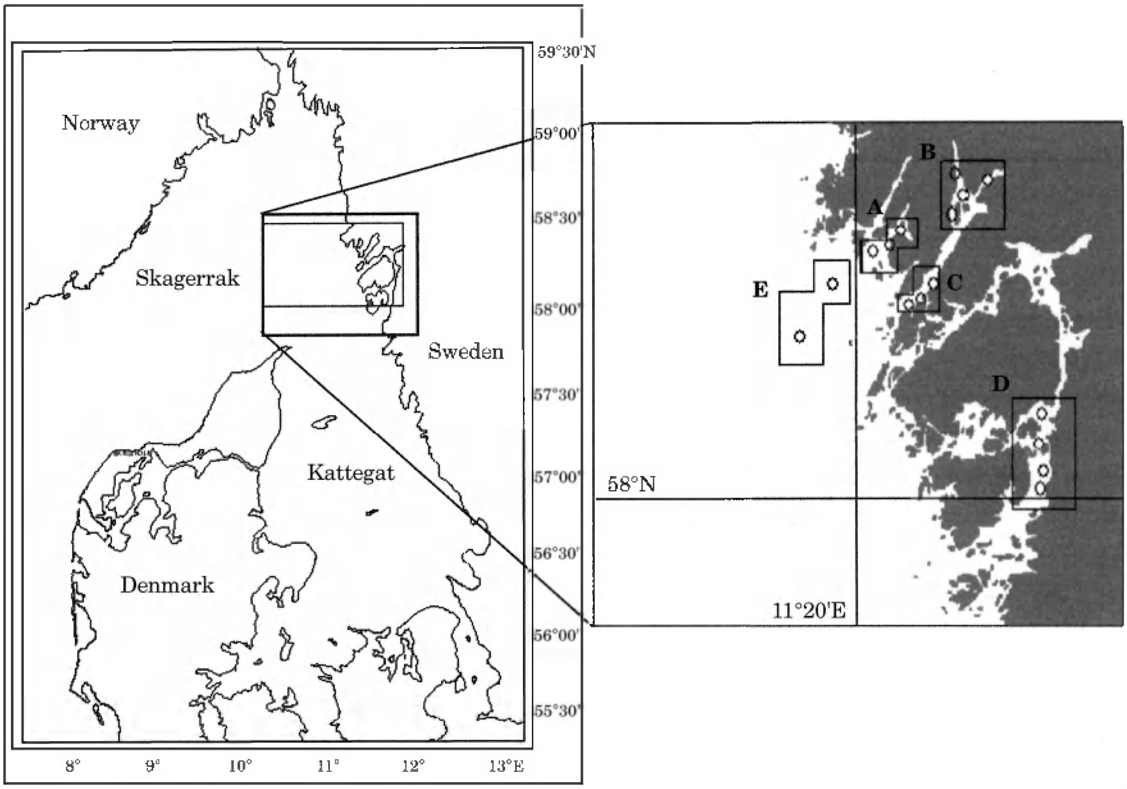

Figure 1. Location of inshore (A–D) and offshore (E) survey areas off the coast of the county of Bohuslän: A: Brofjord, B: inner Gullmarfjord, C: outer Gullmarfjord, D: Hakefjord, E: offshore localities. Log-book data of the Nephrops fishery used refer to the rectangle inside the enlarged box (58°–58°30′N; 10°–12°E).

Table 1. Total cpue of demersal fish in weight and number by survey and area, 2000–2001 (n: number of hauls).

				Cpue			
				$kg\ h^{-1}$		$n\ h^{-1}$	
Area	Year	Month	n	Mean	± s.d.	Mean	± s.d.
Inshore	2000	Mar	15	46	31	476	314
		Jun	13	68	51	675	199
		Oct	11	113	65	1204	571
		Dec	19	71	69	806	798
	2001	Feb	17	61	41	644	868
		May	11	44	30	563	417
		Oct	13	83	44	984	42
Offshore	2000	Mar	2	30	12	415	187
		Jun	3	32	16	307	125
		Oct	4	63	5	1034	289
		Dec	5	61	17	537	212
	2001	Feb	6	47	42	562	506
		May	3	30	3	346	9
		Oct	3	36	25	480	435

To facilitate management advice, marine fish are often assessed by fixed fishing areas, which supposes the existence of isolated stocks. This introduces an obvious risk of neglecting structuring elements within the unit stock area such as the existence of more or less isolated subpopulations, migratory behaviour, spawning site fidelity and dispersal patterns. Apparently, there is a general lack of information about the population structure of many important fish species – including cod – both in a genetical sense (Mork *et al.*, 1985; Hutchinson *et al.*, 2001) and with regards to spatial distribution of spawning sites (Brander, 1994; Munk *et al.*, 1999) as well as to homing and migratory behaviour (Arnold *et al.*, 1994; Righton *et al.*, 2001). However, recent studies on the cod stock complex off Newfoundland and Labrador have pointed out important structuring elements. Ruzzante *et al.* (1996, 2001) and Green and Wroblewski (2000) provide evidence of discrete cod (sub-) populations in the coastal waters relative to offshore populations. Hutchings *et al.* (1993) and Lawson and Rose (2000) showed a widespread distribution of spawning sites in both inshore and offshore waters. Despite variation in migratory behaviour, spawning site fidelity was often high (Green and Wroblewski, 2000; Robichaud and Rose, 2001).

The potential existence of local (sub-)populations of demersal species along the Skagerrak coast is still

Table 2. Cpue in weight of cod in the Brofjord area by survey, 1968–1980 (n: number of hauls).

Year	Month	n	kg h^{-1}
1968	Sep	3	67
	Oct	3	38
1969	May	4	88
	Jul	4	54
	Aug	4	146
	Oct	3	46
	Nov	4	45
	Dec	3	77
1970	Apr	3	77
	Jan	3	220
	Sep	4	17
	Oct	4	22
	Dec	3	52
1971	Feb	3	147
	Mar	4	297
	May	4	86
	Sep	4	28
	Nov	4	42
1973	May	4	98
	July	4	70
	Sep	4	33
	Nov	4	85
1974	Jan	4	337
	April	4	94
	June	4	48
1978	Nov	4	40
1979	May	4	144
	June	4	150
	Sep	4	52
1980	Jan	3	205
	Sep	3	44

an unsettled question (Danielssen, 1969; Pihl and Ulmestrand, 1993; Danielssen and Gjøsæter, 1994; Godø, 1995; Munk *et al.*, 1999), as well as their abundance relative to offshore components of the stock in terms of recruitment and biomass. However, inshore spawning aggregations of cod, whatever their affinity to offshore spawners, have been observed on both the Norwegian (Knutsen *et al.*, 2000) and Swedish coast (Hallbäck *et al.*, 1974).

Offshore spawning aggregations as far away as the northeastern North Sea may supply recruits to the Skagerrak coastal areas, because Munk *et al.* (1999) found clear indications of a major transport of eggs and larvae of cod, whiting (*Merlangus merlangus* L.), haddock (*Melanogrammus aeglefinus*), Norway pout (*Trisopterus esmarki* Nilsson) and saithe (*Pollachius virens* L.) in this direction. Thus, a further objective has been to disentangle the complicated population dynamics in the eastern Skagerrak of the most abundant demersal fish species during the period studied.

Material and methods

Survey data

In 2000 and 2001, trawl surveys have been carried out by RV "Ancylus" in inshore (A–D) and offshore (E) waters of Bohuslän county (Figure 1). The stations were selected partly on previously fished stations as well as new information about suitable fishing grounds. All areas were monitored during four surveys in 2000 and three surveys in 2001 (Table 1). The gear was a 140-feet Nephrops trawl (Ulmestrand and Larsson, 1991) with small bobbins (10 cm in diameter), and a codend mesh size of 70 mm. All hauls were made in full daylight at a speed of 2.5 knots. In most cases, haul duration was 30 min. After sorting by species, catch weights of all demersal fish species was recorded (0.1 kg). Presence of pelagic species was noted but they were excluded from the analysis. Of most species all individuals caught were measured to the nearest cm, but if the catch of a species of a species was large, a random subsample was taken.

During the period 1968–1980, the Institute of Marine Research has made various Nephrops trawl surveys in the Brofjord area (Figure 1), but codend mesh size varied (45–70 mm) and the number of hauls per survey was limited (Table 2). Haul duration varied between 20 and 150 min. The catches were recorded by weight and converted to kg h^{-1}. For 1973, information on mean length distribution of various demersal species (cod, haddock, whiting, plaice, dab – *Limanda limanda* L., long rough dab – *Hippoglossoides platessoides* Fab., and flounder – *Platichthys flesus* L.) has been collated from Hallbäck *et al.* (1974). To compare the development of cod abundance in the Brofjord area with the adjacent offshore area (58°–58°30′N, 10°–12°E), an index was derived from log-book data for 1978–1999 on landings of cod in weight by commercial fishing vessels equipped with Nephrops trawls (70 mm codend mesh). This fishery is targeting Norwegian lobster *Nephrops norvegicus* and cod is taken merely as a by-catch. Therefore, annual cpue data (kg h^{-1}) for cod >30 cm (the current minimum landing size) provide a suitable index of abundance.

Information on length distributions of cod has also been collected during trawl surveys between 1923 and 1956 for three fjords: Brofjord area (30 hauls), Gullmarfjord (59 hauls) and Hakefjord (26 hauls). These surveys were made at different times of year with gears varying in design and variable codend mesh sizes, but the horizontal opening as well as mesh size were always smaller than of the gear used in recent surveys. Haul duration varied between 15 and 75 min. Because of all

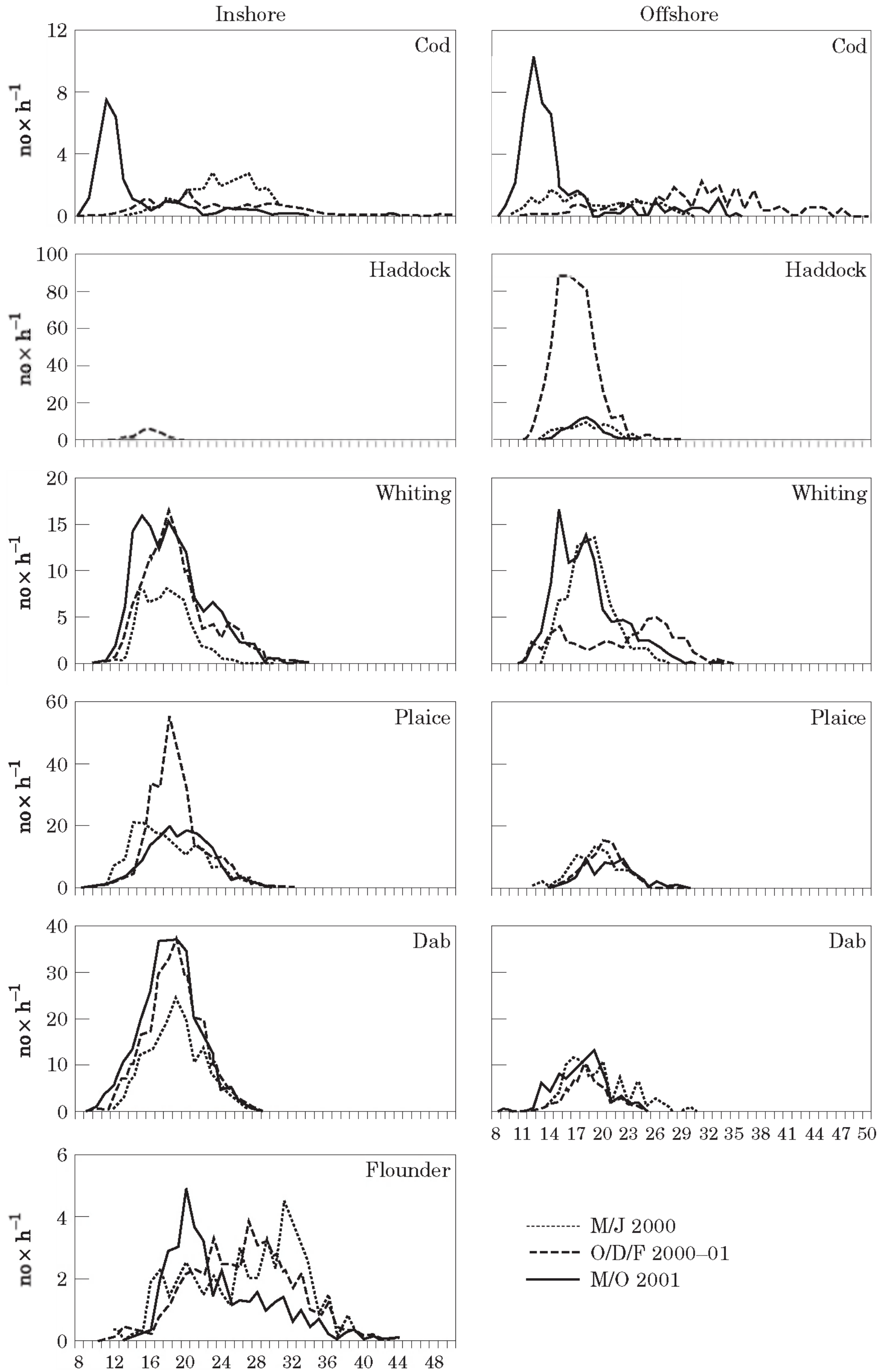

Figure 2. Mean abundance by length class for cod, haddock, whiting, plaice, dab and flounder in inshore (left panels) and offshore (right panels) in 2000–2001.

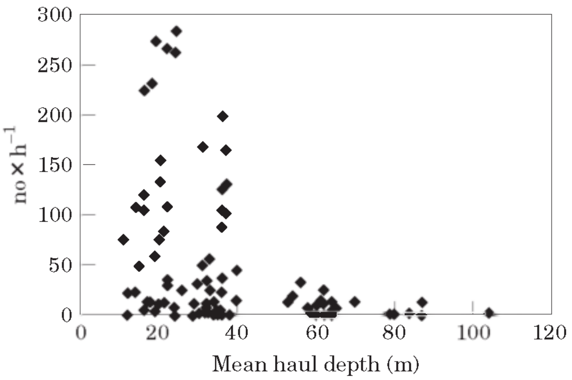

Figure 3. Relation between cpue of flounder and mean haul depth in the 2000/2001 surveys (all hauls).

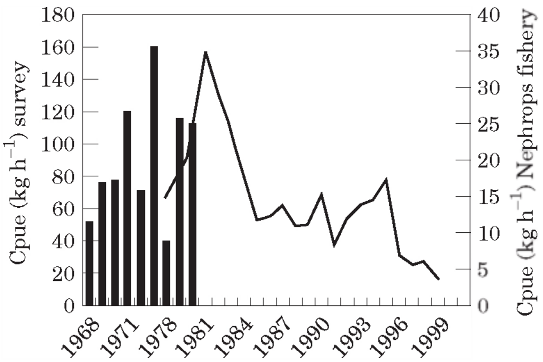

Figure 4. Mean cpue of cod by year: survey data from the Brofjord area, 1968–1980 and 2000–2001 (bars) and landings of the offshore Nephrops fishery, 1978–1999 (line).

this variability, length compositions have simply been pooled.

Data treatment

Total cpue was calculated as number or weight (kg) of fish caught per hour for each haul. Mean values were then estimated for all hauls within each area for each survey. For individual species in the inshore area, the mean cpue in numbers by fjord unit (A–D) were averaged by survey and these were then combined to a grand mean for 3 periods (March/June 2000, October/December 2000 and February 2001, May/October 2001). Differences between recent and historic length distributions were evaluated by means of Mann–Whitney tests and two-sample Kolmogorov–Smirnov tests (Sokal and Rohlf, 1981).

Results

Recent surveys

Total cpue of all demersal species increased in both areas through 2000 to a peak value in October, and decreased thereafter until October 2001, but the value in the offshore area remained much lower all through 2001 (Table 1). With reference to species composition by area and year (Table 3), flatfish clearly dominated the inshore catches, whereas gadoids dominated the catch at the offshore localities. Among the flatfishes, dab and plaice were the most abundant species, both inshore and offshore. Among the gadoids, whiting dominated in the inshore area, whereas haddock was most abundant offshore. Of the other species, grey gurnard (*Eutrigla gurnardus* L.) was frequently caught, especially in the inner part of the Gullmarfjord. Of note, no pollack were caught in any haul.

The inshore abundance of cod >30 cm (presumably ≥2 years old) was low (Figure 2). In March/June 2000, a cohort in the size range of 15–35 cm, was present, which progressively disappeared during the later surveys. In contrast, offshore abundance of 15–35 cm cod in May/June 2000 was lower than in inshore areas, but the 25–40 cm group was well represented later that year. In 2001, a new year class in the range of 8–15 cm (0-group) recruited in both areas.

Offshore abundance of haddock was much higher than inshore abundance (Figure 2). The size distribution in 2000 clearly suggests the predominance of a single year class (presumably 1999), which entered the area in late 2000 and disappeared therafter, when it was replaced by a new but less abundant cohort in the same size range.

The inshore surveys in March/June 2000 indicated a narrow band of whiting of 14–24 cm with two humps (Figure 2). Subsequently, the length composition shifted to larger sizes and abundance increased, while in summer 2001 a new cohort appeared. Offshore, peak abundance in May/June 2000 was shifted to larger fish and this was even more pronounced in late 2000/early 2001. Later in 2001, inshore and offshore size compositions as well as overall abundances were similar. In both areas, abundance of whiting >30 cm was negligible.

Plaice and dab were much more abundant inshore than offshore (Figure 2), but the size distributions were very similar. They appear to be represented by several cohorts and do not show clear dynamic, but plaice >25 cm appear to be notably absent at all sites and times.

Flounder abundance showed a clear relationship with depth (Figure 3), being highest in shallow inshore waters (areas A, B and D; Figure 1). Compared to other species, the number of fish >25 cm was high, particularly during May/June 2000. Subsequently, the size distribution shifted markedly to progressively smaller fish.

Comparisons with previous surveys

Cpue of cod (in weight) in the Brofjord area was drastically lower in 2000 and 2001 (unweighted mean for

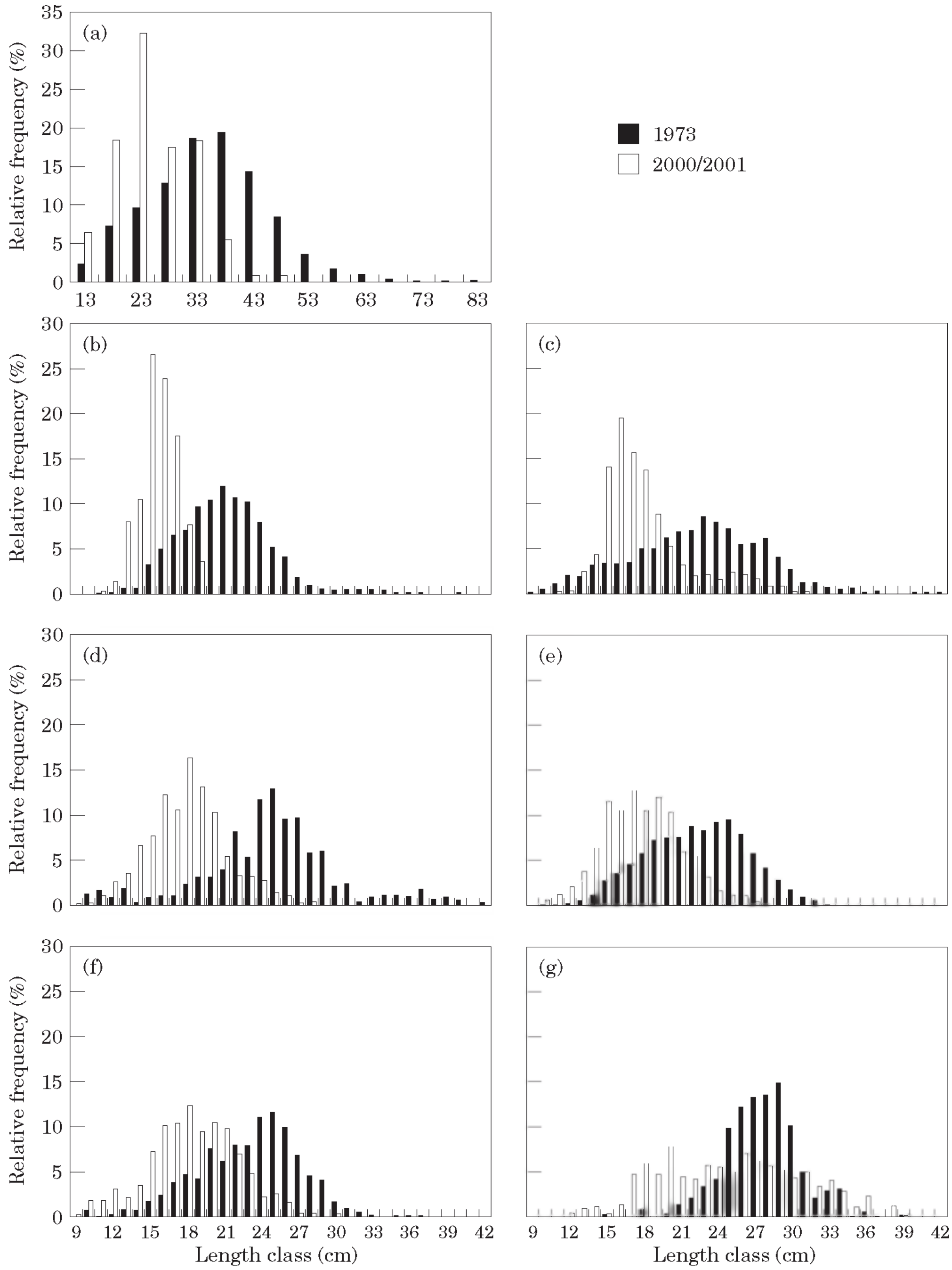

Figure 5. Length frequency distributions for the pooled catch of (a) cod, (b) haddock, (c) whiting, (d) plaice, (e) dab, (f) long rough dab and (g) flounder in the Brofjord area in 1973 (filled bars; from Hallbäck *et al.*, 1974) and in 2000/2001 (open bars).

seven surveys: 1.5 kg h^{-1}) compared to values obtained during similar surveys in 1968–1980 (mean value 96 kg h^{-1}; n=32; Figure 4). The log-book information derived from the offshore Nephrops fishery indicates a likewise but slightly less decline in cod cpue.

The length frequency distributions for 1973 and 2000/2001 from the Brofjord area show highly significant (Mann–Whitney test and two-sample Kolmogorov–Smirnov test: $p<0.001$ in all cases) differences for cod, haddock, whiting, plaice, dab and long rough dab

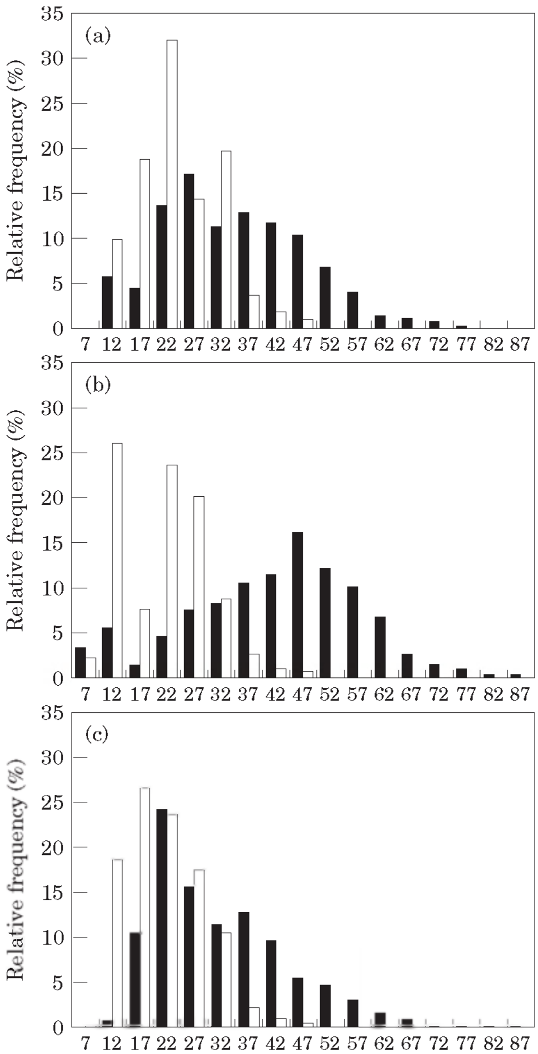

Figure 6. Length frequency distributions of the pooled catch of cod in 1923–1956 (filled bars) and in 2000–2001 (open bars) in (a) Brofjord, (b) Gullmarfjord, and (c) Hakefjord.

(Figure 5). Clearly the relative abundance of larger, adult or maturing fish has been substantially reduced during the intervening period. Flounder presented a noteworthy exception from this pattern, because the length distribution had widened in 2000–2001 compared to 1973: the relative frequency at both the smaller and larger length range have increased since 1973 ($p<0.01$ for both tests).

Comparisons of cod length frequency distributions from surveys during 1923–1956 and those in 2000/2001 also showed significant differences for the Brofjord, Gullmarfjord, and Hakefjord (all $p<0.001$ for both tests; Figure 6).

Discussion

Hagström *et al.* (1990) and Pihl and Ulmestrand (1993) already indicated a declining abundance of cod and other demersal fish off the Swedish westcoast. However, the new surveys in 2000 and 2001 indicate a much more profound decline for the entire inshore demersal fish community than has been previously reported. The new data clearly show that fish abundance in the size range >30 cm was extremely low in the inshore area.

This result is unlikely to be affected by gear differences, because catchability of the gear used in the recent surveys is expected to exceed the catchability of the trawls used in previous surveys, because the horizontal opening is wider. In other words, the observed decline in abundance of large fish should be even steeper, making the conclusion even more robust.

In contrast to the decline in abundance of larger fish, the results indicate that the coastal area still serves as an important area for immature fish of different demersal species, including plaice, cod and whiting. This is the more remarkable, because the (relative) abundance of small fish would have been expected to be less, because of the larger mesh size used in 2000/2001 compared to many of the older surveys. It should be noted that the left-hand side of the length compositions reported may be heavily influenced by mesh selection and the true nursery function of these areas can therefore not be evaluated. Nevertheless, the hypothesis of a major and persistent recruitment failure caused by negative or hazardous environmental factor(s) in the coastal zone of the Skagerrak is not supported by these results, in accordance with the conclusions of Fromentin *et al.* (1998).

Flounder was the only common demersal species with a size spectrum encompassing both small and large individuals. Flounder has a low commercial value and a relatively stationary behaviour (Molander, 1942). Its whole life-cycle is spent in coastal or shallow waters, as emphasized by its depth distribution (Figure 3). This implies that flounder is one of the few demersal species only partially exposed to trawl gears. While long rough dab is another species of negligible commercial value, it shows the same shift to smaller sizes as the demersal species targeted by fisheries. However, long rough dab is less stationary than flounder and also common at greater depths, making it more exposed to demersal fishing.

The observation that the major part of the demersal inshore fish community above a certain size has been affected points to a strong size-selective mortality. Absence of large fish is likely to be an effect of high fishing pressure. For instance, Rice and Gislason (1996) explain the continuing shift in the size spectrum of the demersal fish community in the North Sea between the 1970s and the 1990s to the increase in exploitation. However, it seems unlikely that the observed shift in

Table 3. Average cpue of demersal fish species in numbers per hour trawling in inshore and offshore areas in 2000 and 2001.

Species	Latin name	Inshore 2000	Inshore 2001	Offshore 2000	Offshore 2001
Cod	*Gadus morhua*	32	26	29	37
Haddock	*Melanogrammus aeglefinus*	20	8	352	209
Poor cod	*Trisopterus minutus*	1	<1	<1	1
Whiting	*Merlangius merlangus*	107	139	125	64
Saithe	*Pollachius virens*	1	75	2	1
Ling	*Molva molva*	—	—	1	1
Hake	*Merluccius merluccius*	—	<1	2	<1
Four-bearded rockling	*Enchelyopus cimbrius*	<1	—	6	2
Gold Sinny	*Ctenolabrus rupestris*	—	<1	—	—
Spotted dragonet	*Callionymus lyra*	<1	1	<1	5
Dragonet	*Callionymus maculatus*	<1	—	1	<1
Snake blenny	*Lumpenus lampretaeformis*	<1	<1	<1	<1
Spotted snake blenny	*Leptoclinus maculatus*	<1	—	<1	<1
Butterfish	*Pholis gunellus*	<1	<1	—	—
Catfish	*Anarhichas lupus*	—	<1	—	<1
Viviparous blenny	*Zoarces viviparus*	<1	<1	—	—
Vahl's eelpout	*Lycodes vahlii*	<1	—	—	—
Black goby	*Gobius niger*	<1	1	—	—
Sand goby	*Pomatoschistus minutus*	<1	—	—	—
Grey gurnard	*Eutrigla gurnardus*	25	22	6	8
Bull rout	*Myoxocephalus scorpius*	9	13	2	2
Pogge	*Agonus cataphractus*	<1	<1	—	—
Lumpfish	*Cyclopterus lumpus*	<1	—	<1	<1
Turbot	*Psetta maxima*	<1	<1	—	—
Brill	*Scophthalmus rhombus*	1	<1	1	<1
Scaldfish	*Arnoglossus laterna*	1	1	<1	1
Topknot	*Zeugopterus punctatus*	—	<1	—	—
Halibut	*Hippoglossus hippoglossus*	—	—	—	<1
Long rough dab	*Hippoglossoides platessoides*	41	49	13	20
Dab	*Limanda limanda*	259	231	62	61
Plaice	*Pleuronectes platessa*	310	110	80	67
Flounder	*Platichthys flesus*	52	38	2	5
Lemon sole	*Microstomus kitt*	<1	<1	2	1
Witch	*Glyptocephalus cynoglossus*	1	<1	1	1
Sole	*Solea solea*	4	3	1	1
Monkfish	*Lophius piscatorius*	—	—	<1	<1

Swedish inshore waters has been caused primarily by the local fishery within the coastal zone, because trawls are forbidden and the remaining commercial and sport fishing activity is presumably low in view of the apparent absence of large fish suitable for consumption. Therefore, the hypothesis has been put forward that the present population dynamics of many of the demersal fish stocks of the eastern Skagerrak coast depend on transport of recruits from offshore spawning areas (Munk *et al.* 1995, 1999), and on offshore migration of juvenile and/or maturing fish when they reach a certain size or age (Pihl and Ulmestrand, 1993). This hypothesis was supported by the observation of a general lack of correlation between recruitment (no trend during the past two decades) and abundance of cod >30 cm (significant decline) in the Skagerrak–Kattegat area (Svedäng and Bardon, 2003).

If the present fish community mainly constitutes offspring from offshore spawning aggregations, the absence of mature fish must have been caused either by depletion of local (sub-)populations and/or reduction of the offshore stock component. A major reduction of offshore stocks might lead to severe declines in the number of adult fish of offshore origin wandering to peripheral areas and thus supporting local coastal stocks. However, the existence of local stocks of for instance cod in the Skagerrak region is still an unsettled question (Danielssen, 1969; Pihl and Ulmestrand, 1993; Danielssen and Gjøsæter, 1994; Godø, 1995; Munk *et al.*, 1995, 1999), and even more so is their relative importance in the coastal fish community in the past. Notwithstanding these uncertainties, historic spawning aggregations are well known from the Skagerrak coast for various species and it may be argued that such aggregations are an important aspect of the coastal demersal fish community, whether representing discrete populations or not. Studies on the spatial dynamics of cod off Newfoundland do support such a view (Hutchings *et al.*, 1993; Green and Wroblewski, 2000; Lawson and Rose, 2000; Robichaud and Rose, 2001).

References

Arnold, G. P., Walker, M. G., Emerson, L. S., and Holford, B. H. 1994. Movements of cod (*Gadus morhua* L.) in relation to the tidal streams in the southern North Sea. ICES Journal of Marine Science, 51: 207–232.

Brander, K. M. 1994. The location and timing of cod spawning around the British Isles. ICES Journal of Marine Science, 51: 71–89.

Danielssen, D. S. 1969. On the migrations of the cod in the Skagerrak shown by tagging experiments in the period 1954–65. Fiskerdirektoratets Skrifter Serie Havunderskelser, 15: 331–338.

Danielssen, D. S., and Gjøsaeter, J. 1994. Release of 0-group cod, *Gadus morhua* L., on the southern coast of Norway in the years 1986–1989. Aquaculture and Fisheries Management, 25: 129–142.

Fromentin, J.-M., Stenseth, N.C., Gjøsæter, J., Johannessen, T., and Planque, B. 1998. Long-term fluctuations in cod and pollack along the Norwegian Skagerrak coast. Marine Ecology Progress Series, 162: 265–278.

Godø, O. R. 1995. Transplantation-tagging-experiments in preliminary studies of migration of cod off Norway. ICES Journal of Marine Science, 52: 953–960.

Green, J. M., and Wroblewski, J. S. 2000. Movement patterns of Atlantic cod in Gilbert Bay, Labrador: evidence for bay residency and spawning site fidelity. Journal of the Marine Biological Association of the UK. 80: 1077–1085.

Hagström, O., Larsson, P-O., and Ulmestrand, M. 1990. Swedish cod data from the international young fish surveys 1981–1990. Demersal Committee CM 1990/G:65.

Hallbäck, H., Hagström, O., and Winström, K. 1974. Fishery biology investigations in the Brofjord 1972–74. Meddelande från Havsfiskelaboratoriet, Lysekil. 175. 45 p. (in Swedish).

Hutchings, J. A., Myers, R. A., and Lilly, G. R. 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Science, 50: 2457–2467.

Hutchinson, W. F., Carvalho, G. R., and Rogers, S. I. 2001. Marked genetic structuring in localised spawning populations of cod *Gadus morhua* in the North Sea and adjoining waters, as revealed by microsatellites. Marine Ecology Progress Series, 223: 251–260.

Knutsen, J. A., Bergstad, O. A., Gjøsæter, J., Eneresen, S. E., and Omli, L. 2000. Mapping of spawning sites and perspeciuous oxygen measurements in the municipalities of Risør, Tvedestrand and Lillesand. Fisken og Havet 13 (in Norwegian with English abstract).

Lawson, G. L., and Rose, G. A. 2000. Small-scale spatial and temporal patterns in spawning of Atlantic cod (*Gadus morhua*) in coastal Newfoundland waters. Canadian Journal of Fisheries and Aquatic Science, 57: 1011–1024.

Molander, R. 1942. The family of flounders, Pleuronectidae. *In* Fiskar och fiske i Norden, pp. 111–147. Ed. by K. A. Andersson. Natur och Kultur, Stockholm. (in Swedish).

Mork, J., Ryman, N., Ståhl, G., Utter, F., and Sundness, G. 1985. Genetic variation in Atlantic cod (*Gadus morhua*) throughout its range. Canadian Journal of Fisheries and Aquatic Science, 42: 1580–1587.

Munk, P., Larsson, P.-O., Danielssen, D.S., and Moksness, E. 1995. Larval and small juvenile cod *Gadus morhua* concentrated in the highly productive areas of a shelf break front. Marine Ecology Progress Series, 125: 21–30.

Munk, P., Larsson, P.-O., Danielssen, D.S., and Moksness, E. 1999. Variability in frontal zone formation and distribution of gadoid fish larvae at the shelf break in the northeastern North Sea. Marine Ecology Progress Series, 177: 221–233.

Pihl, L., and Ulmestrand, M. 1993. Migration pattern of juvenile cod (*Gadus morhua*) on the Swedish west coast. ICES Journal of Marine Science, 50: 63–70.

Rice, J., and Gislason, H. 1996. Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. ICES Journal of Marine Science, 53: 1214–1225.

Righton, D., Metcalfe, J., and Connolly, P. 2001. Different behaviour of North and Irish Sea cod. Nature, 482: 156.

Robichaud, D., and Rose, G. A. 2001. Multiyear homing of Atlantic cod to a spawning ground. Canadien Journal of Fisheries and Aquatic Science, 58: 2325–2329.

Ruzzante, D. E., Taggart, C. T., Cook, D., and Goddard, S. 1996. Genetic differentiation between inshore and offshore Atlantic cod (*Gadus morhua*) off Newfoundland: Microsatellite DNA variation and antifreeze level. Canadian Journal of Fisheries and Aquatic Sciences, 53: 634–645.

Ruzzante, D. E., Taggart, C. T., Doyle, R. W., and Cook, D. 2001. Stability in the historical pattern of genetic structure of Newfoundland cod (*Gadus morhua*) despite the catastrophic decline in population size from 1964 to 1994. Conservation Genetics, 2: 257–269.

Sokal, R. S., and Rohlf, F. J. 1981. Biometry. W. H. Freeman, San Francisco. 859 pp.

Svedäng, H., and Bardon, G. 2003. Spatial and temporal aspects of the decline in cod (*Gadus morhua* L.) abundance in the Kattegat and eastern Skagerrak. ICES Journal of Marine Science, 60: 32–37.

Ulmestrand, M., and Larsson, P-O. 1991. Experiments with a square mesh window in the top panel of a Nephrops trawl. ICES CM 1991/B: 50.