

Transition to an alternate state in a continental shelf ecosystem

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Abstract: The collapse of Atlantic cod (*Gadus morhua*) stocks in the northwest Atlantic Ocean ranks among the most dramatic and widely known ecological changes of the 20th century. Less widely known are the systemic changes that occurred within these areas prior to and coincident with the cod collapse. Our analysis of a fishery-independent, long-term, standardized database collected on the eastern Scotian Shelf off Nova Scotia revealed that during the past four decades, coherent, community-level reductions in body size, biomass, and physiological condition have occurred in the resident demersal fish species. The changes occurred over large spatial ($>10^4$ km²) and short temporal (<10 years) scales, suggesting a progressive decline in the nature and extent of the energy flow through the benthic system. The unexpected and persistent poor condition of a variety of morphologically and functionally dissimilar demersal fish species, living in an environment of reduced intra- and inter-specific competition, suggests a decoupling of the benthic-pelagic systems. This decoupling appears to be attributable to a cascading series of processes involving the cumulative removal of biomass resulting from commercial fishing, compensatory and self-stabilizing increases in pelagic fish biomass, and a decline in groundfish productivity exacerbated by decadal scale variability in water temperature and stratification.

Résumé : L'effondrement des stocks de morues de l'Atlantique (*Gadus morhua*) dans le nord-ouest de l'océan Atlantique constitue l'un des changements écologiques les plus spectaculaires et les mieux connus du 20^{ième} siècle. Ce qui demeure moins bien documenté, ce sont les changements systémiques qui sont survenus dans ces régions avant et pendant l'effondrement des populations de morues. Notre analyse d'une banque de données standardisées et récoltées sur une longue période indépendamment de la pêche commerciale sur l'est de la plate-forme Néo-écossaise au large de la Nouvelle-Écosse révèle qu'au cours des quatre dernières décennies, il s'est produit au niveau de la communauté des réductions coordonnées de la taille corporelle, de la biomasse et de la condition physiologique chez les espèces locales de poissons démersaux. Ces changements ont eu lieu sur une vaste échelle spatiale ($>10^4$ km²) et une courte échelle temporelle (<10 ans), ce qui laisse croire à un déclin progressif de la nature et de l'importance du flux d'énergie dans le système benthique. La mauvaise condition physiologique, à la fois imprévue et persistante, d'une variété d'espèces de poissons démersaux à morphologie et biologie différentes qui vivent dans un milieu de faible compétition intra- et inter-spécifique semble indiquer une dissociation entre les systèmes benthique et pélagique. Ce découplage paraît être causé par une série de processus en cascade reliés au retrait cumulatif de la biomasse par la pêche commerciale, à l'augmentation par auto-stabilisation de la biomasse des poissons pélagiques et au déclin de la productivité des poissons de fond, le tout aggravé par une variabilité à l'échelle de la décennie de la température et de la stratification de l'eau.

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Introduction

In 1993, after centuries of commercial fishing, the once extensive fishery for cod (*Gadus morhua*) on the eastern Scotian Shelf off the coast of Nova Scotia, Canada, collapsed and a moratorium on directed fishing was declared. A decade later, with this management measure still in effect, there is no evidence of recovery. The spectacular nature of this collapse and the scientific and public attention that it received has obscured the much more profound coincident ecological collapse of an entire complex of previously abundant demersal fishes, many of which were subjected to only modest exploitation. These rapid, large-scale changes suggest the involvement of broader ecosystem-level influences. In this paper we explore and describe the structural and functional changes that have occurred in the fish community and use them as indicators of ecological change. We then speculate on the probable causes of this catastrophic decline of the formerly dominant demersal community and transition of the system to an alternate state.

Methods

Our evaluation relied heavily upon research surveys of commercial and noncommercial fish species resident on the eastern half of the Scotian Shelf off Nova Scotia. This widely used, randomized, depth-stratified summer survey consists of an average of 100 sets each year and has been conducted annually by the Canadian Department of Fisheries and Oceans from 1970 to present. Although designed to capture bottom-dwelling species (mainly groundfish), other species such as small pelagics are routinely captured (Table 1). The catch for each set is sorted by species, enumerated, and weighed. Additional measurements include individual length and weight for most of the species. These data were used to compute body size and biomass trends over time. No changes have been made to the survey design, although a few changes associated with gear and vessel have occurred. Gear type changed once from the Yankee 36 to the Western IIA in 1982 and vessel changes occurred between 1981 and 1983. Comparative fishing experiments yielded catchability corrections for cod, haddock (*Melanogrammus aeglefinus*), witch flounder (*Glyptocephalus cynoglossus*), yellowtail flounder (*Limanda ferruginea*), winter flounder (*Pseudopleuronectes americanus*), American plaice (*Hippoglossoides platessoides*), silver hake (*Merluccius bilinearis*), and white hake (*Urophycis tenuis*), which have been applied to the data for 1970 to 1981.

Species composition was assessed using correspondence analysis, a robust multivariate ordination technique, in a spatially explicit manner. The numerical abundance per unit effort at each sampling location was used, after $\log_{10}(n + 1)$ transformation to normalize the data. Significance levels for Pearson product-moment correlations were not adjusted for temporal autocorrelation.

Individual fish lengths and weights were used to compute indices of physiological condition. Condition was expressed as the probability value associated with the average standardized residual mass of a given set location using the Z-score transform (residuals were normally distributed). The residuals were determined from unique $\log_{10}(\text{length})$ versus

$\log_{10}(\text{weight})$ linear regression models established for each of the species. Length and weight measurements were available for the dominant species only, which amounted to 53 species. Low probability values (e.g., <0.05) indicate that a community's physiological condition is lower than normal and high probability values (e.g., >0.95) represent communities with higher than normal physiological condition. The data set was complete with the exception that during 1986 to 1994, the lengths and weights of only the six most important commercial species (cod, haddock, pollock (*Pollachius virens*), silver hake, redfish (*Sebastes* spp.), American plaice) were recorded (Table 1). All data analysis was conducted with R (<http://www.R-project.org>). Data were mapped after discretization to a 2-min grid size and spatially interpolated within a 40-km radius using the continuous curvature "splines-in-tension" algorithm in GMT (<http://gmt.soest.hawaii.edu>; tension = 0.2).

Results and discussion

Structural changes

Body size

Spatially coherent, within- and between-species reductions of mean body size were observed (Fig. 1a). Throughout the 1970s and 1980s, large individuals dominated the northeastern half of the shelf. Individuals >8 kg were found in $>75\%$ of the area sampled and by the 1990s had declined to 40%. Currently large fish occur on only 10% of the area surveyed and are restricted to the northeastern edge of the shelf. Numerically, the magnitude of this change was profound. Relative to the 1970s, there are currently 95% fewer fish >8 kg and fish of intermediate size (1–8 kg) are 60% lower in abundance. Conversely, small fish (<0.1 kg and 0.1–1 kg) have increased by 375% and 100%, respectively. These changes in body size result from variations in species composition, size-specific mortality, and reduced growth rates (Department of Fisheries and Oceans (DFO) 2003).

Biomass

Fish biomass was partitioned between groundfish and pelagic species (Figs. 1b, 1c). Historically, groundfish biomass dominated the Scotian Shelf ecosystem (Zwanenburg et al. 2002). Here too, the changes were profound. In the central portion of the shelf, groundfish biomass per standard tow progressively declined throughout the 1970s and 1980s and by the 1990s was two orders of magnitude lower relative to the 1970s. The areal extent of biomass >100 kg per tow decreased from 32% and 49% in the 1970s and 1980s, respectively, to $<1\%$ in the 1990s and 2000s. This decline was mainly associated with the collapse of cod and haddock but was also accompanied by reductions of other less heavily exploited commercial species (Table 1). Biomass levels remained relatively high in only two areas: adjacent to the central region, where a large (14 000 km²) marine protected area was established in 1987, and on the slope along the northeastern edge of the shelf.

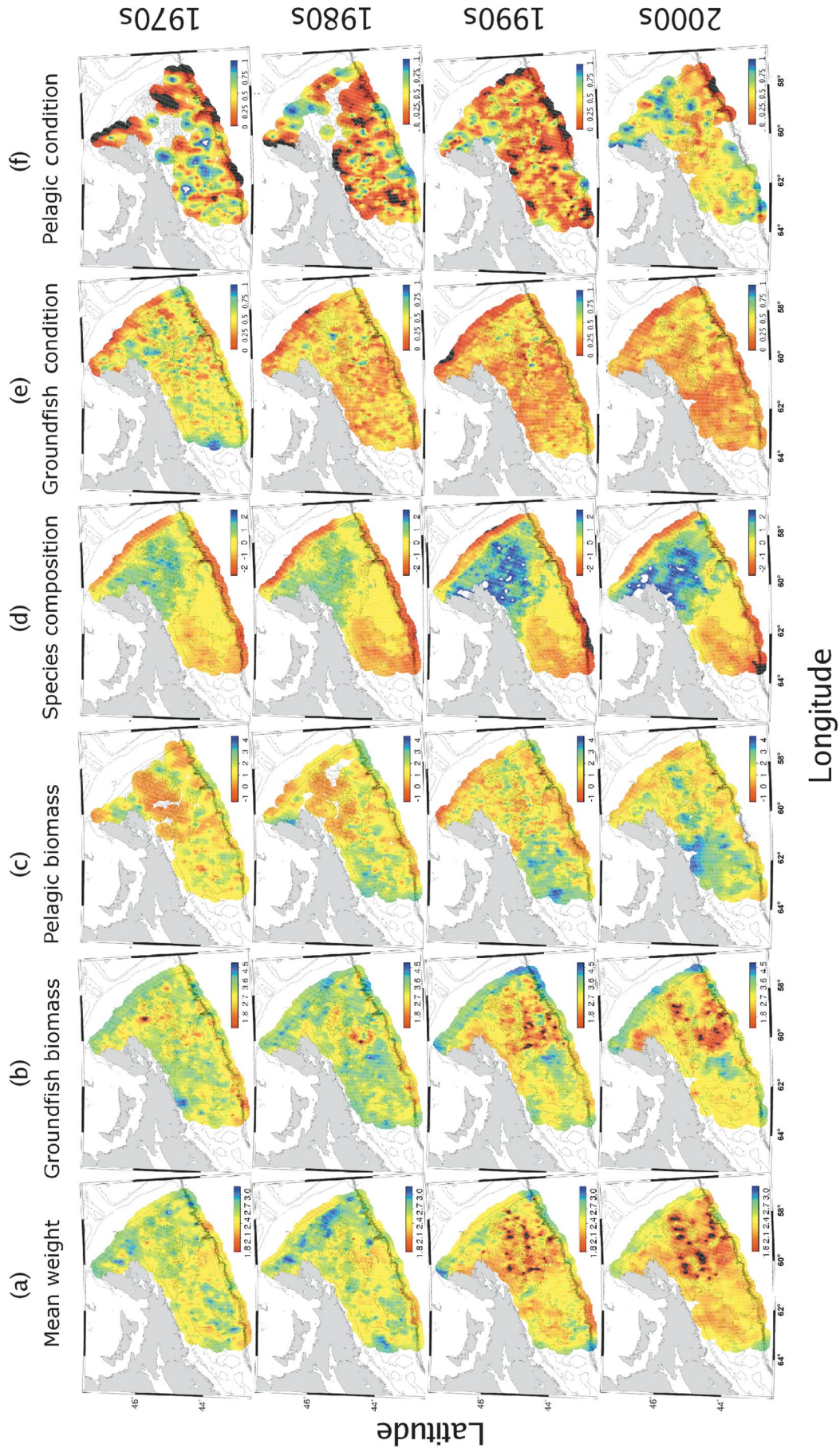
Pelagic biomass was uniformly low during the 1970s and 1980s. In no area did the biomass of pelagic fish species exceed 10 kg per standard tow. By the 2000s, catches containing pelagic biomass >10 kg per standard tow had increased

Table 1. List of fish species used in the analysis of condition.

Scientific name	Common name	C/NC	D/P	Biomass	<i>r</i>	<i>n</i>	<i>p</i> value
<i>Centroscyllium fabricii</i>	Black dogfish	0	0	19.23	-0.73	3	0.48
<i>Lycodes lavalaei</i>	Laval's eelpout	0	0	17.03	-0.70	4	0.30
<i>Melanogrammus aeglefinus</i>	Haddock	1	0	1098.68	-0.66	34	<0.001
<i>Cryptacanthodes maculatus</i>	Wrymouth	0	0	17.18	-0.62	7	0.14
<i>Gadus morthua</i>	Cod	1	0	815.69	-0.55	34	<0.001
<i>Merluccius bilinearis</i>	Silver hake	1	0	404.37	-0.51	34	<0.001
<i>Scophthalmus aquosus</i>	Brill/windowpane	1	0	23.59	-0.51	10	0.14
<i>Merluccius albidus</i>	Offshore hake	0	0	66.99	-0.49	17	0.05
<i>Lycodes reticulatus</i>	Arctic eelpout	0	0	32.24	-0.48	7	0.27
<i>Tautoglabrus adspersus</i>	Cunner	0	0	37.69	-0.48	6	0.34
<i>Urophycis chuss</i>	Red hake	1	0	47.79	-0.47	20	0.04
<i>Peprilus triacanthus</i>	Butterfish	0	1	22.48	-0.46	8	0.25
<i>Sebastes</i> sp.	Redfish	1	0	821.14	-0.46	32	0.01
<i>Pseudopleuronectes americanus</i>	Winter flounder	1	0	154.09	-0.45	25	0.02
<i>Raja erinacea</i>	Little skate	0	0	88.94	-0.40	14	0.15
<i>Cyclopterus lumpus</i>	Lumpfish	0	0	66.00	-0.39	7	0.38
<i>Macrozoarces americanus</i>	Ocean pout	0	0	30.41	-0.39	23	0.07
<i>Phycis chesteri</i>	Longfin hake	0	0	43.08	-0.36	24	0.08
<i>Hippoglossus hippoglossus</i>	Atlantic halibut	1	0	130.51	-0.32	26	0.11
<i>Raja ocellata</i>	Winter skate	1	0	319.96	-0.32	24	0.13
<i>Glyptocephalus cynoglossus</i>	Witch flounder	1	0	48.13	-0.31	26	0.13
<i>Lycodes terraenovae</i>	Eelpout (Nfld.)	0	0	19.79	-0.27	5	0.67
<i>Limanda ferruginea</i>	Yellowtail flounder	1	0	283.66	-0.26	25	0.20
<i>Hippoglossoides platessoides</i>	American plaice	1	0	298.66	-0.26	34	0.14
<i>Lophius americanus</i>	Monkfish	1	0	126.76	-0.22	25	0.29
<i>Agonus decagonus</i>	Sea poacher	0	0	1.1	-0.20	9	0.60
<i>Helicolenus dactylopterus</i>	Blackbelly rosefish	0	0	5.88	-0.20	3	0.87
<i>Hemitripterus americanus</i>	Sea raven	0	0	59.3	-0.17	23	0.43
<i>Argentina silus</i>	Argentine	0	1	66.51	-0.16	23	0.45
<i>Pollachius virens</i>	Pollock	1	0	588.37	-0.14	34	0.44
<i>Lycodes vahlii</i>	Shorttailed eelpout	0	0	26.73	-0.13	18	0.62
<i>Notolepis rissoi kroyeri</i>	White barracudina	0	0	3.00	-0.10	8	0.81
<i>Myoxocephalus octodecemspinosus</i>	Longhorn sculpin	0	0	76.1	-0.05	24	0.82
<i>Myoxocephalus scorpius</i>	Shorthorn sculpin	0	0	17.02	-0.05	7	0.92
<i>Squalus acanthias</i>	Spiny dogfish	1	0	355.91	-0.01	18	0.98
<i>Scomber scombrus</i>	Mackerel	1	1	159.57	0.04	23	0.87
<i>Myxine glutinosa</i>	Northern hagfish	0	0	10.39	0.06	17	0.81
<i>Raja senta</i>	Smooth skate	0	0	20.17	0.13	24	0.53
<i>Urophycis tenuis</i>	White hake	1	0	203.44	0.17	25	0.42
<i>Clupea harengus</i>	Herring	1	1	552.94	0.18	22	0.42
<i>Enchelyopus cimbrius</i>	Fourbeard rockling	0	0	2.50	0.19	20	0.41
<i>Anarhichas denticulatus</i>	Northern wolffish	1	0	191.42	0.22	4	0.78
<i>Nezumia bairdi</i>	Marlinspike grenadier	0	0	8.02	0.24	24	0.25
<i>Anarhichas lupus</i>	Striped Atlantic wolffish	1	0	103.17	0.25	23	0.25
<i>Brosme brosme</i>	Cusk	1	0	128.38	0.26	19	0.28
<i>Raja radiata</i>	Thorny skate	1	0	159.64	0.27	25	0.19
<i>Reinhardtius hippoglossoides</i>	Greenland halibut	1	0	73.39	0.39	24	0.06
<i>Lycodes</i> sp.	Eelpouts	0	0	70.33	0.53	7	0.22
<i>Lumpenus lumpretaeformis</i>	Snake blenny	0	0	5.29	0.88	10	<0.001
<i>Raja laevis</i>	Barndoor skate	0	0	535.79	0.92	4	0.08
<i>Alosa sapidissima</i>	American shad	0	1	31.86	0.97	3	0.15
<i>Paralichthys oblongus</i>	Fourspot flounder	0	0	18.59	1.00	3	0.03
<i>Mallotus villosus</i>	Capelin	0	1	31.86	—	*	—
<i>Alosa pseudoharengus</i>	Alewife	0	1	10.25	—	*	—
<i>Anarhichas minor</i>	Spotted wolffish	1	0	126.45	—	2	—

Note: Species are listed as being either commercial, C (1), or noncommercial, NC (0), and pelagic, P (1), or demersal, D (0). Geometric mean biomass (kg·km⁻²) from 1970 to 2003 is also shown, as well as the temporal correlation of condition (*r*), associated *p* values, and sample size for each species (*n*). The species list has been sorted by the sign and strength of the Pearson correlation coefficient. Variable sample sizes are due to changing protocols, absence of species in some years, or a cutoff criterion imposed on fish less than 20 cm because of the unreliability of weight measurements at these smaller sizes that occurred during the 1970s and 1980s (denoted by an asterisk (*)). Most demersal species exhibited negative temporal trends in condition with about a dozen species showing relatively strong trends.

Fig. 1. Spatiotemporal depictions of selected metrics of the eastern Scotian Shelf fish community. (Column *a*) Geometric mean weight of all groundfish species for each decade expressed in units of $\log_{10}(\text{weight})$; *g*). Note the dramatic reduction of body size throughout the eastern Scotian Shelf. (Columns *b* and *c*) Geometric mean biomass per standard tow of groundfish and pelagic fish species in units of $\log_{10}(\text{biomass; kg})$. Biomass of groundfish and pelagic fish has been declining throughout the region with the exception of the western side where pelagic biomass has recently increased. (Column *d*) Species composition expressed as a depth gradient (i.e., contrasting deep-water to shallow-water assemblages). The first axis of variation accounted for 7.0% of the total variance and was associated with a depth gradient (i.e., contrasting deep-water to shallow-water assemblages). The second axis of variation was associated with bottom temperatures, accounting for 6.8% of the total variance. (Columns *e* and *f*) Community condition index of groundfish and pelagic fish species expressed as the significance level of the mean standardized residual weight of all individuals sampled in a survey. Note the erosion of physiological condition of the majority of groundfish and the increase in condition of pelagic fish species over the last four decades.



to 23% of the total area. The greatest increases in pelagic catches occurred in the west and in a few isolated regions to the east. Current pelagic biomass estimates are approximately two orders of magnitude higher than those of the 1970s. This is attributable primarily to the increased abundance of herring (*Clupea harengus*) in the west, capelin (*Mallotus villosus*) in the east, and sandlance (*Ammodytes dubius*) throughout. These increases in abundance were accompanied by the development of a large offshore herring fishery on the outer banks of the central Scotian Shelf where none had existed before 1996 (DFO 2003).

Increases in pelagic biomass are, in part, related to predation release (Swain and Sinclair 2000), and their reciprocal abundance patterns ($r_{\text{Pearson}} = -0.55$, $df = 31$, $p < 0.001$) support this conclusion. However, none of the groundfish species studied is strictly piscivorous, with most feeding on a wide variety of benthic macroinvertebrates (Garrison and Link 2000). This fact probably accounts for the high residual variance in the relationship. Comparative studies have also shown that in temperate marine fish communities, pelagic species tend to proliferate in areas where water column stratification is stronger (Steele and Schumacher 2000). Temporal increases in stratification intensity were positively correlated with pelagic biomass ($r_{\text{Pearson}} = 0.50$, $df = 31$, $p < 0.001$). Also, the increased capacity of the pelagic community to compete and prey upon groundfish, particularly their early life stages, which themselves tend to also be pelagic, may also have contributed to their increased relative dominance in the region. This autocatalytic positive-feedback mechanism in which pelagic fish regulate the recruitment of their former predators has been documented elsewhere (Swain and Sinclair 2000).

Species composition

A spatially explicit, multivariate ordination of species abundances revealed dramatic changes in community structure (Fig. 1d). First, the ordination revealed a distinct temporal trend towards increasing dominance of shallow-water species (principally pelagic species). Second, species new to the area associated with variations in bottom temperatures were evident. This latter gradient was portrayed spatially; during the 1970s and 1980s, community composition was relatively stable, the eastern half of the region being distinct (colder-water species) from the west (warmer-water species). By the 1990s, the eastern region had become dominated by smaller-bodied species of subarctic origin. Only minor changes were observed to the west.

Functional changes

Condition

During the 1970s, aggregate “condition” was higher than normal in 44% of the survey area. By the 1980s, this value had plummeted to 7% and continued to decline in the 1990s to 3% and finally to 2% by the 2000s, reflecting a sustained reduction in physiological condition (Fig. 1e). The most dramatic reductions occurred in the western half of the region where the community composition remained relatively stable. Collectively, these patterns reveal progressive erosion in the bioenergetic “well-being” of the resident groundfish community. The species that exhibited the strongest trends in condition were quite diverse in terms of their morphology,

dietary preferences, and general life history characteristics (Table 1). Only in the east where species composition became dominated by invading subarctic species associated with the incursion of colder water did the condition index remain greater than normal.

Aggregate condition of pelagic species (Table 1) was variable throughout the survey area: the estimated surface area occupied by pelagics with greater than normal condition changed from 34%, 27%, 14%, and 42% during the 1970s, 1980s, 1990s, and 2000s, respectively (Fig. 1f). The spatial and temporal patterns contrast sharply with those observed in the condition of groundfish.

Speculation on the causes of the transition

Why was there a widespread occurrence of a diverse assemblage of groundfish species in poor condition at a time (mid-1980s to 2000s) when intra- and inter-specific competition for food resources was expected to be low? We consider one of the leading hypotheses to explain this poor health of the resident groundfish to be energy depletion in the system. Two primary factors causing this energy depletion involve cumulative biomass removal and abiotic change.

The removal of biomass from the eastern Scotian Shelf ecosystem as a result of fishing was enormous. Since 1960 (i.e., ignoring all previous human exploitation), fishing removed 9000 kt of fish and macroinvertebrates without replacement (of which groundfish represented ~80%). A conservative estimate of the “net primary production required” to accommodate or sustain this removal of groundfish biomass is of the order of $200 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ (assuming a trophic transfer efficiency of 10% and three feeding steps, as per Pauly and Christensen 1995). This value is of the same order of magnitude as the net primary production observed in many temperate continental shelf systems (Nixon 1988) and that of the Scotian Shelf ($<100 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$; Dauchez et al. 1996). To compensate for the biologically useful biomass removed on the Scotian Shelf would require that every unit of net primary production be shunted into groundfish biomass production, and likely much more. This by-product of benthic biomass removal may, in turn, have contributed to and accelerated the decline in the dominance of the groundfish.

Although some possibly compensatory increases in the abundance of exploited benthic macroinvertebrates (shrimp (*Pandalus borealis*) and snow crab (*Chionoecetes opilio*)) have been observed (current biomass estimate of 60 kt), such increases are still low relative to the peak groundfish abundance in the 1970s and 1980s (DFO 2003). Insufficient data exist to evaluate the abundance of other benthic invertebrate species and it is therefore highly uncertain whether or not the benthic system is energy poor. However, the prolonged period of low and declining condition reflected in dozens of diverse groundfish species is indicative of limited abundance of a broad spectrum of benthic prey types (Fig. 1d).

Abiotic conditions known to influence ecosystem productivity underwent major changes coincident with the community and population level changes observed on the eastern Scotian Shelf. The kinetic energy regime on the eastern Scotian Shelf has been dominated since 1987 by increased density stratification in the top 50 m of the water column (primarily due to surface advection of low-salinity waters

from the north; Drinkwater et al. 2003). This diminished the intermixing of surface and deep water layers and is likely to have reduced the exchange of limiting nutrients between them (i.e., new production). It is noteworthy that current rates of ocean primary production are estimated to have declined ~6.7% in the North Atlantic based on remote sensing data, relative to the early 1980s (Gregg et al. 2003). This would, in turn, reduce the degree to which the pelagic ecosystem acts as an engine of energy production for the benthic community. In addition, there was an increased presence of cold subsurface waters in the region. Bottom temperatures declined throughout the 1980s, dropped below the long-term mean in 1985, and reached a new sustained minimum in the early 1990s. This 15+-year period of colder than normal temperatures is unprecedented in the 50+-year temperature record for the region (Drinkwater et al. 2003). The consequences of these temperature changes are particularly limiting for the growth and recruitment of the component populations of the demersal fish community whose habitat is, by definition, largely restricted to the bottom. Pelagic fishes, in contrast, are more flexible in their capacity to choose and so optimize their use of temperature gradients and resources throughout the water column thereby reducing the influence of such changes.

Future outlook

A convergence of individuals within the groundfish community of the Scotian Shelf to a narrow range of small body sizes has occurred over the past 30+ years. This suggests a functional bottlenecking among species unlike anything recorded in the past leading to (i) a shortening of the characteristic time scales of the population dynamic processes relevant to the groundfish (growth, reproduction, mortality) and (ii) a less energetically efficient system as mass-specific heat production increases as organism size decreases as a consequence of the allometry of biological rate processes (Peters 1983). These characteristics, reflected in the changes seen in the groundfish community of the eastern Scotian Shelf, are indicative of a severely perturbed system with reduced functional diversity (Choi and Patten 2001). Clearly a hysteresis has occurred in the Scotian Shelf ecosystem. This makes the prediction of the conditions required for stock recovery and their associated time scales difficult and highly uncertain. The complexity of the interacting factors involved in the dramatic restructuring of the Scotian Shelf ecosystem highlights the problems inherent in attempting to manage individual species within the framework of a complex and dynamic ecosystem.

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