Uiblein, F., Ott, J., Stachowitsch, M. (Eds), 1996: Deep-sea and extreme shallow water habitats: affinities and adaptations. - Biosystematics and Ecology Series 11: 233-260.

The cycling of organic matter in food-limited environments

G.T. ROWE

Abstract: The abyssal plains below the central gyres of the major ocean basins are examples of extremely food-limited (oligotrophic) environments. Standing stocks are orders of magnitude below adjacent continental margins. This is assumed to be a function of the slow and meagre rain of particulate detritus from the euphotic zone. These abyssal deserts are also characterized by low rates of aerobic metabolism in and on oxic sediments, with minimal mineral accumulation. The low biomass and metabolism correlate well with the rate of particulate organic carbon (POC) input measured with sediment traps. The biomass distribution among size groups of organisms displays an increase in the relative percentages of microbiota (bacteria and meiofauna) and, in some systems, of the megafauna, but the latter may not be a universal trait. Data on standing stocks and community metabolism from several different food-limited systems are used in a mathematical model to simulate the community responses to pulses of organic matter and possible predator-prey interactions. Processes in the deep central North Pacific are compared with a polynya on the east coast of Greenland and the continental shelf of the western Gulf of Mexico. The simulated responses suggest that carbon cycling in some benthic sub-systems may be affected by "top down" (predation) as well as "bottom up" (POC sedimentation) processes.

Introduction

The abyssal plains below the central gyres of the major ocean basins are extreme examples of food-limited (oligotrophic) environments (GAGE and TYLER 1991). The standing stocks of the biota are several orders of magnitude lower (SPARCK 1956, ROWE 1983) than those on adjacent continental margins, in trenches and canyons, or near hydrothermal vents. The observed low biomass is assumed to be a function of the slow and meagre rain of particulate detritus from the euphotic zone (AGASSIZ 1888). These abyssal deserts are also characterized by low rates of aerobic metabolism in and on oxic sediments (SMITH and HINGA 1983) with minimal mineral accumulation. The low biomass and metabolism correlate well with the rate of particulate organic carbon (POC) input into sediment traps (ROWE et al. 1991), but not with the low and rather static concentration of organic matter within the sea floor (MARTIN and BENDER 1988). This deep, food-limited environment favors small organisms (THIEL 1975), and the relative biomass distribution among size groups of organisms shifts to bi-modal under such conditions (POLLONI et al. 1979), with an increase in the relative percentages of the motile carcass-feeding forms (the megafauna and fishes) (HAEDRICH and ROWE 1977) and the microbiota (meiofauna: TIETJEN et al. 1989; heterotrophic bacteria: ROWE et al. 1991), which are presumably able to remobilize relatively unreactive detritus (RICHARDSON and YOUNG 1987, DEMING and BAROSS 1993, ANDERSON et al. 1994). While the input of particulates exhibits a seasonal pattern in many oceans, how this is cycled up a food chain or through food webs is not well documented. Sediment whole-community metabolism appears to vary in a seasonal pattern following the variation in POC fluxes in the North Pacific (SMITH 1992) but not in the deep west central North Atlantic (SAYLES et al. 1994). The latter authors use the model of MARTIN and BENDER (1988) to infer that a community response in total oxygen demand would not be expected in the Atlantic, given the observed low fluxes of what is assumed to be relatively refractory particulate organic matter to the sea floor. In the Pacific the measured POC flux is less than the measured total community metabolism (SMITH 1987); it has been suggested that this results from the sediment traps missing seasonal pulses of POC (SMITH et al. 1989), lateral input from the continental margin (JAHNKE et al. 1990, ROWE et al. 1994), or migration (SMITH 1987).

Following the original verification that seasonal cycles in POC input could be detected in deep-ocean sediment traps (DEUSER et al. 1981), time-lapse bottom photography documented a rain of intact cellular material to great depths with little apparent degradation in the water column (LAMPITT 1985, RICE et al. 1986). Some megafauna display seasonal spawning, which could be a response to such variations in POC input (CAMPOS-CREASEY et al. 1994), but such a response is not universal in most major taxa (TYLER 1988). Biomass and metabolic activity of protists and other small heterotrophs appear to respond quickly to new supplies of energy (PFANNKUCHE and THIEL 1987, GOODAY and LAMBSHEAD1989, GRAF 1989, TURLEY and LOCHTE 1990, LINKE 1992, PFANNKUCHKE 1993), even in laboratory experiments (LINKE et al. 1995).

Much of the deep sea is by definition a "food-limited" environment. Just as an arid desert lacks water to support photosynthesis, the absence of light prevents photosynthesis. But what defines food limitation? "Substrate limitation" (or food limitation in this case) is inferred when a process, such as growth, feeding rate, enzyme activity, etc., responds to increases in the substrate. Therefore, food limitation might also be inferred in other marine ecosystems if a benthic community parameter, such as benthic biomass, sediment oxygen demand, etc., responds directly to POC input from primary producers, regardless of depth. For example, areas with minimal input of "new" nutrients are characterized by relatively low primary production, and a resultant low benthic biomass could be considered a result of "food limitation". An example might be the continental shelf of the western Gulf of Mexico, where low macrobenthic biomass has been attributed to low primary production (ROWE et al. 1974). On the other hand, if the NW Gulf of Mexico is food-limited, how does it support major shrimp fisheries (FLINT and RABALAIS 1981)? A quite opposite example of hypothetical food limitation might be those polar environments where ice cover for much of the year limits primary production to a brief seasonal pulse. Indeed, bacterial activity often appears to be limited in cold polar environments (POMEROY and DEIBEL 1986). On the other hand, the high benthic biomass in some areas at high latitudes suggests that the ecosystem is **not** "food limited" (GREBMEIER et al. 1988). In fact, in some locales the high rates of energy transfer up polar food chains to amphipods, whales, and birds suggest just the opposite (HIGHSMITH and COYLE 1990, OBST and HUNT 1990).

In the present paper, data on standing stocks and community metabolism from several different marine benthic sub-systems (continental shelf of the western Gulf of Mexico, the deep region below the central gyre of the central North Pacific, and the northeast Greenland polynya) are compared to determine the degree to which is each "food limited". Input of POC, community and population respiration rates, and stock sizes are used in sets of coupled differential equations to simulate the dynamic responses of the different benthic communities to temporal alterations in sedimenting POC, including seasonal pulses. Potential predator-prey interactions are also used to investigate possible "top down" control of standing stocks and detrital carbon reservoirs. The "accuracy" of the simulations is tested by subjecting the simulations to limited sensitivity analyses and by comparing model output with data available in the different benthic sub-systems considered (DE BOVEE and LABAT 1993).

Materials and Methods

The primary data in this review are already published or are to be published elsewhere. The data consist of quantitative standing stocks, in terms of biomass, obtained using standard quantitative sampling which is described in the original papers. For the most part, this has been with a USNEL 0.25 m^2 spade core. The second important kind of information reviewed are those biological processes which are transfers of carbon into, out of, or between the standing stocks. This information, too, for the most part has been generated in previous work. The principal process which has been measured directly in the studies reviewed is respiration. This was measured with only minor modifications of standard techniques. Sediment whole-community respiration was measured using benthic chambers, the respiration of megafauna, where possible, by incubating individuals. The information comes from three geographic areas to be compared: a time-series station at a depth of 5.8 km in the east central North Pacific, based on SMITH (1992); the deep troughs (200 to 500 m) in the continental margin below a polynya on the northeast coast of Greenland, based on several recent papers (AMBROSE and RENAUD 1995, DEMING et al. 1995, ESCOBAR-BRIONES 1995, ROWE et al., in revision); and the broad, flat continental shelf of the northwest Gulf of Mexico, for which the data and the techniques used can be found in a series of studies (ROWE et al. 1974, GETTLESON 1976, FLINT and RABALAIS 1981, CRUZ-KAEGI 1992).

The benthic oxygen fluxes (converted to carbon) and standing stocks, in terms of carbon, are used for simplified, comparative ecosystem carbon budgets (Figs 1 and 7). These simple budgets are then expanded to models of food webs or food chains of varying complexity for each area (Figs 2, 8 and 11). In these models, the state variables are pictured as boxes: 1) organic detritus (or organic carbon), 2) bacteria, 3) meiofauna, 4) macrofauna, and 5) megafauna (= penaeid shrimp in the third model from the Gulf of Mexico), or some aggregation of these five. Units for each are mg $C{\cdot}m^{-2}$. Fluxes are represented by the larger open arrows [attached to circles (="valves")]: 1) respiration for each living state variable, represented by arrows leading to cloud-like figures; 2) "predator-prey" transfers, represented by arrows between boxes; 3) defecation (in the second model on the NE Greenland polynya), which are arrows leading from living components back to the detritus box; and 4) an input term, called the "pelagic POC pulse" (or phytoplankton in model 3), which is an arrow representing the rain of particulate matter from above. The units of the fluxes are all mg $C{\cdot}m^{-2}{\cdot}d^{-1}$.

The total carbon flow and the sum of its concentration in the stocks are ultimately controlled by the input of POC, whose value, where possible, has been determined from deep or near-bottom, moored sediment traps. Mass has to be balanced: the total biomass and resulting respiration cannot be greater than the input of POC plus the carbon present in the system under the initial conditions.

The software used for the models is STELLA II, Version 3.0, available from High Performance Systems, Hanover, New Hampshire, U.S.A. The models were run on a Macintosh Quadra 610 or Power Book 140. Solutions employ Euler's Method of numerical integration. First-order respiration coefficients were based on the biomass of each category of organisms, and that category's measured or inferred respiration rate, where

Respiration(i) = k(i) ∗ [biomass(i)], or,
k(i) = Respiration(i)/[biomass(i)], with units of time^{-1}.

and where (i) refers to a particular "group" or stock of organisms. The growth of each stock is a function of the flows into the stock minus the flows out of the stock. For growth to occur, the inflow to a stock must be greater than the losses (respiration, feces and predation). Initial feeding rates (arrows into a box) were determined by assuming steady state (no growth), and in this case assimilation equaled respiration. Where growth rate as well as respiration rate estimates were available for specific groups, this information was used to calculated initial assimilation and feeding rates. Then a first order feeding rate is calculated, where

Feeding(i) = k(i) ∗ [biomass(i)].

The megafauna, where included, was parameterized as a predator on macrofauna. As above, respiration was assumed to be a first-order decay process that is a function of biomass. It was assumed that the megafauna produced little or no gonad material and have no predators. Growth by this group was a function of the balance between feeding rate, respiration, and defecation. Defecation, where included, was assumed to be a constant fraction of the feeding rate (20 to 50 %).

First-order and second-order dynamics have alternately been experimented with in the predator - prey relationships. In second-order relationships, the predation rate was assumed to be a function of the sizes of both the donor (prey(i)) and the recipient (predator(j)) variables:

Carbon Transfer Rate (i,j) = k(i,j) ∗ [biomass of the prey(i)] ∗ [biomass of the predator(j)]

The predation or grazing rate coefficients were calculated by assuming steady state and then dividing the predation rate by the biomass of the two stocks involved.

Equations written for each state variable of the three areas are presented in the appendix. After the equation for each variable, there is also a description of the "inflows" and the "outflows" for each variable, and the initial concentration of each variable. In addition to the state variables (the boxes) and the fluxes (the arrows with "valves"), the values of the coefficients in the parameterizations are given in the appendix. These controlling coefficients are represented by circles in the figures, with small arrows directed into the fluxes that they control (Figs 2, 8, and 11). The values of these coefficients are adjacent to the labeled "circles" at the end of each set of equations. The little solid arrows are not fluxes, but features of the STELLA II software. Their purpose is to identify functional relationships within an equation describing the dynamics of a flux. These arrows illustrate how a state variable (origin of the arrow) and a constant (origin of another related arrow) exert mathematical control over a flux (at the head of the arrow). Note, for example, that the number of variables or constants used to calculate each flux rate is equal to the number of arrowheads entering the circle (valve) on each open flux arrow.

Results and Discussion

The deep North Central Pacific

A traditional approach for portraying the most important biogeochemical processes of an ecosystem is a generic "flux" diagram. Such a diagram portrays the living reservoirs as a box or set of boxes, with transfers or fluxes between the reservoirs as arrows. Such an illustration is particularly useful for describing benthic ecosystems in terms of fluxes of organic matter and the remineralization of metabolic by-products from organic matter (Fig. 1). In a natural abyssal benthic sub-system the key input of organic matter is assumed to be a very slow rain of particulate detritus; the standing stocks of living organisms will be low; detrital organics will be low and rather non-reactive or refractory; and community metabolism will be confined principally to low rates of aerobic respiration (GAGE and TYLER 1991). A basic question for an abyssal benthic sub-system is how an extremely food-limited community of organisms and its biological processes will respond to seasonal fluxes or pulses of organic input. An increase in the organic matter input (Fig. 1) should push an oligotrophic benthic sub-system characteristic of abyssal plains below central gyres toward a less food-limited situation. The models presented will attempt to simulate this progression of responses.

Published data for time-series observations at a benthic boundary layer station in the Pacific at a depth of ca. 5.8 km (SMITH 1992) have been utilized to investigate how a food-limited community responds to time-varying input of POC. This site was chosen because available information is more complete than for practically any other single site on an abyssal plain. SMITH's units and some of his categories of stocks have been changed and simplified to better fit the goals of the simulation experiments. For example, the units in the model for standing stocks are mg $C{\cdot}m^{-2}$, with fluxes in the same units but with time in days. (SMITH used g $C{\cdot}km^{-2}{\cdot}d^{-1}$) The present simulation has been simplified from SMITH's original conceptual steady state budget on the principle of Occam's Razor: don't make models overly complicated. Simplification to some degree is also justified on the basis of SMITH's data. For example, SMITH could define 6 living state variables or standing stocks, but the simulations dealt with only three state variables (Fig. 2): all the biota dwelling within the sediments were aggregated together into one compartment (called "heterotrophs") and all the water column biota were excluded, except for the megafauna living on the sediments, which was a target group for experimenting with effects of predation on community size structure. The biomass of the biota in the sediments is the sum of SMITH's values for sediment-dwelling organisms [for microbiota (=bacteria principally), meiofauna, and macrofauna], the megafauna value is directly from SMITH: it included no fishes or carcasses. The vertical scale was the original top 5.5 cm of the sediments. The biomass "initial conditions" came directly from SMITH's mean values but on a per-square-meter basis.

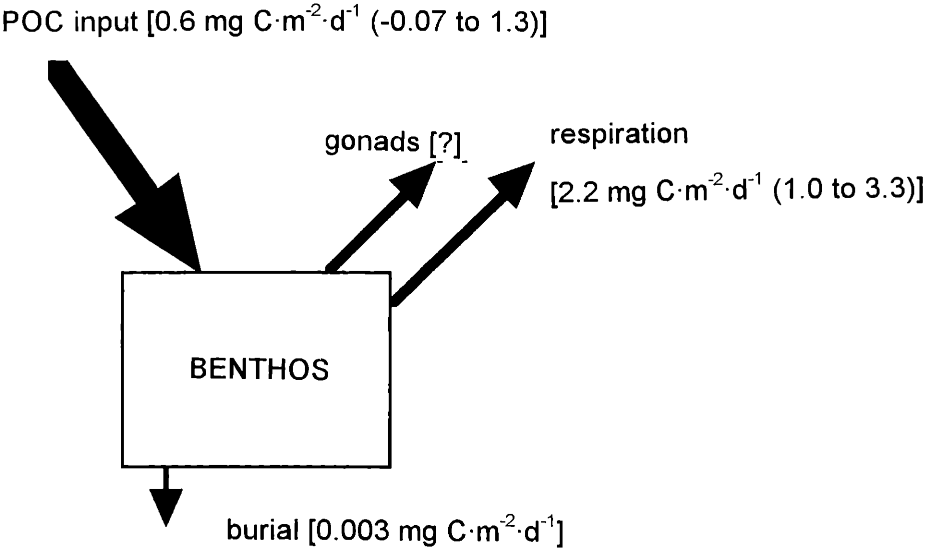

Fig. 1: Simplified flux diagram for benthic community, with data from Smith (1992).

First, the input necessary for steady state was solved for. SMITH, in earlier work (1987), pointed out that the input measured in sediment traps was less than the summed utilization (based on oxygen demand) for the various components of the system. While this could be made up for by migration

(SMITH 1987), lateral input of particulate organic matter (JAHNKE et al. 1990), lack of steady state within the system, or experimental error, I have assumed that it was a failure of the sediment traps to measure vertical pulses of particulate organic matter (SMITH et al. 1989).

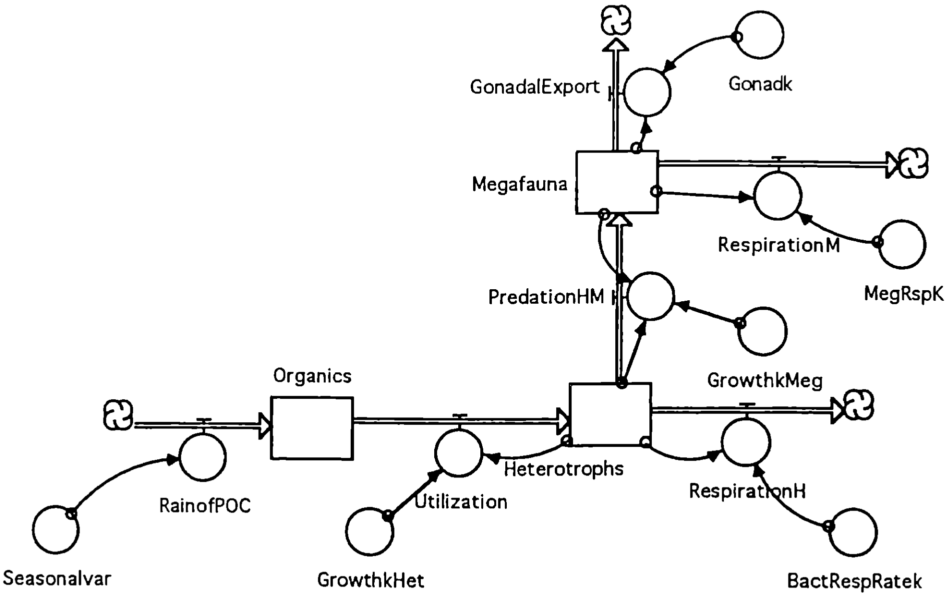

Fig. 2: Conceptual model of a 3 compartment deep-sea food chain (modified from SMITH 1992) associated with the benthic boundary layer in the deep North Pacific, but with some compartments combined or re-named (see text). This formulation is used as the basis for a simulation of the fluxes and stocks over time, based on the initial conditions, fluxes, and standing stocks in Smith's study. Units are mg $C \cdot m^{-2} \cdot d^{-1}$ for fluxes (4 and 5) and mg $C \cdot m^{-2}$ for standing stocks (1 through 3).

The simplest simulation was a two-compartment system consisting of "organic matter" and "heterotrophs" driven by an unvarying input flow of POC (rain of particles). After determining the input required to achieve steady state for that over-simplified situation, a seasonal cycle for POC input which mimics the general pattern observed in sediment trap deployments (DEUSER et al. 1981), including that in the north Pacific (SMITH et al. 1992), was incorporated into the equations. Then an additional living component, the "megafauna", was included (Fig. 2). These preyed on the "heterotrophs." Growth in the "heterotroph" component was accomplished by setting the feeding rate a little bit larger than the respiration (e.g., the first-order growth constant was slightly larger than the first-order respiration rate constant). The feeding rate of the "megafauna" was parameterized as a second-order function of biomass of the donor (heterotroph) and recipient (megafauna) stocks. The rate constants used were calculated from SMITH's original data, as explained in the introduction above. The carbon in the sediments was defined as "total organic carbon". Unfortunately, much of the detrital organic matter in sediments cannot be characterized chemically and in deep water much of it is apparently relatively unreactive, with marginal value as food (KHRIPOUNOFF and ROWE 1985). Therefore, rather than using an initial condition of several hundred grams of organic carbon in the top 5.5 cm of a square meter, as in SMITH, the initial condition was reduced to approximately 10 % of that, or 25 000 mg $C{\cdot}m^{-2}$. This 3 box model was run for 10 years.

This simplified simulation has some fascinating properties (Fig. 3). A pulse of organic matter with a maximum of 12 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$ was entered every year of the 10-year period. Rather than responding to this on a seasonal basis, as might be expected, the "heterotrophs" responded in two peaks more or less evenly spaced over the 10-year period. Their predators, the "megafauna", followed with a peak in each case several months later. The intensity of the predation almost wiped the "heterotrophs" out for a two-year period. The sediment "organics" declined abruptly when the "heterotrophs" were abundant, but increased slowly when the "megafauna" had nearly wiped the "heterotrophs" out. Steady state was not achieved, and several of the variables did not agree with the state variable values SMITH presented: both the "heterotrophs" and the "megafauna" reached values far higher than any observed by SMITH. Because of this lack of agreement between data and the model output, a series of alterations were made in both the parameters and the initial values of the state variables. In these model experiments, an interesting disparity was observed between the sediment detrital carbon stock size as measured by SMITH and the model output (Fig. 3). The use of 25 g $C{\cdot}m^{-2}$, which was about an order of magnitude lower than the actual value, pushed the "heterotrophs" up to unrealistically high values never found in such oligotrophic environments (approaching 1.5 g $C{\cdot}m^{-2}$) (Fig. 3). This was followed by unrealistic values for the "megafauna" preying on them. When the seemingly small initial "organics" (Fig. 3) was reduced to an initial value of 2.2 g $C{\cdot}m^{-2}$ (5.5 cm depth), the biomass values agreed much better with those measured (Fig. 4). This is only a few percent of the total carbon. In this case, note that the "heterotrophs" and the "organics" peaked every two years, but on alternate years. The "megafauna" slowly declined throughout the 10 year-period.

There may be some "top down" control of population levels and of "organics", rather than "bottom up" (POC flux) control. When "megafauna" overate their prey ("heterotrophs") down to a small value, the "heterotrophs" were in essence wiped out, and then the "megafauna" crashed because they had too little to eat. As "megafauna" slowly declined (Fig. 4), a slight increase was evident in the metazoans in the first several years, after which the pattern stabilized. What has been observed in these models are cycles that are typical of predator-prey or Lotka -Volterra relationships. There is a possibility that this was realistic: many such cycles are observed in both terrestrial and aquatic ecosystems (KREBS et al. 1995). It is also possible, however, that this was an artifact of the over-simplification of the food chain itself.

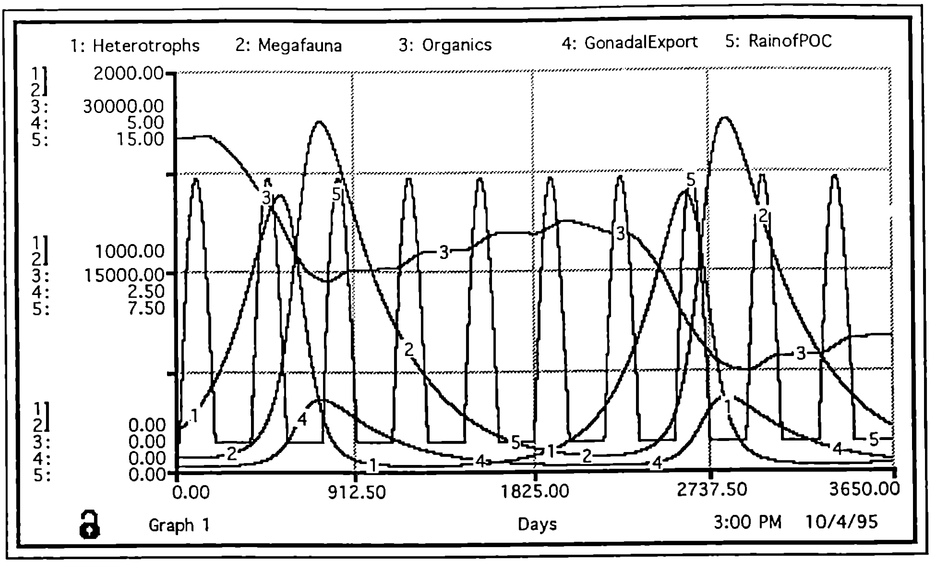

Fig. 3: Output of a numerical simulation of the deep-sea food chain in SMITH (1992). Units for fluxes are mg $C \cdot m^{-2} \cdot d^{-1}$; units for standing stocks are mg C/m^2 down to 5.5 cm in the sediments. Initial value of detrital "organics" is approximately 10% of that measured. Biomass of "megafauna" and "heterotrophs" (all sediment organisms) peak twice in a 10-year simulation, and their values are several times higher than mean values measured.

The next model experiment involved the effects of the "megafauna" on not only the "heterotrophs" but also indirectly on "organics" concentrations. In Fig. 5 the growth rate coefficient for the "megafauna" was increased by 50 %. In this case the "megafauna" consumed enough of the "heterotrophs" that "organics" was conserved. That is, the residual, stored carbon was higher with the "megafauna" than without them. This is contrasted with a case in which the "megafauna" were eliminated completely (Fig. 6). In this case, resulting detrital "organics" was somewhat lower because the biomass of the "heterotrophs" was not controlled by a higher level in the food chain.

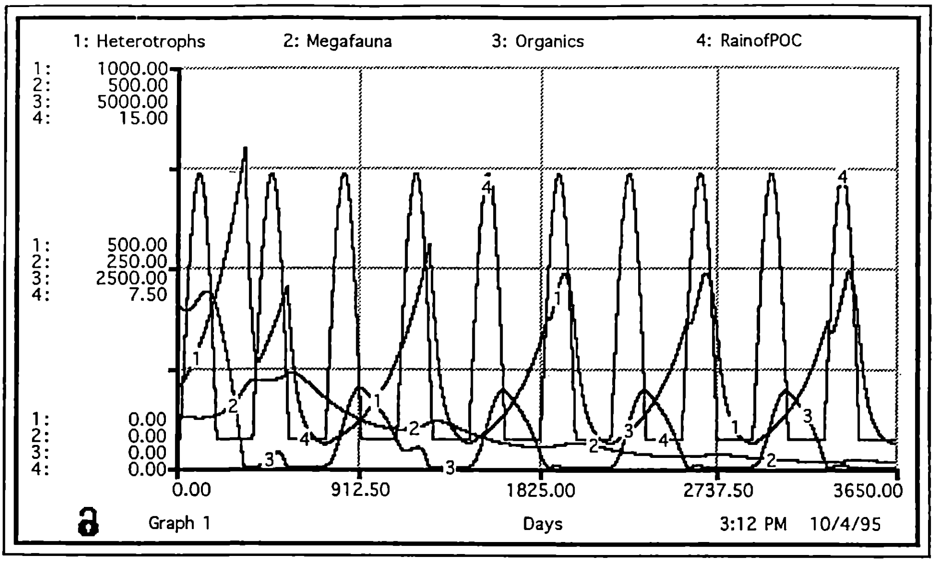

Fig. 4: Output of a numerical simulation, as in Fig. 3, but with initial value of "organics" set at about 1% of measured values. "Heterotroph" and "megafauna" biomass levels are more realistic than in Figure 3. "Megafauna" is not in steady state but continues to decline over the 10-year run. Note that "heterotrophs" and "megafauna" exhibit an evenly spaced periodicity, but at alternating two-year intervals instead of the one-year pulses of POC (4). "Organics" (3) is eliminated on alternate years.

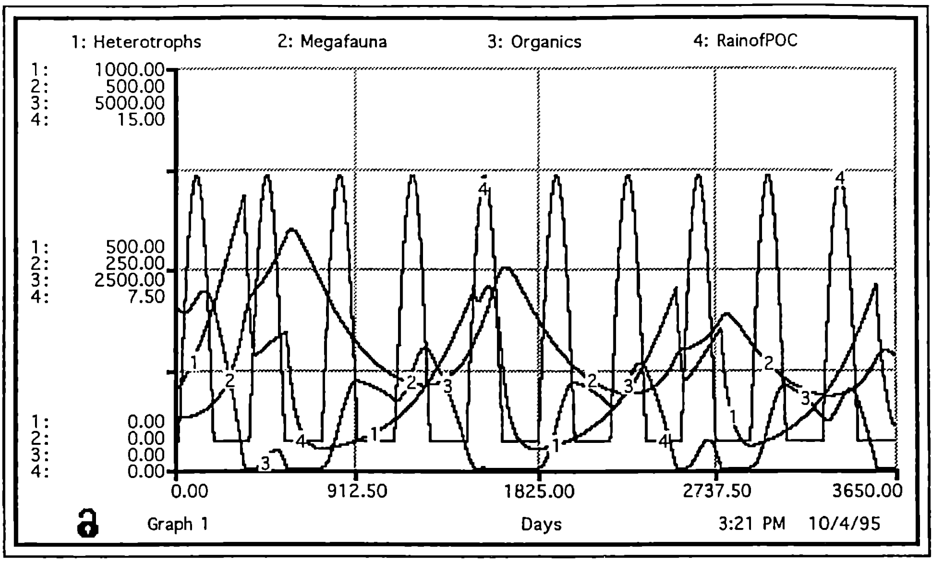

Fig. 5: Output of numerical simulation, as in Figs 3 and 4, but with the growth rate of the "megafauna" increased by increasing the 2nd order feeding rate coefficient from $1 \cdot 10^{-5}$ to $1.5 \cdot 10^{-5}$.

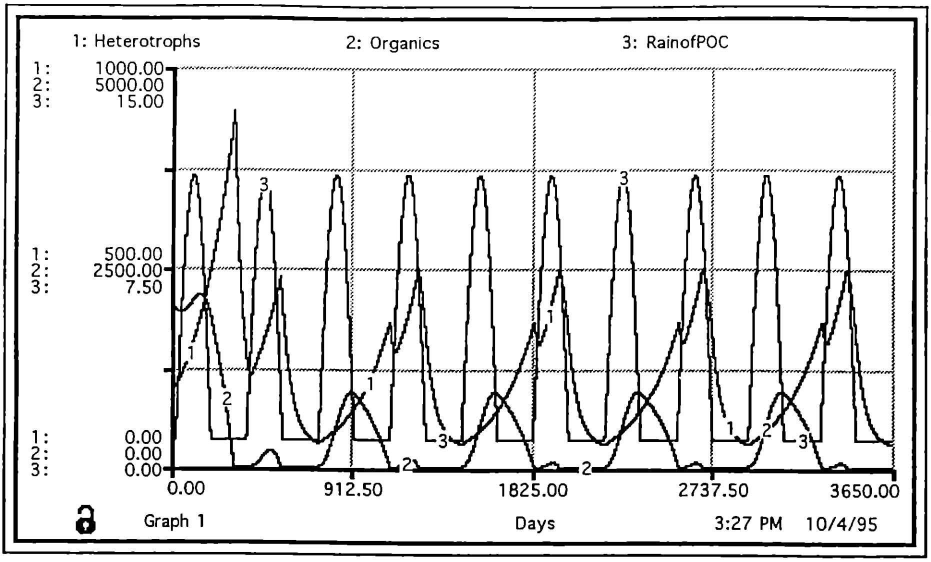

Fig. 6: Output of numerical simulation, as in Figs 3 to 5, but with "megafauna" eliminated. In this case the "organics" and the "heterotroph" biomass reach maxima at two year intervals on alternate years. The "organics" is held to lower values, but the "heterotrophs" are only slightly higher than in Fig. 5 where they were subject to predation.

The above interpretation of the food chain assumes that a resident "megafauna" grows in response to the growth of its presumed prey, a group of smaller invertebrates and bacteria referred to as "heterotrophs". The model does not differentiate between recruitment of new larvae or juveniles from reproduction and growth of species already in the area. In terms of the growth response of the "megafauna", this may not make any difference to the final outcome: increases in predator biomass will depend on increases in prey biomass. It is well-documented that widely-ranging scavengers such as rattail fishes and relatively large crustaceans (Amphipoda) are almost immediately attracted to carcasses anchored to the sea floor, and so biomass increases in all groups under consideration may result from recruitment as well as growth.

The Northeast Greenland continental shelf polynya

The Northeast Water Polynya (NEWP) on the continental margin of northeast Greenland has provided the opportunity to study the effects of a seasonal pulse of organic matter into marginal troughs at intermediate depths of 200 to 500 m. The input of material is limited to only that brief time period when the polynya is open (BAUERFEIND et al. 1995). Little degradation might be expected because physical transit through the water column is "efficient" with little degradation, thus maximizing effects on the benthic environment (AMBROSE and RENAUD1995).

Sediment community metabolism (oxygen demand and inorganic nutrient production) was measured in the NEWP employing two methods: in situ benthic chambers deployed with a benthic lander and shipboard laboratory incubations of "cores" recovered from USNEL box cores (ESCOBAR-BRIONES et al. 1995; ROWE, ESCOBAR-BRIONES, BOLAND, NEWTON, CRUZ-KAEGI, WALSH unpubl. manuscript). A key component in the Greenland study was the benthic lander and in situ chambers developed at Texas A&M University (POMEROY et al. 1991, ROWE et al. 1994). As utilized in the work of SMITH in the Pacific, these chambers remain on the bottom over periods of a few hours up to several days, depending on the expected rate of oxygen utilization and the resulting time required to obtain a reliable time-series measurement.

Standard techniques were used to determine the biomass and abundance of the biota, and these data are reported in a series of papers on different functional and size groups of organisms (AMBROSE and RENAUD 1995, NEWTON and ROWE 1995, DEMING et al. 1995). The same spade cores also provided the samples for the deck incubation chambers, and at the end of each incubation similar analyses of the sediments were made to determine standing stocks within the chambers. The incubation chamber standing stock biomass data for bacteria, meiofauna, and macrofauna were used as the "initial conditions" in the polynya simulations. In 1992, the total sediment biomass in the deck incubation chambers had a mean of 1.48 g $C{\cdot}m^2$ at 6 locations (σ=+0.76, n=6). Macrofauna, meiofauna and bacteria had means of 1.09 (σ=+0.7, ν=6); 0.06(σ=+0.7, ν=8); αvδ 0.292 (σ=+0.17, n=8) g $C{\cdot}m^{-2}$. In 1993, the total sediment biomass was 1.36 g $C{\cdot}m^{-2}$. The macrofauna mean was 0.58 g $C{\cdot}m^{-2}$ (σ=+0.47, n=13), whereas the bacteria mean was 0.59 g $C{\cdot}m^{-2}$ (σ=+0.25, n=13). No statistically significant differences in biomass could be detected between 1992 and 1993. The mean of the total biomass for both years was 1.42 g $C{\cdot}m^{-2}$.

The mean benthic respiration rate at the deep stations, combining the mean of the ship-board incubations and the mean of 5 in situ chamber fluxes, was equivalent to a remineralization rate of 20.4 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$ (Fig. 7), assuming a Respiratory Quotient of 0.85. This represents ca. 10% of the average net primary production measured in 1992 (SMITH 1995). Average carbon residence time in the biota, calculated by dividing the biomass by the respiration, was on the order of 70 days, which is comparable to continental margins at temperate latitudes (ROWE et al. 1991).

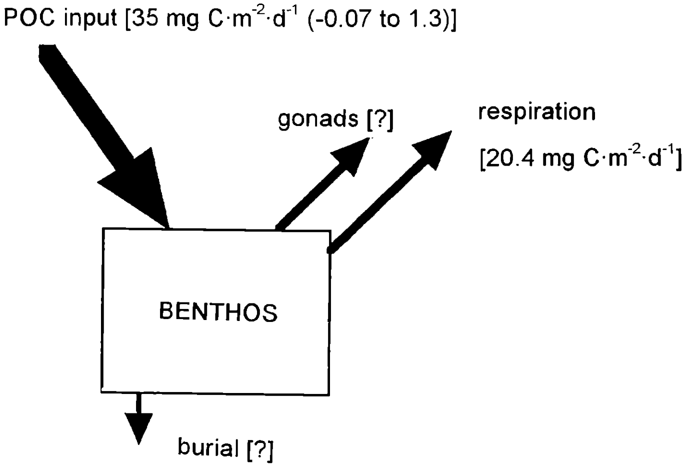

Fig. 7: Benthic sub-system flux diagram, as in Fig. 1. Data from the northeast Greenland continental shelf polynya.

The input of POC into the bottom sediment traps has been "mimicked" as a positive sine function, as in the seasonal variation in the Pacific model. A single pulse of POC extended over a 6 month period, with a maximum rate of just over 100 mg $C \cdot m^{-2} \cdot d^{-1}$ concentrated in a period of 6 weeks. An integration of the pulse and non-pulse periods over an entire year averaged about 35 mg $C \cdot m^{-2} \cdot d^{-1}$, or approximately what was recorded in the near-bottom (50 m off) sediment traps (Fig. 7) as primary input (directly from the water column) and additional material entering laterally from the trough margins or shallow banks.

This second model of an Arctic polynya was designed to be more complex (Fig. 8) than the abyssal Pacific model. It contained 5 state variables: "detritus", "bacteria", meiofauna", "macrofauna", and "megafauna". Fecal production returned organic matter to the detrital pool. The "bacteria", the "meiofauna", the "macrofauna", and the "megafauna" were arranged in a food chain based on increasing sizes, but the three smaller groups were also arranged in a food web in which they could share or compete for "detritus" stocks. In this situation, the absence of one of these groups would not necessarily protect the food source because the other groups could also utilize it. This presumed, however, that the "bacteria" were not necessarily a vital intermediary between relatively refractory "detritus" and the metazoans (RICHARDSON and YOUNG 1987). This assumption was made because the material is thought to be fresh input to the bottom. While the biomass of the individual groups of sediment organisms was fairly well established, the respiration value was for the total community and not its individual size components. Therefore, precise parameterization of the respiration rates of each size component was not possible. The respiration rates and the growth rates of the groups are adjusted within the boundary imposed by the total community respiration rate and the predation required to support the megafauna at steady state. A series of iterations are then run until the most reasonable relationship among the stocks, the rates, and actual data are achieved. The "megafauna" biomass and respiration was kindly supplied by Dieter PIEPENBURG. This model was run for 5 years.

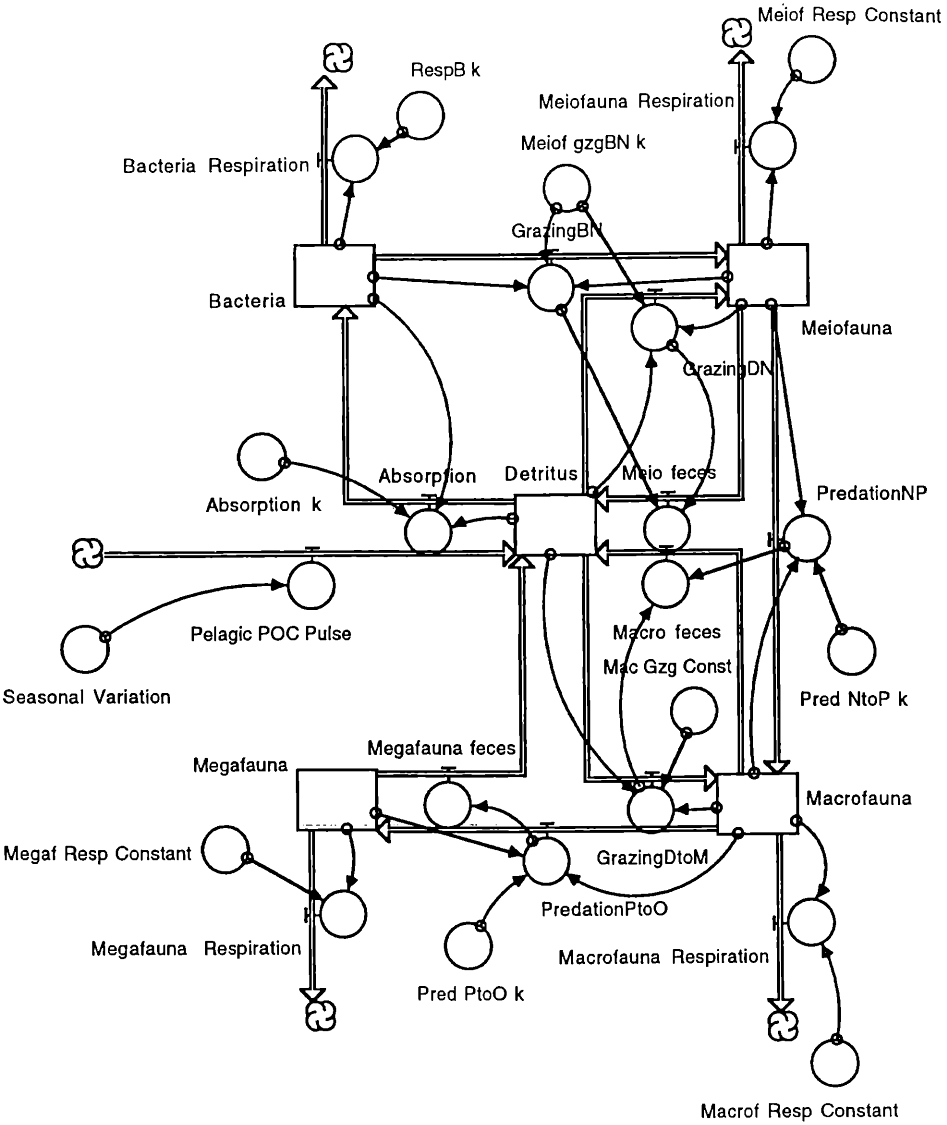

Fig. 8: Carbon model of benthic food chain in the Northeast Water Polynya, Greenland. Equations in appendix. State variables as in Fig. 2, but with heterotrophs split into bacteria, meiofauna, and macrofauna. Organics in Fig. 2 is Detritus in this figure. Fecal production is set as varying fractions of consumption (see second set of model equations in appendix).

The general behavior of the stocks and the rates was a dynamic response to the POC pulse each season (Fig. 9), as might be expected. All responses were annual, rather than bi-annual or tri-annual, as in the various runs of the abyssal model. The "bacteria" increased dramatically following the pulsed input. They reached a maximum of about 5000 mg $C{\cdot}m^{-2}$ about 40 to 50 days after the pulse maximum, which was near the upper range of values recorded. Then it fell continuously to minimal values during the rest of the year when little POC was entering the shelf trough environment. This might have been predicted, but there is presently no way to take winter samples to verify the model. The "macrofauna" biomass at first dropped slowly from the "initial value", but then jumped up from around 0.5 to over 1.5 g $C{\cdot}m^{-2}$ over a short span of about 2 weeks. This coincided with a drop in "bacteria" biomass and respiration. While it is reasonable to presume that the two were related, note, however, that in the model (Fig. 8) the "macrofauna" did not directly consume the "bacteria". Any effect therefore must be indirect. "Megafauna" varied, but less markedly, probably because their responses were dampened by being higher up the food chain. Interestingly, elimination of the "megafauna" had little perceptible effect on other state variables (Fig. 10).

An interesting phenomenon in the model was the degree to which carbon was sequestered as biomass. The "macrofauna", for example, decreased in biomass down to about 350 mg $C{\cdot}m^{-2}$ after about 3 months, but then abruptly increased up to just over 1,500 mg $C{\cdot}m^{-2}$ within a few weeks following the pulse (Fig 9). This was equivalent to a secondary production of about 60 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$. Then, as their food was depleted, they declined in biomass for the rest of the year down to almost nothing due to their own respiration and predation by the "megafauna". The maximum values, however, were well within the range measured (AMBROSE and RENAUD 1995).

A final experiment (not shown) with the model has been to increase the POC pulse appreciably to test the hypothesis that the community was "food limited". When the pulse was pumped up to 6 times that value measured with the sediment traps (maximum of 600 mg $C{\cdot}m^{-2}$ per day), the model behaved in essentially the same manner: in a 3-month period the bacterial respiration tracked the pulse of POC fairly closely, and the "macrofauna" (polychaete worms in this case) steadily increased with wide but characteristic (model) oscillations. The polychaetes reached a biomass of 5 g $C{\cdot}m^{-2}$ within three months, and the respiration was approaching 300 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$. Actual values of this magnitude for the polychaete biomass were approached only at a single station near the outer fringe of the area, or "down stream" where organic-rich particulates were accumulating (AMBROSE and RENAUD1995).

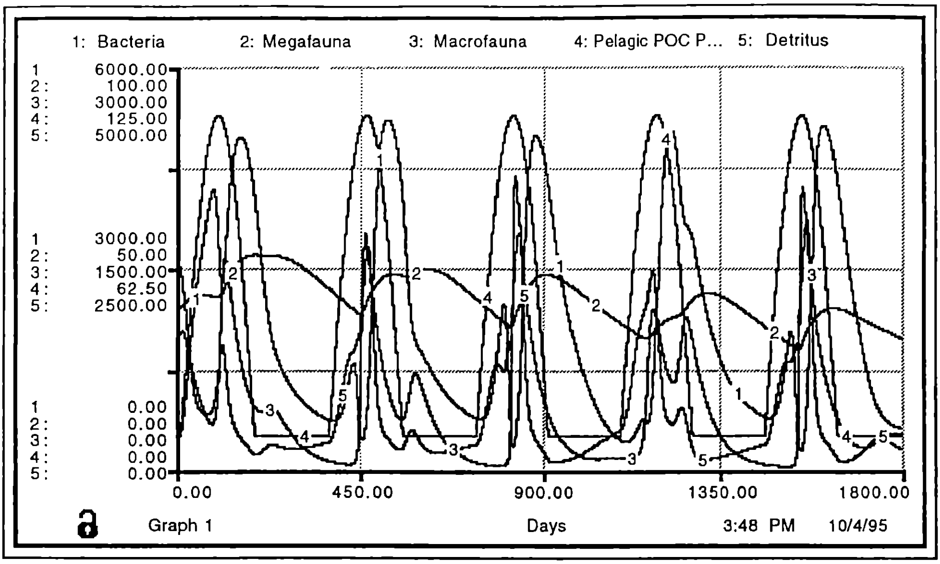

Fig. 9: Two- year simulation of polynya benthic food web (Fig. 8). "Megafauna" slowly decline. Note that responses to the annual pulse of organic input are seasonal, rather than bi-annual or longer, as in the abyssal model.

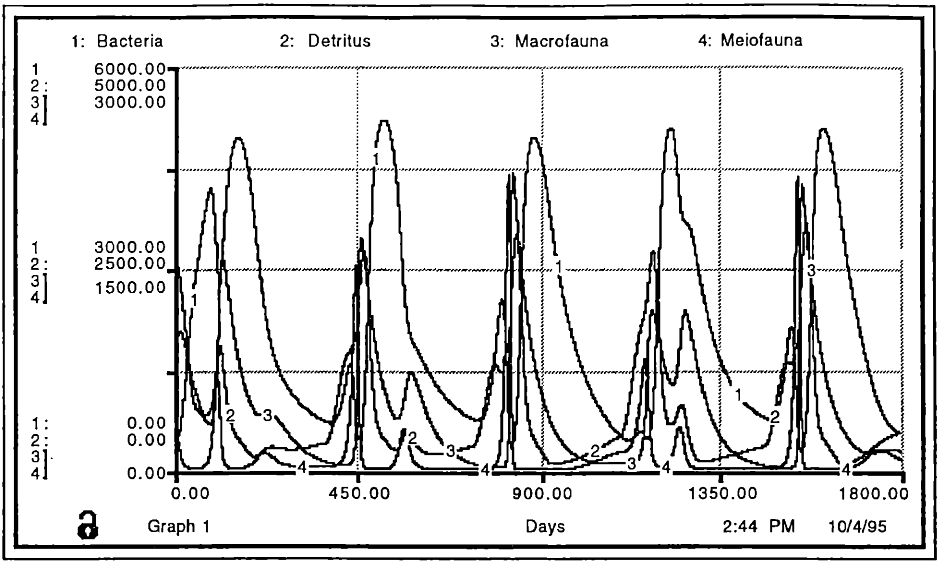

Fig. 10. Repeat of the two-year simulation of the polynya benthic food web, as in Fig. 9, but with the "megafauna" eliminated. Little change can be observed in the groups of smaller components.

The relatively low mean biomass of all the size groups sampled and the low rates of benthic metabolism suggest that the northeast Greenland polynya is an oligotrophic or "food-limited" ecosystem. Both the stocks and rates encountered in the Barents Sea, at similar latitudes, are not unlike those measured here (PFANNKUCHE and THIEL 1987, PIEPENBURG et al. 1995), but other Arctic regions, such as the St. Lawrence Island polynya off Alaska (GREBMEIER and COOPER 1995), are characterized by a higher biomass and metabolism than that measured in this study. This is probably related to the relatively modest rates of primary production in surface waters off east Greenland (SMITH 1995), rather than low temperature.

The continental shelf of the NW Gulf of Mexico

The infaunal macrobenthos of the NW Gulf of Mexico has a biomass significantly lower than seemingly comparable continental shelves (GETTLESON 1976). It has been suggested that this is a function of low primary production (ROWE et al. 1974). However, the NW Gulf of Mexico is also the site of extensive penaeid shrimp fisheries, the most valuable commercial fisheries in the United States. If the benthic biomass is food limited due to low primary production, how can this fishery continue to be persistently productive? A possible explanation of this paradox is that recruitment of macrofauna taxa is prevented by intense grazing pressure and competition from dominant, commercially important keystone species: *Penaeus duorarum*, *P. aztecus*, and *P. setiferus*, the pink, brown, and white shrimp. This section uses a time-dependent numerical simulation of a simplified NW Gulf of Mexico continental shelf food web to explore the possibility that "top down" control can be exerted by the shrimp.

This model has four state variables (Fig. 11): organic "detritus", "bacteria", "metazoans" (aggregated macrofauna and meiofauna), and "shrimp". Standing stock data are available in the works of GETTLESON (1976), CRUZ-KAEGI (1992), and FLINT and RABALAIS (1981). No POC fluxes have been measured with sediment traps on the Texas shelf, and therefore a maximum input of 300 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$ was assumed to drive the reactions. Again, input was set up to be seasonal, as in the previous two models. All exchanges were parameterized as first-order, donor- (prey-) dependent relationships. No fecal matter feedback into the detrital pool was included. Therefore the consumption rates were equal to assimilation rates. A single experiment will be presented here: the system with and without "shrimp". When "shrimp" were included as natural inhabitants of the continental shelf ecosystem, the "metazoan" biomass was held down to trivial levels (Fig. 12) in a simulation of two years. When the "shrimp" were removed, the "metazoans" grew to a maximum of about 7 g C·m^{-2} each season (Fig. 13). This maximum was reached about 3 months after the maximum input to the bottom. This illustrates possible "top down" control of the community and supports the hypothesis that "shrimp" are keystone species which have the potential to control the structure of the infaunal community.

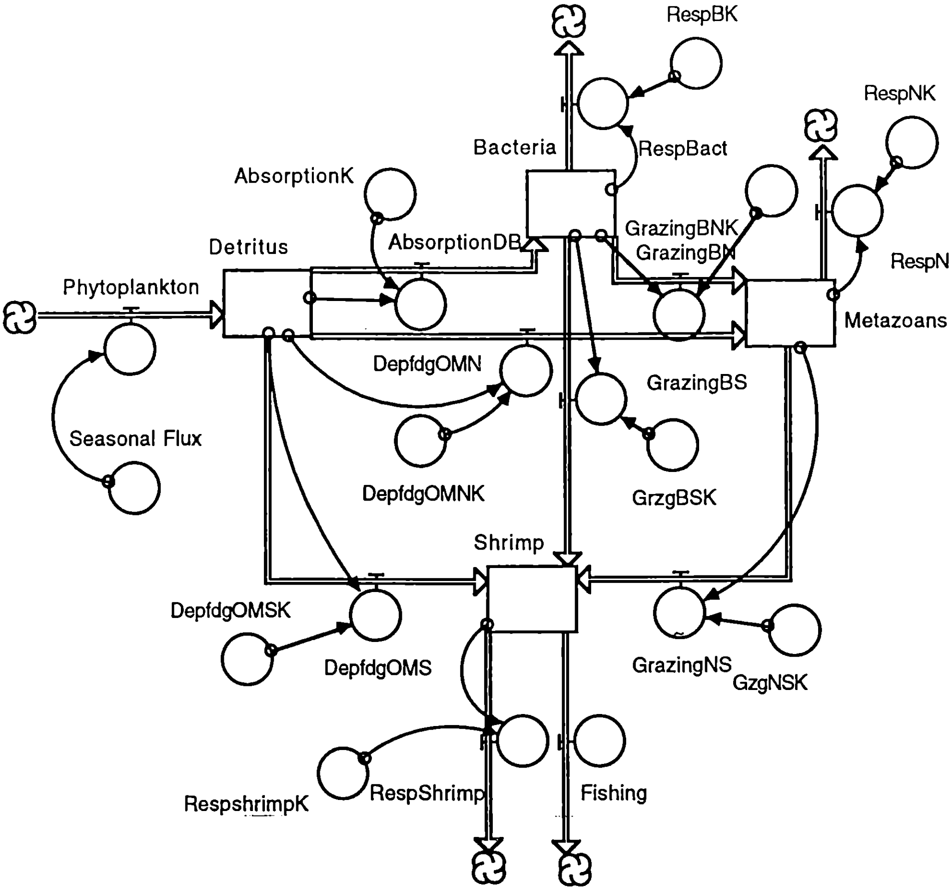

Fig. 11: Diagram of simplified food web on the continental shelf of the NW Gulf of Mexico. See text for sources of data. Equations for the model can be found in part 3 of the appendix. Experiments were run by altering the grazing levels of shrimp on metazoans.

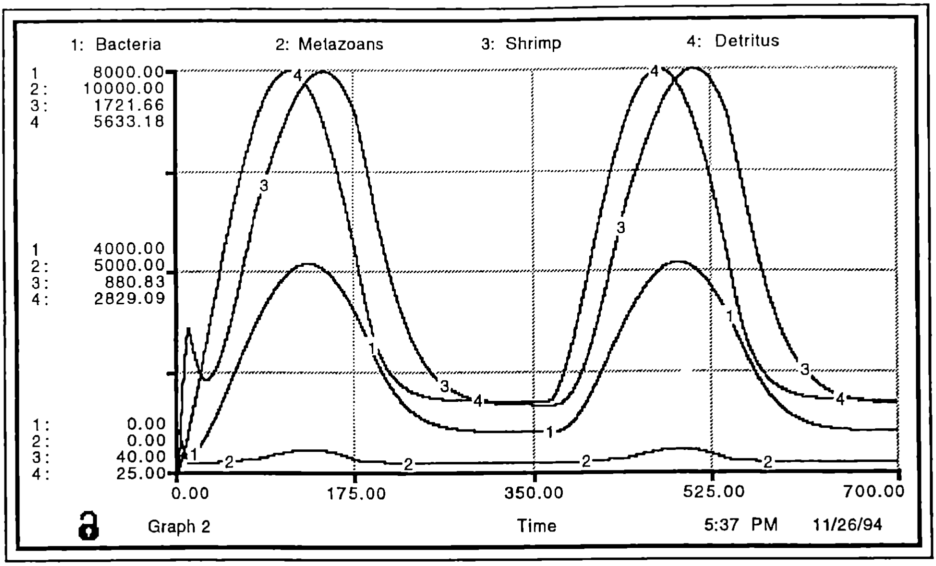

Fig. 12: Two-year simulation of Gulf of Mexico northwestern continental shelf food web. Note low levels of "metazoans". See text for sources of data.

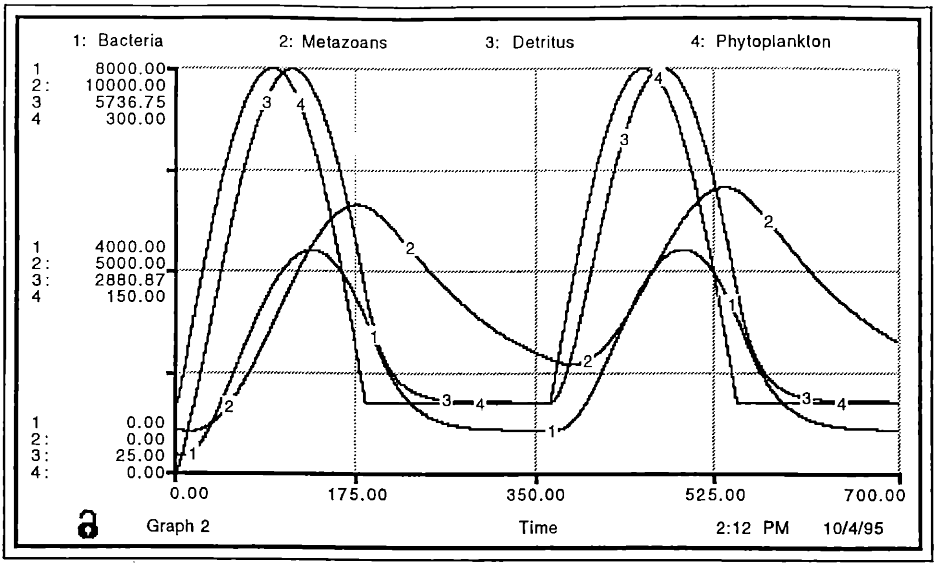

Fig. 13: Two-year simulation of Gulf of Mexico northwestern continental shelf food web, as in Fig. 12, but with "shrimp" removed. Note increased "metazoans" biomass. "Detritus" is unaffected.

Conclusions

The transfer of carbon in low energy ecosystems can be modeled with reasonable success if the models are not overly complex and adequate standing stock and flux data are available. Such simulations are especially valuable in areas where the variables are approaching detection limits because they are "food limited" and where complicating environmental variables (pressure, ice, cold, heat, etc.) preclude adequate sampling. In all three ecosystems, the ranges over which simulated fluxes and standing stocks varied were approximately equal to the standard deviations associated with observed flux and standing stock data. The natural biological "lag-times" observed between fluxes and stocks can help to explain why carbon budgets in dynamic ecosystems are difficult to balance.

The simulations suggest that top down control of living and detrital carbon reservoirs may be more significant than previously thought. This control appears more likely to occur in food chains rather than in food webs where organisms share and therefore compete for limited resources, and where they can switch to alternate food sources when necessary. The degree to which the benthic sub-systems under study are food webs or food chains is not well established.

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Address of the author:

GIL T. ROWE, Department of Oceanography, Texas A&M University, College Station,
Texas 77843, U.S.A.
e-mail: growe@ocean.tamu.edu

Appendix

Three sets of equations for the deep abyssal Pacific, the northeast Greenland polynya and the NW Gulf of Mexico. Units are mg $C\cdot m^{-2}\cdot d^{-1}$, mg $C\cdot m^{-2}$, and day^{-1}. See text for details.

First set of Equations: Abyssal Pacific

Heterotrophs(t) = Heterotrophs(t - dt) + (Utilization - RespirationH - PredationHM) * dt
INIT Heterotrophs = 200
INFLOWS:
Utilization = Heterotrophs*GrowthkHet
OUTFLOWS:
RespirationH = If Heterotrophs 10 then 0 else Heterotrophs*BactRespRatek
PredationHM = Heterotrophs*Megafauna*GrowthkMeg
Megafauna(t) = Megafauna(t - dt) + (PredationHM - RespirationM - GonadalExport) * dt
INIT Megafauna = 63
INFLOWS:
PredationHM = Heterotrophs*Megafauna*GrowthkMeg
OUTFLOWS:
RespirationM = Megafauna*MegRspK
GonadalExport = Megafauna*Gonadk
Organics(t) = Organics(t - dt) + (RainofPOC - Utilization) * dt
INIT Organics = 2000
INFLOWS:
RainofPOC = IF Seasonalvar 0 then 1 else (seasonalvar*10) + 1
OUTFLOWS:
Utilization = Heterotrophs*GrowthkHet
BactRespRatek = .02
Gonadk = .0005
GrowthkHet = .025
GrowthkMeg = .000015
MegRspK = .0025
Seasonalvar = SIN(PI*TIME/182.5)

Second set of Equations: NE Greenland polynya

Bacteria(t) = Bacteria(t - dt) + (Absorption - Bacteria_Respiration - GrazingBN) * dt
INIT Bacteria = 500
INFLOWS:
Absorption = Bacteria*Detritus*Absorption_k
OUTFLOWS:
Bacteria_Respiration = Bacteria*RespB_k
GrazingBN = Bacteria*Meiofauna*Meiof_gzgBN_k
Detritus(t) = Detritus(t - dt) + (Pelagic_POC_Pulse + Meio_feces + Macro_feces + Megafauna_feces - Absorption - GrazingDN - GrazingDtoM) * dt
INIT Detritus = 2500
INFLOWS:
Pelagic_POC_Pulse = If Seasonal_Variation THEN(10) ELSE(Seasonal_Variation*100)+10
Meio_feces = .5*GrazingBN+.5*GrazingDN

```
Macro_feces = .3*PredationNP+.6*GrazingDtoM
Megafauna_feces = .2*PredationPtoO
OUTFLOWS:
Absorption = Bacteria*Detritus*Absorption_k
GrazingDN = Detritus*Meiofauna*Meiof_gzgBN_k
GrazingDtoM = Detritus*Macrofauna*Mac_Gzg_Const
Macrofauna(t) = Macrofauna(t - dt) + (PredationNP + GrazingDtoM - Macrofauna_Respiration - PredationPtoO - Macro_feces) * dt
INIT Macrofauna = 1000
INFLOWS:
PredationNP = Meiofauna*Macrofauna*Pred_NtoP_k
GrazingDtoM = Detritus*Macrofauna*Mac_Gzg_Const
OUTFLOWS:
Macrofauna_Respiration = Macrofauna*Macrof_Resp_Constant
PredationPtoO = Macrofauna*Megafauna*Pred_PtoO_k
Macro_feces = .3*PredationNP+.6*GrazingDtoM
Megafauna(t) = Megafauna(t - dt) + (PredationPtoO - Megafauna__Respiration - Megafauna_feces) * dt
INIT Megafauna = 40
INFLOWS:
PredationPtoO = Macrofauna*Megafauna*Pred_PtoO_k
OUTFLOWS:
Megafauna__Respiration = Megafauna*Megaf_Resp_Constant
Megafauna_feces = .2*PredationPtoO
Meiofauna(t) = Meiofauna(t - dt) + (GrazingBN + GrazingDN - Meiofauna_Respiration - PredationNP - Meio_feces) * dt
INIT Meiofauna = 200
INFLOWS:
GrazingBN = Bacteria*Meiofauna*Meiof_gzgBN_k
GrazingDN = Detritus*Meiofauna*Meiof_gzgBN_k
OUTFLOWS:
Meiofauna_Respiration = Meiofauna*Meiof_Resp_Constant
PredationNP = Meiofauna*Macrofauna*Pred_NtoP_k
Meio_feces = .5*GrazingBN+.5*GrazingDN
Absorption_k = 4E-5
Macrof_Resp_Constant = .02
Mac_Gzg_Const = 6E-8
Megaf_Resp_Constant = .0022
Meiof_gzgBN_k = 1.0E-4
Meiof_Resp_Constant = .03
Pred_NtoP_k = 2.5E-4
Pred_PtoO_k = 6E-6
RespB_k = .015
Seasonal_Variation = SIN(PI*TIME/182.5)
```

Third set of Equations: NW Gulf of Mexico

```
Bacteria(t) = Bacteria(t - dt) + (AbsorptionDB - RespBact - GrazingBN - GrazingBS) * dt
INIT Bacteria = 300
```

```
INFLOWS:
AbsorptionDB = Detritus*AbsorptionK
OUTFLOWS:
RespBact = Bacteria*RespBK
GrazingBN = Bacteria*GrazingBNK
GrazingBS = Bacteria*GrzgBSK
Detritus(t) = Detritus(t - dt) + (Phytoplankton - DepfdgOMS - DepfdgOMN - Absorp-
tionDB) * dt
INIT Detritus = 25
INFLOWS:
Phytoplankton = IF(Seasonal_Flux)THEN(50)ELSE(Seasonal_Flux*250)+50
OUTFLOWS:
DepfdgOMS = DepfdgOMSK*Detritus
DepfdgOMN = Detritus*DepfdgOMNK
AbsorptionDB = Detritus*AbsorptionK
Metazoans(t) = Metazoans(t - dt) + (GrazingBN + DepfdgOMN - RespN - GrazingNS) *
dt
INIT Metazoans = 1000
INFLOWS:
GrazingBN = Bacteria*GrazingBNK
DepfdgOMN = Detritus*DepfdgOMNK
OUTFLOWS:
RespN = Metazoans*RespNK
GrazingNS = GRAPH(Metazoans*GzgNSK)
(0.00, 0.00), (10.0, 0.00), (20.0, 70.5), (30.0, 81.0), (40.0, 90.0), (50.0, 94.5), (60.0, 99.5),
(70.0, 100), (80.0, 99.5), (90.0, 100), (100, 100)
Shrimp(t) = Shrimp(t - dt) + (DepfdgOMS + GrazingBS + GrazingNS - RespShrimp -
Fishing) * dt
INIT Shrimp = 40
INFLOWS:
DepfdgOMS = DepfdgOMSK*Detritus
GrazingBS = Bacteria*GrzgBSK
GrazingNS = GRAPH(Metazoans*GzgNSK)
(0.00, 0.00), (10.0, 0.00), (20.0, 70.5), (30.0, 81.0), (40.0, 90.0), (50.0, 94.5), (60.0, 99.5),
(70.0, 100), (80.0, 99.5), (90.0, 100), (100, 100)
OUTFLOWS:
RespShrimp = Shrimp*RespshrimpK
Fishing = .0008
AbsorptionK = .04
DepfdgOMNK = .01
DepfdgOMSK = .001
GrazingBNK = .01
GrzgBSK = .0025
GzgNSK = .08
RespBK = .04
RespNK = .01
RespshrimpK = .06
Seasonal_Flux = SIN(PI*TIME/182.5)
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Zeitschrift/Journal: Biosystematics and Ecology

Jahr/Year: 1996

Band/Volume: 11

Autor(en)/Author(s): Rowe Gil T.

Artikel/Article: III. Food scarcity. The cycling of organic matter in food-limited environments. In: Deep Sea and Extreme Shallow-water Habitats: Affinities and Adaptations. 233-260