Balancing end-to-end budgets of the Georges Bank ecosystem

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Abstract

Oceanographic regimes on the continental shelf display a great range in the time scales of physical exchange, biochemical processes and trophic transfers. The close surface-to-seabed physical coupling at intermediate scales of weeks to months means that the open ocean simplification to a purely pelagic food web is inadequate. Top-down trophic depictions, starting from the fish populations, are insufficient to constrain a system involving extensive nutrient recycling at lower trophic levels and subject to physical forcing as well as fishing. These pelagic-benthic interactions are found on all continental shelves but are particularly important on the relatively shallow Georges Bank in the northwest Atlantic. We have generated budgets for the

lower food web for three physical regimes (well mixed, transitional and stratified) and for three seasons (spring, summer and fall/winter). The calculations show that vertical mixing and lateral exchange between the three regimes are important for zooplankton production as well as for nutrient input. Benthic suspension feeders are an additional critical pathway for transfers to higher trophic levels. Estimates of production by mesozooplankton, benthic suspension feeders and deposit feeders, derived primarily from data collected during the GLOBEC years of 1995-1999, provide input to an upper food web. Diets of commercial fish populations are used to calculate food requirements in three fish categories, planktivores, benthivores and piscivores, for four decades, 1963-2002, between which there were major changes in the fish communities. Comparisons of inputs from the lower web with fish energetic requirements for plankton and benthos indicate that we obtained reasonable agreement for the last three decades, 1973 to 2002. However, for the first decade, the fish food requirements were significantly less than the inputs. This decade, 1963-1972, corresponds to a period characterized by a strong Labrador Current and lower nitrate levels at the shelf edge, demonstrating how strong bottom-up physical forcing may determine overall fish yields.

Keywords: bottom-up, energy budget, food web, Georges Bank, physical forcing, top-down

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1. Introduction

The primary objective of this study is to construct a budget for the fluxes of nutrients and carbon through the Georges Bank ecosystem. Energy or material flows within ecosystems are usually portrayed as steady-state networks in which the nodes are trophic groups and the links are fluxes from one node to another. The mass balance relations are linear in the sense that the output from any node is proportional to the input. The earliest networks for marine ecosystems had relatively simple uni-directional flows of carbon or biomass from primary production to fishery yields (e.g. Steele, 1965; Sissenwine et al., 1984). Since then our appreciation of the importance of recycling of nutrients within the microbial loop (Azam et al., 1983) has complicated analysis of the lower web. In addition, increasing knowledge of fish stocks and their diets has encouraged a top-down approach to food web fluxes through the upper levels of the web (Christensen and Pauly, 1993)

We use a linear steady-state representation of the food web. Because of the great range in time scales – from phytoplankton to fish – and the different units – nitrogen and carbon - it is necessary to split the web into two components, lower and upper webs (Fig. 1). For the lower web we take nitrate input and ammonium recycling as the drivers for this system and calculate the output as plankton and benthos production. For the upper web we use biomass and diet data for the fish stocks as the driver for a top-down calculation of the fish food requirements in terms of plankton and benthos. The data for the lower web are derived predominantly from the 1980's and 1990's, especially the GLOBEC surveys during 1995-1999 (Wiebe et al., 2003). The data on fish biomass span four decades, 1963-2002. For an initial integration of upper and lower webs, we use the period 1993-2002. We compare the bottom-up and top-down carbon fluxes, and reconcile these inputs by seeking values for the fluxes through the carnivorous plankton and benthos. We then evaluate how far these solutions can be applied to the fish populations in the three earlier decades. Lastly we compare the estimates of plankton and benthos with available observations. These comparisons provide a broad check on the solutions obtained for the intermediate trophic levels.

The structure of the paper is as follows.

(1) We begin with a review of the necessary units and conversion factors for this wide range of ecological components.

(2) We then describe the calculations for the lower web in terms of the physical processes of vertical and horizontal mixing on Georges Bank and the recycling of nutrients. We

determine the annual production, in carbon units, of plankton and benthos averaged over the entire Bank.

(3) For the upper web, we estimate food intake by three fish guilds, planktivores, benthivores and piscivores, from fish biomass and diet data (Garrison and Link, 2000; Link and Almeida, 2000). These values are transformed to give food requirements for plankton and benthos in carbon units for the four decades.

(4) Using these estimates for the lower and upper webs, we calculate the values of fluxes through the invertebrate planktonic and benthic carnivores (Fig. 1) that will satisfy the top-down estimates for the four decades, 1963-2002, and bottom up estimates based on 1995-1999. For the decade 1963-1972, where there is no match of the fish consumption of plankton with the production estimates, we seek an explanation within the changing physical regime.

(5) As a test of these results, we compare data on plankton and benthos biomass with estimates from the budget calculations transformed from fluxes to carbon concentrations.

(6) We compare our results with work in other areas.

2. Units and Conversion Factors

Studies of components of the Georges Bank food web (Fig. 1) range from biogeochemical analyses of nitrogen fluxes in the lower web, to biomass estimates of individual fish populations. To combine these we need to (1) compare measures in units of biomass, carbon and nitrogen, (2) convert biomass estimates to production and consumption, and vice versa, and (3) transfer these measures between different trophic levels.

2.1. Biomass units

Carbon is the common currency in the upper and lower trophic webs. There can be considerable variation in the carbon:nitrogen ratios for different components of the microbial loop, such as phytoplankton, microzooplankton and detritus (Parsons and Takahashi, 1973; Harris et al., 2000) and at different times and regions (Sambrotto et al, 1993). We do not attempt to incorporate these variations but use the traditional Redfield C:N ratio of 106:16 by atoms. When presenting outputs from the lower web the nitrogen fluxes are converted to g C.m^{-2}. For the upper web, biomass is measured as wet weight (or live weight) of organisms. There are a wide range of estimates for carbon:biomass ratios for fish. Because we are dealing with Georges Bank communities, we use the value obtained from these communities, carbon:biomass = 0.114 (Grosslein et al. 1980). Zooplankton, carbon is converted from wet weight (0.12) and displacement volume (0.096) according to Harris et al (2000). Benthic biomass data are given in kilocalories and converted to carbon units according to Parsons and Takahashi (1973), where 1 g C=11 kcal.

2.2. Transfer efficiency

The fraction of food intake converted to growth is a critical factor affecting estimates of flux through the food web (Ryther, 1969). Again, there are a wide variety of estimates. Rather than apply particular values to individual species or situations, we use general ranges from the literature for the non-dimensional ratios of growth:intake. For actively growing copepods, the

ratio may be as high as 0.30-0.45 (Mullin and Brooks, 1970), but a value of 0.30 is typically used (Harris et al, 2000). We take a range of 0.10-0.30. In the calculations for the lower food web, we find this is consistent with the range of winter to spring and summer values corresponding to expected components of the mesozooplankton life cycles (see below). For fish, a transfer efficiency of 0.10 is generally used (Christensen and Pauly, 1993), but Rothschild (1986) and others query this low value. We use 0.10 for the recruited stocks and 0.30 for the juveniles. For the meio-, macro- and predatory benthos we use an intermediate value of 0.20. In the lower web we need to account for all of the other "outputs" by plankton. We assume that the fraction of intake that is particulate fecal material is equal to the growth fraction. The remainder of the nitrogen intake goes to soluble excretion and, via bacteria, to recycled ammonium.

2.3. Consumption to biomass (C:B) ratios

The basic units in the calculations are fluxes between food web components. The common unit is g $C.m^{-2}.yr^{-1}$. The survey data for fish are in biomass units. To convert these to consumption requires estimates of the C:B ratios. We use the Grosslein et al.'s (1980) values of 3.9 yr^{-1} for benthivores, 4.1 yr^{-1} for piscivores, and 4.4 yr^{-1} for planktivores. To convert seasonal estimates of plankton flux to biomass, it is necessary to consider temperature and size. We use the Hirst and Lampitt (1998) formulation for all species and take an average value of 0.25 for the transfer efficiency. Because the C:B ratios of phytoplankton, bacteria and microzooplankton are higher than those of zooplankton, values of 0.5-1.0 d^{-1} are used here (Table 1). This leaves detritus, an omnipresent but ill-defined component. Although these values remain uncertain, we have used values in the "meso" rather than the "micro" range for turnover rates.

3. Lower Food web

Georges Bank is an off-shore shallow shelf located to the southeast of the Gulf of Maine

in the northwest Atlantic (Fig. 2a). We characterize its spatial structure by specifying three

regimes in terms of vertical hydrographic processes after Pingree et al. (1978) (Fig. 2b, 2c, and

2d). The regimes are Mixed (always well mixed), Transitional (episodically mixed) and

Stratified (seasonally stratified). These correspond to regions defined from tidal and shelf-edge

fronts and seasonal mixing (Simpson & Hunter, 1974). The sizes of the spatial domains (Table 2)

were determined from analysis of satellite-derived sea surface temperature fields (Mavor and

Bisagni, 2001). The seasonal components of the annual production are defined by the

temperature and nitrate cycles and are represented by a Spring period (May-June) of nutrient

draw down, a Summer period (July-October) characterized by constant, low nutrients, and a

Fall/Winter period (November-April) when nutrients rebuild or regenerate. The result is a

combined space-time division into nine separate scenarios. For each scenario, a steady state is

assumed for the fluxes of nitrogen through the ecosystem. The sum of these fluxes provides the

input to the upper web.

3.1. New and total primary production

The underlying assumption from open ocean studies is that ammonium (NH_4) uptake

represents the recycled component of production whereas nitrate (NO_3) uptake determines new

production because the NO_3 comes from deeper water below the euphotic zone (Eppley and

Peterson, 1979; Laws et al., 2000). In contrast to the open ocean, the benthic food web is an important component of nutrient recycling on continental shelves. Nitrification of organic matter to NO_3 is usually considered to be a relatively slow process (Harvey, 1957). Although nitrifying bacteria are widely distributed in the ocean, they are rarely abundant and their growth rates are believed to be slow. The extent to which heterotrophic bacteria oxidize NH_4 to NO_2 and NO_3 is not well understood (Karl and Michaels, 2001), except that it is inhibited by light and occurs below the 10% light level (Ward, 2000). Karl and Michaels (2001) cite experimental work by von Brand and Rakestraw (see Harvey, 1957) done more than 50 years ago that shows a two-month time lag for the formation of NO_3 from NH_4. Anderson and Williams (1998) propose a value of 0.033 d^{-1} for the rate of conversion of organic nitrogen in the sediment compartment to ammonium, and 0.03 d^{-1} for nitrification in the water column. Observations and models of phosphate regeneration below the euphotic zone in the North Sea suggest the same time scale from uptake to reappearance in the water column (Steele, 1956; Luff and Moll, 2004). The residence time of NH_4 in the euphotic zone during spring, summer and fall is on the order of days, and should be shorter than regeneration in winter. On this basis we assume that any significant input of NO_3 to the euphotic zone comes from deep water.

The daily rate of NO_3 uptake by phytoplankton over any interval Δt can be calculated from the sum of the draw-down of NO_3 over the euphotic zone, depth z^*, plus the flux of NO_3 through the base of the euphotic zone (Bisagni, 2003), determined by the vertical eddy diffusivity, K_z in nitrogen units

$$NP = \Delta \left[\int_{z*} NO_3.dz\right] / \Delta t - \left[K_z.\partial \, NO_3/\partial z\right]_{z*} \tag{1}$$

where NP is new production. The potential new production (PNP) in carbon units ($g \, C.m^{-2}.d^{-1}$) is

$$PNP = 79.5 \, . \, NP.$$

Values for integrated total primary production ($ITPP$) from the surface to the base of the euphotic zone are determined from ^{14}C uptake data for 1977-1982 (O'Reilly et al; 1987). The f-ratio used here is defined as

$$f = PNP/ITPP.$$

This ratio is *not* equivalent to that of Eppley and Peterson (1979), i.e., the ratio of the assimilation rate of new inorganic nitrogen [NO_3] to total inorganic nitrogen [$NO_3 + NH_4$].

The values of PNP, $ITTP$ and f-ratio for the nine scenarios on Georges Bank were determined as follows. PNP was calculated as 5-day averages using equation (1) based on estimates of the vertical eddy diffusivity on Georges Bank. Values of $ITPP$, PNP and f were calculated using the mean annual cycle curves from Bisagni (2003) for each of the nine scenarios (Table 3). Seasonally, new production is highest in the spring, reflecting the supply of new NO_3 onto the Bank. New production and corresponding f-ratios are highest in the Transition region (Table 3). High total primary production in summer is sustained by recycled nutrients.

3.2. Physical exchange rates

The general pattern in these production estimates agrees well with other studies such as the 3-dimensional model of Franks and Chen (2001). However, the flux calculations for new production (Table 3) are purely 1-dimensional, estimating how much NO_3 must be utilized within the euphotic zone plus mixing of NO_3 into this zone (Eq. 1). This does not consider the lateral flux of NO_3 needed to provide replenishment in the deeper layers (Fig. 3). We use estimates of this lateral nutrient flux to calculate the required physical exchanges (Table 4). These horizontal fluxes are determined for the three regions and three seasons by estimating the lateral exchange of water needed to provide the excess NO_3 required for new production, over that available within the water column (Table 4). These inward fluxes in deeper water require physical losses in the upper layers that will export plankton.

The physical losses, *F*, in Table 4, are calculated as the fraction of water exported laterally per day from the euphotic (40m) zone to allow for import of deeper nutrient-rich water (see Fig. 3).

$$F = (NP/40 + \Delta NO_3/\Delta t)/(DeepNO_3 - SurfaceNO_3) \qquad (2)$$

Where *NP* is new primary production, ΔNO_3 is the seasonal increase in NO_3 in the euphotic zone, and Δt is length of season.

At steady state in summer there must be a flux of NO_3 into the euphotic zone to balance the uptake for *NP*. In fall and winter, the flux of NO_3 from deep water must meet both new production and $\Delta NO_3/\Delta t$ in the upper layer, although there may be some contribution from *in situ* regeneration. Correspondingly, in spring much of *NP* occurs as draw-down of NO_3 and the decrease in NO_3 can offset much of the *NP*. For the Stratified region, the flux of NO_3 occurs vertically across the bottom of the euphotic zone. For the Transition region there is flux through the deep boundary with the Stratified region (Fig. 3). The flux for the Mixed region is assumed to occur with deeper Transition region water. This is difficult to estimate, but the Mixed region is relatively small. These factors are reflected in the "Deep" values in Table 4 used to calculate *F*. We assume that the flux out of the Transition region into the Stratified region is balanced by similar loss from the Stratified region. The losses from the Mixed region are from a relatively small area and are assumed to go directly off the shelf, possibly to the northeast.

The available calculations of nutrient flux based on observations are confined to the spring months. Townsend and Pettigrew (1997) estimated the flux into areas < 60 m depth as 3.4 $mM.m^{-2}.d^{-1}$, or 0.085 mM $m^{-3}.d^{-1}$ for a 40 m euphotic zone. The calculated values of fractional exchange rates for the Mixed and Transition zones in spring give a range of 0.05-0.13 mM $m^{-3}.d^{-1}$ (Table 4). Townsend and Pettigrew (1997) considered Horne et al.'s (1989) flux estimates to be significantly too high, and we agree.

These estimates of fractional exchange rates out of the regions are important for the plankton components of the webs because they can result in eventual wash-out from the Bank. Such advection has long been recognized as a potentially limiting factor for the transfer of

production to higher trophic levels, especially by the mesozooplankton (Cohen et al., 1982; Klein, 1987). Comparison of the mesozooplankton C:B values (Table 1) with the physical flux rates (Table 4) shows that the latter are comparable in winter but are an order of magnitude lower in summer. Thus physical fluxes play a significant, but variable, role in the budget.

3.3. Network for the lower food web

Energy or material flows within ecosystems are usually portrayed as linear steady-state networks in which the nodes are trophic groups and the links are fluxes from one node to another. The earliest networks for marine ecosystems (e.g. Steele, 1965; Sissenwine et al., 1984) had relatively simple uni-directional flows of carbon or biomass from primary production to fishery yields. In contemporary ecosystem models, nutrient recycling is a central component of the microbial web.

For the lower web, where all soluble and particulate pathways for nitrogen are accounted for by recycling of nitrogen

$$X_i \ = \ \sum_j a_{ij}. \ X_j \ + A_i\text{-} F_i. \ X_i \tag{3}$$

where X_i is production by i^{th} trophic group ("compartment"),

a_{ij} is allocation of production to X_i from other boxes X_j; $\sum_i a_{ij} = 1$,

A_i are external inputs $(A_i > 0)$,

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F_i are fractional physical losses from X_i. $F_i = F/(C_i/B_i)$, with F for each

scenario from Table 4,

and

C_i/B_i is turnover rate from Table 1 for the ith component.

The ecosystem is contained within the euphotic zone for the Stratified and Transition regions but occupies the mixed layer in the Mixed region. Output occurs from (1) pelagic predation on mesozooplankton, (2) sinking of mesozooplankton fecal pellets to the seabed and their consumption by deposit feeders, and (3) filtering of large phytoplankton and microzooplankton by benthic suspension feeders.

There are obvious differences among the three regions. We assume there are no benthic suspension feeders in the Stratified region, and no deposit feeders in the Mixed region. This implies that there is no sinking in the Mixed region and all feces go directly to detritus in the water column. The most interesting and most productive area, the Transition region, has both types of benthic feeders. The problem for this region is to apportion consumption of large phytoplankton and microzooplankton between mesozooplankton and benthic suspension feeders. There are no relevant estimates of consumption by suspension versus deposit feeding benthos. Because the biomasses of these components are about equal, we assume that suspension feeders consume about the same amount as deposit feeders whose food source, feces, is taken to be 30% of the mesozooplankton intake. On this basis, 23% of the large phytoplankton plus microzooplankton and detritus are allocated to the suspension feeders, with the remainder going to the mesozooplankton. Thus we define three different lower webs for the three regions.

A major variable in Fig. 1 is the "small" size fraction of phytoplankton production that goes to the microzooplankton, with the remainder (large phytoplankton and detritus) going to mesozooplankton and suspension feeders. This fraction is based on cell size, with 20 μm dividing small and large cells (Sieburth et al., 1978). Chlorophyll is assumed to be an indicator of the relative production in the two size fractions, and the values from O'Reilly et al. (1987) are used as a measure of this parameter (Table 3).

In equations of the form (3), if a_{ij}, F_i and A_i are known, then a unique solution for X_i can be obtained by matrix inversion. In practice some of a_{ij} are unknown, but there are also constraints on the X_i. If the unknowns equal the constraints, then a solution may be found by searching parameter space. For the lower web we have one major constraint, the *f*-ratio, for each of the nine scenarios. The nature and rates of production of detritus and subsequent pathways are the most intractable of the processes in Fig. 1. This uncertainty includes the role of bacteria in transforming detritus to food for plankton or to NH_4. We take the fraction of detritus (DR) that is recycled to NH_4 as the major unknown. By allowing the proportions of growth, feces and nutrient excretion for zooplankton to vary seasonally we have a second possible unknown in terms of the Transfer efficiency, TE. Here we assume that 0.1<TE<0.3; and that TE takes the maximum value within the constraints.

For each of the nine budgets we then seek values of the two parameters, TE and DR, that satisfy the constraint given by the *f*-ratio (Table 3) and lie within the ranges 0.10<TE< 0.30 and 0< DR<1.0. When these are satisfied, then the assumption that TE will take the maximum value

in the range gives values for TE and DR (Table 5). In 8 of the 9 scenarios this is an acceptable solution. The high *f*-ratio for Fall/Transition (Table 1), gives TE >> 0.3. Because this high value is inconsistent with the other data, we use an interpolated value of *f* = 0.52. The Fall/Winter period is the most heterogeneous and has the least data, rendering the calculations for this period least reliable. Nevertheless, lower values of TE for the winter periods are reasonable. With this correction, a consistent picture of the lower web emerges from the calculations.

The budgets for the nine scenarios can be summed (weighted by area and time) to give an integrated annual budget in carbon units for the lower food web of the entire Bank (Fig 4). The fecal material from mesozooplankton and suspension feeders is assumed to go to deposit feeders, where appropriate. This output requires conversion to production by deposit feeding macrobenthos. There are no data for the role of meiobenthos on Georges Bank. Steele (1965) derived a fraction of 40% for detritus input to meiobenthos in the North Sea. Given the much smaller fraction of Georges Bank that is primarily sedimentary, we use a value of 20%. Assuming that the macrobenthos eat the meiobenthos, and that both have a 20% transfer efficiency, the overall transfer efficiency is 16.8%, giving a value of 4.8 g C m^{-2}.yr^{-1} for production of deposit feeding macrobenthos.

The estimated outputs of plankton and benthos to the upper web are then 27.0 and 10.5 g C. m^{-2}.yr^{-1}, respectively. These form the input of food available to invertebrate carnivores and fish. Note that physical losses by advection off the Bank, 66 g C.m^{-2}.yr^{-1} account for approximately half of the new production, but they are a much smaller fraction of net production, 362 g C.m^{-2}.yr^{-1}.

4. Upper food web

4.1. Fish biomass

The biomass of 35 important fish and squid species (Table 6) was obtained from the Northeast Fisheries Science Center (NEFSC) standardized bottom-trawl survey (Azarovitz, 1981; NEFSC, 1988; Smith, 2004). These species comprise more than 95% of the biomass of fish and squid on Georges Bank. Relative biomass estimates were converted to densities based on estimates of relative catch efficiencies (Edwards, 1960; Harley and Myers, 2001). The spring and fall trawl survey data were averaged to reduce interannual variability. The 35 species were grouped into three trophic categories—benthivores, piscivores and planktivores—based on the NEFSC food-habits database (Link and Almeida, 2000).

Most of the variability in the fish and squid community arises from significant changes in the abundances of individual fish species (Fig. 5). Biomass of the principal commercial species—cod, haddock and flounder—was reduced by fishing pressure in the 1970s and 1980s (Mayo et al., 1992; Fogarty and Murawski, 1998; Collie and deLong, 1999). Among the planktivorous fish, there was a peak in sand lance in the late 1970s and early 1980s (Fig. 5a). Herring and mackerel biomass increased in the most recent years, producing a sharp peak in planktivore biomass. Piscivore biomass was maximal during the late 1970s and 1980s, largely because of increases in elasmobranches, winter skate and spiny dogfish (Fig. 5b). The biomass of benthivorous fish declined with the reduction of haddock in the late 1960s, but has been

relatively constant since then (Fig. 5c). Several non-commercial species, including ocean pout, sculpin, and little skate, compensated for the reduction in commercial species.

4.2 Fish food requirements

The biomass data for the fish feeding guilds were grouped into four decades. Average diet composition data, weighted by the biomass of individual species, were calculated for each guild and decade (Table 7). Conversion factors for biomass to carbon and for consumption-to-biomass (C:B) ratios (see section 2) were used to convert the biomass data to food consumption in units of g C.m^{-2}.yr^{-1} (Fig. 6a).

The nominal members of each trophic category do not, understandably, confine themselves to a single diet type (Table 7). This omnivory is particularly true for the piscivores, which obtain only 1/3 of their diet from fish, but half from benthos, and the remainder from plankton (Garrison and Link, 2000). Additionally, the planktivores consume some benthos. The biomass estimates were combined with the food-habits data to estimate the actual consumption of benthos, fish and plankton over the four decades (Fig. 6b). This calculation converts the fish categories to functional groups rather than species guilds.

The estimates of fish dietary requirements do not include the pre-recruit fish of each species. Sissenwine et al. (1984) estimated the production of pre-recruit fish based on the assumption that cohort biomass is constant from larva to recruit (i.e., Mortality=Growth). They deduced that pre-recruit production was 33 to 50% of the total recruit production. Jones (1984)

demonstrated that the pre-recruit/recruit ratio can vary by a factor of four, depending on the

population trajectory from larva to recruit. Houde (1996) showed that the trajectory is concave

downwards. Given these uncertainties, we derived alternate estimates. We assumed that the

piscivores eat only pre-recruits (including their own) and are the dominant predator on the pre-

recruits (Overholtz et al., 2000). Piscivore consumption therefore provides an independent

estimate of pre-recruit production. Based on the diet data, our value is about 12% of recruit fish

production, in agreement with Houde (1996). Further, we assumed that the pre-recruits eat

predominantly zooplankton and we allowed 25% of their diet to be benthos. By taking the

production/consumption ratio of pre-recruit fish as 0.3 (see Section 2), we obtain an estimate of

their consumption of plankton and benthos. Given these assumptions, it is now possible to

calculate the total consumption of plankton and benthos in each of the four decades (Fig. 6c).

4.3. Comparisons with the lower web.

We now have estimates of consumption by fish, and production from the lower food web,

linked by other trophic groups (Fig. 7a). This introduces two poorly known, but critical,

components-- invertebrate predators on the plankton and benthic inputs from the lower web. The

reconciliation of top-down and bottom-up forcing of the food web is reduced to solving for two

key variables, consumption by the planktonic and benthic invertebrate predators (Fig. 7a). If we

assume that all of the invertebrate carnivores are eaten by pelagic and demersal fish, then the

quantity of consumption by invertebrate predators is calculated by

Fish consumption = (Input – Predator consumption) + Predator production

Invertebrate predator production/consumption = 0.2 (section 2), then

$$\text{Predator consumption} = (\text{Input} - \text{Fish consumption})/0.8. \qquad (4)$$

This gives values for the planktonic and benthic predator consumption with the constraint that

$$\text{Predator consumption} \leq \text{Input.} \qquad\qquad (5)$$

This constraint assumes there are no significant losses of invertebrate predators to sources other than fish consumption.

This comparison of results from the upper and lower web applies directly to the last decade when the data for fish consumption during 1993-2002, overlap with the years of the GLOBEC surveys 1995-1999. Solutions for the last decade (1993-2002) were found for both plankton and benthos (Figs. 7b, 7c). We then used the GLOBEC production values for the lower web to search for solutions for the fish food requirements for the three earlier decades.

In five of the six cases for the earlier decades, all of the production input to the upper food web is consumed either directly by fish or indirectly through invertebrate carnivores (Fig. 7b, c). For the plankton in the first decade, the fish food requirement is so small that there is no exact solution that satisfies constraint (5). The best fit for this decade is that all food intake by the recruited fish is in the form of predatory plankton, but even then the plankton consumption is

less than the production in the last decade. For the benthos, the food intake of the fish can be balanced by the benthic production in all four decades. However, in the first decade (1963-1972), the predator intake needs to be 34% greater than that of the fourth decade, indicating again a significant decrease in the benthic fish requirement in that decade (Fig 7c). The combined fish food requirement for plankton and benthos is 41% of that in the fourth decade but there is a much greater reduction in the plankton requirement compared to the benthos.

4.4. The decade 1963-1972

We need to consider possible causes for differences in the first decade when planktonic food appears to be significantly greater than required by fish. However these budgets for the lower web are based on NO_3 data from the 1980s and 1990s. There are no nutrient observations for Georges Bank for the years 1960-1970, but there is a repeated section on the Central Scotian Shelf that documents an increase in the influence of the Labrador Current from 1960-1970 (Petrie and Yeats, 2000) (Fig.8). The interannual-to-decadal variability of the physical environment on the Scotian Shelf, Gulf of Maine and Georges Bank is largely determined by the fluctuating strength and position of the cold Labrador Current (Pershing et al., 2001). Its signature is evident in the temperature at 100-150 m (Loder et al., 2001). There was a marked cold period during 1960-1970, followed by 25 warm years and then a brief cold spell in 1997-1998 (Thomas et al., 2003) (Fig. 8b). The cold period is also seen in bottom temperatures measured on Georges Bank (Fig. 8c). In the cold years, NO_3 concentration was significantly lower than in warm years by as much as 5-10 $mM.m^{-3}$ (Fig. 8a).

There are no continuous data for plankton covering the four decades. The MARMAP data (Sherman et al, 2002) from 1977 to 2000 show little change during that period. However, data collected with the Continuous Plankton Recorder in the Gulf of Maine show lower phytoplankton color (Zwanenburg et al., 2002) and lower zooplankton biomass (Jossi & Goulet, 1993) for the period 1965-1975 compared with succeeding decades, and there are some decreases in the two dominant mesozooplankton biomass components, *Calanus finmarchicus* and *Pseudocalanus* spp. These sequences confirm the indications from the food web fluxes, that the period 1963-1972 had significantly lower primary production that propagated through higher trophic levels to overall fish production and may be linked to larger spatial patterns such as the North Atlantic Oscillation (Pershing et al., 2001).

If we assume that the lower fish food requirements in the first decade were due to lower NO_3 input, then for this linearly based lower food web, (equation 3) we would expect export to the higher trophic levels to change proportionately within and between the benthic and planktonic components. We can use equation (4) to apportion this production between fish and invertebrate carnivores. In this "low-N" scenario we assume that the same proportions of invertebrate to vertebrate carnivores found in the fourth decade would be achieved in the first decade (Fig. 7). This requires 28% of the plankton and 71% of the benthos fluxes compared with the GLOBEC values. These very different percentages imply that invariant web proportionality does not hold under varying physical regimes. Some web parameters would have to be changed in a low-N regime, but reduced nutrient input could account for the lower fish food requirements in the first decade.

5. Comparisons with Observations

The nutrient data on new and recycled production, and the data on fish biomass and diet are used as drivers for the food web and are not appropriate to test the output. For this we use the available data on the intermediate trophic levels.

5.1. Phytoplankton size categories

A critical assumption in the web calculations is that the fraction of chlorophyll in large cells (Table 1, O'Reilly et al., 1987) provides a measure of the fraction of primary production grazed by mesozooplankton. A comparison of the percentage of primary production grazed by copepods in April, July and October, 1978 (Dagg and Turner, 1982) with the percentage of total chlorophyll as large cells (Table 8) shows considerable overlap except for the Mixed region.

5.2. Microzooplankton

Microplankton and nanoplankton are defined operationally on the basis of size (Sieburth et al., 1978). Both categories include autotrophs and heterotrophs as well as mixotrophic forms. The autotroph standing stock is partitioned into small (<20μm) and large (>20μm) phytoplankton. All heterotrophs and mixotrophs <200μm are assigned to a single box, defined inclusively as microzooplankton. There are no published seasonal or synoptic surveys of microzooplankton on Georges Bank. Here, we use *in situ* data for standing stocks of nanoplankton, microplankton and chlorophyll-*a* collected during five cruises to Georges Bank between January and June 1995 (D.J. Gifford and M.E. Sieracki, unpublished). Seawater was

collected from rosette-mounted 10-l teflon-lined Go-Flo bottles. At stations where the water

column was well-mixed, samples were collected at the top, middle and bottom of the water

column. At stations where the water column was stratified, water was collected above, within

and below the pycnocline and at other targeted depths. Separate samples were collected for

analysis of chlorophyll *a*, nanoplankton and microplankton. Chlorophyll-*a* was analyzed by

fluorometry according to Knap et al. (1996). Nanoplankton samples were processed after

Sieracki et al. (1993) and carbon content was calculated according to Verity et al. (1992).

Microplankton samples were processed and analyzed according to Gifford and Caron (2000) and

carbon content was calculated according to Putt and Stoecker (1989) for ciliates and Lessard

(1991) for heterotrophic dinoflagellates.

Inspection of the microzooplankton data showed increases in standing stocks from winter

to spring (there are no summer data), but no detectable spatial pattern over the three Bank

regions. Thus the data were grouped into winter and spring categories, with each group

containing 15 and 10 values respectively. The median values (± standard deviation) for winter

and spring were 14 (±6) and 40 (±8) mg C.m^{-3}, after removing anomalous outliers. To convert

the standing stocks to energy flow, we assumed that intake (C:B) is in the range 0.5 (winter) to

1.0 (summer) d^{-1} over 40m depth (Table 3). Flux through the microzooplankton in winter is then

0.28 (±0.12) g C.m^{-2}d^{-1} and in spring is 1.20 (±0.24) g C.m^{-2}.d^{-1}, based on a C:B ratio of 0.75).

Estimated fluxes through the microzooplankton from the lower web budgets (Table 9) agree with

observed winter values but are about 75% of observed spring fluxes. Given the variability of the

measurements and uncertainty of conversion factors, this comparison is not unsatisfactory.

5.3 Mesozooplankton

In the Georges Bank GLOBEC field program, mesozooplankton were collected with a 1 m^2 MOCNESS equipped with 0.15-mm nets that sampled the copepodid stages of the dominant species quantitatively (Wiebe et al, 2003). A pump system with 0.035 to 0.050 mm nets was used to sample nauplii (Durbin et al., 2000). Analyses for dry weights were made at 12 stations on the Bank at approximately monthly intervals between January and June 1995-1999. 10 - 20 mesozooplankton samples were collected each month in each region of the Bank and are used here to calculate monthly mean biomasses (± standard deviations) (Fig. 9).

The estimated mesozooplankton fluxes from the budget calculations were converted to carbon biomass using the Hirst and Lampitt (1998) formulae. The C:B ratios are temperature and size dependent. *Calanus finmarchicus* and *Pseudocalanus* spp. are dominant on the Bank during the GLOBEC surveys. We take their weights, 70 and 7 μg C respectively (Lynch et al., 2001), to represent the principal size categories of mesozooplankton. A range of values is given in Table 1. The general pattern of species distribution is that *Pseudocalanus* spp. are dominant on the crest and *C. finmarchicus* near the shelf edge (Lynch et al., 2001; Meise and O'Reilly, 1996). We formalize this by assigning "small" (7 μg C) mesozooplankton to the Mixed region and "large" (70 μg C) mesozooplanktonto the Stratified region, with equal weights of the two species in the Transition zone. These averages for the three seasons are superimposed on the graphs of observed zooplankton biomass (Fig. 9). The estimated biomasses are within the broad limits given by the data, except for spring in the Mixed region, where the estimated spring bloom is too high and the observed value is closer to the summer estimate.

The zooplankton biomass estimates from the lower food web can also be compared with the MARMAP average data for 1977-1999 (Sherman et al., 2002). The MARMAP data (displacement volume . 100 m^{-3}) were converted to g C . 50 m^{-3} using the conversion factor: 1.0 cc displacement volume = 0.1 g C (Harris et al., 2000). The MARMAP averages for the three seasons are 1.2, 3.8 and 2.0 g . 50 m^{-3}. The ranges of estimated values from the budget calculations are 0.5-1.1, 3.2-5.6 and 1.3-2.6 g . 50m^{-3} for winter spring and summer, respectively Because the MARMAP samples were collected with a 330 µm net that undersampled smaller mesozooplankton life history stages, they are likely to underestimate total mesozooplankton biomass. Although the MARMAP data differ in detail from the web calculations, the main trends in the data are similar.

5.4. Carnivorous zooplankton

As part of the GLOBEC Georges Bank sampling program, four categories of pelagic invertebrate predators were collected for the period January to June, 1995-1999: chaetognaths, ctenophores, predatory copepods and hydroids. Rates of their intake of mesozooplankton prey were derived from these data by applying available estimates of consumption.

Chaetognaths. Ingestion by chaetognaths on Georges Bank ranges from 2-8% body weight.d^{-1} (Davis, 1984). From analysis of gut contents of *Sagitta elegans* during 1994-1995 (B.K. Sullivan, unpublished) we use a daily feeding rate of 4% body weight.d^{-1}. Applying this feeding rate to chaetognath abundances in 1995-1999 gives average consumption rates of 1.36, 1.04, 1.80, 0.57, 1.88 and 3.17 mg C m^{-2}.d^{-1} in the months of January, February, March, April,

May and June, respectively. Using averages of 1.19 for six months of "winter" and 2.52 for "spring" plus "summer", consumption in winter is 214 mg C.m^{-2}, consumption in Spring/summer is 454 mg C.m^{-2}, and annual food intake by the chaetognaths is 0.7 g C m^{-2}.yr^{-1}.

Ctenophores. Estimates of ctenophore feeding rates are based on experiments with *Pleurobrachia* spp. (Davis, 1984). When combined with abundance data, intake rates are, 5.3, 6.9, 2.1, 5.9, 3.1 and 4.9 mg C m^{-2}.d^{-1} in January, February, March, April, May and June, respectively. The average intake is 4.7 mg C m^{-2}.d^{-1} with no seasonal pattern. Application of this value over the entire year gives an annual intake of 1.6 g C m^{-2}.yr^{-1}.

Predatory copepods. The "predatory" copepods, principally *Centropages typicus*, feed on microzooplankton, and on copepod eggs and nauplii. Here, only the latter components are "predatory"; feeding on microzooplankton is subsumed in the mesozooplankton. From data on copepod nauplii densities (E.G. Durbin, unpublished; see also Durbin et al., 2000; Lynch et al., 2001) the mean values (ranges) for winter (Jan-April) and spring (May-June) are 2.1 μg C.l^{-1} (1.2 –2.9) and 4.5 μg C.l^{-1} (2.6-6.5), respectively. Combining these values with a clearance rate of 0.2 l predator^{-1}.d^{-1} (Sell et al., 2001), and a carbon weight for the predator of 7 μg C (Davis, 1984), the predation rates are 0.06 and 0.13 mg C.predator C^{-1}.day^{-1} for winter and spring, respectively. The 5-year average densities of predatory copepods (E.G. Durbin, unpublished; B.K. Sullivan, unpublished) were 0.07 and 0.27 g C.m^{-2} for winter (January–April) and spring (May-June), respectively. Assuming that each value applies to six months, yearly predation is 7.0 g C.m^{-2}.

Hydroids. The pelagic phase of hydroids (dominated by *Clytia* spp.) on Georges Bank is erratic in timing, but they appear to be abundant on the Bank crest for approximately two months (Concelman et al., 2001). The maximum annual population densities, averaged over the two months of hydroid occurrence were 0.25, 0.45, 0.12, 0.30 and 0.20 g C.m^{-2} in 1995, 1996, 1997, 1998 and 1999, respectively (E.G. Durbin, unpublished; B.K. Sullivan, unpublished). The average 5-year population size was 0.25 g C.m^{-2} (B.K. Sullivan, unpublished). Hydroid growth rate at 8°C is 0.15 d^{-1} (B.K. Sullivan, unpublished). Assuming a transfer efficiency of 0.3, then food intake is ~ 0.5 d^{-1}. The average population (0.24 g C.m^{-2}) food requirement for 60 days is then equivalent to 7.2 g C m^{-2}.yr^{-1}.

In summary, the total invertebrate predation rate on the mesozooplankton is on the order of 16.4 g C m^{-2}.yr^{-1}. Given the variability in the data and the uncertainties in assigning rates to summer and fall, the range could be at least ± 50% or 8.2-24.6 g C m^{-2}.yr^{-1}.

To make a comparison with the calculations for the upper web, we assume that the pelagic invertebrate predators can out-compete the fish but the fish eat all of the predators. There is then 13.9 g C.m^{-2}.yr^{-1} available for the fish. The intake required by the pelagic feeding fish for the last decade, when comparison is appropriate, is 12.2 g C.m^{-2}.yr^{-1} (Fig. 8c). This is close because it is unlikely that carnivores such as gelatinous zooplankton would be totally consumed. These values indicate that predatory plankton are a critical competitor with fish in the consumption of mesozooplankton, in agreement with Davis (1984), who concluded that invertebrate predators are able to control copepod populations on Georges Bank.

5.5. Benthic Fauna

Diet information has been compiled for 24 benthic species that are abundant on Georges Bank (Theroux & Wigley, 1998). The suspension feeders filter microplankton (diatoms, flagellates and microzooplankton) and the deposit feeders consume organic matter on sediment grains. The predators eat mainly deposit feeders, some fish eggs, juvenile fish, and small bivalves. Scavengers eat a combination of deposit feeders and detritivores. There are no herbivores feeding on macroalgae on Georges Bank. As a first-order approximation, we assume that suspension-feeding benthos eat microplankton and deposit-feeding benthos eat detritus.

Benthic production on Georges Bank has been estimated with a variety of direct and indirect methods. For a few cases in which the same stations have been sampled repetitively over time, the production of scallops (Hermsen et al., 2003), amphipods, and sand dollars has been estimated with the growth-increment method. Hynes size-frequency method was used to estimate production from samples having size-frequency data but insufficient numbers to follow cohorts (Hermsen et al., 2003). Steimle (1987) used literature values of P:B ratios to estimate benthic production on the Bank. Total production based on the Theroux and Wigley (1998) samples is 102 kcal m^{-2}.yr^{-1} with an overall P:B ratio of 1.2 (Table 10). The same P:B ratios, applied to Michael et al.'s (1983) data from the southern flank give a total production of 92 kcal.m^{-2}.yr^{-1} and an overall P:B of 1.3. Applying the same P:B ratios as Steimle to the data from the Georges Bank Benthic Infauna Monitoring Program (Maciolek-Blake et al. 1985) resulted in a total production of 86 kcal.m^{-2}.yr^{-1} and an overall P:B of 1.4. In Hermsen et al.'s (2003) study a combination of direct and indirect methods was used to estimate benthic production at stations

on the northern edge of the Bank. Total production ranged from 40 to 382 kcal.m^{-2}.yr^{-1}. The highest value was attributable to high densities of sea scallops, with a P:B ratio of 0.33.

In summary, benthic production on Georges Bank ranges from 86 to 105 kcal.m^{-2}.yr^{-1} (Table 10). Although production has been estimated for different time periods, temporal comparisons are not possible, except at locations that have been sampled repeatedly over time. On the northern edge of the Bank, there has been a marked increase in benthic biomass within the area closed to fishing since 1994 (Hermsen et al., 2003). Here, biomass and production are partitioned into suspension and deposit feeding benthos for inclusion in the energy budget (Table 10). The suspension feeders consist primarily of large bivalves with lower P:B ratios than the deposit feeders. The deposit feeders likely include some carnivorous or omnivorous species, but it was not possible to separate these species in the aggregate data. There was a wide range in the ratio of suspension-to-deposit feeders, but on average, suspension feeder biomass was 54 kcal.m^{-2} and production was 36 kcal.m^{-2}.yr^{-1}, for a P:B ratio of 0.7. Average deposit feeder biomass was 51 kcal.m^{-2} and production was 60 kcal.m^{-2}.yr^{-1}, for a P:B of 1.2. We take a ratio of 11 kcal = 1 g C to obtain a total benthic production of 8.8 g C.m^{-2}.yr^{-1} .

Total macro-benthic production (deposit feeding plus suspension feeding) from the budget calculations is estimated as 10.5 g C.m^{-2}.yr^{-1}, in reasonable agreement with the average observed value of 8.8 g C.m^{-2}yr^{-1}. The calculated proportions of suspended and detritus feeders are within the observed range (Table 10).

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6. Discussion

6.1 Results of analysis

Our calculations agree broadly, but not in detail, with earlier energy budgets for Georges Bank (Cohen et al., 1982; Sissenwine et al, 1984; Cohen and Grosslein, 1987). For example, Cohen and Grosslein (1987) estimated macrozooplankton production as 20.2 g $C.m^{-2}.yr^{-1}$, lower than our estimate of 27.0. The estimates of exploitable fish production are also comparable, because these were calculated with the same P:B ratios. Consumption by juvenile fish is less than was estimated by Sissenwine et al. (1984). On the other hand, the high consumption of carnivorous zooplankton, including gelatinous forms, confirms their importance as pelagic predators (Davis, 1984). The detailed and quantitative treatment of the lower food web is a major improvement over earlier energy budgets. The recycling of nutrients through the microbial loop in combination with advective losses of zooplankton off the bank, explains why Georges Bank has high total primary production, yet comparatively low zooplankton production.

Solving the lower and upper food webs separately has the advantage that both can be modeled at appropriate space and time scales and with different approaches. Starting with estimates of new and total production based on data from 1980-2000, linear steady-state budgets of the lower food web provide values for fluxes of micro- and mesoplankton, and for suspension and deposit feeding benthos. Starting with data on fish populations and their diets over four decades, the upper food web calculates the fluxes of mesozooplankton and predatory zooplankton, and total benthos required for fish consumption.

In the budgets for fluxes through the food web, we used the best estimates available in the literature for a large number of parameters, such as transfer efficiency and consumption–to–biomass ratios, rather than explore the limits for some of the factors in individual applications. We restricted the choice of unknowns to three – detritus recycling, and planktonic and benthic carnivore consumption - because they apply to the critical trophic transfers on Georges Bank. Thus, we have a constrained comparison of the inputs at the top and bottom of the food web that determines possible solutions. This was preferable to a general use of data on the various planktonic and benthic components because, as described here, these would have had such wide upper and lower bounds that any solution, including the first decade, might have been acceptable.

The planktonic and benthic fluxes can be reconciled with the fish food requirements for the last three decades, and the estimated values of biomass of plankton and benthos fall within the wide range of variation of available observations. However for the first decade, 1963-72, the plankton requirements of the fish populations were significantly lower than the fluxes estimated for the succeeding three decades, and the benthic fish requirements were also lower than the later periods. Examination of the available physical, nutrient, and plankton data for the period 1960-1975 suggests that decreased NO_3 input during this decade resulted in significantly decreased plankton production.

A year-by-year examination of this change shows that the ratio of benthic to total food requirement trends down fairly regularly over the four decades (Fig. 10). There are two types of

possible explanation for this trend: changes within the lower food web and changes in the fishery. The assumption of fixed linear relations between variable components in the food web (eq. 3) is an obvious over-simplification, particularly when there are marked changes in physical forcing and nutrient input. The intrusion of the cold Labrador Current could induce changes in the physical fluxes (Fig. 3) that would alter the retention of plankton on the Bank. Decreased new production could also affect the *f*-ratio, as calculated with data from the later decades.

Ascribing observed changes in fish populations to physical environmental processes or to changes in fishing effort is a persistent problem. Usually both factors operate at the same time, as is certainly true for the four decades described here. There was major restructuring of fishing effort on Georges Bank after the 1976 extension of national jurisdiction, with a marked decrease in fishing for pelagic species but an increase in effort for preferred demersal stocks of cod, haddock, and flounder. Fishing depleted the principal groundfish stocks, but these changes appear to be balanced by alterations in other fish species (Fig. 5). High benthivore biomass in the 1960s shifted to high piscivore biomass in the 1980s, and subsequently to high planktivore biomass in the late 1990s. Thus the shift to greater planktonic intake may be in part the result of changes in fishing pressure. An alternative, or additional, explanation is that the increased intensity of bottom trawling, combined with greater technology (NRC, 2002; Hermsen et al, 2003) has depleted the suspension feeding epibenthos that are significant consumers of primary production as well as competitors with the plankton.

We have omitted some food web components, but they are unlikely to be sufficiently large to affect the food web balance. Exploited invertebrates (e.g., lobsters & scallops) would

remove some of the benthic production. For example, the harvest of scallops from the Canadian portion of Georges Bank was estimated at 1 g C.m^{-2}.yr^{-1} (Horne et al., 1989). Inclusion of these removals in the energy budget would require the benthivorous fish to consume more of the benthos directly, with less consumption of the carnivorous benthos (Fig. 10). Top predators (i.e., marine mammals, sharks, turtles, and seabirds) were not included in the upper food web. These predators have been estimated to consume about 1 g C.m^{-2}.yr^{-1} from the pelagic food web (Cohen and Grosslein, 1987). To the extent that the top predators eat pelagic fish, the feeding demands do not increase because the consumption of planktivorous fish was estimated directly from fish biomass. To the extent that the top predators eat zooplankton, there is room in the budget for some of the zooplankton production to be diverted away from fish while still maintaining the food web in balance.

6.2   *Functional diversity*.

This food-web analysis requires that changes in community composition and species diversity must accommodate the overall fluxes. Increases in abundance of certain members of a guild necessitate decreases elsewhere. Such compensation has implications for attempts to reconstruct past conditions when, for example, single species such as cod were considerably more abundant (Kurlansky, 1997; Fogarty and Murawski, 1998). Compensation also indicates likely constraints on attempts at recovery of particular stocks, when the overall balance requires reduction in abundance of other species. The marked fluctuations in abundance of both exploited and non-commercial species supports Tilman's (1999) conclusion that the relation between diversity and stability is best expressed as "increases in diversity cause *community* stability to

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increase but *population* stability to decrease" (our italics). As discussed above, our linear

analysis describes the context for fish stocks, it does not determine the nature of the constraints,

nor methods for their removal. To restore dominance of a single species, Tilman's doctrine

would require a decrease in the stability of the existing community.

6.3 *Climatic change*.

Changes in the physical environment can affect the ecosystem in a variety of ways,

through trends in static properties such as temperature or salinity, or in physical rate processes

such as currents or vertical mixing. The effects may be direct through temperature tolerance or

advective losses for particular species, or they can be indirect through nutrient fluxes up the food

web. Our approach focuses on the latter, and the results indicate a probable connection between

the shelf-edge Labrador Current and fluxes up through the food web to plankton consumption by

fish. In turn there appears to be a connection between this current and a broader climatic index,

the North Atlantic Oscillation linking these changes to larger spatial patterns (Pershing et al.,

2001).

6.4 *Trophic cascades*.

There is considerable controversy over the definition (Polis et al., 2000) and

determination (Shurin et al., 2002) of trophic cascades. The concept of aquatic cascades

originated in studies of fresh water lakes (Carpenter and Kitchell, 1993) with alternating

dominance of successive trophic levels from piscivorous fish to phytoplankton. Reviews of

open-sea marine systems suggest that there are partial cascades from fish to zooplankton but not to nutrients (Micheli, 1999; Richardson and Schoeman, 2004; Shurin et al., 2002; Worm and Myers, 2003). However individual studies range from no evidence of end-to-end cascades on Georges Bank (Sherman et al., 1998;) or the North Sea (Heath, 2005), to complete cascades from piscivores to nitrate on the north-east Scotian Shelf (Frank et al., 2005) based on correlations between components of the food web. The problem in our analyses arises from the difficulty in defining integral trophic cascades. Nominal "piscivores" such as cod can consume as much benthos as fish. At the other end, variations in f-ratios are an index of the variable fraction of mesoplankton intake that is carnivorous or herbivorous. Fractional trophic levels are now accepted (Pauly et al., 1998), reflecting the diversity and openness of marine food webs and making it impractical to construct cascades based on quantitative flux data.

6.5 Comparison with other regions

Heath (2005) performed an extensive analysis of the North Sea food web for the years 1973-2000, using data on zooplankton and benthos biomass as input. Heath's budgets start from mid-trophic levels and assume that inter-annual changes in plankton are forced by climatic factors. Heath's results indicate that the pelagic food web of the North Sea is controlled from the bottom-up. In contrast to Georges Bank, there has been no expansion of alternate fish species to fill the niche of commercial species depleted by overfishing. Instead, in the North Sea, fisheries for benthic invertebrates have developed. Heath's general conclusions of bottom-up pelagic and top-down benthic control fits, to some extent, with the Georges Bank results. However, the expansion in benthic invertebrates in the North Sea and on the Scotian Shelf (Worm and Myers,

2003) was not observed on Georges Bank, where there appears to have been replacement by other benthic feeding fish.

On the Eastern Scotian Shelf, there have been various explanations for marked changes over the last four decades. Frank et al. (2005) describe a trophic cascade of alternate increasing and decreasing trends in abundance at decreasing trophic levels driven by the collapse in cod stocks and extending to NO_3 concentration. The same group (Choi et al., 2004) propose a "transition to an alternate state" caused by "biomass removal and abiotic change", and resulting in a hysteresis inhibiting return to an earlier state. These varying conclusions about the same geographic region are based on mainly visual correlations to support inferences for causation by physical factors (low nutrient supply), linear sequences (cascades), or non-linear regime shifts. It should be noted that there are significant differences between the Eastern and Western Scotian Shelves (Zwanenburg et al., 2002). The former is under the influence of the St Lawrence River outflow, whereas the latter is influenced primarily by the Labrador Current.

There are similarities and differences among Georges Bank, the North Sea and the Scotian Shelf in their physical, chemical and ecological regimes. Any general theories for the dynamics of shelf ecosystems will need to account for such features. There are also differences in the sequences of fishing effort, but the most prominent feature–the depletion of cod stocks–is remarkably similar for the three ecosystems. The North Atlantic Oscillation may affect the three regions in different ways, but could impose similar periodicities. As a start, there are striking differences in the bottom topography and physical oceanography of the regions. As discussed in this study, the distribution of different regimes of vertical mixing–Mixed, Transition and

Stratified—plays a critical role in the assessment of the productivity of Georges Bank. The episodically mixed Transition domain forms about half of Georges Bank, whereas in the North Sea (Pingree et al., 1978) it is only about 20%, and it appears to be significantly less on the Scotian Shelf (Iles and Sinclair, 1982). These proportions not only determine the new production but also its allocation to zooplankton, to detritus and especially to suspension feeding benthos such as scallops. These factors can account for the differing proportion in the yields of pelagic and demersal fish in the North Sea versus Georges Bank noted by Cohen et al. (1982)

6.6 Management Issues.

The problems facing fisheries management are often posed as a choice between control of inter-annual to decadal changes in resource abundance by fishing effort (top-down) or by climatic change (bottom-up). A major conclusion of this study is that both can operate at the same time, but in different ways. In this context, the primary use of ecosystem budgets is to elucidate the problems in quantifying the interactions between external forcing and internal structure. This analysis for Georges Bank illustrates the difficulties but also demonstrates the necessity for end-to-end food web calculations. No single top-down or bottom-up process determines the observed patterns. As a result of selective fishing pressures, there may be decimation of top predators (Myers and Worm, 2003), but first-order piscivores can be replaced by other species, albeit less commercially attractive ones. Certain major fish components such as plankton feeders may be limited by the basic productivity of the ecosystem, while consumption of benthos in some systems has switched to invertebrate predators. Management of the diversity of fishery resources requires an approach based on a full appreciation of the entire food web.

Acknowledgements

References

Anderson, T.R., Williams, P.J. leB., 1998. Modelling the seasonal cycle of dissolved organic carbon at Station E1 in the English Channel. Estuarine, Coastal and Marine Science 46, 93-100.

Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A., Thingstad, F. 1983. The ecological role of water column microbes in the sea. Marine Ecology Progress Series 10, 257-263.

Azarovitz, T.R. 1981. A brief historical review of the Woods Hole laboratory trawl survey time series. In: Doubleday, W.G., Rivard, D., (Eds.), Bottom Trawl Surveys, Canadian Special Publication of Fisheries and Aquatic Science 58, 62-67.

Bisagni, J.J. 2003. Seasonal variability of nitrate supply and potential new production in the Gulf of Maine and Georges Bank regions. Journal of Geophysical Research 108, c11: 8015.

Carpenter, S.R., Kitchell, J.K. 1993. The trophic cascade in lakes. Cambridge University Press, Cambridge,

Christensen, V., Pauly, D. (Eds.) 1993. Trophic models of aquatic ecosystems. The International Center for Living Aquatic Resources Management (ICLARM) Conference Proceedings, 26, ICLARM, Manila, Philippines.

Choi, J.S., Frank, K.T., Leggett, W.C., Drinkwater, K. 2004. Transition to an alternate state in a continental shelf ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 61, 505-510.

Cohen, E.B., Grosslein, M.D., Sissenwine, M.P. 1982. Energy budget of Georges Bank. Canadian Special Publications in Fisheries and Aquatic Science 59, 95-107.

Cohen, E.B., Grosslein, M.D. 1987. Production on Georges Bank compared with other shelf ecosystems. In: Backus, R.H., Bourne, D.W. (Eds.), Georges Bank, MIT Press, Cambridge pp. 382-391.

Collie, J.S. , DeLong, A.K. 1999. Multispecies interactions in the Georges Bank fish community. In: Alaska Sea Grant College Program, Ecosystem Approaches for Fisheries Management, Alaska Sea Grant Publication AK-SG-99-01, pp. 187-210.

Concelman, S., Bollens, S.M., Sullivan, B.K. Madin, L.P. Horgan, E., Butler, M. , Van Keuren, D.M. 2001. Distribution abundance and benthic-pelagic coupling of suspended hydroids on Georges Bank, Deep-sea Research. II 48, 645-658.

Dagg, M.J., Turner, J.T 1982. The impact of copepod grazing on the phytoplankton of Georges Bank and the New York Bight. Canadian Journal of Fisheries and Aquatic Science 39, 979-990.

Davis, C.S. 1984. Predatory control of copepod seasonal cycles on Georges Bank. Marine Biology 82, 31-40.

Durbin, E.G., Garrahan, P.R., Casas, M.C. 2000. Abundance and distribution of *Calanus finmarchicus* on Georges Bank during 1995 and 1996. ICES Journal of Marine Science 57, 1664-1685.

Edwards, R.L. 1960. Fishery Resources of the North Atlantic area. In: Gilbert, D.W. (Ed.). The future of the Fishing Industry of the United States. University of Washington, Seattle, pp. 52-60.

Eppley, R.W., Peterson, B.J. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282, 677-680.

Fogarty, M.J., Murawski, S.A. 1998. Large scale disturbance and the structure of marine systems: fisheries impacts on Georges Bank. Ecological Applications 8 (Suppl.), S6-22.

Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science 308, 1621-1623.

Franks, P. J. S., Chen, C. 2001. A 3-D prognostic numerical model study of the Georges Bank ecosystem. Part II: biological-physical model. Deep-Sea Research II 48, 457-482.

Garrison, L.P., Link, J.S. 2000. Dietary guild structure of the fish community in the north-east United States continental shelf ecosystem. Marine Ecology Progress Series 202, 231-240.

Gifford, D.G., Caron, D.A. 2000. Sampling, preservation, enumeration and biomass of marine protozooplankton. In: Harris, R.P., Wiebe, P.H., Lenz, J, Skjoldal, H.R., Huntley, M.E. (Eds.) ICES Zooplankton Methodology Manual Academic Press, London, pp. 193-221.

Grosslein, M.D., Langton, R.W., Sissenwine, M.P. 1980. Recent fluctuations in pelagic fish stocks of the north-west Atlantic, Georges Bank region in relation to species interactions. Rapports et procès-verbaux des réunions /Commission internationale pour l'exploration scientifique de la Mer 177, 374-404.

Harley, S.J., Myers, R.A. 2001. Hierarchical Bayesian models of length-specific catchability of research trawl surveys. Canadian Journal of Fisheries and Aquatic Science 58, 1569-1584.

Harris, R.P., Wiebe, P.H., Lenz, J, Skjoldal, H.R., Huntley, M.E. (Eds.) 2000. ICES Zooplankton Methodology Manual. Academic Press, London.

Harvey, H.W. 1957. The Chemistry and Fertility of Sea Waters. Cambridge University Press, Cambridge.

Heath, M.R. 2005. Changes in the structure and function of the North Sea fish food web, 1973-2000, and the impacts of fishing and climate. ICES Journal of Marine Science 62, 847-868.

Hermsen, J., Collie, J.S., Valentine, P.C. 2003. Mobile fishing gear reduces benthic megafaunal production on Georges Bank. Marine Ecology Progress Series 260, 97-108.

Hirst, A.G., Lampitt, R.S. 1998. Towards a global model of in situ weight-specific growth in marine

    copepods. Marine Biology 132, 247-257.

Horne, E.P.W., Loder, J.W. Harrison, W.G., Mohn, R., Lewis, M.R., Irwin, B., Platt, T. 1989. Nitrate

    supply and demand at the Georges Bank tidal front. Scientia Marina 53, 145-158.

Houde, E.D. 1996. Evaluating stage-specific survival during the early life of fish. In: Watanabe, Y.,

    Tamashita, Y., Oozeki, Y. (Eds.) Survival strategies in early life stages of marine resources.

    Balkema, Rotterdam, pp. 51-66.

Iles, T.D., Sinclair, M. 1982. Atlantic herring: stock discreteness and abundance. Science 215, 627-633.

Jones, R. 1984. Species interactions in the North Sea. Canadian Special Publication of Fisheries and

    Aquatic Science 59, 48-63.

Jossi, J.W., Goulet, J.R. 1993. Zooplankton trends: US north-east shelf ecosystem and adjacent regions

    differ from north-east Atlantic and North Sea. ICES Journal of Marine Science 50, 303-313.

Karl, D.M., Michaels, A.F. 2001. Nitrogen Cycle. In: Steele, J.H., Thorpe, S., Turekian, K. (Eds.).

    Encyclopedia of Ocean Sciences, Academic Press. New York, pp. 1876-1884.

Klein, P. 1987. Assimilation of some physical and biological interactions. In: Backus, R.H., Bourne

    D.W. (Eds.), Georges Bank. MIT Press, Cambridge, pp. 395-405.

Knap, A., Michaels, A., Close, A., Ducklow, H., Dickson, A. (Eds.) 1996. Protocols for the Joint Global

    Ocean Flux Study (JGOFS) Core Measurements. JGOFS Report No. 19. Reprint of the IOC

    Manuals and Guides No. 29, UNESCO 1994.

Kurlansky, M. 1997. Cod: A biography of the fish that changed the world. Walker and Co., New York.

Laws, E.A., Falkowski, P.G., Smith, W.O, Ducklow, H., McCarthy, J.J. 2000. Temperature effects on

    export production in the open ocean. Global Biogeochemical Cycles 14, 1231-1246.

Lessard, E.J. 1991. The role of heterotrophic dinoflagellates in diverse marine environments. Marine

    Microbial Food Webs 5, 49-58.

Link, J.S., Almeida, F.P. 2000. An Overview and History of the Food Web Dynamics Program of the

    Northeast Fisheries Science Center, Woods Hole, Massachusetts. NOAA Tech. Memo. F/NE-

    159.

Loder, J.W., Shore, J.A., Hannah, C.G., Petrie, B.D. 2001. Decadal-scale hydrographic and circulation

    variability in the Scotia-Maine region. Deep-sea Research II 48, 3-36.

Luff, R., Moll, A. 2004. Seasonal dynamics of the North Sea sediments using a three-dimensional coupled sediment-water model system. Continental Shelf Research 24, 1099-1127.

Lynch, D.R., Lewis, C.V., Werner, F. E. 2001. Can Georges Bank larval cod survive on a calanoid diet? Deep-Sea Research II 48, 609-630.

Maciolek-Blake, N., Grassle, J.F., Neff, J.M. 1985. Georges Bank Benthic Infauna Monitoring Program: Volume 2, Final Report for the third year of sampling. U.S. Department of the Interior, Minerals management Service, Washington, DC.

Mavor, T. P., Bisagni, J.J. 2001. Seasonal variability of sea-surface temperature fronts on Georges Bank. Deep-Sea Research II 48, 215-243.

Mayo, R. K., M. J. Fogarty, Serchuk, F.M. 1992. Trends in aggregate fish biomass and production on Georges Bank. Journal of Northwest Atlantic Fisheries Science 14, 59-78.

Meise, C.J., O'Reilly, J.E. 1996. Spatial and seasonal patterns in abundance and age composition of *Calanus finmarchicus* in the Gulf of Main and on Georges Bank: 1977-1987. Deep-sea Research II 43, 1473-1501.

Michael, A.D., Longs, C.D., Maurer, D., McGrath, R.A., 1983. Georges Bank benthic infaunal historical study. Final Report to U.S.D.I Minerals Management Service, Washington, D.C.

Micheli, F. 1999. Eutrophication, fisheries and consumer-resource dynamics in marine pelagic
ecosystems. Science 285, 325-326.

Mullin M.M., Brooks, E.R. 1970. Growth and metabolism of two marine copepods as influenced by
temperature and type of food. In: Steele, J.H. (Ed.), Marine Food Chains, Oliver and Boyd,
Edinburgh, pp. 74-95.

Myers, R.A., Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. Nature 423:
280-283

National Research Council 2002. Effects of Trawling and Dredging on Seafloor Habitat. National
Academy Press, Washington DC

Northeast Fisheries Center (NEFC) 1988. An evaluation of the bottom trawl survey program of the
Northeast Fisheries Center. NOAA Technical Memorandum NMFS-F/NEC-52, Woods Hole.

O'Reilly, J.E., Evans-Zetlin, C., Busch, D.A. 1987. Primary Production. In: Backus, R.H., Bourne,
D.W. (Eds.), *Georges Bank* (pp. .220-234), MIT Press, Cambridge.

Overholtz, W.J., Link, J.S., Suslowicz, L.E. 2000. Consumption of important pelagic fish in the
northeastern USA shelf ecosystem with some fishery comparisons. ICES Journal of Marine
Science 57, 1147-1159.

Parsons, T.R., Takahashi, M. 1973. Biological Oceanographic Processes. Pergamon Press, Oxford.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres Jr., F. 1998. Fishing down marine food webs. Science 279, 860-863.

Pershing, A.J., Greene, C.H., Hannah, C., Sameoto, D., Head, E., Mountain, D.G., Jossi, J., Benfield, M., Reid, P.C.R., Durbin, E.G. 2001. Oceanographic response to climate in the northwest Atlantic. Oceanography 14, 76-82.

Petrie, B., Yeats, P. 2000. Annual and interannual variability of nutrients and their estimated fluxes in the Scotian Shelf-Gulf of Maine region. Canadian Journal of Fisheries and Aquatic Sciences 57, 2536-2546.

Pingree, R.D., Holligan, P.M., Mardell, G.T. 1978. The effects of vertical stability on phytoplankton distributions in the summer on the north-west European shelf. Deep-sea Research 25, 1011-1028.

Polis, G.A., Sears, A.L.W., Huzel, G.R., Strong, D.R., Maron, J. 2000. When is a trophic cascade a trophic cascade? Trends in Ecology and Evolution 15, 473-475.

Putt, M., Stoecker, D.K. 1989. An experimentally determined carbon:volume ratio for marine "oligotrichous" ciliates from estuarine and coastal waters. Limnology and Oceanography 34, 1097-1103.

Richardson, A.J., Schoeman, D.S. (2004). Climate impact on plankton ecosystems in the North-east Atlantic. *Science*, 305, 1609-1612.

Rothschild, B. J. 1986. Dynamics of marine fish populations. Harvard University Press, Cambridge.

Ryther, J. H. 1969. Photosynthesis and fish production in the sea. Science 166, 72-76.

Sambrotto, R. N., Savidge, G., Robinson, C., Boyd, P., Takahashi, T, Karl, D., Langdon, C., Chipman, D., Marra, J., Codispoti, L. 1993 Elevated consumption of carbon relative to nitrogen in the surface ocean. Nature 363, 248-250.

Sell, A.D., Van Keuren, D.M., Madin, L.P. 2001. Predation by omnivorous copepods on early developmental stages of *Calanus finmarchicus* and *Pseudocalanus* spp. Limnology and Oceanography 46, 953-959.

Sherman, K., Kane, J., Murawski, S., Overholtz, W., Solow,A. 2002. The U.S. northeast large marine ecosystem. In: Sherman. K., H.R. Skjoldal (Eds.), Large marine ecosystems of the North Atlantic: changing states and sustainability, Elsevier, Amsterdam, pp. 195-215.

Sherman, K., Solow, A., Jossi, J., Kane, J. 1998. Biodiversity and abundance of the zooplankton of the Northeast Shelf ecosystem. ICES Journal of Marine Science 55, 730-738.

Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B., Cooper, S.D., Halpern, B.S. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5, 785-791.

Sieburth, J. McN., Smetacek, V., Lenz, J. 1978. Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. Limnology and Oceanography 23,1256-1263.

Sieracki, M.E., Vereity, P.G., Stoecker, D.K. 1993. Plankton community response to sequential silicate and nitrate depletion during the 1989 North Atlantic spring bloom. Deep Sea Research-II 40, 213-225.

Simpson, H.J., Hunter, J.R. 1974. Fronts in the Irish Sea. Nature 1250, 404-406.

Sissenwine, M.P., Cohen, E.B., Grosslein, M.D. 1984. Structure of the Georges Bank ecosystem. Rapports et procès-verbaux des réunions /Commission internationale pour l'exploration scientifique de la Mer 183, 243-254.

Smith, T.D. 2004. The Woods Hole bottom trawl resource survey: development of fisheries-independent multi-species monitoring. ICES Marine Science Symposium 215, 474-482.

Steele, J.H. 1956. Plant production on the Fladen Ground. Journal of the Marine Biological Association of the United Kingdom 35, 1-33.

Steele, J.H. 1965. Some Problems in the Study of Marine Resources. In: International Commission for

    the Northwest Atlantic Fisheries (ICNAF), ICNAF Special Publication No. 6., pp. 463-476.

Steimle, F.W. 1987 . Production by the benthic fauna. In: Backus, R.H., Bourne, D.W. (Eds.). Georges

    Bank, MIT Press, Cambridge pp. 310-314.

Theroux, R.B., Wigley, R.L. 1998. Quantitative composition and distribution of the macrobenthic

    invertebrate fauna of the continental shelf ecosytems of the northeastern United States. U.S.

    Department of Commerce, NOAA Technical Report NMFS 140.

Thomas, A.C., Townsend, D.W., Weaherbee, R. 2003. Satellite-measured phytoplankton variability in

    the Gulf of Maine. Continental Shelf Research 23, 971-989.

Tilman, D. 1999. The ecological consequences of changes in biodiversity. Ecology 80, 1455-1474.

Townsend, D.W., Pettigrew, N.R. 1997. Nutrient limitation of secondary production on Georges Bank.

    Journal of Plankton Research 19, 221-236.

Verity, P.G., Robertson, C.Y., Tronzo, C.R., Andrews, M.G, Nelson, J.R., Sieracki, M.E. 1992.

    Relationships between cell volume and the carbon and nitrogen content of marine photosynthetic

    nanoplankton. Limnology and Oceanography 37, 1434-1446.

Ward, B. B. 2000. Nitrification and the marine nitrogen cycle. In: D. L. Kirchman (Ed.), Microbial ecology of the oceans. Wiley-Liss, New York, pp. 427-454.

Wiebe, P.H., Beardsley, R.C., Bucklin, A.C., Mountain, D.G. (Eds.) 2003. Coupled biological and physical studies of plankton populations: Georges Bank and related North Atlantic regions. Deep-sea Research 48: 1-684.

Worm, B., Myers, R.A. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology 84, 162-173.

Zwanenburg, K.C.T., Bowen, D., Bundy, A., Drinkwater, K. Frank, K., O'Boyle, R., Sameoto, D., Sinclair, M. 2002. Decadal changes in the Scotian Shelf large marine ecosystem. In: Sherman, K., Skjoldal, H.R. (Eds.), Large marine ecosystems of the North Atlantic: changing states and sustainability, Elsevier, Amsterdam, pp. 105-150.

Table 1. Turnover rates ($C:B.d^{-1}$) of lower web components as a function of temperature.

	Fall/Winter	Spring	Summer
Temperature	6	8	15
Phytoplankton	0.5	1.0	1.0
Bacteria	0.5	1.0	1.0
Microzooplankton	0.5	1.0	1.0
Mesozooplankton	0.07-0.15	0.08-0.17	0.11-0.24
Detritus	0.1	0.12	0.16

Table 2. Fractions of Georges Bank allocated to the three regions and seasons (see text Section 3).

	Fall/Winter	Spring	Summer
Stratified	0.35	0.52	0.64
Transition	0.57	0.39	0.28
Mixed	0.08	0.08	0.08

Table 3. Estimates of Potential New Production (*PNP*), Integrated Total Primary Production (*ITPP*), *f*-ratio and chlorophyll > 20 μm for the three Bank regions and three seasons (from Bisagni, 2003; O'Reilly et al., 1978, Figure 21.5; see text Section 3.1 for details).

Region	Fall/Winter	Spring	Summer
Potential New Production (mgC m^{-2}.d^{-1})			
Stratified	180	306	242
Transition	487	627	462
Mixed	263	314	207
Integrated Total Primary Production (mgC m^{-2}.d^{-1})			
Stratified	598	1060	1095
Transition	639	1352	1228
Mixed	980	1189	1263
f-ratio			
Stratified	0.30	0.29	0.22
Transition	0.76	0.46	0.38
Mixed	0.27	0.26	0.16
Fraction of chlorophyll > 20μm			
Stratified	0.55	0.87	0.76
Transition	0.39	0.58	0.80
Mixed	0.30	0.44	0.43

Table 4. Calculations of physical fluxes, F, for the three Bank regions. See section 3.2 of text and Fig. 4 for details.

Region	Fall	Spring	Summer
Surface $NO_3.m^{-3}$ (from Townsend & Thomas, 2002)			
Stratified	7.0	1.0	1.0
Transition	5.0	1.0	1.0
Mixed	2.5	0.0	0.0
"Deep" $NO_3 .m^{-3}$ (from Horne et al., 1989)			
Stratified	10.0	10.0	10.0
Transition	8.0	8.0	8.0
Mixed	5.0	5.0	5.0
Calculated values for daily exchange coefficient, F			
Stratified, F_S	0.0299	0.0005	0.0085
Transition, F_T	0.0583	0.0186	0.0207
Mixed, F_M	0.0493	0.0097	0.0130

Table 5. Parameter estimates for the lower food web. Values for Fall/Transition are corrected.

Region	Fall	Spring	Summer
TE = Maximum growth/intake ratio (in the range 0.1-0.3)			
Stratified	0.10	0.30	0.26
Transition	>0.3 (0.16)	0.30	0.30
Mixed	0.10	0.30	0.24
DR = Fraction of detritus recycled to NH_4 (to satisfy constraints)			
Stratified	1.0	0.55	1.0
Transition	0.0 (1.0)	0.75	0.65
Mixed	1.0	0.40	1.0

Table 6. Feeding guilds of 35 species of fish and squid on Georges Bank.

Piscivores	Benthivores	Planktivores
Spiny Dogfish	Smooth Dogfish	Atlantic Herring
Winter Skate	Barndoor Skate	Butterfish
Silver Hake	Little Skate	Acadian Redfish
Atlantic Cod	Thorny Skate	Northern Sandlance
Pollock	Haddock	Atlantic Mackerel
White Hake	Red Hake	Windowpane
Spottted Hake	American Plaice	*Loligo* squid
Atlantic Halibut	Yellowtail Flounder	*Illex* squid
Summer Flounder	Winter Flounder	Smooth Skate
Bluefish	Witch Flounder	
Sea Raven	Longhorn Sculpin	
Goosefish	Cunner	
	Ocean Pout	
	Fourspot Flounder	

Table 7. Average diet composition (proportion by weight) of the three fish guilds, weighted by the biomass of individual fish species.

1963-1972	Benthivores	Piscivores	Planktivores
Benthic fish	0.00	0.04	0.00
Deposit feeding benthos	0.78	0.34	0.25
Mesozooplankton	0.14	0.16	0.47
Pelagic invertebrate predators	0.00	0.02	0.28
Piscivorous fish	0.01	0.15	0.00
Planktonic fish	0.00	0.17	0.00
Suspension feeding benthos	0.08	0.11	0.00

1973-1982			
Benthic fish	0.00	0.03	0.00
Deposit feeding benthos	0.78	0.28	0.10
Mesozooplankton	0.14	0.21	0.73
Pelagic invertebrate predators	0.00	0.05	0.17
Piscivorous fish	0.00	0.15	0.00
Planktonic fish	0.00	0.18	0.00
Suspension feeding benthos	0.07	0.09	0.00

1983-1992			
Benthic fish	0.00	0.02	0.00
Deposit feeding benthos	0.79	0.36	0.03
Mesozooplankton	0.08	0.18	0.85
	0.00	0.07	0.06

Table 7, continued

Pelagic invertebrate predators

Piscivorous fish	0.03	0.09	0.05
Planktonic fish	0.01	0.17	0.01
Suspension feeding benthos	0.09	0.11	0.00

1993-2002

Benthic fish	0.01	0.01	0.00
Deposit feeding benthos	0.75	0.27	0.16
Mesozooplankton	0.08	0.16	0.54
Pelagic invertebrate predators	0.00	0.13	0.21
Piscivorous fish	0.03	0.12	0.09
Planktonic fish	0.07	0.21	0.01
Suspension feeding benthos	0.07	0.10	0.00

Table 8. Estimated percentage of primary production grazed by mesozooplankton: (A) mean (and range) from experiments with copepods (Dagg & Turner, 1982), and (B) mean (range) of large (>20μm) size fraction of chlorophyll, for the three regions on the Bank.

	Stratified	Transition	Mixed
(A)	48 (19-65)	44 (14-75)	9 (6-13)
(B)	73 (55-76)	59 (39-80)	39 (30-43)

Table 9. Estimated consumption by microzooplankton in the lower food web (g C m^{-2}.d^{-1})

	Fall/Winter	Spring	Summer
Stratified	0.21	0.95	0.92
Transition	0.28	0.90	0.90
Mixed	0.19	0.64	0.74

Table 10. Summary of benthic macrofaunal biomass and production on Georges Bank. Data
sources: 1: Steimle (1987), 2: Michael et al. (1983), 3: Maciolek-Blake et al. (1985): 4: Hermsen
et al. (2003).

Time Period	Location	Feeding mode	Biomass $(kcal.m^{-2})$	P:B	Production $(kcal.m\text{-}2.yr^{-2)}$
1960s	Entire Bank[1]	Suspension	19	0.9	16
		Deposit	64	1.5	86
		Total	83	1.2	102
1977	Southern Flank[2]	Suspension	54	1.0	54
		Deposit	20	1.7	39
		Total	74	1.3	92
1983	Southern Flank[3]	Suspension	30	1.0	30
		Deposit	31	2.0	56
			61	1.4	86
1990s	Northern Edge[4]	Suspension	113	0.5	45
		Deposit	89	0.7	60
		Total	202	0.5	105

Figure captions

Figure 1. Georges Bank food web. Rectangles are components of the web. Solid arrows represent fluxes. Dashed lines represent nutrient recycling, and dash-dot lines represent fish recruitment. Dotted lines leading to diamonds are physical losses. Ovals are inputs (NO_3) and outputs (zooplankton feces) to higher trophic levels. Thick arrows denote export from the lower web. Circles indicate where upper and lower fluxes join. For the lower web the arrows denote the flow of nutrients up to plankton and benthos. For the upper web the arrows trace consumption by fish down to plankton and benthos, where the upper and lower webs meet.

Figure 2. a. Map of the Georges Bank region showing the depth contours. b. Spatial domains in Fall/Winter. c. Spatial domains in Spring. d. Spatial domains in summer.

Figure 3. Representation of three mixing regimes on Georges Bank. The fluxes, F_M, F_T, and F_S, represent the loss rates estimated in Table 4.

Figure 4. Fluxes in the lower food web integrated over the three Bank regions and three seasons to give outputs in g C. $m^{-2}.yr^{-1}$. The upper boxes represent the fluxes to the upper web. P is phytoplankton; M is microzooplankton; Z is mesozooplankton; SB is suspension feeding benthos; D is detritus; B is bacteria (recycling NH). Sediment Feeding Benthos represents the transformation of fecal material to benthos (see text Section 3.3).

Figure 5. Time series of major fish species on Georges Bank. Data are averages from the Northeast Fisheries Science Center spring and fall trawl surveys.

Figure 6. (a) Food requirements of recruited fish guilds. (b) Fish consumption expressed in terms of prey groups. (a) and (b) differ because the nominal fish trophic groups eat all three prey groups (Table 8). (c) Food requirements of all fish (including pre-recruits) in plankton and benthos equivalents.

Figure 7. Matching the output from the lower food web with the requirements of the fish communities. (a) Upper food web simplified to show direct consumption of benthos and plankton by fish and indirect consumption through invertebrate carnivores. (b) Zooplankton production of 27.0 g C.m^{-2}.yr^{-1} is matched for the last three decades with varying abundance of invertebrate pelagic predators, but no match is possible for the first decade. (c) Benthic production of 10.5 g C.m^{-2}.yr^{-1} is matched for all four stanzas but with nearly double the apparent abundance of invertebrate benthic predators in the first decade. The "low nitrate" scenario shows that with reduced NO_3 input in the 1963-1972 decade, fish consumption can balance production from the lower food web.

Figure 8. Changes in (a) NO_3 and (b) temperature at 150 m on the edge of the Scotian Shelf, as indicators of the cold Labrador current that flowed south to Georges Bank in the 1960s. (c) Bottom temperature anomalies on Georges Bank suggest that the same cold water mass was present in the 1960s. Adapted from Petrie & Yeats (2000) with temperature data from the National Marine Fisheries Service.

Figure 9. Mean and standard deviations of GLOBEC mesozooplankton biomass data for the three Bank regions with the values calculated for the three seasons from the lower food web superimposed as dashed lines.

Figure 10. (a) Year-by-year estimates of plankton and benthos food requirements by the Georges Bank fish stocks. (b) The benthos component as a fraction of the total food requirement.
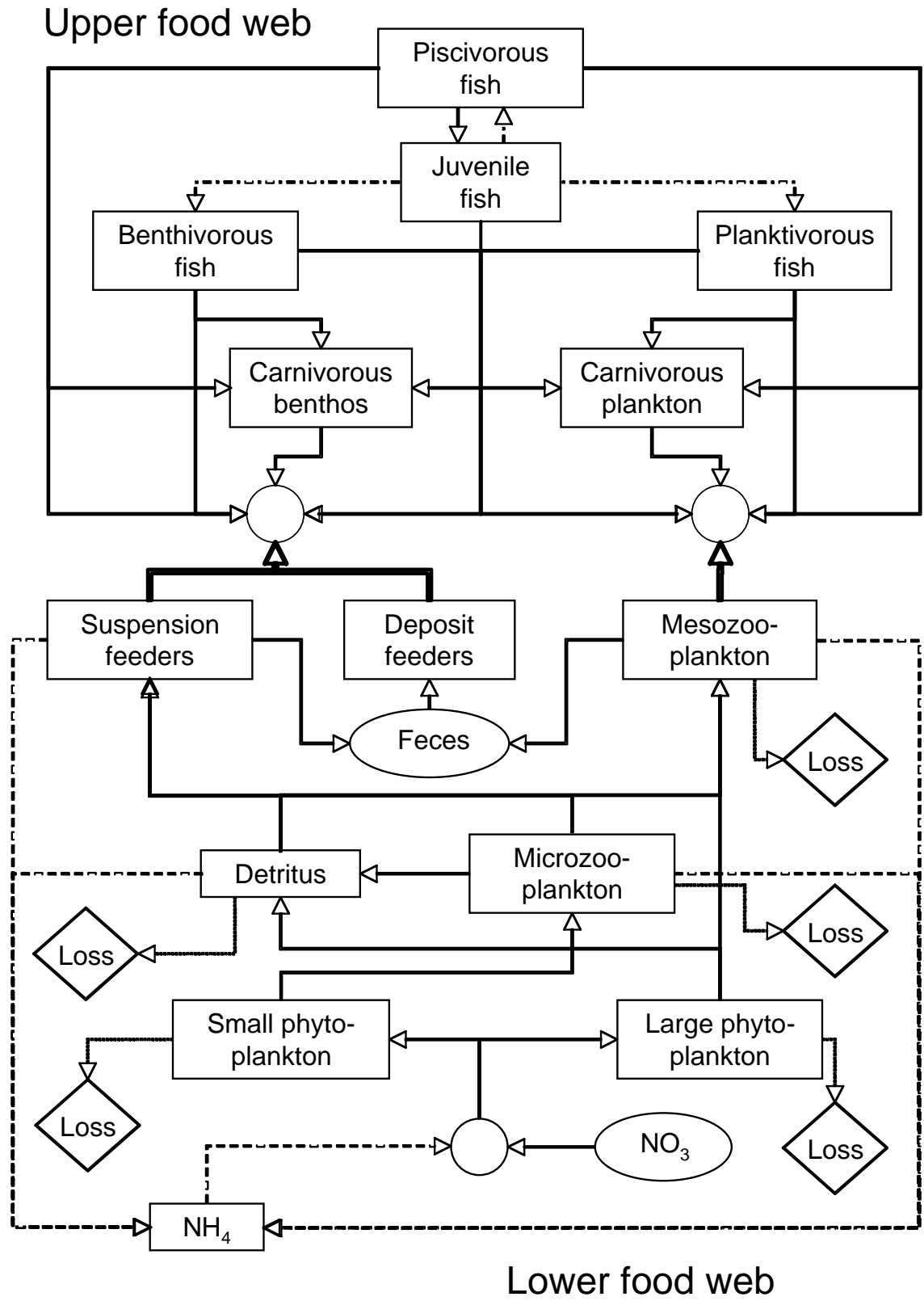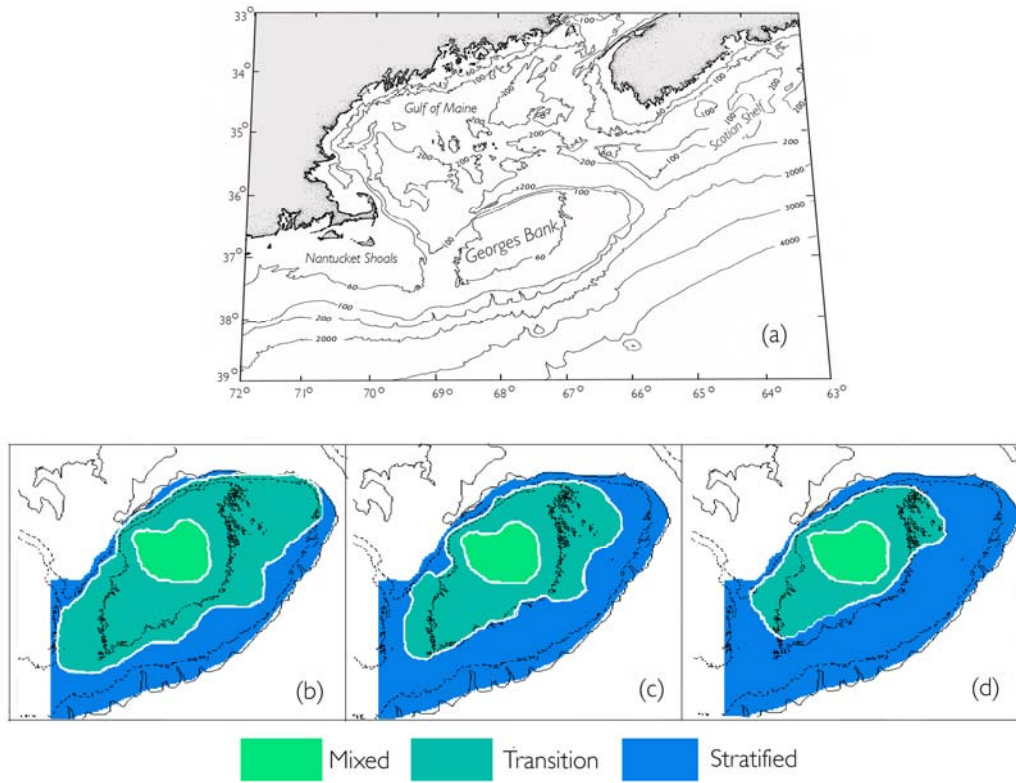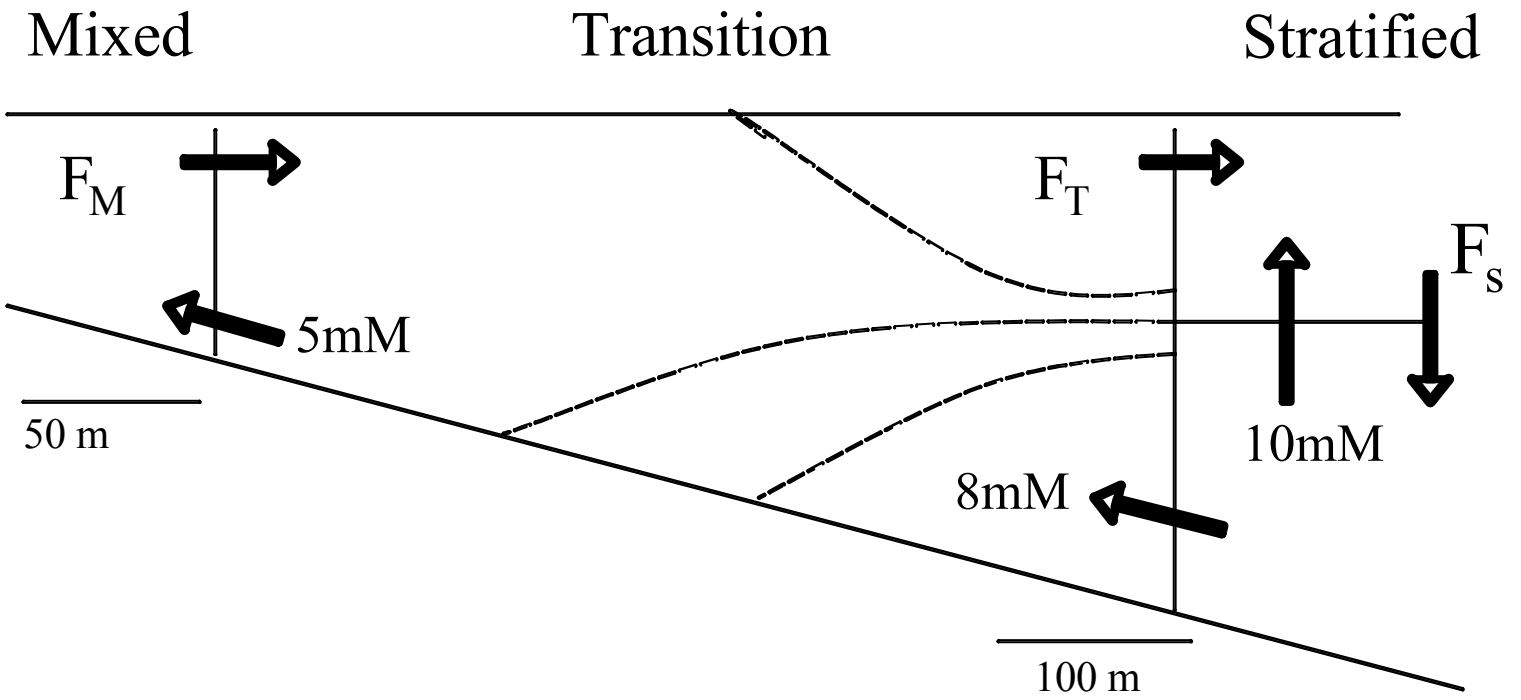
Figure 1

Figure 2

Mixed   Transition   Stratified

F_M

F_T

F_S

5mM

10mM

8mM

50 m

100 m

Figure 3

Figure 4

Predators Benthos

Sediment Feeding Benthos

Predators Plankton

Feces

5.7

4.8

4.8

5.5

7

SB

M

42

Z

24

27

1.8

209

68

22

19

90

16

108

47

9

B

235

P

27

D

10

17

53

10

New Production
127 gC m^{-2} year^{-1}

Figure 5

(a) Planktivores

(b) Piscivores

(c) Benthivores
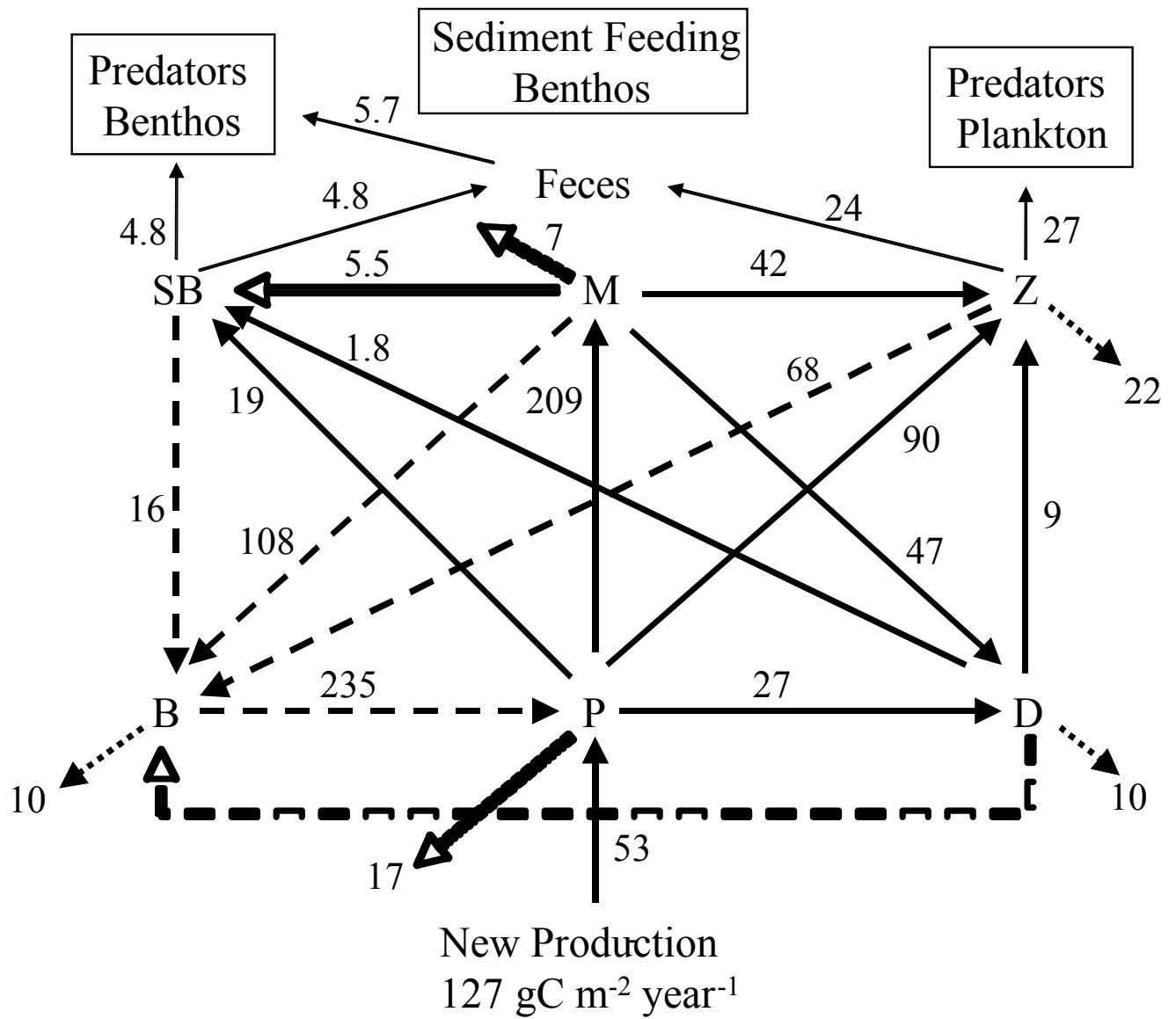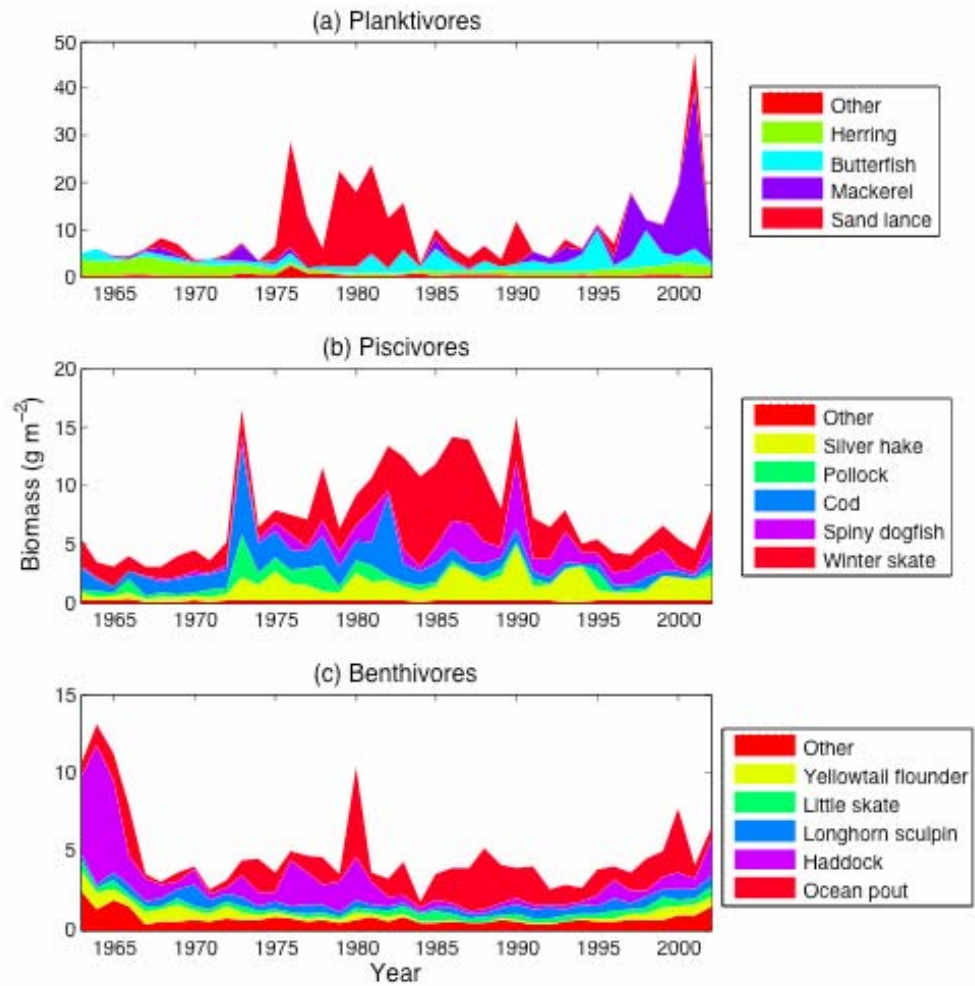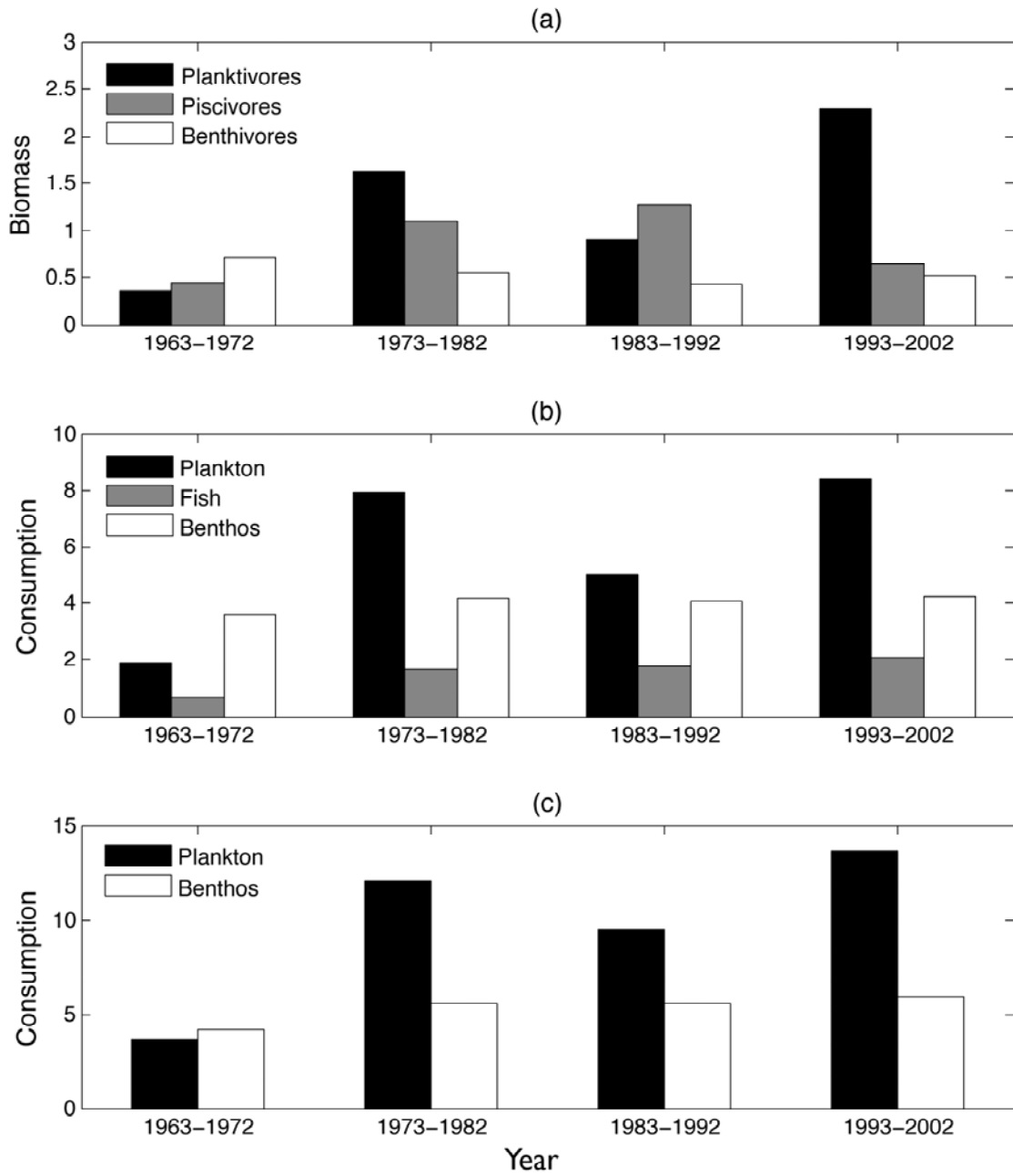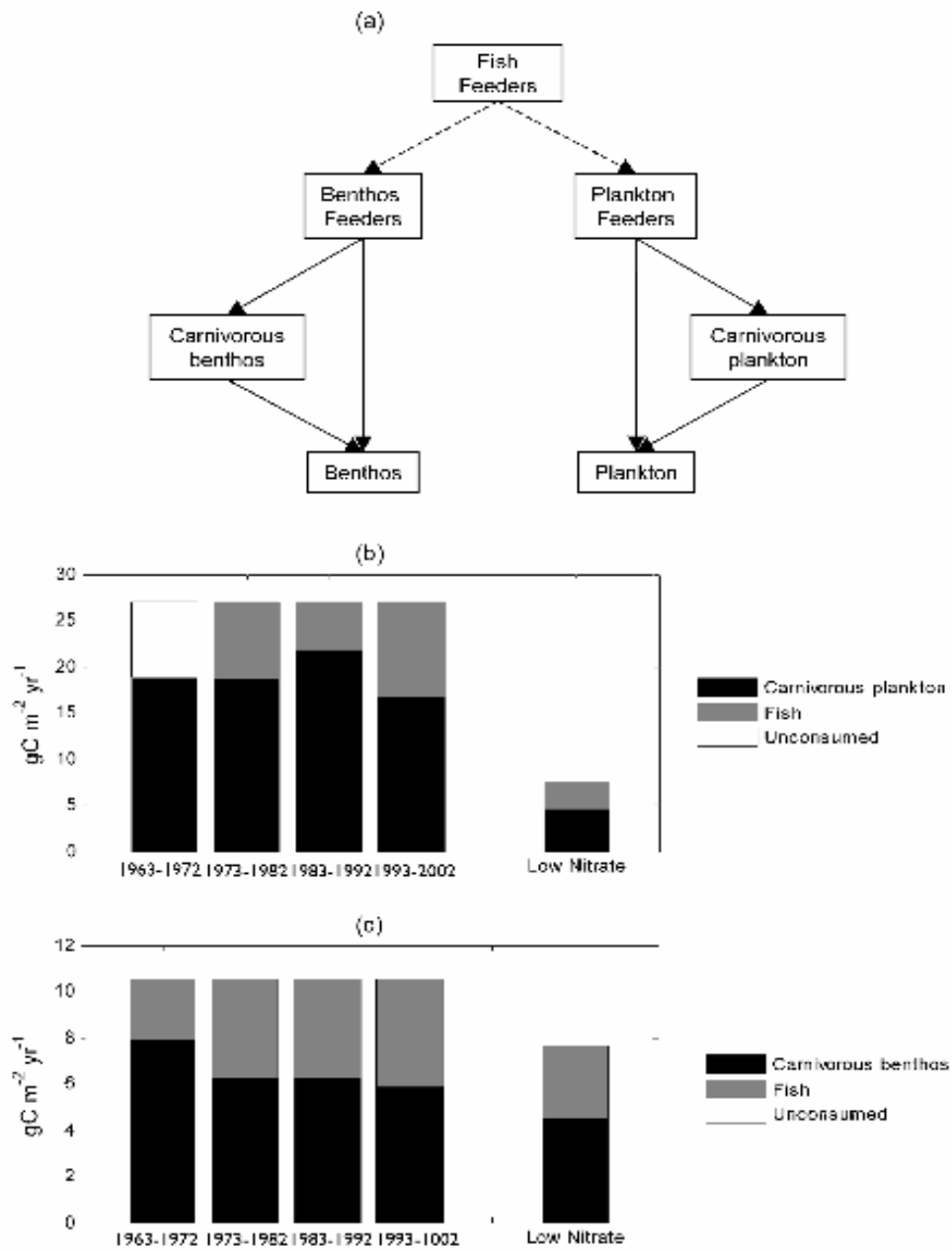
Figure 6

Figure 7

Figure 8

Figure 9

Figure 10