



Review

Eastern Scotian Shelf trophic dynamics: A review of the evidence for diverse hypotheses



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ABSTRACT

Two hypotheses have been proposed to account for trophic dynamic control of the eastern Scotian Shelf ecosystem off Atlantic Canada: (1) top-down: *fishery induced trophic cascade* and (2) bottom-up: *climate variability*. We evaluate the evidence in support of these hypotheses: including observations on top-down drivers (fishing effort and predation by grey seals), bottom-up drivers (nutrient supply and water column stratification), and the several trophic levels (groundfish, macro-invertebrates, small pelagic fish, and plankton). There is limited support for the *fishery-induced trophic cascade* hypothesis. The predictions of the *climate variability* hypothesis are generally met for the lower and middle trophic levels, but the ongoing high levels of natural mortality of groundfish are not accounted for. We propose an alternative hypothesis encompassing concurrent top-down and bottom-up processes, and conclude that many species of groundfish (including cod) and small pelagic fish stocks (including herring) will not recover with the ongoing high levels of natural mortality generated by grey seal predation. Predictions on future trends in abundance of the commercially important macro-invertebrate species (lobster, snow crab, and shrimp) are not possible based on the available evidence.

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1. Introduction

The fisheries oceanography literature has generally highlighted three conceptual models with respect to the functioning of marine ecosystems: bottom-up, top-down and wasp-waist (Cury et al., 2003, 2008) (Fig. 1). Under the bottom-up model the food web components are regulated by either primary producers or the input of limited nutrients through changes in the physical environment (i.e. controlled by the physical environment). Under top-down con-

trol the regulation of ecosystem components at lower trophic levels is by species at higher trophic levels (i.e. control by predation or fishing effort). Under the wasp-waist model, which is primarily related to upwelling ecosystems, the environmental processes directly cause changes in abundance on the small pelagic fish populations, with subsequent cascading effects upwards in the ecosystem (i.e. on the groundfish population abundance) and downwards (on the plankton productivity). In this paper we examine the dynamics of the eastern Scotian Shelf off Nova Scotia, Canada with respect to the factors controlling ecosystem dynamics. The biomass of large demersal fishes, in particular Atlantic cod, collapsed in this ecosystem in the late 1980s and early 1990s due to overfishing. These fishes, in particular Atlantic cod, have shown no sustained recovery in the more than two decades since the collapse, despite reductions in fishing mortality to negligible levels following a moratorium on the cod-directed fishery starting in 1993.

The Scotian Shelf off Canada's east coast is comprised of two ecosystems: respectively the eastern Scotian Shelf (ESS) and the western Scotian Shelf (WSS) (Fig. 2). The ESS ecosystem in particular has been the subject of a number of interpretations of the relative importance of the ecological and oceanographic processes (top-down and bottom-up, but not wasp-waist) on the changes observed during the past four and a half decades. The region is characterized by some of the largest spatial gradients in oceanographic properties in the global oceans (Longhurst, 1998), with the ESS being a transition area between temperate and sub-arctic fish communities (Mahon et al., 1998). This spatial complexity in the oceanographic setting and a biogeographic transition would be expected to complicate interpretation of the observed temporal changes in ecosystem structure.

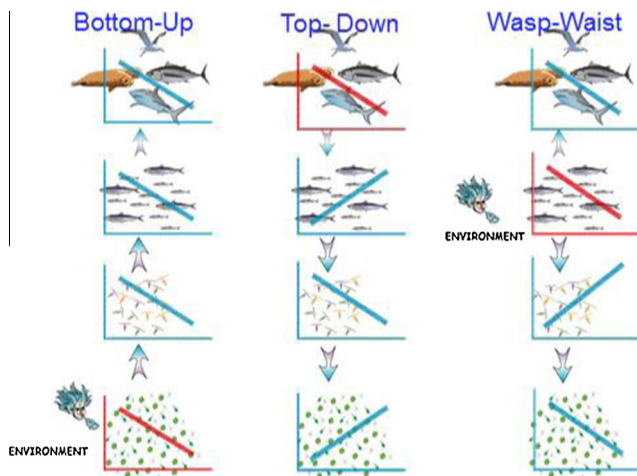


Fig. 1. Conceptual models addressing the controls of abundance of fish populations: (a) top-down, (b) bottom-up, and (c) wasp-waist (from Cury et al., 2003).

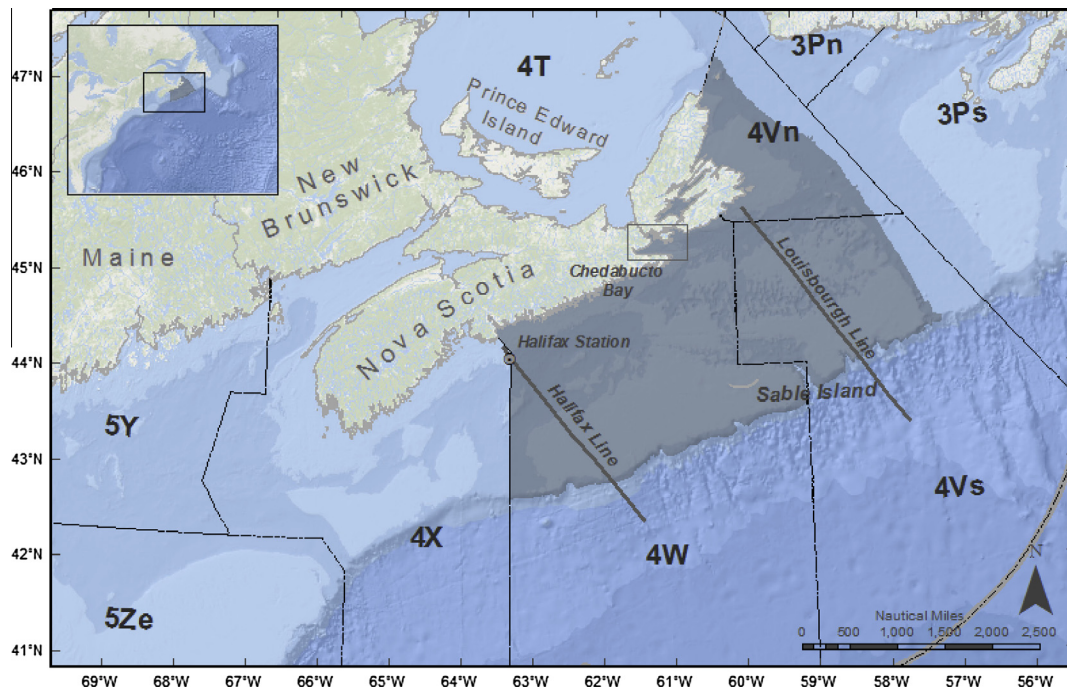


Fig. 2. Scotian Shelf (NAFO Area 4VWX). ESS comprises NAFO areas 4Vn, 4Vs, and 4W. WSS is the shelf area within 4X. The Halifax station, and the Louisbourg and Halifax lines, of the Atlantic Zone Monitoring Program (AZMP) are also shown.

Halliday and Pinhorn (2009) conclude that increases in natural mortality of cod began in the late 1980s, coincident with the collapses of the several cod stocks off Atlantic Canada, and that this phenomenon was widespread. They suggest that environmental conditions, at the scale of the Northwest Atlantic, influenced the productivity of demersal fish species on decadal time scales and that a combination of overfishing and climate variability has been responsible for the observed fluctuations in demersal fish populations.

Bundy (2004, 2005) and Bundy and Fanning (2005) use a trophic dynamic modelling approach (ECOPATH) to evaluate the relative importance of various processes in the lack of recovery of cod in ESS following the reduction in fishing mortality in 1993. They conclude that the removal of large fish (primarily cod) by fishing has resulted, through a trophic cascade, in an increase in the abundance of species at the middle trophic levels. They argue that predation and competition by these species on early life-stages of cod have resulted in reduced condition and increased mortality of small cod. Bundy et al. (2010) use a similar modelling approach to compare four geographic areas off Atlantic Canada (including ESS), concluding that the forage species out-compete small cod for small zooplankton. In addition they suggest that these competitors prey on larval cod (thus generating lower levels of recruitment success).

A series of papers use an integrated assessment approach to the evaluation of the processes responsible for the ESS trophic dynamic temporal patterns (Choi et al., 2004, 2005; Frank et al., 2005, 2006, 2007, 2011; Shackell and Frank, 2007; Shackell et al., 2010). Choi et al. (2004) describe community-level reductions in the body size, biomass, and physiological condition in demersal fish species; and conclude that there has been a reduction in the energy flow to the benthic system with a decoupling of the benthic and pelagic systems. This decoupling is considered to have been due to a complex set of factors that were triggered by the cumulative removal of biomass of demersal species and exacerbated by decadal scale variability in bottom temperature and water column stratification.

Frank et al. (2005) conclude that the ESS trophic level changes are due to the cascading impacts of the removal of large fish (in particular the larger cod). In essence the release of predation on groundfish caused by overfishing is interpreted to have led to increases in the relative abundance of small pelagic species (such as herring) and of benthic invertebrates (such as snow crab). This in turn is interpreted to have caused decreases in zooplankton abundance and thus lower predation on phytoplankton (resulting in higher biomass at the base of the food-chain). Frank et al. (2007) conclude that top-down impacts due to overfishing are more prevalent in ecosystems with lower species diversity and lower temperatures (such as the ESS ecosystem) than in ecosystems with higher diversity and temperatures (e.g. WSS). Under this interpretation the ESS ecosystem is less resilient than the WSS ecosystem. Frank et al. (2011) updated the assessment of the Eastern Scotian Shelf to include recent observations and conclude that the ecosystem structure is returning to that observed during the 1980s. They interpret that the forage species (i.e. sand lance, capelin, and herring) have outstripped the zooplankton production resulting in a reversal of the trophic cascade, and propose that the decline in forage species has led to a recovery of the previously dominant benthic predators (e.g. cod, pollock, and silver hake).

There have been recent studies which suggest that the changes in ESS may not be due to trophic cascades. McQuinn (2009) concludes that the trawl survey time series showing an outburst of small pelagic species on the Scotian Shelf during the 1990s is an artefact of changes in the depth distribution of herring, capelin, and sand lance. Swain and Mohn (2012) examine the relationships between forage fish biomass and recruitment dynamics and condition of ESS cod. They conclude that the lack of recovery of ESS cod,

as well as the recent short term increase in biomass, is due to factors other than interactions with forage fish (and the proposed trophic cascade processes). Frank et al. (2013a, 2013b) respond to critiques of Greene (2013) and McQuinn (2009) on respectively (1) the role of bottom-up drivers on plankton decadal trends, and (2) an alternate interpretation of decadal trends in small pelagic fishes.

There have been a number of studies that more narrowly consider the predator–prey interactions between grey seals and cod in ESS. These evaluations of the impact of seals on the cod stocks are contradictory. Mohn and Bowen (1996) develop a predator/prey model for the eastern Scotian Shelf area (4VsW) for the 1970–1994 period, and conclude that grey seals were not a major factor in the collapse of the cod stock. Sinclair et al. (1997), based on a comparative analysis of fisheries management practices on the eastern (4VsW) and western (4X) Scotian Shelf, conclude that a combination of poor environmental conditions and increases in natural mortality (in part due to seal predation) contributed to the decline in stock production and recruitment. Fu et al. (2001) evaluate the causes of the lack of recovery of cod in ESS following the 1993 fishery closure concluding that seal predation was not a significant factor. Trzcinski et al. (2006, 2009) also focus on the lack of recovery of cod since 1993. They conclude that grey seals had made some contribution to increases in cod natural mortality in the post fishery closure period, but that overall it was minor and that “*unknown sources of mortality ... are contributing to the failure of cod to recover*”. O’Boyle and Sinclair (2012) re-evaluate the impact of grey seals on 4VsW cod abundance. In contrast to the above predator–prey studies their review of the global literature on grey seal diets suggests that cod is a significant prey item. Their model results indicate that the cod consumption by grey seals in ESS accounts for the increases in natural mortality beginning in the late 1980s, as well the lack of recovery of the stock since the fisheries moratorium initiated in 1993.

1.1. Two hypotheses defined

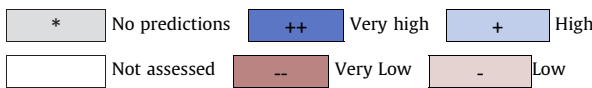
The literature on ESS ecosystem dynamics demonstrates a lack of consensus on the relative importance of potential drivers. The diverse interpretations of the ecosystem dynamics can be grouped within two hypotheses. The first hypothesis (e.g. Bundy, 2005; Bundy and Fanning, 2005; Frank et al., 2005, 2011) is that fishery induced top-down processes have generated a trophic cascade covering several levels from large-bodied groundfish to nutrients (with ecosystem transitions occurring in 1991/1992 and 2005/2006). The “*cultivation/depensation*” interactions (e.g. Bundy et al., 2010) are considered here to be a component of this first *fishery-induced trophic cascade* hypothesis. The second hypothesis, defined as *climate variability*, includes the importance of bottom-up processes (in addition to overfishing) in the interpretation of the observed trends (Greene, 2013; Greene and Pershing, 2007; Greene et al., 2008; Halliday and Pinhorn, 2009; Rothschild, 2011). This paper undertakes an examination of the evidence supporting the two hypotheses, systematically examining the predictions of each (Table 1), in order to evaluate which processes have been instrumental in causing the decadal changes in the ESS ecosystem.

2. Review of the evidence

Given that the preponderance of interpretations of the ecosystem dynamics of ESS are top-down, the review of the evidence begins with the observations on fishing effort and grey seals, followed by those on the middle and lower trophic levels, and ending

Table 1
The predictions of trophic level relative abundance levels (very high, high, or low) for the two hypotheses on the control of ecosystem dynamics in ESS during the following time periods (prior to 1992, 1992–2005, after 2005).

Trophic level	Prior to 1992		1992–2005		After 2005	
	Cascade	Climate	Cascade	Climate	Cascade	Climate
<i>Top-down drivers</i>						
Groundfish effort	+	+	–	–	–	–
Grey seal fish consumption	*	*	*	*	*	*
<i>Fish and macro-invertebrates</i>						
Groundfish	+	+	–	–	+	–
Macroinvertebrates	–	*	+	*	–	*
Small pelagics	–	+	++	–	–	–
Fish natural mortality	*	*	*	*	*	*
<i>Plankton</i>						
Large bodied zooplankton	+	+	–	–	+	–
Small bodied zooplankton	*	+	*	–	*	–
Phytoplankton	–	+	+	–	–	–
<i>Environmental drivers</i>						
Nutrients	+	+	–	–	–	–
Stratification	–	–	+	+	+	+



with the bottom-up drivers (nutrients and water column stratification). The data sources and methods are provided in Text S1.

2.1. Top-down factors: fishing effort and landings

DFO (1996) provides a summary of the trends in fishing effort on three of the major groundfish species (i.e. cod, haddock and pollock) in 4VsW for 1977–1995. It was concluded that the rough indices of trends in effort (i.e. the annual # of trips by vessel categories) indicate a general increase from 1977 to 1992, followed by a sharp decline. Following a similar approach, the number of trips/year (aggregated for all gear types) targeting cod, haddock and pollock are updated to provide the trends in effort since 1986 (Fig. 3a).

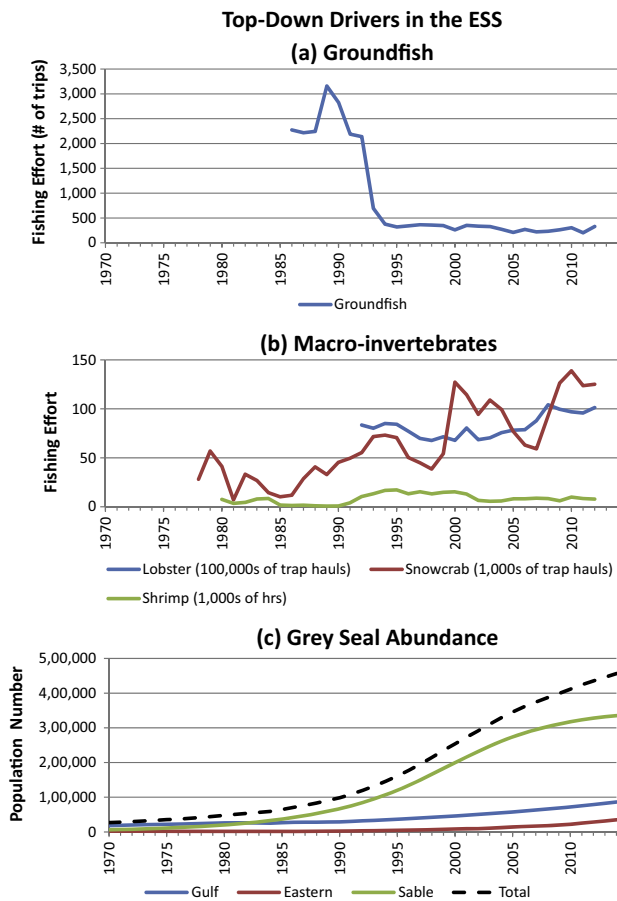


Fig. 3. Temporal trends in the top-down drivers in ESS. Groundfish effort: cod, haddock, and pollock (tonnage classes 2 and 3) numbers of trips using gears 11, 12 and 51 in ESS (1986–2012). Macro-invertebrates effort: American lobster effort (1000s of trap hauls); shrimp effort (1000s of hours); and snow crab effort (1000s of trap hauls). Grey seal abundance (1970–2013) from three herds (Sable Island, Gulf of St. Lawrence, and coastal Nova Scotia).

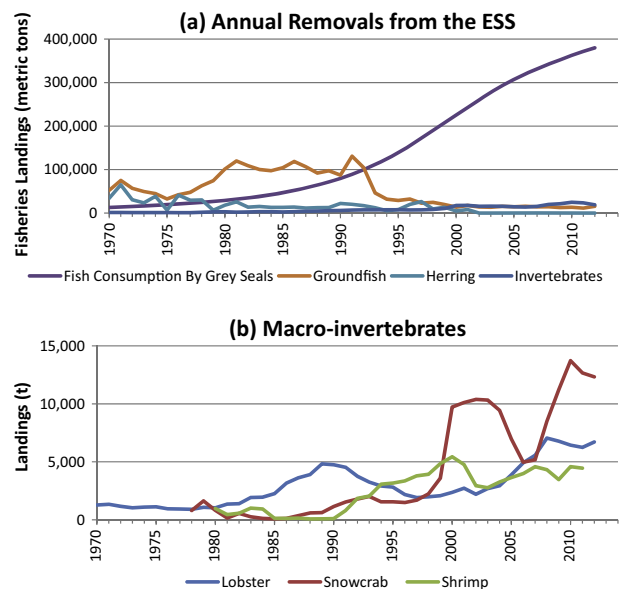


Fig. 4. Annual fish removals from ESS (metric tonnes) by top-down drivers: (a) estimates of the total fish consumption by grey seals in comparison with the landings of groundfish, small pelagics and invertebrate fisheries (squid not included); (b) reported landings of American lobster, shrimp, and snow crab.

Table 2

Estimated annual discards (in tonnes) of groundfish and small pelagics in 4VW from 2002 to 2006 (extracted from Gavaris et al., 2010).

Species	2002	2003	2004	2005	2006
Cod	0.702	1.26	0.646	3.861	0.419
Haddock	0.022	1.254	0.005	0.002	0
Atlantic halibut	41.274	33.98	24.44	36.495	11.91
Herring	42.692	8.413	65.206	181.318	8.49
Redfish	0.569	2.03	2.241	24.293	28.769
Silver hake	0	2.471	1.726	22.482	47.53
Smooth skate	0.755	2.045	10.06	0	5.156
Thorny skate	11.351	69.615	34.03	50.879	3.828
Greenland halibut	0	0.035	22.789	4.657	0.14
White hake	2.857	1.297	0.012	6.828	0
Winter skate	28.252	54.134	94.701	13.914	37.629

The restrictive measures put in place starting in 1993 (i.e. the groundfish moratorium) have essentially eliminated the fishing effort directed at these species. The trends in effort on small pelagic species are not well documented (DFO, 2015).

Groundfish landings were high during the 1970s to the late 1980s, followed by a sharp decline due to reduction in abundance of several groundfish species and the implementation of the moratorium (Fig. 4a, and Supplementary Figs. S2 and S3a). Landings of small pelagic species (predominantly herring) approached the levels of groundfish in the 1970s, but have been mostly below 20,000 t per year since the late 1970s (Fig. 4a). There has been no fishery on sand lance, and occasional landings of capelin. The herring landings have been declining in recent years (DFO, 2015). Gavaris et al. (2010) estimated the discards from Canadian commercial fisheries on the ESS during 2002–2006 (Table 2). The annual discard levels of groundfish species have generally been much less than 100 tons since the imposition of the moratorium, with the herring discards somewhat higher.

Overall, the fishing effort and associated reported landings (and estimated discards) on groundfish in ESS since the 1993 moratorium

Table 3

(a) Annual proportions of grey seal diets comprised respectively of small pelagic fish and groundfish as estimated from the scat samples from Sable Island; (b) ranking of the relative importance of groundfish species in the diet of grey seals.

Panel A		
Year	% Pelagics	% Groundfish
1991	79	21
1992	88	12
1993	86	14
1994	72	28
1995	58	42
1996	86	14
1997	70	30
1998	75	25
2010	91	9

Panel B	
Species	Rank
Sandlance	1
Flounders CMB	2
Cod	3
Longhorn sculpin	4
Silver hake	5
Capelin	6
Atlantic herring	7
Redfish	8
Ocean pout	9
Haddock	10
Pollock	11
Urophycis	12
Squid CMB	13
Fourbeard rockling	14

have been very low compared with the 1970s and 1980s. A rough index of exploitation for cod (the ratio of the annual commercial landings to the RV survey biomass) indicates that fishing mortality has dropped to negligible levels since the early 1990s (Fig. S3b). This trend in fishing exploitation rate for cod is considered representative of that for many of the groundfish species on the ESS (i.e. those species impacted by the fishing moratorium that started in 1993). Fishing effort on small pelagic species in ESS is not well documented, but is considered to be low. The landings from the ESS coastal herring fisheries have been low (DFO, 2015).

Lobster fishing effort fluctuated from 1992 to 2006 then increased by about 20% by 2010 (Fig. 3b). Annual landings peaked at more than 4700 t in the late 1980s and declined to 2000–3000 t from the late 1990s to early 2000s (Fig. 4b). Between 2005 and 2008, landings increased to more than 7000 t and have stayed at this level since then. Most of this increase occurred in the area of Chedabucto Bay. Unlike lobster, shrimp and snow crab are managed by annual quotas. Eastern Scotian Shelf shrimp quotas and landings increased substantially from 1990 (104 t) to 2000 (5436 t), and since then have fluctuated in the range of 3000–4500 t (Fig. 4b). Effort has declined from the high levels of the mid- to late 1990s. Snow crab landings and quotas have been on an upward trajectory since 1990 with the exception of the low period from 2005 to 2008. Snow crab landings have tracked fishing effort since 1998 (Figs. 3b and 4b).

In summary, the top-down driver of fishing effort on groundfish increased substantially following the extension of jurisdiction to 200 miles in 1977, but has been reduced to very low levels since 1993. The trends in effort on three macro-invertebrate species have been more complex, with relatively higher levels during the past two decades compared to the earlier period.

2.2. Top-down factors: grey seals

Three grey seal herds spend part of the year on the ESS. The Sable Island herd has been doubling in abundance about every seven years during the past several decades, whilst the Gulf of St. Lawrence and coastal Nova Scotian herds are increasing at lower rates (Fig. 3c and database S1) (DFO, 2014). Although there is controversy about the diet composition of marine mammals (see Rosen and Tollit, 2012 for a recent perspective), there is general agreement in the literature that the annual fish consumption in ESS by grey seals is about 1.5–2 tonnes per individual (Mohn and Bowen, 1996; Trzcinski et al., 2006; Smith et al., 2015). By the mid-1980s, annual fish consumption by grey seals within ESS exceeded commercial fish landings (Fig. 4a). The 2010 estimate

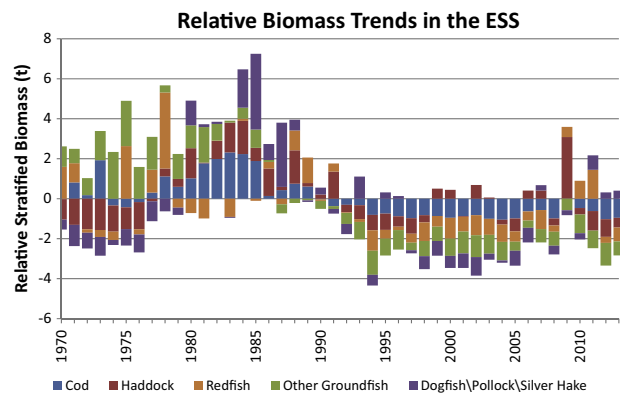


Fig. 5. Groundfish biomass trends (1970–2013) for 18 species in ESS. No corrections have been made for temporal catchability differences between species, or due to gear changes in the trawl survey.

of fish consumption by grey seals is about seven times higher than the pre-moratorium total groundfish and small pelagic species annual landings.

Table 4

Ranking of the “ratio” metric and “log ratio” from the “tilt” analysis for the 18 large bodied groundfish species. Species ranking or “tilt” based on the ratio of the biomass in the most recent 10 years of survey with the first 10 years. Classification of “risers” with ratio greater than 1.0, “fast droppers” with ratio less than 0.4 and “slow droppers” as ratios between 0.4 and 1.0.

Rank	Species	Ratio	Log (ratio)	Category
1	Greenland halibut	19.12	2.95	Risers
3	Red hake	2.84	1.04	Risers
5	Halibut	2.5	0.92	Risers
6	Haddock	2.36	0.86	Risers
8	Witch flounder	0.68	-0.38	Slow droppers
9	Redfish	0.68	-0.38	Slow droppers
10	Winter flounder	0.6	-0.51	Slow droppers
11	White hake	0.52	-0.65	Slow droppers
12	Yellowtail flounder	0.44	-0.81	Slow droppers
13	American plaice	0.4	-0.91	Slow droppers
14	Longfin hake	0.32	-1.13	Fast droppers
15	Cod	0.31	-1.18	Fast droppers
16	Thorny skate	0.18	-1.71	Fast droppers
17	Winter skate	0.09	-2.43	Fast droppers
18	Cusk	0.01	-4.66	Fast droppers
2	Dogfish	7.22	1.98	Semi-pelagic
4	Silver hake	2.56	0.94	Semi-pelagic
7	Pollock	2.03	0.71	Semi-pelagic

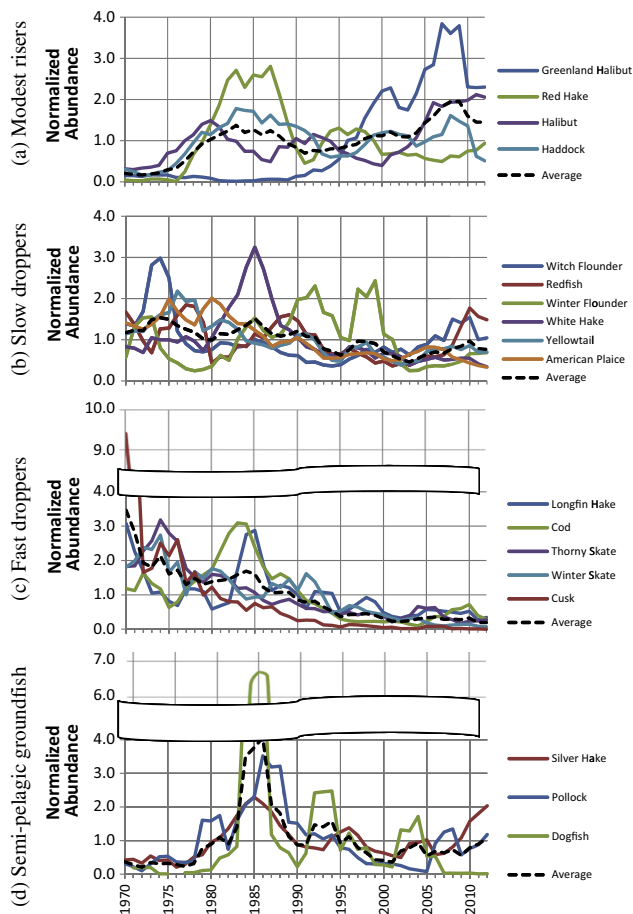


Fig. 6. Trends in abundance of four clusters of groundfish species. (a) The first group (the “modest risers”) has a “tilt” ratio greater than 1. (b) The second group (the “slow droppers”) has a ratio between 0.68 and 0.40. (c) The third group (the “fast droppers”) has a ratio from 0.32 and 0.01. (d) The semi-pelagic groundfish species from 1983 to 2012.

The diet information, as derived from the scat collected on Sable Island from 1991 to 2010 (Table 3a and b) provides estimates of the relative importance of different species (and species groups). There is considerable short-term variability in the proportion of the diet represented by the various small pelagic and groundfish species, but there is no obvious trend in estimated species composition in the diet during the two decades of scat sampling on Sable Island. The single year recent estimate in 2010 indicates a very high proportion of the diet being comprised of small pelagic species. For the small pelagic species in the diet (Table 3b), the ranking (highest to lowest) is: sandlance, capelin, herring and squid (all species). For groundfish species the ranking (highest to lowest) is: flounder (all species), cod, sculpin, silver hake, redfish, ocean pout, haddock, pollock, hake (all species), and forbear rockling.

Diets of grey seals in ESS have also been estimated based on the fatty acid composition of the blubber (Quantitative Fatty Acid Signature Analysis, QFASA, Iverson et al., 2004). However, a number of issues have been raised for this methodology (e.g. Rosen and Tollit, 2012). Recent sampling of grey seals foraging on cod aggregations indicate that cod can be the dominant component of the diet (up to 64–80% by weight for males and 35–54% for females) with a high proportion being large cod (Hammill et al., 2014). In conclusion, whilst there is general agreement on the abundance levels of the three grey seal herds (Fig. 3c) and their annual fish consumption in ESS (Fig. 4a), there is considerable uncertainty with respect to the diet composition.

2.3. Large-bodied benthic fishes

There was a rapid decline in demersal fish biomass in the late 1980s and early 1990s, including a sharp decline in the biomass of Atlantic cod (Fig. 5). There are however species specific trends (Table 4, Figs. 6, S1 and S2). Several species (Greenland halibut, red hake, halibut and haddock) increased in abundance during the four decades (the “risers” in Fig. 6). Several other species experienced a slow and fairly steady biomass decline from high values in the 1970s to low values in the 2000s (i.e. the “slow droppers”: redfish, white hake, American plaice, witch flounder, winter flounder, and yellowtail flounder). A third category (the “fast droppers”) includes cod, longfin hake, thorny skate, winter skate and cusk. Due to gear changes in survey in 1982 (see text S1) the trends in abundance of the semi-pelagic groundfish species (silver hake, pollock and dogfish) are not considered to be representative (Figs. 6d and S1). These species-specific trends in biomass suggest complicated ecosystem dynamics. Rothschild and Jiao (2012) and Halliday and Pinhorn (2009), both of which cover the broader area of the northwest Atlantic, also report diverse temporal trajectories of groundfish within ESS.

Overfishing was an important cause of the collapse of cod in the late 1980s and early 1990s (Angel et al., 1994), and was a factor in the steady decline in some other demersal fishes from the 1970s to the 1990s (e.g. Swain et al., 2013). However, other factors must be responsible for the lack of recovery or continued decline in these fishes following reductions in fishing effort to negligible levels in 1993 (Fig. 3a). Frank et al. (2011) attributed this lack of recovery to competition with and/or predation on early life stages of demersal fishes by pelagic fishes. However, productivity of early life stages of demersal fishes was high in the 1990s and 2000s (e.g. Swain and Mohn, 2012; Swain et al., 2013), indicating that some other processes were involved.

The main factor preventing the recovery of ESS cod appears to be the unusually high natural mortality (M) of adults in recent decades (O’Boyle and Sinclair, 2012; Swain and Mohn, 2012). Mohn and Rowe (2011) and Swain and Mohn (2012), estimate that M for adult cod increased to very high levels (near 1, or about 63% annually) in the mid-1990s to the mid-2000s, then declining to a

value near 0.4 (33% annually). However the recent estimates of M were strongly influenced by the high survey index in 2009 (Fig. 5). Since then, the survey index has declined, returning to extremely low levels in 2012 and 2013 (Fig. 5). To obtain more recent estimates of M we updated the analysis of Swain and Mohn (2012)

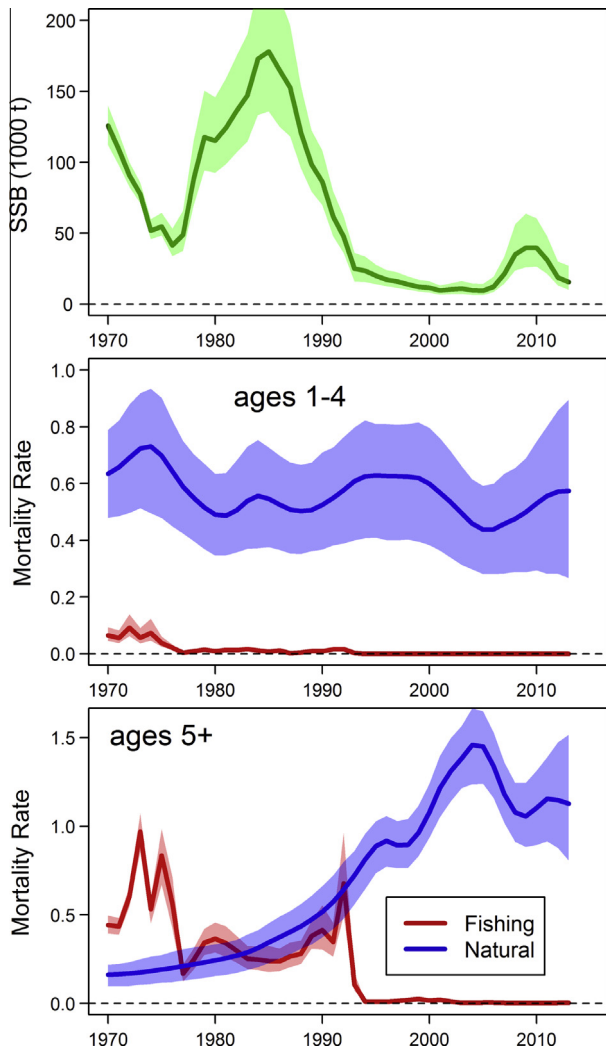


Fig. 7. Annual estimates the instantaneous rates of fishing and natural mortality of 4Vsw cod (1970–2013), as well as the trends in spawning stock biomass (SSB). Lines show the estimates and shading their 95% confidence intervals.

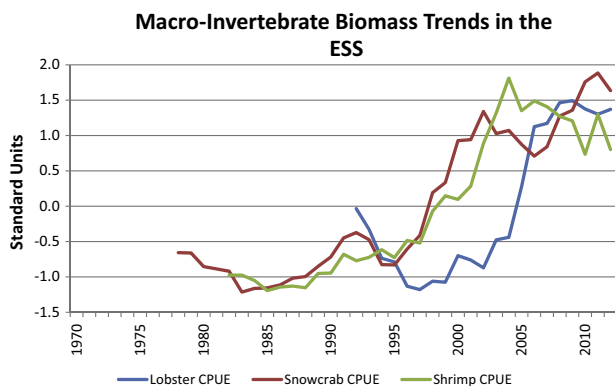


Fig. 8. Macro-invertebrate (shrimp, crab, and lobster) biomass trends in ESS (based on commercial catch rates as a proxy).

with the recent data. The analysis is a virtual population analysis, the standard assessment model used for cod in Atlantic Canada. Model inputs are annual fishery catches at ages 1–12+ (12 years and older), and survey catch rates at ages 1–10 years. In addition to estimating abundance-at-age and catchability-at-age to the survey, the model used here estimates time trends in the instantaneous rate of natural mortality (M) for two age groups, cod ages 1–4 years and cod 5 years and older (5+). Modelling details are provided in text S2.

Based on the updated analysis, M of adults (5+) cod increased throughout the 1970s, 1980s and 1990s, rising gradually to levels above 0.8 since 1995 and above 1.0 (i.e. above 63% annually) since 2007 (Fig. 7). Unlike older cod, no trend in M is evident for cod aged 1–4 years. Contrary to the suggestion by Frank et al. (2011), there is no indication that cod are on the path to recovery (Figs. 5, 6 and 7). Estimated adult biomass did increase in the late 2000s due to recruitment of the relatively strong 2004 year-class. However, due to high M of age 5+ cod, this year-class was rapidly lost for the population after reaching the age of 5 years and adult biomass declined, approaching the record low levels of the early 2000s by 2013 (Figs. 5 and 7).

Natural mortality is also estimated to have increased for silver hake (Stone et al., 2013), and large individuals of thorny, winter and smooth skates on the ESS (Swain et al., 2013). Population models that estimate changes in M have not been developed for other species in ESS; but in the contiguous southern Gulf of St. Lawrence ecosystem natural mortality appears to be at elevated levels among large individuals of most large-bodied demersal fishes (Swain and Benoit, 2015).

In summary, the analysis and interpretation of the temporal patterns of the aggregate biomass of the 18 large bodied benthic fishes (Fig. S1) masks a diversity of species specific trends (Figs. S2 and 6a–d). There is considerable evidence that overfishing in the 1980s following the extension of jurisdiction in 1977, as well as increases in natural mortality due to grey seal predation, generated rapid declines in the abundance of several groundfish species within ESS. Although a few species have shown recent increases of abundance (Fig. 6a), there is no evidence of a sustained recovery of cod in the past decade (Figs. 5, 6c and 7). The observed groundfish trends in abundance (and natural mortality of several species) are inconsistent with the predictions of both the *fishery induced trophic cascade* and the *climate variability* hypotheses.

2.4. Benthic macro-invertebrates

The decadal trends in abundance of snow crab, shrimp, and lobster to the end of 2012 are shown in Fig. 8. These fishery-based data (i.e. catch per unit of effort) are the longest time series available and are correlated with other abundance measures where the time series overlap. The trends for shrimp and snow crab are similar: abundance increased beginning in the mid-1990s, and peaked in the early 2000s with a plateau since then. The lobster trend (although shorter in coverage) is different: relatively constant abundance levels until the early 2000s, followed by a sharp increase for a few years and a plateau since 2006.

Snow crab and shrimp have, on aggregate, a negative relationship with the total groundfish abundance estimates (comparison of Figs. 5 and 8). Several studies have addressed the issue of predatory control of the abundance of these three macro-invertebrates in the North Atlantic. While not universal, the consensus is that predatory control is important for shrimp. Worm and Myers (2003) conducted a meta-analysis of cod–shrimp interactions in nine areas in the North Atlantic and found a strong negative correlation between shrimp and cod abundances in 8 areas, with no correlation between shrimp and temperature. Wieland and Siegfstad (2012) reported that off West Greenland, cod and shrimp biomass

were negatively linked until the early 1990s when cod declined. During 1993–2011 bottom temperature and Greenland halibut (predator) were most important in their model. [Jonsson et al. \(2012\)](#) reported that in two locations off Iceland, cod had an adverse effect on shrimp biomass. They note that shrimp are also regulated by other factors such as temperature.

Evidence for predatory control of snow crab abundance by cod is more mixed. A meta-analysis of 10 regions with multiple lags found that snow crab abundance was negatively correlated with temperature and with cod abundance, and concluded that snow crab is influenced by temperature during early post-settlement and by cod during the years approaching recruitment to the fishery ([Boudreau et al., 2011](#)). Another analysis of three ecosystems outside of the ESS found no evidence for a consistent effect of gadoid biomass on subsequent snow crab recruitment, arguing for the primacy of water temperature in determining snow crab recruitment success ([Marcello et al., 2012](#)). [Windle et al. \(2012\)](#) concluded that for the Newfoundland–Labrador Shelf snow crab abundance was best predicted by environmental variables, while shrimp was influenced both by the environment and predator abundance. [Choi et al. \(2013\)](#) reviewed several potential population control factors for ESS snow crab including environment, predation, resource limitation, competition, disease and human influence. They do not give priority to any one factor, but note that predatory groundfish may have been an important regulating factor controlling the recruitment of snow crab prior to the 1990s.

The substantial increase in lobster abundance in the Gulf of Maine has been attributed to a release from predation ([Steneck, 2006](#); [Boudreau and Worm, 2010](#); [Steneck and Wahle, 2013](#)) based on the negative correlation between the abundances of lobster and groundfish. There is also direct evidence for groundfish predation on lobster in the Gulf of Maine (cited in [Steneck and Wahle, 2013](#)). The effect of climate is acknowledged to have affected lobster distribution and disease in the Gulf of Maine. In contrast to the Gulf of Maine, stomach content analysis of fish in the southern Gulf of St. Lawrence (also adjacent to ESS) indicates commercially fished groundfish are not important predators of lobster ([Hanson, 2009](#)). Instead, non-commercial species such as shorthorn sculpin, cunner and thorny skate were found to be the most important predators.

Overall the observed trends in abundance of lobster, snow crab and shrimp are partially consistent with the expectations of the *fishery induced trophic cascade* hypothesis. However, under this hypothesis it is predicted that *runaway consumption dynamics* of small pelagic species and the associated predicted recovery of groundfish species would have generated a decline in the abundance of macro-invertebrates since 2005, which is not observed. A gradual reduction in plankton productivity, predicted by the *climate variability* hypothesis, is also not consistent with the multi-decadal increase in macro-invertebrate abundance. The differences in the temporal patterns amongst the commercially important macro-invertebrate species (as well as the relevant literature on the interpretation of their population dynamics) suggest that species specific interactions are important.

2.5. Small pelagic planktivorous fish species

A key challenge in the evaluation of the hypotheses is the degree to which there was a small pelagic outburst within ESS beginning in the late 1980s/early 1990s (as described by [Frank et al., 2005, 2011, 2013a](#)). Trends in ESS groundfish estimates of abundance for three small pelagic species (herring, capelin, sandlance) are characterized by different patterns ([Fig. 9](#)). Survey catches of herring increased in the mid-1980s, and have remained relatively high (although variable) since then. Sandlance catches in the groundfish survey increased in the late 1990s, followed by a gradual decline. Capelin catches by the survey have been at low

levels of abundance except for a few years in the mid-1990s. However, the groundfish bottom-trawl survey does not sample small pelagic species efficiently, as these species are more frequently distributed within the water column rather than close to the sea floor. Furthermore, the changes in the trawl survey gear described in the groundfish methods section ([Text S1](#)) imply a significant change in catchability of small pelagic species to the RV survey in 1982. [McQuinn \(2009\)](#) and [Frank et al. \(2013a\)](#) provide contrasting perspectives on these trends, with the former concluding that changes in the vertical distribution of herring within the water column, which imply a temporal change in survey catchability (q) of herring, are responsible for these trends. In other words, the small pelagic outburst is a sampling artifact.

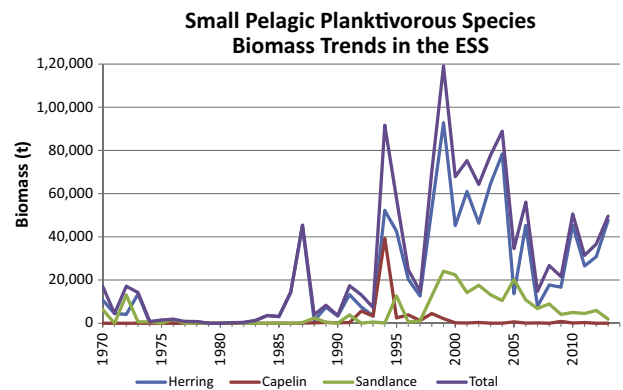


Fig. 9. Small pelagic planktivorous species (herring, capelin, sandlance) biomass trends in ESS based on groundfish trawl survey estimates (1970–2013) of abundance (with no adjustments made for changes in catchability).

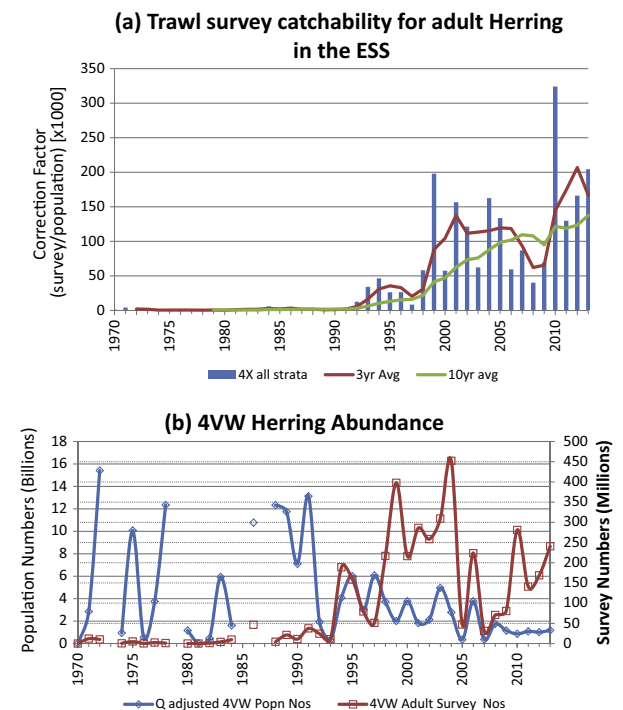


Fig. 10. (a) Trawl survey catchability (q) estimates for adult herring in 4X (based on total survey numbers for herring ≥ 23 cm) and a smoothed series using 3 and 10 year averages. (b) Herring (4VW) abundance estimates from the July trawl survey (stratified total numbers) and Q-adjusted 4VW population numbers. Population estimates larger than 10 billion (larger than 4X historical maximum) were removed for 4VW in 1970, 1973, 1985 and 1989.

An analytical assessment of ESS herring is not available to directly examine whether a temporal change in survey q has occurred. However, both an analytical assessment of herring abundance as well as groundfish survey estimates are available for the herring populations in the western Scotian Shelf (4X in Fig. 2). These data sets and analyses allow examination of trends in the herring groundfish survey q within 4X, which are considered to be applicable to ESS (see text S3). Trends in survey q were estimated by dividing the survey abundance index for adult herring (equal and greater than 23 cm) by the VPA estimate of age 3+ abundance. Results indicate that there was a dramatic increase in q starting in the early 1990s with higher and relatively stable estimates since 2000 (Fig. 10a). These q trends in WSS are consistent with herring being increasingly distributed closer to the bottom over the 3 decades, and thus more catchable by the bottom trawl survey with time. This behavioural change is confirmed by observations from the herring acoustic surveys which have been conducted in collaboration with the herring industry since 1997, during which backscatter estimates indicate that herring have been closer to the bottom since the early 2000s (Power et al., 2006). Furthermore the trends in survey indices of adult abundance and mean length are very similar between 4X and 4VW (Fig. 2 in text S3). This also supports the inference that trends in the survey catchability (using the same vessel) are similar for the two areas.

With the trends in catchability of the trawl survey (Fig. 10a) taken into consideration, there is no evidence of an increase in abundance of herring within ESS during the early 1990s (Fig. 10b). Rather the pattern is reversed, with herring abundance declining starting the 1990s with no subsequent recovery. It is inferred that both the survey gear change in 1982, and subsequently behavioural changes of herring within ESS beginning in the late 1980s/early 1990s, have caused the herring to become increasingly available to the survey gear. It is of interest to speculate on the processes that would cause herring to be distributed closer to the bottom since the early 1990s. This is the time period during which the Sable Island grey seal herd dramatically increased in abundance (Fig. 3c). It is not clear how much influence this may have had within the western Scotian Shelf (4X), but within ESS (the centre of distribution of this herd) it is to be expected that herring (a major prey item of grey seals) would attempt to avoid this predator. An avoidance behaviour of this type would be consistent with the forage-arena functional relationship defined by Walters and Martell (2004).

It is not possible to estimate survey catchability trends for capelin and sand lance because there are no independent estimates of abundance. However, the uncorrected trends in Fig. 9 are informative. The observations of capelin in ESS (whatever their actual biomass) were short-lived and occurred well after the survey gear change of 1982. As such, the trawl survey may have been capturing a distributional change for this species. Frank et al. (1996) conclude that the increase in capelin on the ESS was due to a relatively short

term decrease in bottom water temperatures. The Scotian Shelf is the southern limit of distribution of capelin, and they interpret the low bottom temperatures as leading to the expansion of the range of populations on the Grand Banks off of Newfoundland and/or the northern Gulf of St. Lawrence. Horseman and Shackell (2009) illustrate this short term spatial extension and subsequent contraction of range for capelin. The sand lance decadal trends are uncertain.

Observations of the diet of grey seals cover the 1991–1998 period well, but there are few samples thereafter (only for 2010). Nevertheless, the proportions in the diet (Table 3a) do not suggest a higher than normal availability of small pelagic species during the period of the proposed outbreak of small pelagic species (1992–2004). Bowen et al. (1993) provide additional observations on the groundfish/pelagic ratios in the diet for the 1988–90 years. A different method was used (i.e. analyses of stomach contents rather than scat samples). For the inshore samples (mostly from the ESS coastline) herring contributed 65.8% and 9% by weight of the stomach content for summer and winter, respectively. For the offshore (Sable Island) the estimates were 32.7% and 75.1% of sand lance for summer and winter, respectively. The diet observations for both the scat and the stomach contents of grey seals do not reflect the conclusion that there was a major increase of small pelagic biomass during 1992–2004 (i.e. there were equally high proportions of small pelagic species in the diet of grey seals prior to and after the early 1990s).

Estimates of larval abundance from ichthyoplankton surveys have also been used to provide an indication of changes in adult biomass for small pelagic fishes, based on the assumption that high larval abundance reflects high spawner biomass (Frank et al., 2013a). To evaluate reliability of this approach, we compare trawl survey estimates of spawner biomass and ichthyoplankton survey estimates of larval abundance of four groundfish species present in the ichthyoplankton data and well sampled as adults by the groundfish trawl survey (Text S4 and Table 5). There are three sources of ichthyoplankton data for ESS: the SSIP surveys conducted in 1978–1982, OPEN surveys conducted in 1991–1992, and the collaborative Dalhousie University/Department of Fisheries and oceans (Dal/DFO) surveys conducted in 1997–1998. Data were extracted from the SSIP database to match as closely as possible the areas covered by the OPEN and Dal/DFO surveys. There was no correspondence between the differences in spawner abundance in the groundfish trawl survey and the differences in the larval abundance estimates between the SSIP and OPEN surveys (Table 5). A similar lack of correspondence was evident using the Dal/DFO survey. Thus, temporal changes in larval abundance in the three ichthyoplankton surveys do not appear to be reliable indicators of changes in spawner biomass.

A potential additional metric of population abundance used by Frank et al. (2013a) is the area occupied based on the presence/absence data from the groundfish trawl survey observations. However, since there have been major changes in catchability of herring

Table 5

Comparison of larval abundance of four groundfish species (#/100 m³) sampled in the Western Bank area of ESS during the SSIP (1978–1982) and OPEN (1991–1992) plankton studies.

Time period	Spawning stock biomass from trawl surveys		SSIP (Western Bank and slope area)	OPEN shelf station	OPEN bank station
	78/82	91/92			
<i>Species</i>					
Atlantic cod	49.92	18.61	4.1	77	538
Yellowtail flounder	7.89	6.95	3.97	14	41
Witch flounder	1.3	0.83	1.99	12	3
Redfish	28.51	30.45	1.2	13	40

in the groundfish trawl survey (Fig. 10a), the analysis is biased and thus not meaningful as a measure of abundance trends. The trend in “area occupied” within ESS during the trawl surveys is more likely to be due to increases in catchability resulting from behavioural changes, than to increases in abundance. By inference, an analysis of the trends in area occupied by sand lance within the groundfish survey is also likely to be flawed.

Changes in physiological condition of pelagic fishes have also been presented as evidence in support of a small pelagics outburst and a subsequent decline due to food limitation (Frank et al., 2011). Weight at a given length is often used as a measure of fish condition. However Frank et al. (2011) used an annual mean individual weight in the trawl survey catch as their index of physiological condition. This index can be strongly affected by changes in length and age composition of the population. Mean length of ESS herring progressively decreased in the survey catches from 1970 to 2014 (Fig. S2-e in text S3). This reflects an increase in abundance of small adult herring (23–30 cm) relative to the abundance of large adults (equal to and larger than 30 cm) (Fig. S2-c in text S3). Thus the observed changes in the index reflect a shift in age composition towards younger fish, with no evidence of a decline in physiological condition of individual fish.

In summary, the evidence for a major increase in small pelagic species during the 1992–2005 years (a key component of the fishery-induced trophic cascade hypothesis) is questionable given: (1) the decline in the trawl survey estimates of herring abundance starting in the early 1990s (Fig. 10b), (2) the lack of trends in the proportion of small pelagic species in grey seal diets, (3) the analyses of the larval fish surveys that compare similar sampling areas and seasons in comparison with groundfish SSB estimates (Table 5), (4) the estimated biases (generated by the catchability changes in the groundfish survey) in the analysis of the geographic area occupied by herring in the groundfish trawl survey, and (5) the sporadic range changes of capelin. Furthermore, the gradual decline in “relative weights” of herring in the groundfish trawls survey (Fig. S4), in parallel with the decline in herring abundance (Fig. 10b), during a period of presumed low fishing mortality, suggests an increase in natural mortality rather than a recent food-limited decline in condition.

To the degree that decadal patterns in abundance of the three small pelagic species can be estimated it is likely that different processes drive their population dynamics. Capelin abundance appears to be driven by bottom temperature changes (Frank et al., 1996). For sand lance, Nelson and Ross (1991) in a review of its biology and population changes in the Gulf of Maine to the Middle Atlantic Bight, indicate that interspecific interactions between mackerel and sand lance may influence the latter's abundance fluctuations (also citing Bowman et al., 1984). Finally, the decline in the herring abundance since the early 1990s, in the absence of much of a fishery, may be due to increasing grey seal predation. However, without a stock assessment for this geographic area, it is not possible to estimate trends in natural mortality directly. The decline in average weight of herring in the trawl survey (Fig. S4) is consistent with a loss of older fish due to an increasing trend in natural mortality. The pattern could also be generated by improved recruitment, but this does not appear to be the case. The herring recruitment trend within an overlapping area (4WX) indicates that recruitment declined sharply in the mid-1980s and has not recovered.

2.6. Synthesis of upper and middle trophic level trends

The groundfish and herring abundance trends are similar: relatively high levels of abundance/biomass until the early 1990s, followed by sharp declines without any sustained recovery (Fig. 11). In contrast, snow crab and shrimp abundance/biomass levels have

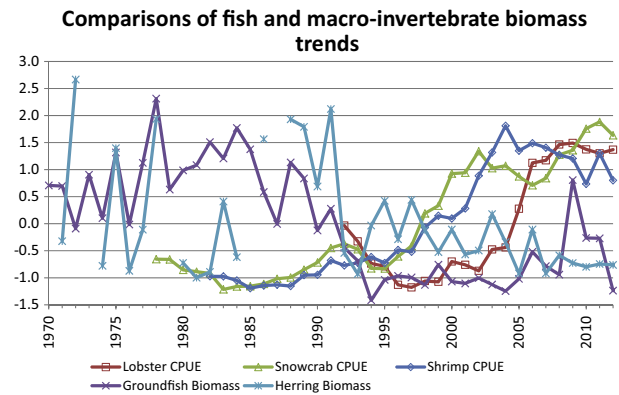


Fig. 11. Comparisons of fish and macro-invertebrate biomass trends: aggregate biomass of 15 groundfish species; lobster, snow crab, and shrimp CPUE; and “q” adjusted herring.

increased since the early 1990s. Lobster trends lag the crab/shrimp increases, but have been high since the mid-2000s (Fig. 11).

2.7. Lower trophic levels

Due to the lack of continuous coverage of ESS plankton using a similar sampling methodology it is difficult to elucidate the temporal trends in plankton abundance (see texts S1 and S5 for a summary of the data sources and selection of zooplankton species considered). The general approach taken here is similar to that of Frank et al. (2005, 2011), in that all the available plankton data from the diverse surveys are “stitched together” in an attempt to illustrate the temporal trends. The longest time series on plankton are derived from the Continuous Plankton Recorder (CPR) program (late 1960s to the present), but with major gaps in the time series. The gaps are filled to a certain degree by comparing the 1978–1982 Scotian Shelf Ichthyoplankton program (SSIP) with the 1999–2004 Atlantic Zone Monitoring program (AZMP), both surveys having used similar sampling gear. The challenge is to ensure that the extractions from the diverse data sets covering different time periods are estimating similar phenomena (i.e. the plankton estimates of abundance and/or biomass from different decades are derived from similar seasons and geographic areas).

2.8. Lower trophic levels: zooplankton

For the selected years with sufficient CPR monthly sampling (text S1 and Table S1), the estimates of annual abundance of the large and small-bodied zooplankton species are shown in Figs. 12a, S5 and S6. Prior to 1992, only 1966, 1969, and 1970 had enough monthly observations to meet our criteria for inclusion. The large-bodied zooplankton (based on the CPR data) show little difference in abundance between the late 1960s/1970 and the 1992/mid-2000s period. There has however been a sharp decline in recent years (Fig. 12a). In contrast there has been a gradual decline in the abundance of small-bodied zooplankton since the early 1990s (Fig. 12a).

To fill the gap for the missing CPR years the average of the SSIP abundance estimates for *Calanus finmarchicus*, *Calanus glacialis*, and *Calanus hyperboreus* (1978–1982) are compared with the AZMP abundance estimates of similar species categories (1999–2004). Given that the SSIP and AZMP cruises cover different seasons, we compared just the spring and autumn cruises for the two time periods (Text S6). In contrast to the conclusions of Frank et al. (2005, 2011), our analysis indicates that *Calanus* abundance levels were similar during both the spring and fall sampling periods in the 1970s/80s and 1990s/early 2000s (Fig. 12b).

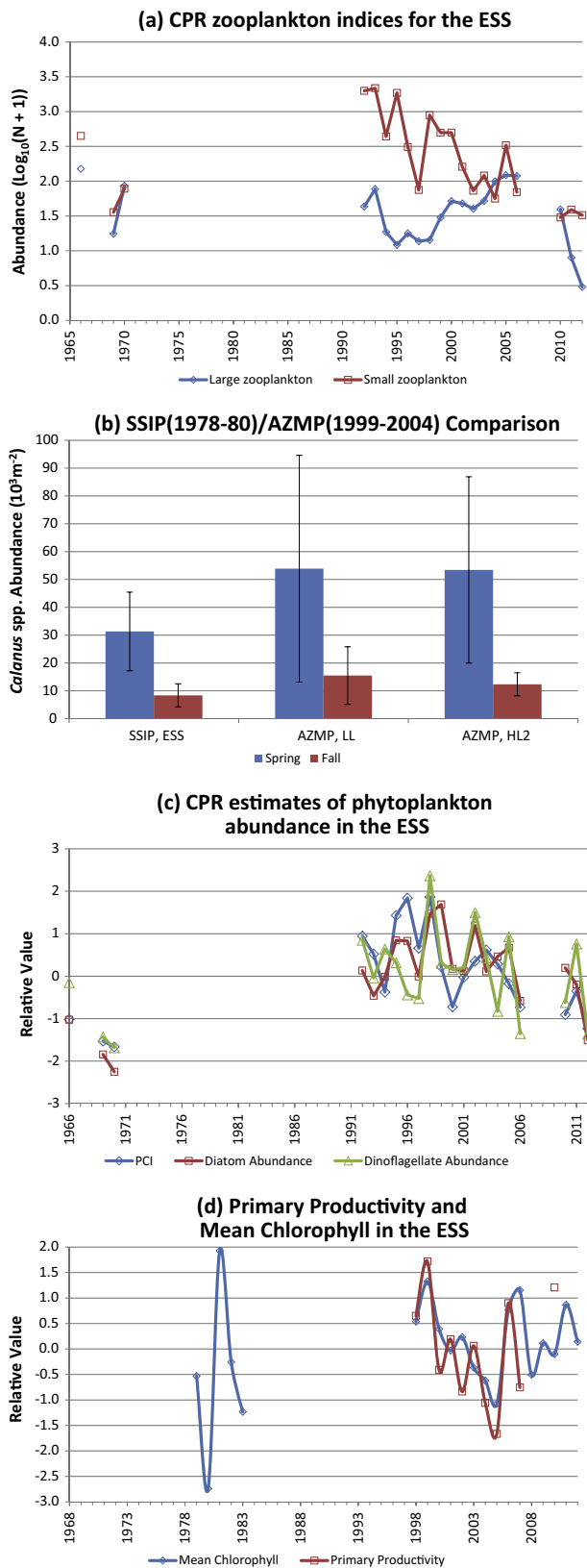


Fig. 12. Plankton abundance trends: (a) large and small aggregate estimates for CPR zooplankton indices for ESS from 1966 to 2012; (b) comparison of SSIP and AZMP estimates of zooplankton abundance; (c) CPR estimates of phytoplankton abundance in ESS from 1966 to 2012; and (d) surface layer chlorophyll and primary production in ESS during the 1970–2012 period (from OCR).

There is seasonal coverage of zooplankton abundance at a fixed station off Halifax (Fig. 2), starting in 1999. Although this inshore sampling station is at the periphery of the ESS, the observations are useful to consider due to the high frequency of sampling. The monthly normalized estimates of *Calanus finmarchicus* and zooplankton biomass are shown in Fig. S7. Based on the observations at this station there has been a slight decline in the estimates of zooplankton abundance during the decade and a half of sampling (i.e. from 1999 to present). The AZMP zooplankton abundance trends from the Louisbourg and Halifax sections, which cross ESS (see Fig. 2), as well as the summer groundfish RV survey plankton summaries of zooplankton abundance in 4VW, are shown in Fig. S8. Based on the AZMP data for the sections and the fixed station, as well as the groundfish RV survey plankton data, large-bodied zooplankton abundance in ESS has been relatively constant since the late 1990s. The CPR decline in large-bodied zooplankton since 2010 is not consistent with the other survey trends.

In summary, it is difficult to develop a coherent picture of decadal trends (late 1960s to the present) in both the large and small-bodied categories of zooplankton; due to (1) the missing months and years for the CPR estimates, and (2) the complexity of comparing the discontinuous CPR estimates with the SSIP, AZMP and groundfish RV survey plankton data sets (each of which have different sampling designs). In contrast to the conclusions of Frank et al. (2005), when only comparable seasons are used in the analysis of respectively the SSIP (1978–1982) and AZMP/groundfish RV plankton surveys (late 1990s/early 2000s), the abundance of large bodied zooplankton are similar in both time periods. Overall (based on the aggregate zooplankton evidence: Figs. 12a, b, S5, S7 and S8) the large-bodied zooplankton abundance estimates are relatively constant from the late 1960s to the present (with the exception of the recent declines shown in the CPR data). If there is any trend it is slightly downwards. The small-bodied zooplankton trends are downwards during the past two decades, with no obvious trends for the earlier period.

2.9. Lower trophic levels: phytoplankton

The CPR data set also provides the only systematic direct comparison that can be made between Scotian Shelf phytoplankton in the late 1960s and recent (post 1990s) period. In this regard, the differences are striking: the average values of the phytoplankton colour index (PCI) are all less than 0.6 units in the early period, and except for 2012 are all greater than 0.6 units in the recent period (Fig. 12c). The post 1970s PCI increase is a widespread phenomenon, evident in many regions: some distant from ESS, such as the central northeast Atlantic and the North Sea (Reid et al., 1998; Raitos et al., 2005); some closer to ESS, such as the Newfoundland Shelf (Head and Sameoto, 2007; Head and Pepin, 2010); and some very close indeed to ESS, such as the WSS, Gulf of Maine/Georges Bank, and St. Pierre Bank (Sameoto, 2001).

Other than the 1966/1969/1970 low estimates of phytoplankton abundance there has been a gradual but slight decline in the CPR phytoplankton indices since the late-1990s (as is the case for the small-bodied zooplankton). Based on the satellite estimates, although the interannual variability in surface layer chlorophyll concentrations is high in the early 1980s, there is no temporal trend (Fig. 12d). The primary production estimates also illustrate considerable interannual variability, with some decline until 2005, followed by a return to the levels estimated for the late 1990s (Fig. 12d). The AZMP fixed station sampling off Halifax shows no trend in average annual chlorophyll concentrations since 1999 (Fig. S9). Based on the AZMP data Li (2014) provides a

detailed analysis of the trends in chlorophyll concentration (as one of several phytoplankton indicators) within ESS for 1997–2013. Over the Scotian Shelf as a whole the spatial–temporal patterns of chlorophyll concentrations are complex with local variations. The trends are generally positive in the spring and negative in the autumn. The counteracting seasonal trends result in a near-neutral bi-seasonal average trend.

As was done for the large-bodied zooplankton, to fill the long gap in the CPR time series the phytoplankton biomass levels in respectively the late 1970s/early 1980s (SSIP) are compared with the 1995–2004 period (AZMP). The chlorophyll data (1979–1982) from the SSIP database for all stations east of the Halifax Line provides an average value of $1.31 \pm 2.63 \text{ mg m}^{-3}$ for the 0–50 m depth layer (Table S3). This analysis of SSIP data allowed us to construct the monthly climatology for chlorophyll in the 4-year period from 1979 to 1982 for the 0–100 m depth layer (Table 6). The climatological average for April was $5.86 \pm 6.33 \text{ mg m}^{-3}$, and that for September was $0.42 \pm 0.33 \text{ mg m}^{-3}$. Within statistical confidence, these seasonal averages overlap the 1997–2013 AZMP chlorophyll averages for spring and fall on the Louisbourg Line and the Halifax Line (Li, 2014). Thus there is no evidence that chlorophyll concentrations in the ESS were higher on average during the AZMP period (1997–2004) compared to the SSIP period (1979–1982). This conclusion is also supported by satellite observations of ocean colour (Fig. 12d).

With the exception of the low phytoplankton abundance and biomass estimates in the late 1960s, the aggregate data leads to the conclusion that from the late 1970s to the present the phytoplankton trends have been relatively constant (with some indication of a slight decline). Although the CPR trends are generally downwards from the early 1990s to the present, the satellite derived estimates show little evidence of trends. There are seasonal and geographic differences in the decadal patterns estimated for the Halifax and Louisbourg lines, but overall there is a near-neutral average trend based on the AZMP surveys (1997–2013). The monthly sampling at the Halifax Station (1999 to present) shows no upward or downward trend. Also the SSIP/AZMP comparison the late 1970s/early 1980s with the late 1990s/early 2000s (i.e. the approach to filling the major gap in the CPR sampling) supports the conclusion of relative constancy.

On a more conceptual level, the plankton trophic level dynamics are based (here and in other interpretations) on the evidence of metazoan zooplankton (large or small) grazing on phytoplankton measured as “green stuff” (PCI). However, it is well-accepted that, on a global basis, protistan zooplankton (i.e. microzooplankton such as ciliates and heterotrophic flagellates) account for the major portion (~60%) of primary production grazed on a daily basis in coastal oceans (Calbet and Landry, 2004). The “green stuff” is the

bulk mass of phytoplankton, but this bulk is partitioned by size selective grazing with metazoans consuming large cells (microphytoplankton consisting mainly of diatoms and dinoflagellates) and protozoans consuming small cells (a polyphyletic mix of nanophytoplankters and picophytoplankters). In other words, a trophic level interaction based on metazoan zooplankton should be based the evidence of microphytoplankton, not bulk “green stuff”. In this regard, on the AZMP Louisbourg Line within ESS, there has been an almost 3-fold decrease in microphytoplankton biomass (measured from diagnostic pigments) in the fall season from 1998 to 2013 (Li, 2014). Li (2014) proposes a bottom-up explanation that considers changes in stratification, nutrients, bulk phytoplankton biomass, and phytoplankton abundance in size classes.

Overall the phytoplankton abundance estimates indicate low levels for the late 1960s, with slight declines from the late 1970s to the present (Fig. 12c and d). Also the AZMP data infers large declines in the microphytoplankton. The plankton evidence is not consistent with the predictions of the *fishery-induced trophic cascade* hypothesis, but does provide some support for the *climate variability* hypothesis.

2.10. Bottom-up factors: nutrients and stratification

Yeats et al. (2010), in a synthesis of the archived data for the Scotian Shelf, shows that there was a gradual decline in nutrient concentrations from 1970 to 2009 (Fig. 13a). The trend, which is shelf-wide, is most obvious in the 50–100 m depth range. According to Yeats (2014), winter nitrate concentrations decreased by close to 50% between 1980–86 and 1995–2005 (for the years when winter conditions were observed) which it was concluded could have had implications for primary productivity. The unusual concurrence of downward trends in both nutrient and oxygen levels suggests a complex underlying mechanism. Based on Smith et al. (2011) and Yeats (2014) suggests that a decline in the input of deeper offshore water (and an associated more sluggish shelf circulation) could account for the long term decline in both nutrients and oxygen. The key point is that nutrient trends were interpreted to be driven predominantly by large scale circulation processes, rather than by top-down influences initiated by the declines in groundfish abundance in the late 1980s (as interpreted in the *fishery-induced trophic cascade* hypothesis).

To further examine the top-down hypothesis at the phytoplankton–nitrate link, we considered whether the inverse relationship, when evident, is stoichiometrically balanced. In other words, does a given incremental increase of phytoplankton expressed in nitrogen molar units give rise to an equal incremental decrease of nitrate in equivalent molar units? If so, the top-down hypothesis may arguably not be falsified at this trophic link. The AZMP time series measurements (1997–2013) of depth-averaged (0–100 m) nitrate and chlorophyll at 7 stations of the Louisbourg Line in spring and fall (Li, 2014) permit a locally-matched test using data-paired time series. The 14 (2 seasons \times 7 stations) multi-year rates of chlorophyll change ($\text{mg Chl m}^{-3} \text{ y}^{-1}$) are converted to rates of phytoplankton-N change ($\text{mmol Phyto-N m}^3 \text{ y}^{-1}$) using a phytoplankton carbon-to-chlorophyll ratio of $40 \text{ mg C mg Chl}^{-1}$, a Redfield carbon-to-nitrogen molar ratio of $6.6 \text{ mol C mol N}^{-1}$, and the atomic weights of the elements. These rates of phytoplankton-N change and nitrate change bear an inverse relationship to each other (Fig. 14). In spring, rates of phytoplankton-N were positive at 6 of 7 stations (“spring-up” phenomenon), and rates of nitrate change were negative at all 7 stations; conversely, in fall, rates of phytoplankton-N were negative at 6 of 7 stations (“fall-down” phenomenon), and rates of nitrate change were positive at 4 of 7 stations. The nitrogen changes in fall are much closer to stoichiometric balance than those in spring, but there

Table 6
Monthly climatology of chlorophyll in the upper 100 m from SSIP (1979–1982) selecting all stations east of the Halifax Line.

Month	Chl (mg/m^3)	Sddev Chl (mg/m^3)	Number of samples
1	0.42	0.24	31
2	0.61	0.29	26
3	6.24	3.92	35
4	5.86	6.33	52
5	0.57	0.52	74
6	0.83	1.89	26
7	1.29	1.56	154
8	0.63	1.89	216
9	0.42	0.33	130
10	0.89	1.27	189
11	1.03	0.79	38
12	0.33	0.14	7
Total	1.24	2.56	978

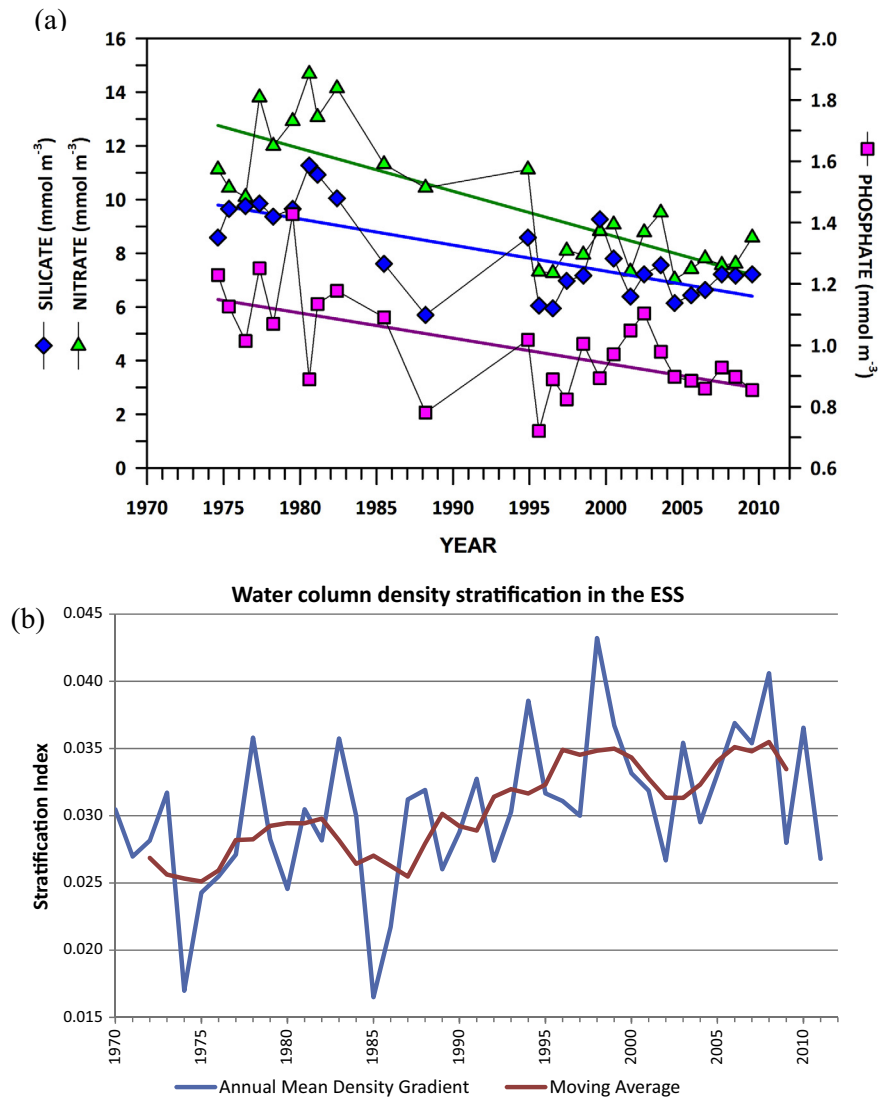


Fig. 13. Environmental trends: (a) nutrient levels (early 1970s to 2010) (adapted from Yeats et al., 2010); (b) water column density stratification (1970–2011).

are seasonal differences in phytoplankton size class composition (microplankton dominant in spring, picoplankton dominant in fall) and probably in nitrogen utilisation preferences (nitrate, ammonium). Notwithstanding seasonal complexities, the consolidated spring and fall dataset taken as a whole indicates a 2.4-fold negative change in nitrate for a unit positive change in phytoplankton-N. The one outlier [the spring time series at Banquereau Bank station (LL-6, where the water column is 66 m in depth)] has a depth-averaged (0–100 m) nitrate concentration which is lower than at other stations, and the chlorophyll concentration higher. Overall, the observed incremental decrease in nitrate is substantially more than is needed to account for the incremental nitrogen removal by phytoplankton.

Elsewhere, in Bedford Basin, Li et al. (2010) have considered the relationship between dissolved nitrate and phytoplankton chlorophyll in a nested hierarchy of time scales: intra-day, intra-annual, inter-annual, and inter-decadal. An inverse relationship between the variables is evident; both at the hourly time scale (physiological processes) and also at the intra-annual time scale over the weeks of nutrient drawdown and nutrient recharge (population dynamics and community assembly). However, at the decadal time scale, the concentrations of nitrate and

chlorophyll are positively related. We conclude that at the multi-year time scale (i.e. the analysis shown in Fig. 14), although the apparent gross inverse relationship supports cause (phytoplankton uptake of nitrogen) and effect (reduction in dissolved nitrate concentration), the variables are too coarse-grained to explain the mechanism. Furthermore the stoichiometric test is found wanting.

The analyses of trends in stratification of the water column within ESS, following the approach of Hebert et al. (2012) for the Scotian Shelf as a whole, are updated to cover the 1970–2011 period (Fig. 13b). Overall, there has been a gradual increase in stratification throughout the four decades, with changes in the near-surface salinity accounting for about 50% of the change in stratification (Hebert et al., 2012).

The gradual declines in nutrient concentrations at all depths over several decades (Fig. 13a), as well as (1) the increase in stratification (Fig. 13b) and (2) the declines in the CPR phytoplankton and small zooplankton indices since the early 1990s (Fig. 12a and c), are consistent with bottom-up processes contributing to the changes in plankton dynamics in ESS. The pattern of multi-decadal declines in nutrients is widespread throughout the northwest Atlantic, from the Labrador Basin and Labrador Sea to the Scotian Shelf (Yeats, 2014; Yeats et al., 2010). The stratification

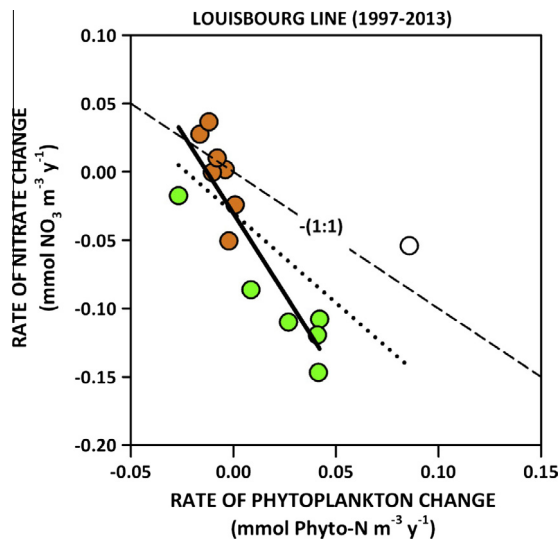


Fig. 14. Rates of molar nitrogen change in phytoplankton and dissolved nitrate based on 17-year time series (1997–2013) at 7 stations on the Louisbourg Line (data from Li, 2014). Spring data (green), fall data (orange), outlier datum (white, see text footnote), line of reciprocal equivalence (dashed line), linear regression omitting outlier (solid line, $y = a + bx$: $a = -0.031 \pm 0.008$, $b = -2.36 \pm 0.34$, $n = 13$, $F = 48$, $r^2 = 0.81$), regression including outlier (dotted line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and nutrient trends may be due to the increasing influence of ice melt in the Arctic Ocean, since the outflow has lower levels of nutrients. Some studies (Smith et al., 2001; Mountain, 2003) have shown a general freshening of the Scotian Shelf/Gulf of Maine area. Pershing et al. (2005) linked freshening in the Gulf of Maine area to increased export of freshwater from the Arctic. Indeed, a series of papers has concluded that large scale bottom-up processes are responsible for the nutrient and plankton trends in the Gulf of Maine area rather than any top-down effects (Frank et al., 2006; Greene, 2013; Greene and Pershing, 2007; Greene et al., 2008; MERCINA Working Group, 2012).

The most parsimonious interpretation of the decadal nutrient trends in ESS is that they are predominantly driven by large scale physical oceanographic processes (Li, 2014; Yeats, 2014), rather than due to top-down plankton drivers under the trophic cascade interpretation (Frank et al., 2005). Also, the stratification trends are considered to be consistent with the bottom-up interpretation of the plankton dynamics. In summary the trends in the bottom-up environmental drivers are consistent with the *climate variability* hypothesis, but not with the *fishery-induced trophic cascade* hypothesis.

3. Summary of the evidence

There was a major decline in the aggregate biomass of groundfish during the late 1980s and early 1990s, but little evidence of a recovery transition centred in 2005/2006. The “tilt analysis” groups the temporal trends of the groundfish species into three categories (the “slow risers”, the “slow droppers”, and the “fast droppers”), suggesting that there have been different drivers of change for the diverse species. Given the survey gear change in 1982 the spiny dogfish, silver hake and pollock abundance trends are suspect. The temporal patterns in abundance suggest that fishing pressure alone does not account for the decadal trends for many of the groundfish species. Furthermore, fishing effort alone was not the sole cause for the cod collapse in the late 1980s and early 1990s

(Bowen and Mohn, 1994; Burke et al., 1996; Mohn and O’Boyle, 1994; Sinclair, 1997; Sinclair et al., 1997).

The predictions of the *fishery-induced trophic cascade* and the *climate variability* hypotheses are not consistent with the documented major changes in natural mortality for several of the groundfish species (e.g. cod, thorny skate, and winter skate) that started in the late 1980s and early 1990s. A more complex interpretation of the trends in abundance of the groundfish species seems warranted. The diet of grey seals suggests that several of the groundfish species, both “fast and slow droppers” (including cod), are preyed upon by this predator. Also, some of the “slow risers” (e.g. haddock and halibut) are not large components of the grey seal diet. That said, recent assessments of haddock on the Scotian Shelf show evidence of a strong retrospective pattern, which suggests increases in natural mortality (Don Clark, personal communication).

The aggregate observations for the patterns of shrimp, snow crab and lobster trends in abundance until the mid-2000s are consistent with the *fishery-induced trophic cascade* hypothesis. However, only one of the three macro-invertebrates shows any decline after 2005–06, as would be predicted by the groundfish recovery proposed by Frank et al. (2011). Alternative explanations include (i) there has not been an increase in groundfish predation on snow crab or lobster beginning in the mid-2000s, (ii) that these three species are responding to predation pressure on different time scales, or (iii) that the population dynamics of these three species are driven by processes other than top-down. As concluded for the groundfish species, the abundance trends for these three macro-invertebrates are species specific and may be driven by different ecological processes, rather than by groundfish fishery induced top-down trophic cascade dynamics.

The estimated increase in catchability of herring in the early 1990s (which has been ongoing) infers a change in behaviour such that herring are closer to the sea-floor (as proposed by McQuinn, 2009), and thus increasingly available to the groundfish trawl. When the catchability changes are taken into consideration, the groundfish survey does not indicate an increase in abundance of herring in the 1990s. Rather the trend is reversed, with an estimated decline in abundance of in 4VW herring during the time period of the putative outbreak of small pelagic species. The temporal and spatial patterns of capelin abundance from the trawl survey indicate a brief (several years) southern extension of the distributional area of this species from its distributional centres in the Gulf of St. Lawrence and the Grand Banks. It is concluded that the sand lance temporal trends cannot be estimated with confidence using the groundfish trawl survey data.

The three surveys for fish larvae in ESS do not appear to track the relative changes in spawning stock abundance for the groundfish species (the trends in the latter species being relatively well estimated using the trawl survey and the stock assessments). Thus it is concluded that the several fish larval surveys do not provide reliable information on decadal trends in the abundance of herring and sand lance. Also, the grey seal diet does not indicate an increase in the proportion of small pelagics during the proposed small pelagic outbreak. The evidence of a decline in condition of the small pelagic species subsequent to the groundfish collapse is equivocal. The decline in average weight of these species (i.e. less large herring, capelin and sand lance captured in the groundfish surveys) is consistent with increasing levels of natural mortality on larger individuals rather than any increase in physiological condition. The diverse temporal patterns of abundance of the small pelagic species suggest that different species-specific driving forces are important drivers of change. Overall the small pelagics evidence is not consistent with the *fishery-induced trophic cascade* hypothesis. The decline in abundance of herring since the early 1990s is not inconsistent with the *climate variability* hypothesis

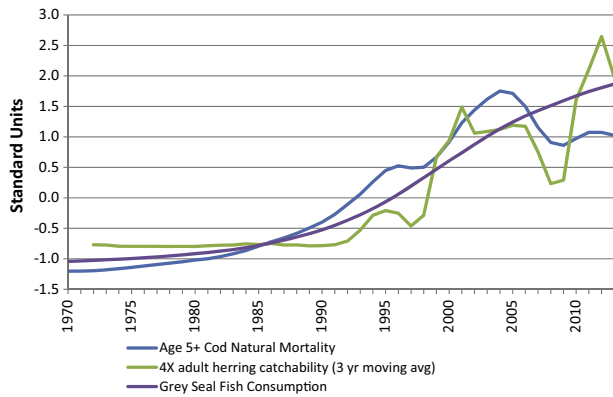


Fig. 15. Comparison of the relative trends in annual grey seal fish consumption, cod natural mortality (M) and herring catchability (q) in the groundfish RV survey. McM new figure, showing the seal fish consumption, q , and M relative trends.

(i.e. a consequence of the declines in plankton biomass levels). However the plankton decadal declines have been slight, whereas the herring decline dramatic.

The evidence for an inverse relationship between zooplankton and phytoplankton trends during the four decades (as predicted under the *fishery-induced trophic cascade* hypothesis) is not supported by the data or the analyses provided here. The CPR time series has many years without any samples, and some years with insufficient seasonal coverage to provide annual abundance estimates. When (1) the issues with the CPR data are taken into account, (2) the additional plankton surveys on the ESS are considered, and (3) the seasonality of the SSIP and AZMP surveys are adjusted for, there is little evidence that either the small or large categories of zooplankton are negatively correlated with the diverse indices of phytoplankton. The comparison of the SSIP and AZMP plankton biomass levels (when the seasonal sampling is taken into consideration) suggest that there was not higher zooplankton and lower phytoplankton abundance levels in the late 1970s/early 1980s relative to the late 1990s and early 2000s. Also, there is no evidence of an increase in abundance of large zooplankton during the mid-2000s, which was proposed to have generated increases in survival of larval groundfish. The aggregate plankton data support a bottom-up interpretation of the plankton dynamics (i.e. consistent with the *climate variability* hypothesis, but inconsistent with the *fishery-induced trophic cascade* hypothesis). However, given the extent of the nutrient decline (coincident with the enhanced stratification over four decades), the nuanced declines in the plankton indices suggest that the linear mechanistic processes in the physical chemical realm can give way to non-linear complexities in the biological realm. Whereas stratification change may guarantee nitrate change, it is not the case that nitrate change is either a necessary or sufficient cause for phytoplankton and zooplankton change.

Finally, when the data are examined on a full annual basis, there is little evidence of a reciprocal relationship between phytoplankton and nutrients within the ESS (as predicted by the *fishery-induced trophic cascade* hypothesis). Rather, consistent with the *climate variability* hypothesis, there is evidence that nutrients have been gradually declining over several decades within the context of large scale circulation and mixing processes (including gradual increases in water column stratification).

4. Conclusions

Murawski (2010) provides a global synthesis of the response of 24 marine fish populations to reductions in fishing effort. With the exception of one cod management unit off Atlantic Canada (that

resident in the southern Gulf of St. Lawrence), essentially all documented cases show substantial recoveries when fishing effort is reduced. Although not included in his synthesis, the lack of recovery of cod in ESS following the fishing moratorium in 1993 is also anomalous. Thus an increased understanding of the ecosystem dynamics that have prevented a recovery in ESS is of broad interest. Furthermore Neubauer et al. (2013) conclude that excessive levels of overfishing (as inferred for the ESS cod) erodes the resilience of populations leading to lengthy and uncertain recovery periods subsequent to reductions in fishing effort. In their synthesis it is assumed that fishing effort is the major component of mortality. If this assumption is incorrect (i.e. for those situations where increases in natural mortality have contributed to the stock collapse and lack of recovery) the conclusions on the erosion of resilience due to overfishing are flawed, and the management options for recovery are unlikely to be successful. In summary, an accurate interpretation of the causes of the ESS trophic level temporal patterns during the past several decades is critical to fisheries management discussions.

The observations of the trends in abundance at each trophic level (grey seals, groundfish, small pelagic fishes, macro-invertebrates, zooplankton, and phytoplankton) and the physical/chemical properties (nutrients and stratification) suggest that a complex set of interactions (a mixture of top-down and bottom-up) have been underway. These interactions include large scale oceanographic forcing, trophic level interactions, and species specific population dynamics. There is limited support for the *fishery-induced trophic cascade* hypothesis (including the proposed cod recovery since 2005).

The role of grey seals in the trends in abundance of some of the groundfish species (including cod, white hake, silver hake, pollock, cusk, thorny skate, and winter skate) and small pelagic species (herring, capelin, and sandlance) is likely of considerable importance. The conclusion of minor impacts of grey seal predation on groundfish and small planktivorous pelagic fish was based, at least in part, on an Ecopath model for the years 1995–2000 (Bundy, 2005; Bundy and Fanning, 2005). However, as the seal population has been growing exponentially, the impact of seals on some fish populations after 2000 (as shown by the rapid increase in annual fish consumption in Fig. 4a) must have been considerably larger than that estimated using the seal abundance observations from these earlier years (i.e. 1995–2000). The multi-decadal trends in the estimates of respectively annual grey seal fish consumption, cod natural mortality (M), and the catchability (q) of herring in the groundfish RV survey (Fig. 15) indicate very similar temporal patterns, which suggest a causal relationship (i.e. the herring are increasingly close to the sea-floor as a tactic of predator avoidance, and the high natural mortality of cod due to increasing predation by grey seals). Among the groundfish, the “fast and the slow droppers” have not recovered during the two decades since the closure of most of the groundfish fishery in ESS (1993 to the present). For the groundfish species for which natural mortality has been estimated, the levels are remarkably high. They are higher than nearly everywhere else in the world (except for the rest of the Scotian Shelf, the southern Gulf of St. Lawrence, and the Gulf of Maine area). Although over-fishing of some groundfish species occurred during the 1970s and 1980s, the accumulated observations since the early 1990s suggest that an additional top-down driver is important for the dynamics of the groundfish and small pelagic species.

An alternative interpretation of the decadal observations within ESS invokes climate variability, species interactions, and a key network species (in the sense of Boyd, 2012); with concurrent bottom-up and top-down processes being of importance. From a bottom-up perspective, the decadal trends of lower surface layer salinities, enhanced stratification, and declines in nutrients are plausibly interpreted by a freshening of the flows of Arctic waters due to

increasing ice melt. As such, large scale oceanographic processes (influenced by climate variability and change) are gradually changing the characteristics of the ESS plankton dynamics. Under this interpretation, the observed physical and chemical oceanographic trends are favouring a redistribution of phytoplankton biomass from the large size class (microphytoplankton) to the small size class (picophytoplankton), leading to a slight decline in bulk phytoplankton biomass. Further, the possibility of earlier spring diatom blooms would be expected to lead to a gradual decline in zooplankton production. A mismatch in diatom blooms with the seasonality of zooplankton production may have resulted in a higher proportion of the plankton production sinking to the benthos (rather than being re-cycled in the water column) as proposed by Head and Pepin (2010). An enhanced energy flow to the benthos may be at least partially responsible for the increasing abundances of the commercially exploited macro-invertebrates.

From a top-down perspective, it is probable that overfishing of groundfish in the 1970s to 1992, in combination with increasing levels of natural mortality of several groundfish species (due at least in part to grey seal predation), resulted in steep declines in the abundance of several groundfish species. Although fishing pressure has essentially been eliminated for most of the groundfish species during the past two decades, natural mortality rates have remained high. As well, total consumption of fish by grey seals has been increasing; leading to the inference that predation is causing the lack of recovery of many species during the ongoing groundfish fisheries moratorium (1993 to the present). Some groundfish species have been doing relatively well (e.g. redfish, Atlantic halibut, Greenland halibut, and haddock). These species are minor components of the diet of grey seals. The increasing level of seal predation may also be contributing to the recent declines in the herring within the ESS area. The release of predation on the macro-invertebrates by the reduced groundfish populations, in combination with enhanced energy flow to the benthos, may be generating the higher productivity of these commercially important invertebrate species. If these multiple interactions reflect reality, the grey seal could well be considered a key network species. Furthermore, the increases in abundance and the broader spatial distribution for both breeding and feeding of grey seals within the Gulf of Maine area and the southern Gulf of St. Lawrence may well be responsible for the observed increases in natural mortality of several fish species, as well as the herring and groundfish fisheries productivity declines in areas contiguous to ESS.

The complexity of the decadal patterns of abundance for groundfish, macro-invertebrates, and small pelagic fish species (and spatial distributions, for capelin for example) suggests that species specific processes rather than trophic level energetic constraints are important for many species. The alternative hypothesis (concurrent top-down and bottom-up drivers) proposed here is supported by much of the evidence (as well as being consistent with the interpretations of McQuinn (2009), Head and Pepin (2010), Rothschild (2011), Greene (2013), Li (2014), and Pershing et al. (2015)). Finally, if our interpretation of ESS ecosystem dynamics is robust, it is inferred that herring and several groundfish species within ESS will continue to generate poor fisheries yields due to the high natural mortality levels under the existing top-down predatory regime. Given the uncertainty in the causes of the decadal patterns in abundance of the commercially important macro-invertebrates (snow crab, shrimp, and lobster), forecasting of their fisheries yields is not possible.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.pocean.2015.09.005>.

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