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Transient dynamics of an altered large marine ecosystem

Kenneth T. Frank¹, Brian Petrie¹, Jonathan A. D. Fisher² & William C. Leggett²

Overfishing of large-bodied benthic fishes and their subsequent population collapses on the Scotian Shelf of Canada's east coast^{1,2} and elsewhere^{3,4} resulted in restructuring of entire food webs now dominated by planktivorous, forage fish species and macroinvertebrates. Despite the imposition of strict management measures in force since the early 1990s, the Scotian Shelf ecosystem has not reverted back to its former structure. Here we provide evidence of the transient nature of this ecosystem and its current return path towards benthic fish species domination. The prolonged duration of the altered food web, and its current recovery, was and is being governed by the oscillatory, runaway consumption dynamics of the forage fish complex. These erupting forage species, which reached biomass levels 900% greater than those prevalent during the pre-collapse years of large benthic predators, are now in decline, having outstripped their zooplankton food supply. This dampening, and the associated reduction in the intensity of predation, was accompanied by lagged increases in species abundances at both lower and higher trophic levels, first witnessed in zooplankton and then in large-bodied predators, all consistent with a return towards the earlier ecosystem structure. We conclude that the reversibility of perturbed ecosystems can occur and that this bodes well for other collapsed fisheries.

The recent demonstration that overfishing of large-bodied predators in the northwest Atlantic initiated a trophic cascade, typified by reciprocal changes in biomass between adjacent trophic levels extending to the base of the food web^{1,2}, overturned the long-held view that large marine ecosystems are resistant to restructuring⁵. It has been proposed^{6,7} that such trophic cascades are characteristic of ecosystems that have been transformed into undesirable states involving large changes in ecological functions and/or economic resources^{8,9}. Although the excessive consumption characteristic of trophic cascades may be unstable⁶, whether, how, and on what time scales such altered, diverse food webs and their key species and functional groups will recover remains unknown^{1,3,4}. This has led to controversy regarding the efficacy of and experimentation with strategies based on conventional management approaches such as moratoria on exploitation, culling and re-stocking intended to return ecosystems to their former structure^{10–13}. Using four decades of high quality, annual, fishery-independent data (see Methods) representative of multiple trophic levels on the eastern Scotian Shelf (Supplementary Fig. 1), we document the transient nature of its altered ecosystem and its return towards dominance by large-bodied predators.

The collapse of the northwest Atlantic cod (*Gadus morhua*) and several other large predatory fishes in the early 1990s (Fig. 1a), caused principally by over-fishing^{14,15}, precipitated the first documented open ocean trophic cascade in a large marine ecosystem¹. The total biomass of cod, one of the ecosystem's dominant species, has hovered at less than 5% of pre-collapse levels for almost two decades despite the implementation of strict regulations forbidding their capture¹⁵.

Recent investigations^{13,16} have provided strong evidence that, following these collapses, the eastern Scotian Shelf, and other northwest Atlantic ecosystems in which similar collapses occurred, moved to

apparent alternate states in which planktivorous forage fishes and macroinvertebrates became the dominant predators³. Released from predation on the eastern Scotian Shelf, the biomass of forage fishes increased by 900% (Fig. 1b) and macroinvertebrates by 200% compared to the pre-collapse years¹³. They then competed directly with and/or preyed upon the early life stages of their once benthic predators, a phenomenon termed predator–prey reversal¹⁷ which seems to be one of the leading causes of the delayed recovery of the benthic fish complex in this and other large marine ecosystems^{4,17,18}. Although forage fish constitute approximately half the diet of an expanding, resident grey seal (*Halichoerus grypus*) population, estimates of their consumption of pelagic fish species (1995–2000) were only 35% of the benthic

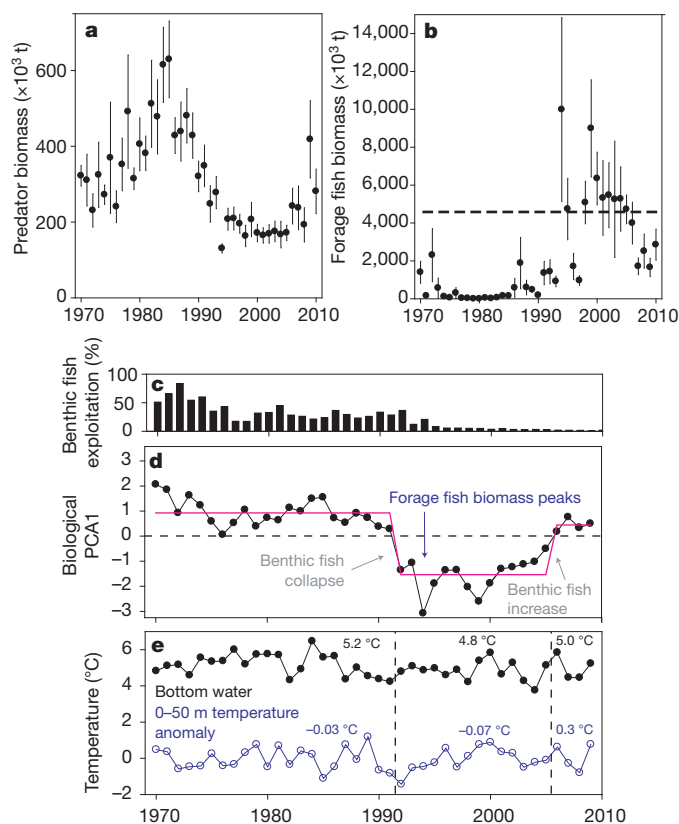


Figure 1 | Variability of the eastern Scotian Shelf ecosystem. a–e, Data (Supplementary Fig. 1) based on large-bodied benthic fish (a), their prey (forage fishes, b) with estimated carrying capacity (dashed line), benthic fish exploitation history expressed as annual per cent biomass removal (c), changing ecosystem structure based on the leading mode (PCA1) of biotic data spanning four trophic levels and the demarcation of regimes²⁹ of 22, 14 and 4 years duration (pink solid line) (d), and temperatures with averages shown for the three regimes (dashed vertical lines) (e). Vertical bars in a and b show \pm s.e.m. ($n = 27$).

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fish complex¹³ and insufficient to suppress the outbreaks and biomass variability of forage fishes (Fig. 1b).

The changing status of the eastern Scotian Shelf ecosystem exhibited two transitions. A period of intensive fishing, when aggregate landings of benthic fishes averaged close to 105,000 tonnes (t) representing annual biomass removals of >50% (Fig. 1c), resulted in the first transition centred in 1991–1992 from a ‘pre-collapse’ state dominated by benthic fish species to a ‘collapsed’ state dominated by forage fish species¹. A cod and haddock fishing moratorium implemented in 1993 had the desired effect of reducing aggregate exploitation (<5% since 2000; Fig. 1c) but did not produce the anticipated recovery (Supplementary Figs 2 and 3). The second transition, centred in 2005–2006, represents a return towards a ‘recovering’ state of benthic fish domination described here (Fig. 1d and Methods). An additional bottom trawl survey, beginning in 1986, revealed a similar pattern of collapse and recent increase in benthic fish biomass (Supplementary Fig. 4).

The physical environment during the three states, assessed using annual bottom temperatures, 0–50 m water temperatures (Fig. 1e) and water column stratification (Supplementary Information), showed only minor changes. The bottom temperatures during the collapsed state were only 0.33 °C and 0.24 °C lower than during the pre-collapse and recovering periods, respectively. The magnitude of this temperature change would have only minimal or no effect on individual and population growth rates as well as other life history traits (Methods). Further, the dominant large-scale atmospheric forcing mechanism in the western North Atlantic (that is, the North Atlantic Oscillation) induces a bimodal response of ocean temperatures with a nodal point in bottom temperature occurring in the middle of the eastern Scotian Shelf⁹. Consequently, the temperature response to such forcing in this region is minimal and is reflected in the dampening of regional variability in other biological properties such as species richness²⁰. Differences in water column temperature anomalies were also slight for the three periods: on average, temperatures during the pre-collapse and collapsed periods were within 0.1 °C, during the forage fish outbreak temperatures were elevated by about 0.4 °C; overall, temperatures varied over a range of about 2 °C. There was no relationship between water column temperatures and forage fish biomass at zero lag (Supplementary Fig. 5; correlation coefficient, $r = 0.02$) or for lags (forage fish biomass relative to temperature) up to four years (Methods). The minor increases in stratification occurred primarily during summer, outside of the peak period of phytoplankton production (Methods). The timing and magnitude of this ongoing recovery of the benthic fish complex was initiated and is being sustained by naturally induced changes in the dynamics of their former prey, and the resulting impact on the total ecosystem, more so than by external climatic influences (Fig. 1e).

The second and most recent ecosystem transition began with a marked decline in the biomass of the unfished, forage fish complex dominated by northern sand lance (*Ammodytes dubius*), capelin (*Mallotus villosus*), and Atlantic herring (*Clupea harengus*). The aggregate biomass of these species peaked in 1994 and 1999 at approximately 10 million t, which exceeded the estimated carrying capacity of 4.3 million t for the eastern Scotian Shelf ecosystem (Fig. 1b; Methods). Subsequently, their total biomass rapidly declined at an average rate of 0.5 million t per year to current levels near 3 million t. Such eruptions followed by crashes involving fast growing, highly opportunistic species are known to occur in other ecosystems freed from predatory control^{21,22}.

Physiological changes and cascading food web effects associated with the overshoot of the pelagic forage fish were evident. Relative weights, an index of physiological condition available since 1970, of the three dominant forage fish species showed coherent changes (31 out of 41 years with same sign) throughout the entire period with relative high condition indices from the 1970s to the early 1990s followed by sustained declines beginning about 1994 (Fig. 2a). This points to the pelagic species having inadequate food resources at

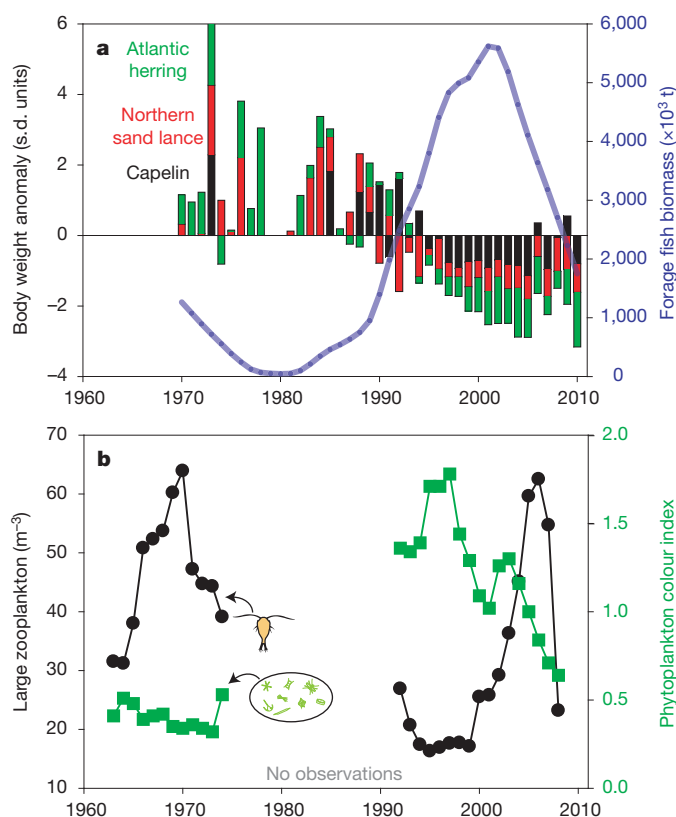


Figure 2 | Physiological changes in forage fish species and resultant food web effects. **a**, Species-specific body weight anomalies (stacked histograms) and smoothed forage fish biomass (solid line; 30% LOESS; Supplementary Fig. 8). **b**, Time series of large-bodied zooplankton abundance and phytoplankton colour index (a measure of abundance) from the Continuous Plankton Recorder survey (<http://www.safhos.ac.uk>). Recent (2000–2007) increases in large-bodied zooplankton, coincident with major reductions in forage fish biomass shown in **a**, indicate a weakening of the inhibitory effects of the predator–prey reversal mechanism to benthic fish species recovery.

increased abundances. The density of large-bodied zooplankton, which has varied inversely ($r = -0.32$, $n = 22$ years) with the forage fish biomass (their principal predators), reached a broad minimum of about 17 individuals per m³ at the approximate peak (1994) of the forage group biomass—a signature of excessive grazing. Large-bodied zooplankton species increased rapidly (1997–2007) by a factor of four in six to seven years to levels observed before the forage fish eruption, the final year in the series being an exception (Fig. 2b). Moreover, the standing stock of phytoplankton, which has varied inversely with the abundance of large-bodied zooplankton ($r = -0.71$), declined by 40% during the ongoing recovery of the benthic fish complex. These reciprocal relationships between adjacent trophic levels are consistent with the trophic cascade model¹.

Most revealing is the fact that the trajectory of forage fish biomass changes following the benthic fish collapse approximates a damped harmonic oscillator (Fig. 3), providing key biological insights from the derived parameter values including estimates of the period, 5 years (the approximate life cycle of this functional group), and dampening time, 7 years. The 7-year dampening represented a 78% decrease in forage fish biomass between 1994, the time of the peak amplitude, and 2005, the end of the regime dominated by this group (Fig. 1d). Studies of terrestrial herbivores indicate that the cycle period is strongly dependent on body size²²; based on the range of body sizes of the forage fishes we studied (weight range: 0.04–0.3 kg), the cycle period is similar to those estimated from outbreaks of similar-sized terrestrial species (3.6 to 5.9 years)²². This dynamic, oscillatory behaviour indicates that the internal damping capacity of the ecosystem, and not solely management

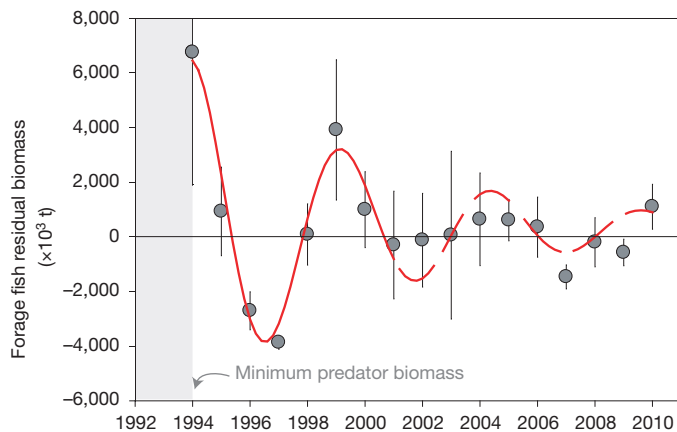


Figure 3 | Post-perturbation forage fish variability. The variability (solid points \pm s.e.m., $n = 27$), described by a damped harmonic oscillator fitting the 1994–2001 observations (solid line), gives an amplitude of $6,100 \times 10^3$ t, dampening rate = 6.9 years, and oscillation period = 5.2 years (Methods). Shaded area indicates period of greatest population growth. Aggregate prey biomass is expressed as an anomaly from the 30% LOESS filter (Supplementary Fig. 8). This solution is extrapolated to the end of the record (broken line). In theory³⁰, a population or functional group that is characterized by damped oscillations will overshoot and then undershoot the carrying capacity.

strategies, probably initiated the return of the eastern Scotian Shelf ecosystem towards its former structure and the restoration of food web stability.

We propose that this crash in forage fish biomass led to a reduction in the intensity of predator–prey reversal which, combined with increased food availability to the benthic fish larval stages resulting from the corresponding and related growth in the abundance of large zooplankton, provided a window of opportunity for the recovery of the once dominant benthic predators. Since 2006 the benthic fish biomass has attained levels approaching those observed during the pre-collapse period (Fig. 1a). Atlantic cod and redfish (*Sebastes* spp.) have reached levels not seen since the early 1990s and haddock (*Melanogrammus aeglefinus*) to an unprecedented high (Supplementary Fig. 6). Enhanced recruitment (by a factor of 5.3, recovering/pre-collapse; Supplementary Fig. 7) and improvements in post-recruitment survivorship, which for cod and haddock has increased by factors of 12 and 70 times compared to the collapsed period, contributed to these changes (Supplementary Table 1). In addition, three of the four benthic fish species which are routinely aged (cod, pollock and silver hake) have shown 8–18% increases in average weight at age during 2006–2010 relative to the 1992–2005 post-collapse period (Supplementary Table 2).

The generally positive response of the large-bodied zooplankton to the declining forage fish biomass supports this hypothesis. The early life stages of most of the benthic fish species form an integral part of the large-bodied zooplankton complex and their survival and contribution to recruitment would have benefited from the same forces that have led to the increase in large-bodied zooplankton abundance noted above. Increased predation by the expanding benthic fish complex on the forage fish community should accelerate this trend.

This unfolding drama held many surprises, including the prolonged recovery of the benthic predator complex, despite the moratorium on directed fishing for cod and haddock, the establishment of a closed area on the western offshore banks that preceded the fishing moratorium²³, and the promotion of new and experimental fisheries²⁴ to divert fishing effort away from the traditional species. Although the current trajectory is positive, several factors could alter ongoing ecosystem recovery. The current high levels of recruitment and survivorship of the benthic fish complex, if sustained, could accelerate the recovery. The current dominance of haddock over cod also raises the question of whether the species makeup of the ecosystem will return to that which prevailed before the collapse. Furthermore, recovery in other over-exploited

ecosystems such as the Black Sea, Northern Benguela, the Sea of Japan, and elsewhere has been delayed by jellyfish blooms²⁵, the presence of invasive species and by eutrophication³, all of which are possible in the system we describe. The widespread body size reductions of benthic fishes documented for other exploited northwest Atlantic systems^{26,27}, if not reversed, could also slow the recovery of the benthic fish complex and adversely affect food web structure²⁶. The evolving global climate could alter the ecosystem positively or negatively.

These uncertainties notwithstanding, the answer to the critical question of whether or not such profound changes in the dynamics of large marine ecosystems are reversible seems to be ‘yes’. This bodes well for other perturbed, formerly cod-dominated systems at latitudes to the north of the eastern Scotian Shelf that have yet to recover. Indeed, subtle signs of cod recovery have been appearing in other sub-arctic northwest Atlantic ecosystems during the past few years²⁸. However, the time scales for their recovery are likely to be greater given the lower water temperatures (equates to slower turnover times) and their reduced species richness and, for some, because of the continued exploitation of cod and other large-bodied benthic fish species^{13,15,18}.

METHODS SUMMARY

Annual fishery-independent, randomly stratified bottom trawl surveys on the continental shelf off eastern Nova Scotia (1970–2010) during July–August provided biomass and variance estimates for functional groupings of fifteen, commercially exploited benthic and three forage fish species. A March survey (1986–2010) was used to assess the benthic fish dynamics further. Benthic fish exploitation levels were expressed as the ratio of landings to survey-estimated biomass. Ageing data, available for four benthic fish species, were used to calculate growth and mortality rates. Correction factors were applied to the typically under-sampled forage species. A 30% linear LOESS filter was applied to the forage fish biomass data to isolate high-frequency variability; the resultant anomalies were least squares fit to a damped harmonic oscillator equation (Methods). We quantified the time-averaged ecosystem carrying capacity of forage fishes using seasonally averaged, zooplankton data and production to biomass ratios obtained from the literature (Methods). Annual anomalies of the individual average body weights (total biomass/total abundance), an index of physiological condition, were derived for each forage species. Lower trophic level data (phytoplankton colour index and zooplankton abundance time series) were obtained from the Continuous Plankton Recorder survey (<http://www.safhos.ac.uk>). Zooplankton were grouped into large (≥ 2 mm carapace length) and small (< 2 mm) species. The eastern Scotian Shelf ecosystem status was assessed by principal components analysis of the five biological time series. To determine whether and when ecosystem transitions occurred, the dominant principal component axis (PCA1) was subjected to a sequential t -test analysis of the regime shift method (STARS)²⁹, which identifies the magnitude and direction of significant shifts. Temperature, salinity and density observations were obtained from directed and opportunistic ship-based sampling.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions K.T.F. developed the overall concept of paper reported here. B.P. and K.T.F. developed the initial hypothesis and assembled the relevant data. Most analyses were performed by B.P. with assistance from J.A.D.F. and K.T.F. All authors contributed to the interpretations and synthesis of the analytical results.

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METHODS

Large-bodied benthic predators, aggregate forage fish biomass, zooplankton functional groups and chlorophyll. The primary data used in the analyses were from July–August surveys, initiated in 1970, that are conducted annually by the Department of Fisheries and Oceans (DFO) of the eastern Scotian Shelf (Supplementary Fig. 1), Canada^{31–34}. Results from a secondary, fishery-independent bottom trawl survey beginning in 1986 and conducted during the month of March were used to assess the benthic fish biomass dynamics further. We consider this a secondary survey because of its reduced geographic coverage, different statistical design, and three missing/incomplete years in comparison to the July–August survey.

The dominant, large-bodied predator species, designated the predator group, are Atlantic cod *Gadus morhua* (L_{\max} = 161 cm), haddock *Melanogrammus aeglefinus* (87 cm), pollock *Pollachius virens* (112 cm), longfin hake *Urophycis chesteri* (71 cm), silver hake *Merluccius bilinearis* (73 cm), white hake *Urophycis tenuis* (142 cm), red hake *Urophycis chuss* (69 cm), redfish *Sebastes* spp. (60 cm), thorny skate *Amblyraja radiata* (120 cm), spiny dogfish *Squalus acanthias* (196 cm), Greenland halibut *Reinhardtius hippoglossoides* (82 cm), American plaice *Hippoglossoides platessoides* (76 cm), winter flounder *Pseudopleuronectes americanus* (64 cm), witch flounder *Glyptocephalus cynoglossus* (67 cm), and yellowtail flounder *Limanda ferruginea* (59 cm). These fifteen species have been commercially exploited, often in mixed fisheries, throughout the continental shelf in depths of less than 200 m. Ages are determined for Atlantic cod, haddock, pollock and silver hake; a growth model for redfish³⁵ applicable to the eastern Scotian Shelf stock and an age–length key for American plaice³⁶ permitted approximations of abundance at age for these two species. The availability of age data permitted the estimation of total mortalities (Supplementary Table 1) and growth rates (Supplementary Table 2).

The forage species group consists of three species: herring *Clupea harengus*, capelin *Mallotus villosus*, and northern sand lance *Ammodytes dubius*, which are under-sampled by the bottom trawl survey. Correction factors have been applied (capelin and sand lance by a factor of 200 and herring by 40 (ref. 37)). Commercial exploitation of these species has been relatively low (herring) or non-existent in this region. Annual anomalies (s.d. units) of individual average body weights (total biomass/total abundance) for each of the three forage species were estimated and used as indices of the temporal variation in physiological condition.

Lower trophic level data (phytoplankton colour index and zooplankton abundance time series) were obtained from Continuous Plankton Recorder (CPR) observations collected on the Scotian Shelf beginning in 1961 at a nominal sampling interval of 1 month. The CPR instrument is towed behind a vessel at about 7 m depth; plankton are collected on a 270 µm silk mesh over a 10 nautical mile tow and stored within the recorder for later identification. Details of the sampling and analysis methods can be found on the Sir Alister Hardy Foundation website (<http://www.sahfos.ac.uk/>).

The number of CPR samples per month by year is shown in Supplementary Table 3. The series consists of two periods of data collection, 1961–1976, when there were many months without samples, and 1991–2008, when most months were sampled. There was a large data gap from 1977–1990. To compensate for missing monthly data, a time series for the period 1961–1976 was created by averaging monthly values over successive 5-year periods. For the better-sampled 1991–2008 period, 3-year averaging blocks were used. The averaging acts like a rough low-pass filter. The positions of all samples are shown in Supplementary Fig. 9.

Zooplankton data obtained from the CPR Program were grouped into large-bodied (≥ 2 mm carapace length) and small-bodied (< 2 mm) species. The large-bodied category comprised all *Calanus* species and their copepodite stages including *C. finmarchicus*, *C. hyperboreus*, *C. helgolandicus* and *C. glacialis*; all *Metridia*, *Euchaeta* and *Pleuromamma* species including *M. lucens*, *M. longa*, *E. marina*, *E. norvegica*, *P. abdominalis* and *P. robusta*; also included were *Candacia* sp., *C. armata*, *Heterorhabdus* sp. and *H. papilliger*, and *Neocalanus gracilis*, *Rhincalanus nasutus*, *Euchirella rostrata* and *Anomalocera patersoni*.

The small-bodied category included: all *Centropages* and *Temora* species including *C. typicus*, *C. hamatus*, *C. bradyi*, *C. chierchiai*, *T. longicornis* and *T. stylifera*; also *Pseudocalanus*, *Candacia*, *Paracalanus*, *Oncaea*, *Sapphirina*, *Lucicutia*, *Scolecithricella*, *Clausocalanus* and *Calocalanus* sp.; and *Acartia* sp., *Acartia danae*, *Corycaeus* sp., *Ctenocalanus vanus*, *Mecynocera clausi*, *Nannocalanus minor*, *Pleuromamma* sp., *Pleuromamma borealis*, *Lucicutia* and *Tortanus discaudatus*. Further details of the species identification protocols used are provided elsewhere³⁸.

Bottom trawl survey precision. The precision of the biomass estimates at both the functional group and species level was evaluated by using the random, stratified survey design (27 strata) to calculate the relative standard error (rse, standard error divided by the mean and expressed as a percentage)³⁹. For the aggregate predator biomass, the rse (averaged over 41 years) equalled 17.5% (range: 8–40%). The rse for the annual forage fish biomass was averaged over a fewer number of surveys (1993 to 2010) because, before 1993, there were very low levels of forage

fish with the majority of survey sets yielding null values ($> 70\%$). The resulting rse was 32% (range: 16–59%). The rse of the annual biomasses of the individual predator species are shown in Supplementary Fig. 6. The average value for cod-like species (35%) compares favourably to surveys in other geographic regions⁴⁰. The forage species biomass estimates averaged 53, 45 and 38%, for capelin, northern sand lance and herring, respectively.

We also considered the probability that the aggregate benthic fish biomass from the relatively constant period of 2000–2004 (168,000 t) was different from the 2010 value (336,000 t) represented by a linear fit to the 2004–2010 observations when the biomass had an average increase of 28,000 t per year. From the analysis above, we took 19% as a representative rse and computed the probability that the 2000–2004 value differed from the 2010 best-fit value. The probability that the 2000–2004 average value was greater than or equal to the best-fit 2010 value was 0.009.

Commercial landings and fishery regulations. Annual eastern Scotian Shelf landings for the benthic species were extracted from databases maintained by the Northwest Atlantic Fisheries Organization (NAFO) and the DFO. The management unit, NAFO Div. 4VW (Supplementary Fig. 1), goes beyond the continental shelf into offshore slope waters where fishing effort was concentrated for certain species, specifically silver hake. Therefore, estimation of meaningful exploitation levels based on the ratio of landings to biomass (derived from the fishery-independent trawl surveys that are constrained to the continental shelf) required the exclusion of the landings data for silver hake. No survey catchability corrections were made for any of the benthic fish species and this may result in annual ratios greater than 1. Hence, this measure of exploitation, often referred to as relative *F* (fishing mortality), is meant to serve as an index of commercial exploitation (Fig. 1c). There are no contemporary (post-2000) estimates of instantaneous fishing mortality rates because of the low levels of fishing associated with the cod and haddock fishing moratorium; for eleven species that were not aged there have never been any estimates of instantaneous fishing mortality rates.

In September of 1993 the eastern Scotian Shelf fishery for cod and haddock was closed while fisheries for flatfish, skates, redfish, silver hake (omitted) and some other minor species have remained open and, since then, total landings have averaged ~6,000 t. For silver hake, landings averaged 16,000 t during this same period and the percentage of cod by-catch associated with this directed fishery was very low (0.01%). The second leading fishery in this area was for redfish (4,500 t) and it incurred by-catches of cod of 0.8%. This information is available at <http://www.dfo-mpo.gc.ca/fm-gp/initiatives/cod-morue/strategic-mar-eng.htm>.

Principal components analysis and regime shift detection. The status of the eastern Scotian Shelf ecosystem was characterized by principal components analysis based on standardized anomalies (s.d. units) from five biological time series (CPR phytoplankton colour index, zooplankton (body size $<$ and ≥ 2 mm), forage fish and large benthic predators) using a method previously described⁴¹. PCA1 and 2 accounted for 56.3% and 18% of the variance, respectively. We compared the time series variability of PCA1 constructed from the correlation matrices based on the data series from 1970–2010, which include data gaps for the three lower trophic levels from 1975–1991 and 2008–2009 and from the period (1970–74; 1992–2007) when all series were complete. The r^2 between the two PCA1 series was 0.99. The loadings based on the 1970–2009 (1970–1974; 1992–2008) series of the five variables on PCA1 were: predators = 0.49 (0.50), forage fish complex = -0.44 (-0.46), large-bodied zooplankton = 0.43 (0.43), small-bodied zooplankton = -0.33 (-0.32), phytoplankton colour index = -0.52 (-0.51).

To objectively determine whether and when ecosystem transitions occurred, the dominant principal component axis (PCA1) from the five-variable biological analysis was subjected to a sequential *t*-test analysis of regime shift method (STARS) that identifies the magnitude and direction of shifts significant at a pre-determined α -level, given both the expected cut-off length for the regime (*L*) and a parameter that designates how much of a difference from the observed mean (in s.d. units) are required before data are considered outliers²⁹ (available at <http://www.beringclimate.noaa.gov/regimes/index.html>). Choice of *L* and α affect the number and duration of regime shifts²⁹. We set *L* = 5 and α = 0.01, in keeping with previous analyses using a subset of ecosystem data where shifts in Scotian Shelf cod–prey states were shown to be relatively insensitive to changes in *L* and *H* (a parameter describing the treatment of outliers) and where the relatively stringent α -value was established to limit regime shift detection to only cases with strong evidence⁴². In our analyses, *L* = 10, *L* = 15 did not affect the timing of the biological regime shifts; setting α = 0.05 only suggested one additional small regime shift in 1975 when *L* = 5.

Carrying capacity estimation. Estimates of the zooplankton biomass on the eastern Scotian Shelf have been compiled⁴³; additional stations were available through the BIOCHEM database (http://www.meds-sdmm.dfo-mpo.gc.ca/biochem/Biochem_e.htm) and courtesy of C. Johnson and B. Casault. Biomass estimates were made using vertical hauls from the bottom to the surface using 200 µm mesh nets. Observations from 1999–2008 provided reasonable spatial

coverage for the months of March, April, July and October. March and July observations were made during ecosystem fisheries surveys; April and October data, from Atlantic Zone Monitoring Program cruises, were collected on three standard, repeated sections at the northeastern (Cabot Strait Section), central (Louisbourg Section) and southwestern end (Halifax Section) of NAFO Div. 4VW (Supplementary Fig. 10).

The zooplankton biomasses are shown in Supplementary Table 4. Taking the simple average of these observations and multiplying by the surface area of the eastern shelf gives a zooplankton standing crop of 4.8×10^6 t. Previous work⁴⁴ estimated a zooplankton production to biomass ratio of 6 to 9.7, and used an average value of 7 as an overall factor applied to zooplankton as a group. Another more rigorous, quantitative analysis⁴⁵, estimated production to biomass (P/B) ratios for nine species, including leading components of the overall biomass, and for a single general category. Their biomass-weighted P/B ratio was 8.9. Multiplying the average biomass in Supplementary Table 4 by this factor yields an overall zooplankton production of approximately 4.3×10^7 t. Using a 10% efficiency relating the zooplankton production to forage fish yields a rough estimate of the forage fish carrying capacity of 4.3×10^6 t.

Similar to our calculation of carrying capacity for forage species, we estimated the annual production of phytoplankton on the eastern Scotian Shelf based on measurements from three sources^{46–48}. The data from two sources^{46,47} covered the months of March–August and November; the observations from the third⁴⁷ consisted of 13 monthly estimates from March 1991 to March 1992. All observations were reported as mg of carbon per m² per hour. We converted mg C to wet weight of phytoplankton using a factor of 42 (ref. 49), thus allowing direct comparison with our estimates of zooplankton production. Combining two sets^{46,47} of results, we estimate the annual production of phytoplankton as 640×10^6 t and 240×10^6 t, respectively. These give ratios of phytoplankton to zooplankton production of 15 and 5.5 which are reasonable if the energy transfer efficiency is ~10%. One crude measure for estimating the carrying capacity for the predator complex involved taking the ratio of peak biomasses of benthic fish predators to forage fishes which is about 1:16.

Damped harmonic oscillator calculations. The input data set was the biomass of the three leading forage species. The period under consideration was 1994–2010. We used a temporally varying background state derived by running a 30% linear LOESS filter through the data. The filter split the variability into two components: a very low frequency component with a period estimated as 56 years from the autocorrelation function and higher frequency variability (Supplementary Fig. 8).

The anomalies indicated a simple damped harmonic oscillator-like (dSHO) variability, particularly from 1994 to 2001, shown as solid grey circles in Fig. 3. We solved for the characteristics of this variability by least squares fitting the observations to the dSHO equation:

$$A_0 + A_1 e^{-d_1 t} \cos(2\pi t/\tau),$$

where A_0 is the mean, A_1 the amplitude of the harmonic oscillation, d_1 the dampening rate, and τ the periodicity of the oscillation. The solution based on optimal fitting of 1994–2001 observations, shown as a solid red line in Fig. 3, gives $A_0 = 347,000$ t, $A_1 = 6,100,000$ t, $1/d_1 = 6.9$ years, $\tau = 5.2$ years.

Environmental indices and their relationship to the pre-collapse, collapse and post-collapse periods. The relationship between forage fish biomass and water column temperatures was evaluated. The results showed no relationship between the two variables at 0 lag (Supplementary Fig. 5). We also lagged the forage fish biomass relative to the temperature; for lags up to 4 years, the r^2 was less than 0.04. At lags of 5 years, $r^2 = 0.21$; however, this is approaching the life cycle of these species and the biological import of the enhanced correlation at this lag is therefore questionable. Finally, we examined integrated temperatures up to 5 years. All r^2 values were less than 0.02.

An examination of the seasonal variability of the stratification index showed that the long-term trend seen in the annual data was due mostly to the summer and secondarily to the fall series (Supplementary Fig. 11). Moreover, the magnitude of the changes during winter and spring (major bloom period) were small compared to those in summer and fall. The period, 1985–1994, of ongoing decline of the benthic fish functional group showed near-normal values of the stratification parameter during the spring bloom period. The outbreak period (1994–2001) of the forage group was weakly ($r^2 = 0.21$) related (not significantly) to the spring stratification.

The seasonal variation of the phytoplankton colour index (Supplementary Fig. 12) and their correlations with the annual index, their averages and deviations

(Supplementary Table 5) indicated that the greatest contributions were from the winter and spring seasons (high correlations and variance), followed by fall (high correlation, moderate variance), and finally by summer (low correlation, lowest variance). This indicated that summer, with the greatest stratification changes, had the least impact on the annual colour index; fall, with the next greatest impact on stratification, made the second least contribution to the index. Further comparisons of the monthly colour indexes with the annual revealed that the greatest contributions were from March and April, typical months for the spring bloom on the eastern Scotian Shelf (Supplementary Table 6).

We assessed the impact of the full range of temperatures observed in the eastern Scotian Shelf using the relationship between the intrinsic rate of population growth, r , age at maturity, a , and bottom temperatures developed previously for 20 stocks of North Atlantic cod⁵⁰. This analysis revealed that the estimates of r and a so derived were, during the pre-collapse period, on average +4% higher and –3% lower, respectively, than during the collapsed period and +3% higher and –2% lower, respectively, for the recovering period. We also note that the period 1987–1991, immediately preceding the cod collapse, featured some of the coldest bottom water temperatures on record. Again applying the approach detailed above, and the r and a data provided⁵⁰, we estimate a maximum 10% decrease in r and a 9% increase in a relative to the collapsed and post-collapse intervals. During this cold period, fishing mortality on cod, based on the ratio of landings to biomass, averaged 65%, which is an extremely high annual rate of biomass removal. This dwarfs any possible impact of the environment as expressed through the effect of temperature on r and a .

The population dynamics and feeding ecology of grey seals on the eastern Scotian Shelf has been assessed since the early 1960s with sampling effort concentrated on the colony inhabiting Sable Island. Total population sizes were estimated from a model fit to census data on pup production (Supplementary Fig. 13).

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