Fishing effects on spatial distribution and trophic guild structure of the fish community in the Georges Bank region

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We examined the changes in the spatial distribution and trophic guild structure of the Georges Bank fish community associated with intense exploitation over the last 30 years. As heavily exploited species declined in abundance, their spatial ranges and degree of overlap with other species declined. The converse was true for weakly exploited species whose populations have increased. Despite dramatic alterations in species composition, the trophic guild structure was consistent over time. There are five major trophic guilds on Georges Bank across gradients from benthic to pelagic feeders and fish to invertebrate prey. Exploitation has strongly impacted the piscivores in this system and has modified species interactions through alterations in species composition.

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Introduction

Fishing pressure has induced significant changes in the fish community on Georges Bank. Since the 1960s, there have been major reductions in the biomass of exploited flatfish and gadids and dramatic increases in the biomass of elasmobranchs and pelagic species (Fogarty and Murawski, 1998). These changes are associated with the direct removal of biomass and indirect effects on unexploited species through alterations in trophic interactions such as predatory or competitive release (Fogarty and Murawski, 1998).

Competing species, or predators and their prey, must overlap in time and space for significant interactions to occur. The geographic ranges of overexploited species typically decline, and stocks are concentrated into smaller regions following population declines (Atkinson *et al.*, 1997). These fishing-induced changes in spatial distribution can have important impacts on species interations. Fishery removals of top predators may also strongly affect the trophic structure of a system. The reduction in predator abundance can have cascading impacts on lower trophic levels (Carpenter and Kitchell, 1993). This presumes strong predator control of prey populations.

While management can regulate the removal of biomass, internal ecosystem dynamics – particularly predator–prey and competitive interactions – ultimately determine the recovery of fish communities (Jennings and Kaiser, 1998). To assess fishing-induced changes in ecosystem processes, we examined changes in the spacial distribution and trophic structure of the Georges Bank fish community. Specifically, we evaluated the changes in spatial and dietary overlap between species and the resulting trophic guild structure.

Materials and methods

Data sources

Data were drawn from seasonal bottom-trawl surveys conducted by the Northeast Fisheries Science Center (NEFSC). The surveys employ a stratified random sampling design with strata defined by depth and latitude. Sample depths ranged between 8 and 400 m on the North American continental shelf between Cape Hatteras, North Carolina and Nova Scotia. Details of the survey sampling design, execution, and efficiency are available in NEFSC (1988).
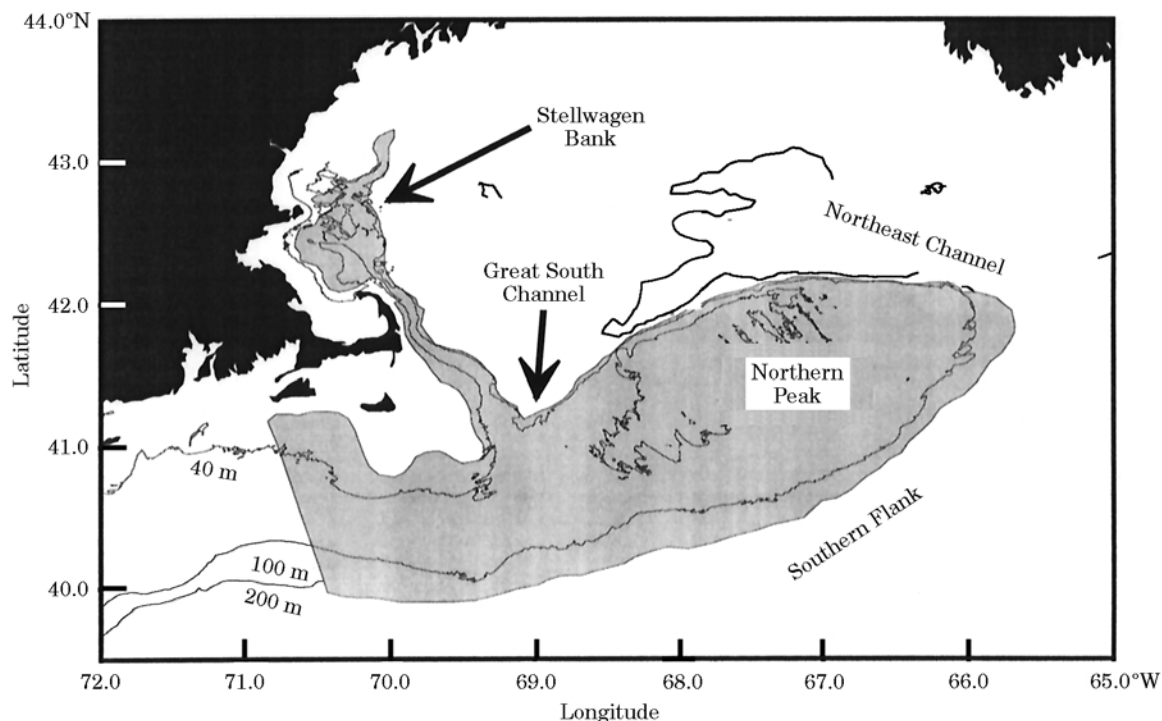
Figure 1. Map of Georges Bank region showing bathymetry. Survey samples from the shaded region were included in the analysis.

In addition to catch data, a subset of trawl tows and species was analyzed for food habits data. The NEFSC has conducted quantitative food habits sampling in seasonal surveys from 1973 to the present. Stomach contents were identified to the lowest possible taxonomic level, focusing particularly on the identification of fish prey to species, and the volume of each prey item in the stomach was quantified. In our analysis, important fish and squid prey were retained at the species level, while less important fish prey were grouped into families. Invertebrate prey were generally lumped into family or order groups.

Our study included tows made during autumn surveys from the Georges Bank region as defined by boundaries in faunal assemblages, including areas south of Cape Cod, Georges Bank, and Stellwagen Bank (Fig. 1), 1963–1997 (diet analyses during 1973–1997). The autumn surveys are available for the longest time period and have the most consistent sampling relative to other seasons. Temporal trends in spatial distribution and trophic structure were evaluated in five-year time blocks: 1963–1967 (space only), 1973–1977, 1983–1987, and 1993–1997. Data are generally homogeneous within five-year blocks, and results from alternating time blocks are presented for brevity.

Twenty-three predator species were examined, including two squid species (Table 1). These were numerically dominant, commercially valuable, and/or ecologically important species on Georges Bank. The predator

species were divided into length categories to account for ontogenetic shifts in diet (Bowman and Michaels, 1984). In all, 60 predator categories were used in the analysis (Table 1).

Spatial overlap and trophic guild analyses

Maps were prepared for selected species to display shifts in spatial distribution. A matrix of spatial overlap indices between all predator pairs was calculated for each five-year time block to assess changes in co-occurrence over time. The index of spatial overlap, S_{ij}, was calculated as the number of tows containing both predator i and predator j divided by the number of tows containing predator i. Because the index is standardized by the number of tows containing predator i, it is not symmetric with regard to species (i.e. $Sij \neq Sji$; Murawski and Finn, 1988).

A matrix of the Bray-Curtis similarity index (Pielou, 1984) was used to assess the dietary overlap between predator pairs. Hierarchical agglomerative clustering methods were used to identify groups of species with common diets based on the mean percent volume of prey items in the diets. The classification of dietary groups was further examined using principal components analysis (PCA). Mean percentage composition of 14 major prey items was plotted for the guilds identified in the cluster and PCA analyses to assess trends in diets.

Table 1. Predators and length categories for diet analyses. Species and size class (S=small, M=medium, L=large, XL=extra large) codes are used in Figures 2 and 4.

Species	Common name	Code	Length categories (cm)			
			S	M	L	XL
Squalus acanthias	Spiny dogfish	SD	10–40	41–60	>60	—
Raja ocellata	Winter skate	WS	10–30	31–60	61–80	>80
Raja erinacea	Little skate	LS	10–30	>30	—	—
Clupea harengus	Atlantic herring	AH	10–20	>20	—	—
Merluccius bilinearis	Silver hake	SH	10–20	21–50	>50	—
Gadus morhua	Atlantic cod	AC	10–20	21–50	51–80	>80
Melanogrammus aeglefinus	Haddock	HA	10–20	21–50	>50	—
Pollachius virens	Pollock	PO	10–20	21–50	51–80	>80
Urophycis tenuis	White hake	WH	10–20	21–40	>40	—
Urophycis chuss	Red hake	RH	10–20	21–40	>40	—
Paralichthys oblongus	Fourspot flounder	4F	10–20	>20	—	—
Paralichthys dentatus	Summer flounder	SF	10–20	21–40	>40	—
Limanda ferruginea	Yellowtail flounder	YF	10–20	21–40	>40	—
Pseudopleuronectes americanus	Winter flounder	WinF	10–20	21–40	>40	
Glyptocephalus cynoglossus	Witch flounder	WitF	10–20	21–40	>40	—
Scophthalmus aquosus	Windowpane	WP	10–20	21–40	>40	—
Scomber scombrus	Atlantic mackerel	AM	10–20	21–35	>35	—
Pomatomus saltatrix	Bluefish	BUF	—	30–70	>70	—
Myoxocephalus octodecemspinosus	Loghorn sculpin	LHS	10–25	>25	—	—
Hemitripterus americanus	Sea raven	SR	10–25	>25	—	—
Lophius americanus	Goosefish	GF	—	—	>60	—
Illex illecebrosus	Shortfin squid	SFS	—	—	—	—
Loligo pealeii	Longfin squid	LFS	—	—	—	—

Results

Spatial distribution and overlap

The community is characterized by a few species that are widespread over the entire region and subsequently have high spatial overlaps with most other species. The most notable of these is silver hake, which has consistently high overlap (>60%) with most species across all time periods (Fig. 2). The mean index of spatial overlap among fish species is approximately 40%.

Trends in spatial overlap generally reflect changes in species abundance. During the 1960s, haddock (Fig. 3A) and yellowtail flounder were widely distributed and had a high spatial overlap with other species. As the abundance of these species declined through the 1970s into the 1990s, their spatial range contracted (e.g. Fig. 3a), and their overlap values with other species subsequently declined (Fig. 2).

In contrast, species whose abundance has increased through time show an expansion of ranges and increased spatial overlap with other species. For example, spiny dogfish currently occurs over a broader region of Georges Bank than during the 1960s (Fig. 3B). Overlaps with spiny dogfish were approximately 40% in the 1960s (Fig. 2A), increased to above 60% in the 1970s and 1980s (Fig. 2B,C), and have declined again in the 1990s (Fig. 2D).

Trophic guild structure

In general, the trophic guild structure has remained static over time, with a mean dietary overlap of approximately 25%. There is some variation in the species composition of minor groups, but the main dietary guilds have remained constant (e.g., Fig. 4A). This community contains five major groups that were indicated in both cluster diagrams and the PCA (Fig. 4B). Major clusters in diet composition were separated at a similarity level ranging from 32% to 37% (Fig. 4A). These dietary groups were separated along two major gradients: from benthic to pelagic prey and from fish to invertebrate prey (Fig. 4B). The first two principal components accounted for 40–50% of the variance in the diet and separated species into the groups identified in the cluster analyses.

The major predator groups were consistent across decades. The first major group included species (e.g. small hakes and small and medium spiny dogfish) that fed primarily on pelagic organisms and shrimps (Shrimp–Pelagic, Fig. 4). The diets of these species were dominated by unidentified fish, pandalid shrimp, crangonid shrimp, and mysids (Fig. 5). The second group included small skates, small and medium Atlantic cod, and longhorn sculpin (Bentho–Pelagic, Fig. 4). While these species also preyed on shrimp such as pandalids and crangonids, their diets also contained benthic
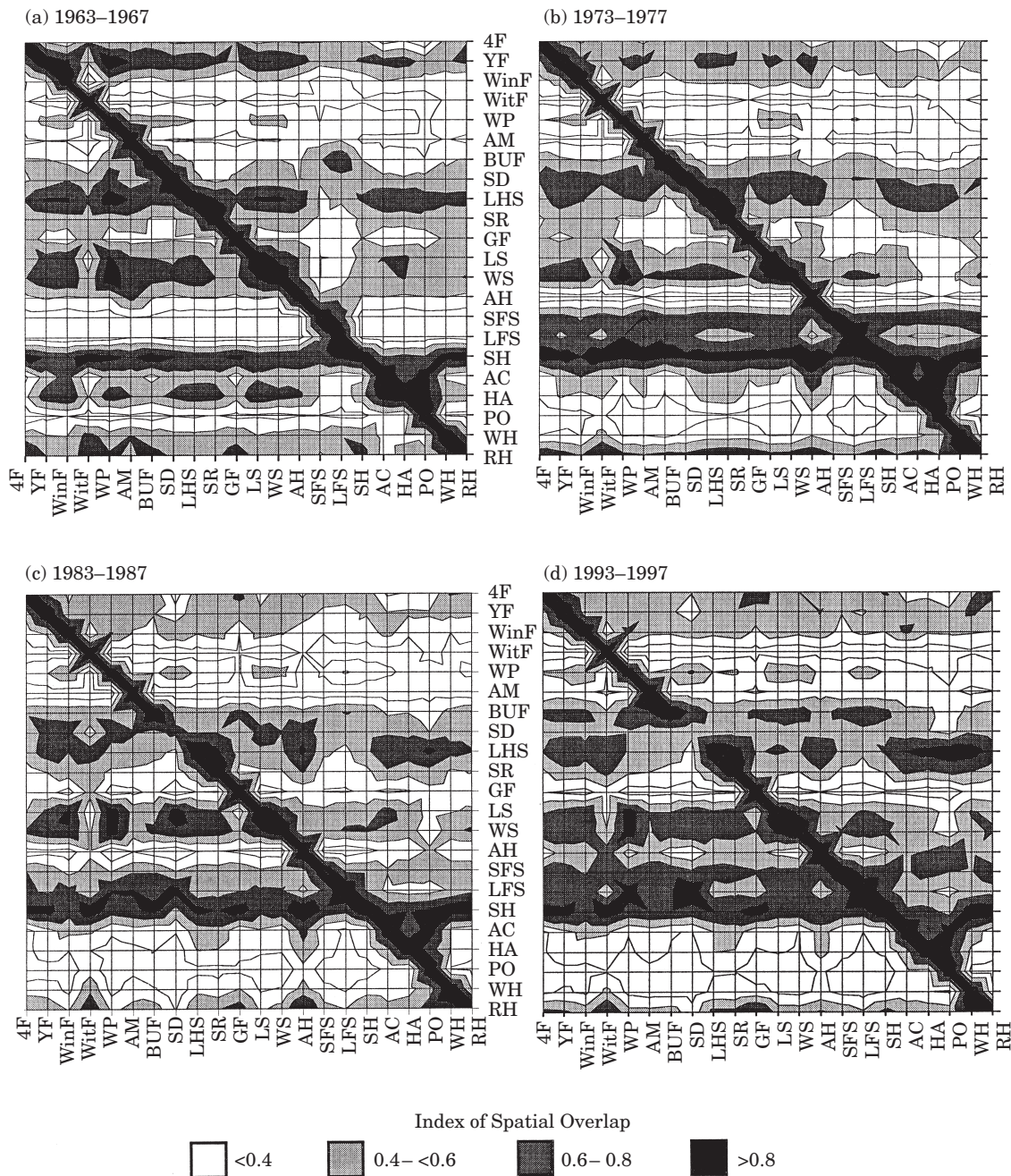
(a) 1963–1967

(b) 1973–1977

(c) 1983–1987

(d) 1993–1997

Index of Spatial Overlap

| <0.4 | 0.4– <0.6 | 0.6– 0.8 | >0.8 |

Figure 2. Contour plots of spatial species overlap matrices for (A) 1963–1967, (B) 1973–1977, (C) 1983–1987, and 1993–1997 bottom trawl surveys. The spatial overlap index is standardized with respect to the species (for code see Table 1) on the horizontal axis.

invertebrates such as gammarid amphipods, polychaetes, and bivalves (Fig. 5). The third group (Benthivores, Fig. 4) included haddock, yellowtail flounder, and winter flounder, and their diets were dominated by small benthic invertebrates, particularly polychaetes (Fig. 5). The food habits sampling in the 1990s did not emphasize

haddock or flatfish; therefore they do not appear in this time period. The large skates dominated the fourth group and were characterized by a combination of fish and benthic prey, with a high proportion of sand lance during the 1980s (Fig. 5). Finally, the piscivorous species included large spiny dogfish, large silver hake, white
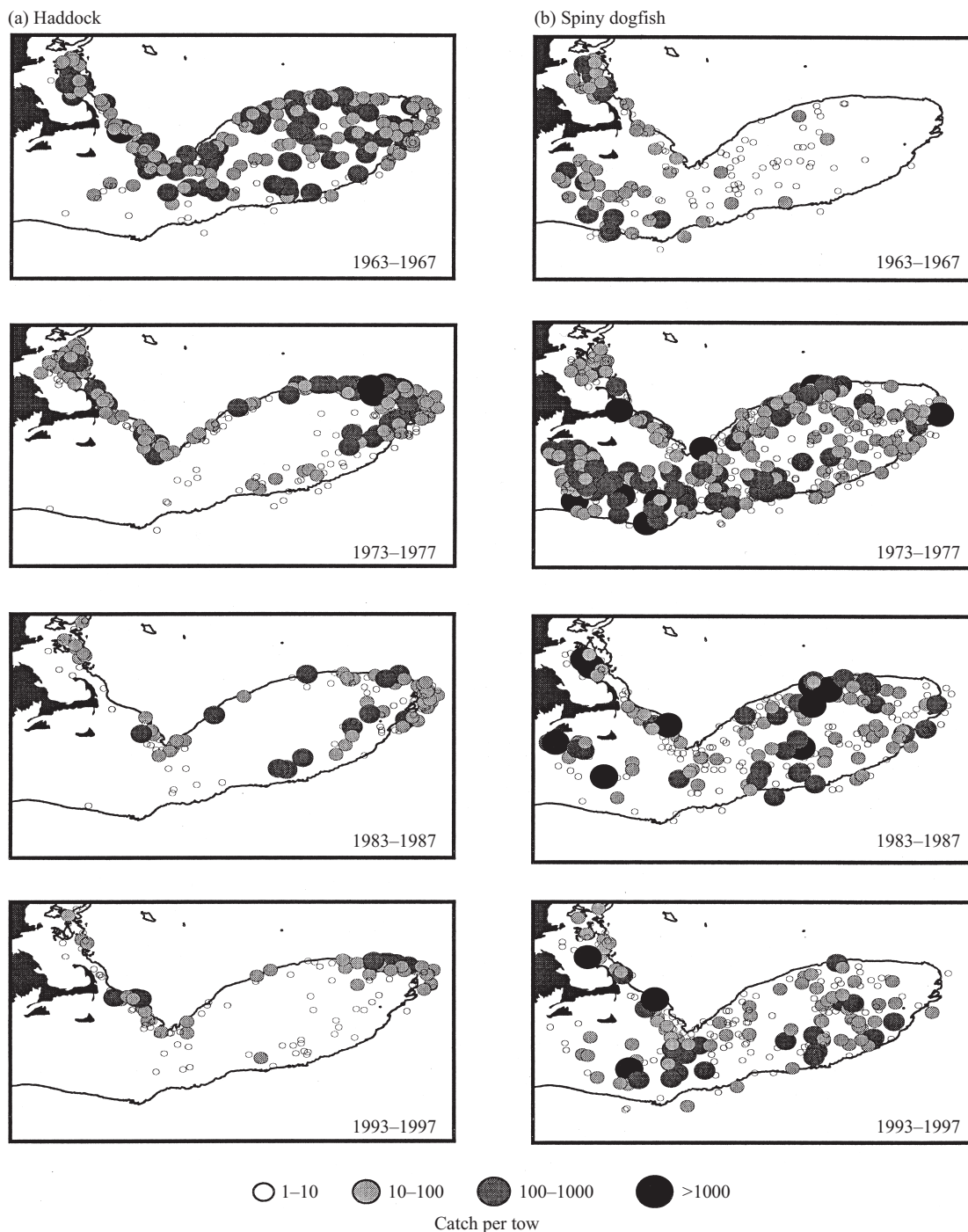
(a) Haddock

(b) Spiny dogfish

Figure 3. Spatial distribution plots showing catch in numbers per tow for (A) haddock and (B) spiny dogfish collected during 1963–1967, 1973–1977, 1983–1987, and 1993–1997 bottom trawl surveys. The 100 m depth contour is shown.

hake, large Atlantic cod, goosefish, and bluefish (Fig. 4). Piscivore diets were dominated by unidentified fish, clupeids, and silver hake throughout the time series (Fig. 5). Planktivores including Atlantic herring and Atlantic mackerel were adequately sampled only during the 1990s. These species feed primarily upon zooplankton, mysid shrimp, and small unidentified fish (Fig. 5C).

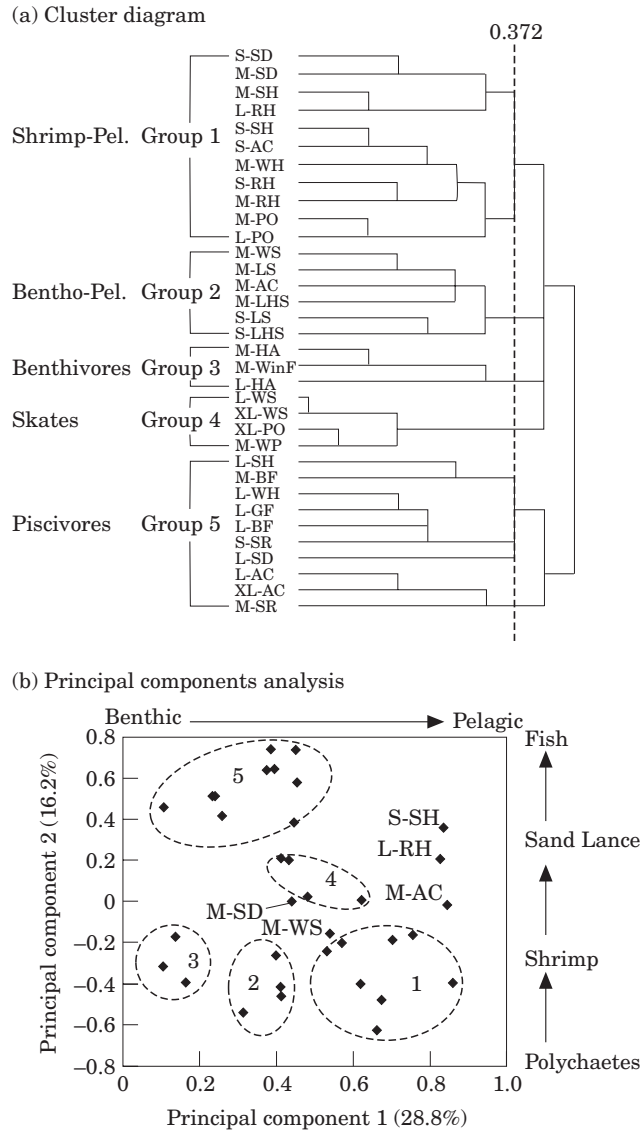(a) Cluster diagram

(b) Principal components analysis

Figure 4. (A) Dendrogram showing major feeding groups among species/size classes based on diet similarity and (B) PCA showing species/size class scores in the multivariate space defined by diet. Results are shown for 1983–1987 as an example, but patterns were stable over time. Group numbers are the same in the two diagrams (for species and size class codes, see Table 1). Predator classes with low sample sizes during the period have been excluded.

Discussion

During the 1960s, yellowtail flounder and haddock were biomass dominants (Fogarty and Murawski, 1998), had broad spatial distributions across the region, and had high spatial overlap with most species. As their populations declined and their ranges contracted, the degree of spatial overlap declined, and their interactions with other species likely also declined. In contrast, species that were much less exploited during the 1960s and 1970s underwent dramatic increases in abundance, most

notably spiny dogfish, winter skate, and little skate (Fogarty and Murawski, 1998), and their distribution expanded accordingly. The strong positive relationship between the abundance of a species and its spatial range confirms the general pattern observed in many fish communities (Atkinson *et al.*, 1997). Similarity in habitat preferences drives the formation of regional and sub-regional assemblages of species that tend to be associated with one another (Overholtz and Tyler, 1985). Fishing alters the species composition within spatial assemblages and thereby alters species
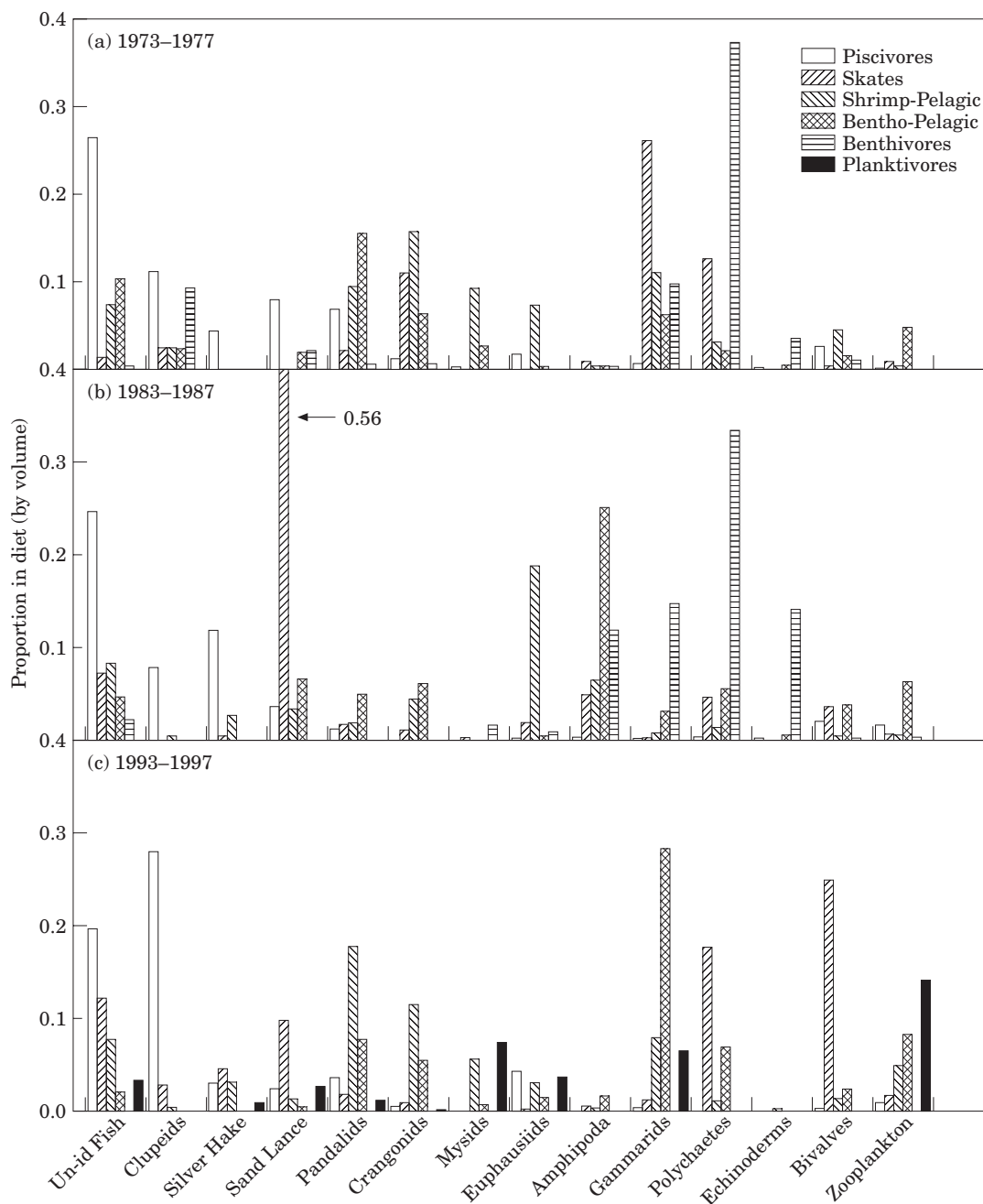
Figure 5. Mean proportion (by volume) of major prey categories in diet groups (cf. Fig. 4A; planktivores added for the last period) identified in the cluster and PCA analyses for (A) 1973–1977, (B) 1983–1987, and (C) 1993–1997 time periods.

interactions. The shift in species interactions associated with changes in spatial distribution is a potentially important, indirect impact of exploitation.

Spatial differences in exploitation rates can also directly modify species distributions. There are at least three alternative mechanisms that may explain why species remain abundant in localized areas despite over-exploitation: (1) habitat characteristics promote sufficient reproductive success to counteract the mortality due to fishing, (2) immigration of individuals from other areas, or (3) fishing effort is locally reduced owing to management restrictions or logistical considerations.

It is noteworthy that the highest concentrations of Atlantic cod, haddock, yellowtail flounder, and spiny dogfish are currently associated with closed areas on the northern peak of Georges Bank and in the Great South Channel (Fogarty and Murawski, 1998), implying that protection from the fishery creates a refuge for resident individuals, recruits, or immigrants into a region. This indicates the importance of fishery removals in driving the abundance and distribution of exploited species.

The trophic guild structure in the Georges Bank community has remained remarkably consistent despite fishery-induced perturbations. Most of these fish species tend to be omnivorous, generalist feeders, dietary overlap is moderate, and many species show strong ontogenetic shifts in diets (Bowman and Michaels, 1984). There are shifts towards increased piscivory with age in many dominant and commercially important species (e.g. skates, silver hake, white hake, spiny dogfish, Atlantic cod). The dietary overlap between species is frequently higher than the overlap between size classes of the same species, and many of these fish occur in different trophic guilds across their life history (Fig. 4). Different size classes within a species may therefore be considered functionally different species in terms of trophic dynamics (Ross, 1986).

While the major dietary groups are consistent through time, the proportion of specific prey items within the diet guilds varies considerably (Fig. 5). Within a suite of available prey, predators freely switch among specific taxa depending upon availability. The generalist nature of predators in this system and their ability to switch among multiple prey precludes strong top-down control of prey populations and trophic cascades following predator removal (Sissenwine *et al.*, 1984; Jennings and Kaiser, 1998). The generally weak interactions observed likely account for the relative stability of the trophic structure despite major changes in community structure.

Overexploitation has altered the dynamics of the Georges Bank ecosystem primarily through the reduction of dominant species and subsequent adjustments in biomass distribution among species. While the trophic guild structure of the community has remained static, fishing pressure has altered the dynamics by targeting two major feeding guilds. Fishing pressure was and is directed primarily at large piscivores (e.g. Atlantic cod, white hake, and goosefish) and large benthivores (e.g. yellowtail flounder and haddock). As a result, the current biomass dominants include pelagic species (spiny dogfish, silver hake), and planktivores (herring, mackerel). The dominant fish species have become smaller and feed at lower trophic levels, and the Georges Bank fish community has shifted from a primarily demersal community to a pelagic community.

Acknowledgements

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