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Irruptive prey dynamics following the groundfish collapse in the Northwest Atlantic: an illusion?

Kenneth T. Frank[1]*, William C. Leggett[2], Brian D. Petrie[1], Jonathan A. D. Fisher[3], Nancy L. Shackell[1], and Christopher T. Taggart[4]

[1]*Department of Fisheries and Oceans, Bedford Institute of Oceanography, PO Box 1006, B2Y 4A2, Dartmouth, Nova Scotia, Canada*
[2]*Department of Biology, Queen's University, K7L 3N6, Kingston, Ontario, Canada*
[3]*Centre for Fisheries Ecosystem Research, Fisheries and Marine Institute of Memorial University of Newfoundland, A1C 5R3, St John's, Newfoundland, Canada*
[4]*Department of Oceanography, Dalhousie University, B3H 4J1, Halifax, Nova Scotia, Canada*

**Corresponding author: tel: 1-902-426-3498; fax: 1-902-426-6927; e-mail: Kenneth.Frank@dfo-mpo-gc.ca*

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The collapse of Northwest Atlantic groundfish in the early 1990s yielded a "natural experiment" within which to explore responses of ecosystems to a major perturbation. The "Pelagic Outburst" hypothesis was developed to explain an up to 900% increase in the abundance of small-bodied forage fishes and macroinvertebrates following this collapse and a subsequent trophic cascade extending across four trophic levels. Recently, this theory has been challenged and an alternative "Suprabenthic Habitat Occupation" (SHO) hypothesis has been advanced; it proposes the prey outburst associated with the forage fish component was an illusion created by changes in the vertical distribution of small pelagic fishes after the cod collapse in favour of a more bottom-oriented distribution that increased their vulnerability to bottom trawls. We evaluated the SHO hypothesis as it applied to the relationship between changes in the biomass of cod and the vertical distribution of herring and sand lance, the major small pelagic species of the Scotian Shelf ecosystem off eastern Nova Scotia. Contrary to predictions of the SHO hypothesis our initial conclusion that a pelagic outburst occurred in that ecosystem was confirmed and we found no evidence of a predator effect on vertical distributions of these species. We also explored the acoustic survey design and execution that generated the data that form the cornerstone of the SHO hypothesis, and the coherence between the behaviour depicted in these data and catch rates in the surface-oriented purse-seine fishery for herring operating at the time of these surveys. In combination, the results of our re-analysis of the population dynamics and behaviour of herring on the eastern Scotian Shelf, lead us to conclude that the SHO hypothesis, at least as it relates to the post-cod collapse dynamics of the affected Northwest Atlantic ecosystems, is not supported.

Keywords: ecosystem dynamics, predator – prey, small pelagics.

Introduction

The growing acceptance that the traditional single species approach to the management of commercial marine resources is inadequate has led to enhanced interest in the applicability of ecosystem-based management models (Link, 2010). Central to this approach is a more complete knowledge of the interdependency of the numerous trophic levels and species interactions that govern the dynamics of large marine ecosystems (Cury *et al.*, 2011; Hunsicker *et al.*, 2011). The well-known collapse of cod (*Gadus morhua*) and other groundfish populations in the western North Atlantic in the early 1990s produced something akin to a natural experiment (Jensen *et al.*, 2012) that has been exploited by several researchers to develop, refine and evaluate ecological theory as it relates to the response of large marine ecosystems to natural and anthropogenic perturbations (Bundy, 2005; Frank *et al.*, 2005, 2011; Savenkoff *et al.*, 2007; Shackell *et al.*, 2010).

Frank *et al.* (2006) documented a suite of post-collapse trophic cascades that involved up to four trophic levels (large-bodied benthic predators, small pelagic fishes, zooplankton, and phytoplankton) in several Northwest Atlantic ecosystems. Small pelagic planktivores, once the primary prey of the collapsed groundfish species on the eastern Scotian Shelf (Figure 1), exhibited a 900%

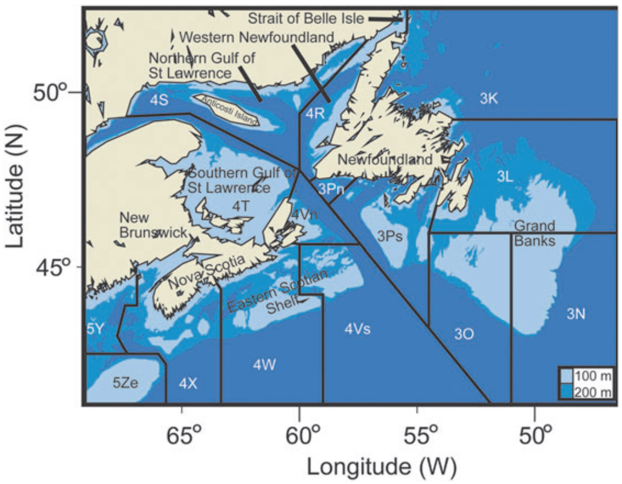

Figure 1. Map of the northwest Atlantic study region, indicating the boundaries and names of Northwest Atlantic Fishery Organization statistical areas and the locations of major offshore features. The 100- and 200-m isobaths are highlighted.

increase in biomass (Frank *et al.*, 2005). Zooplankton species, their principal prey, declined and phytoplankton concentrations increased. Petrie *et al.* (2009) subsequently demonstrated that the differential susceptibility of large marine ecosystems to such top-down alterations was linked in a predictable way to water temperature and species richness—colder and less species rich ecosystems being more vulnerable to top-down forcing.

Detailed studies of the dynamics of the altered eastern Scotian Shelf ecosystem led Frank *et al.* (2011) to inquire whether these lower trophic level effects, and the failure of cod and other collapsed groundfish species to recover in spite of a > 20-year moratorium on exploitation, resulted from the post-collapse increase in the abundance and biomass of small pelagic fishes, notably herring (*Clupea harengus harengus*), sand lance (*Ammodytes dubius*) and capelin (*Mallotus villous*). The same authors hypothesized that this produced a predator–prey role reversal in which the once pelagic fish prey became important predators of the now diminished egg and larval stages of the collapsed demersal species, thereby inhibiting their recovery.

McQuinn (2009) developed an alternate view of the post-collapse dynamics of these small pelagic species by focusing on herring. McQuinn's analysis of the post-collapse vertical distribution of commercially exploited herring in the waters off western Newfoundland (Figure 1), as reflected in acoustic surveys conducted at night between 1991 and 2002, led to the conclusion that the collapse of cod in the region resulted in a rapid (<2 year), dramatic, and persistent (decadal) behavioural change in which the classic night-time, near-surface distribution of herring (e.g. Horwood and Cushing, 1978; Blaxter and Hunter, 1982; Cardinale *et al.*, 2003) was no longer evident. The acoustic survey data indicated that in the years following the collapse of cod approximately 80% of the population was distributed within 6 m of the bottom at night at depths in excess of 80 m compared with 10% estimated from one acoustic survey conducted in 1989 before cod collapsed. McQuinn (2009) attributed this apparent behavioural change to reduced predation pressure resulting from the collapse of cod, a behaviour characterized as Suprabenthic Habitat Occupation (SHO). This hypothesis was then generalized to apply to other small-bodied forage fishes known to be prey of cod (e.g. sand lance), and to all times of day, seasons and years following the collapse of cod across all formerly cod-dominated ecosystems in the Northwest Atlantic.

On the basis of these findings, McQuinn (2009) concluded that the "Pelagic Outburst" reported in other ecosystems affected by the collapse of cod (Frank *et al.*, 2005; Bundy 2005; Benoît and Swain, 2008; Petrie *et al.*, 2009) was an artefact of the apparently enhanced benthic-oriented behaviour and increased susceptibility of herring and other small pelagic species to capture by bottom trawls. Scientific surveys using bottom trawls remain the primary monitoring tool for assessing the abundance and distribution of groundfish and small pelagic fishes in these ecosystems. Distinguishing between these competing mechanisms is thus crucial to increasing our knowledge of predator, prey and ecosystem dynamics.

Changes in predator abundance have been shown to influence prey behaviour, activity patterns, habitat use, foraging rate, growth, reproduction and diel vertical migration in aquatic invertebrates and vertebrates (Lima, 1998; Preisser *et al.*, 2005; Peckarsky *et al.*, 2008). Diel vertical migration (DVM) is generally viewed as a behavioural strategy that achieves trade-offs between foraging efficiency, predator or competitor avoidance, and bioenergetic efficiency (Neilson and Perry, 1990; Hays, 2003). Hays *et al.* (1996) demonstrated that an index of DVM behaviour (based on the ratio of day- to night-time catch rates) for *Calanus finmarchicus* and several other abundant zooplankton taxa in the North Sea, was positively correlated with herring biomass during the period 1958–1994; Gliwicz (1986) showed that the depth distributions of zooplankton did not change between day and night in fishless lakes but did so, in dramatic fashion, in lakes with planktivorous fish. The reported change in vertical migration and distribution of herring off western Newfoundland that was reflected in the acoustic data developed by McQuinn (2009) is, therefore, not without some analogs.

The Pelagic Outburst (Frank *et al.*, 2005, 2011) and the SHO hypotheses (McQuinn, 2009) present very different interpretations of the dynamics of these important Northwest Atlantic ecosystems following cod collapses. In this paper we re-examine the relationship between temporal changes in the biomass of herring and their principal predator (cod) in the eastern Scotian Shelf ecosystem (Figure 1), the focus of our earlier investigations (Frank *et al.*, 2005, 2011), and we evaluate the post-cod collapse vertical distributions of herring there. Similar analyses were conducted for sand lance. We then re-evaluate the analyses of the vertical distribution patterns of the western Newfoundland herring that led to the SHO hypothesis and compare the predictions leading from those distributions with the success of the commercial purse-seine fishery for herring in that survey area.

Methods

The target herring population we examined—fall spawning herring resident on the offshore areas of the eastern Scotian Shelf (Harris and Stephenson, 1999)—form part of a larger complex of independently managed sub-stocks distributed contiguously in three other regions within NAFO Division 4VWX (Figure 1; DFO, 2002). This offshore population has remained largely unexploited with the exception of a foreign fishery that operated during the period 1963–1973 with reported annual landings as high as 120 kt (Stephenson *et al.*, 1998). A limited fishery was re-established in 1996 with an annual quota of 12 kt (DFO, 2002). We also investigated the temporal dynamics and vertical distribution of the unexploited sand lance population on the eastern Scotian Shelf, an important prey of cod (Cook and Bundy, 2010). McQuinn (2009) concluded that the similarity of the temporal population dynamics of sand lance and herring on the eastern Scotian Shelf was supportive of the SHO hypothesis, i.e. that both species reacted similarly to the absence of a mutual predator.

Temporal trends in the biomass of herring, sand lance and cod were assessed from annual fishery-independent, bottom trawl surveys conducted on the eastern Scotian Shelf during July from 1970–2011 in Division 4VW (Figure 1). This is the only systematically developed, scientifically rigorous source of data available with which to conduct such an evaluation. The survey uses a stratified random sampling design with stratification by depth and geographic location. The eastern Scotian Shelf consists of 27 strata [see Shackell and Frank (2003) for map illustrating stratum boundaries and locations]. Finfish were captured using a standard bottom trawl equipped with a 19-mm codend liner which was towed at a constant speed of 3.5 knots for approximately 30 min. Set allocation was generally proportional to stratum area and sampling was conducted around the clock. Because there was no fixed schedule, the allocation of day and night samples varied randomly among strata and years (Chadwick *et al*., 2007).

Day and night biomass series were generated for both forage species. These were used to assess the extent, if any, of changes in the vertical distribution of herring and sand lance in relation to changes in the biomass of cod. We estimated the average biomass per tow from annual bottom trawl survey tows for day (07:00–21:59) and night (22:00–06:59) components (sunrise and sunset). There were 2940 day sets and 1720 night sets of data during 1970–2011.The ratio of day-to-night catch rates was employed as an index of DVM. Several applications of this approach have been successfully used to assess vertical migration behaviour in fishes (Pillar and Barange, 1997; Casey and Myers, 1998; Aglen *et al*., 1999; Petrakis *et al*., 2001; Krutzikowsky and Emmett, 2005).

If a major change in the diel vertical distribution of the two forage species (herring and sand lance) had occurred in this ecosystem, as hypothesized by McQuinn (2009), our expectations would be: (i) that the magnitude of the ratio of day-to-night catches would be positively correlated with the biomass of cod spanning the pre- and post-cod collapse period; and (ii) that the day-to-night catch ratio for herring and sand lance would not deviate significantly from 1 (i.e. no difference between day and night catch rates) following the cod collapse.

In a separate and independent evaluation of the abundance of herring in the pre- and post-cod collapse years, we employed a secondary metric of population abundance (area occupied based on presence/absence data), which has been shown to scale positively with the abundance of herring (Overholtz, 2002; Overholtz and Friedland, 2002; Benoît *et al*., 2003) and for many other animal taxa (Gaston *et al*., 2000). We also developed estimates of trends in herring larval abundances as a surrogate indicator of changes in adult abundance over time due to the expected positive relationship between stock size and reproductive output. Quantitative estimation of larval abundances based on standard sampling protocols has been commonly used as an indirect method for assessing adult stock biomass (Heath, 1993; Richardson *et al*., 2010). Estimates of herring larval abundance (based on ichthyoplankton surveys) have been developed periodically throughout the eastern Scotian Shelf region since the mid-1970s (Harris and Stephenson, 1999). The data we used were derived from the Scotian Shelf Ichthyoplankton Program (SSIP) 1979–1981, from the Ocean Production Enhancement Network (OPEN) larval surveys executed from 1991–1992, and from joint DFO/Dalhousie University larval surveys undertaken from 1997–1998 (Harris and Stephenson, 1999). Sand lance larval abundance data were only available from the SSIP and OPEN surveys.

In our re-assessment of the data upon which the SHO hypothesis was founded, we researched the original technical reports, which provide specifics of the design and execution of the acoustic surveys in western Newfoundland (Division 4R; Figure 1), and we assessed the consistency between the behavioural changes reflected in those data and the success of the commercial herring purse-seine fishery that was operating simultaneously in space and time with the acoustic surveys.

Results and Discussion

Herring biomass (developed from herring catches in the bottom trawl survey) was low from 1970–1993 (average of 2.1 kg per tow) when cod biomass was relatively high (average of 38.9 kg per tow). With the exception of 1987, herring weight per tow never exceeded 6 kg (Figure 2a). Herring weight per tow increased rapidly after the collapse of cod and averaged 15.5 kg per tow from 1994–2011. The highest biomass values occurred during the late 1990s to mid-2000s (maximum = 35 kg per tow in 1999) when cod biomass featured a broad minimum of 4.6 kg per tow. More recently (since 2005), with the development of early signs of cod recovery (Frank *et al*., 2011; Swain and Mohn, 2012), herring biomass has been declining (Figure 2a). Sand lance biomass exhibited a similar temporal pattern. Average weight per tow increased by

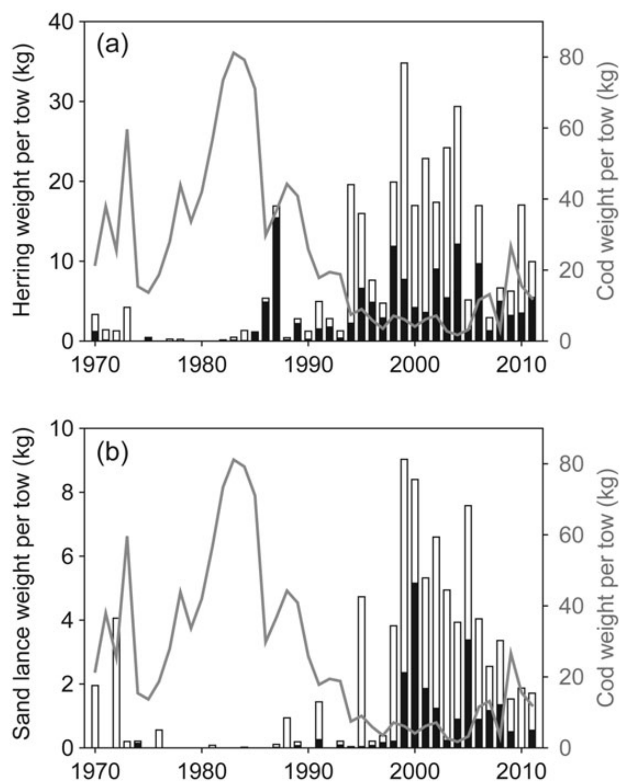

Figure 2. **(a)** Time series of herring weight per tow during daytime (open bars) and night-time (closed bars) in relation to the biomass of cod (grey line) from bottom trawl surveys of the eastern Scotian Shelf, 1970–2011. **(b)** Same as (a) except for sand lance.

nearly an order of magnitude after cod collapsed (1970–1993: 0.42 vs. 1994–2011: 3.89 kg per tow), and it too has recently been declining (Figure 2b).

We found that for herring on the eastern Scotian Shelf, the second metric of population abundance (area occupied based on presence/absence data) increased threefold from the pre- to post-cod collapse period (12 vs. 38%); a similar increase was observed for sand lance (6 vs. 28%) between the two periods (Figure 3).

Estimates of larval herring abundance for the eastern Scotia Shelf provide a fishery-independent estimate of herring spawning stock biomass. They also revealed a progression from extremely low levels in the late 1970s/early 1980s to much higher levels during the 1990s. Data from the SSIP indicate that annual larval herring concentrations on the eastern Scotian Shelf were 0.013, 0.016 and 0.005 m^{-3} during 1979, 1980 and 1981, respectively. Those very low concentrations led O'Boyle *et al.* (1984) to exclude herring from their characterization of the ichthyoplankton community structure of the Scotian Shelf. Monthly sampling of herring larvae from March 1991 to March 1992 from two stations in the Sable Island Bank region surveyed by OPEN yielded densities of herring larvae averaging 1.43 m^{-3} from an on-bank location at 50 m depth; at the other station to the northeast of the shelf at 80 m depth, average densities of herring larvae were 0.08 m^{-3} (Mousseau *et al.*, 1998). The on-bank densities of herring larvae were >250 times higher than the densities encountered during the pre-cod collapse years associated with SSIP. A fall ichthyoplankton survey in the Western/Sable Island Banks region conducted in 1997 yielded average concentrations of herring larvae of 0.08 m^{-3} (maximum = 0.6 m^{-3}; Reiss *et al.*, 2000). The survey was repeated in 1998 and yielded an average of 1.2 herring larvae m^{-3} (maximum = 7.1 m^{-3}). Despite the limited number of larval fish surveys there was a positive correlation between herring weight per tow from the bottom trawl survey and herring larval concentration ($r = 0.7$, $n = 6$). Sand lance larval concentrations averaged 0.29, 0.19 and 0.22 m^{-3} for 1979, 1980 and 1981, respectively, during the SSIP but were one to two orders of magnitude higher during the 1991–1992 OPEN surveys, averaging 1.74 and 11.11 m^{-3} for the shelf and bank station, respectively (Mousseau *et al.*, 1998).

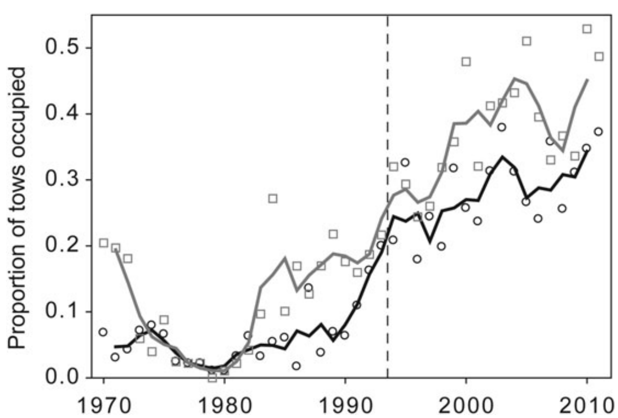

Figure 3. An annual index of distributional change for herring (open squares and grey line) and sand lance (open circles and black line) for the eastern Scotian Shelf (Division 4VW) from 1970–2011 based on the July bottom trawl survey. Catches were treated as either present or absent and the index represents the number of locations (or tows) with positive catches relative to the total sampling effort in each year. Smoothed lines represent the three-year, centre-weighted running mean. Dashed vertical line separates pre- and post-cod collapse periods.

Collectively, these data are consistent with the hypothesis that the biomass and productivity of herring and sand lance increased dramatically following the collapse of cod on the eastern Scotian Shelf. It is worth noting, also, that the biomass of two macroinvertebrate prey of cod, adult snow crab *Chionecetes opilio*, which do not exhibit diel vertical migration, and adult shrimp *Pandulus borealis*, which do exhibit a typical pattern of DVM (D. Hardie, Population Ecology Division, Bedford Institute of Oceanography, pers. comm.) also increased on the eastern Scotian Shelf following the collapse of cod (Frank *et al.*, 2005) and have since sustained economically lucrative fisheries (Koeller *et al.*, 2011; Choi *et al.*, 2012).

Changed vertical migratory behaviour of herring on the eastern Scotian Shelf due to cod collapse: yes or no?

Notwithstanding the evidence provided above regarding changes in the biomass of herring and sand lance over time in relation to the collapse of cod on the eastern Scotian Shelf, the possibility remains that the behaviour hypothesized in the SHO (McQuinn, 2009) may have influenced these changes, at least in part. We therefore examined patterns of day and night catches of herring and sand lance in that ecosystem.

The typically reported pattern of DVM in herring is a shallower distribution at night during vertical feeding excursions, followed by deeper distributions during the day as the fish move to deeper, darker waters to avoid detection and predation (Cardinale *et al.*, 2003; Huse *et al.*, 2012). Hence, all else being equal, and under typical patterns of DVM, the expectation is that daytime catches in bottom trawls should exceed night-time catches (i.e. the ratio of day-to-night catches should exceed 1). We found that in years following the collapse of cod when cod weight per tow was comparable with the levels characteristic of western Newfoundland when McQuinn (2009) conducted his study (see Table 11 from Fréchet *et al.*, 2005), daytime catch rates of herring (based on weight per tow) were, on average, 4.17 kg higher than night-time catch rates [significantly higher (1-tailed t-test: $n = 18$, $t = 2.380$, $p = 0.015$)]. The ratio of day-to-night catch rates averaged 1.7 when based on weight per tow, and 1.7 when based on numbers per tow at length captured during day and night (Figure 4a). Moreover, the average total lengths of herring captured during day and night sets were nearly identical (day = 26.8 cm, night = 26.5 cm) and a comparison between the day and night length frequency distributions revealed no difference (Figure 4; Komolgorov Smirnov test: D = 0.098, $p = 0.967$).

A similar pattern was observed for sand lance during the post-collapse period. Daytime catch rates were higher than night-time catch rates with an average difference of 1.62 kg (1-tailed t-test: $n = 18$, $t = 3.656$, $p = 0.001$). The ratio of day-to-night catch rates averaged 2.4 when based on weight per tow, and 2.1 when based on numbers per tow at length captured during day and night (Figure 4b). The average total length for sand lance collected during the day (19.5 cm) and night (19.1 cm) were virtually identical, with no difference between the day and night length frequency distributions (Figure 4; K-S test: D = 0.157, $p = 0.557$). Unlike herring, sand lance are obligate benthic inhabitants closely associated with sandy bottoms that are used for refuge during extended periods in winter (van der Kooij *et al.*, 2008). In the North Sea during summer, sand lance undergoes a DVM pattern similar to that of herring (Greenstreet *et al.*, 2006), and our results are consistent with this observation.

McQuinn (2009) concluded that, consistent with this well-established pattern, during times of high cod abundance, the

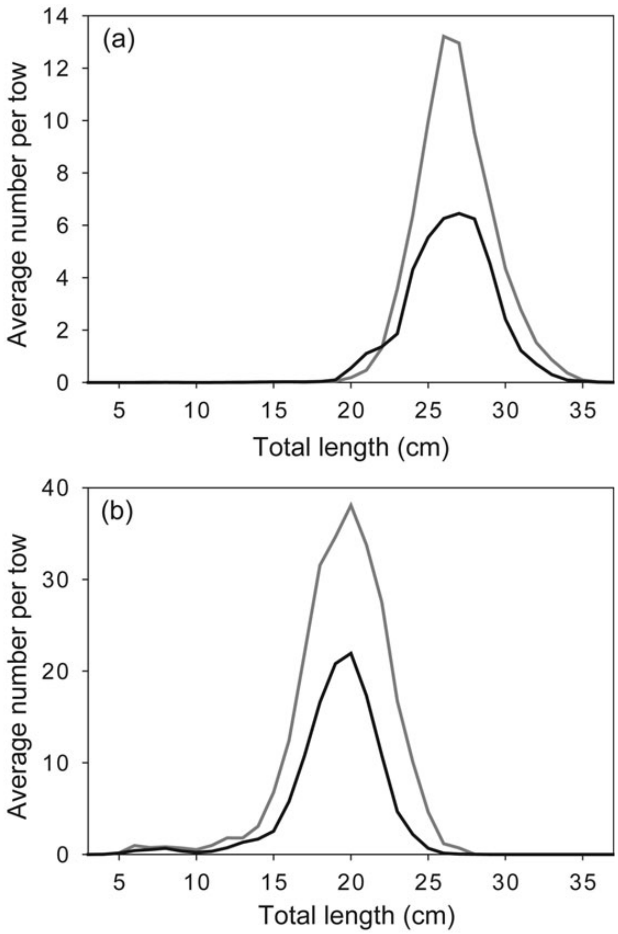

Figure 4. Average number per tow at length from day (grey lines) and night (black lines) during the post-cod collapse period (1994–2011) for (**a**) herring and (**b**) sand lance. Daytime catch rates exceeded night-time rates by 1.7 for herring and 2.1 sand lance, based on the ratios of the areas under each curve. Length frequency distributions were not statistically different between day and night for either species (K-S test; $p > 0.0.5$).

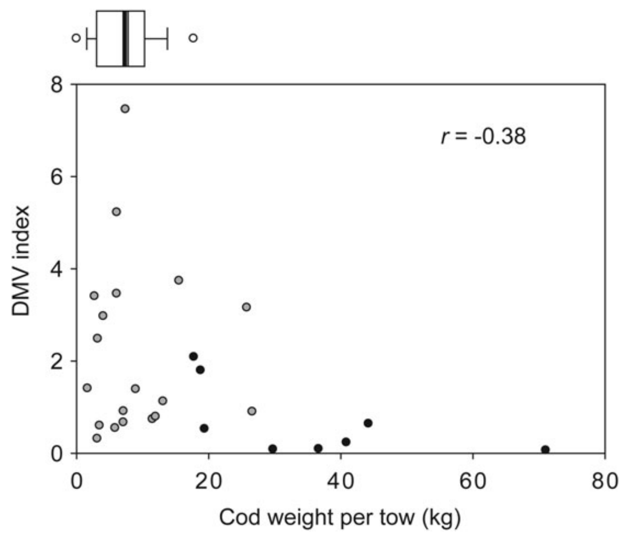

Figure 5. Relationship between the annual index of herring diel vertical migration (DVM) and cod biomass from 1985–2011 from the eastern Scotian Shelf. Post-cod collapse data points are in grey and pre-cod collapse data points are in black. The box and whisker plot at the top of the figure was derived from annual cod-weight-per-tow data from research vessel surveys conducted off western Newfoundland (Division 4R) from 1991–2002 (see Table 11 from Fréchet *et al.*, 2005)—the post-cod collapse period during which McQuinn (2009) conducted herring acoustic surveys, and illustrative of the near complete overlap of the post-collapse cod biomass levels between the two locations.

typical pattern of vertical migration behaviour for western Newfoundland herring involves ascending to shallow depths at night and descending in daytime. This would translate to lower catches near the bottom at night and higher catch rates near the bottom during the day. Following the collapse of cod, a persistent near-bottom occupancy at night was revealed in herring acoustic surveys conducted in the western Newfoundland region and interpreted as a "major behavioural shift" (McQuinn, 2009). Given this interpretation one would expect the day-to-night catch ratios for herring as determined from bottom trawls surveys to be positively related to cod biomass, with low values characteristic of weak predation pressure and higher values (i.e. in excess of 1) when predator biomass was high.

Contrary to this expectation under the SHO hypothesis on the eastern Scotian Shelf, a weak inverse relationship ($r = -0.38$, $p > 0.05$, $n = 27$) was found between the day-to-night catch ratio and cod biomass (Figure 5) during the transition from cod dominance to collapse (1985–2011). Annual day-to-night catch ratios became progressively higher and somewhat more variable as cod biomass estimates fell below 10 kg per tow. These estimates are virtually identical to those from the western Newfoundland region (Division 4R) where the McQuinn (2009) acoustic surveys were conducted (see box and whisker plot within Figure 5). Similarly, there was no relationship between the day-to-night catch ratio for sand lance and cod biomass ($r = -0.12$, $p > 0.05$, $n = 27$).

Given the above results, the two expectations derived from the SHO hypothesis (McQuinn, 2009) are not supported since: (i) the day-to-night catch ratio for herring (and sand lance) deviated significantly from 1; and (ii) the magnitude of the ratio of day-to-night catches was not positively correlated with the biomass of cod for the pre- and post-cod collapse period combined.

We conclude that all available evidence continues to indicate that the pelagic outburst on the eastern Scotion Shelf hypothesized by Frank *et al*. (2005) was "real" [see also Bundy (2005)], and that it resulted from reduced natural mortality caused by a dramatic decline in predation associated with the collapse of cod and other groundfish species, and not from behaviourally mediated changes in their susceptibility to capture as hypothesized by McQuinn (2009).

Herring behaviour in western Newfoundland

Given these inconsistencies between the predictions of the SHO hypothesis as developed from the acoustic surveys conducted in western Newfoundland waters and our findings for the eastern Scotian Shelf ecosystem, we conducted a detailed re-evaluation of the analyses that gave rise to the SHO hypothesis.

In contrast to the offshore herring stock of the eastern Scotian Shelf, the Division 4R western Newfoundland herring stock, an amalgam of spring and fall spawners, is heavily fished, principally by a purse-seine fishery (DFO, 2006). This stock experienced a 60% reduction in biomass from a high of 224 kt in 1986 to a low of 91 kt in 1998. The decline, which was largely coincident with the collapse and prolonged impoverished state of the cod population in the ecosystem, has been attributed primarily to overfishing (Grégoire *et al*., 2004).

The western Newfoundland herring acoustic surveys, the data which formed the basis of the SHO hypothesis, began in 1989 and continued through to 2002 with the primary aim of developing estimates of herring biomass for stock assessment purposes. The cornerstone of the SHO hypothesis was a comparison of the vertical distributions of herring in western Newfoundland waters in 1989 with those of 1991 through 2002**.** The 1989 survey differed from those that followed. It was the only survey in which sampling was undertaken during day and night (McQuinn and Levebvre, 1995). All subsequent surveys were conducted exclusively at night (17:00–05:00; Beaulieu *et al*., 2010). The data derived from later surveys differ markedly (see Table 1 and Figure 2 from McQuinn, 2009) from the 1989 data that revealed herring distributed from surface to bottom (10.8% in the bottom 6 m) with a slight bias toward deeper waters. In contrast, those for 1991–2002 indicated that all herring were concentrated near the bottom (average of 77%, range, 45–99%). This difference in the apparent vertical distribution of herring prior to and subsequent to the collapse of cod constituted the genesis of McQuinn's (2009) formulation of the SHO hypothesis.

Details of the design and execution of the acoustic surveys that led to the formulation of the SHO hypothesis are provided in a series of technical reports (McQuinn and Lefebvre, 1995, 1996, 1999). These reveal that the survey methods employed underwent a significant evolution in their annual timing, the type of acoustic surveying equipment employed, the ground-truthing protocols, and the survey vessel employed. Significant technological issues are documented including deployment of a defective transducer (McQuinn and Lefebvre, 1995, 1999), variable survey coverage due to weather and other factors (McQuinn and Lefebvre, 1999), vessel noise that may have obscured the acoustic signal (McQuinn and Lefebvre, 1995), and software problems that resulted in data loss (McQuinn and Lefebvre, 1995). During the 1990 survey so few herring were detected, even in areas where the commercial purse-seine fleet was successfully operating (McQuinn and Lefebvre, 1995), that data from 1990 were excluded from the analysis that led to the SHO hypothesis (McQuinn, 2009). More critical to the assessment of the reliability of the data that framed the SHO hypothesis, however, is the fact that data from the 1989 survey were excluded from use in analyses of herring biomass in that and subsequent years (McQuinn *et al*., 1999), and from analyses of distributional patterns of herring along western Newfoundland (Beaulieu *et al*., 2010) "due to the poor performance of the transducer and incertitude as to the proper calibration parameters" (McQuinn and Lefebvre, 1999). Subsequent surveys (all conducted at night) showed herring to be heavily concentrated in the bottom waters. In fact, in each of the six surveys conducted after 1989, the maximum reported acoustic target densities occurred within the 2 m layer next to the bottom (depths in excess of 80 m), which is coincident with the acoustic dead zone where fish are less detectable by echosounders since they cannot be distinguished from the strong acoustic echo from the seabed (Aglen *et al*., 1999; DFO, 2007). If the seabed is even partly integrated, the result is a large overestimation of fish density (MacLennan *et al*., 2004).

Herring are often referred to in the literature as a classic example of a vertically migrating species (Horwood and Cushing, 1978; Blaxter and Hunter, 1982). In the North Sea and elsewhere this classic behaviour is reflected in well-defined schools located near the seabed or in midwater by day, and dispersed into the surface waters at night (Huse and Korneliussen, 2000; Orlowski, 2005). This behaviour is known to result in acoustic undersampling of herring during periods of darkness, a consequence of a surface "blind zone" when fish are located above the ensonified portion of the water column (Totland *et al*., 2009). This problem is so acute that the international herring acoustic survey program of ICES suspends acoustic sampling during periods of maximum darkness when herring are concentrated closest to the surface (ICES, 2011). This surface blind zone effect, combined with the restriction of acoustic sampling to night hours during the post-cod collapse years (1991–2002), may have contributed to the apparent behavioural shift reflected in the post-1989 survey data.

In a further attempt to assess the validity of hypothesized changes in herring vertical distribution implied by the acoustic data underlying the SHO hypothesis, we examined herring landings data from the western Newfoundland purse-seine fishery for the years prior to and during which the acoustic surveys were conducted. Purse-seines, whose landings account annually for 80–90% of the total reported in western Newfoundland waters since the mid-1980s (McQuinn *et al*., 1999; Beaulieu *et al*., 2010), are designed to capture herring in the upper 20–50 m and are generally deployed at night to exploit the herring's classic night-time surface-oriented vertical migratory behaviour. A gillnet fishery accounts for an average of 15% of the reported landings with an assortment of other fishery gears making up the remainder (e.g. shrimp trawls, bar seines, cod traps, midwater trawls, etc.). Assuming the apparent extreme, post-1990 bottom-oriented behaviour of herring revealed in the acoustic surveys that McQuinn (2009) concluded occurred as a consequence of the collapse of cod was a real phenomenon, purse-seine catches in Division 4R should have exhibited a significant decline as herring became progressively less abundant in the surface waters. This did not occur. Commercial purse-seine landings of herring during the months of October and November alone (coincident in time and space with the acoustic surveys) constituted, on average, 22% of the

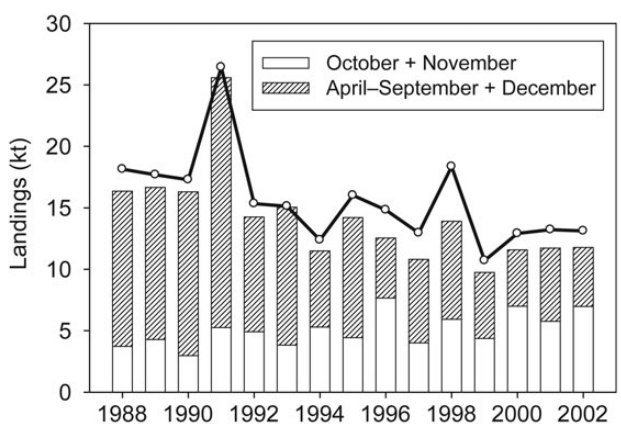

Figure 6. Total landings of herring (black line) in NAFO Division 4R and monthly landings (histograms) by purse-seines ($< 65' + > 65'$ vessel lengths) from 1988–2002. Beginning in 1988, an over-the-side market to Russian vessels resulted in the spring fishery contribution rising to a peak of 12 400 t in 1991; the spring fishery accounted for over 70% of the total catch in 1990 and 1993; this proportion diminished to $<$40% in 1994 and subsequent years when the spring fishery in some of the coastal embayments was closed due to concerns about a potential collapse of the spring spawning component.

total landings in western Newfoundland waters in the pre-cod collapse years 1988–1990. In the post collapse years, 1991–2002 herring landings in these months averaged 38% of the total annual landings for the region, and in some years exceeded 50% (Grégoire *et al.*, 2002). Specifically, in 2002 when the acoustic surveys indicated that 82.9% of western Newfoundland herring were concentrated within 6 m of the bottom (McQuinn, 2009), 56% of the total annual landings of herring from these waters were derived from the October and November purse-seine fishery (Figure 6).

The inconsistencies in the acoustic survey and the associated potential shortcomings of the acoustic data underpinning the SHO hypothesis, and the contrasting expectations regarding purse-seine landings under the SHO hypothesis and the realized catches, are sufficient to challenge the validity of the SHO hypothesis, at least as it is applied to herring and sand lance in the Northwest Atlantic.

Conclusion

We conclude that the pelagic outbreak previously reported for the eastern Scotian Shelf ecosystem following the collapse of cod and other groundfish is strongly supported by the evidence and by additional analyses presented here; it is not an artefact of any change in the vertical migratory behaviour of the forage fishes following their release from predation. This finding also lends credence to the hypothesis that other cold-water, species-poor ecosystems in the Northwest Atlantic experienced similar ecological transitions following the collapse of cod (Petrie *et al.*, 2009), a hypothesis that is fully consistent with the well-documented parallel responses of a wide range of animal groups to fluctuations in the abundance of their major predators (Strong and Frank, 2010; Estes *et al.*, 2011). We also conclude that the data underpinning the SHO hypothesis potentially suffer from technological and sampling problems, and that the hypothesis as it applies to the dynamics of the eastern Scotian Shelf ecosystem in particular, and by extension to other Northwest Atlantic ecosystems affected by the collapse of cod and other demersal predators, is not supported by the evidence.

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