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Constructing end-to-end budgets for the Georges Bank ecosystem

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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 –weeks to months – means that the open ocean paradigm of a relatively autonomous microbial loop is inadequate. But purely top-down trophic depictions are insufficient to constrain a system subject to physical forcing as well as fishing. These processes are found on most continental shelves but are particularly important on Georges Bank in the north-west Atlantic where the weeks-to-months regime is dominant in relative area and in productivity.

We have generated budgets for the microbial food web for three physical regimes– well mixed, sporadically mixed 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. Also benthic suspension feeders (anchored plankton) are a critical pathway for transfers to higher trophic levels. Estimates of production by mesozooplankton, benthic suspension feeders and deposit feeders provide input to an upper trophic food web. Then diets of commercial fish populations are used to calculate food requirements in three categories, planktivores, benthivores and piscivores, for four decades or stanzas, between which there were major changes in the fish communities.

Comparisons of food requirements for fish with inputs from the microbial web indicate that (1) piscivore needs are relatively constant, even though there are major species shifts, and these needs can be met by the production of pelagic juvenile pre-recruits. (2) recent large increases in pelagic fish stocks would appear to limit food for pre-recruits or for invertebrate predators such as "jellies" (3) benthivorous fish requirements) benthivorous fish requirements match the production by suspension plus detritus feeding benthos, if 50-75% of the benthic production flows to fish via benthic invertebrate predators.

Keywords: Georges Bank, ecosystem, fisheries, microbial food web, physical forcing

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The microbial food web

The open ocean pattern of a "fast" microbial web in the upper layers with a very "slow" regeneration of exported nutrient to NO3 in deep water, does not hold on the continental shelf, Fig. 1.Thus the ocean paradigm (Eppley and Peterson, 1979; Laws et al, 2000) that the f-ratio of new:net production increases monotonically with net production breaks down completely in shallower water, Fig. 2, (Richardson and Pedresen, 1998; Bisagni, 2003). Since it is the "new" not the "net" production that is exported, this difference requires a complete revision of previous estimates of export to higher trophic levels (Cohen et al, 1982). New production (NP) is calculated (Bisagni, 2003) as the sum of *in situ* changes in NO3 in the euphotic zone plus fluxes of NO3 into this layer from deeper water. The season cycles of temperature and NO3, Fig. 3, have three phases – spring draw-down of nutrients, low summer concentrations, and recharge in the fall and winter. We take these three phases as distinct periods.

The three regions in Fig. 2 have been determined for these three periods, Fig. 4. The flux of water high in NO3 into the euphotic zone implies a corresponding loss. Specifically, the productive **Transition** region, Fig. 2, depends on an influx of deep **Stratified** water and a loss to the system through the upper layers of this sector. The calculated turnover time for this loss varies between 100 days in summer and 10 days in winter; similar to earlier estimates (Klein, 1987). These times overlap with the turnover times of the mesozooplankton (Hirst and Lampitt, 1998) that are in the range 5-15 days, summer to winter, so plankton loss from water exchange can be significant and is estimated for these budgets. In this environment, benthic suspension feeders – anchored plankton – have an advantage, as evidenced by the abundance of scallops in the **Transition** region (Horne et al, 1989).

Given these estimates of mixing and new production NP, fluxes in a microbial food web, Fig. 5, were estimated for the three regions and three seasons. For each season and region we have measures of the f-ratio and of the fraction of chlorophyll in small ($<20\mu$) cells (O'Reilly et al, 1987; Gifford, unpublished). This allows us to estimate two critical unknowns in this web; the fraction of NP going to microzooplankton, and the fraction of detritus that is recycled. These calculations are in terms of nitrogen, and the results are converted to carbon using an average C/N ratio = 7. The output from these calculations for the regions and seasons, Fig. 4, can be integrated to give the averaged trophic exports from the Bank; as

Mesozooplankton = 26.4 Suspension feeders = 5.6 Detritus = 28.9 gC.m⁻².year⁻¹

Note that the total export, 61 gC.m⁻².year⁻¹ is significantly less than the new production. This is a consequence of the leaks in the system due to the physical exchanges, Fig. 2; principally of zooplankton and detritus.

There is a final step. Detritus is consumed by deposit feeding macro- and meio-benthos, with an estimated 20% efficiency. We have no information on the meiobenthos. For the North Sea, Steele (1974), derived a fraction of 40% going to meiobenthos. We use 20%,

giving a biomass estimate of 4.8 for the deposit feeding macrobenthos. The filter feeding macrobenthos are dominated by scallops which are harvested at an approximate rate of 1.0 gC.m^{-2} .year⁻¹ (Horne et al, 1989) giving an available production of 4.6 and a total of 9.4 gC.m⁻².year⁻¹. Collie (unpublished) gives values based on observations of 3.8 and 6.1 gC.m⁻².year⁻¹ respectively for suspension and deposit production.

The upper level web

The simplest web that captures the main components, Fig. 7, has three top-down inputs, the food requirements of the fish, estimated from the NMFS trawl surveys (Fogarty, unpublished) and analysis of stomach contents (Garrison and Link, 2000); and expressed in terms of planktivores, piscivores and benthivores plus the predominantly planktonic food for the pre-recruit stages. From the microbial web calculations, we have two other inputs; the mesozooplankton production and the combined production of suspension and deposit feeding benthos. There are two "unknown" boxes for invertebrate predators; the pelagic invertebrate carnivores such as chaetognaths, ctenophores and other "jellies" that are notoriously difficult to sample; and benthic invertebrate carnivores – shrimps, crabs etc. Both groups of invertebrate predators are eaten by fish but these links are difficult to quantify with the present data.

The fish community is usually divided into these three feeding types, planktivores, piscivores and benthivores, but the nominal members of each category do not, understandably, confine themselves to a single diet type. This is particularly true for the piscivores which, based on Garrison and Link(2000) take only 1/3 of their diet from fish, but half from benthos, and the remainder from plankton. In turn, the planktivores consume some benthos. So we have combined the stock estimates with the Garrison and Link data to estimate the actual consumption of benthos, fish and plankton over the four stanzas, Fig8 upper.

Next we assume that the piscivores are feeding indiscriminately on the pre-recruit fish. If we assume that they are the predominant predators on the pre-recruits, then estimates of piscivore consumption are also estimates of pre-recruit production. By taking the ratio of production/consumption = 0.3, we can then estimate the food requirements of the prerecruit fish. If further, we assume the pre-recruits eat plankton, we can express all the fish consumption in terms of requirements for plankton and benthos, Fig.8 lower. At first sight it appears that available food is about 1.5 - 2.0 times the requirement. But this ignores the intermediate components in this food web; the carnivorous plankton and benthos. Not only are the carnivores in the plankton difficult to sample, especially the ctenophores and chaetognaths, but the estimates of energy requirements vary greatly.(Davis, 1984). Estimates of these plus Centropages spp and Hydroids, from the 1995-99 GLOBEC data lead to a value of 18 gC.m⁻².year⁻¹ (Sullivan and Chang, unpublished) for their food requirement, compared with a mesozooplankton production of 26.4 gC.m⁻².year⁻¹. Their conclusion, that invertebrate predators are the main consumer of copepods is in broad agreement with earlier work by Davis (1984). If we assume that invertebrate carnivores are eaten by planktivorous fish then the food remaining for these fish is 12 gC.m⁻².year⁻¹; just about enough on average but not for the

highest populations in the last decade. A major anomaly is that the Garrison and Link data indicate that very little of the fish food for recruits is in the invertebrate planktonic predator category. But this may be because of difficulty in identifying ctenophores, chaetognaths and predatory copepods such as *Centropages*. Also, the "predator" data is highly variable from year to year. Another possibility is to assume that some fraction of the pre-recruit diet for piscivores and benthivores is from the benthos. This would decrease the pressure on the mesozooplankton.

A second problem concerns the estimation of pre-recruit production. Sissenwine et al (1984) calculate a value about 1/3 the total recruit production based on the assumption that biomass is constant from larvae to recruit (Mortality=Growth). The value here is about 1/8. However Jones (1982) demonstrated that this ratio can vary by a factor of 4, depending on the population trajectory from larvae to recruit, and Houde (1996) showed that the trajectory is concave downwards. Given these uncertainties, we use this lower value, based on the assumption that piscivore consumption is the sole source of pre-recruit mortality.

Lastly we calculate the consumption by predatory benthos required to balance this part of the web, assuming that the predators are consumed by fish. For the four stanzas, the predators consume 74, 50, 50, 45% of benthic production, respectively. This number appears high.

Discussion

The basic premise is that detailed and quantitative knowledge of the microbial food web is essential to an understanding of ecosystems on the continental shelf. The implication is that top-down changes in fish populations are constrained by the output from the lower components so that, for example, detritus is not a free variable (Christensen and Pauly, 1998). Rather we would expect variations in nutrient supply to propagate through the system as changes in productivity at all trophic levels. The only major change in the upper levels occurs pre- to post-1973 when there was such a marked increase in fish stocks. It is not clear whether this can be attributed to environmental changes or is related to the extension of territorial limits in 1976. The latter resulted in a marked decrease in fishing on pelagic stocks; and these are the ones that show the largest increase.

The picture that emerges after 1973 is very different from the trajectories for the major fish stocks, Fig. 9 (Collie and deLong 1999); or from historical estimates of abundance of cod or haddock. The two- to three-fold increase in plankton eaters is explainable in terms of the removal of foreign fishing fleets. But the increase in benthic feeders pre- to post-1973 and the relative constancy thereafter seems difficult to reconcile with trends in commercial stocks, Fig. 9. This relative constancy in benthic intake results from significant contributions to benthic biomass from ocean pout, longhorn sculpin, red hake,

little skate and, recently, barndoor skate. So there appears to be switching to compensate for overfishing of the commercial species.

There is a similar picture for the piscivores as Garrison and Link (2000) have pointed out, with switching between winter skate, silver hake, dogfish and cod. There is much interest in the declines in top predators such as sharks, swordfish etc (Myers and Worms, 2003). It is of interest that our calculated requirements of piscivorous fish change little. in spite of a major switch in species composition from cod and hake to dogfish and winter skate.

Unlike the piscivores, the estimates for pelagic fish, including the pre-recruits, vary significantly over the four stanzas, in response to major increases in populations of herring and mackerel; to the point where estimates ofrequirement exceed those for supply. It should be noted that the adult populations are migratory and spend part of their annual cycle away from the Bank. It is difficult to estimate the invertebrate predators on the mesozooplankton, particularly the "jellies" such as ctenophores, but populations of these predators sampled in 1995-1999 would be expected to have significant food requirements at certain seasons. Given these uncertainties, the general conclusion is that the pelagic fish populations are likely to be limited by food supply through competition from other predators. It should be noted that this group includes the pre-recruits of the major groups and such limitation by large populations of adult plankton feeders could be a factor affecting recruitment of species such as cod and haddock (but not so much dogfish?).

The story is rather different for benthivorous fish over the last few decades. There would appear to be some superfluous production in the benthic, particularly pre-1973, but only if the fish feed directly on the suspension and deposit feeders. There is little evidence for a capacity for dramatic increase in the benthivorous fish stocks.. In other areas such as Newfoundland (Worm and Myers, 2003) and the North Sea (Heath, 2005), decline in commercial benthivorous fish is linked to increases in commercial catches of crabs, shrimp and lobsters. Georges Bank appears to be quite different, with switching to other non-commercial benthic fish feeders.

Conclusions

These results require estimates of a great range and diversity of parameters. Even more important, they depend on assumptions about processes such as long term nutrient fluxes and pre-recruit dynamics, where we have little direct evidence. Nevertheless, the results seem intuitively reasonable and are in line with calculations for fish stocks in a similar ecosystem, the North Sea (Heath, 2005). The underlying postulate, that each of the stanzas can be described by a linear steady state budget, is patently inadequate. It needs to be complemented by some process of punctuated equilibrium for switching between stanzas. Such "regime shifts" (Collie et al, 2004; Steele and Collie, 2005) must be incorporated for a fuller description of these systems.

The main 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 of having end-to-end food web calculations. No single top-down or bottom-up process determines the observed patterns. A significant role for benthic suspension feeders emerges from the physical constraints. There may be decimation of top predators but first order piscivores can switch successfully to other species, albeit less commercially attractive ones. Certain major fish components such as plankton feeders may be limited by competition for the basic productivity of the ecosystem, while consumption of benthos by fish implies that 45-74% 0f their diet is invertebrate predators. Management of the diversity of fishery resources requires an approach based on a full appreciation of the whole food web.

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Figure1. Coastal processes: (a) time scales – days to years - of top-to-bottom physical mixing are related to frontal systems determined in part by depth and tidal currents, (b) regeneration of organic matter appears to have time scales of weeks to months (Karl and Michaels 2001), (c) food web expressed in terms of time scales (from Steele and Collie, 2005)



Figure 2. Representation of three mixing regimes on Georges Bank New production data Bisagni (2003; unpublished); net production O'Reilly et al (1987) Units gC.m⁻² .year⁻¹



Figure 3. The seasonal changes in nitrate as a function of temperature on Georges Bank (Bisagni, unpublished)



Figure 4. The three regions during the three periods for which budgets were calculated for the microbial web. (Bisagni, unpublished)



Figure 5 The microbial food web based on nitrogen budgeting. Rectangles, components of the web: Ovals, input of NO3 and exports to upper trophic levels: Diamonds, physical losses due to mixing and advection: Dashed lines, recycling through bacteria and NH4.

Georges Bank Mesozoo Prodn



Figure 6. The production in the microbial food web that is exported to higher trophic levels. We assume that there is no suspension feeding in the **Stratified** region and no deposit feeding in the **Mixed**.



Figure 7. The upper web. Solid arrows denote estimated food requirements from fish diets. Dashed arrows are the unknown links. Inputs to D./S.B. and H.P. are from the microbial food web. Marine mammals are not considered significant here .

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Fish food consumption (gC/m²/year)





Figure 8. Top: The food requirements of plankton, benthos and fish eating fish (gC.m⁻²).year⁻¹); plus the total. Bottom: A comparison of plankton and benthos fish food requirement with the available production estimated from the microbial food web.







Figure 9. Biomass of the major commercial stocks on Georges Bank (Collie and deLong, 1999)