End-to-end food web control of fish production on Georges Bank

Jeremy S. Collie, Dian J. Gifford, and John H. Steele


Abstract

The ecosystem approach to management requires the productivity of individual fish stocks to be considered in the context of the entire ecosystem. In this paper, we derive an annual end-to-end budget for the Georges Bank ecosystem, based on data from the GLOBEC program and fisheries surveys for the years 1993-2002. We use this budget as the basis to construct scenarios that describe the consequences of various alterations in the Georges Bank trophic web: reduced nutrient input, increased benthic production, removal of carnivorous plankton such as jellyfish, and changes in species dominance within fish guilds. We calculate potential yields of cod and haddock for the different scenarios, and compare the results with historic catches and estimates of maximum sustainable yield (MSY) from recent stock assessments. The MSYs of cod and haddock can be met if the fish community is restructured to make them the dominant species in their respective diet-defined guilds. A return to the balance of fish species present in the first half of the 20th century would depend on an increase in the fraction of primary production going to the benthos rather than to plankton. Estimates of energy flux through
the Georges Bank trophic web indicate that rebuilding the principal groundfish species to their MSY levels requires restructuring of the fish community and repartitioning of energy within the food web.

Keywords: community dynamics, ecosystem-based management, Georges Bank, marine fish, end-to-end.

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Introduction

The super-abundance of cod on the fishing grounds of the northwest Atlantic fueled the development of early settlements in North America (Kurlansky, 1997; Rosenberg et al., 2005). The collapse of cod and other principal groundfish stocks was caused primarily by excessive fishing mortality, but the delayed recovery of some stocks has been attributed to several factors in addition to over-fishing. Climate change (Beaugrand et al., 2003), regime shifts (Choi et al., 2004), trophic cascades (Frank et al., 2005), and habitat disturbance (National Research Council, 2002) have all been invoked
as causes of ecosystem change, while proliferation of pelagic fish species (Frank et al., 2005), elasmobranchs (Myers et al., 2007), jellyfish (Jackson et al., 2001) and crustaceans (Worm and Myers, 2003) are described as consequences. These explanations are based predominantly on correlations between individual species or trophic groups and do not quantify the changes in energy fluxes within the overall food web.

Measures to halt over-fishing and to rebuild depleted ground-fish stocks (effort reduction, gear modification, and area closures) were implemented by the New England Fishery Management Council starting in 1993 and are continuing with subsequent amendments to the fishery management plans (Fogarty and Murawski, 1998). The US Sustainable Fisheries Act mandates rebuilding of over-fished stocks to levels capable of sustaining maximum sustainable yield (MSY) within 10 years (Safina et al., 2005). MSY estimates are uncertain, not only because they require knowledge of the productivity and compensatory capacity of each stock, but also because they often imply rebuilding to levels beyond those observed in recent decades. Further, it is very difficult to derive quantitative estimates of the abundance of the pristine stocks, either from historical data (Rosenberg et al., 2005) or by solving for the unfished biomass from population models (Myers et al., 2001). As fish stocks begin to rebuild there is some doubt as to whether MSY levels of individual stocks can be attained collectively, given increases in non-commercial species (Link, 2007) and other changes in the marine ecosystem. Decreased growth rates, particularly in haddock (Northeast Fisheries Science Center, 2008), can be interpreted as density-dependent growth caused by limited food supply.

A new assessment of the Georges Bank ecosystem (Fig. 1) provides estimates of production at all trophic levels (Steele et al., 2007). We use a unified version of this web
to calculate the effects on all trophic groups of a range of adjustments to the internal
structure of the ecosystem. These different scenarios determine the consequent changes in
production of the three fish guilds, planktivores, benthivores and piscivores (Fig. 1). We
estimate the potential production of cod, a piscivore and haddock, a benthivore, under
different food-web scenarios by using the maximum fraction that the individual species
contribute to the trophic guilds. We compare these scenarios with observed patterns of
yields of cod and haddock during the 20th century. Finally, we evaluate the extent to
which rebuilding the cod and haddock stocks to MSY levels is constrained by the basic
productivity of the ecosystem.

Food-web Analysis [main heading]

A general equation for a prey-predator food web (Steele, 2009) is

\[
\frac{dB_i}{dt} = e_i \left( \sum_j Q_{ij} + G_i \right) - \sum_i Q_{ij} - L_i
\]

(1)

where \( B_i \) = the biomass of “trophic component” \( i \), \( Q_{ij} \) = rate at which \( B_j \) is consumed by \( B_i \), \( G_i \) = gains from external sources, \( L_i \) = losses from the system, and \( G_i, L_i > 0 \). The
transfer efficiency, \( e_i \) = Production \( (P_i) \)/Consumption \( (C_i) \), is assumed constant for each
component \( i \).

The units of biomass can be energy, live weight, particulate organic carbon or a
nutrient such as nitrogen. In the last case, “consumption” can include nutrients recycled
from heterotrophs to autotrophs. This is the most general formulation, with the $Q_{ij}$ as
variables. Because there are typically many more $Q_{ij}$ than equations, the usual practice is
to associate a single variable with each compartment – biomass, production or
consumption rate – and to linearize the system, permitting matrix solutions for the steady
state. There are two options:

(A) $Q_{ij} = a_{ij} P_j \quad a_{ij} \geq 0 \quad$ (bottom-up)

and

(B) $Q_{ij} = b_{ji} C_i \quad b_{ji} \geq 0 \quad$ (top-down).

Option (A) follows the expected direction of energy flux, with production by prey
determining intake by predators (e.g. Steele, 1974; Sissenwine et al., 1984). Whereas for
(B) consumption by the predator determines output from the prey (Christensen and Pauly,
1993). Thus (A) describes “bottom-up” and (B) describes “top-down” control.

Application to Georges Bank [subheading]

Recently, the desire to construct end-to-end budgets that encompass external
forcing from both climatic change and fishing, has led to combinations of the two
approaches (Aydin et al., 2005; Field et al., 2006; Plaganyi, 2007) with bottom-up
depictions forced by nutrient fluxes into the system (e.g. NEMURO; Fuji et al., 2002)
and top-down treatments starting from fisheries yields (e.g. ECOPATH; Christensen and
Pauly, 1993). Steele et al. (2007) followed this general approach, dividing the ecosystem
components into a lower and upper trophic webs because of their disparate space/time
scales and different relation to physical processes (Steele and Collie, 2005). The lower
food web is driven by nutrient recycling, and by physical influx of NO₃-rich deeper water
with concomitant export off Georges Bank of near-surface water and associated plankton.
To encompass the spatial and temporal variability Steele et al. (2007) constructed nine
budgets for three seasons in three distinct hydrographic regimes on Georges Bank. The
output from the nine budgets was used to estimate the annual average fluxes from the
lower to the upper components of the web. The data on NO₃ fluxes to drive this part of
the system, and the data on plankton and benthos to constrain the output were derived
largely from GLOBEC surveys from 1995 to 1999 (Wiebe et al., 2001). The output is
expressed as annual average production (gC m⁻² yr⁻¹) of mesozooplankton, suspension-
feeding macrobenthos, and deposit-feeding macrobenthos (Fig.1).

Fish biomass data from trawl surveys on Georges Bank from 1963 to 2002
(Smith, 2004; Steele et al., 2007) were partitioned as piscivores, planktivores and
benthivores (Table 1) based on fish diets (Garrison and Link, 2000). For the budget
calculations we used the decade 1993-2002, which is coincident with the period of the
Georges Bank GLOBEC field program. Further, we assumed (1) the fish eaten by other
fish are juvenile pre-recruits (Overholtz, 2000) that eat predominantly zooplankton, and
(2) this piscivory is the dominant source of mortality for the pre-recruits. These data and
assumptions permitted us to make top-down estimates of the food requirements of the
fish communities on Georges Bank in terms of two functional, rather than species,
groups—total plankton and total benthos (Fig. 1). The top-down and bottom-up fluxes
were matched for the decade 1993-2002 by estimating the required fluxes through the
invertebrate carnivore components of the plankton and benthos (Fig. 1) and comparing
these fluxes with the available observations (Steele et al., 2007). Flux estimates for these components of the food web generally have relatively large uncertainties, and so are often used to reconcile web budgets (Mackinson and Daskalov, 2007; Link et al., 2008).

Main findings of previous work [subheading]

Three patterns of variability in the Georges Bank ecosystem, which are influenced by some combination of climatic change and fishing pressure, are relevant to this analysis.

(1) The 40 years of data for fish populations revealed great inter-annual and inter-decadal variation in species composition (Steele et al., 2007; Gifford et al., 2009) and in the three feeding guilds (Fig. 2a). Over time the species composition shifted from benthivores in the first decade, to piscivores in the third decade, and planktivores in the second and last decades (Fig. 2a). The species in each trophic guild actually feed to different degrees on all three prey categories (Table 1). Benthivores (e.g., haddock and ocean pout) and planktivores (e.g., herring and mackerel) are more restricted in their diets, but piscivores (e.g., cod and winter skate) have an average intake spread fairly evenly among plankton, benthos and juvenile fish. The piscivores should in fact be termed omnivores, but we retain the conventional nomenclature to emphasize predation on fish in the food web. Partitioning of consumption among guilds will be altered by changes in the lower trophic web.

(2) Fish consumption of plankton plus benthos (Fig. 2b) showed a marked increase in total food intake by fish after the first decade of the time series. Steele et al. (2007) attributed the markedly lower consumption during 1963-1972 to lower primary
production resulting from a significantly decreased concentration of NO$_3$ (Petrie and Yeats, 2000) in an intrusion of the cold Labrador Current (Pershing et al., 2001) at the shelf edge. Because the food web model assumes linear responses, reductions in primary production are distributed proportionally among the three trophic groups.

(3) There was a marked decrease in benthos as a fraction of total food consumption by fish (Fig. 2c). Steele et al (2007) attributed this to a decrease in the epifaunal suspension feeders that compete for phytoplankton (Fig. 1), possibly due to habitat destruction (National Research Council, 2002; Hermsen et al., 2003).

Bottom-up representation of the end-to-end food web [main heading]

In this study, we have converted the top-down and bottom-up components to a single bottom-up representation of the annual average production by each element of the total food web in carbon units. For the fish components, we took averages for the decade 1993-2002, which corresponds most closely to the GLOBEC years used for the lower web calculations. For the lower web, we took weighted averages over the spatial domains and seasons.

From equation (1) the resultant expression for a bottom-up food web at steady state is:

\[ e_i \left( \sum_j a_{ij} P_j + G_i \right) - \sum_i a_{ij} P_j - f_i P_i = 0. \]  

Since \( \sum_i a_{ij} = 1 \), then
The matrix $[a_{ij}]$ is given in Table 2, and the vectors for $e_i$ and $f_i$ in Table 3. Upper closure is obtained by total removal of fish guilds by fishing and top predators. Marine mammals and sea birds are implicit as top predators in this budget. Estimates of their consumption of fish (Yodzis, 2001) are approximately 4% and 1% respectively. The coupled set of equations (3) was solved by matrix inversion to obtain the annual production of each trophic component (Table 3). These results were used as a baseline (Scenario 0) for comparing production in other scenarios.

Food-web scenarios [subheading]

Our goal is to examine the consequences of alterations in particular ecosystem processes on the yields of the benthivore, haddock ($Melanogrammus aeglefinus$) and the piscivore, Atlantic cod ($Gadus morhua$). To do this, we first estimate changes in the fish feeding guilds produced by changes in internal food web processes. To translate from guilds to species requires estimates of the maximum, or expected, fraction contributed by member species to the total biomass of each guild. Using Steele et al.’s (2007) fish biomass data, we calculated the maximum fractional abundance of each guild member for each year and then found the 40-year maximum and mean, as percentages, for the three guilds (Table 4).

A variety of explanations have been invoked to explain the major changes in the fish communities on Georges Bank and other fishing grounds in the western North
Atlantic (Beaugrand et al., 2003; Choi et al., 2004; Frank et al., 2005; Myers et al., 2007; Jackson et al., 2001; Worm and Myers, 2003). We consider a set of scenarios that simulate such changes in the trophic groups resulting from adaptations in internal food-web processes. These scenarios are produced by altering the relative magnitudes of fluxes in the food web from the baseline 1993-2002 production values (Table 3). Technically, this is done by changing values in the production matrix (Table 2; see Appendix for changes). The results are expressed as percent changes from the baseline values in the production of plankton, benthos, and juvenile fish as prey (Fig. 3a) and in the production of planktivores, benthivores, and piscivores as consumers (Fig. 3b).

**Scenario I: Piscivores are the dominant fish guild.** We transferred 70% of the production of planktivores and benthivores to the piscivores, while retaining the proportions of juvenile fish, plankton and benthos in the piscivore diet. This change gave the piscivore guild 66% of total production, matching the maximum in Fig. 2a. The result was a 200% increase in piscivore production (Fig. 3b). Total fish production is reduced because more food goes through the juvenile fish.

**Scenario II: Benthivores are the dominant guild.** The benthivore diet consists predominantly of benthos, so relatively little food can be reallocated from the other fish guilds, especially planktivores. Switching some benthos production from piscivores to benthivores increases benthivore production by only 111% (Fig. 3b).

**Scenario III: Carnivorous zooplankton are eliminated.** There are numerous suggestions in the recent literature (Pauly et al., 1998; Mills, 2001; Jackson et al., 2001; Lyman et al., 2006) that over-fishing has produced a marked increase in gelatinous zooplankton. On Georges Bank the invertebrate predators on the mesozooplankton
include ctenophores, chaetognaths, hydroids and carnivorous copepods. As an extreme case, we have removed them from the food web so that mesozooplankton production goes directly to fish. This removal increases piscivore production by only 51% (Fig. 3b). Understandably planktivore production also increases, but the benthivore increase is negligible.

**Scenario IV: Carnivorous benthos is eliminated.** Increases in shrimp, crabs and lobster in the North Atlantic (Worms and Myers, 2003) and the North Sea (Heath, 2005) have been attributed to over-fishing of cod and other demersal species. An increase in crustaceans has not been reported on Georges Bank, but as an extreme case we eliminated all benthic invertebrate carnivores. Elimination of this link results in an increase of only 32% in piscivore production, but 60% in benthivore production (Fig. 3b).

**Scenario V: Production of suspension feeding benthos is increased.** In the analysis of food consumption by fish over the four decades, consumption of benthos as a percentage of the total fish intake decreased from >60% at the beginning of the time series to ~30% in later decades (Fig. 2a) (Steele et al., 2007). We simulated this process by redirecting the fluxes of phytoplankton from mesozooplankton to suspension feeding benthos. This reallocation changed the percent of benthos in the aggregate fish diet from 31% to 65%, close to the observed change. The switch from plankton to benthos also increases the total (plankton plus benthos) food available because the benthos, unlike the plankton, is not subject to fractional loss by physical export off the Bank. This change resulted in a large increase in benthivore production and a much smaller increase in piscivores (Fig. 3b).
Scenario VI: The role of microzooplankton is reduced. It is not evident that changes in fish stocks will restructure the lower trophic web, but this type of trophic cascade has been said to occur in other ecosystems (Frank et al., 2005; Oguz and Gilbert, 2007). To illustrate changes within the lower web, we reduced consumption of phytoplankton by microzooplankton by 1/3 and redirected it to the suspension feeding benthos. As expected, this scenario produced a large increase in benthivore production (219%) and smaller gains in piscivores (88%) (Fig. 3b).

Scenario VII: Direct input of phytoplankton to detritus is eliminated. Bacterial decomposition of detritus in recycling nutrients is a critical process, but its magnitude in any system is uncertain. In calculating energy budgets for Georges Bank Steele et al. (2007) took the fraction of detritus recycled to NH₄ as an unknown and used it to match the calculated and observed rates of recycling. To illustrate the possible effects of decreased recycling, we eliminated the direct input of phytoplankton to detritus. Again, the benthivores gained more than the piscivores (Fig 3b).

The general conclusion from these scenarios (Fig. 3b) is that, for piscivores, including cod, the main factors increasing production occur at the higher trophic levels by redistributing fish food (Scenario I) or removing pelagic invertebrate predators (Scenario III). For benthivores, including haddock, the primary increases occur at lower trophic levels and depend predominantly on the switch from mesozooplankton to suspension feeding benthos (Scenarios V, VI). The changes produced by Scenario IV are relatively small and, because there is no evidence of increased carnivore populations in the benthos on Georges Bank, we do not consider this scenario further. Similarly there is no evidence
for changes in the lowest trophic levels, so Scenarios VI and VII are not considered further, although they could potentially enhance the switch to benthivores.

Relation to fishery yields [subheading]

As a prelude to considering future changes, we can evaluate how well food-web Scenarios I-VII explain past fishery yields. Several authors (Pauly, 1995; Kurlansky, 1997; Myers et al., 2007) have pointed out the problems of “shifting baselines” and emphasized the difficulty of reconstructing the pristine structure of ecosystems such as Georges Bank that have been exploited for centuries (Hennemuth and Rockwell, 1987; Steele and Schumacher, 1999). Quantitative data for landings of cod and haddock extend back to the beginnings of the 20th century (Fig. 4). The early dominance of cod landings is attributed to the fact that haddock did not salt well (Hennemuth and Rockwell, 1987). From 1921 to 1950 the stocks were not considered to be over-fished (Hennemuth and Rockwell, 1987), providing one set of reference values (Fig. 5). After the combined period of low basic productivity and excessive fishing effort in the 1960s and early 1970s (Gifford et al., 2009), the relative magnitude of cod and haddock catches was reversed for the two decades 1971-1990 (Fig. 5). Lastly, for the decade used to construct the food-web budget, 1993-2002, both fisheries were at a low level (Fig. 5). These observations provide a baseline for comparison with the food-web scenarios (Fig. 3).

The values for MSY of cod and haddock in Fig. 5 are taken from the most recent available estimates (NEFSC, 2008). To relate haddock and cod production to the scenarios for their respective guilds, we take 71% and 74% as the maximum percentage production for a single species in the respective guilds (Table 4). We use the following
formula to convert the food-web production rates, \( P \) (gC m\(^{-2}\) yr\(^{-1}\)), to fishery yields, \( Y \) (t yr\(^{-1}\)) for the whole of Georges Bank

\[
Y = \frac{F}{C/B} \times \frac{P \cdot A}{P/B} \times \frac{MSY}{B_{MSY}}
\]

where, \( F \) is the fraction of guild production allocated to cod or haddock (Table 4), \( A \) is the area of Georges Bank (43,000 km\(^2\)), \( C/B \) is the ratio of carbon to biomass (0.114) and \( P/B \) is the production-biomass ratio of piscivores (0.41) or benthivores (0.39) (Steele et al., 2007). We used the most recent estimates of \( MSY \) and biomass at \( MSY \) \( (B_{MSY}) \) (NEFSC, 2008) to calculate the exploitation rate \( (U_{MSY}) \) and hence the fraction of production required to support the fishery at \( MSY \) (Table 5).

In Fig. 5, Scenario 0 represents the maximum potential yields of cod and haddock assuming no change from the 1993-2002 food-web configuration in terms of fish diets (Table 1), other than realizing maximum dominance of these species within their respective guilds. The yields are intermediate between the earlier (1921-1950) and middle (1971-1990) periods, and can almost achieve the \( MSY \) levels for haddock and cod if both species are at their maximum achievable abundances within their respective guilds (Table 4). If cod and haddock abundances are closer to the recent 40-year average dominance (Table 4), yields would be well below estimated \( MSY \). Thus it is necessary to consider the consequences of changes within the food web.

Scenario I switches the available food toward cod (Fig. 5), but this switch does not benefit haddock and requires a massive reduction in pelagic fish (Fig. 3b). Another possibility is to reduce significantly the role of invertebrate pelagic predators (Scenario...
III, Fig. 5). This scenario increases the abundance of all fish guilds and, in particular,
corresponds to the relative abundance of cod and haddock in the period 1971-1990.
Although there is increasing speculation about such ecosystem alterations (Mills, 2001;
Jackson et al., 2001; Lyman et al., 2006), there is no direct evidence of such a change in
the Georges Bank food web.

Scenario V involves the redistribution of primary production from
mesozooplankton to benthos, particularly epifaunal suspension feeders (Fig. 5). This
change produces relative abundances of cod and haddock similar to the earlier 1921-1950
period. The overall increase in production of all fish guilds (Fig. 3) arises from the
decrease in washout of plankton from Georges Bank when the benthos is dominant.
Washout of plankton from this relatively small off-shore fishing ground is more
significant than for larger coastal ecosystems (Klein, 1987). This scenario explains the
relative abundance of benthic feeding fish in the decades before 1970, compared with
areas such as the North Sea (Cohen and Grosslein, 1987) and compared with the present
Georges Bank ecosystem. Steele et al. (2007) showed that the fraction of benthic food in
the aggregate fish diet declined from ~0.6 in the early 1960s to ~0.3 after 1980 (Fig. 2c).
This shift can be linked to the greatly increased habitat disturbance occasioned by
modern trawling methods (Hermsen et al., 2003) and/or to environmental changes (Collie
et al., 2008).

Discussion
The use of scenarios in this analysis depends on the acceptance of a linear steady-state description of the Georges Bank trophic web. The natural system is unlikely to be linear and certainly is not at steady state, even as an annual average. But non-linear dynamic simulation models with large numbers of state variables are unlikely to be more realistic and they have less heuristic value (Oreskes et al., 1994; Ginsberg and Jensen, 2004). Because linear bottom-up simulations of food webs are generally donor controlled (Steele, 2009) and therefore stable, these scenarios represent asymptotic solutions in dynamic simulations (Steele, 2009). We have not performed specific sensitivity analyses, but the scenarios approximate the sensitivity of the system to changes in the parameters (Appendix). Given these caveats, four inferences may be drawn from these calculations and from Steele et al (2007), beginning with physical processes at the base of the trophic web.

(1) Physical forcing, demonstrated by the changes occurring in 1963-1972, can decrease production by a factor of two compared with the later decades and must be considered a “natural” process influencing fish production. Our linear budget model implies that any change in nutrient flux affects the fish guilds equally. Large changes in nutrient supply could affect the partitioning of energy in the lower trophic web, but we have no evidence for a non-linear assumption in continental-shelf ecosystems. It seems unlikely that top-down cascades would alter nitrogen recycling within the microbial web significantly. Possible connections to climatic change (Pershing et al., 2001) suggest a link to periods of negative NAO index. Because the years 1955-1972 experienced the most sustained negative NAO index during the last century (Wisbeck et al., 2001), the total productivity in earlier and later decades may be comparable.
Within this overall productivity, a long-term switch from benthic to pelagic production occurring in the 1970s is indicated by a 50% reduction in the fraction of benthos in the aggregate fish diet (Steele et al., 2007). This switch can be attributed to habitat destruction by mobile fishing gear (Hermsen et al., 2003). If nutrient fluxes were comparable for the interwar period and the decade 1993-2002, then the yields of haddock and cod during 1921-1950 would be achieved with 56% and 40% presence in their respective guilds. This is significantly less than the maximum observed value of 72% required with the status quo, and is closer to the long-term averages (Table 4).

In the various scenarios, the largest changes in cod and haddock stocks arise from major restructuring of the fish community that changes the pattern of species dominance within the fish diet guilds. The marked decline of cod after the 1980s was balanced by an outburst of another piscivore, winter skate (Leucoraja ocellata), a predator of sand lance (Ammodytes americanus) (Gifford et al., 2009). The subsequent decline in winter skate corresponded to an increase in other piscivorous species, principally spiny dogfish (Squalus acanthias). The decline in haddock corresponds to a reduction in the proportion of benthic food in the aggregate fish diet (Steele et al., 2007) and also with some increase in another benthivore, ocean pout (Macrozoarces americanus).

Possible increases in pelagic and benthic invertebrate predators are frequently proposed as factors that could result in significant diversion of food energy from vertebrates (Jackson et al., 2001; Worm and Myers, 2003). There is no evidence of an empty fish niche on Georges Bank, nor should we expect such evidence. Significant increases in one fish guild require decreases in others, or major changes within the food
web. An increase in cod, within the piscivore guild would require decreases in other
piscivores—such as the elasmobranches, winter skate or spiny dogfish—or changes in
other guild species such as haddock, herring or mackerel, which maintain the overall
balance in the diet of plankton, benthos and juvenile fish.

The present challenge is to rebuild the principal demersal species, including cod
and haddock, in an ecosystem with an altered fish species composition. Thanks to the
very large 2003 year class, Georges Bank haddock is now considered to be in the process
of rebuilding (Northeast Fisheries Science Center, 2008), but recent low growth rates
suggest that production of benthic food may limit recovery. The yields of other species
in the fish community must also be considered. For example, the combined $MSY$ of the
benthivores haddock, yellowtail ($Limanda ferruginea$), and winter flounder
($Pseudopleuronectes americanus$) totals 45.6 kt (Table 5). Under Scenario 0, the entire
production of the benthivore guild would be required to support this combined yield.
Scenarios III, IV or V would be required to allow production of the other 11 species in
the benthivore guild (Steele et al., 2007). There are several migratory species for which
it is difficult to assign a yield to Georges Bank. Of these, Atlantic herring ($Clupea
harengus$) and Atlantic mackerel ($Scomber scombrus$) are at historically high abundance
levels (Steele et al., 2007), a situation that exacerbates the challenge of recovering
demersal fish stocks in a pelagic-dominated ecosystem.

In summary, we cannot specify whether past or future mechanisms of change,
such as regime shifts (Collie et al., 2004), are responsible for the decline of cod and
haddock stocks, or are required for their recovery. Our approach cannot define the cause
of transitions from one state to another, nor the modifications required to rebuild the
demersal fish stocks on Georges Bank. The observed trends in the patterns of dominance within the fish community implicate over-fishing as a primary cause of past changes on Georges Bank, and any future increase in commercial stocks will require significant redistribution within the fish community. A return to the balance of species present during the first half of the 20th century will depend on an increase in the fraction of primary production going to the benthos and may require changes in benthic habitats.

Acknowledgements

We acknowledge NOAA-CICOR award NA17RJ1233 (J.H. Steele) and NSF award OCE0217399 (D.J. Gifford and J.S. Collie). We thank M.J. Fogarty for providing data and comments on an earlier draft. Contribution number ### of the US-GLOBEC Georges Bank program.


Table 1. Percentage diets of the three fish guilds. Average and range for the four decades 1963-2002 (after Garrison and Link 2000).

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<th>Benthos</th>
<th>Plankton</th>
<th>Fish</th>
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<tr>
<td>Benthivores</td>
<td>85 (82-88)</td>
<td>11 (8-14)</td>
<td>4 (0-10)</td>
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<tr>
<td>Planktivores</td>
<td>14 (3-25)</td>
<td>82 (74-91)</td>
<td>4 (0-10)</td>
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<tr>
<td>Piscivores</td>
<td>42 (37-45)</td>
<td>24 (18-29)</td>
<td>34 (28-37)</td>
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Table 2. The production matrix, $AP = [a_{ij}]$ for an end-to-end Georges Bank food web, expressed as the percentage of nitrogen or carbon transferred from food web component $j$ (columns) to component $i$ (rows) including recycling in the lower web. (Note that in the actual calculations (Eq. 3) the $a_{ij}$ are proportions.)

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Table 3. Annual values of nutrient input ($G$), transfer efficiency ($e$) fractional physical loss ($f$) for equation (3) and the resultant rate of annual production $P$. $G$ and $P$ are in units of gC m$^{-2}$ yr$^{-1}$

<table>
<thead>
<tr>
<th>Food-web component</th>
<th>$G$</th>
<th>$e$</th>
<th>$f$</th>
<th>$P$</th>
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Table 4. Maximum and mean fractions of biomass contributed by the annual dominant species within each of the three fish guilds over the 40 years, 1963-2002.

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<thead>
<tr>
<th></th>
<th>Piscivores</th>
<th>Benthivores</th>
<th>Planktivores</th>
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<tr>
<td>Maximum</td>
<td>0.71</td>
<td>0.74</td>
<td>0.92</td>
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<tr>
<td>Mean</td>
<td>0.41</td>
<td>0.43</td>
<td>0.59</td>
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Table 5. Maximum sustainable yield (MSY), biomass at MSY (B_{MSY}) and exploitation rate at MSY (U_{MSY}) for four Georges Bank fish stocks (from NEFSC, 2008).

<table>
<thead>
<tr>
<th>Species</th>
<th>MSY (kt)</th>
<th>B_{MSY} (kt)</th>
<th>U_{MSY}</th>
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<tr>
<td>Cod</td>
<td>31.159</td>
<td>148.084</td>
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<td>Haddock</td>
<td>32.746</td>
<td>158.873</td>
<td>0.206</td>
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<td>Yellowtail flounder</td>
<td>9.400</td>
<td>43.200</td>
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<td>Winter flounder</td>
<td>3.500</td>
<td>16.000</td>
<td>0.219</td>
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Figure legends

Figure 1. Georges Bank food web. Solid arrows represent predator-prey links. The input, NO₃, drives the microbial food web including recycling of nitrogen as NH₄ (dashed lines). Dotted lines are physical losses. The ovals for Total Plankton and Total Benthos indicate the food available for the fish guilds. See Table 3 for the flux values.

Figure 2. Time series of (a) percentage biomass in the three fish guilds, (b) consumption of benthos and plankton by the fish community, and (c) fraction of benthos in the total food intake—plankton plus benthos.

Figure 3. Effects of individual food web scenarios, I-VII, on (a) percentage changes in production of total plankton and benthos available as food for fish and of juvenile fish that form part of the diet of piscivores, and (b) the production of the three feeding guilds.

Figure 4. Landings of cod and haddock from Georges Bank (kt yr⁻¹) (from NOAA web site www.nefsc.noaa.gov/nefsc/publications/)

Figure 5. Average biomass yields of haddock and cod for three periods on Georges Bank compared with maximum sustainable yields (MSY) and with yields estimated from various food-web scenarios assuming that cod and haddock yields are 71% and 74% of their respective guilds (see text).
Appendix. Changes to the percentages in matrix $\mathbf{AP} = [a_{ij}]$ (Table 2) required for the seven Scenarios.

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<td>AP(17,14)=94;</td>
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