PERSPECTIVE / PERSPECTIVE

Pelagic fish outburst or suprabenthic habitat occupation: legacy of the Atlantic cod (*Gadus morhua*) collapse in eastern Canada

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Abstract: The use of bottom-trawl research survey data to estimate population trends for small pelagic fishes, despite the extremely low selectivity of this gear for these species, has created the impression of a pelagic fish outburst along eastern Canada in the 1990s as a top-down response resulting from the demise of the Atlantic cod (*Gadus morhua*) and other groundfish. Using Atlantic herring (*Clupea harengus*) population assessments, fisheries statistics, and an acoustic database, as well as grey seal (*Halichoerus grypus*) diet studies, I demonstrate that contrary to a pelagic outburst, pelagic catches in research bottom trawls increased in several eastern Canadian ecosystems as these species increasingly occupied the suprabenthic habitat vacated by their diminishing groundfish predators. Although several herring populations were actually decreasing in abundance, bottom-trawl indices (BTIs) were dramatically increasing as their availability to research bottom-trawl surveys increased. Studies using BTIs have systematically underestimated pelagic fish abundances before the cod decline and therefore have dramatically overestimated their importance since, seriously biasing our view of the past and present state of many Canadian east coast ecosystems.

Résumé : L'utilisation des données de relevés de recherche au chalut de fond pour estimer les tendances démographiques des petits poissons pélagiques, bien que ces engins soient extrêmement peu sélectifs pour ces espèces, a créé l'impression qu'il y avait eu une profusion des poissons pélagiques le long de la côte est du Canada dans les années 1990 en réaction descendante à l'effondrement de la morue franche (*Gadus morhua*) et des autres poissons de fond. À l'aide d'évaluations de populations de harengs de l'Atlantique (*Clupea harengus*), de statistiques des pêches, de banques de données acoustiques et d'études de régime alimentaire de phoques, il m'a été possible de démontrer qu'au lieu d'une forte hausse pélagique, il y a eu une augmentation des captures pélagiques dans les relevés au chalut de fond dans plusieurs écosystèmes de l'est du Canada parce que ces espèces occupaient de plus en plus l'habitat suprabenthique abandonné par les populations décroissantes de poissons de fond prédateurs. Alors que certaines populations de harengs affichaient en réalité un déclin de leur abondance, leurs indices des relevés de chalut de fond (BTI) augmentaient de façon spectaculaire à mesure que croissait leur disponibilité dans ces relevés. Les études qui utilisent les BTI ont systématiquement sous-estimé les abondances des poissons pélagiques avant le déclin de la morue; elles ont ainsi considérablement surestimé leur importance depuis lors, ce qui fournit une image erronée de l'état passé et actuel de plusieurs écosystèmes côtiers de l'est du Canada.

[Traduit par la Rédaction]

Introduction

With the collapse in the early 1990s of many groundfish fisheries in eastern Canada, notably several populations of Atlantic cod (*Gadus morhua*), the Canadian government has embarked on a major policy shift towards the ecosystem approach for fisheries management (http://www.dfo-mpo.gc.ca/afpr-rppa/link_policy_framework_e.htm). It is generally believed that monospecific population management has not delivered the anticipated results and a more ecologically oriented, process-based direction is required. The ecosystem approach has a major advantage over single-species assessment because it considers ecological processes explicitly in the modeling and prediction of population dynamics and trophic interactions. Experience has shown us that the lack of emphasis on ecological processes when developing fisheries policies and management measures can have unforeseen negative impacts. For example, although overfishing was undoubtedly the ultimate cause for the collapse of the Atlantic cod (Myers et al. 1997), failure to predict environmen-

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tally induced changes in demographic rates (e.g., mortality, recruitment, production) hampered our ability to foresee and adequately react to the decline (Lambert and Dutil 1997), whereas an increase in predation pressure and, in some cases, continued fishing has certainly impeded population recovery (Fu et al. 2001).

This precipitous decline in the abundance of fisheries-targeted top predators throughout the western Atlantic (Myers et al. 1996) has nonetheless created an opportunity to study the effects of major shifts in the biological forcing within several coastal marine ecosystems. This has lead to a proliferation of investigations of evidence for top-down or bottom-up controls linking species at various tropic levels (Greene and Pershing 2007; Myers et al. 2007; Worm and Myers 2003) and the development of ecosystem models (Bundy 2001; Savenkoff et al. 2004*b*) to investigate ecosystem-scale trophic relationships and decadal-scale regime shifts (Bundy 2005; Savenkoff et al. 2007*a*). For example, in a top-down controlled system in which cod is a near-apex predator, a decrease in cod abundance should release predation pressure and lead to an increase in the abundance of their prey, e.g., planktivorous fishes and invertebrates. In contrast, in a bottom-up controlled system, it is the availability of prey and nutrient resources that controls the abundance of consumers. A third system has been described whereby forage species (e.g., small pelagic fish) at some intermediate trophic level occupy a keystone position in a "wasp-waist" model, exerting top-down control on lower tropic levels and bottom-up influence on higher predators (Rice 1995; Cury et al. 2000). The wasp-waist analogy comes from the observation that only a few species occupy this intermediate level within the food web and therefore their abundance fluctuations have a disproportionate impact on the trophic dynamics of the ecosystem.

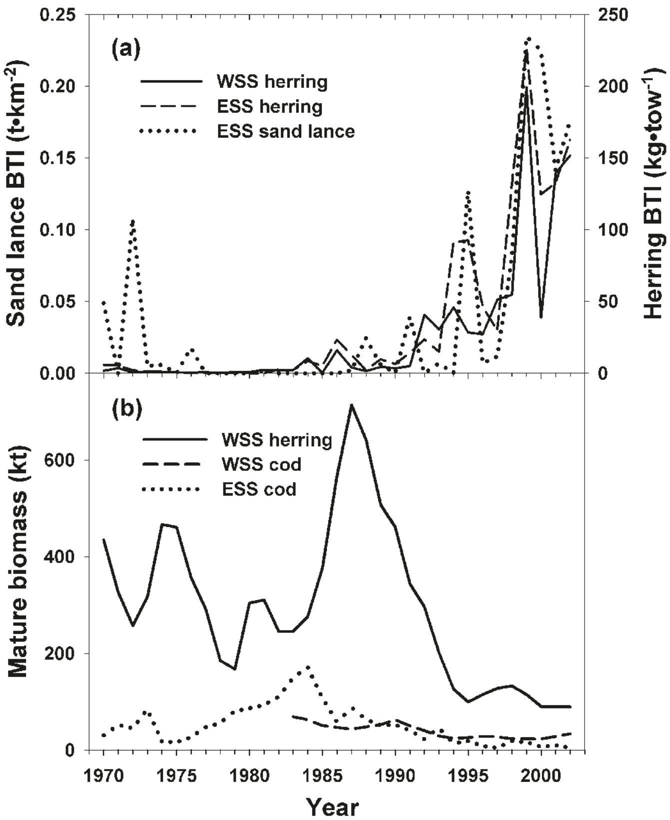
Worm and Myers (2003) presented statistical evidence using data collected between 1970 and 2000 throughout the northern Atlantic for a widespread top-down effect on shrimp populations, which they argued was due to fluctuations in the abundance of associated cod populations. Further, Frank et al. (2005) presented correlative evidence suggesting a top-down, five-level trophic cascade on the eastern Scotian Shelf (ESS) involving groundfish – small pelagic fish – zooplankton – phytoplankton – nutrients. A trophic cascade is a special case of a top-down control in which the effects of varying abundance at the upper levels of the food web are felt down through several trophic levels. Fundamental to the demonstration of the ESS trophic cascade is evidence of an exponential increase in the abundance of small pelagic planktivorous fishes beginning in the late 1980s, coincident with the collapse of commercially important near-apex predatory groundfish populations. The presumed pelagic outburst is hypothesized to have reduced the herbivorous copepod biomass, resulting in an increase in average phytoplankton density and finally a decrease in nutrient levels. This proposed new regime leaves small pelagic planktivorous fishes as the dominant vertebrate biomass in the ESS ecosystem (Bundy 2005).

Although the new emphasis on the ecosystem approach has produced an increased interest in the population dynamics of species at all trophic levels, decades of single-species, population-based thinking has left major gaps in basic demographic information. In many jurisdictions, the main investment of scientific and monitoring effort for marine resource assessment was on commercially important species such as groundfish. However, the requirements of ecosystem models (Bundy 2004; Savenkoff et al. 2004*a*) and bottom-up – top-down dynamic studies (Worm and Myers 2003; Frank et al. 2005) has increased the demand for population-trend indices for less commercially important species, and time series of key components within each trophic level are at a premium. A case in point is the group of fish species collectively known as small pelagics.

Small pelagic fishes are recognized as a key group within the coastal marine ecosystems off eastern Canada and include species whose primary ecological function is to transform zooplankton biomass to fish biomass for consumption by higher-level predators. However, evidence for the small pelagic outburst on the ESS, central to the trophic cascade hypothesis, comes solely from a catch index estimated from an annual scientific bottom-trawl survey conducted since 1970 on the Scotian Shelf (Frank et al. 2005). This small pelagic bottom-trawl index (BTI), estimated as the mean catch per standard tow ($kg \cdot tow^{-1}$), includes Atlantic mackerel (*Scomber scombrus*), Atlantic argentine (*Argentina silus*), and capelin (*Mallotus villosus*) in various years, although the main contributing species on the ESS are Atlantic herring (*Clupea harengus*) and northern sand lance (*Ammodytes dubius*), comprising 77% and 21% of the pelagic index by weight, respectively (see Bundy 2004). The apparent exponential increase in these two herbivorous zooplankton consumers (Fig. 1*a*) between 1986 and 2002 supports the notion of a top-down cascade. Conversely, without an abundance outburst in these species, there cannot have been a cascading trophic linkage between top predators and herbivorous zooplankton within this system.

Time series of small pelagic fish catches from annual stratified random bottom-trawl surveys have been available for several ecosystems in eastern Canada since the 1970s but have garnered little attention until recent years. Catches of small pelagics in these surveys have historically been very low; their catchability in bottom trawls have been estimated at between 0.009% and 2.48%, depending on the species (Harley et al. 2001). Nonetheless, BTIs for various pelagic species have shown remarkable increases in most of these surveys since the late 1980s, consistent with the notion of a demographic expansion. Obviously, estimates of population trends from gear with such low selectivity are accompanied by high uncertainty. Hydroacoustic surveys are the preferred method worldwide for assessing biomass of pelagic species (Simmonds and MacLennan 2005) given their low availability to trawls. Unfortunately, no regular acoustic surveys have been conducted on the ESS, and several historical time series for other eastern Canadian ecosystems have been interrupted. For the present study, I re-examined the abundance indices for small pelagic fishes used in the construction of the ESS ecosystem model (Bundy 2005) and as a major element in the top-down hypotheses in Atlantic coastal ecosystems (Frank et al. 2006) in relation to other available indicators of pelagic fish population abundance trends.

Fig. 1. Trends in pelagic research bottom-trawl survey indices compared with Scotian Shelf cod (*Gadus morhua*) and herring (*Clupea harengus*) population biomass from analytical stock assessments: (*a*) bottom-trawl indices (BTIs) for eastern Scotian Shelf (ESS) and western Scotian Shelf (WSS) herring and ESS sand lance (*Ammodytes dubius*); (*b*) spawning-stock biomass for WSS herring and ESS cod (1970–2002) and WSS cod (1983–2002).



Material and methods

Scientific stratified random bottom-trawl surveys have been conducted by Fisheries and Oceans Canada each July since 1970 on the Scotian Shelf and each August since 1984 in the northern Gulf of St. Lawrence (GSL), providing data on catches per standard tow (kg·tow^{-1}) for all captured species, including pelagic fishes. BTIs estimated from these surveys for eastern and western Scotian Shelf herring were obtained from Power et al. (2006) and for the eastern Scotian Shelf sand lance from Bundy (2004). The western Newfoundland herring BTI (Table 1) was estimated using the Fisheries and Oceans Canada standard survey database (H. Bourdages, Fisheries and Oceans Canada, Institut Maurice Lamontagne, Mont-Joli, QC G5H 3Z4, personal communication). The index was estimated for Atlantic herring (spring and autumn spawning populations combined) within NAFO division 4R (western Newfoundland) to be directly comparable with the area covered by the biennial western Newfoundland herring acoustic survey (McQuinn and Lefebvre 1999), conducted between 1989 and 2002, to produce a population index for the analytical stock assessment. All acoustic area backscatter (s_a) from this survey that was classified as herring was integrated with respect to depth for each year and proportioned over 2 m vertical bins referenced to the sea floor to determine their annual vertical distribution at the time of the survey.

Table 1. Western Newfoundland (WN) annual herring (*Clupea harengus*) biomass (t) from the stock assessment, the WN herring bottom-trawl index (BTI), and the amount of herring available to a research survey bottom trawl (B_a; within 0–6 m of bottom) for the years when the acoustic survey was conducted.

Year	Biomass (t)	BTI (kg·tow^{-1})	B_a (t)	B_a (%)
1984	162 978	0.093	—	—
1985	179 896	0.142	—	—
1986	224 244	0.231	—	—
1987	222 741	0.611	—	—
1988	196 837	0.101	—	—
1989	177 418	0.044	19 175	10.8
1990	163 324	2.037	—	—
1991	151 877	1.349	92 018	60.6
1992	124 802	0.810	—	—
1993	121 043	1.693	103 409	85.4
1994	127 890	3.784	—	—
1995	118 304	2.894	117 030	98.9
1996	102 643	1.138	—	—
1997	94 904	0.132	42 921	45.2
1998	91 350	0.136	—	—
1999	99 853	0.807	88 707	88.8
2000	122 832	0.371	—	—
2001	112 419	0.614	—	—
2002	121 224	0.405	100 452	82.9

Population trend data were obtained through CSAS (http://www.dfo-mpo.gc.ca/csas/) from research documents detailing the analytical stock assessments for Scotian Shelf herring (Power et al. 2006), western Newfoundland spring- and autumn-spawning herring (Grégoire et al. 2004), eastern Scotian Shelf cod (Fanning et al. 2003), western Scotian Shelf cod (Clark et al. 2002), and northern Gulf cod (Fréchet et al. 2007). These analytical stock assessments used virtual population analyses, incorporated all available data, and were rigorously peer-reviewed in open committee. Mature biomass, B_m, used to standardize comparisons between populations and species, was defined as the portion of the total population that spawns in a given year and was calculated as

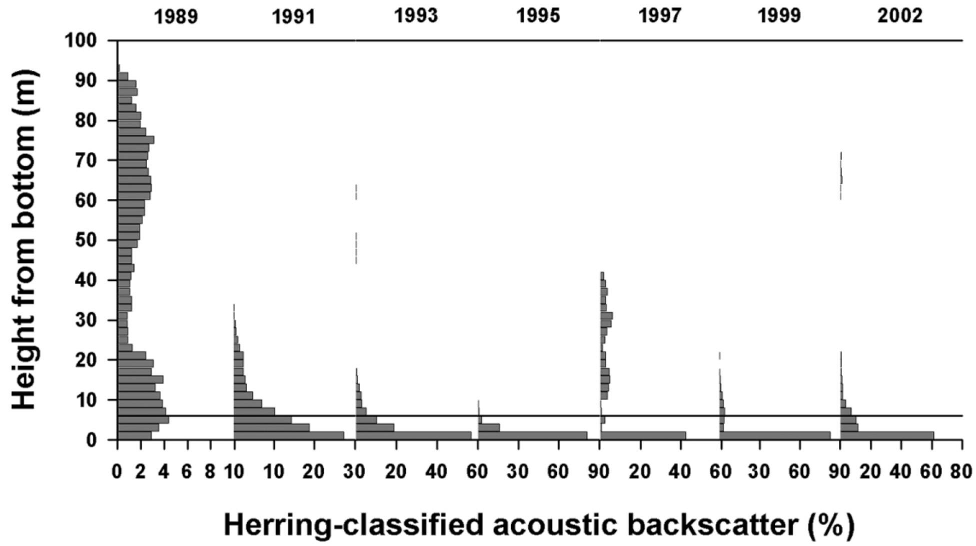
$$B_m = \sum N_i \cdot m_i \cdot w_i$$

where N_i is the population numbers at age i, m_i is the fraction of age group i that has or will have matured during the year, and w_i is the mean weight of an individual at age i. Finally, the amount of western Newfoundland herring biomass (t) available to the northern Gulf bottom-trawl survey, B_a, was estimated by multiplying the annual herring biomass (t) from the analytical stock assessment (Grégoire et al. 2004) by the annual proportion of herring found within 6 m from the sea floor (the approximate trawl height) estimated from the western Newfoundland acoustic survey data (Table 1).

Results

During the period of exponentially increasing pelagic BTIs, the western Scotian Shelf (WSS) herring analytical population assessment showed a dramatic decrease in bio-

Fig. 2. Increasing occupancy of the suprabenthic habitat by western Newfoundland herring (*Clupea harengus*). Proportion of the acoustic backscatter (s_a) attributed to herring found within 2 m layers relative to the sea floor from the biennial herring acoustic survey between 1989 and 2002. The horizontal line indicates the approximate vertical opening of the bottom trawl used in the annual bottom-trawl survey.



mass between 1987 and 1995 and remained low for a decade (Fig. 1*b*). The herring fishery based on this population followed a similar pattern: annual landings ranged from 78 to 200 kt (mean, 137 kt) between 1963 to 1993 and then declined to between 90 and 50 kt (mean, 72 kt), despite higher quotas. This fishery therefore experienced its highest yields when the BTIs (both WSS and ESS) were at their lowest (Fig. 1*a*). When the indices showed a 200-fold increase in herring biomass, the fishery was in decline and the estimated biomass from the analytical assessment was at an historical low. Surely, if the population had grown as much as indicated by the BTI, there should be independent signs of increased abundance. The fishery is mainly conducted inshore on or near the spawning grounds in the WSS; therefore, the increased abundance on the ESS could have been the expansion of the offshore population that occurred since the demise of the cod population. However, the herring BTI shows the same pattern (Fig. 1*a*) whether estimated for the inshore areas (WSS) or the offshore areas (ESS). Curiously, the ESS sand lance BTI shows the same pattern (Fig. 1*a*), following the annual increases and decreases in unison with the herring indices.

At about the same time as the cod decline in eastern Canada, a behavioural change was noted in the biennial (1989–2002) Atlantic herring acoustic survey (McQuinn and Lefebvre 1996) conducted along western Newfoundland (WN) where a similar cod population collapse had occurred (Savenkoff et al. 2007*b*). Between 1989 and 1995, herring were less and less likely to form pelagic schools in the water column, but instead exhibited a conspicuous preference for the suprabenthic habitat, as measured by the annual mean vertical distribution (Fig. 2) and, in doing so, significantly increased their availability to bottom trawls. In fact, the proportion of the herring population found within 0–6 m from the bottom and thus available to the survey gear increased from 11% to above 80% in most years as the cod biomass decreased (Fig. 3*a*). As would be expected, the annual northern GSL bottom-trawl survey conducted in this area (similar to the Scotian Shelf survey and targeting mainly groundfish and shrimp) showed a 10-fold increase in the WN herring BTI (Fig. 3*b*; Table 1) (mean 1984–1989, 0.20 kg·tow^{-1}; mean 1990–1996, 1.96 kg·tow^{-1}). The index had a strong nonlinear correlation (r^2 = 0.91) with B_a, the fraction of the WN herring population (kt) available to the trawl (Fig. 4), and can be approximated by

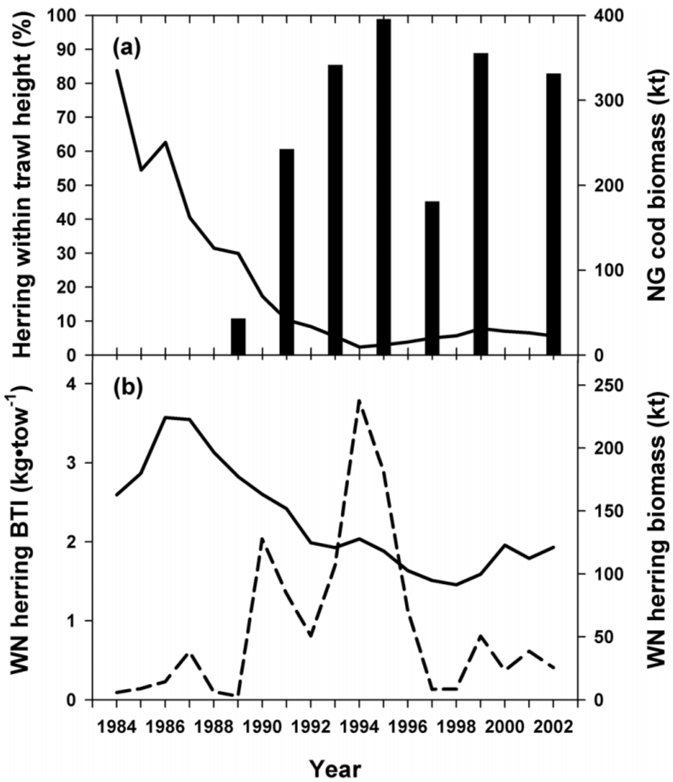
$$\mathrm{BTI} = 0.0095e^{0.0486B_a}$$

This analysis also suggests that when the B_a of this herring population falls below ~70 kt (or 2 t·km^{-2}), the bottom-trawl survey does not catch significant amounts of herring. This is mostly due to the decreasing probability of encountering schools at lower densities.

Discussion

These results show that the rising trend in the WN herring BTI was not dependant on population biomass but rather on the annual patterns in available biomass near the sea floor. The index was close to zero when the herring population was at a 20-year maximum and the cod biomass was high and increased dramatically with the decline of the local cod population. The WN herring acoustic data showed that a distributional shift towards the bottom caused a major increase in their availability to bottom trawls, whereas the analytical assessment showed that the herring biomass was actually declining through this period. The same pattern can be observed in both the ESS and WSS herring BTIs, which are virtually zero in many years throughout the 1980s when the WSS herring population biomass was known to be very high and increased dramatically along with the decline of the cod predators in both areas. On the ESS, both the herring and sand lance BTIs varied in unison, which would be expected if their occupancy of the suprabenthic habitat varied through a behavioural reaction to extrinsic influences such as the presence or absence of a mutual predator. This would not be expected through a synchrony of their population dynamics (e.g., interannual recruitment and mortality rates).

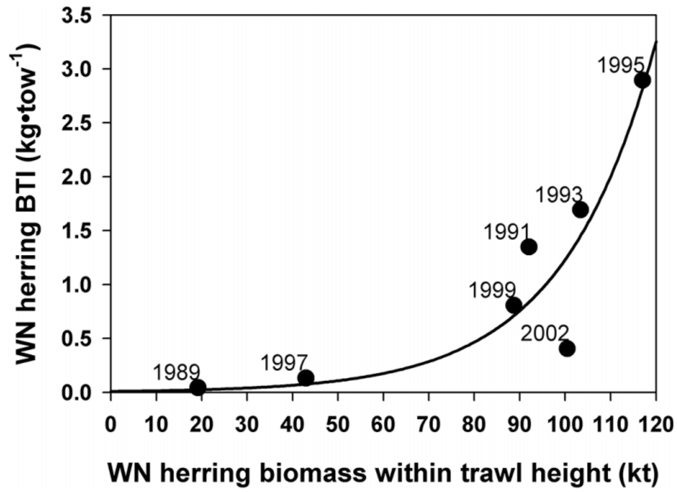
Fig. 3. Combined effects of the declining northern Gulf (NG) cod (*Gadus morhua*) and western Newfoundland (WN) herring (*Clupea harengus*) populations on the herring vertical distribution and bottom-trawl index (BTI): (*a*) NG cod mature biomass (line) from the stock assessment (1984–2002) and the proportion of the WN herring population found within 6 m of the bottom (vertical bars) from the biennial herring acoustic survey (1989–2002); (*b*) WN herring mature biomass (continuous line) from the stock assessment (1984–2002) and WN herring BTI (broken line).



Capelin has also been caught on the ESS during certain periods (Frank et al. 1996), and indeed, capelin catches increased substantially in the ESS research bottom-trawl survey in the 1970s and again in the 1990s. Frank et al. (1996) argued that this was due to below-normal temperatures on the Scotian Shelf but presumed that low capelin abundance explained why capelin bottom-trawl catches did not increase during a similar cold period in the 1980s. However, cod abundance was low on the ESS during the 1970s and 1990s but was high during the 1980s. Colder temperatures may favour the horizontal expansion of capelin habitat, but the absence of cod would favour its vertical expansion. Mowbray (2002) found that capelin in Newfoundland have aggregated significantly closer to the seabed since 1991 and that this deepening of vertical distribution was correlated with the absence of cod. Therefore, the capelin BTI would be susceptible to the same increase in trawl catchability as herring, as capelin increase their exploitation of the suprabenthic habitat.

The striking effect that the presence of cod has on capelin vertical distribution was dramatically illustrated by Rose (1993). He presented acoustic recordings showing capelin, which were clearly occupying the suprabenthic layer, rising 50 m into the water column as migrating cod advanced into

Fig. 4. The response of the western Newfoundland (WN) bottom-trawl index (BTI) to annual variations in herring (*Clupea harengus*) biomass (kt) available to the trawl. WN herring BTI versus the fraction of the WN herring population available to the annual bottom-trawl survey (the proportion within 0–6 m from the bottom × population biomass estimate from the analytical stock assessment). Data labels refer to the years of the survey.



the area. A similar avoidance effect has been documented in the Bay of Biscay, where the pelagic anchovy were found to be distributed higher in the water column in the presence of horse mackerel, a suprabenthic predator (Massé et al. 1996).

Unfortunately, there are no targeted abundance indices for these pelagic populations on the ESS to confirm whether the increase in bottom-trawl catches was due to a change in abundance or vertical distribution. However, Bowen et al. (2006) proposed the monitoring of grey seal (*Halichoerus grypus*) behavioural, dietary, and life history variables to track forage-species abundance as ecosystem indicators based on the premise that seals are opportunistic feeders and therefore their diet and dive characteristics should reflect local prey abundance. Although sand lance is a major component in the ESS grey seal diet, they observed no trend in the proportion of sand lance in the seal diet from 1993 to 2001 (Bowen et al. 2006), while the ESS sand lance BTI fluctuated by several orders of magnitude following an exponentially increasing trend. Likewise, herring was an insignificant prey species for Sable Island grey seals in the early 1990s (Bowen et al. 1993) and remained a marginal component of their diet during this period of a 15-fold increase in the herring BTI. In contrast, the diet composition of grey seals inshore along the coast of Nova Scotia where herring are known to be distributed was dominated by herring between 1988 and 1990 (Bowen et al. 1993), showing their preference for this prey when it is available. These observations do not support a dramatic increase in herring or sand lance abundance in the offshore throughout the 1990s.

It is concluded, therefore, that time series of pelagic fish biomass, inferred from these bottom-trawl indices, severely underestimated population abundances before the cod decline and have, by contrast, dramatically overestimated their importance as pelagic fish catchability subsequently increased. The present study underlines the pitfalls of monitoring population trends of marine organisms from low-selectivity sampling gears that can be severely influenced by simple behavioural shifts. Such indices must be critically evaluated to determine whether the ecological and demographic patterns that they suggest can be corroborated through independent observations and evidence. Although Bundy (2004, 2005) assumed that part of the dramatic increase in the ESS sand lance and herring BTIs was due to an increase in their catchability (Q) and adjusted the biomass estimates for this, these adjustments were arbitrary and nonetheless implied that there was an order of magnitude increase in these species on the ESS between the late 1980s and the 1990s. Further, this Q-adjusted ESS herring BTI also implies that this population averaged 0.9 million tonnes between 1995 and 2000, i.e., is one of the biggest herring populations in the Northwest Atlantic. Yet, acoustic explorations by industry and research vessels on the ESS have found few important concentrations of herring, and the purse-seine industry has not caught its 12 kt quota since 2001 (Power et al. 2006), partly because herring are reportedly too deep, as would be expected if they preferentially occupied the suprabenthic habitat during these years. It is quite possible that there was no increase in ESS herring biomass following the decline of the cod population, and judging from the herring biomass trend on the WSS, there may even have been a decline. The lack of correlation between Sable Island grey seal diet composition and the small pelagic BTIs caused Bowen et al. (2006) to doubt the usefulness of seal diet as an ecosystem indicator. The present study suggests that it is rather the BTIs that do not reflect pelagic fish abundance, which would explain the seal diet – prey anomaly exposed by Bowen et al. (2006). Perhaps the decrease in groundfish predation and the increase in the seal population between the 1980s and 1990s also explain the preference by small pelagic fish for the suprabenthic habitat, as a major predation threat would have come from below in the early period and from above in the latter period.

The results of this study introduce serious doubts concerning a pelagic outburst in the majority of coastal ecosystems in the Northwest Atlantic (Frank et al. 2006). They do not support the conclusions of ecosystem studies suggesting a regime shift towards planktivorous pelagic grazers (Bundy 2005; Bundy and Fanning 2005) or the hypothesized large marine ecosystem top-down trophic cascade on the eastern Scotian Shelf (Frank et al. 2005). Head and Sameoto (2007) also questioned the top-down control of phytoplankton by herbivorous zooplankton within the cascade proposed by Frank et al. (2005), noting the lack of temporal overlap between the grazers and their potential prey that would be necessary to support a top-down mechanism. Further, Greene and Pershing (2007) argued that climatic forcing originating in the High Arctic induced oceanographic changes in coastal waters of the Northwest Atlantic resulting in a bottom-up controlled regime shift of the lower trophic levels on the ESS.

The lack of corroborative evidence for a pelagic outburst in eastern Canadian coastal ecosystems compromises the interpretation of ecosystem models using these same pelagic population-trend indices. Given that these species are presumed to dominate these ecosystems at present, if evidence for these large proposed biomasses cannot be found, these models should be re-evaluated with more realistic abundance estimates for these pelagic species. At the very least, some quantitative validation of these indices should be conducted before assuming that such a major regime shift has occurred. In ecosystems where herring population abundances are assessed analytically, e.g., western Newfoundland, eastern Newfoundland, and the WSS, the herring population outburst did not occur, despite the demise of the cod and other groundfish populations in each of these areas. In contrast to the hypothesized pelagic outburst on the ESS, ecosystem models in the GSL using herring population trends from analytical assessments confirmed a decrease in herring biomass following the cod collapse (Savenkoff et al. 2007*b*), although capelin biomass increased dramatically, again based on a BTI.

In conclusion, failing to implement standard pelagic monitoring programs throughout eastern Canada when pelagics fisheries were of lesser commercial importance has had lasting detrimental effects on our ability to detect changes in this important component of marine ecosystems and on our ability to understand the impacts that future environmental change may exert. Data from just a small-scale acoustic monitoring program were able to document other important changes that have occurred in these ecosystems beside trophic regime shifts, i.e., a major behavioural shift in suprabenthic habitat use. Recognising the importance of monitoring each trophic level as an integral part of the ecosystem approach may be one of the most important lessons to be learned from the failures of the single-species approach. In the mean time, we must not sacrifice sound scientific method and rigour in the race to develop the new paradigm.

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