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Inverse Model Analysis of Plankton Food Webs in the North Atlantic and Western Antarctic Peninsula

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Inverse Model Analysis of Plankton Food Webs in the North Atlantic and Western Antarctic Peninsula

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Master of Science

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by

Robert M. Daniels

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This thesis is submitted in partial fulfillment of
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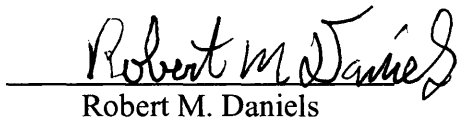
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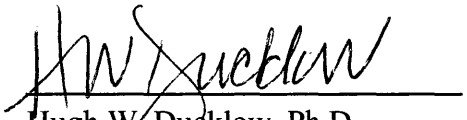
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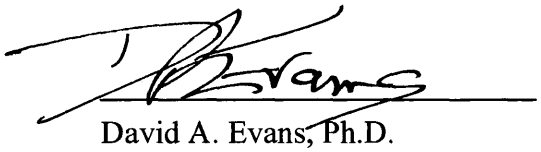
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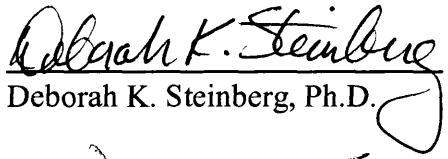
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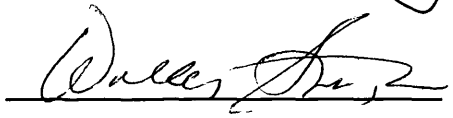
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ABSTRACT

The relationship between food web structure and function across two ocean biomes was investigated, using an inverse method to recover solutions of food web carbon and nitrogen flows. The study focused on food webs in the North Atlantic Ocean and the western Antarctic Peninsula. Plankton food web data were synthesized for input into the inverse solution method, including measured flows and biomasses from the North Atlantic Bloom Experiment (NABE study) and the western Antarctic Peninsula (WAP: Palmer Station LTER study). Inverse food web solutions were recovered for NABE and the WAP. The inverse model solutions were analyzed with network analysis, sensitivity analysis and other techniques.

North Atlantic carbon and nitrogen inverse solutions were found representing 2 weeks in May 1989, during the spring phytoplankton bloom. Microzooplankton and protozoan grazing dominated in both the nitrogen and carbon solutions. Detritus was less important in these solutions than DOC and DON. Active recycling was seen, especially in the nitrogen solution, and much of the new production was not realized in the export of particulate organic matter from the surface ocean, but was stored and recycled in the food web. Carbon inverse solutions for the western Antarctic Peninsula were found for January 1996, following a year of relatively high areal coverage of sea ice and high primary production and January 1999, following a year of relatively low areal coverage of sea ice and low primary production. Krill grazing was the dominant flow of carbon in the food web in both years. Salps played a significant role in altering the food web structure and function in 1999. A comparison between the NABE carbon inverse solution and the WAP 1996 carbon inverse solution showed key differences in the food webs. Recycling and the activity of the microbial food web were much more important in the NABE food web than in the WAP. However in the WAP inverse solution, the microbial food web was just as significant as the short food web (diatoms to krill to penguins), that is traditionally believed to be dominant.

INVERSE MODEL ANALYSIS OF PLANKTON FOOD WEBS IN THE NORTH ATLANTIC AND WESTERN ANTARCTIC PENINSULA

Chapter I. Introduction

The goal of my project was to investigate the relationship between food web structure and function in different ocean ecosystems (biomes). Food web structure refers to the organisms within a food web and the flows of matter, such as carbon and nitrogen, between them. Ocean environments in different regions of the world have different food web structures that have adapted to the regional conditions (Lochte et al., 1993; McCarthy et al. 1996; Karl, 1999(1)). Two very different regions, where large studies of food webs have been done are the North Atlantic and the western Antarctic Peninsula. I used a modeling technique known as the inverse method (Vezina & Platt, 1988; Jackson & Eldridge, 1992) to describe fully plankton food web structure in these regions. The inverse method uses observed data to recover snapshots that provide estimates of all the flows within a food web, many of which have rarely been measured.

Important processes in food webs that are influenced by food web structure include particle export, nutrient regeneration, and dissolved organic matter (DOM) production. Particle export is the loss of matter through the sinking of dead organisms, attachment of detrital matter to sinking particles, or the packaging of matter into the dense fecal pellets of mesozooplankton (Eppley & Peterson, 1979; Karl, 1999). Nutrient regeneration includes the processes that recycle phytoplankton nutrients (Dugdale & Goering, 1967). New production is defined as the amount of phytoplankton production that is driven by the supply of allochthonous nutrient inputs to the euphotic zone, while regenerated production is that primary production that is driven by nutrients recycled

within the euphotic zone (Eppley & Peterson, 1979). Ocean environments are often described with an f-ratio, the amount of new production divided by the total production (new + regenerated), indicating the degree of reliance on external inputs. Ocean environments that have a large input of new nutrients have a large f-ratio that is close to 1, and environments with a small input of new nutrients have low f-ratios close to 0. Dissolved organic carbon (DOC) includes dissolved carbon compounds that have been released by plankton through various processes including direct release, inefficient grazing ("sloppy feeding"), excretion and death (Karl, 1999(1)). DOC has been shown to play a significant role in the export of carbon (Carlson et al., 1994) and also is a major resource for bacterial consumption. There is a large pool of DOC in the ocean but little is known about DOC production and DOC flux within food webs (Legendre and Gosselin, 1989). The lack of knowledge of the DOC pool presents a significant roadblock to modeling the open-ocean microbial food web (Karl, 1999(1)).

Previous researchers have investigated and found links between food web structure and the behavior of key food web processes. Eppley and Peterson (1979) related ocean environments with very different food web structures to the export of particulate organic matter out of the surface ocean. They calculated f-ratios for regions ranging from the oligotrophic central North Pacific to the highly productive upwelling region off the coast of Peru. The central North Pacific had a low f-ratio of about 0.05, indicating a system dominated by the recycling of nitrogen and a relatively high residence time for nitrogen in the surface ocean. In the Peru upwelling region, half of the total production was new production fueled by nitrate upwelled from the deep waters, giving an f-ratio of about 0.5. Legendre and Rassoulzadegan (1996) investigated links

between food web structure and the export of carbon with a model and data from the literature. They concluded that the flows of biogenic carbon are strongly influenced by the size distribution of the primary producers and the matching between primary producers and grazers (Legendre & Rassoulzadegan, 1996), two key aspects of food web structure.

The specific objectives of this study were:

Objective 1: Synthesize plankton food web data including measured flows and biomasses from the North Atlantic Bloom Experiment (NABE study) and the western Antarctic Peninsula (WAP: Palmer Station Long Term Ecological Research study) for input into the inverse solution method. Obtain both carbon and nitrogen data for the NABE study and carbon data for the WAP inverse solutions. Gather and average data over specified time periods, and convert to standard depth integrated units for flows (mmols $m^{-2}d^{-1}$of Carbon or Nitrogen) and biomass (mmols m^{-2} of Carbon or Nitrogen). Define constraints on biological processes (respiration, assimilation, etc.).

Objective 2: Recover inverse food web solutions for the North Atlantic (NABE) and the western Antarctic Peninsula (WAP). Use generic models for both systems as well as region-specific models. The solutions include all of the inter-compartmental flows within each model, staying consistent with measured data and the biological constraints.

Objective 3: Analyze the inverse model solutions for the NABE and WAP food webs with network analysis, sensitivity/stability analysis and other techniques such as the food web classification used by Legendre and Rassoulzadegan (1996).

Background

Ocean Carbon Cycle and Biological Pump:

The euphotic zone plays a key role in delivering carbon to the deep ocean through the biological, carbonate, and solubility "pumps". The ocean contains by far the largest pool of freely exchanging carbon on the earth equal to 4×10^{19} g with 97% in the form of dissolved inorganic carbon (Karl, 1999(1)). The "biological pump" is the sum of the processes carried out by the pelagic ecosystem in taking up dissolved inorganic carbon from the surface ocean and converting it into soft tissue that can be exported to the interior of the ocean (Longhurst & Harrison, 1989). Some organisms convert dissolved inorganic carbon into hard parts like calcite and aragonite that can also be exported to the interior of the ocean through the "carbonate pump" (Longhurst & Harrison, 1989). Over geological time, the carbonate pump has made the most significant contribution to sequestering carbon in sediments (Lalli & Parsons, 1993). On shorter time scales of concern to society, the biological pump along with the carbonate pump is important in exporting carbon below the euphotic zone where it remains for tens to hundreds of years (Longhurst & Harrison, 1989). The biological pump starts with phytoplankton reducing dissolved inorganic carbon and combining it with dissolved nitrogen and phosphorous into soft organic tissue. The resultant organic matter provides energy for organisms both within the surface ocean and below in the deep ocean. This "biological pump" exports carbon out of the surface ocean by gravitational settling of phytoplankton and detritus, the advection and diffusion of dissolved organic matter, and the vertical migrations of heterotrophic organisms and phytoplankton (Karl, 1999(1)). The solubility pump is the

downward flux of dissolved inorganic carbon driven by the differential solubility along the vertical temperature gradient (Longhurst & Harrison, 1989). This flux proceeds independently of biology and is difficult to monitor and quantify.

Ocean Plankton as Components of the Biological Pump:

The structure of the plankton community dictates the activity of the biological pump. The type of organisms in the plankton food web and the size and distribution of flows between them make up the food web structure. Eppley & Peterson (1979) proposed that the export of organic carbon from the surface ocean was equal to the new production by phytoplankton. Other researchers have gone on to investigate the relationship between community or food web structure and the amount of new production and export. By using a simple model of oceanic food webs, Michaels and Silver (1988) concluded that the size distribution of phytoplankton and the trophic structure of the consumer populations control the type and quantity of export. Legendre and Rassoulzadegan (1996), also using a simple model, found that the size structure of the phytoplankton and the degree of matching between primary production and grazing largely determined export. In a review of changing views of the North Pacific Subtropical Gyre (NPSG), Karl (1999(1), p197) states: "Community structure controls all." Karl discusses the role of large eukaryotic autotrophs like diatoms in controlling export in a system that is normally driven by the recycling of nutrients. In the NPSG, the normal background community of small phytoplankton dominated by prokaryotic autotrophs is at times of external nutrient supply, "overprinted" by large eukaryotic algae like diatoms. Diatoms usually either sink out of the euphotic zone after dying or are grazed upon by zooplankton, which can package unassimilated food into dense fecal

pellets that also rapidly sink to depth. Thus episodic inputs of new nutrients foster enhanced growth of large organisms and their export.

Legendre and Rassoulzadegan (1996) describe a method of predicting the function of five different types of plankton food webs, ranging from a system dominated by the sinking of ungrazed phytoplankton (high export) to the microbial loop (low export). The primary production within the food web is given three fates including sinking out of the euphotic zone, remineralization within the euphotic zone, and transfer through the food web. For each type of food web, values for the three potential fates of the primary production were calculated depending upon the amount of primary production that is accounted for by large vs. small phytoplankton and by the matching between grazing and primary production. The microbial loop is described as an almost closed system with low primary production and consisting mainly of heterotrophic bacteria and nanoflagellate grazers. The grazers feed on the bacteria and release DOM that is in turn used as a substrate by the bacteria. The microbial loop is believed to be an unstable and transient system (Legendre & Rassoulzadegan, 1996). On the other hand, the multivorous food web with characteristics in between the two extremes mentioned above, is considered to be a stable system in which mesozooplankton and microzooplankton grazing are closely matched with primary production.

Regional Variations & Contrasts:

Food web structure varies throughout the world's oceans. Upwelling regions have classically been characterized by short food webs consisting of three main trophic levels: large phytoplankton, mesozooplankton grazers, and fish (Ryther, 1969), with high

f-ratios and high export. Oligotrophic gyres are characterized by a more complex food web consisting of small phytoplankton, protozoans, microzooplankton, mesozooplankton grazers, and finally fish (Karl, 1999(1)). For example, the North Pacific Subtropical Gyre (NPSG) is considered to be a "microbial ecosystem" dominated by prokaryotic autotrophs that are grazed upon by active protozoan and microzooplankton communities (Karl, 1999(1)). High nutrient, low chlorophyll (HNLC) areas of the ocean have relatively high concentrations of macronutrients and lower than expected phytoplankton biomass. The Equatorial Pacific, subarctic Pacific and the Southern Ocean are all HNLC regions (Landry et al., 2000). In the Equatorial Pacific small phytoplankton usually dominate the autotrophic community and are grazed on by an active microzooplankton community (Landry et al., 1995). High latitude systems are characterized by diatom blooms and mismatches between production and grazing (Pesant et al., 1998).

WAP vs. NABE:

The North Atlantic is among the areas of the open ocean that absorb the most CO_2 from the atmosphere, and the western Antarctic Peninsula is also believed to be a strong sink of CO_2. Comparing and contrasting the roles of the different plankton food webs in these two regions will help further knowledge of the biological pump. The western Antarctic Peninsula has a relatively short food web with as few as two links between the primary producers and apex predators. The North Atlantic has a short food web during the beginning of the spring bloom but also a longer food web that develops soon after the bloom starts that depends more on smaller organisms and the microbial loop. Comparing the amount of recycling and export between these two different food webs will be helpful in understanding the effects of food web structure on food web function. In a previous

study in the area of the WAP (Karl et al. 1996), the bacterial community was uncoupled from the phytoplankton community during bloom conditions, while in NABE the bacterial community was more closely coupled with the phytoplankton bloom (Ducklow et al., 1993). The differences in the role of the microbial loop may shed further light on its function in both areas and on its role in the cycling of DOC.

Methods

The following methods apply to the inverse solutions for both the North Atlantic and the western Antarctic Peninsula. Specific methods sections for the two regions can be found in each respective chapter. I use an inverse method to recover solutions of food webs. The method uses measured values and assumptions to obtain an inverse solution to the food web that gives estimates for all the flows in the system. This method has been borrowed and adapted from the physical sciences (Parker 1977; Wunsch, 1978). It is has also been adapted by Pauly & Christensen (2000) to infer stocks of fish species using the program, ECOPATH. It was first used for plankton food webs by Vezina & Platt (1988) for an English coastal system and then later by other researchers (Jackson & Eldridge, 1992; Eldridge & Jackson, 1993; Vezina & Pace, 1994; Donali et al., 1998, Niquil et al., 1998).

The inverse method uses as much of the observed data as possible to arrive at a solution to the desired unknowns in the system. In the physical sciences, the inverse method has been used in such problems as inferring ocean circulation from current, temperature and salinity measurements (Wunsch and Minster, 1982) and in estimating the inner structure of the earth from seismic waves (Wiggins, 1972). In each of these problems, as with plankton food webs, the number of unknown variables can far outnumber the independent measurements taken. The inverse technique supplies a solution to these problems that is consistent with the measured data and other known constraints (Vezina & Platt, 1988). Usually models of food webs use the *a priori* approach of assuming rate parameters and running the model over time to observe

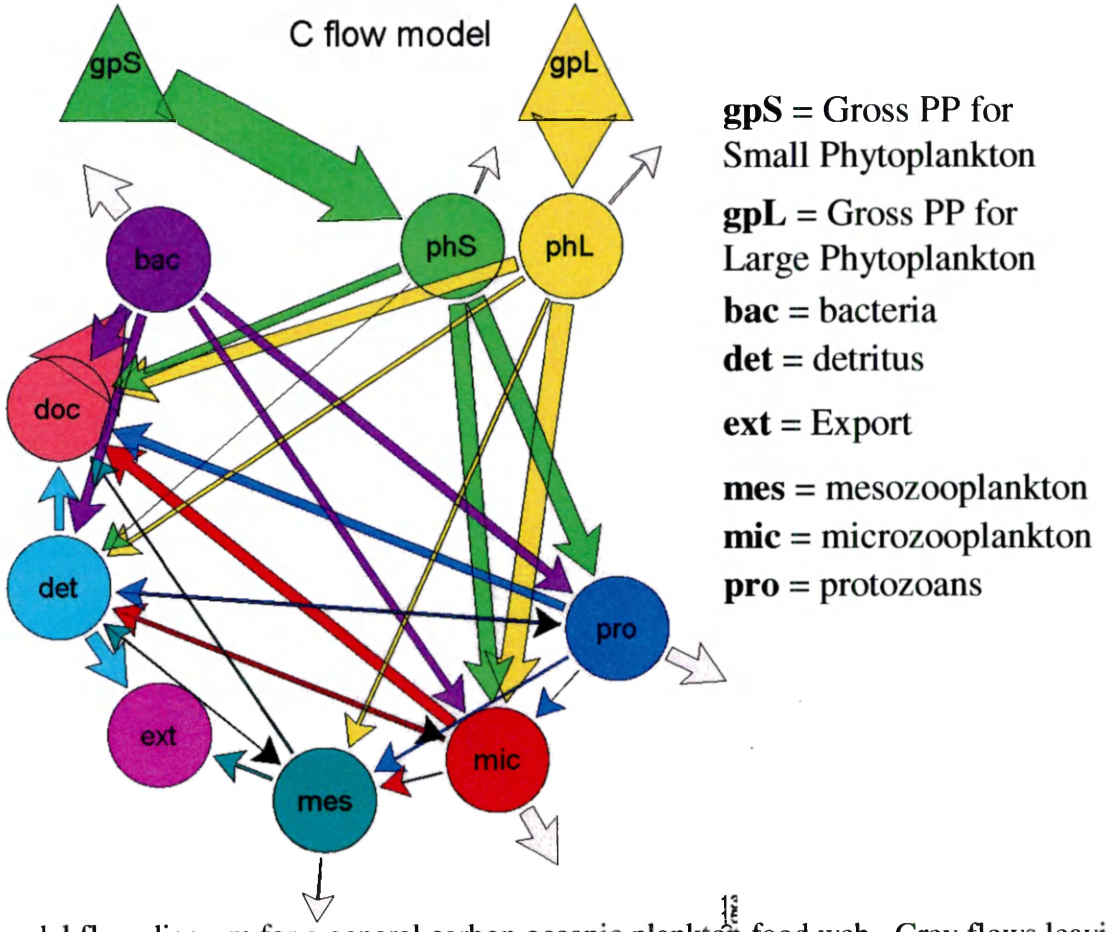


Figure 1. Inverse model flow diagram for a general carbon oceanic plankton food web. Grey flows leaving compartments are losses to respiration. Inputs are from gross primary production for small phytoplankton (gps) and large phytoplankton (gpl). Export from the surface ocean enters the ext compartment.

changes in the system. Direct measurements of most of the flows and rate parameters in food webs are usually not available (Vezina & Platt, 1988). The inverse method works opposite from *a priori* models in that it uses observations of the standing stocks and flows, along with known biological constraints to solve for unknown flows and rate parameters in the system. The solution is consistent with real data from the system, satisfies conservation of mass, and obeys biological constraints (Vezina & Platt, 1988).

The first step in the inverse method for food webs is deciding on the components of the model and the possible flows between them. Groups are categorized by their function and or size, such as large and small primary producers. Figure 1 shows the model components and carbon flows for a general oceanic plankton food web, based on the Vezina and Platt (1988) food web for the North Atlantic off the English coast and the Jackson and Eldridge (1992) food web for the southern California Bight. The living components are small phytoplankton, large phytoplankton, bacteria, protozoans, microzooplankton, and mesozooplankton. The nonliving components are DOC and detritus. Inputs to the system are the gross primary production for large phytoplankton and small phytoplankton, respectively. Outputs from the system are sinking detritus, mesozooplankton production that is consumed by higher trophic levels not represented in the model, and respiration. Export is represented by the flows entering the export compartment and respiration by the gray arrows pointing away from the center of the diagram. The export of fecal pellets from the euphotic zone follows the path from the mesozooplankton to detritus to the export box. Phytoplankton were split into large (>5 μm) and small (0.2 – 5 μm) size fractions. These classes were used by Legendre and Rassoulzadegan (1996), in a general open ocean plankton model to distinguish the

smaller phytoplankton that mesozooplankton can't efficiently graze from the larger phytoplankton that mesozooplankton can graze. Also, the large phytoplankton along with other particles >5 μm are more likely to form aggregates and sink to depth. The protozoans represent the smallest heterotrophic organisms (< 10 μm) including zooflagellates and ciliates (Capriulo, 1990) that feed upon bacteria and each other. Microzooplankton include heterotrophic organisms between 10–200 μm such as large zooflagellates and dinoflagellates, ciliates, sarcodines and copepod nauplii (Verity, 1993). Heterotrophic organisms greater than 200 μm that can be captured in plankton nets such as copepods and euphausiids make up the mesozooplankton (Vezina & Platt, 1988). The mesozooplankton are restricted from grazing on the small phytoplankton in the model, hence there is not a flow arrow from small phytoplankton to mesozooplankton. The grazers, including the protozoans, microzooplankton and mesozooplankton are allowed to consume other grazers, as long as their food source is smaller in size. However, the mesozooplankton are restricted from grazing on bacteria, which like small phytoplankton fall into the class of organisms less than 5 μm that they can't graze efficiently. All of the grazers are allowed to consume detritus. All of the living components are permitted to contribute to DOC.

Sensitivity analysis and various network analysis techniques were used to analyze model results. Two of the important network analysis techniques used were dependency coefficients and effective trophic levels. Dependency coefficients give an indication of the proportion of a component's input or diet that comes from another component over direct or indirect pathways. Effective trophic levels rank each component according to where they feed in the food web. The input parametes to the models were varied by +/-

10% in order to test the sensitivity of the model flows to small changes in the inputs. The sensitivity analysis highlights measurements that the modeled food web is sensitive to, as well as organisms in the model that are sensitive. Detailed descriptions of the network analysis techniques used to analyze model output and the sensitivity analysis can be found in the Appendix. Also, a detailed description of the inverse method is in the Appendix.

Chapter II. The North Atlantic Bloom Experiment

Introduction

The Joint Global Ocean Flux Study (JGOFS) began in 1987, with the goal of understanding the mechanisms that affect the flux of carbon and its associated elements in the ocean (SCOR, 1987). JGOFS was a multinational and multidisciplinary program involving scientists from more than 30 nations (Buessler et al., 2001). One of the major tasks of JGOFS was conducting multidisciplinary regional process studies. Four such studies were done across the world's oceans including the North Atlantic, Equatorial Pacific, Arabian Sea, and the Southern Ocean. The Synthesis and Modeling Project (SMP) is an initiative within JGOFS that set out to model the data obtained in JGOFS studies. One goal of the SMP is to understand mechanistic controls of local carbon balances, especially the role of food web structure in controlling particle flux, particle export, nutrient regeneration and DOC production. This project is part of the JGOFS – SMP.

The pilot regional process study of JGOFS was the North Atlantic Bloom Experiment (NABE). Each year in the spring, an enormous phytoplankton bloom takes place across the North Atlantic Ocean. The bloom is obvious from space in satellite chlorophyll maps (Feldman, 1993). In late winter deep mixing in the eastern North Atlantic brings nitrate up from the depths to the surface ocean (Ducklow and Harris, 1993). As the temperature increases and winds calm down in April-May, the surface ocean stratifies and phytoplankton thrive.

NABE included seven primary stations from 18° N to 72° N, sampled from March – July 1989 by six research vessels from the U.S.A., Canada, Germany, the Netherlands and the U.K. (Ducklow and Harris, 1993). During NABE researchers developed and refined analytical techniques for CO_2 analysis and collected a large number of surface pCO_2 measurements. At 47°N, 20°W, CO_2 was removed from the mixed layer at a rate of about 75% of primary production (Ducklow and Harris, 1993). Some findings did not conform to the classical idea of a bloom. The most surprising feature of NABE was the intense nutrient recycling during a diatom bloom with f-ratios across the study area ranging from 0.3 in the western North Atlantic (Harrison et al., 1993) to 0.45 in the eastern North Atlantic (Martin et al., 1993). All of the new production may not have been exported due to the intense recycling (Garside and Garside, 1993). Over 50% of the primary production was by cells less than 5 um, which is indicative of recycling (Lochte et al., 1993). Mesozooplankton contributed only a small portion to the total plankton biomass and grazed a small percentage of the primary production (Dam et al., 1993). Dam et al. also concluded that mesozooplankton fecal pellets contributed less than five percent of the export. However, Lenz et al. (1993) aboard the R. V. Meteor believed that the particle flux was dominated by mesozooplankton fecal pellets, because of their estimated high community grazing rates for mesozooplankton and the low amount of chlorophyll found in sediment traps. The Meteor was at 46° N and 17.5 – 19 ° W during May, but not within the same water mass that Dam's measurements were taken from at 47°N, 20°W. Also, the grazing estimates by Lenz et al. (1993) were maximum consumption rates, because they assumed that the zooplankton only acted as herbivores. Dam et al. (1993), upon comparing measured

phytoplankton ingestion with estimated metabolic and excretion rates, suggest that just 50% of the mesozooplankton diet came from phytoplankton.

High microbial activity was seen during NABE. Bacterial biomass increased fivefold at 47°N, 20°W (Ducklow et al., 1993). Bacterial production measured at 47°N, 20°W was on average thirty percent of the primary production and was most likely supported by grazer mediated release and particle decay (Ducklow et al., 1993). Mesoscale eddies were prevalent during the study. Three large eddies were tracked in the vicinity of 47°N, 20°W by the GeoSat satellite measuring sea-surface height and through the use of XBT's released from ships (Robinson et al., 1993). The eddy structure complicates sampling as well as analyses of the resulting data.

The inverse method is useful to better estimate the food web exchanges that led to the observations in the NABE study. The organisms and processes most responsible for the intense recycling can be better understood by inferring the unknown flows in the food web. The inverse method will also help identify potential pathways for the new production that was not realized in the export.

Methods

The majority of the data for the NABE inverse model was taken from the May 18 –31, 1989 cruise by the research vessel Atlantis II. This period has the most inclusive data for the study, including in most cases daily measurements of phytoplankton production and biomass, new and regenerated production, bacterial production and biomass, microzooplankton grazing and biomass, mesozooplankton grazing and biomass, and export. The carbon model components and the possible flow interconnections for NABE are the same as seen in Figure 1 for the general open ocean model. Carbon and nitrogen measurements were averaged over the two-week observation period to arrive at mean values to be used in the inverse analysis. The measurements were integrated to 35 m, the depth of thorium estimates of export (Buessler et al., 1992). The components and interconnections of the nitrogen model are shown in Figure 19. A detailed description of the inverse method can be found in the Appendix. Data were downloaded from http://usjgofs.whoi.edu/jg/serv/jgofs/nabe/atlantisII and are also available from the United States JGOFS Process Study Data 1989-1998 CD-ROM, released by the Woods Hole Oceanographic Institution that is referenced as the source for the measurements. A number of techniques were used to analyze the output of the models including descriptions of the fate of the primary production, the zooplankton diet, and the particulate export. Also network analysis techniques were used to characterize the solutions including the index of recycling, indices of relative activity, dependency coefficients, and effective trophic levels. Further details of these techniques can be found in the Appendix. A sensitivity analysis was performed to determine the effects on the solution resulting from varying the input parameters by a small amount (+/- 10%).

Results

Data Synthesis

Primary Production and Phytoplankton Biomass

The net primary production measurements (Martin et al., 1993) were used to indirectly supply the inputs for the system. The average primary production was assumed to be split evenly between the small phytoplankton and large phytoplankton, because the week before May 18, Joint et al. (1993) found that the large and small phytoplankton each contributed 50% of the primary production (Lochte et al., 1993). The inputs to the system are in terms of gross primary production, so the model was configured to back-calculate the gross primary production based on the measured net primary production plus the inferred phytoplankton respiration.

The carbon primary production was measured about every other day over the period of May 18-31, 1989 by Martin et al. (1993) aboard the Atlantis II (Figure 2a). Carbon-14 incorporation was measured in water samples to a depth of 65 m at 5 to 15 m intervals. The primary production measurements were integrated to a depth of 35 m, equal to the depth of export measurements made by Buessler et al. (1992) using ^{234}Th: ^{238}U disequilibria. On the days primary production was not measured, it was estimated from the measured PAR (photosynthetic available radiation), using a regression equation defined by Martin et al. (1993), who found that production varied strongly with light over the cruise (r^2=0.88). The average primary production integrated to 35 m was 88 mmols $Cm^{-2}d^{-1}$ and nearly equal to the production integrated to the depth of the entire euphotic zone of 90.4 mmols $Cm^{-2}d^{-1}$ (Martin et al., 1993).

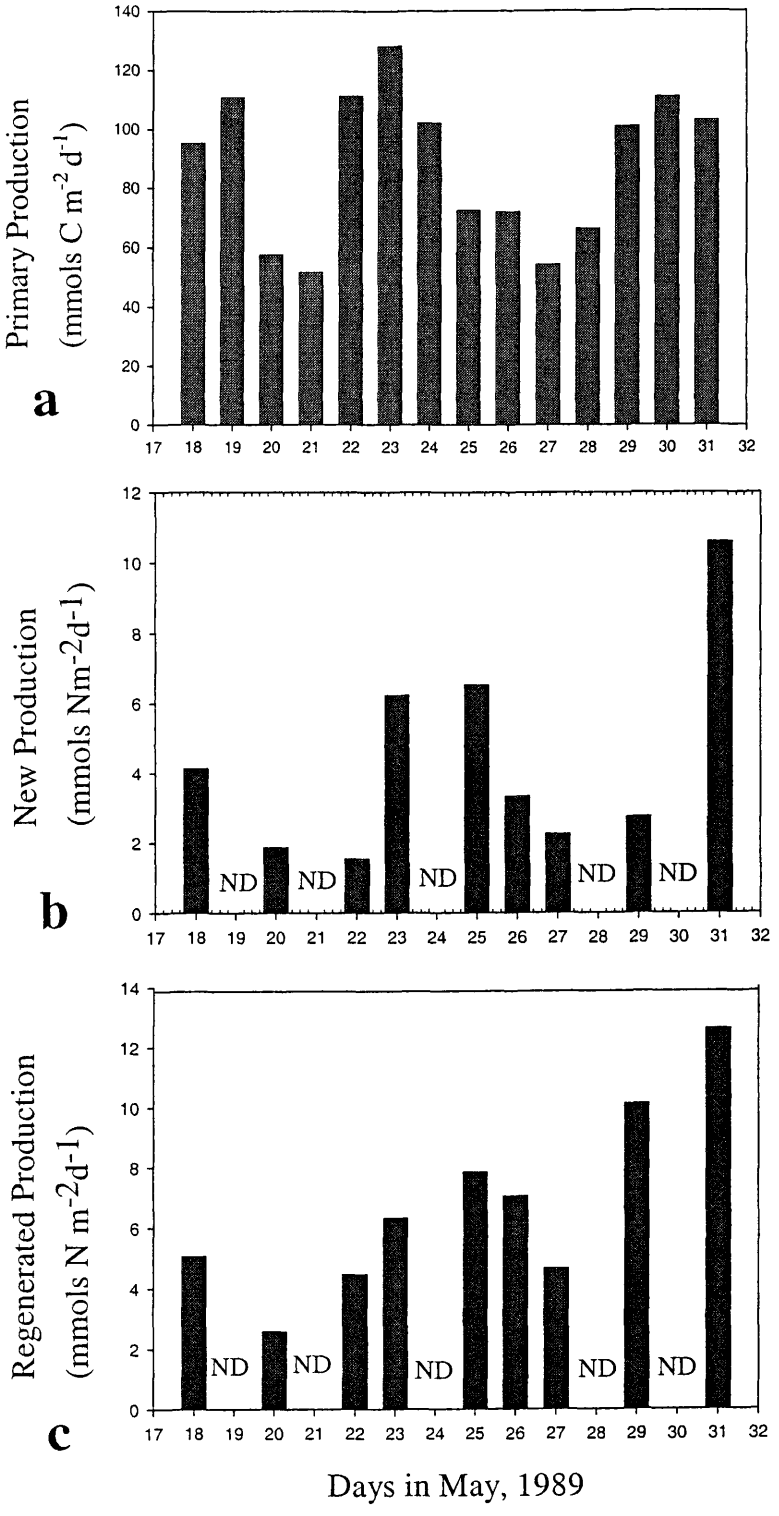


Figure 2. Carbon and nitrogen primary production measurements made aboard the Atlantis II at 47°N, 20° W. Figure **2a**: Carbon primary production measurements using ^{14}C by Martin et al. (1989). Figure **2b**: New production by NO_3 incorporation (McCarthy and Nevens, 1989). Figure **2c**: Regenerated production measured by NH_4 uptake by McCarthy and Nevins (1989). ND = no data taken on that day.

Nitrogen-based primary production was measured using NH_4, urea and NO_3 uptake experiments taken about every other day by McCarthy and Nevins (1989) on the Atlantis II. New production was estimated by integrating the NO_3 uptake measurements to 35 m (Figure 2b). Regenerated production was estimated by integrating the NH_4 and urea uptake measurements to 35 m (Figure 2c). The urea measurements were only made on four days. The ratio of NH_4 uptake to urea uptake ratio over these four days was used to infer the urea uptake on the days it was not measured.

Phytoplankton biomass (Figure 3) was estimated from Chl a measurements made by Dan Repeta (1989) using HPLC (High Performance Liquid Chromatography). The Chl a measurements were integrated to 35 m and then converted to carbon units using a C:Chl a ratio of 80 (Ducklow et al., 1993). Nitrogen phytoplankton biomass was estimated from the carbon phytoplankton mass using Redfield ratio of 6.6 C : 1 N.

Bacterial Productivity and Biomass

Bacterial production was estimated daily from May 18-31 by Ducklow et al. (1993) on the Atlantis II using ^{3}H-thymidine incorporation. Measurements were downloaded from the JGOFs database (Ducklow et al., 1989), and integrated to 35 m (Figure 4). Nitrogen bacterial production was estimated by using the ratio 4.5 C: 1 N (Goldman et al., 1987). Bacterial biomass was measured daily by acridine orange direct counts (Figure 5) for nitrogen and carbon. Numbers of cells were converted to carbon biomass using the factor of 2×10^{-14} g C cell^{-1} (Duckow et al., 1993; Lee and Fuhrman, 1987). Bacterial nitrogen biomass was derived using the conversion of 4.5 C: 1 N.

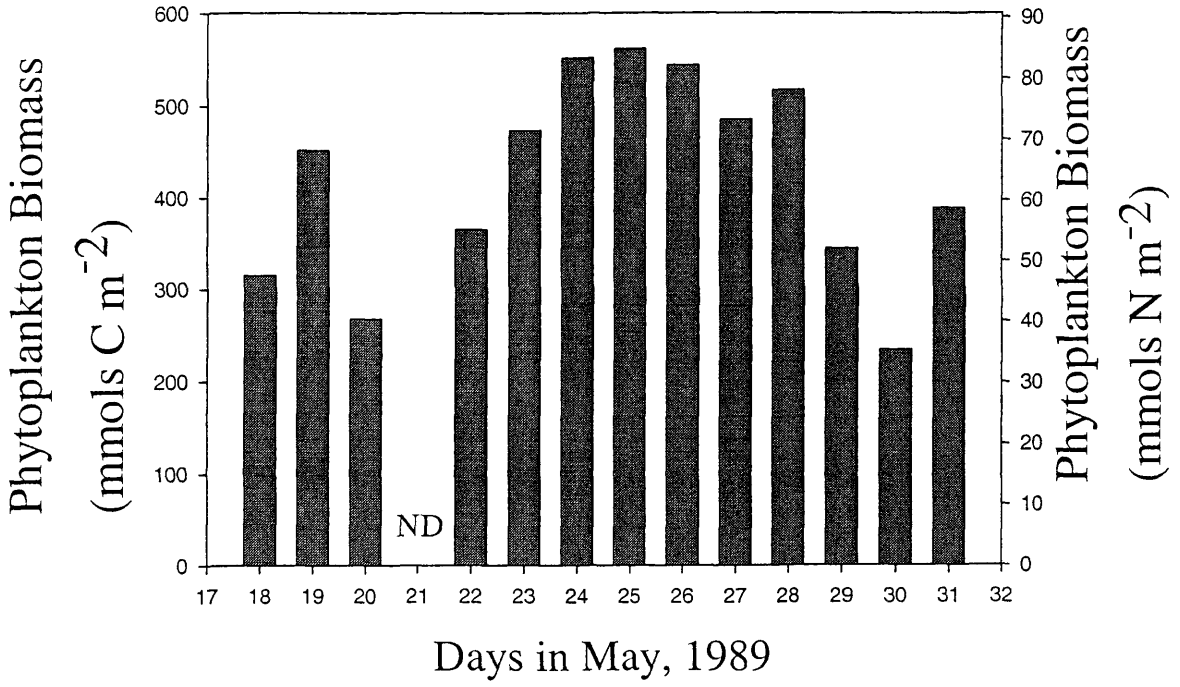


Figure 3. Phytoplankton biomass at 47° N, 20° W measured by Repeta et al. (1989). Nitrogen biomass was derived by dividing the carbon measurements by the Redfield ratio (6.625 C:N). ND = no measurement taken on that day.

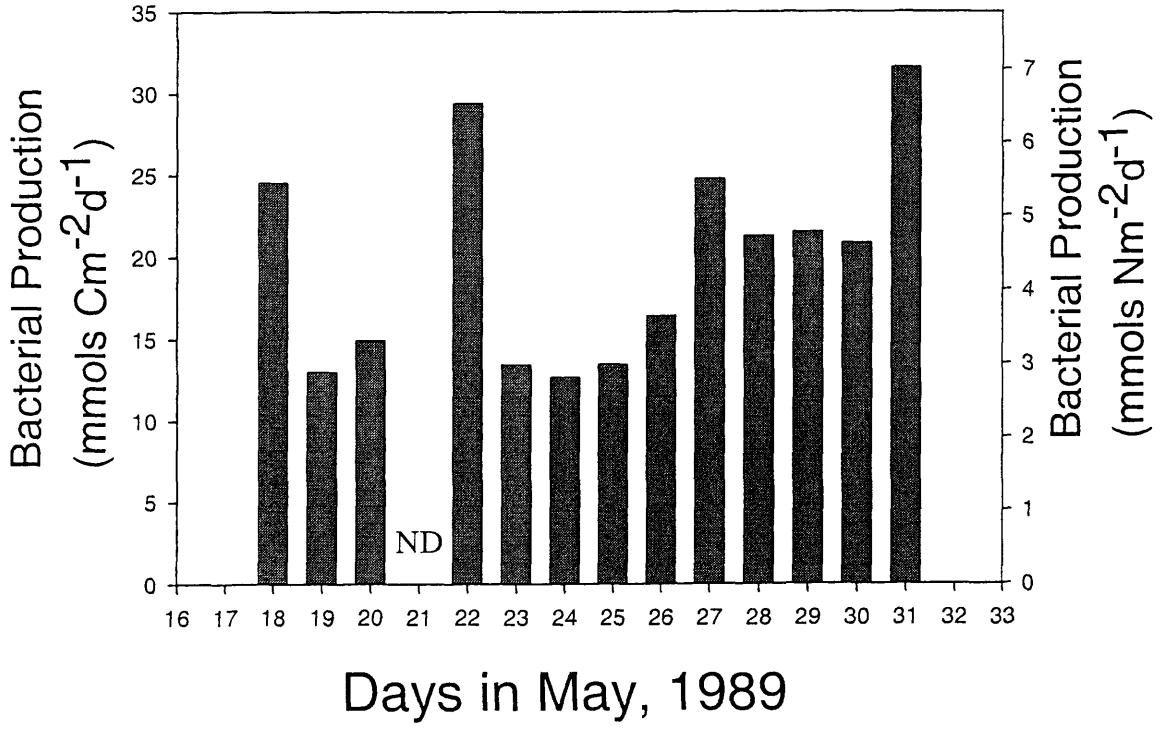


Figure 4. Bacterial production at 47° N, 20° W measured by Ducklow et al. (1992) using thymidine incorporation. Nitrogen production was derived using a C:N for bacteria of 4.5 (Goldman et. al, 1987). ND = no measurement made on that day.

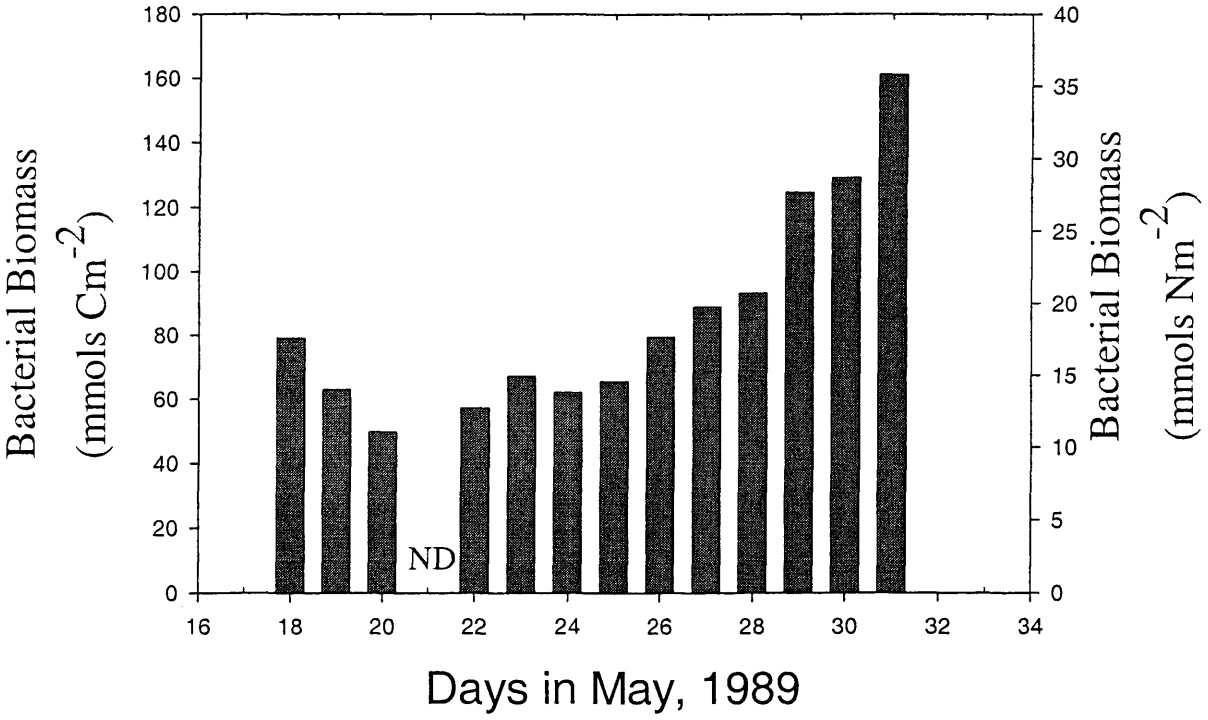


Figure 5. Bacterial biomass at 47° N, 20° W in the North Atlantic measured by acridine orange direct counts (Ducklow et. al, 1993). Nitrogen biomass derived by dividing carbon biomass by a C:N ratio of 4.5 (Goldman et al., 1987).

ND = no data measurement on that day.

Microzooplankton Grazing and Biomass

Dilution experiments were done on 3 days of the Atlantis II cruise and provide grazing rates for zooplankton smaller than 200 μm, including both the protozoan and microzooplankton size classes in the models (Verity et al., 1993). The 'protozoans' in the model represent microzooplankton less than 10 μm in diameter. While, the 'microzooplankton' include the size class of 10 – 200 μm. Water for the experiments was taken from 10 meters. The grazing rates, expressed in terms of a fraction of the primary production, were multiplied by 88 mmols C $m^{-2}d^{-1}$, the average production for the upper 35 meters (Figure 6a). Microzooplankton grazing in terms of nitrogen was derived by multiplying the fraction of the primary production grazed by the nitrogen total primary production (Figure 6b).

Total microzooplankton biomass (Figure 7) was derived from measurements of density and group specific biomass of ciliates, dinoflagellates, and microflagellates (Verity et al., 1993). Nitrogen microzooplankton biomass was derived by multiplying the carbon biomass by a C:N ratio of 4.5 (Moloney & Field, 1991).

Mesozooplankton Grazing and Biomass

Mesozooplankton grazing and biomass were estimated from trawl surveys aboard the Atlantis II (Dam et al. 1989, 1993). Dam et al. (1993) estimated grazing using gut fluorescence and gut clearance experiments for mesozooplankton split into three size classes: 0.2 – 0.5mm, 0.5 – 1.0 mm and 1.0 – 2.0 mm. Dam et al. (1993) estimated the total zooplankton grazing to be an average of 2.7% of daily primary production for the

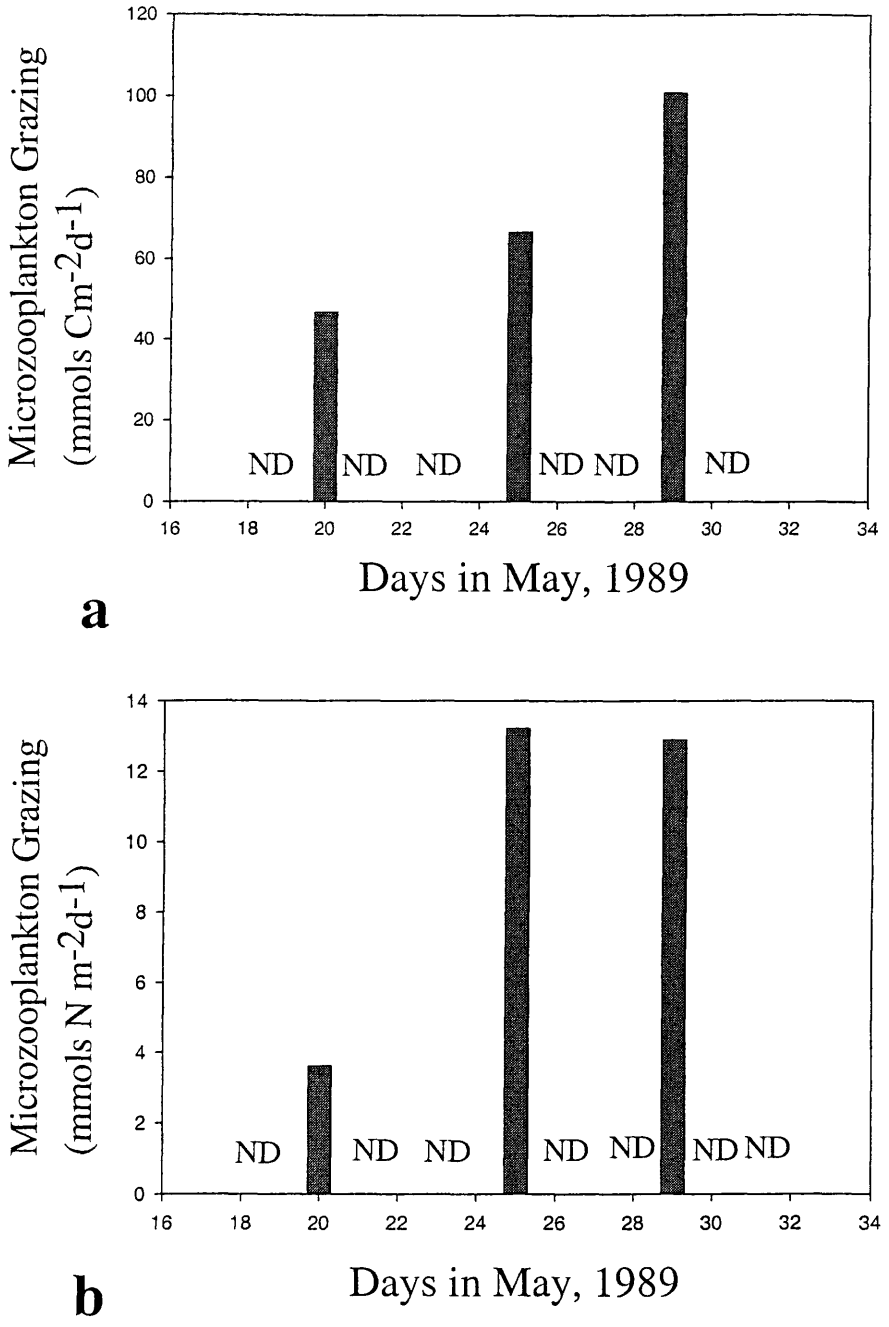


Figure 6. Microzooplankton Grazing at 47° N, 20° W in the North Atlantic measured by dilution experiments by Verity et al. (1993). The carbon grazing is shown in Figure 6a and the nitrogen grazing in Figure 6b. Grazing rates, originally given as a fraction of the carbon primary production and the nitrogen primary production (new + regenerated production), were multiplied by the daily primary production integrated to 35 m. ND = no measurement made on that day.

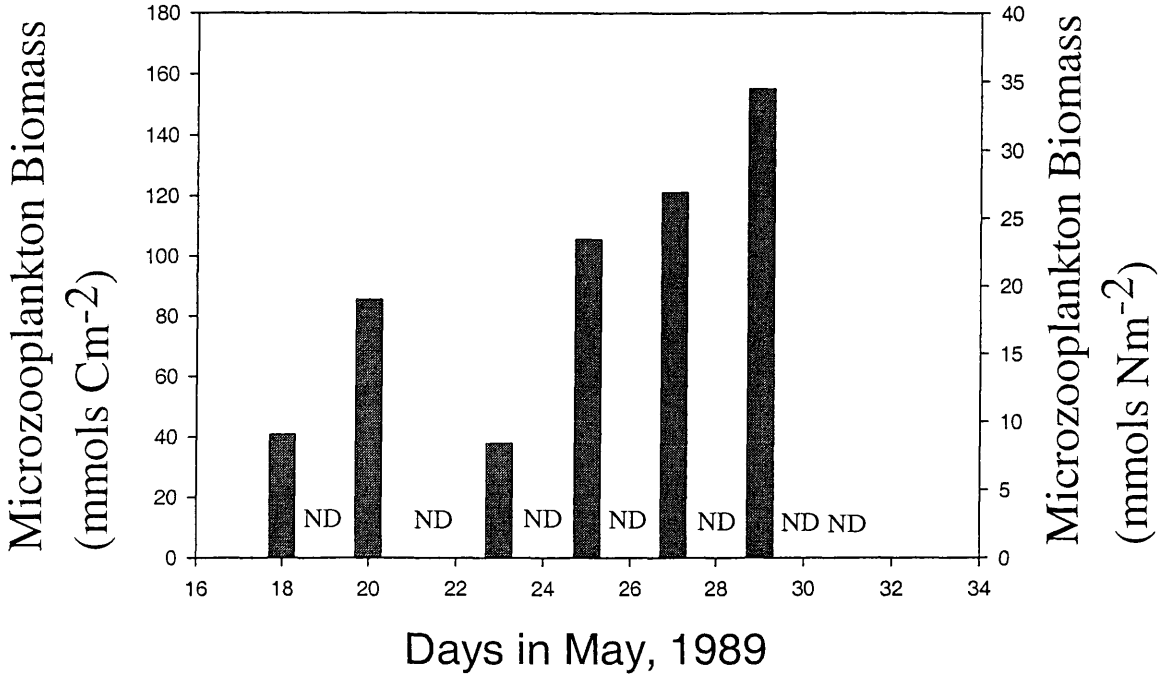


Figure 7. Microzooplankton Biomass at 47° N, 20° W in the North Atlantic measured by Verity et al. (1993). Abundance and individual carbon content from Table 8 in Verity et al. (1993) were used to estimate the total biomass of microzooplankton. The nitrogen biomass was found by dividing the carbon values by a C:N ratio of 4.5 for microzooplankton (Moloney & Field, 1991). ND = no measurement made on that day.

periods, April 25 – May 7 and May 18-31, with no significant difference in the grazing between these periods (Figure 8). The nitrogen mesozooplankton grazing was calculated as 2.7% of the nitrogen primary production (Figure 8). Dam et al. (1989) measured mesozooplankton carbon biomass (Figure 9a) and nitrogen biomass (Figure 9b) independently from the trawls and these were each integrated to 35 meters.

Export

The export from the system was estimated from measurements of ^{234}Th: ^{238}U disequilibria (Buessler et al., 1992). Buessler reported low and high estimates at 35 m and 150 m for both carbon and nitrogen export. The estimates at 35 m were used to constrain the export for the carbon and nitrogen models and are shown along with all of the model input data in Tables 1 and 2.

Model Inputs

Each of the above measurements was averaged over the period May 18 – 31 and is shown in Table 1 for carbon and Table 2 for nitrogen. The standard deviations of the rate measurements were used to set minimum and maximum constraints on the calculated flows. The measurements, +/- one standard deviation, were entered into the constraint equation for the model. In cases where the standard deviation was not available, such as for microzooplankton grazing, minimum and maximum constraints of 0.5 X and 1.5 X the measured value were used.

Regressions were performed on the biomass measurements vs. time to determine if there were significant changes over the study period. Changes were found in bacteria,

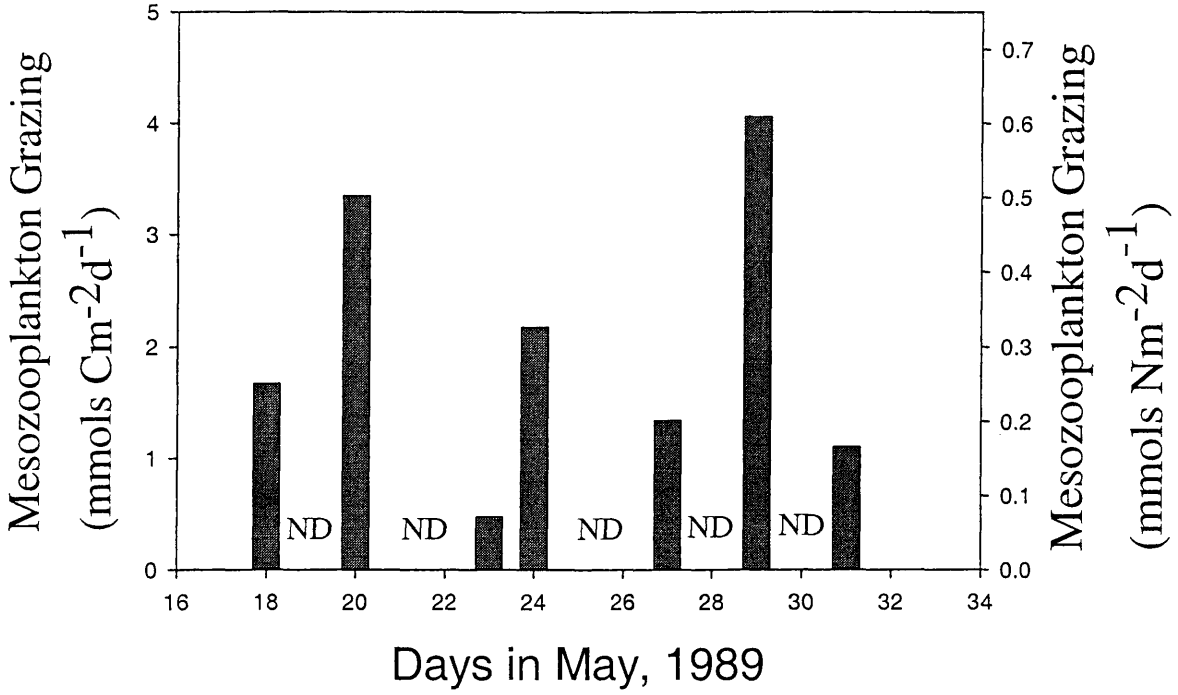


Figure 8. Mesozooplankton Grazing at 47° N, 20° W in the North Atlantic estimated from copepod gut flourescence and gut clearance experiments by Dam et al. (1993). Grazing is the total from 3 size classes: 0.2 - 0.5 mm, 0.5 - 1 mm, and 1 - 2 mm. Grazing of nitrogen component of phytoplankton was estimated using the Redfield ratio, C:N of 6.625. ND = no measurements made on that day.

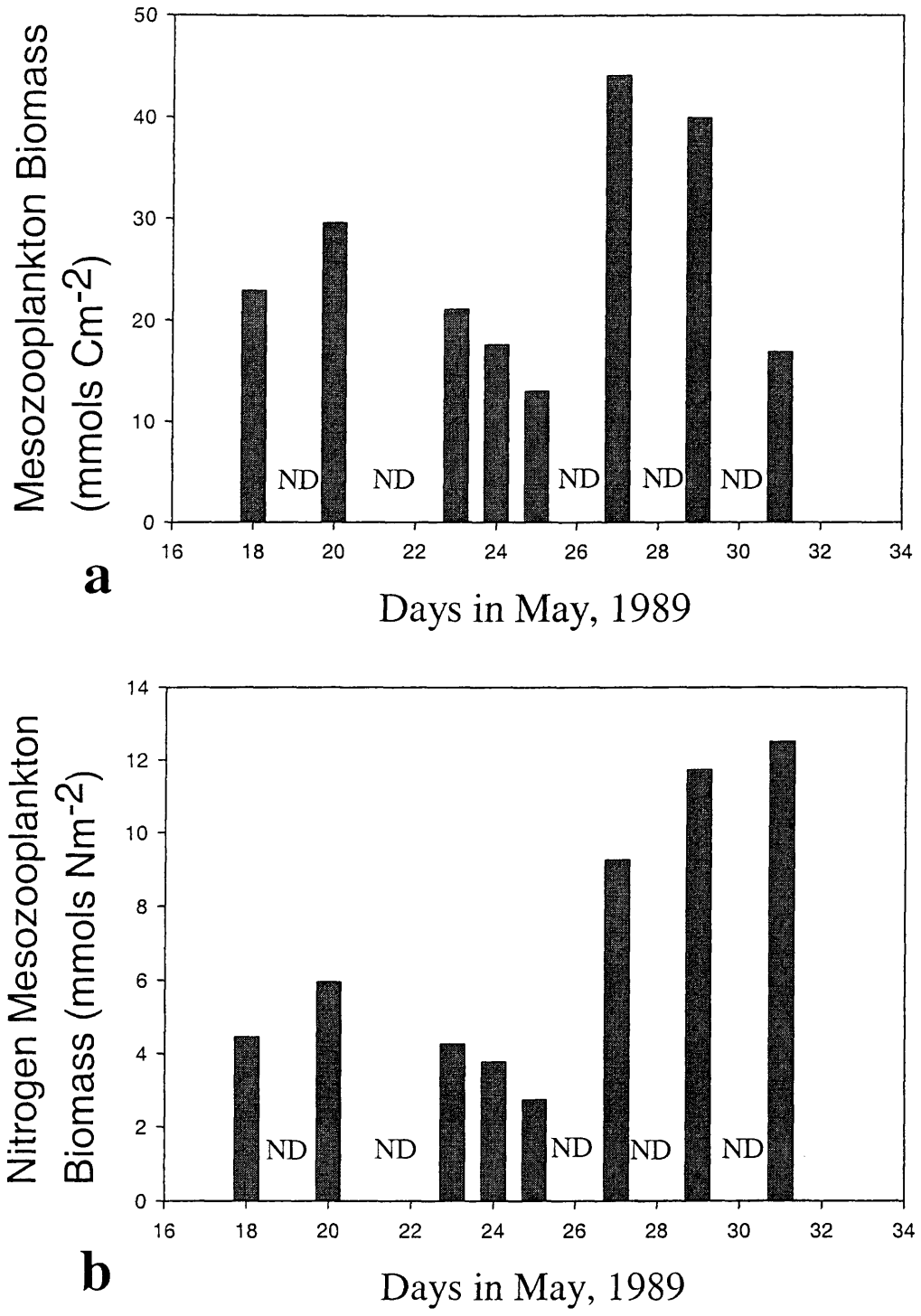


Figure 9. Mesozooplankton biomass at 47° N, 20° W in the North Atlantic from trawls by Dam et al. (1993). Biomass is the total from 3 size classes: 0.2 - 0.5mm, 0.5 - 1mm, and 1 - 2 mm. Figure 9a shows the carbon biomass. Figure 9b shows the nitrogen biomass measured independently from the carbon biomass.

ND = no data taken on that day.

Table 1. North Atlantic carbon model inputs. Daily measurements are shown with averages over the period May 18 - 31.
The change in measurements is shown if regression analysis showed a significant increase or decrease over the period.
ND = no measurements taken that day.

	Phytoplankton Production (mmol C $m^{-2}d^{-1}$)	Phytoplankton Biomass (mmol C m^{-2})	Bacterial Productivity (mmol C $m^{-2}d^{-1}$)	Bacterial biomass (mmol C m^{-2})	Microzooplankton Grazing (mmol C $m^{-2}d^{-1}$)	Micozooplankton Biomass (mmol C m^{-2})	Mesozooplankton Grazing (mmol C $m^{-2}d^{-1}$)	Mesozooplankton Biomass (mmol C m^{-2})	Export (Thorium 35m Low) (mmol C $m^{-2}d^{-1}$)	Export (Thorium 35m High) (mmol C $m^{-2}d^{-1}$)
18-May	95	315	25	79	ND	40.8		2.4		
19-May	111	452	13	63	ND	ND		ND		
20-May	58	268	15	50	47	85.5		ND		
21-May	52	ND	ND	ND	ND	ND		ND		
22-May	111	366	29	57	ND	ND		ND		
23-May	128	473	13	67	ND	37.9		ND		
24-May	102	552	13	62	ND	ND		3.8		
25-May	72	561	13	66	67	105.6		ND		
26-May	72	544	16	79	ND	ND		ND		
27-May	54	485	25	89	ND	121.0		9.3		
28-May	66	517	21	93	ND	ND		ND		
29-May	101	344	21	125	101	155.2		16.2		
30-May	111	234	21	129	ND	ND		ND		
31-May	103	389	32	161	ND	ND		5.1		
AVG	88	423	20	86	81	91.0	2	7.4	7.7	23.6
Change	0	0	0	6.33	0	9.2	0	0		
Standard dev.	25	111	6	33		46		6		

Table 2. North Atlantic nitrogen model inputs. Daily measurements are shown with averages over the period May 18 - 31.
The change in measurements is shown if regression analysis showed a significant increase or decrease over the period.
ND = no measurements taken that day.

Date	New Production (mmols N $m^{-2}d^{-1}$)	Regenerated Production (mmols N $m^{-2}d^{-1}$)	Phytoplankton Production (mmols N m^{-2} d^{-1})	NO_3 Pool (mmols m^{-2})	NH_4 Pool (mmols m^{-2})	Phytoplankton Biomass (mmols N m^{-2})	Bacterial Productivity (mmols N m^{-2} d^{-1})	Bacterial Biomass (mmols N m^{-2})	Microzooplankton Biomass (mmols N m^{-2})	Microzooplankton Grazing (mmols N m^{-2} d^{-1})	Mesozooplankton Biomass (mmols N m^{-2})	Mesozooplankton Grazing (mmols N m^{-2} d^{-1})	Export (Thorium - 35m Low)	Export (Thorium - 35m High)
18-May	4.1	5.1	9	59.8	1.38	48	5.4	18	7.8	ND	6.5			
19-May	ND	ND	ND	160.7	0	68	2.9	14	ND	ND	ND			
20-May	1.9	2.6	4	56.7	6.06	40	3.3	11	16.3	4	ND			
21-May	ND	ND	ND	ND	ND	55	ND	ND	ND	ND	ND			
22-May	1.5	4.5	6	72.0	4.87	55	6.5	13	ND	ND	ND			
23-May	6.2	6.3	13	57.4	3.96	71	3.0	15	7.2	ND	ND			
24-May	ND	ND	ND	63.3	ND	83	2.8	14	ND	ND	3.8			
25-May	6.5	7.9	14	47.8	6.775	85	3.0	15	20.1	13	ND			
26-May	3.3	7.1	10	53.7	6.775	82	3.6	18	ND	ND	ND			
27-May	2.3	4.7	7	44.7	4.645	73	5.5	20	23.1	ND	9.3			
28-May	ND	0.0	ND	35.4	3.64	78	4.7	21	ND	ND	ND			
29-May	2.8	10.1	13	29.9	5.925	52	4.8	28	29.6	13	16.2			
30-May	ND	ND	ND	37.8	ND	35	4.6	36	ND	ND	ND			
31-May	10.6	12.6	23	28.8	7	59	7.0	19	ND	ND	5.1			
AVG	3.9	6.8	11	53.4	3.6	63	4.1	17	17.3	10	8.2	0.30	1.4	3.5
Change/Day	0	0.6	0	-5.4	0	0	0.0	1.4	2.0	0	0	0		
Stand Dev	2.9	3.1	5.6			16.3	1.4	6.8	8.8		5.6			

microzooplankton, and NO_3 (Tables 1 and 2, Figure 7). Bacterial biomass showed increases of 6.3 mmols $Cm^{-2}\,day^{-1}$ and 1.4 mmols $Nm^{-2}\,day^{-1}$. Microzooplankton biomass showed increases of 9.2 mmols $Cm^{-2}day^{-1}$and 2.0 mmols $Nm^{-2}day^{-1}$. The NO_3 pool decreased 5.3 mmols $Nm^{-2}day^{-1}$. The changes for bacterial and microzooplankton biomass were entered into the balance equations for bacteria and microzooplankton, respectively, forcing the model to account for the increases in these compartments. The decrease in the NO_3 pool could not be included in the model, because the NO_3 pool is an external source in the model, with a supply rate that is the average of NO_3 uptake over the study period. A significant change in the NO_3 pool would have affected the daily NO_3 uptake rates.

Constraints on respiration, ingestion, excretion, assimilation, and production for all living components were included for the nitrogen and carbon models (Tables 3 and 4). The average biomasses were used as inputs to the allometric equation described by Moloney and Field (1989) to constrain the maintenance respiration for each component.

Model Results

The bacterial ingestion of DOM and grazing by microzooplankton and protozoans dominated the flows of carbon and nitrogen in the inverse solutions. Flow diagrams for the carbon and nitrogen inverse solutions are shown in Figures 10 and 11, with the widths of the arrows between components proportional to the magnitudes of the flows. Arrows that are black represent allowed flows the model found to be equal to zero. Bacterial ingestion of DOC was the largest flow in the carbon model (40.7 mmols $Cm^{-2}\,d^{-1}$) and was equal to 65% of the net primary production (Figure 10 and Table 5). The largest

Table 3. Biological contraints for the NABE carbon inverse solution. The temperature, T is equal to 15 ° C and is the average of the surface temperature of 17 ° C and the temperature at 50 meters of 13 ° C from Weeks et al. (1993).

Mbac = pmols of carbon / bacteria cell, Cbacteria = biomass of bacteria in mmols C m^{-2},

MicC = pmols of carbon / microzooplankton cell, Cmicro = biomass of microzooplankton in mmols C m^{-2},

MesC = pmols of carbon / individual mesozooplankton, Cmesozoo = biomass of mesozooplankton in mmols C m^{-2}.

All biomass measurements were integrated to 35 m.

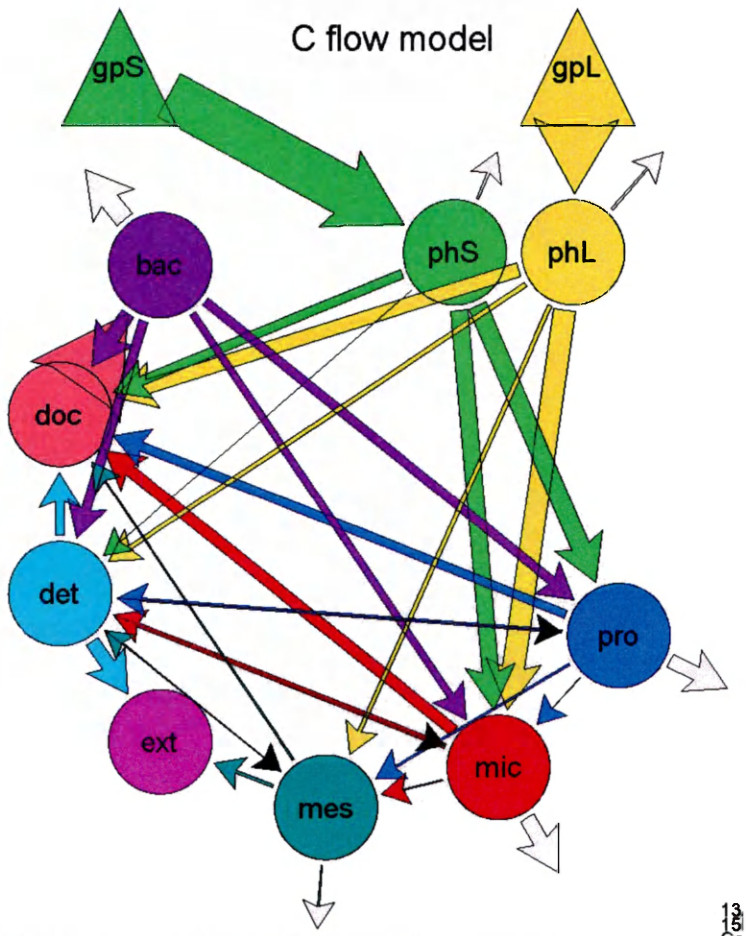
Biological Constraints	Lower Bound	Upper Bound	Reference
Respiration			
Bacteria	20 % of consumption of DOC	(1.7*(Mbac)^-0.25*EXP(0.0693*(T-20)))*Cbacteria	1
Large Phytoplankton	5 % of GPP	30 % of gross primary production	2
Small Phytoplankton	5 % of GPP	30 % of gross primary production	2
Protozoa	20 % of total C intake	none	
Microzooplankton	20 % of total C intake	(14*('MicC')^-0.25*EXP(0.0693*(T-20)))*'Cmicro'	1
Mesozooplankton	20 % of total C intake	(14*(mesC)^-0.25*EXP(0.0693*(T-20)))*Cmesozoo	1
Excretion			
Large Phytoplankton	2 % of large phytoplankton NPP	55 % of large phytoplankton NPP	2
Small Phytoplankton	2 % of small phytoplankton NPP	55 % of small phytoplankton NPP	2
Protozoa	10 % of total C intake	100 % of protozoan respiration	3
Microzooplankton	10 % of total C intake	100 % of microzooplankton respiration	3
Mesozooplankton	10 % of total C intake	100 % of mesozooplankton respiration	3
Assimilation efficiency			
Protozoa	C output to Detritus <= 50% of total C intake	C output to Detritus >= 10% of total C intake	2
Microzooplankton	C output to Detritus <= 50% of total C intake	C output to Detritus >= 10% of total C intake	2
Mesozooplankton	C output to Detritus <= 50% of total C intake	C output to Detritus >= 10% of total C intake	2
Net production efficiency			
Bacteria	bacteria to DOC + bacterial respiration <= 95% DOC to bacteria	bacteria to DOC + bacterial respiration >= 50% DOC to bacteria	3
Gross production efficiency			
Protozoa	losses to respiration + detritus + DOC <= 90 % of total carbon intake	losses to respiration + dertritus + DOC >= 60 % of total carbon intake	3
Microzooplankton	losses to respiration + detritus + DOC <= 90 % of total carbon intake	losses to respiration + dertritus + DOC >= 60 % of total carbon intake	3
Mesozooplankton	losses to respiration + detritus + DOC <= 90 % of total carbon intake	losses to respiration + dertritus + DOC >= 60 % of total carbon intake	3
Ingestion			
Bacteria	none	(3.6*(Mbac)^-0.25*EXP(0.0693*(T-20)))*Cbacteria	1
Mesozooplankton	none	(63*(mesC)^-0.25*EXP(0.0693*(T-20)))*Cmesozoo	1

References. 1. Moloney & Field (1989) 2. Vezina & Platt (1989) 3. Richardson & Jackson, pers. comm.(2001)

Table 4. Biological constraints for the NABE nitrogen inverse solutions. The temperature, T is equal to 15 ° C and is the average of the surface temperature of 17 ° C and the temperature at 50 meters of 13 ° C from Weeks et al. (1993).
Mbac = pmols of nitrogen / bacteria cell, Nbacteria = biomass of bacteria in mmols N m^{-2},
MicN = pmols of nitrogen / microzooplankton cell, Nmicro= biomass of microzooplankton in mmols N m^{-2},
MesN = pmols of nitrogen / individual mesozooplantkon, Nmesozoo = biomass of mesozooplankton in mmols N m^{-2}.
All biomass measurements were integrated to 35 m.

Biological Constraints	Lower Bound	Upper Bound	Reference
Excretion			
Large Phytoplankton	2 % of large phytoplankton Net Primary Production	55 % of large phytoplankton Net Primary Production	2
Small Phytoplankton	2 % of small phytoplankton Net Primary Production	55 % of small phytoplankton Net Primary Production	2
Protozoa	10 % of total N intake	None	3
Microzooplankton	10 % of total N intake	None	3
Mesozooplankton	10 % of total N intake	None	3
Assimilation efficiency			
Protozoa	N output to Detritus <= 50% of total N intake	N output to Detritus >= 10% of total N intake	2
Microzooplankton	N output to Detritus <= 50% of total N intake	N output to Detritus >= 10% of total N intake	2
Mesozooplankton	N output to Detritus <= 50% of total N intake	N output to Detritus >= 10% of total N intake	2
Gross production efficiency			
Bacteria	bacteria to DON <= 95% DON to bacteria	bacteria to DON >= 50% DON to bacteria	3
Net production efficiency			
Protozoa	losses to NH4 + detritus + DON <= 90 % of total nitrogen intake	losses to NH4 + dertritus + DON >= 60 % of total nitrogen intake	3
Microzooplankton	losses to NH4 + detritus + DON <= 90 % of total nitrogen intake	losses to NH4 + dertritus + DON >= 60 % of total nitrogen intake	3
Mesozooplankton	losses to NH4 + detritus + DON <= 90 % of total nitrogen intake	losses to NH4 + dertritus + DON >= 60 % of total nitrogen intake	3
Ingestion			
Bacteria	none	(3.6*(Mbac)^-0.25*EXP(0.0693*(T-20)))*Nbacteria/4.5	1
Mesozooplankton	none	(63*(mesN)^-0.25*EXP(0.0693*(T-20)))*Nmesozoo/6.63	1

References. 1. Moloney & Field (1989) 2. Vezina & Platt (1989) 3. Richardson & Jackson, pers. comm.(2001)



gpS = Gross PP for Small Phytoplankton

gpL = Gross PP for Large Phytoplankton

bac = bacteria

det = detritus

ext = Export

mes = mesozooplankton

mic = microzooplankton

pro = protozoans

Figure 10. NABE inverse carbon solution with measurements set as constraints. The width of the flows are proportional to their magnitudes. Inputs are from gross primay production for small phytoplankton (gpS) and large phytoplankton (gpL). Gray flows leaving compartments are losses to respiration. Export from the top 35 m enters the ext compartment.

Table 5. NABE Carbon flows generated using the inverse method with measurements as constraints. Flows are expressed as absolute flows in mmols C $m^{-2}d^{-1}$ and as a fraction of the net primary production.

Flows	mmols C $m^{-2}d^{-1}$	Normalized to Net PP
Large phytoplankton gross primary production	33.2	0.53
Large phytoplankton respiration	1.7	0.03
Microzooplankton grazing of large phytoplankton	15.3	0.24
Mesozooplankton grazing of large phytoplankton	3.2	0.05
Large phytoplankton sinking	3.9	0.06
Large phytoplankton release of DOC	9.2	0.15
Small phytoplankton gross primary production	33.2	0.53
Small phytoplankton respiration	1.7	0.03
Protozoan grazing of small phytoplankton	13.3	0.21
Microzooplankton grazing of small phytoplankton	11.9	0.19
Small phytoplankton to detritus	0.5	0.01
Small phytoplankton release of DOC	5.8	0.09
Microzooplankton consumption of protozoans	0.5	0.01
Mesozooplankton consumption of protozoans	1.4	0.02
Protozoan respiration	9.8	0.16
Protozoans to detritus	1.8	0.03
Protozoans to DOC	4.9	0.08
Microzooplankton respiration	11.6	0.18
Mesozooplantkton consumption of microzooplankton	0.7	0.01
Microzooplankton to detritus	3.1	0.05
Microzooplankton to DOC	6.7	0.11
Mesozooplankton respiration	1.2	0.02
Mesozooplankton to detritus (Faecal pellets)	0.8	0.01
Mesozooplankton to DOC	1.2	0.02
Bacterial respiration	12.6	0.20
Bacteria to protozoans	5.1	0.08
Bacteria to microzooplankton	3.7	0.06
Bacteria to detritus	5.2	0.08
Bacteria to DOC	7.7	0.12
Protozoan consumption of detritus	0.0	0.00
Microzooplankton consumption of detritus	0.0	0.00
Mesozooplankton consumption of detritus	0.0	0.00
Detritus to DOC	5.3	0.08
Bacterial ingestion of DOC	40.7	0.65
Total Particulate Export out of the top 35 m	10.2	0.16
Mesozooplankton to export (Consumption by higher trophic levels or death)	2.1	0.03

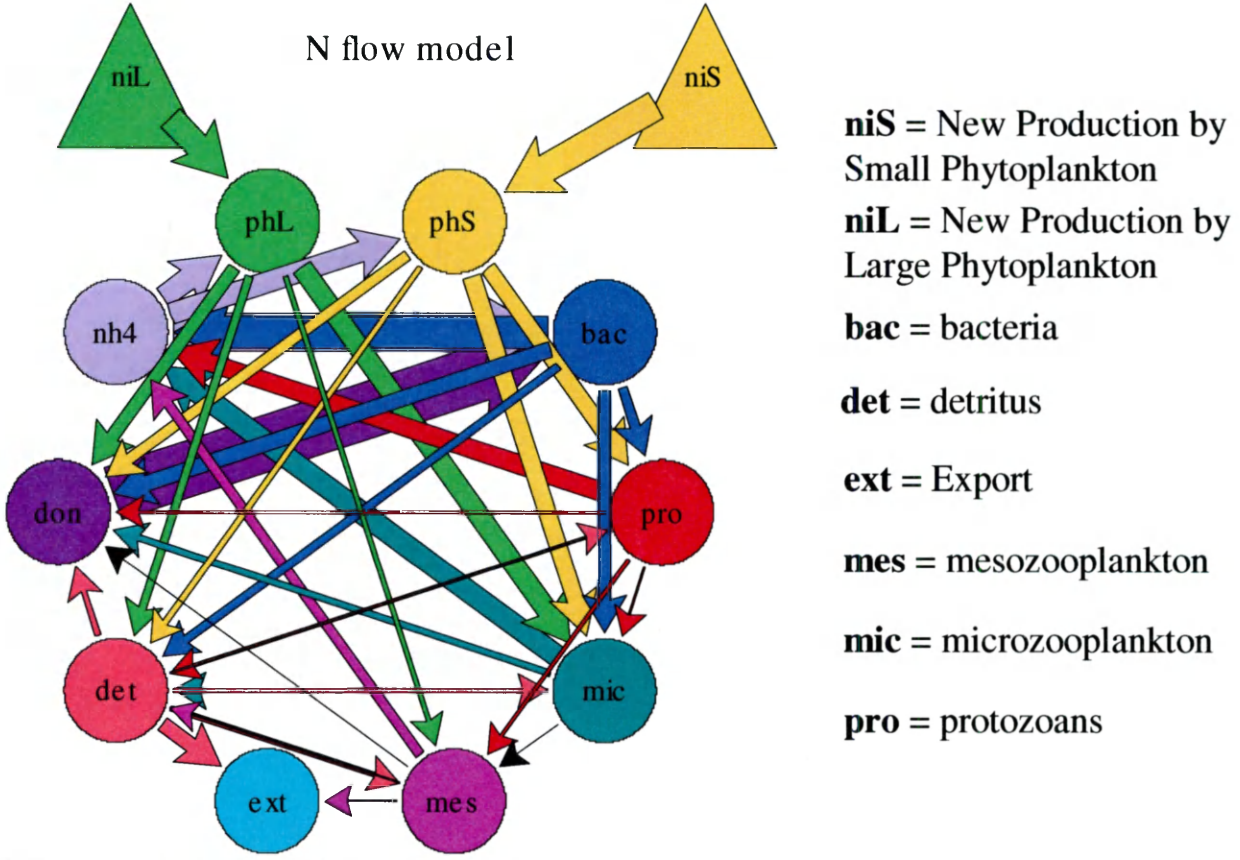


Figure 11. NABE inverse nitrogen solution with measurements set as constraints. The width of the flows are proportional to their magnitudes. Inputs are from new production for small phytoplankton (niS) and large phytoplankton (niL). Export from the top 35 m enters the ext compartment.

Table 6. NABE Nitrogen flows generated using the inverse method with measurements as constraints. Flows are expressed as absolute flows in mmols N $m^{-2}d^{-1}$ and as a fraction of the total new primary production and the total primary production.

Flows	mmols C $m^{-2}d^{-1}$	Normalized to Total New Production	Normalized to Total Primary Production
Large phytoplankton new production	2.33	0.48	0.27
Microzooplankton grazing of large phytoplankton	1.85	0.38	0.21
Mesozooplankton grazing of large phytoplankton	0.45	0.09	0.05
Large phytoplankton sinking	0.71	0.15	0.08
Large phytoplankton release of DON	1.17	0.24	0.14
Small phytoplankton new production	2.58	0.52	0.30
Protozoan grazing of small phytoplankton	1.42	0.29	0.17
Microzooplankton grazing of small phytoplankton	1.60	0.33	0.19
Small phytoplankton to detritus	0.47	0.10	0.05
Small phytoplankton release of DON	0.93	0.19	0.11
Small phytoplankton regenerated production	1.85	0.38	0.21
Large phytoplankton regenerated production	1.85	0.38	0.21
Bacterial uptake of NH4	3.43	0.70	0.40
Microzooplankton consumption of protozoans	0.14	0.03	0.02
Mesozooplankton consumption of protozoans	0.22	0.04	0.03
Protozoans to detritus	0.25	0.05	0.03
Protozoans to DON	0.26	0.05	0.03
Protozoans to NH4	1.61	0.33	0.19
Mesozooplantkton consumption of microzooplankton	0.00	0.00	0.00
Microzooplankton to detritus	0.50	0.10	0.06
Microzooplankton to DON	0.58	0.12	0.07
Microzooplankton to NH4	1.92	0.39	0.22
Mesozooplankton to detritus (Fecal pellets)	0.11	0.02	0.01
Mesozooplankton to DON	0.00	0.00	0.00
Mesozooplankton to NH4	0.87	0.18	0.10
Protozoan consumption of bacteria	0.89	0.18	0.10
Microzooplankton consumption of bacteria	1.07	0.22	0.12
Bacteria to detritus	0.73	0.15	0.09
Bacteria to DON	1.38	0.28	0.16
Bacteria to NH4	2.72	0.55	0.32
Protozoan consumption of detritus	0.16	0.03	0.02
Microzooplankton consumption of detritus	0.34	0.07	0.04
Mesozooplankton consumption of detritus	0.42	0.09	0.05
Detritus to DON	0.46	0.09	0.05
Bacterial ingestion of DON	4.77	0.97	0.55
Total Particulate Export out of the top 35 m	1.40	0.29	0.16
Mesozooplankton to export (Consumption by higher trophic levels or death)	0.11	0.02	0.01

flow in the nitrogen solution is the bacterial ingestion of DON (4.77 mmols $Nm^{-2}d^{-1}$), and is equal to 97% of the new production and 55% of the total production (Table 6 and Figure 11). The microzooplankton and protozoans dominated grazing in the carbon and nitrogen solutions. Microzooplankton grazing of small and large phytoplankton carbon is equivalent to 43% of the net primary production (Table 5). Microzooplankton grazing of small and large phytoplankton nitrogen accounted for 71% of the total new production and 40% of the total nitrogen production (Table 6). Protozoan grazing of small phytoplankton is equal to 21% of the net carbon primary production (Table 5) and 17% of the total nitrogen production (Table 6). Mesozooplankton grazing of large phytoplankton is equal to just 5% of both the net carbon primary production and the total nitrogen primary production.

The inferred large phytoplankton and small phytoplankton carbon primary production were equal (Figure 10 and Table 5). The small phytoplankton nitrogen production was slightly larger than the large phytoplankton nitrogen production in the solution: 2.58 vs. 2.33 mmols $Nm^{-2}d^{-1}$, respectively (Table 6). Although the nitrogen production is assumed to be equally split among small and large phytoplankton, the standard deviation of the data used in the constraint equations for the model allows for variance from a 50% split in the solution.

The total throughputs of the dissolved organic matter pools are 2 –3 times that of the detritus pool in the carbon and nitrogen solutions. The total throughput of the detritus pool in the carbon solution is 15.4 mmols $Cm^{-2}day^{-1}$, equal to 24% of the net primary production. The total throughput of the DOC pool is 40.6 mmols $Cm^{-2}day^{-1}$ equal to 65%

of the net primary production. The largest flow leaving the carbon detritus pool is the particulate export, 10.2 mmols $Cm^{-2}\,d^{-1}$ and the next largest flow is detrital decompositon into the DOC pool, 5.3 mmols $Cm^{-2}\,d^{-1}$. The total throughput of the detritus pool in the nitrogen solution is 2.8 mmols $Nm^{-2}day^{-1}$, equal to 32% of the net primary production. The total throughput of the DON pool is 4.8 mmols $Nm^{-2}d^{-1}$ or 55% of the total nitrogen primary production. The largest flow leaving the detritus pool is the particulate export, 1.4 mmols $Nm^{-2}d^{-1}$ and the next largest flow is detrital decompostion into the DON pool, 0.46 mmols $Nm^{-2}d^{-1}$.

The particulate nitrogen and carbon export sinking out of the top 35 m are equal to 16% of both the net carbon primary production and the total nitrogen primary production (Table 7). Two components of the detrital export, mesozooplankton fecal pellets and the sinking of large phytoplankton, account for 7% of the carbon primary production and 9% of the nitrogen primary production (Table 7). These flows are represented in the model by the paths from large phytoplankton to detritus and from mesozooplankton to detritus (Figures 10 and 11). It is assumed that these contributions to the detritus pool sink readily, taking the model pathway from detritus to export. The remaining detrital export, equal to 9% of the net carbon primary production and 7% of the total nitrogen primary production, comes from the aggregation of detritus from other living sources, into particles that are large enough to sink. The model solution does not explicitly assign this export to specific components. However, examining the contributions to the detritus pool shown in Table 8, gives some insight as to the relative contributions of the living components to sinking particles. Small phytoplankton, bacteria, protozoans, and microzooplankton make up 69% of the carbon inputs to the

Table 7. Export flows from the upper 35 m in the NABE carbon and nitrogen models. The sinking of large phytoplankton, mesozooplankton fecal pellets, and detrital particles formed from the aggregation of other living components (See Table 8). Flows are expressed as a % of the net carbon primary production and the total nitrogen primary production.

	% of Net Carbon PP	% of Total Nitrogen PP
Sinking of Large Phytoplankton	6	8
Mesozooplankton Fecal Pellets	1	1
Aggregation of Detritus into sinking particles	9	7
Total Detrital Export	16	16

Table 8. Contributions to the detritus pool from the upper 35 m, in terms of carbon and nitrogen as a % of the total inputs to the pool.

	% Contribution to Detritus Pool	
	Carbon	Nitrogen
Large Phytoplankton	25	26
Small Phytoplankton	3	17
Bacteria	34	26
Protozoans	12	9
Microzooplankton	20	18
Mesozooplankton	5	4

detritus pool and 70% of the nitrogen inputs. These small particles likely aggregate into particles that are large enough to sink, explaining the difference between large sinking particles, including large phytoplankton and mesozooplankton fecal pellets, and the total detrital export in Table 7. Bacteria make the greatest contributions to the detritus pool equal to 34% of the carbon and 36% of the nitrogen. Microzooplankton, the largest sized organism in Table 8, contribute 20% of the carbon and 18% of the nitrogen entering the detrital pool. Due to their size (20-200 μm), the microzooplankton are the most likely contributors to sinking by the aggregation of small detrital particles.

Another potential export flow, separate from the detrital export, is mesozooplankton production that is equal to 3% of the carbon net primary production (Table 5) and 1% of the nitrogen total primary production (Table 6). Mesozooplankton production represents the growth of mesozooplankton that can be consumed by higher trophic levels or can sink out of the surface ocean when the mesozooplankton die. The mesozooplankton production and the particulate export together make up the model's estimated export ratio or e-ratio. In the carbon solution, the e_C-ratio is 0.16 + 0.03 = 0.19 and in the nitrogen solution the e_N-ratio is 0.16 + 0.01 = 0.17. The f-ratio can be estimated from the flows for large and small phytoplankton in the nitrogen solution:

f = New Production / (New + Regenerated Production) =

(2.33 + 2.58) mmols $Nm^{-2}d^{-1}$ /(2.33 + 2.58 + 1.85 + 1.85) mmols $Nm^{-2}d^{-1}$ = 0.57

The model e-ratios are much lower than the f-ratio of 0.45, estimated for the same area by Martin et al. (1993), and the model f-ratio is larger than Martin's estimate.

The dominance of microzooplankton and protozoan grazing is also shown in the fates of both the net carbon primary production (Figures 12a) and the total nitrogen production (Figure12b). The microzooplankton consumed 48% of the large phytoplankton carbon production and 37% of the small phytoplankton carbon production (Figure 12a). Protozoans consumed 43% of the small phytoplankton carbon production (Figure 12a). Mesozooplankton grazing was relatively small, equal to 10% of the large phytoplankton carbon production. The fate of the nitrogen primary production in the food web (Figure 12b) is similar to the fate of the carbon primary production, except the protozoans graze about 10% more of the small primary production in the carbon solution and the detritus pool receives 7% more of the primary production in the carbon solution. The differences in the fates of carbon and nitrogen are most likely the result of obtaining separate solutions for carbon and nitrogen. In nature one would expect the carbon and nitrogen fates to be equal, because a grazer can't consume carbon without nitrogen. This could be addressed in future simulations by using a C/N ratio as a constraint on the zooplankton feeding to bring agreement between the carbon and nitrogen solutions.

The three zooplankton classes relied mainly on phytoplankton in their diet and the consumption of detritus was important in the nitrogen solution but was absent in the carbon solution (Figures 13a and 13b). Protozoans receive about 72% of their carbon diet from small phytoplankton and 28% from bacteria (Figure 13a). Small phytoplankton make up a smaller proportion of the protozoan diet, 57% in the nitrogen solution and bacteria is more important in the protozoan nitrogen diet, making up 37% of the nitrogen diet (Figure 13b). Microzooplankton have the most varied diet in both the nitrogen and the carbon solution (Figures 13a and 13b). Large phytoplankton and small phytoplankton

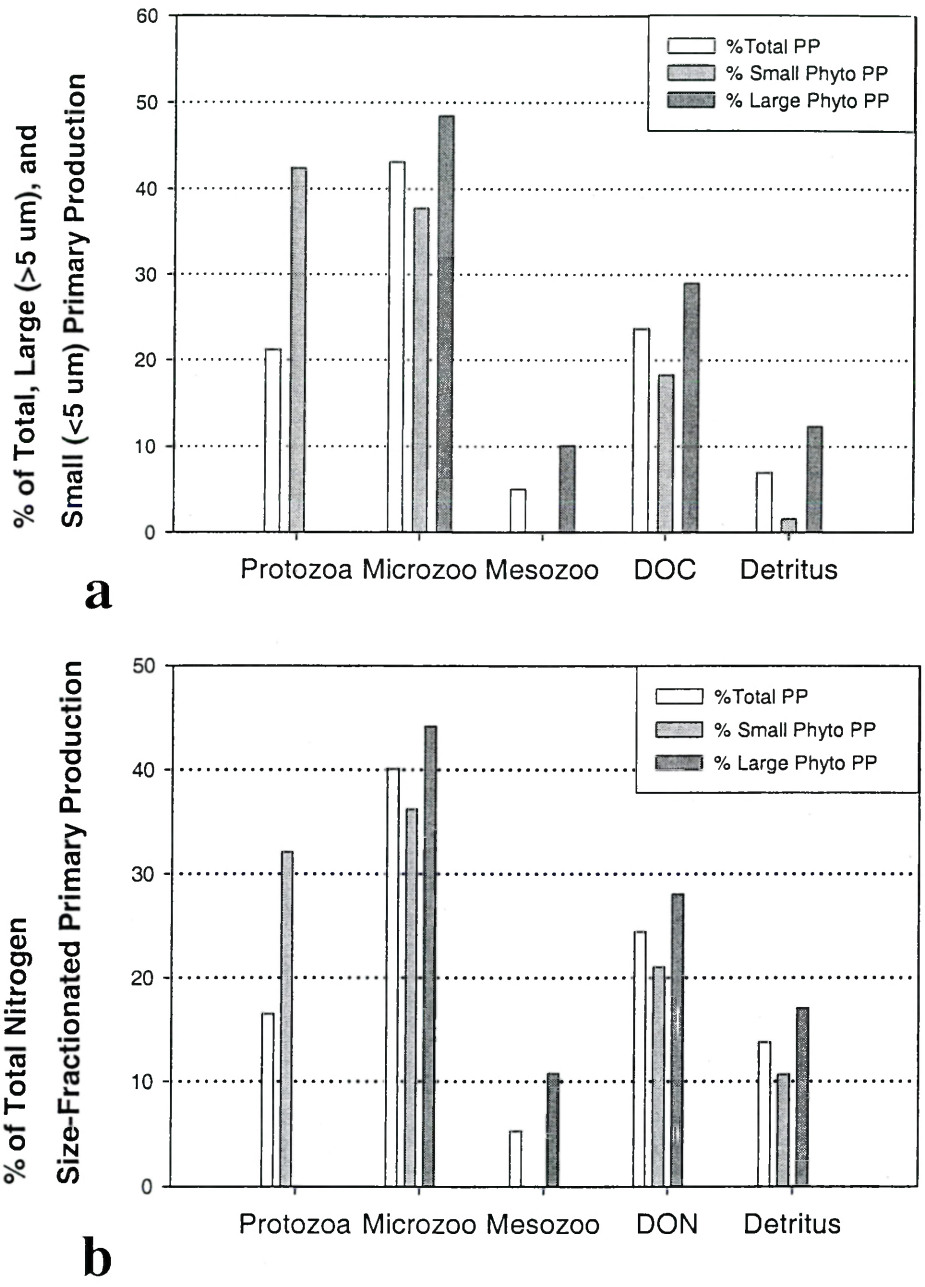


Figure 12. The fate of the carbon (a) and nitrogen (b) primary production for NABE. The primary production is expressed as total, large (>5 μm), and small (<5 μm) primary production that is consumed by the 3 size classes of zooplankton:protozoans (<10 μm), microzooplankton (10-200 μm), and mesozooplankton (> 200 μm), goes to detritus, or is released as DOC / DON.

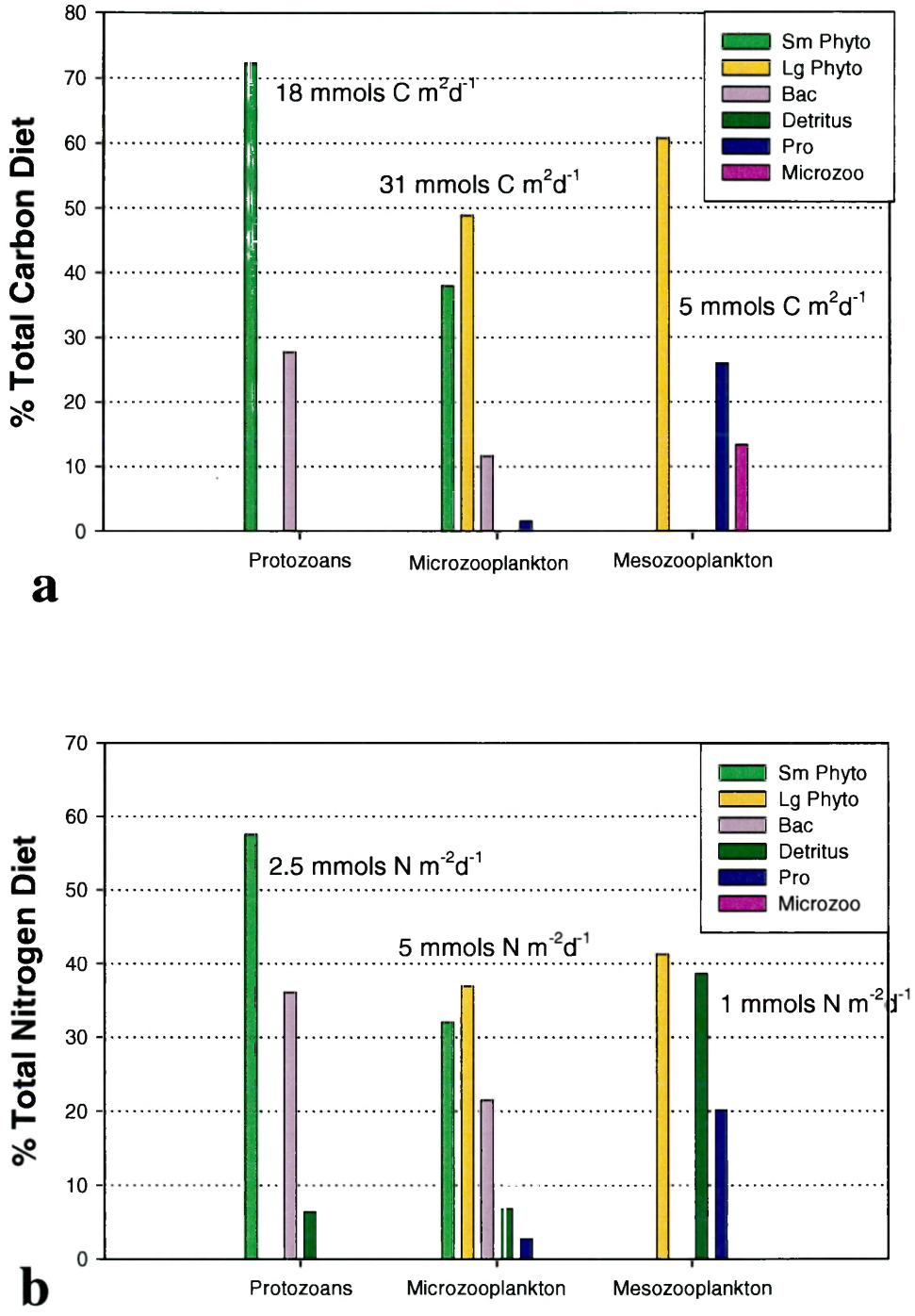


Figure 13. Zooplankton diet composition for the carbon (a) and nitrogen (b) solutions for NABE. The percentage of the diet contents for each zooplankton size class is shown. The total input in mmols C m^{-2} d^{-1} for each zooplankton size class is also shown.

make up 48% and 38% of their carbon diet, respectively. The microzooplankton consume the most carbon (31 mmols $Cm^{-2}d^{-1}$) and nitrogen (5 mmols $Nm^{-2}d^{-1}$) of the zooplankton. Microzooplankton consume twice as much bacteria, as a percentage of their diet, in the nitrogen solution than they do in the carbon solution. Detritus makes up 7% of the microzooplankton nitrogen diet. Mesozooplankton consume the least amount of carbon (5 mmols $Cm^{-2}d^{-1}$) and nitrogen (1 mmol $Nm^{-2}d^{-1}$) of the zooplankton, which they mostly receive from grazing of large phytoplankton. Detritus is a large part of the mesozooplankton nitrogen diet equal to 38%. Mesozooplankton do not consume any microzooplankton in the nitrogen solution but gain 13% of their diet from microzooplankton in the carbon solution. (Figures 13a and 13b). The consumption of detritus for all three zooplankton classes takes place in the nitrogen solution, but was zero for all in the carbon solution. This result is impossible in nature, like the differences in the fate of phytoplankton described above. Differences in zooplankton diet composition of nitrogen and carbon could also be resolved by using a C/N ration between the carbon and nitrogen solutions. However, some differences are possible, if for example microzooplantkon were more nitrogen rich than protozoans, the microzooplantkon would make up a greater percentage of the mesozooplankton's nitrogen diet than their carbon diet.

The greatest contributors to the DOC and DON pools are large phytoplankton and bacteria (Figures 14 a and 14 b). None of the inputs to the DOC and DON pools were measured. Large phytoplankton and bacteria each contribute 21% of the inputs to the DOC pool (Figure 14 a). Bacteria are the greatest contributors to DON (31%). Large phytoplankton are the second greatest contributor to the DON pool, providing 26% of the

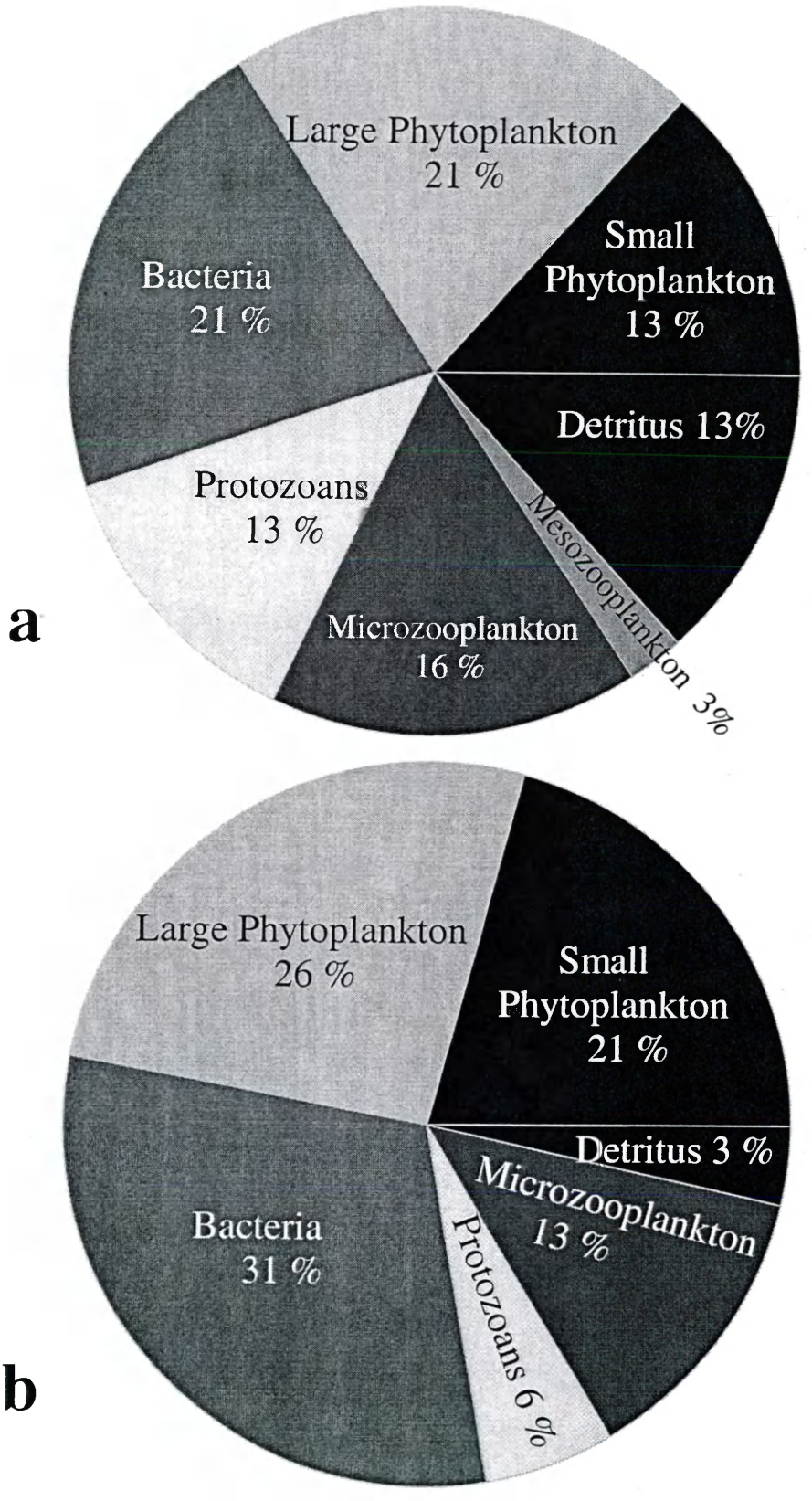


Figure 14. Contributions to the DOC (a) and DON (b) pools in the NABE inverse solutions as a % of the total flows entering.

nitrogen (Figure 14b). Protozoans made a smaller contribution to the DON (6%) pool than the DOC pool (21%). Detritus also made a smaller contribution to the DON pool (3%) than the DOC pool (13%). Note that some components of the DOC pool could lack nitrogen, explaining the uncoupling of these flows.

Network Analysis

Network analysis indices were calculated for the solution (Table 8). The index of recycling, ***L*** is an estimate of the number of times an average carbon atom passes through the system before leaving (Jackson & Eldridge, 1992). ***L*** is calculated by dividing the total of all internal flows within the system by the net primary production. This index revealed that the average carbon atom is cycled through the food web 2.6 times and the average nitrogen atom 7.2 times before leaving through respiration (carbon only), sinking detritus, or fecal pellets (Table 9). Another index of recycling, the **Total ingestion / pp** is equal to all of the zooplankton ingestion flows plus the bacterial ingestion of DOC divided by the net primary production (Table 9). The **Total ingestion/ pp** of 1.6 for the carbon solution indicates that 60% of the carbon ingestion comes from recycling in the food web. For the nitrogen solution, this index was 2.5 indicating 150% of the ingestion was from recycled nitrogen.

Other indices were used to show the relative activity of each living compartment. ***Fbac*** is equal to the ratio of bacterial production to net primary production. ***Fpro***, ***Fmic***, and ***Fmes*** are the ratios of the total flows through each compartment to the total flows through all three grazer compartments (Niquil et al., 1998). The bacterial production was equal to 22% of the net carbon primary production and 55% of the total nitrogen

Table 9. Network analysis indices for the NABE carbon and nitrogen solutions. **L** is the index of recycling equal to the number of times a carbon atom cycles through the food web before leaving through respiration (for carbon only), sinking, or predation by higher trophic levels. The **Total ingestion / PP** is the total ingestion of all zooplankton components plus the ingestion of DOC / DON by bacteria divided by the net primary production. **Fbac** is the ratio of bacterial production to net carbon primary production or total nitrogen production. **Fpro, Fmic, and Fmes** are the ratios of the total flows through protozoans, microzooplankton, and mesozooplankton, respectively to the total flows through all three grazer compartments.

Index	Carbon	Nitrogen
L	2.4	7.2
Total Ingestion/ PP	1.6	2.5
Fbac (%)	22.2	55.0
Fpro (%)	40.3	33.0
Fmic (%)	48.4	52.5
Fmes (%)	11.4	14.6

production as shown by ***Fbac*** (Table 9). The microzooplankton processed the most carbon (***Fmic*** = 48%), followed by the protozoans (***Fpro*** = 41%) and mesozooplankton (***Fmes*** = 11%) (Table 9). The same order of consumption was seen in the nitrogen solution.

The dependency coefficients, calculated by the network analysis program by Ulanowicz (1986), indicate the percentage of a component's input that passes through a donor compartment on its way to the recipient compartment, over all possible pathways (Table 10). For example, 85% of the carbon ingestion of protozoans passed through small phytoplankton before reaching the protozoans (Table 10a). Diagonal elements represent the amount of carbon that passed through the same compartment earlier, cycled through the food web and was returned to the compartment. The small phytoplankton and large phytoplankton columns are filled with zeros because the input of carbon is an external flow and is not supplied by recycling of carbon within the food web. This is a reasonable assumption for carbon models because carbon is not a limiting nutrient for phytoplankton in the ocean.

The protozoan carbon diet depends heavily on small phytoplankton with 85% of their input passing through them (Table 10a). Protozoans depend on bacteria for 28% of their carbon diet, which they mostly consume directly. Large phytoplankton have a significant indirect effect on the protozoan carbon diet equal to a 15% dependency, even though large phytoplankton are too large for them to consume directly. Microzooplankton depend heavily on large and small phytoplankton for 55 and 45% of their diet, as shown previously in the summary of the carbon flows (Table 5) and in the

Table 10a. Dependency coefficients for the NABE carbon inverse solution. The fraction of the total ingestion by a component j (column designation) that passes through a component i (row designation) on its way to component j. Network Analysis program, NETWRK.exe by Ulanowicz(1986) provided the values shown. For example, 85 % of the input to protozoans is mediated by small phytoplankton.

	Entering							
Leaving	Small Phytoplankton	Large Phytoplankton	Protozoans	Microzooplankton	Mesozooplankton	Bacteria	Detritus	DOC
Small Phytoplankton	0.00	0.00	0.85	0.45	0.28	0.47	0.39	0.47
Large Phytoplankton	0.00	0.00	0.15	0.55	0.72	0.53	0.60	0.53
Protozoans	0.00	0.00	0.06	0.04	0.27	0.20	0.20	0.20
Microzooplankton	0.00	0.00	0.07	0.03	0.15	0.27	0.31	0.27
Mesozooplankton	0.00	0.00	0.01	0.01	0.00	0.05	0.07	0.05
Bacteria	0.00	0.00	0.28	0.12	0.09	0.30	0.40	0.30
Detritus	0.00	0.00	0.05	0.02	0.02	0.17	0.07	0.17
DOC	0.00	0.00	0.28	0.12	0.09	1.00	0.40	0.30

Table 10b. Dependency coefficients for the NABE nitrogen inverse solution. The fraction of the total ingestion by a component j (column designation) that passes through a component i (row designation) on its way to component j. For example, 40 % of the input to protozoans is mediated by large phytoplankton. Network Analysis program, NETWRK.exe by Ulanowicz(1986) provided the values shown.

	Entering								
Leaving	Large Phytoplankton	Small Phytoplankton	Protozoans	Microzooplankton	Mesozooplankton	Bacteria	NH4	DON	Detritus
Large Phytoplankton	0.26	0.24	0.40	0.63	0.74	0.61	0.58	0.63	0.64
Small Phytoplankton	0.30	0.29	0.85	0.64	0.54	0.66	0.68	0.64	0.64
Protozoans	0.23	0.22	0.30	0.30	0.44	0.42	0.52	0.34	0.37
Microzooplankton	0.26	0.24	0.35	0.32	0.36	0.50	0.58	0.44	0.47
Mesozooplankton	0.12	0.11	0.15	0.14	0.15	0.20	0.27	0.15	0.18
Bacteria	0.31	0.29	0.56	0.47	0.45	0.61	0.69	0.56	0.55
NH4	0.44	0.42	0.54	0.51	0.50	0.74	0.60	0.54	0.54
DON	0.25	0.24	0.46	0.39	0.37	0.82	0.56	0.46	0.45
Detritus	0.12	0.11	0.22	0.21	0.48	0.26	0.26	0.26	0.20

zooplankton diet composition (Figure 15). Bacteria are the next most significant contributor to the microzooplankton diet accounting for 12%. Protozoans, mesozooplankton, and detritus each contribute less than 5% of the microzooplankton, diet either directly or indirectly.

Mesozooplankton depend on small phytoplankton for 28% of their carbon diet, even though they do not consume small phytoplankton directly (Table 10a). Bacteria depend on DOC for 100% of their diet, because all of their carbon ingestion comes from the DOC pool. Bacteria depend indirectly on small phytoplankton for 47% of their diet and large phytoplankton for 53% of their diet. This DOC from the primary producers comes from direct release and sloppy feeding. Bacteria depend on microzooplankton the most of the zooplankton, which indirectly account for 27% of their diet. Protozoans also contribute a significant portion of the bacteria carbon diet, equal to 20%. The detrital pool depends on all of the other components for significant contributions. The mesozooplankton contribute just 7% of the input but this contribution represents zooplankton fecal pellets, which sink quickly out of the surface ocean. The DOC pool receives contributions making up at least 20% of its diet from each of the other components, except for mesozooplankton and detritus. The diagonal elements in Table 10a are in most cases less than 10% indicating very low recycling of carbon. This is another result of the recycling flows for carbon not being modeled, except for recycling through the DOC and detritus pools. The bacteria and DOC diagonal elements are each 30%, indicating recycling of carbon through these components.

Large dependencies can be found throughout the dependency matrix for the nitrogen solution (Table 10b), indicating active recycling of nitrogen in the food web. All nitrogen components rely significantly on bacteria, which mediate at least 30% of each component's diet (Table 10b). Also, all components are very dependent upon the NH_4 pool, resulting in dependency coefficients no less than 0.4. The large phytoplankton depended upon the NH_4 pool for 44% of their nitrogen input. This agrees closely with the calculated f-ratio above of 0.57 that indicated 57% of the primary production was equal to new production and 43% regenerated production, fueled by NH_4. Large phytoplankton were dependent upon bacteria next, which mediate 31% of their nitrogen input. Small phytoplankton mediate 30% of the large phytoplankton nitrogen input. The small phytoplankton rely on the NH_4 pool for 42% of their nitrogen input. This also agrees closely with the f-ratio calculated earlier. Bacteria mediate 29% of the small phytoplankton's nitrogen input.

The effective trophic levels of the carbon and nitrogen components show similarities for the mesozooplankton and differences for the protozoans and microzooplantkon (Table 11). Due to the simplified nature of the model food web, no consumer has a trophic level of 3 or more. The primary producers, and nonliving components including DOC and detritus, are assigned trophic levels of 1 in the carbon solution. In the nitrogen solution, the small and large phytoplankton have trophic levels greater than 1, because the uptake of NH_4 is modeled and NH_4 has a trophic level equal to 1. The bacteria have a trophic level of 2, because their diet comes entirely from DOC or DON with a trophic level of 1. In both the carbon and nitrogen solution, the mesozooplankton ingest herbivores and large phytoplankton in an equal amount, giving

Table 11. Effective trophic level of the components in the NABE carbon and nitrogen models, found using the network analysis program, NETWRK.exe by Ulanawicz (1986). The nonliving components, DOC, DON, NH_4 and Detritus are assigned trophic levels of 1.

	Effective Trophic Level	
Component	Carbon	Nitrogen
Small Phytoplankton	1	1.42
Large Phytoplankton	1	1.44
Protozoans	2.28	2.6
Microzooplankton	2.14	2.56
Mesozooplankton	2.49	2.51
Bacteria	2	2
DOC / DON	1	1
Detritus	1	1
NH_4	-	1

them trophic levels of 2.49 and 2.51 for the carbon and nitrogen solutions, respectively. The mesozooplankton trophic level equal to 2.51 agrees closely with its carbon trophic level of 2.49. The protozoans and microzooplantkon have carbon trophic levels close to 2, indicating they mainly act as herbivores. In the nitrogen solution, their trophic levels are each above 2.5, indicating they act as carnivores more often than herbivores. For the protozoans, this increase is entirely the result of the increase of protozoan bacterivory and a decrease in grazing of phytoplankton in the nitrogen solution vs. the carbon solution. For microzooplankton, the increase is largely due to the increase in microzooplankton bacterivory and also to a small increase in the consumption of protozoans in the nitrogen solution.

Sensitivity Analysis

The input parameters to the carbon and nitrogen models were successively varied by + and – 10% and the inverse solution was recalculated for each change to assess the sensitivity of the model. The input parameters that had the greatest effect on the carbon solution were the net large and small primary production (Figure 15), and microzooplankton grazing (Figure 16). Each of these brought about changes greater than 10% in between 11 and 13 of the 36 total food web flows (Tables 12 and 13). The flows that were the most sensitive to changes in the input parameters were small phytoplankton to detritus and the mesozooplankton consumption of microzooplankton. Small phytoplankton to detritus increased 450% with an increase in 10% on the net small primary production and decreased to 0 with a decrease of 10% in the net small primary production (Figure 15). Mesozooplankton consumption of microzooplankton increased

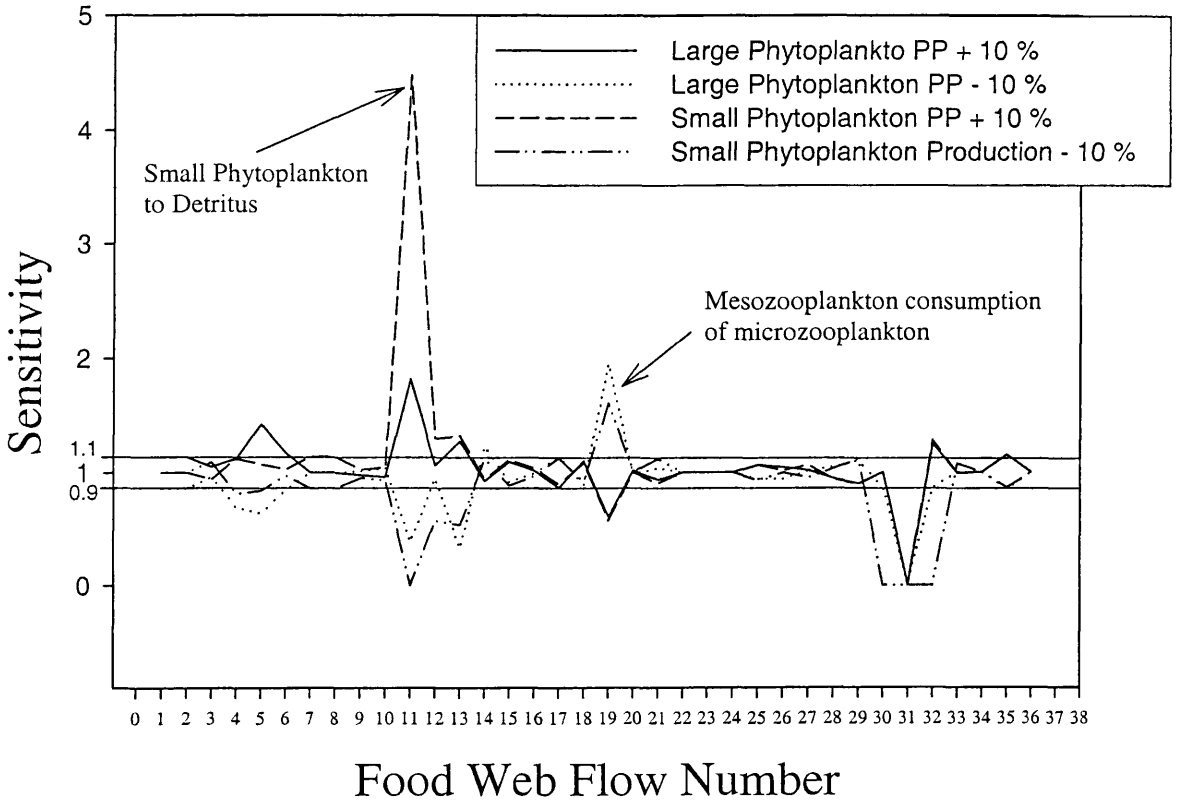


Figure 15. Sensitivity analysis for changes in the input parameters: large and small phytoplankton production in the North Atlantic carbon model. The input parameters, representing measurements, were varied by + and - 10 %, individually. The response of the food web flow is the new value resulting from the +/- 10 % change in the input parameter divided by the original value of the flow. Food web flow numbers are described in Tables 12 and 13.

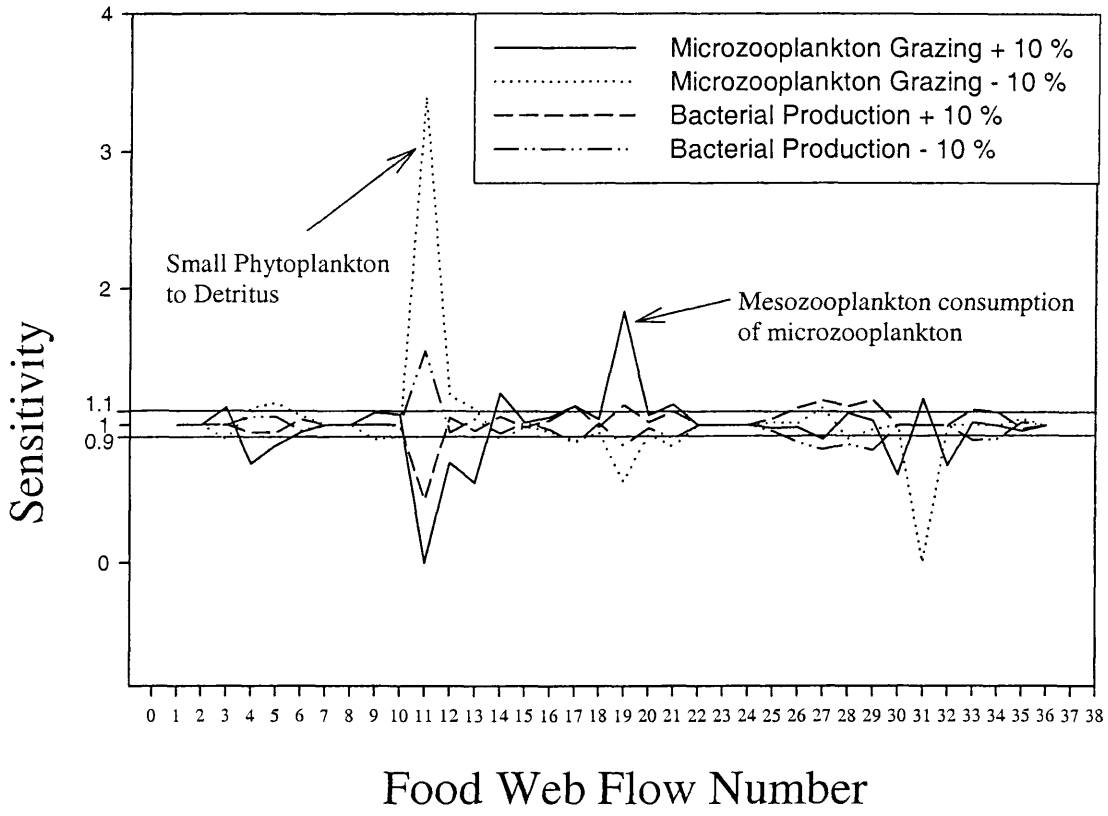


Figure 16. Sensitivity analysis for changes in the input parameters: microzooplankton grazing and bacterial production in the North Atlantic carbon model. The input parameters, representing measurements, were varied by + and - 10 %, individually. The response of the food web flow is the new value resulting from the +/- 10 % change in the input parameter divided by the original value of the flow. Food web flow numbers are described in Tables 12 and 13.

Table 12. Sensitivity Analysis with change in input parameters by + 10 %. The ratio shown is the model flow with the 10 % change in the input parameter divided by the original model flow. A '+' before a value indicates the value was 0 in the original solution and increased to the # mmols C $m^{-2}d^{-1}$ shown.

Flow #		Net Large Primary Production	Net Small Primary Production	Minimum Export Constraint	Maximum Export Constraint	Bacterial Production	Bacterial Biomass	Microzooplankton Biomass	Microzooplankton Feeding	Temperature	Change in Bacterial Biomass	Change in Microzooplankton Biomass	Mesozooplankton grazing
1	Large phytoplankton gross primary production	1.14	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
2	Large phytoplankton respiration	1.14	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
3	Microzooplankton grazing of large phytoplankton	1.05	0.94	1.00	1.00	1.00	1.00	1.00	1.13	1.00	1.00	1.00	1.00
4	Mesozooplankton grazing of large phytoplankton	1.12	1.12	1.00	1.00	0.94	1.00	1.00	0.72	1.00	0.98	1.03	1.00
5	Large phytoplankton sinking	1.42	1.07	1.00	1.00	0.94	1.00	1.00	0.85	1.00	0.99	0.98	1.00
6	Large phytoplankton release of DOC	1.17	1.03	1.00	1.00	1.04	1.00	1.00	0.95	1.00	1.01	1.00	1.00
7	Small phytoplankton gross primary production	1.00	1.14	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
8	Small phytoplankton respiration	1.00	1.14	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
9	Protozoan grazing of small phytoplankton	0.98	1.03	1.00	1.00	1.00	1.00	1.00	1.09	1.00	1.00	0.99	1.00
10	Microzooplankton grazing of small phytoplankton	0.96	1.05	1.00	1.00	1.00	1.00	1.00	1.08	1.00	1.00	1.01	1.00
11	Small phytoplankton to detritus	1.82	4.48	1.00	1.00	0.46	1.00	1.00	0.00	1.00	0.86	0.98	1.00
12	Small phytoplankton release of DOC	1.06	1.30	1.00	1.00	1.05	1.00	1.00	0.73	1.00	1.01	1.01	1.00
13	Microzooplankton consumption of protozoans	1.27	1.32	1.00	1.00	0.96	1.00	1.00	0.58	1.00	0.96	1.02	1.00
14	Mesozooplankton consumption of protozoans	0.92	0.94	1.00	1.00	1.06	1.00	1.00	1.23	1.00	1.01	0.98	1.00
15	Protozoan respiration	1.09	1.11	1.00	1.00	0.98	1.00	1.00	1.02	1.00	0.98	0.98	1.00
16	Protozoans to detritus	1.02	1.04	1.00	1.00	1.03	1.00	1.00	1.06	1.00	1.00	0.99	1.00
17	Protozoans to DOC	0.86	0.90	1.00	1.00	1.13	1.00	1.00	1.14	1.00	1.04	1.01	1.00
18	Microzooplankton respiration	1.10	1.08	1.00	1.00	0.98	1.00	1.00	1.04	1.00	0.98	0.96	1.00
19	Mesozooplankton consumption of microzooplankton	0.60	0.57	1.00	1.00	1.15	1.00	1.00	1.83	1.00	1.05	0.91	1.00
20	Microzooplankton to detritus	1.02	1.00	1.00	1.00	1.02	1.00	1.00	1.07	1.00	1.00	1.01	1.00
21	Microzooplankton to DOC	0.93	0.90	1.00	1.00	1.10	1.00	1.00	1.15	1.00	1.03	0.97	1.00
22	Mesozooplankton respiration	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
23	Mesozooplankton to detritus (Faecal pellets)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
24	Mesozooplankton to DOC	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
25	Bacterial respiration	1.06	1.06	1.00	1.00	1.05	1.00	1.00	0.98	1.00	1.01	0.99	1.00
26	Bacteria to protozoans	1.04	1.02	1.00	1.00	1.13	1.00	1.00	0.98	1.00	1.00	0.99	1.00
27	Bacteria to microzooplankton	1.02	1.06	1.00	1.00	1.18	1.00	1.00	0.90	1.00	1.00	1.04	1.00
28	Bacteria to detritus	0.95	0.94	1.00	1.00	1.14	1.00	1.00	1.09	1.00	1.00	0.99	1.00
29	Bacteria to DOC	0.90	0.90	1.00	1.00	1.18	1.00	1.00	1.03	1.00	1.07	1.02	1.00
30	Protozoan consumption of detritus	+ 0.38	+ 0.28	1.00	1.00	1.00	1.00	1.00	0.64	1.00	0.89	1.01	1.00
31	Microzooplankton consumption of detritus	0.00	0.00	1.00	1.00	1.00	1.00	1.00	1.19	1.00	0.00	0.00	1.00
32	Mesozooplankton consumption of detritus	1.25	1.28	1.00	1.00	1.00	1.00	1.00	0.71	1.00	0.79	0.89	1.00
33	Detritus to DOC	0.99	0.99	1.00	1.00	1.11	1.00	1.00	1.02	1.00	1.03	1.01	1.00
34	Bacterial ingestion of DOC	1.00	1.00	1.00	1.00	1.10	1.00	1.00	1.00	1.00	1.03	1.00	1.00
35	Total Particulate Export out of the top 35 m	1.15	1.15	1.00	1.00	0.98	1.00	1.00	0.96	1.00	0.97	0.98	1.00
36	Mesozooplankton to export (Consumption by higher trophic levels or death)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 13. Sensitivity Analysis with change in input parameters by - 10 %. The ratio shown is the model flow with the 10 % change in the input parameter divided by the original model flow. A '+' before a value indicates the value was 0 in the original solution and increased to the # mmols of C $m^{-2}d^{-1}$ shown.

Flow #		Net Large Primary Production	Net Small Primary Production	Minimum Export Constraint	Maximum Export Constraint	Bacterial Production	Bacterial Biomass	Microzooplankton Biomass	Microzooplankton Feeding	Temperature	Change in Bacterial Biomass	Change in Microzooplankton Biomass	Mesozooplankton grazing
1	Large phytoplankton gross primary production	0.86	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
2	Large phytoplankton respiration	0.86	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
3	Microzooplankton grazing of large phytoplankton	0.96	1.09	1.00	1.00	1.00	1.00	1.00	0.89	1.00	1.00	1.00	1.00
4	Mesozooplankton grazing of large phytoplankton	0.69	0.82	1.00	1.00	1.06	1.00	1.00	1.12	1.00	1.02	0.97	1.00
5	Large phytoplankton sinking	0.64	0.84	1.00	1.00	1.06	1.00	1.00	1.16	1.00	1.01	1.02	1.00
6	Large phytoplankton release of DOC	0.85	0.98	1.00	1.00	0.96	1.00	1.00	1.07	1.00	0.99	1.00	1.00
7	Small phytoplankton gross primary production	1.00	0.86	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
8	Small phytoplankton respiration	1.00	0.86	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
9	Protozoan grazing of small phytoplankton	1.01	0.95	1.00	1.00	1.00	1.00	1.00	0.89	1.00	1.00	1.01	1.00
10	Microzooplankton grazing of small phytoplankton	1.04	0.93	1.00	1.00	1.00	1.00	1.00	0.91	1.00	1.00	0.99	1.00
11	Small phytoplankton to detritus	0.39	0.00	1.00	1.00	1.54	1.00	1.00	3.40	1.00	1.14	1.02	1.00
12	Small phytoplankton release of DOC	0.95	0.57	1.00	1.00	0.95	1.00	1.00	1.21	1.00	0.99	0.99	1.00
13	Microzooplankton consumption of protozoans	0.33	0.53	1.00	1.00	1.04	1.00	1.00	1.12	1.00	1.04	0.98	1.00
14	Mesozooplankton consumption of protozoans	1.23	1.12	1.00	1.00	0.94	1.00	1.00	0.89	1.00	0.99	1.02	1.00
15	Protozoan respiration	0.92	0.88	1.00	1.00	1.02	1.00	1.00	0.99	1.00	1.02	1.02	1.00
16	Protozoans to detritus	0.99	0.96	1.00	1.00	0.97	1.00	1.00	0.95	1.00	1.00	1.01	1.00
17	Protozoans to DOC	1.14	1.13	1.00	1.00	0.87	1.00	1.00	0.88	1.00	0.96	0.99	1.00
18	Microzooplankton respiration	0.89	0.91	1.00	1.00	1.02	1.00	1.00	0.95	1.00	1.02	1.04	1.00
19	Mesozooplantkton consumption of microzooplankton	1.95	1.61	1.00	1.00	0.85	1.00	1.00	0.59	1.00	0.95	1.09	1.00
20	Microzooplankton to detritus	0.99	1.01	1.00	1.00	0.98	1.00	1.00	0.93	1.00	1.00	0.99	1.00
21	Microzooplankton to DOC	1.04	1.12	1.00	1.00	0.90	1.00	1.00	0.84	1.00	0.97	1.03	1.00
22	Mesozooplankton respiration	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
23	Mesozooplankton to detritus (Faecal pellets)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
24	Mesozooplankton to DOC	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
25	Bacterial respiration	0.94	0.93	1.00	1.00	0.95	1.00	1.00	1.02	1.00	0.99	1.01	1.00
26	Bacteria to protozoans	0.94	1.00	1.00	1.00	0.87	1.00	1.00	1.01	1.00	1.00	1.01	1.00
27	Bacteria to microzooplankton	1.01	0.95	1.00	1.00	0.82	1.00	1.00	1.12	1.00	1.00	0.96	1.00
28	Bacteria to detritus	1.05	1.03	1.00	1.00	0.86	1.00	1.00	0.90	1.00	1.00	1.01	1.00
29	Bacteria to DOC	1.10	1.11	1.00	1.00	0.82	1.00	1.00	0.97	1.00	0.93	0.98	1.00
30	Protozoan consumption of detritus	0.86	0.00	1.00	1.00	1.00	1.00	1.00	+ 0.457	1.00	1.12	0.95	1.00
31	Microzooplankton consumption of detritus	0.00	0.00	1.00	1.00	1.00	1.00	1.00	0.00	1.00	0.00	3.45	1.00
32	Mesozooplankton consumption of detritus	0.87	0.00	1.00	1.00	1.00	1.00	1.00	+ 0.055	1.00	0.97	1.04	1.00
33	Detritus to DOC	1.00	1.07	1.00	1.00	0.89	1.00	1.00	1.00	1.00	0.97	0.99	1.00
34	Bacterial ingestion of DOC	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00	1.00	0.97	1.00	1.00
35	Total Particulate Export out of the top 35 m	0.85	0.86	1.00	1.00	1.02	1.00	1.00	1.05	1.00	1.03	1.02	1.00
36	Mesozooplankton to export (Consumption by higher trophic levels or death)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

95% with a decrease of 10% in the net large primary production and decreased by about 40% with increases in both the net small and large primary production (Figure 15). Changes in the input parameters also brought about the consumption of detritus in some cases. In the original solution the consumption of detritus by all three zooplankton size classes was zero. However, with a 10% decrease in the microzooplankton feeding, the protozoans consumed 0.46 mmols $Cm^{-2}d^{-1}$ and the mesozooplankton 0.055 mmols $Cm^{-2}d^{-1}$ (Figure 16 and Table 13). With the increases in the net small and large primary production, the protozoans consumed 0.28 and 0.38 mmols $Cm^{-2}d^{-1}$ of detritus, respectively (Figure 15 and Table 12).

In the nitrogen solution, the input parameters that showed the greatest effects on the flows were the change in microzooplankton biomass, and the small and large regenerated production. Manipulations of + and – 10% in the change in microzooplankton biomass, brought about changes greater than 10% in 10 of the total 36 flows (Figure 17, Tables 14 and 15). Changes in the small and large regenerated production, triggered changes greater than 10% in 4 of the flows (Figure 18, Tables 14 and 15). The flows that were the most sensitive were the microzooplankton consumption of protozoans and detritus. The microzooplankton consumption of protozoans increased 101% with a 10% increase in the change in microzooplankton biomass and decreased to 0 with a 10% decrease (Figure 17). The microzooplankton consumption of detritus increased 50% with a 10% increase in the change in microzooplankton biomass and decreased 50% with a decrease. There were much fewer changes greater than 10% in the flows for the nitrogen sensitivity analysis than for the carbon sensitivity analysis.

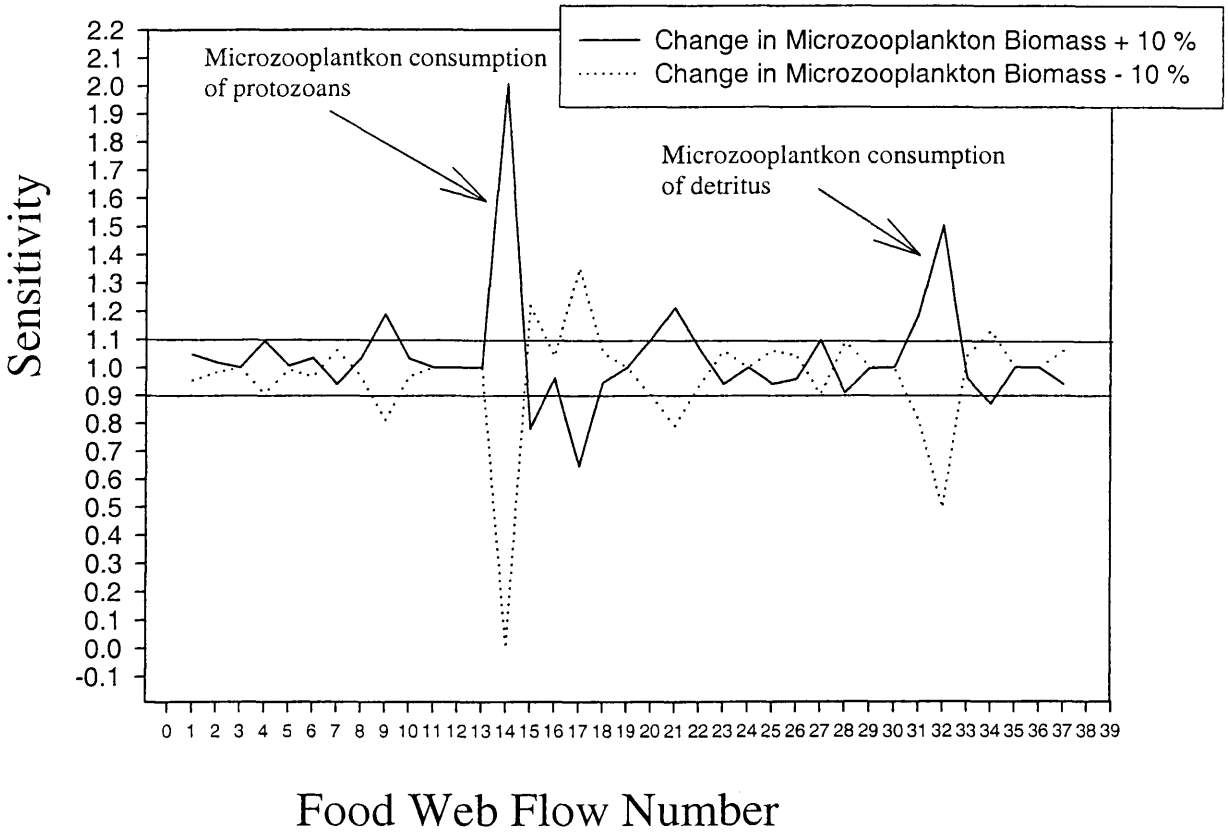


Figure 17. Sensitivity analysis for changes in the input parameter, change in microzooplankton biomass in the North Atlantic nitrogen model. The input parameters, representing measurements, were varied by + and - 10 %, individually. The response of the food web flow is the new value resulting from the +/- 10 % change in the input parameter divided by the original value of the flow. Food web flow numbers are described in Tables 14 and 15.

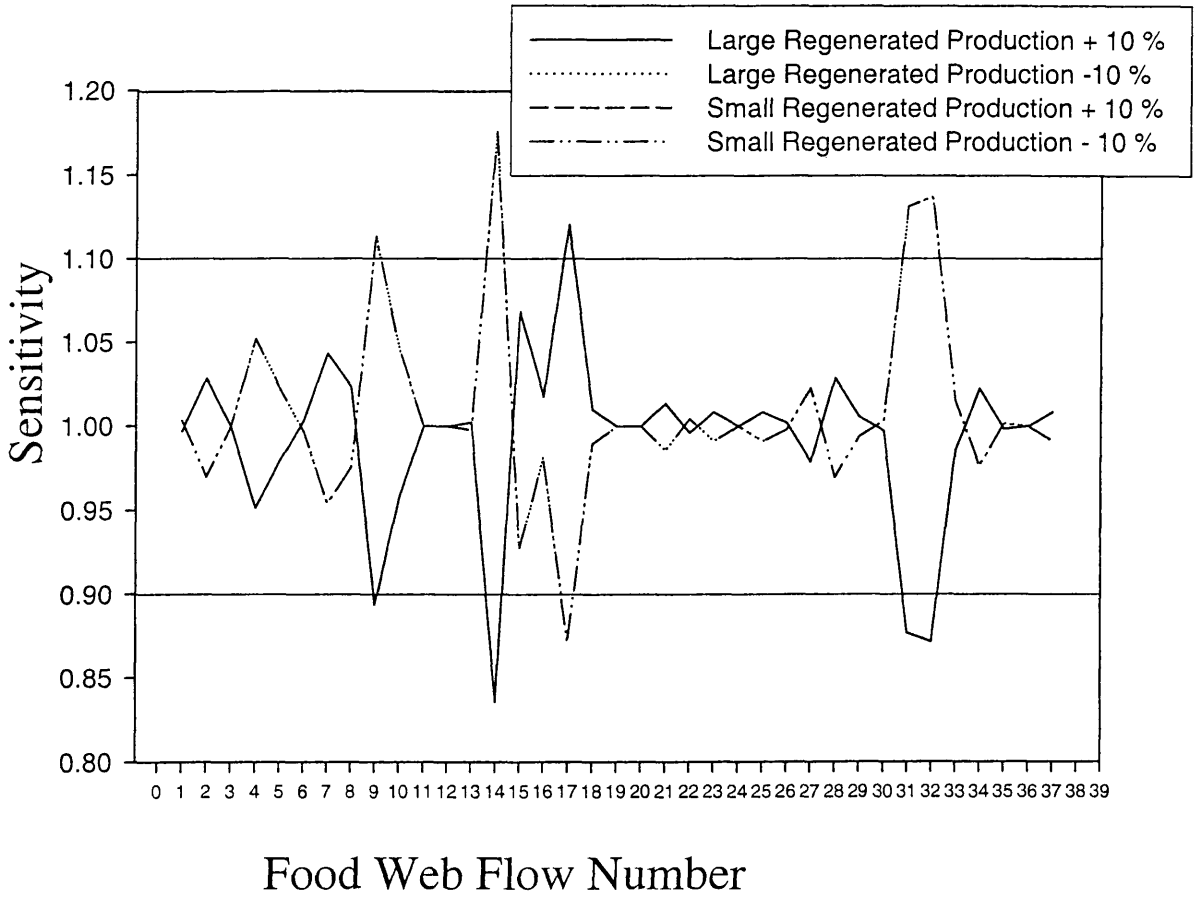


Figure 18. Sensitivity analysis for changes in the input parameters: large and small phytoplankon regenerated production in the North Atlantic nitrogen model. The input parameters, representing measurements, were varied by + and - 10 %, individually. The response of the food web flow is the new value resulting from the +/- 10 % change in the input parameter divided by the original value of the flow. Food web flow numbers are described in Tables 14 and 15.

Table 14. Sensitivity Analysis for the nitrogen inverse solution with changes in input parameters by + 10 %.
The ratio shown is the model flow resulting from the 10 % change in the input parameter divided by the original model flow.
A '+' before a value indicates the value was 0 in original solution and increased to the # mmols C $m^{-2}d^{-1}$ shown.

						Input Parameters									
Flow #	Food web Flow	Small New Production	Large New Production	Large Regenerated Production	Small Regenerated Production	Minimum Export Constraint	Maximum Export Constraint	Bacterial Production	Bacterial Biomass	Microzooplankton Grazing	Mesozooplankton g	Temperature	Change in Bacterial Biomass	Change in Microzooplankton Biomass	Change in NH4 Pool
1	Large phytoplankton new production	1.00	1.00	1.00	1.00	1.03	1.00	1.00	1.00	1.00	1.00	1.00	1.03	1.05	1.00
2	Microzooplankton grazing of large phytoplankton	1.02	1.02	1.03	1.03	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.02	1.00
3	Mesozooplankton grazing of large phytoplankton	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
4	Large phytoplankton sinking	0.97	0.97	0.95	0.95	1.06	1.00	1.00	1.00	1.00	1.00	1.00	1.04	1.09	1.00
5	Large phytoplankton release of DON	0.99	0.99	0.98	0.98	1.02	1.00	1.00	1.00	1.00	1.00	1.00	1.04	1.01	1.00
6	Small phytoplankton new production	1.00	1.00	1.00	1.00	1.03	1.00	1.00	1.00	1.00	1.00	1.00	1.03	1.03	1.00
7	Protozoan grazing of small phytoplankton	1.03	1.03	1.04	1.04	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.94	1.00
8	Microzooplankton grazing of small phytoplankton	1.01	1.01	1.02	1.02	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.03	1.00
9	Small phytoplankton to detritus	0.94	0.94	0.89	0.89	1.10	1.00	1.00	1.00	1.00	1.00	1.00	1.06	1.19	1.00
10	Small phytoplankton release of DON	0.97	0.97	0.96	0.96	1.03	1.00	1.00	1.00	1.00	1.00	1.00	1.05	1.03	1.00
11	Small phytoplankton regenerated production	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
12	Large phytoplankton regenerated production	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
13	Bacterial uptake of NH4	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.04	1.00	1.00
14	Microzooplankton consumption of protozoans	0.90	0.90	0.84	0.84	1.03	1.00	1.00	1.00	1.00	1.00	1.00	0.95	2.01	1.00
15	Mesozooplankton consumption of protozoans	1.04	1.04	1.07	1.07	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.78	1.00
16	Protozoans to detritus	1.01	1.01	1.02	1.02	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.01	0.96	1.00
17	Protozoans to DON	1.07	1.07	1.12	1.12	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.01	0.65	1.00
18	Protozoans to NH4	1.01	1.01	1.01	1.01	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.02	0.95	1.00
19	Mesozooplantkton consumption of microzooplankto	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
20	Microzooplankton to detritus	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00
21	Microzooplankton to DON	1.01	1.01	1.01	1.01	0.99	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1.21	1.00
22	Microzooplankton to NH4	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01	1.07	1.00
23	Mesozooplankton to detritus (Fecal pellets)	1.01	1.01	1.01	1.01	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.01	0.94	1.00
24	Mesozooplankton to DON	1.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
25	Mesozooplankton to NH4	1.01	1.01	1.01	1.01	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.01	0.94	1.00
26	Protozoan consumption of bacteria	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01	0.96	1.00
27	Microzooplankton consumption of bacteria	0.99	0.99	0.98	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00
28	Bacteria to detritus	1.02	1.02	1.03	1.03	1.01	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.91	1.00
29	Bacteria to DON	1.00	1.00	1.01	1.01	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.04	1.00	1.00
30	Bacteria to NH4	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.03	1.00	1.00
31	Protozoan consumption of detritus	0.93	0.93	0.88	0.88	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.08	1.19	1.00
32	Microzooplankton consumption of detritus	0.92	0.92	0.87	0.87	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.02	1.50	1.00
33	Mesozooplankton consumption of detritus	0.99	0.99	0.99	0.99	0.97	1.00	1.00	1.00	1.00	1.00	1.00	1.03	0.96	1.00
34	Detritus to DON	1.01	1.01	1.02	1.02	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.04	0.87	1.00
35	Bacterial ingestion of DON	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.03	1.00	1.00
36	Total Particulate Export out of the top 35 m	1.00	1.00	1.00	1.00	1.10	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
37	Mesozooplankton to export (Consumption by higher trophic levels or death)	1.01	1.01	1.01	1.01	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.01	0.94	1.00

Table 15. Sensitivity Analysis for the nitrogen inverse solution with changes in input parameters by - 10 %.
The ratio shown is the model flow resulting from the 10 % change in the input parameter divided by the original model flow.
A '+' before a value indicates the value was 0 in original solution and increased to the # mmols C $m^{-2}d^{-1}$ shown.

Flow #	Food web Flow	Small New Production	Large New Production	Large Regenerated Production	Small Regenerated Production	Minimum Export Constraint	Maximum Export Constraint	Bacterial Production	Bacterial Biomass	Microzooplankton Grazing	Mesozooplankton grazing	Temperature	Change in Bacterial Biomass	Change in Microzooplankton Biomass	Change in NH4 Pool
1	Large phytoplankton new production	1.00	1.00	1.00	1.00	0.97	1.00	1.00	1.00	1.00	1.00	1.00	0.97	0.95	1.00
2	Microzooplankton grazing of large phytoplankton	0.98	0.98	0.97	0.97	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1.00
3	Mesozooplankton grazing of large phytoplankton	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
4	Large phytoplankton sinking	1.03	1.03	1.05	1.05	0.94	1.00	1.00	1.00	1.00	1.00	1.00	0.96	0.91	1.00
5	Large phytoplankton release of DON	1.01	1.01	1.02	1.02	0.98	1.00	1.00	1.00	1.00	1.00	1.00	0.96	0.99	1.00
6	Small phytoplankton new production	1.00	1.00	1.00	1.00	0.97	1.00	1.00	1.00	1.00	1.00	1.00	0.97	0.97	1.00
7	Protozoan grazing of small phytoplankton	0.97	0.97	0.95	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.06	1.00
8	Microzooplankton grazing of small phytoplankton	0.99	0.99	0.98	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.97	1.00
9	Small phytoplankton to detritus	1.06	1.06	1.11	1.11	0.90	1.00	1.00	1.00	1.00	1.00	1.00	0.94	0.81	1.00
10	Small phytoplankton release of DON	1.03	1.03	1.05	1.05	0.97	1.00	1.00	1.00	1.00	1.00	1.00	0.95	0.97	1.00
11	Small phytoplankton regenerated production	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
12	Large phytoplankton regenerated production	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
13	Bacterial uptake of NH4	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.96	1.00	1.00
14	Microzooplankton consumption of protozoans	1.10	1.10	1.18	1.18	0.97	1.00	1.00	1.00	1.00	1.00	1.00	1.05	0.00	1.00
15	Mesozooplankton consumption of protozoans	0.96	0.96	0.93	0.93	1.01	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.22	1.00
16	Protozoans to detritus	0.99	0.99	0.98	0.98	1.01	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.04	1.00
17	Protozoans to DON	0.93	0.93	0.87	0.87	1.05	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.35	1.00
18	Protozoans to NH4	0.99	0.99	0.99	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1.05	1.00
19	Mesozooplantkton consumption of microzooplankton	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
20	Microzooplankton to detritus	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00
21	Microzooplankton to DON	0.99	0.99	0.99	0.99	1.01	1.00	1.00	1.00	1.00	1.00	1.00	1.02	0.79	1.00
22	Microzooplankton to NH4	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.93	1.00
23	Mesozooplankton to detritus (Fecal pellets)	1.00	1.00	0.99	0.99	1.01	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.06	1.00
24	Mesozooplankton to DON	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
25	Mesozooplankton to NH4	1.00	1.00	0.99	0.99	1.01	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.06	1.00
26	Protozoan consumption of bacteria	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.04	1.00
27	Microzooplankton consumption of bacteria	1.01	1.01	1.02	1.02	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00
28	Bacteria to detritus	0.98	0.98	0.97	0.97	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.01	1.09	1.00
29	Bacteria to DON	1.00	1.00	0.99	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.96	1.00	1.00
30	Bacteria to NH4	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.97	1.00	1.00
31	Protozoan consumption of detritus	1.07	1.07	1.13	1.13	1.05	1.00	1.00	1.00	1.00	1.00	1.00	0.92	0.81	1.00
32	Microzooplankton consumption of detritus	1.08	1.08	1.14	1.14	1.02	1.00	1.00	1.00	1.00	1.00	1.00	0.98	0.50	1.00
33	Mesozooplankton consumption of detritus	1.01	1.01	1.02	1.02	1.03	1.00	1.00	1.00	1.00	1.00	1.00	0.97	1.04	1.00
34	Detritus to DON	0.99	0.99	0.98	0.98	1.05	1.00	1.00	1.00	1.00	1.00	1.00	0.96	1.13	1.00
35	Bacterial ingestion of DON	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.97	1.00	1.00
36	Total Particulate Export out of the top 35 m	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
37	Mesozooplankton to export (Consumption by higher trophic levels or death)	1.00	1.00	0.99	0.99	1.01	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.06	1.00

Discussion

The largest flow in each model was the consumption of dissolved organic matter. Bacteria consumed 65% of the carbon primary production as DOC and 55% of the nitrogen primary production as DON. Microzooplankton and protozoan grazing dominated in both the carbon and nitrogen solutions. Microzooplankton grazed 43% of the carbon primary production and 40% of the total nitrogen primary production. Protozoans grazed 21% of the carbon primary production and 17% of the total nitrogen primary production. Mesozooplankton grazed a much smaller proportion, 5% of both the carbon and nitrogen primary production.

Recycling was important in the North Atlantic food web. The indices of recycling, **L** = 2.4 for carbon and **L** = 7.2 for nitrogen indicated that carbon and nitrogen atoms were actively recycled in the food web. The **Total ingestion / PP** for carbon and nitrogen revealed that 60% of the carbon ingestion and 150% of the nitrogen ingestion were provided by recycling. The higher indices are seen in the nitrogen solution, where metabolic products are recycled rather than respired. In the carbon solution, respired carbon goes to an infinite sink and is not recycled. The high dependency coefficients found for almost all the components in the nitrogen solution (Table 10b) are also indicative of high recycling.

Detritus was less important in these solutions than DOC. The throughput was 24% of net carbon primary production vs. 74% for DOC and 32% of total nitrogen primary production vs. 55% for DON, indicating a system dominated by DOC and DON. The results are similar to measurements of the activity of DOC in the Sargasso Sea, a

subtropical, low nutrient region, where the accumulation of DOC during blooms made up 86% of the total organic carbon, while particulate organic carbon or detritus accounted for 14% (Carlson et al., 1998). Even though the productivity is normally higher in the North Atlantic than the Sargasso Sea, the NABE models suggest the production and cycling of DOC is high in North Atlantic blooms also.

After bacteria, the microzooplankton and protozoans were the most active processors of carbon and nitrogen. Microzooplankton and protozoans were important in the sensitivity analysis, where changes in the microzooplankton grazing (including protozoan grazing) and in the observed increase in microzooplankton biomass brought about many significant changes in the estimated food web flows. Microzooplankton have been shown to be significant grazers in the ocean, passing organic matter up the food web and recycling nutrients for primary producers (Landry et al., 1982; Gaul et al., 1999; Verity et al., 1985). Researchers at 47°N, 20°W did witness a very active microzooplankton community at times consuming up to 100% of the primary production (Verity, 1993). This high degree of grazing is not uncommon. Measurements of microzooplankton grazing in the equatorial pacific showed that microzooplankton balanced primary production by pyrmesiophytes, and consumed a high proportion of the picoplankton production (Verity et al., 1996).

The contribution to export by mesozooplankton fecal pellets in the model was only 3% of the carbon net primary production and 1% of the nitrogen primary production. Dam et al. (1993) found mesozooplankton fecal pellets were less than 5% of the particulate organic carbon flux at 47°N, 20°W. The modeled mesozooplankton export

was 8% of the particulate carbon flux in the carbon inverse solution, slightly higher than the findings by Dam et al. (1993). The modeled nitrogen export was consistent with the carbon solution and equal to 8% of the particulate nitrogen flux. Lenz et al. (1993), who found no ungrazed phytoplankton in sediment traps at 46° N, 19° W in May, 1989 and estimated much higher grazing rates than Dam, concluded that zooplankton fecal pellets dominated the particle flux. Lenz found a mesozooplankton biomass of 313 mg $Cm^{-2}d^{-1}$, much higher than the biomass of 90 mmols $Cm^{-2}d^{-1}$ found by Dam at 47°N, 20°W. There was a difference in the study area (i.e. different water mass), but also Dam and Lenz made very different assumptions in their calculations of the impact of mesozooplankton. Dam estimated mesozooplankton grazing using copepod gut pigment and gut fluorescence anlalyses, while Lenz used mesozooplantkon biomass and respiration measurements along with an assumption that during bloom conditions, mesozooplankton respiration was equal to 1/3 of ingestion. Lenz assumed that mesozooplankton only ingested phytoplankton. Dam estimated that about 50% of the mesozooplankton ingestion was from phytoplankton, by comparing measured nitrogen excretion rates with daily ingestion of carbon and nitrogen. Lenz admitted that the ingestion of microzooplankton and detritus would have decreased their grazing estimates. The effective trophic levels of mesozooplantkon in the carbon and nitrogen inverse model solutions (Table 11) agree with Dam's conclusions about the mesozooplankton diet and suggest that the mesozooplankton received 50% of their diet from phytoplankton and the remaining food from microzooplankton and detritus (nitrogen solution only). It is likely that Lenz's estimates of mesozooplankton grazing and contributions to the export flux were overestimated.

The differences between the export ratios and f-ratios calculated from the models suggest a very different view of export than the traditional view of export equaling new production. The export ratios from the carbon and nitrogen solutions were very similar: 0.19 and 0.17. The f-ratio calculated from the nitrogen solution was 0.57. The much lower export ratios indicate that much of the new production was not exported during May 18- 31, but remained in the food web. Garside and Garside (1993) modeled the seasonal new production in the North Atlantic using measurements of nitrate from the NABE study and historical data of deep-water nitrate concentrations and mixed layer depths. They concluded that the new production is not immediately exported during the bloom, but may be incorporated into the food web and recycled during the year. In the models, increases in the components and the flows of matter through the recycling pools balanced the difference between the f-ratio and e-ratios. Carbon and nitrogen that was not exported remained in the system in a recycled form or went into the biomass of bacteria and microzooplakton. The Garside and Garside (1993) modeling study covered seasonal production, starting with the beginning of the bloom and ending in early June. The inverse model solutions for NABE covered just a 2-week period during the late bloom ending at the end of May. It is not surprising that the export was not equal to the new production in the inverse solutions, when they were not equal in a study encompassing the entire bloom period.

Chapter III. Western Antarctic Peninsula

Introduction

The western Antarctic Peninsula (WAP) has been intensely studied for the past 12 years (1990- 2002) under the leadership of the Long-Term Ecological Research Program (LTER). The LTER program was started by the National Science Foundation in 1980 in order to monitor and compare long-term ecological phenomena across different ecosystems and now includes 24 sites (LTER website: http://lternet.edu/, 2002). The research at WAP is led by the Palmer Long-Term Ecological Research program (PAL) and based out of Palmer Station, Antarctica. A central tenet of PAL is that the annual advance and retreat of sea ice drives changes in the structure and function of the food webs in the area (Smith et al., 1998). A sampling grid was set up by PAL, encompassing an area 900 km along the west coast of the Antarctic Peninsula by 200 km offshore (Smith et al., 1998). The research has included ten annual summer cruises (1993 – 2002) coincident with the Adélie penguin nesting period and five cruises investigating fall, winter, and spring processes. Also, weekly sampling was carried out each year, by zodiac between October/November and March/April, within a two-mile boundary of Palmer Station. The measurements taken at Palmer Station include: primary production, phytoplankton pigments, nutrient concentrations, sediment trap flux, bacterial abundance and production, krill biomass and reproduction, and penguin abundance and feeding (Smith et al., 1998).

The food web in the western Antarctica Peninsula (WAP) is very short with only a few links between primary producers and apex predators (Smith et al., 1998). The shortest path through the food web is from large autotrophs like diatoms to krill (*Euphausia superba*) to the apex predator, Adélie penguins (*Pygoscelis adeliae*). The other key apex predator is the south polar skua (*Catharacta maccormicki*) whose favored prey is silverfish *(Pleuragramma antarcticum*). Although short paths through the food web are available, the microbial loop is still present in the WAP as it is throughout the world's oceans (Smith et al., 1998; Karl et al. 1996). Microbial processes in the Southern Ocean are poorly understood, mainly because of the ever changing physical environment and the barriers to sampling presented by ice (Karl et al. 1996). During the RACER program, a previous study in the WAP, measurements during bloom conditions revealed an uncoupling between the bacteria and phytoplankton assemblages (Karl et al. 1996). The bacterial biomass and production remained very low relative to the phytoplankton biomass and production.

The western Antarctica Peninsula is characterized by two functional subdivisions, a highly productive Coastal and Continental Shelf Zone (CCSZ) and a productive Seasonal Ice Zone (SIZ) (Tréguer and Jacques, 1992; Smith et al., 1998). The CCSZ is the area close to the Peninsula that usually exhibits large blooms (Smith et al., 1998). The SIZ is the area of expanding and retreating ice that can overtake the CCSZ and modify the intensity of the blooms (Smith et al., 1998). The WAP is also characterized by two distinct climates: to the north a maritime climate of relatively warm moist air and to the south a continental climate of cool dry air (Smith et al., 1998). Through paleoecological and historical data Smith et al. (1998) show that the WAP region has

been warming rapidly over the last century, coincident with a shift in abundance and distribution of penguin species. The warming of 4 to 5 °C during midwinter observed over the last fifty years is believed to be responsible for a decline in Adélie penguins, monitored by William Fraser of Montanna State University (Kaiser, 1997). A decrease in frequency of heavy ice years, resulting from increasing temperatures is believed to be the main cause behind the large decline of over one third of the breeding pairs of Adélies from 1975 to 1997 (Kaiser, 1997). In addition, Fraser found Adélies abandoning nesting sites on the southwest sides of islands where snow accumulation was greatest, and believes it is possible that an increase in snowfall over the period contributed to the decline in Adélies (Kaiser, 1997). Increased precipitation is a consequence of climate warming. The historical record of snowfall in the WAP is too limited to make a conclusion but other regions in Antarctica have shown an increase in snowfall since 1975.

The inverse method can illuminate the many unknown flows within the plankton food web in the western Antarctic Peninsula. A better understanding of this food web will help answer questions like: "What are the relative roles of the short and microbial food webs?" and "What are the differences in the food web between a year of relatively high sea ice and high primary production and a year with relatively low sea ice and low primary production?". Answers to these questions are key to understanding the response of the food web to climate change.

Methods

The WAP measurements used for the model inputs were taken from the January cruises in 1996 and 1999 in the Palmer LTER regional grid (Figure 19) and from sampling near Palmer Station (Figure 20), also during January. January is a crucial time for Adélie penguin chick development and is coincident with the crèche period, when both parents leave the chicks on land and forage, doubling the food provided to the chicks (Salihoglu et al., 2000). Data for the models was taken from stations within the foraging area of the Adélie penguins (Figure 21). The sampling areas are defined by a circular area with its center on Anvers Island, the home of the local Adélie colony, and with a radius equal to the foraging distance of the adult Adélies. The back 1/3 of the circular area was not included in the sampling area because this area lies over land. The foraging distance was estimated from the measured durations of foraging trips, found with radio transmitters fixed to adult Adélies (Fraser pers.comm., 2003 and Salihoglu et al., 2000) and assuming an average swimming speed for Adélies (Fraser pers.comm., 2003 and Culik & Wilson, 1991). For the 1995-1996 field season, the maximum foraging range was 113 km and for the 1998-1999 field season, it was 208 km (Fraser, 2003 pers.comm.).

The basic carbon model components and the possible flow interconnections for the WAP are shown in Figure 1, for the general open ocean model. Carbon measurements were averaged over the month of January for both 1996 and 1999 to arrive at mean values to be used in the inverse analysis. Krill were the only mesozooplankton represented in the model because they are usually the dominant zoolplankton in the area

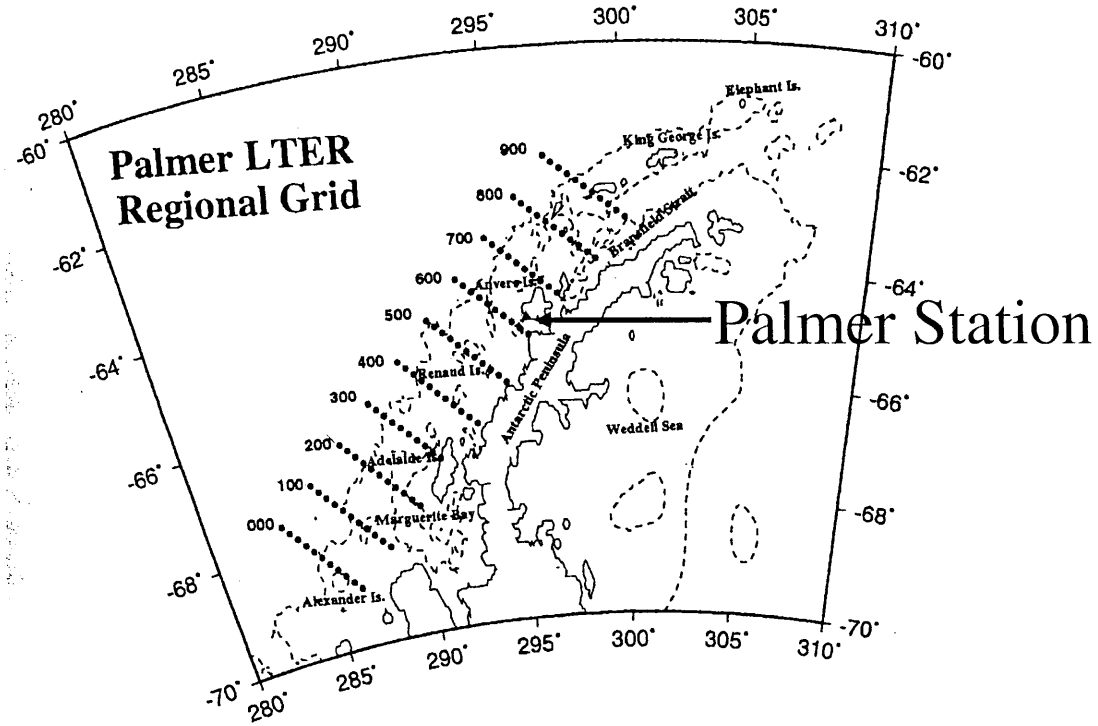


Figure 19. Palmer LTER regional grid that is sampled during the annual January cruise. The grid lines are every 100 kms along the coast of the western Antarctic Peninsula, and the stations are every 20 kms along a grid line, extending 200 kms offshore (Smith et al., 1995).

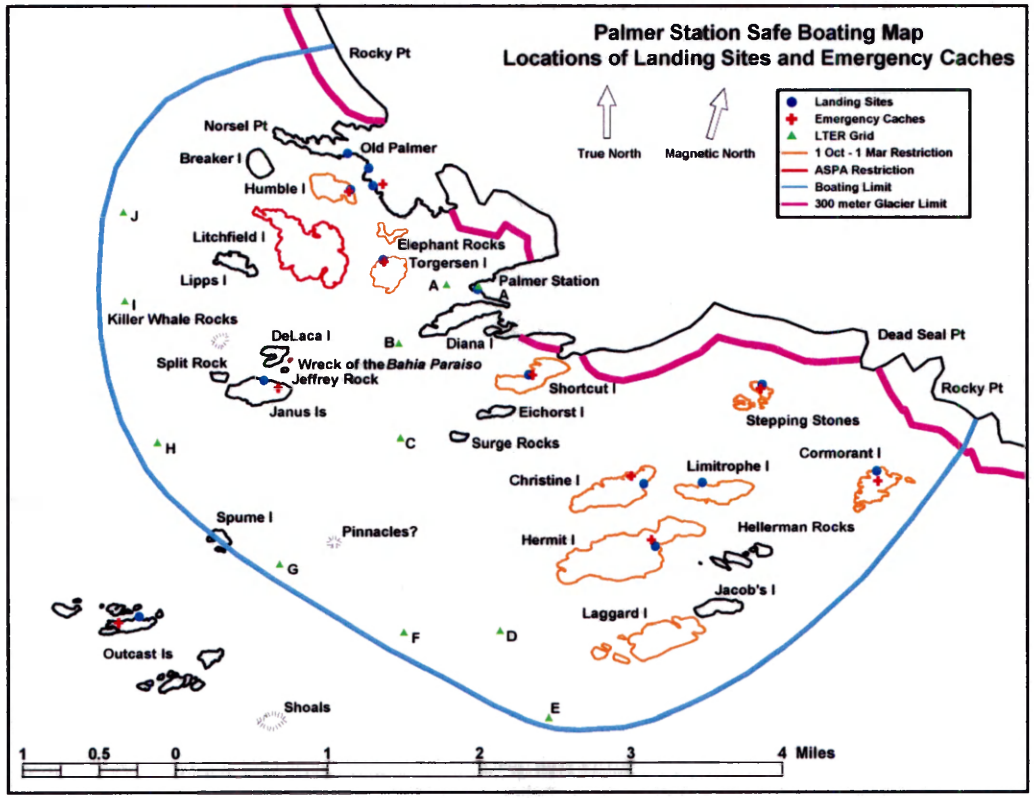


Figure 20. Palmer Station near shore grid, sampled by zodiac from Palmer Station (Smith et al., 1995).

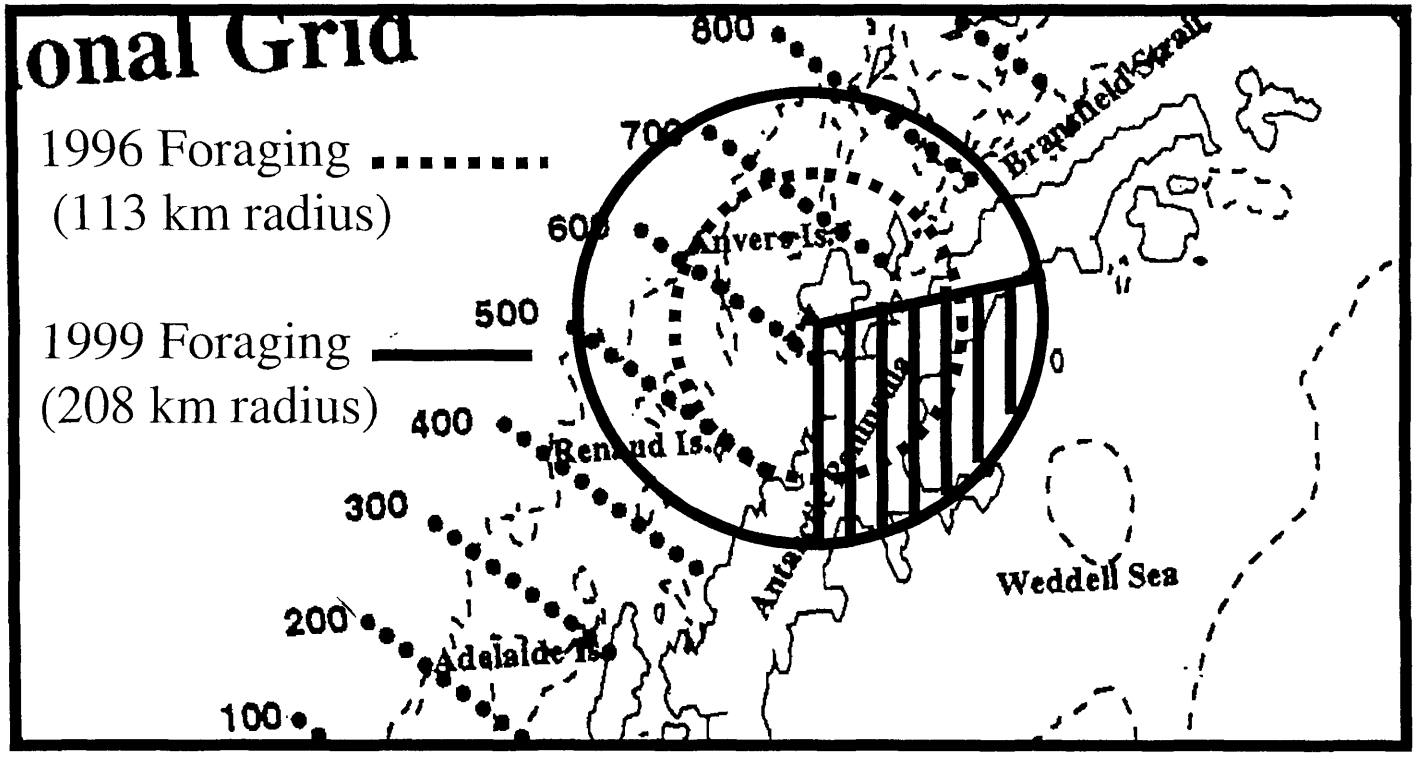


Figure 21. Adelie penguin foraging areas for 1996 and 1999, estimated from foraging duration times measured using radio transmitters attached to adults (Fraser, 2003 pers.comm.and Salihoglu et al., 2000). Hatched area is 1/3 of the circle which lies over the land.

(Ross et al., 1996). Also, even though there may have been significant numbers of other zooplankton such as copepods, the model was designed to estimate the impact of the traditional short food web including large phytoplankton, krill, and penguins. For the 1996 model, myctophids and Adélie penguins were included (Figure 28). In the 1999 model, myctophids, Adélie penguins, and salps were included in the model (Figure 34). A detailed description of the inverse method can be found in the Appendix. A number of techniques were used to analyze the output of the models including descriptions of the fate of the primary production, the zooplankton diet, and the particulate export. Network analysis techniques were used to characterize the solutions including the index of recycling, indices of relative activity, dependency coefficients, and effective trophic levels. Further details of these techniques can be found in the Appendix. A sensitivity analysis was performed to determine the effects on the solution resulting from varying the input parameters by a small amount (+/- 10%).

Results

Data Synthesis

Primary Production and Biomass

Primary production for January 1996 (Figure 22, was measured using Carbon-14 incorporation in water samples collected to the 2% light level (Smith et al., 1998 and LTER website: http://lternet.edu/, 2002) and was integrated to a depth of 35 m to allow comparison with the North Atlantic models. The 2% light level was almost always above 35 m, so the integrated production is representative of the entire euphotic zone. Production measurements at stations within the Adélie foraging area with a radius of 113 km were averaged, along with the near shore stations. Figure 23 shows the primary production measured for January 1999, also using Carbon-14 incorporation in water samples collected to the 1% light level (Smith et al., 1998 and LTER website: http://lternet.edu/, 2002). Stations were sampled within the Adélie foraging area with a radius of 208 km. The primary production was integrated to 35 m, which was much shallower than the depth of the euphotic zone with an average depth for the 1% light level of 69 m. However, the average integrated primary production for the full euphotic zone, (35 mmols $Cm^{-2}d^{-1}$) was not very different from the upper 35 m (29 mmols $Cm^{-2}d^{-1}$).

Phytoplankton Biomass was measured by flourometry in water samples taken down to depths of at least 50 m (Smith et al., 1998 and LTER website: http://lternet.edu/, 2002). Chlorophyll a was converted to carbon, using a C:Chl ratio of 50 (Mitchell &

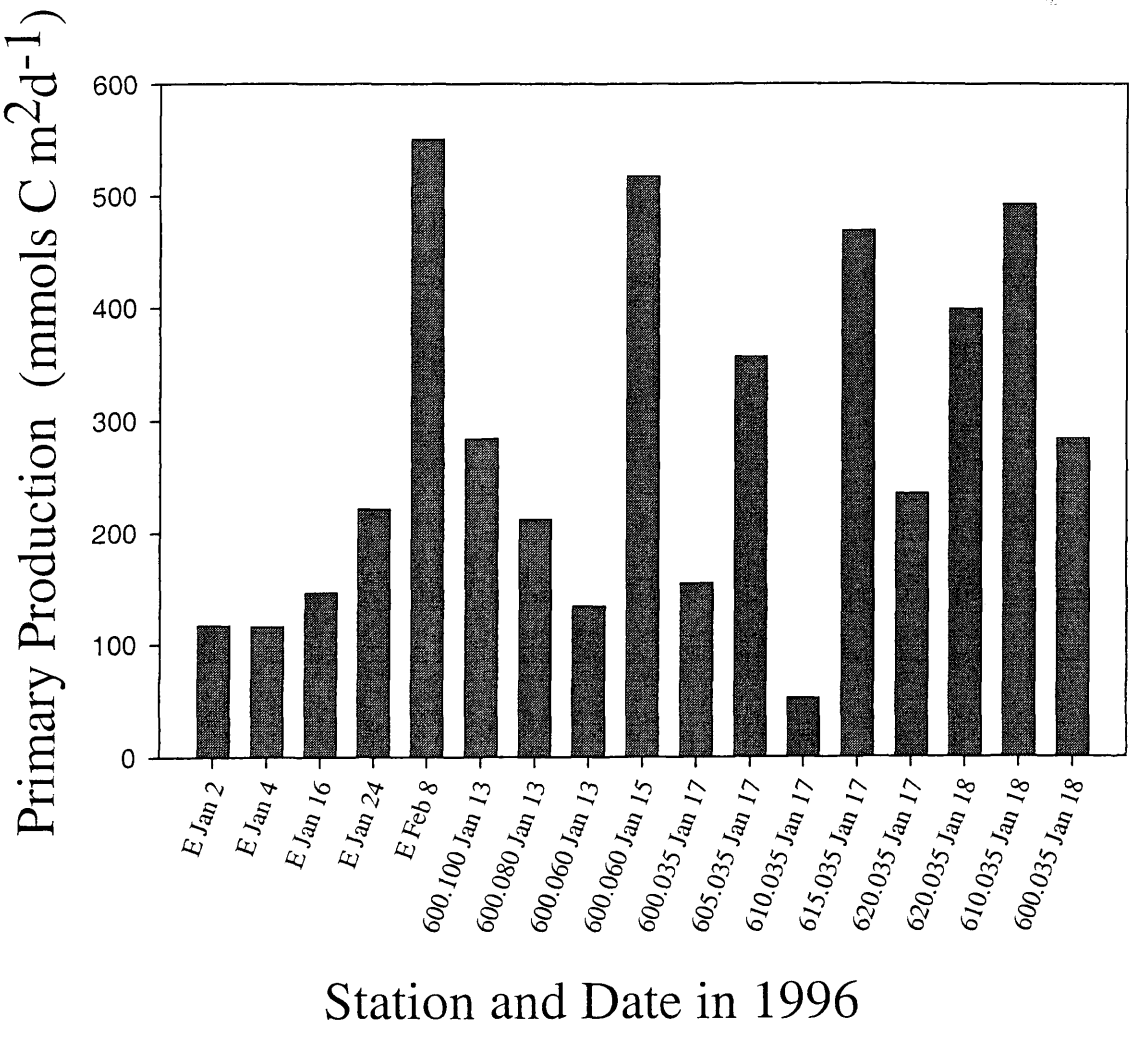


Figure 22. WAP Primary Production measurements from January, 1996 regional cruise and Palmer near shore station E, using ^{14}C incorporation (Smith et al., 1995 and LTER website: http://lternet.edu/, 2002). For the regional grid stations, the first 3 numbers are grid line along shore and the last 3 after the "." are the km offshore. For example station, 600.100 is on the 600 grid line and is 100 km offshore and 600.035 is on the 600 grid line and 35 km offshore.

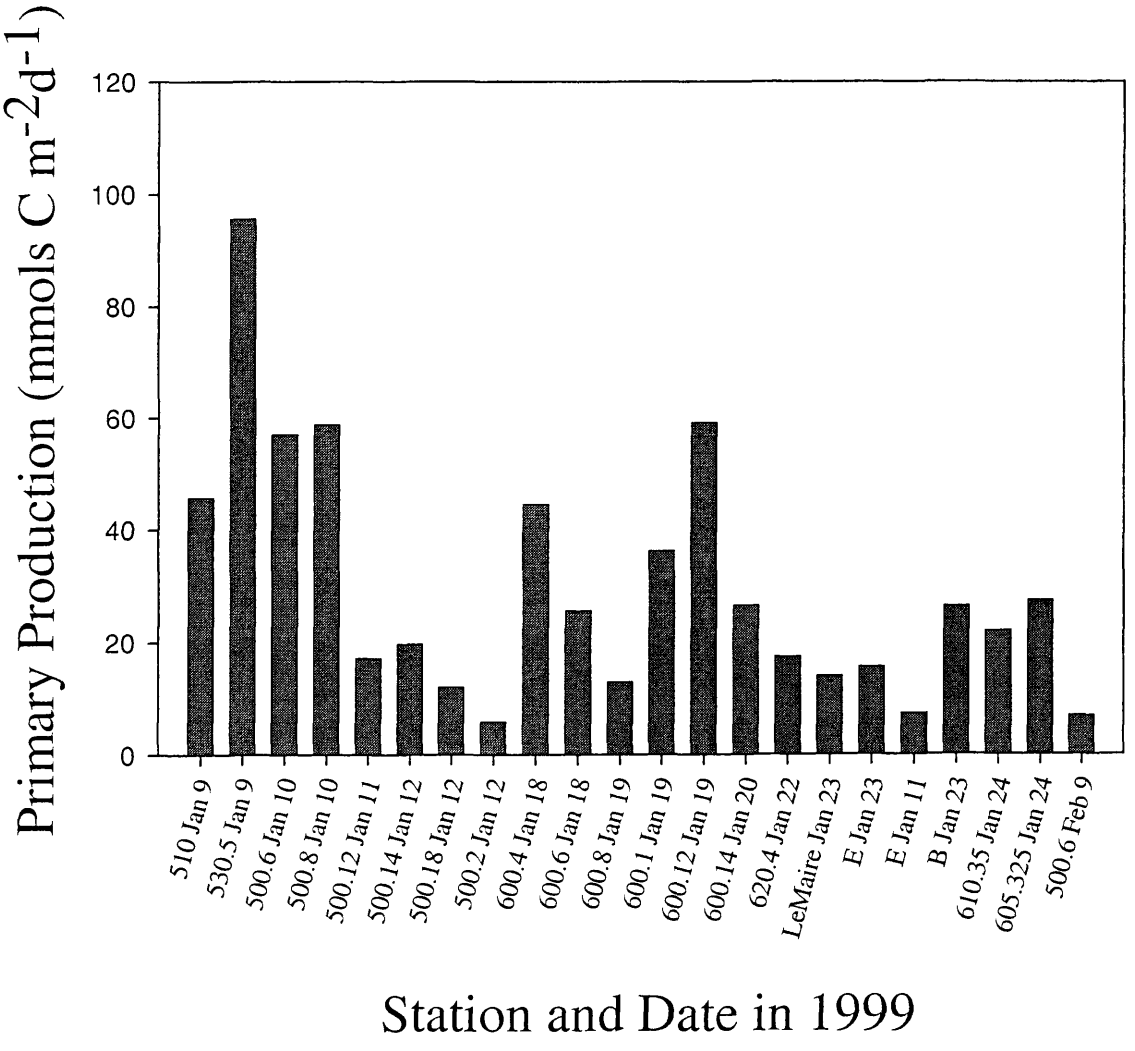


Figure 23. WAP Primary Production measurements from January, 1999 regional cruise and Palmer near shore stations B and E, using ^{14}C incorporation (Smith et al., 1995 and LTER website: http://lternet.edu/, 2002).

Holm-Hansen, 1991) and the biomass was integrated to 35 m. Figures 4 and 5 show the phytoplankton biomasses for January 1996 and January 1999, respectively.

Bacterial Production and Biomass

Bacterial production was estimated by ^{3}H labeled-leucine incorporation (Karl et al.,1996 and LTER website: http://lternet.edu/, 2002). Data required for the conversion to carbon mass units were not given, so the results reported in the website were not used. Instead bacterial production was defined as a percentage of the primary production. The bacterial production was constrained between zero and fifty percent of the primary production for both 1996 and 1999.

Bacterial biomass was determined from measurements of particulate lipopolysaccharide (Karl et al., 1996 and LTER website: http://lternet.edu/, 2002). Water samples from depths down to at least 75 m were analyzed for bacterial carbon and the measurements were integrated to 35 m. Figures 30 and 31 show the bacterial biomass for January 1996 and January 1999, respectively.

Microzooplankton Grazing and Biomass

Microzooplankton grazing, including protozoans with diameters < 20 micrometers and microzooplankton 20 - 200 micrometers in diameter, was not measured as part of the Palmer LTER study. Estimates from the literature from different areas of the Southern Ocean including the Ross Sea (Caron et al., 2000), and the Atlantic sector (Froneman and Perissinotto, 1996; Becquevort, 1995) were used to provide a wide range of potential microzooplankton grazing from 0 – 75% of primary production.

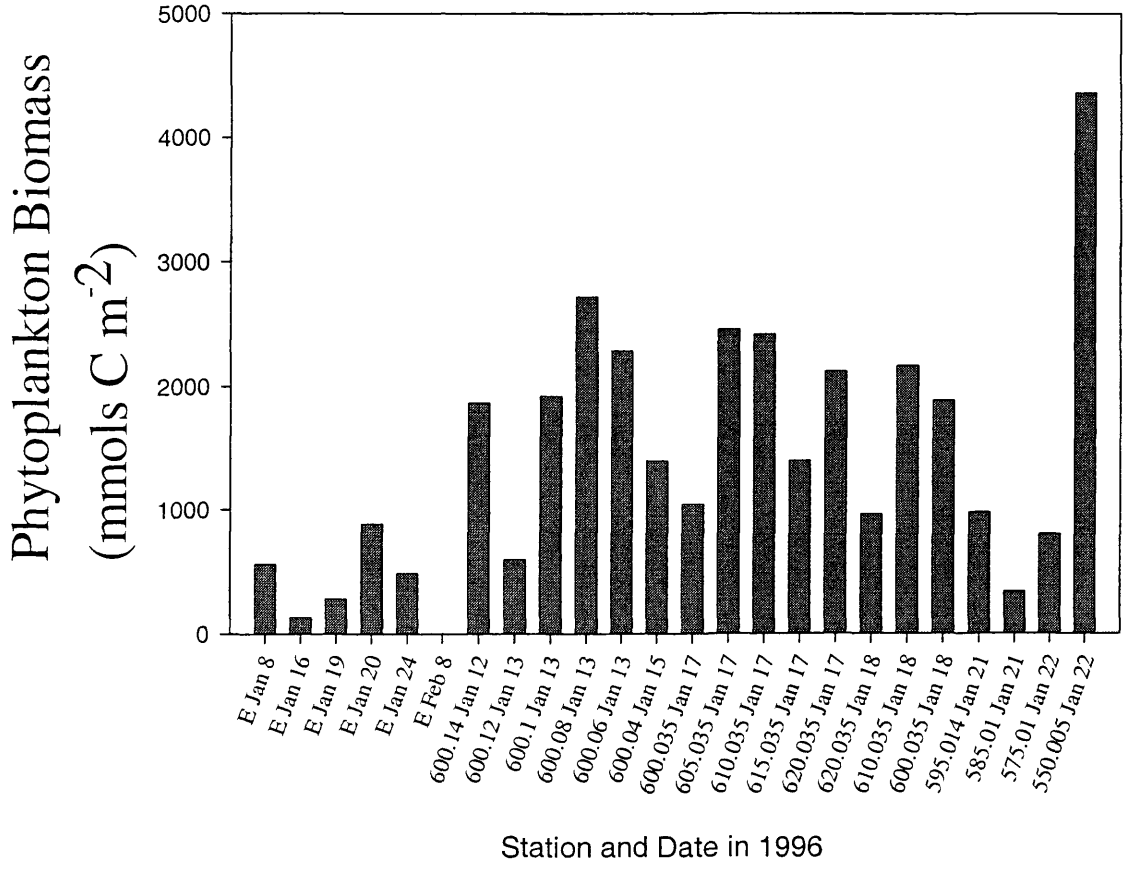


Figure 24. WAP Phytoplankton Biomass measurements from January, 1996 regional cruise and Palmer near shore station E (Smith et al., 1995 and LTER website: http://lternet.edu/, 2002).

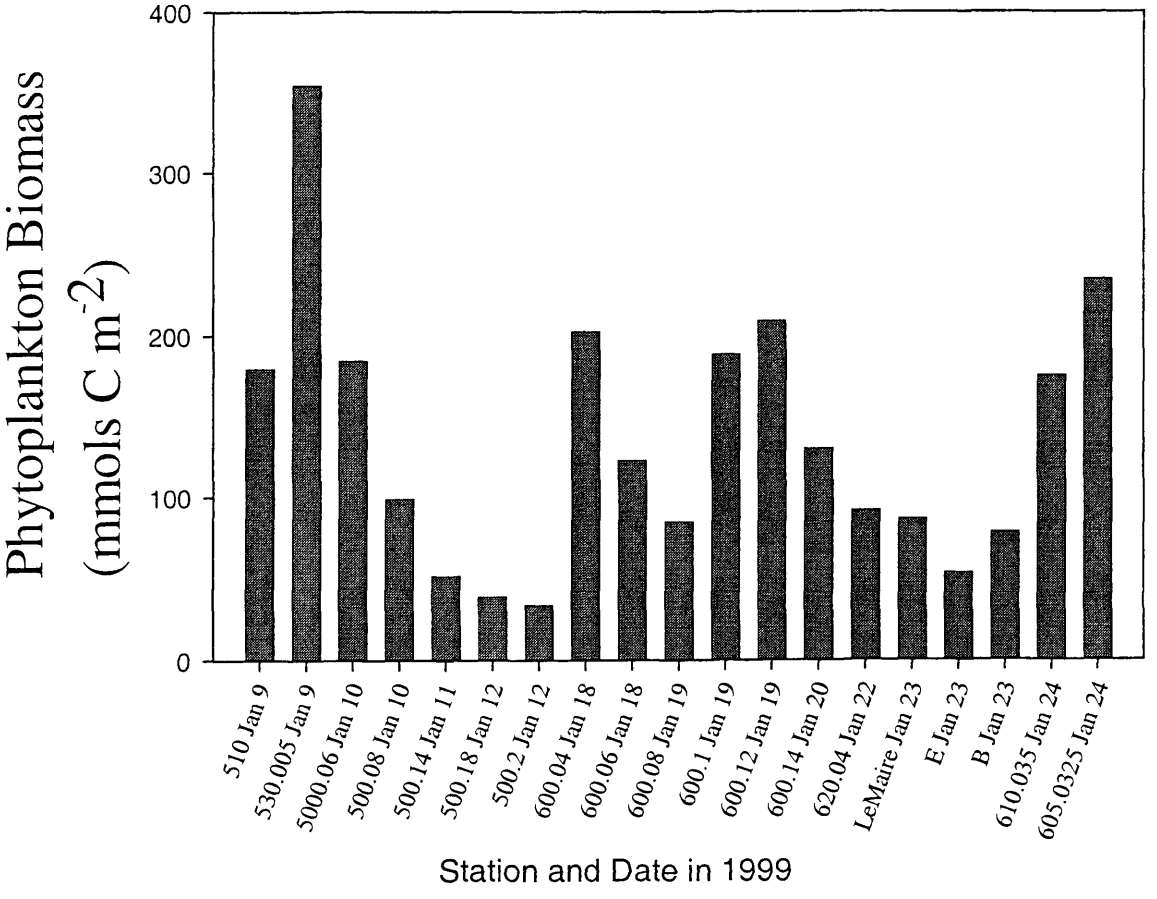


Figure 25. WAP Phytoplankton Biomass measurements from January, 1999 regional cruise and Palmer near shore stations E, B, and LeMaire. Fluorometry was used to find Chl a (Smith et al.,1998 and LTER website: http://lternet.edu/, 2002) and biomass was found by using a C:Chl a ratio of 50 (Mitchell & Holm-Hansen, 1991) and integrating to 35m.

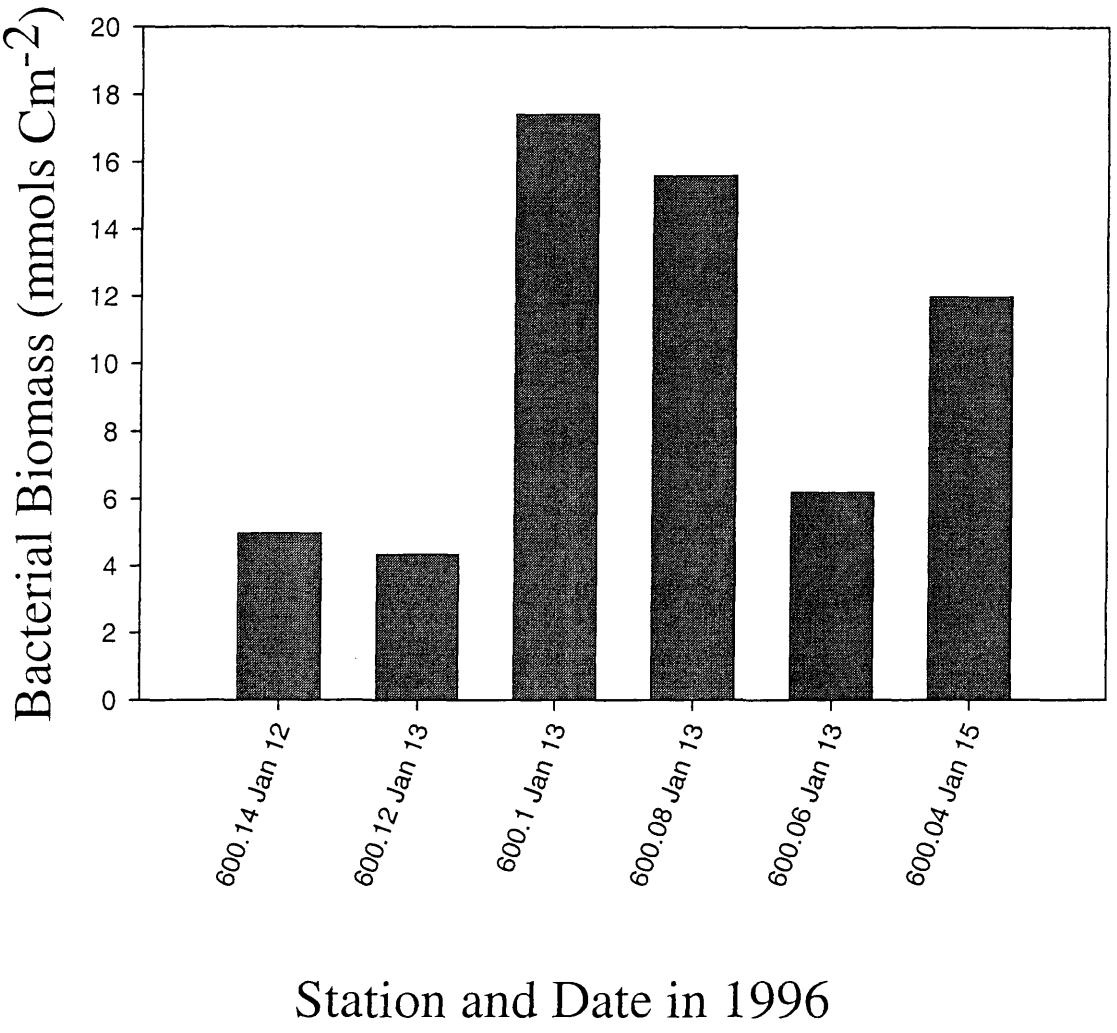


Figure 26. Bacterial Biomass determined from measurements of particulate lipopolysaccharide (Karl et. al, 1996 and LTER website: http://lternet.edu/, 2002). Biomass was integrated to 35 m. For example station, 600.100 is on the 600 grid line and is 100 km offshore and 600.035 is on the 600 grid line and 35 km offshore.

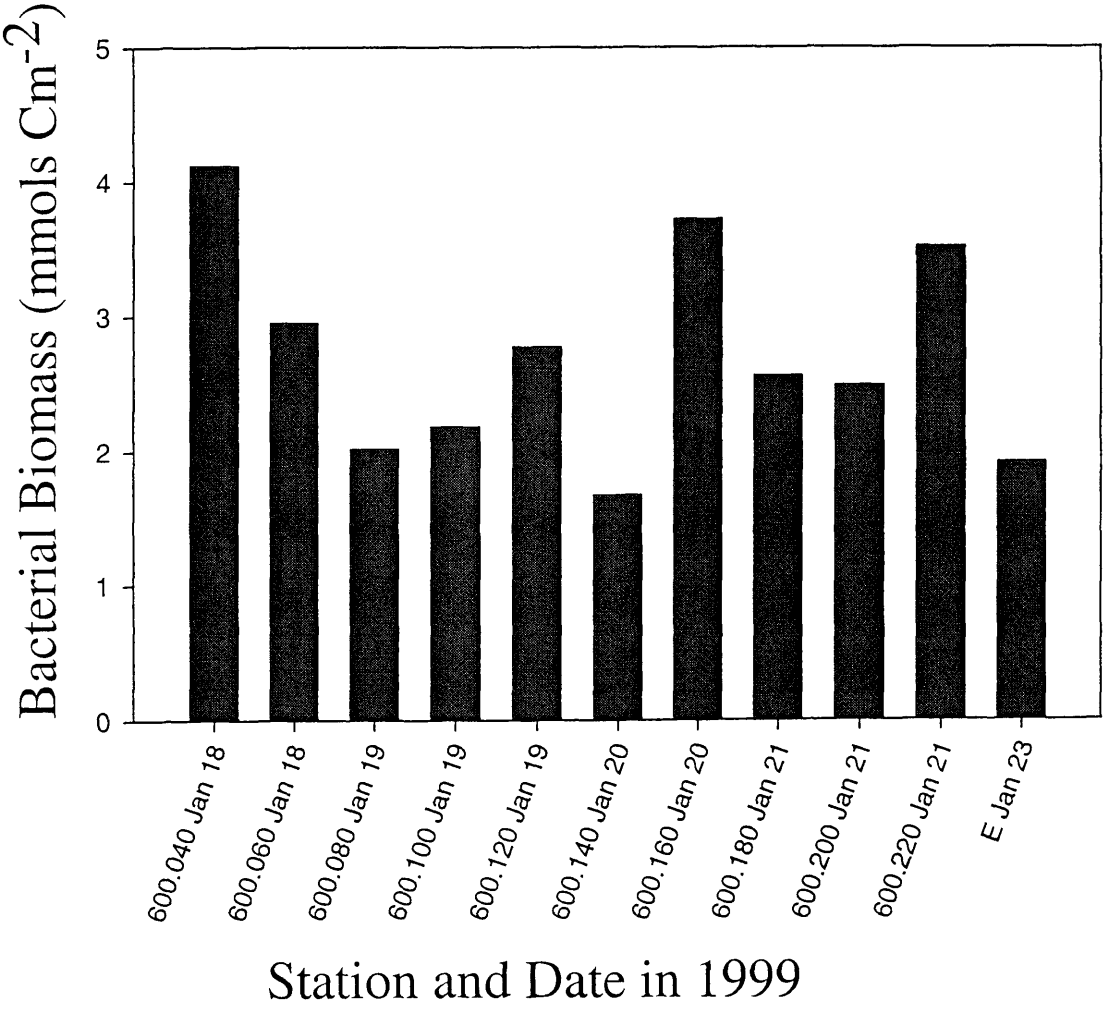


Figure 27. Bacterial Biomass determined from measurements of particulate lipopolysaccharide (Karl et. al, 1996 and LTER website: http://lternet.edu/, 2002). Biomass was integrated to 35 m.

Microzooplankton biomass was not measured, so the microzooplankton respiration was left unconstrained.

Krill Grazing and Biomass

Antarctic krill (*Euphasia superba*) biomass was estimated from penguin stomach content data, trawl data, and from estimates from the literature (Table 16). Penguins are opportunistic visual predators that do not discriminate between different sizes of krill, so the size distribution of krill in their stomachs is a good approximation of the size distribution of krill in the area (Salihoglu et al., 2001). Fraser (unpublished data) provided the size distribution of over 2000 krill from penguin stomach contents for both the 1995-1996 and 1998-1999 summer seasons. The average sizes for 1995-1996 and 1998-1999 were 48 mms and 43 mms, respectively. The average krill sizes were used to estimate the individual wet weight of an average krill, using regressions found by Ross and Quetin (unpublished, 2003 and LTER website: http://lternet.edu/, 2002) between length and wet weight of krill measured in trawl catches. The density of krill measured in trawls was then used to find the biomass of krill (Table16). The biomass of krill was also estimated from acoustic data (Table 16), taken with an echo sounder from the regional grid (Lascara et al., 1999).

Krill grazing was estimated from a feeding relationship, found by experiments during 1991 and 1992 by Ross et al. (1998), (Table 17). The average phytoplankton concentration in the upper 35 m was used in the feeding relationship to estimate the specific feeding rate of krill. The acoustic and trawl biomass measurements were used to find grazing estimates for the krill community for January 1996 and January 1999.

Table 16. Krill Biomass in the western Antarctic Peninsula estimated from trawl catches and from acoustic measurements.

Krill Biomass	1995-96	1998-99	References
Mean Krill Length (mm)	48	43	Fraser - 2002: stomach contents of penguins: In 95-96 the 41-45 mm size class had the highest frequency (29.7%) in penguins. In 98-99, the 46-50 mm size class had the highest frequency in penguins (40.8 %).
Mass of indiv. Krill WW (g /indiv.)	1.08	0.66	Ross - LTER Database and regressions on Wet weight vs. Total Length.
Mass of indiv. Krill DW (g /indiv.)	0.23	0.14	Lascara & Hofmann 2000: conversion from WW to DW = 0.216.
Density of Krill (# / m^2)	29.60	2.90	Ross - LTER Database: trawl catch files, 2 m net data.
Biomass (g krill/m^2)	32.06	1.91	Lascara & Hofmann, 2000: conversion from DW to CW: CW = 0.366DW^1.037.
Biomass (g C/m^2)	2.72	0.15	Lascara & Hofmann 2000: conversion from WW to DW = 0.216, conversion from DW to CW: CW = 0.366DW^1.037.
Biomass (mmols C/m^2)	226.88	12.16	
Acoustic Biomass (g krill/m^2)	345.80	42.30	Ross - LTER Database: Acoustic transect data, files: AcouBiojan96.xls and AcouBiojan99.xls.
St Deviation (Acoustic Biomass g krill/m^2)	508.52	65.31	Ross - LTER Database: Acoustic transect data, files: AcouBiojan96.xls and AcouBiojan99.xls.
Acoustic Biomass (g C/m^2)	32.07	3.63	Lascara & Hofmann 2000: conversion from WW to DW = 0.216, conversion from DW to CW: CW = 0.366DW^1.037.
Acoustic Biomass (mmols C/m^2)	2672.33	302.44	

Table 17. Krill grazing estimated from biomasses found in Table 10 and from linear feeding function found by Ross, Quetin, and Haberman (1998).

Krill Grazing	1995-96	1998-99	References
Phyto Conc.in top 35m (µg Chl a /l)	9.86	0.94	Data from LTER database and Integrated to 35m.
Grazing (ug Chla a / g WW/ hour)	11.57	0.71	Ross, Quetin, and Haberman (1998) Linear feeding function: 1.218*(Phyto. Concentration in (µg Chl a /l)) - 0.435 from experiments in 1991 and 1992.
Grazing - Trawl estimate (µg Chla / m^2 /hour)	371.05	1.35	
Grazing - trawl estimate (mmols C/ m^2/day)	37.10	0.13	Assumes 24 hour feeding.
Grazing - Acoustic Bio estimate (µg Chla / m^2 /hour)	4002.25	29.86	
Grazing - Acou Bio estimate (mmols C/ m^2/day)	400.22	2.99	

Adélie Penguin Grazing and Biomass

The Adélie penguin grazing was estimated using counts of penguins and grazing estimates from a modeling simulation of penguin chick feeding. The total number of penguins to be included in the model was tallied from surveys of penguins on the islands within the vicinity of Palmer Station that were likely to feed in the Adélie foraging areas (Fraser et al., unpublished data), (Table 18). Penguins were tallied from the local islands within a 2-mile radius of Palmer Station including Christine, Cormorant, Humble, Litchfield, and Torgersen Islands, and nearby colonies including Biscoe Point and Dream Island (Table 18). An additional 10,000 penguins were added to include estimates of uncounted Adélie and Gentoo penguins south of Palmer Station that also are active in the area (Fraser, pers. comm., 2003). Surveys of chicks on the islands were used to find a ratio of chicks/adult pairs (Table 18). The feeding rate, in mmols $Cm^{-2}d^{-1}$ for chicks was then found (Table 18) based on a modeling study that estimated the feeding required for Adélie chicks to acquire experimentally measured fledging weights, which are remarkably consistent from year to year (Salihoglu, Fraser, and Hoffman, 2001). The feeding rate was an average value for the crèche period, equal to the feeding at day 40 in the simulation (Fig 3 A in Salihoglu, Fraser, and Hoffman, 2001). The feeding rate for all penguins, in mmols $Cm^{-2}d^{-1}$, including adults and chicks was estimated by using the assumption that the adults provide a maximum of 54% of their stomach contents to the chicks during the crèche period (Salihoglu, Fraser, and Hoffman, 2001).

The penguin biomass was estimated from penguin weights for males, females, and chicks measured on Torgensen Island by Fraser et al. (unpublished data, 2003;

Table 18. Adelie penguin feeding and biomass estimated by penguin surveys by Fraser (2002) and from chick feeding rate used by Salihoglu, Fraser, and Hoffman (2001).

	1995-96	1998-99	Reference
Penguin Pop'n (pairs of Adults on Local Islands)	11063	8423	Fraser, 2002
Penguin Pop'n (pairs of Adults on Biscoe Point)	735	444	Fraser, 2002
Penguin Pop'n (pairs of Adults on Dream Island)	6582	4827	Fraser, 2002
Penguin Pop'n Estimate of Penguins not counted and Gentoos S. of Palmer	10000	10000	Fraser, 2002
Total Penguin pop'n (Adult Pairs)	28380	23694	
Penguin Chicks (Local Islands)	15267	10781	Fraser, 2002
Penguin Chicks (Biscoe and Night Islands)	1010	941	Fraser, 2002
Penguin Chicks (Dream Island)	9081	6381	Estimated using Chicks / Adult ratio
Total Chicks	16277	11722	Fraser, 2002
Chicks/Adult Pair on Local, Biscoe, and Night Islands	1.379640617	1.32198038	
Foraging Area	**1995-96**	**1998-99**	
Foraging distance (km from Palmer)	113	208	Fraser, 2002
Foraging Area (m^2)	2.67E+10	9.06E+10	Assume foraging area is a 2/3 of a circle with its center at Palmer and radius equal to the foraging distance.
Feeding			
# Adult pairs/m^2	1.06E-06	2.61E-07	
# Chicks/m^2	1.46E-06	3.46E-07	
Food (mmols C/chick/day)	27416.66667	27416.6667	Average value for the creche period equal to the feeding at day 40 in the simulation by Salihoglu, Fraser, and Hoffman 2001 (Fig 3 A).
Chick feeding (mmols C/ m^2/day)	4.01E-02	9.48E-03	
Adult and Chick feeding (mmols C/ m^2/day)	7.38E-02	1.74E-02	Salihoglu,Fraser, Hoffman 2001: Chick receives max. of 54 % of parents stomach content before fledging.
Biomass			
Adult Male mean wt (g)	4658	4790	Penguins weighed on Torgersen Islands - Fraser, 2002.
Adult Female mean wt (g)	4288	4034	Penguins weighed on Torgersen Islands - Fraser, 2002.
Chick fledgling wt (g)	2921	3012	Penguins weighed on Torgersen Islands - Fraser, 2002.
C as % of wet wt. For Adelies	50	50	
Penguin Biomass (g C)	87244428.5	69922296	
Penguin Biomass (mmols C/m^2)	2.72E-01	6.43E-02	

Salihoglu, Fraser, and Hoffman, 2001). The total number of penguins was used along with the weights to find the penguin biomass in mmols Cm^{-2} for January 1996 and January 1999 (Table 18).

Myctophid Grazing and Biomass

Biomass and grazing estimates from the literature were used to estimate the impact of myctophids in the western Antarctic Peninsula (Table 19). Data for the silverfish, *Pleuragramma antarcticum*, common to the area were not found, but data for other myctophid species were used, including the most abundant fish in the Southern Ocean, *Electrona antarctica* (Greely et al., 1999). The growth rate of *Electrona antarctica* is consistent with the growth rates of all other myctophid species investigated (Greely et al., 1999). Minimum and maximum densities of myctophids were taken from measurements made in 1988 as part of the AMERIEZ study in the Marginal Ice Zone in the Atlantic sector of the Southern Ocean (Lancraft et al., 1991 in Pakhomov et al., 1996), (Table 19). Conversion factors for wet weight (Donnelly et al., 1990) and carbon content (Childress et al., 1990) were used to calculate an average biomass in mmols Cm^{-2} (Table 19).

Myctophid Grazing was estimated using specific grazing rates and the biomass estimates (Table 19). Minimum and maximum grazing estimates were taken from Pakhomov et al. (1996), who used data from five South African cruises to the Southern Ocean from 1985 – 1995.

Table 19. Myctophid biomass and grazing estimated from surveys in the Marginal Ice Zone, Atlantic sector of the Southern Ocean by Pakhamov et al. (1996).

Myctophid Biomass		**References**
Min Biomass (g dry wt / m^2)	0.36	MIZ Atlantic Sector, Pakhamov et. al 1996, Lancraft et al (1991) for various species of Myctophids.
Max Biomass (g dry wt / m^2)	0.73	MIZ Atlantic Sector, Pakhamov et. al 1996, Lancraft et al (1991) for various species of Myctophids.
Average Biomass(g dry wt / m^2)	0.545	
Water as % of Wet Wt	69	Donnelly et. al. 1990: *Electrona antarctica* from Weddell/ Scotia Sea region.
Average Biomass(g wet wt / m^2)	1.76	
C as % of Wet Wt	9.25	Average C as % of Wet Wt from Table 1: Myctophidae species from Childress et. al 1990 (See Sheet 2).
Average Biomass (mmols C / m^2)	13.55	
Max Wet Wt. Of indiv (g)	6.00	Donnelly et. al. 1990: Electrona antarctica from Weddell/ Scotia Sea region.
Max C of indiv (mmoles)	46.24	
Myctophid Grazing		
Min grazing % dry body wt /day	0.46	Pakhomov et. al. 1996 Min value found in study (Table 6).
Max grazing % dry body wt /day	8.00	Pakhomov et. al. 1996 pg. 11 based on highest ISF found in literature: Kozlov & Tarverdieva,1989.
Min grazing (mmol C / m^2 / day)	0.06	
Max grazing (mmol C / m^2 / day)	1.08	

Salp Grazing and Biomass

Salp grazing was estimated from the measured abundance of salps caught in zooplankton trawl surveys, as part of the regional cruise (Ross et al., LTER website: http://lternet.edu/, 2002), (Table 20). Salp grazing is only shown for 1999, because in 1996 salps were not observed in the trawls. Minimum and maximum specific grazing rates are from a study in the Lazarev Sea (Perissinotto and Pakhomov, 1998). The abundance of salps was multiplied by the specific grazing rates to find minimum and maximum limits for the salp grazing in mmols $Cm^{-2}d^{-1}$.

Export

The export was measured at a sediment trap located near Palmer Station at a depth of 350 m (Karl et al, LTER website: http://lternet.edu/, 2002), (Table 21). The export at 35 m was estimated using the measurements at 350 m and assuming a normalized power function derived for open ocean environments by Martin et al.(1987): $F = F_{100} (z/100)^b$. The known export at 350 m was used to estimate F_{100} using the above equation and assuming b = - 0.858 (Martin et al., 1987). The export at 35 m was then estimated using the above equation.

Model Inputs

The measurements were each averaged over the month of January to provide an average value to use in the models for 1996 and 1999 (Table 21). The standard deviations of the rate measurements were used to set minimum and maximum constraints on the calculated flows. The measurements, +/- one standard deviation, were entered into

Table 20. 1999 Salp Grazing based on trawl surveys (Ross & Quetin, LTER Database) and feeding relationship used by Perissonotto and Pakhomov (1998).

Salp Grazing Estimates		References
Average # Salps/1000 m^3	122.39	
Minimum grazing rate ug Chl a /salp day	3.00	Perissonotto and Pakhomov (1998) for Larger salps > 5 cm.
Maximum grazing rate ug Chl a/ salp day	160.00	Perissonotto and Pakhomov (1998) for Larger salps > 5 cm.
Minimum grazing rate ug C /salp day	154.65	Conversion to Carbon from Chl using rel. from Pakhomov (1998): C=80*(Chl a)^0.6.
Maximum grazing rate ug C/ salp day	1680.98	
Minimum grazing rate mmols C /salp day	0.01	
Maximum grazing rate mmols C/ salp day	0.14	
Min Grazing mmols C/m^2 day	0.06	
Max Grazing mmols C/m^2 day	0.60	

Table 21. Data input for WAP carbon inverse models.

	Phytoplankton Production (mmol C $m^{-2}d^{-1}$)	Small Phytoplankton Production (mmol C $m^{-2}d^{-1}$)	Large Phytoplankton Production (mmol C $m^{-2}d^{-1}$)	Phytoplankton Biomass (mmol C m^{-2})	Bacterial Productivity (mmol C $m^{-2}d^{-1}$)	Bacterial biomass (mmol C m^{-2})	Microzooplankton Grazing (mmol C $m^{-2}d^{-1}$)	Krill Grazing (mmol C $m^{-2}d^{-1}$)	Krill Biomass Acoustic Est. (mmol C m^{-2})	Adelie Grazing (mmol C $m^{-2}d^{-1}$)	Myctophid Grazing (mmol C $m^{-2}d^{-1}$)	Myctophid Biomass (mmol C m^{-2})	Export (Sed Traps 300 m) (mmol C $m^{-2}d^{-1}$)	Salp Grazing (mmol C $m^{-2}d^{-1}$)
January 1996														
Jan AVG	255	85	170	1437.84		10.09			2672.33	0.07			11.93	
Min	88	29	59		0.00		0.00	37.10		0.03	0.06	0.36	5.97	
Max	421	140	280		50 % of PP		75 % of PP	400.20		0.10	1.08	0.73	17.90	
St Dev	166.2	55	111	1007.68		5.70								
January 1999										0.5				
January AVG	30	10	20	137		2.78		0.13	302.44	0.02			3.60	
Min	7	2	5	54	0	1.88	0.00	2.99		0.01	0.06	0.36	1.80	0.06
Max	52	17	35	219	50 % of PP	3.68	75 % of PP			0.02	1.08	0.73	5.40	0.61
St Dev	22.3	7	15	82.3		0.90								

the constraint equation for the model. The measured biomasses are used to set the maximum constraints for respiration, so there are no minimum and maximum constraints listed for the biomasses. For some of the measurements, such as salp grazing and myctophid grazing, the minimum and maximum constraints were provided by the assumptions used from the literature. For other measurements, where the standard deviation was not available (e.g. Adélie grazing and export), the minimum and maximum constraints were set equal to 0.5 and 1.5 X the January average.

The measurements for the western Antarctic Peninsula were not a time series, like in NABE, but were taken across different sites throughout the regional and local grids over the month of January. Given the sampling scheme, it was not possible to estimate changes in the biomasses of food web components over the study period. It was assumed that biomass did not change over the month and the balance equations for each component were set to zero.

The average biomasses were used as inputs to the allometric equation from Moloney and Field (1989) to constrain the maintenance respiration for each component (Table 22). Additional constraints on ingestion, excretion, assimilation, and production for all living components were included (Table 22).

The primary production was split among the small, < 5 μm and large > 5 μm phytoplankton, with 2/3 of the measured production assigned to the large phytoplankton and 1/3 to the small. The phytoplankton community in the southern ocean is believed to be dominated by larger cells during bloom conditions (Laws, 1985). The standard deviation of the data to be used in the constraints for the primary production was split in

Table 22. Biological contraints for the WAP inverse carbon solutions. The temperature, T is equal to -2 deg C.

Mbac = pmoles of C/ bacteria cell, Cbacteria = biomass of bacteria in mmols Cm^{-2}, MicC = pmoles of C / microzooplankton cell, Cmicro = biomass of microzooplankton in mmols Cm-2, MesC = pmoles of C / individual mesozooplantkon, Cmesozoo = biomass of mesozooplankton in mmols C / m^2.

Biological Constraints	Lower Bound	Upper Bound	Reference
Respiration			
Bacteria	20 % of consumption of DOC	(1.7*(Mbac)^-0.25*EXP(0.0693*(T-20)))*Cbacteria	Moloney & Field, 1989, Richardson & Jackson, 2001pers. comm.
Large Phytoplankton	5 % of GPP	30 % of gross primary production	Vezina & Platt, 1989
Small Phytoplankton	5 % of GPP	30 % of gross primary production	Vezina & Platt, 1989
Protozoa	20 % of total C intake	none	
Microzooplankton	20 % of total C intake	(14*('MicC')^-0.25*EXP(0.0693*(T-20)))*'Cmicro'	Moloney & Field, 1989, Richardson & Jackson, 2001pers. comm.
Krill	20 % of total C intake	(14*(krillC)^-0.25*EXP(0.0693*(T-20)))*Ckrill	Moloney & Field, 1989, Richardson & Jackson, 2001pers. comm.
Myctophids	20 % of total C intake	(14*(mycC)^-0.25*EXP(0.0693*(T-20)))*Cmyc	Moloney & Field, 1989, Richardson & Jackson, 2001pers. comm.
Salps	20 % of total C intake	(None)	
Adelies	20 % of total C intake	(None)	
Excretion			
Large Phytoplankton	2 % of large phytoplankton NPP	55 % of large phytoplankton NPP	Vezina & Platt, 1989
Small Phytoplankton	2 % of small phytoplankton NPP	55 % of small phytoplankton NPP	Vezina & Platt, 1989
Protozoa	10 % of total C intake	100 % of protozoan respiration	Richardson & Jackson, 2001pers. comm.
Microzooplankton	10 % of total C intake	100 % of microzooplankton respiration	Richardson & Jackson, 2001pers. comm.
Krill	10 % of total C intake	100 % of mesozooplankton respiration	Richardson & Jackson, 2001pers. comm.
Myctophids	10 % of total C intake	100 % of myctophid respiration	Richardson & Jackson, 2001pers. comm.
Salps	10 % of total C intake	100 % of salp respiration	
Adelies	10 % of total C intake	100 % of adelie respiration	Richardson & Jackson, 2001pers. comm.
Assimilation efficiency			
Protozoa	C output to Detritus <= 50% of total C intake	C output to Detritus >= 10% of total C intake	Vezina & Platt, 1989
Microzooplankton	C output to Detritus <= 50% of total C intake	C output to Detritus >= 10% of total C intake	Kato, 1982
Krill	C output to Detritus <= 28% of total C intake	C output to Detritus >= 6% of total C intake	Kato, 1982
Myctophids	C output to Detritus <= 50% of total C intake	C output to Detritus >= 10% of total C intake	
Adelies	C output to Detritus <= 50% of total C intake	C output to Detritus >= 10% of total C intake	Salihoglu, Fraser, Hoffman A.E. =0.8 for chicks
Salps	C output to Detritus <= 50% of total C intake	C output to Detritus >= 30% of total C intake	
Net production efficiency			
Bacteria	bacteria to DOC + bacterial respiration <= 95% DOC to bacteria	bacteria to DOC + bacterial respiration >= 50% DOC to bacteria	Richardson & Jackson, 2001pers. comm.
Gross production efficiency			
Protozoa	losses to respiration + detritus + DOC <= 90 % of total carbon intake	losses to respiration + detritus + DOC >= 60 % of total carbon intake	Richardson & Jackson, 2001pers. comm.
Microzooplankton	losses to respiration + detritus + DOC <= 90 % of total carbon intake	losses to respiration + detritus + DOC >= 60 % of total carbon intake	Richardson & Jackson, 2001pers. comm.
Krill	losses to respiration + detritus + DOC <= 90 % of total carbon intake	losses to respiration + detritus + DOC >= 60 % of total carbon intake	Richardson & Jackson, 2001pers. comm.
Myctophids	losses to respiration + detritus + DOC <= 90 % of total carbon intake	losses to respiration + detritus + DOC >= 60 % of total carbon intake	Richardson & Jackson, 2001pers. comm.
Adelies	losses to respiration + detritus + DOC <= 90 % of total carbon intake	losses to respiration + detritus + DOC >= 60 % of total carbon intake	Richardson & Jackson, 2001pers. comm.
Salps	losses to respiration + detritus + DOC <= 90 % of total carbon intake	losses to respiration + detritus + DOC >= 60 % of total carbon intake	
Ingestion			
Bacteria	none	(3.6*(Mbac)^-0.25*EXP(0.0693*(T-20)))*Cbacteria	Moloney & Field, 1989, Richardson & Jackson, 2001pers. comm.

the same ratio as the production with 2/3 assigned to the large phytoplankton and 1/3 to the small.

1996 Carbon Model Results

The largest flows within the food web, inferred by the 1996 carbon model inverse solution, are krill grazing and respiration (Figure 28 and Table 23). The next most important flows are microzooplankton respiration and bacterial ingestion of DOC, channeling a significant amount of carbon into the microbial food web. The inferred small and large gross primary production are 31 and 62 mmols $Cm^{-2}d^{-1}$, respectively, just slightly above their minimum constraints of 29 and 59 mmols $Cm^{-2}d^{-1}$, respectively (Table 23). The largest flow within the food web is the grazing of large phytoplankton by krill equal to 37 mmols $Cm^{-2}d^{-1}$ and 42% of the net primary production (Table 23). Krill respiration is the second largest flow equal to 17 mmols $Cm^{-2}d^{-1}$and 20% of the primary production. The third largest flow is the ingestion of DOC by bacteria, equal to 13 mmols $Cm^{-2}d^{-1}$ or 14% of the net primary production. The fourth largest flow is microzooplankton respiration equal to 15 mmols $Cm^{-2}d^{-1}$or 16% of the net primary production.

The flows for the upper trophic levels including penguins and myctophids are much smaller than for the lower trophic levels. Myctophids consume 1.08 mmols $Cm^{-2}d^{-1}$ of krill equal to 1% of the net primary production and the penguins consume 0.11 mmols $Cm^{-2}d^{-1}$ of krill equal to 0.1% of the production, an order of magnitude less than myctophids.

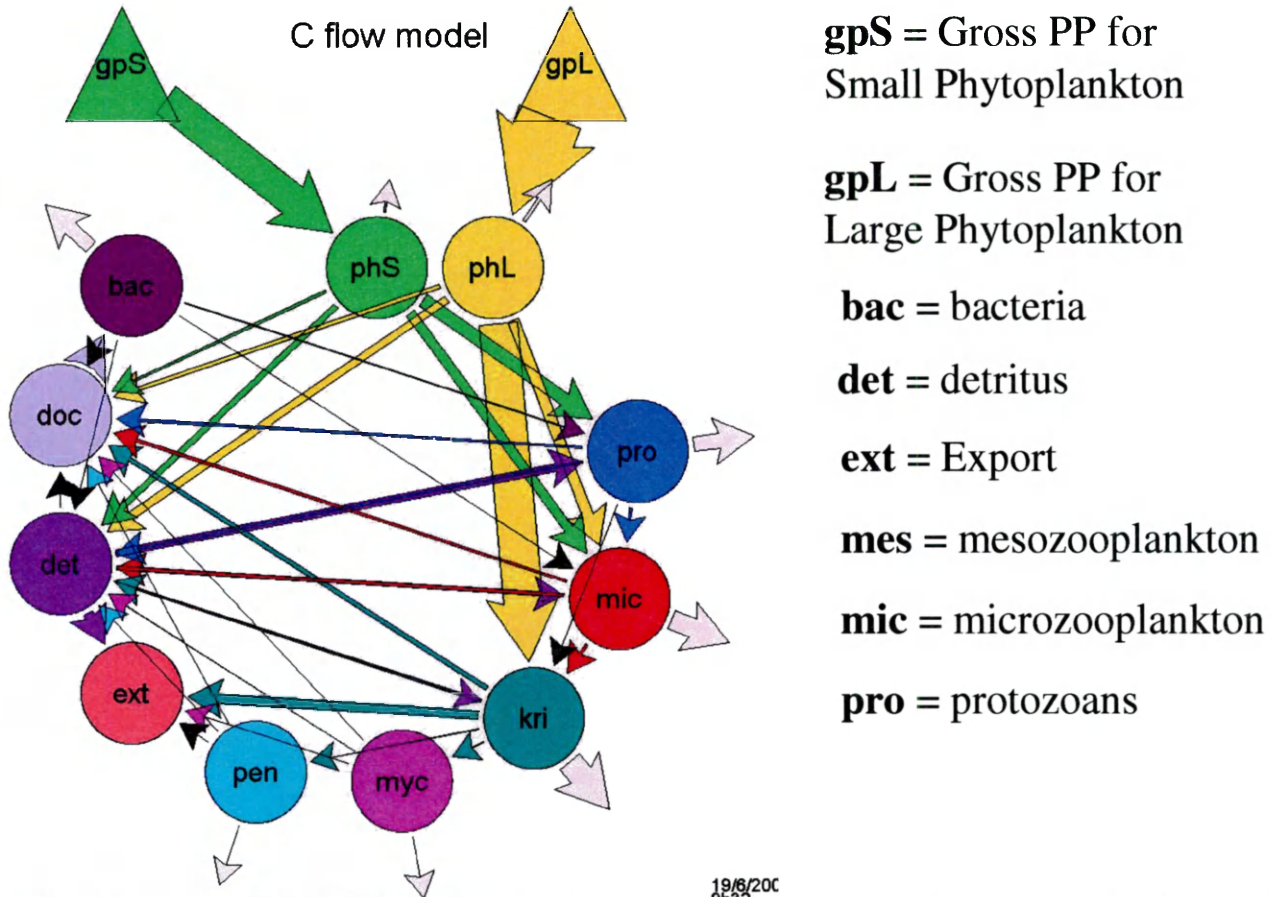


Figure 28. Carbon flow diagram for 1996 WAP inverse solution Inputs are from gross primary production for small phytoplankton (gps) and large phytoplankton (gpl). Export from the surface ocean enters the ext compartment. Black arrows represent flows the model found to be zero.

Table 23. WAP 1996 carbon inverse solution flows. Flows are expressed as absolute flows in mmols C /m^2/d and as a fraction of the net primary production.

Flows	mmols C $m^{-2}d^{-1}$	Normalized to Net PP
Large phytoplankton gross primary production	62.32	0.70
Large phytoplankton respiration	3.12	0.04
Microzooplankton grazing of large phytoplankton	9.84	0.11
krill grazing of large phytoplankton	37.10	0.42
Large phytoplankton sinking	8.86	0.10
Large phytoplankton release of DOC	3.40	0.04
Small phytoplankton gross primary production	31.16	0.35
Small phytoplankton respiration	1.56	0.02
Protozoan grazing of small phytoplankton	11.43	0.13
Microzooplankton grazing of small phytoplankton	8.72	0.10
Small phytoplankton to detritus	7.75	0.09
Small phytoplankton release of DOC	1.70	0.02
Microzooplankton consumption of protozoans	1.20	0.01
krill consumption of protozoans	0.37	0.00
Protozoan respiration	11.03	0.12
Protozoans to detritus	1.58	0.02
Protozoans to DOC	1.58	0.02
Microzooplankton respiration	14.52	0.16
Mesozooplantkton consumption of microzooplankton	2.07	0.02
Microzooplankton to detritus	2.07	0.02
Microzooplankton to DOC	2.07	0.02
krill respiration	17.46	0.20
krill to detritus (Faecal pellets)	2.38	0.03
krill to DOC	3.97	0.04
Bacterial respiration	12.20	0.14
Bacteria to protozoans	0.64	0.01
Bacteria to microzooplankton	0.00	0.00
Bacteria to detritus	0.00	0.00
Bacteria to DOC	0.00	0.00
Protozoan consumption of detritus	3.69	0.04
Microzooplankton consumption of detritus	0.98	0.01
krill consumption of detritus	0.14	0.00
Detritus to DOC	0.00	0.00
Bacterial ingestion of DOC	12.84	0.14
Total Particulate Export out of the top 35 m	17.83	0.20
Krill to export (Consumption by higher trophic levels or death	14.69	0.17
Myctophid consumption of krill	1.08	0.01
Penguins consumption of krill	0.11	0.001
Penguins to detritus	0.03	0.000
Penguins to DOC	0.01	0.000
Penguin respiration	0.03	0.000
Penguin to export (Consumption by higher trophic levels or death)	0.03	0.000
Myctophids to detritus	0.32	0.004
Myctophids to DOC	0.11	0.001
Myctophids to respiration	0.32	0.004
Myctophids to export (Consumption by higher trophic levels or death)	0.32	0.004

The particulate export sinking out of the top 35 m is equal to 18 mmols $Cm^{-2}d^{-1}$ or 21% of the primary production (Table 23). The export of krill, representing krill production that can be consumed by higher trophic levels or can sink when the krill die, is 15 mmols $Cm^{-2}d^{-1}$ or 17% of the primary production. The estimated e-ratio is equal to the sum of the particulate export, the krill export, the penguin export and the myctophid export in terms of the primary production:

e-ratio = 0.20 + 0.17 + 0 + 0.004 = 0.37.

The total carbon throughput of the paticulate organic carbon or detritus pool is about twice that of the dissolved organic carbon (DOC) pool. The total throughput of the detritus pool is 23 mmols $Cm^{-2}d^{-1}$ or 26% of the primary production. The total throughput of the DOC pool is 13 mmols $Cm^{-2}d^{-1}$ or 14% of the primary production.

Krill grazing dominates the fate of the carbon primary production (Figure 29). Krill consume 42% of the total primary production. Microzooplankton consume 21% and protozoans 13% of the total primary production. The detrital pool receives 26% of the small phytoplankton production and 15% of the large phytoplankton production. The DOC pool receives 6% of the total primary production.

The krill consumed the most carbon of the zooplankton (40 mmols $Cm^{-2}d^{-1}$), 94% of which consisted of large phytoplankton (Figure 30). Microzooplankton consumed less carbon than krill (21 mmols $Cm^{-2}d^{-1}$), receiving most of their carbon from small (42%) and large phytoplankton (47%) and smaller contributions from protozoans (6%) and detritus (5%). Protozoans consumed the least amount of carbon (16 mmols $Cm^{-2}d^{-1}$) and received a small portion of their diet (4%), from bacteria and a large portion from detritus

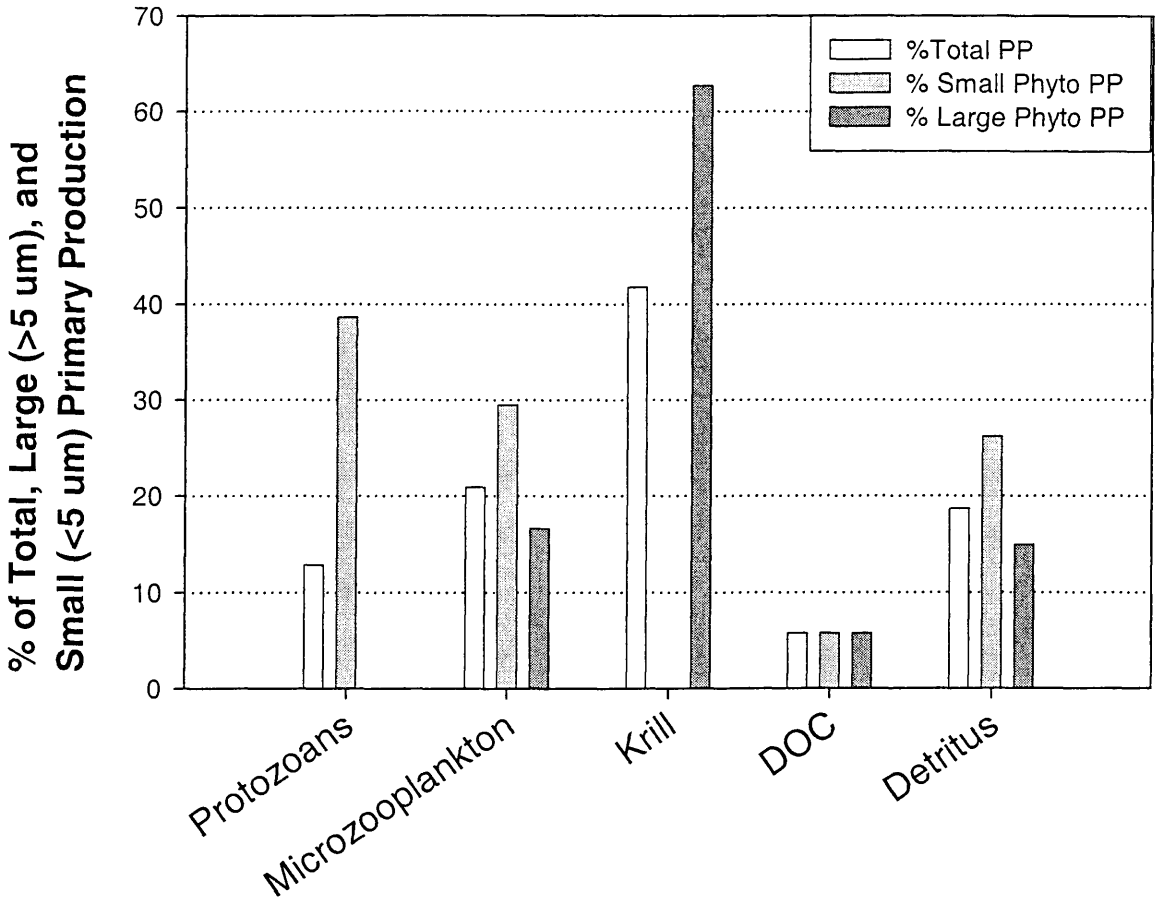


Figure 29. The fate of the carbon primary production for the western Antarctic Peninsula in January, 1996. The primary production is expressed as total, large (>5 μm), and small (<5 μm) primary production that is consumed by protozoans, microzooplankton, or krill, goes to detritus or is released as DOC.
goes to detritus, or is released as DOC.

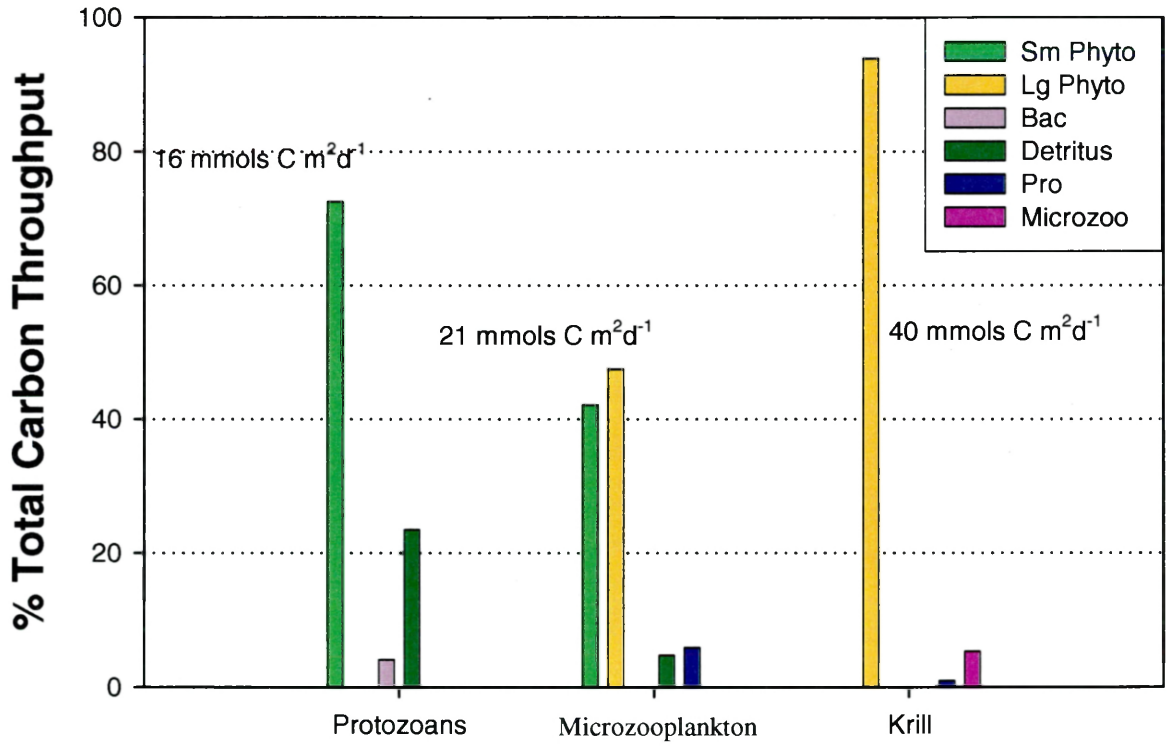


Figure 30. Zooplankton diet composition for the carbon solution for the western Antarctic Peninsula in January, 1996. The percentage of the diet contents for each zooplankton size class is shown. The total input in mmols $Cm^{-2}\ d^{-1}$ for each zooplankton size class is also shown.

(5%). The diet compositions of the myctophids and penguins are not shown here, because the only food source provided for them in the model was krill, their main food source in the western Antarctic Peninsula.

The exports from the surface ocean are shown in Table 24. The sinking of large phytoplankton, equal to 10% of the primary production, makes the greatest contribution to the flux. The aggregation of detritus from smaller particles into sinking particles is equal to 7% of the primary production and krill fecal pellets account for 3% of the primary production. The contributors to the particulate carbon pool, not shown in Table 24, that can provide smaller particles that can aggregate and sink are small phytoplankton, protozoans, and microzooplankton (Table 25). Small phytoplankton contribute 34% of the carbon to the particulate carbon pool, protozoans, 9% and microzooplankton, 7%.

Krill and large phytoplankton make the greatest contributions to the DOC pool, 31% and 27% respectively (Figure 31). Significant contributions also come from microzooplankton (16%), small phytoplankton (13%), and protozoans (12%).

Network Analysis (1996 Carbon Model)

The index of recycling, ***L*** revealed that the average carbon atom is cycled through the food web 1.4 times before leaving through respiration, sinking detritus, or fecal pellets (Table 26), about the same as in NABE (Ch. 2). Another index of recycling, the **Total ingestion / pp** equal to 1.3 indicates that 30% of the carbon ingestion comes from recycling in the food web. The bacterial production was equal to only 0.7% of the net primary production as shown by ***Fbac*** (Table 26). The krill processed the most carbon

Table 24. Export flows from the upper 35 m in the 1996 WAP carbon model. The sinking of large phytoplankton, and mesozooplankton fecal pellets contribute to the total detrital export. These two flows that are likely to sink are much greater than the Total Detrital Export. The consumption of detritus by protozoans is very high in the model, acting as a sink for detritus (see Table 30).

	% of Net PP exported
Sinking of Large Phytoplankton	10
Krill Fecal Pellets	3
Aggregation of Detritus into Sinking Particles	7
Total Detrital Export	20

Table 25. Contributions to the detritus pool as a % of the total inputs to the pool for the WAP 1996 carbon inverse solution.

	% Contribution to Detritus Pool
Small Phytoplankton	34
Large Phtyoplankton	39
Bacteria	0
Protozoans	7
Microzooplankton	9
Krill	10
Myctophids	1.4
Penguins	0.1

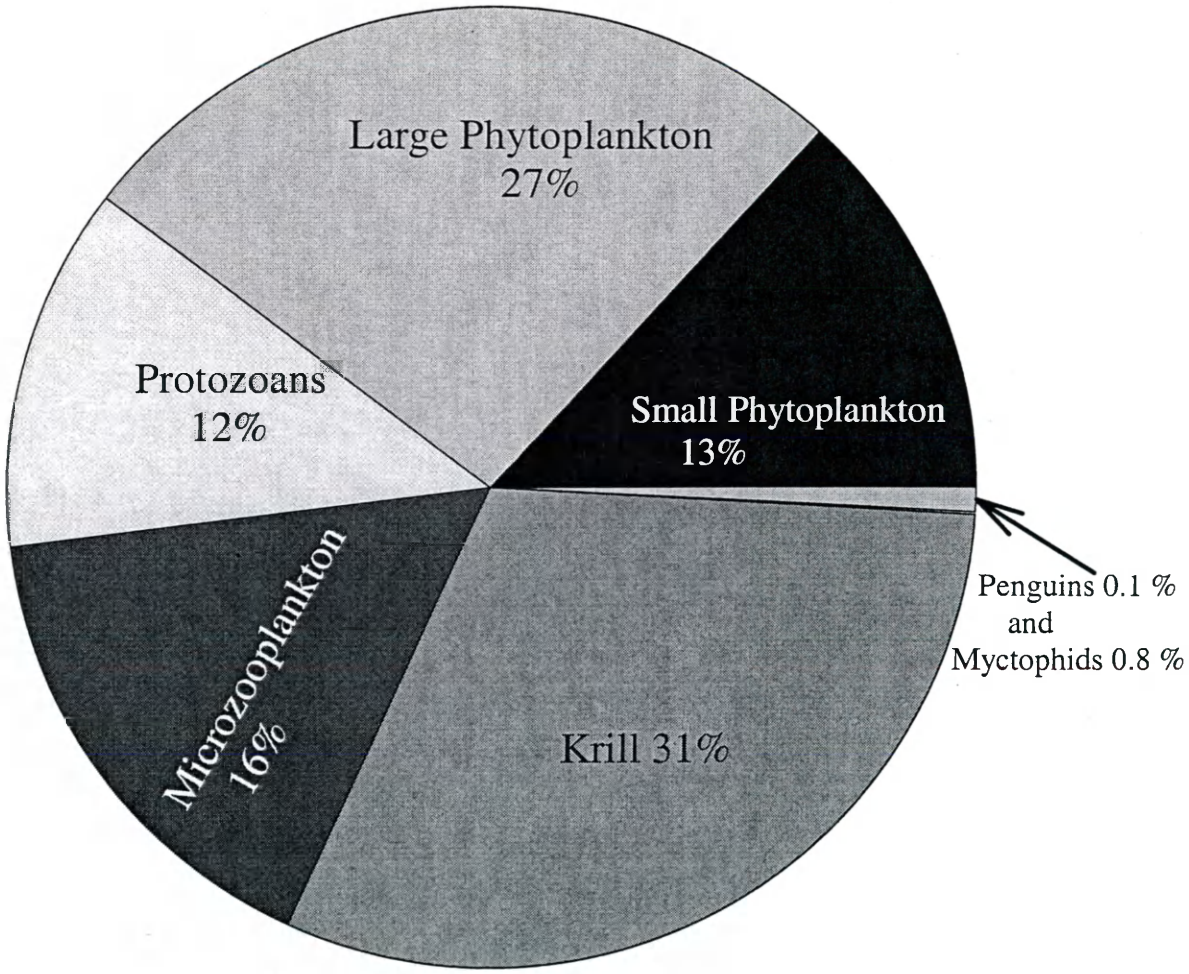


Figure 31. Contributions to the DOC pool as a % of the total flows entering it in the 1996 western Antarctic Peninsula carbon inverse solution.

(***Fkri*** = 51%), followed by the microzooplankton (***Fmic*** = 27%) and protozoans (***Fpro*** = 21%).

The bacteria depend on small phytoplankton for 33% of their carbon input and large phytoplankton for 67% (Table 27). All of the direct uptake of carbon comes to bacteria through the DOC pool, so the bacterial dependency on DOC is 1.0. Bacteria depend indirectly on protozoans, microzooplankton, and krill for between 14 and 33% of their uptake of carbon. Protozoans depend upon large phytoplankton for 16% of their diet, by way of indirect pathways, because they can not consume large phytoplankton directly. Protozoans have the highest dependency on detritus of any organism, equal to 24% of their diet.

The krill depend almost exclusively on large phytoplankton for 97% of their diet. Krill depend on other sources for a maximum of 5% (microzooplankton) of their diet. The myctophids and penguins both depend on krill for 100% of their diet as designated in the model structure. The other dependencies for myctophids and penguins mirror the dependencies of krill, because each predator inherits the krill dependencies by relying 100% on krill as a food source. The DOC pool depends strongly on phytoplankton for 33% and 67% of its inputs from small and large phytoplankton, respectively. Protozoans, microzooplankton, and krill all make siginificant contributions to the DOC pool by direct or indirect pathways, resulting in dependencies between 14 and 33%.

The effective trophic levels indicate the protozoans mainly act as grazers on small phytoplankton and consume only a relatively small amount of bacteria, giving them a trophic level of 2.04 (Table 28). Microzooplankton and krill both act chiefly as grazers

Table 26. Network analysis indices for the WAP 1996 carbon inverse solution.
L is the index of recycling equal to the number of times a carbon atom cycles through the food web before leaving through respiration, sinking, or predation by higher trophic levels
The **Total ingestion/ PP** is the total ingestion of all animal components plus the ingestion of DOC by bacteria divided by the net primary production.
Fbac is the ratio of bacterial production to net primary production.
Fpro, Fmic, and Fkri, Fmyc, and **Fpen** are the ratios of the total flows through each compartment to the total flows through all five animal compartments.

Index	
L	1.4
Total Ingestion/ PP	1.2
Fbac (%)	0.7
Fpro (%)	20.7
Fmic (%)	27.2
Fkri (%)	50.5
Fmyc (%)	1.4
Fpen (%)	0.1

Table 27. Dependency coefficients for the WAP 1996 carbon inverse solution. The fraction of the total ingestion by a component j (column designation) that passes through a component i (row designation) on its way to component j. For example, 48 % of the input to microzooplankton is mediated by small phytoplankton. Network Analysis program, NETWRK.exe by Ulanowicz (1986) provided the values shown.

	Entering								
Leaving	Small Phytoplankton	Large Phytoplankton	Bacteria	Protozoans	Microzooplankton	Krill	Myctophids	Penguins	DOC
Small Phytoplankton	0.00	0.00	0.33	0.84	0.49	0.04	0.04	0.04	0.33
Large Phytoplankton	0.00	0.00	0.67	0.16	0.51	0.97	0.97	0.97	0.67
Bacteria	0.00	0.00	0.01	0.04	0.00	0.00	0.00	0.00	0.01
Protozoans	0.00	0.00	0.14	0.02	0.06	0.01	0.01	0.01	0.14
Microzooplankton	0.00	0.00	0.18	0.03	0.01	0.05	0.05	0.05	0.18
Krill	0.00	0.00	0.33	0.04	0.01	0.00	1.00	1.00	0.33
Myctophids	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01
Penguins	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
DOC	0.00	0.00	1.00	0.04	0.00	0.00	0.00	0.00	0.01
Detritus	0.00	0.00	0.04	0.24	0.06	0.01	0.01	0.01	0.04

of phytoplankton, giving them trophic levels of 2.06 and 2.07, respectively. Myctophids and penguins have trophic levels exactly 1.0 greater than the krill trophic level, because they both depend on krill for 100% of their diets.

1999 Carbon Model Results

Krill and microzooplankton grazing were the largest flows within the food web in carbon model inverse solution for 1999 (Figure 32 and Table 29). The inferred small and large gross primary production were equal to 2.7 and 5.4 mmols $Cm^{-2}d^{-1}$, just slightly above their minimum constraints of 2 and 5 mmols $Cm^{-2}d^{-1}$ and equal to just about 10% of the 1996 production (Table 29). The largest flow within the food web is krill grazing of large phytoplankton equal to 1.6 mmols $Cm^{-2}d^{-1}$ or 21% of the primary production. The next largest flow within the food web is microzooplankton grazing of large phytoplankton equal to 1.2 mmols $Cm^{-2}d^{-1}$or 17% of primary production. Other large flows in the food web include large phytoplankton sinking, microzooplankton respiration, and bacterial respiration equal to 16, 15, and 15% of the primary production, respectively.

The particulate export sinking out of the top 35 m is equal to 1.4 mmols $Cm^{-2}d^{-1}$ or 18% of the primary production. The export of krill, representing krill production that can be consumed by higher trophic levels or can sink when the krill die, is 0.6 mmols $Cm^{-2}d^{-1}$ or 8% of the primary production. The estimated e-ratio is equal to the sum of the particulate export, the krill export, the penguin export, the myctophid export, and the salp export as a fraction of the primary production (Table 29):

e-ratio = 0.18 + 0.08 + 0 + 0.01 + 0.08 = 0.35.

Table 28. Effective trophic levels of the components in the WAP 1996 carbon model, found using the network analysis program, NETWRK.exe by Ulanawicz (1986). The nonliving components, DOC and Detritus are assigned trophic levels of 1.

Component	Effective Trophic Level
Small Phytoplankton	1
Large Phytoplankton	1
Bacteria	2
Protozoans	2.04
Microzooplankton	2.06
Krill	2.07
Myctophids	3.07
Penguins	3.07
DOC	1

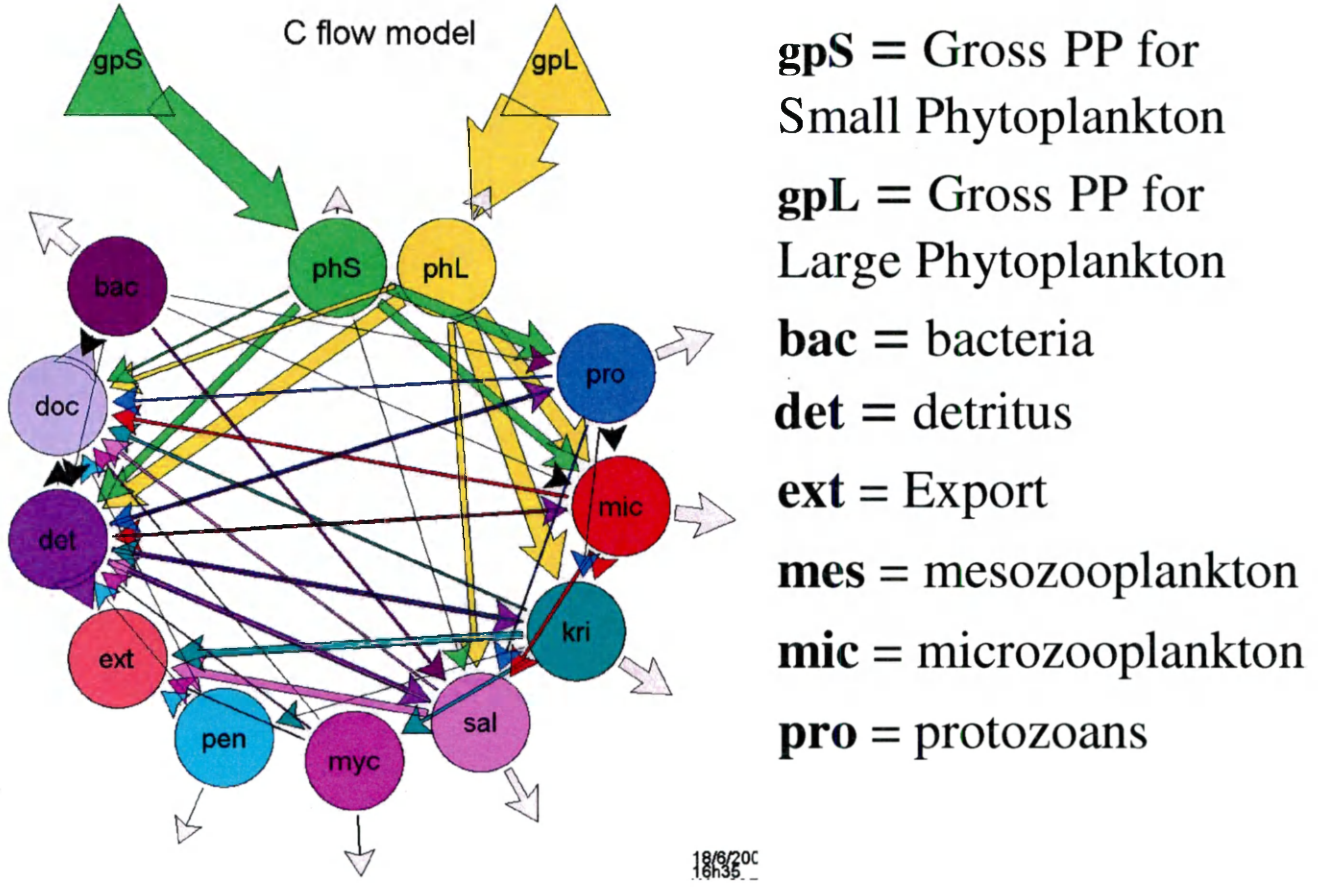


Figure 32. Carbon flow diagram for 1999 WAP inverse solution. Inputs are from gross primary production for small phytoplankton (gps) and large phytoplantkon (gpl). Export from the surface ocean enters the ext compartment. Black arrows represent flows the model found to be zero.

Table 29. WAP 1999 carbon inverse solution flows. Flows are expressed as absolute flows in mmols C /m^2/d and as a fraction of the net primary production.

Flows	mmols C $m^{-2}d^{-1}$	Normalized to Net PP
Large phytoplankton gross primary production	5.400	0.70
Large phytoplankton respiration	0.270	0.04
Microzooplankton grazing of large phytoplankton	1.271	0.17
krill grazing of large phytoplankton	1.627	0.21
Large phytoplankton sinking	1.246	0.16
Large phytoplankton release of DOC	0.400	0.05
Small phytoplankton gross primary production	2.705	0.35
Small phytoplankton respiration	0.135	0.02
Protozoan grazing of small phytoplankton	0.958	0.12
Microzooplankton grazing of small phytoplankton	0.707	0.09
Small phytoplankton to detritus	0.682	0.09
Small phytoplankton release of DOC	0.200	0.03
Microzooplankton consumption of protozoans	0.000	0.00
krill consumption of protozoans	0.021	0.00
Protozoan respiration	0.870	0.11
Protozoans to detritus	0.124	0.02
Protozoans to DOC	0.124	0.02
Microzooplankton respiration	1.186	0.15
Mesozooplantkton consumption of microzooplankton	0.167	0.02
Microzooplankton to detritus	0.200	0.03
Microzooplankton to DOC	0.200	0.03
krill respiration	0.966	0.13
krill to detritus (Fecal pellets)	0.132	0.02
krill to DOC	0.220	0.03
Bacterial respiration	1.132	0.15
Bacteria to protozoans	0.008	0.00
Bacteria to microzooplankton	0.000	0.00
Bacteria to detritus	0.000	0.00
Bacteria to DOC	0.000	0.00
Protozoan consumption of detritus	0.276	0.04
Microzooplankton consumption of detritus	0.025	0.00
krill consumption of detritus	0.381	0.05
Detritus to DOC	0.000	0.00
Bacterial ingestion of DOC	1.335	0.17
Total Particulate Export out of the top 35 m	1.401	0.18
Krill to export (Consumption by higher trophic levels or death)	0.584	0.08
Myctophid consumption of krill	0.264	0.03
Penguins consumption of krill	0.030	0.00
Penguins to detritus	0.009	0.00
Penguins to DOC	0.003	0.00
Penguin respiration	0.009	0.00
Penguin to export (Consumption by higher trophic levels or death)	0.009	0.00
Myctophids to detritus	0.079	0.01
Myctophids to DOC	0.026	0.00
Myctophids to respiration	0.079	0.01
Myctophids to export (Consumption by higher trophic levels or death)	0.079	0.01
Salps consumption of large phytoplankton	0.587	0.08
Salps consumption of small phytoplankton	0.023	0.00
Salps consumption of bacteria	0.195	0.03
Salps consumption of protozoans	0.103	0.01
Salps consumption of microzooplankton	0.249	0.03
Salps consumption of detritus	0.463	0.06
Salps respiration	0.648	0.08
Salps to detritus (fecal pellets)	0.162	0.02
Salps to DOC	0.162	0.02
Salps to export	0.648	0.08

The total throughput of the detritus pool is twice that of the DOC pool, like in the WAP 1996 solution. The total throughput of the detritus pool is 2.6 mmols $Cm^{-2}d^{-1}$ or 34% of the primary production. The throughput of the DOC pool is 1.3 mmols $Cm^{-2}d^{-1}$ or 17% of the primary production.

The total primary production is more evenly split among grazers, detritus and DOC than in the January 1996 inverse solution (Figure 33). Microzooplankton consume the highest amount of the total primary production (26 %). Krill consume 21% of the total production in 1999, much less than the 42% in 1996 (Figure 33). Other differences between the 1999 and 1996 fates of the primary production are the amount of production going to detritus and the introduction of salps. Salps consume 8% of the total primary production, the majority coming from the large phytoplankton of which they consume 11%. More production goes to detritus in the 1999 solution, 25% vs. 18% for 1996.

Krill consume the most carbon, and 90 % of their diet is large phytoplankton (2.3 mmols $Cm^{-2}d^{-1}$), (Figure 34). The microzooplankton consume a little less carbon than the krill (2.1 mmols $Cm^{-2}d^{-1}$) and have a less varied diet in 1999 than in 1996, consuming mainly large and small phytoplankton (Figure 34). Protozoans consume the least carbon, 1.5 mmols $Cm^{-2}d^{-1}$, 77% coming from small phytoplankton and a significant portion, 25% coming from detritus. Salps have the most varied diet, with 36% coming from large phytoplankton, 29% from detritus and the rest from bacteria, protozoans, and microzooplankton (Figure 34).

The sum of the large particle flows that one would expect to contribute to sinking is 22% of the primary production and exceeds the model's estimated sinking flux by 4%

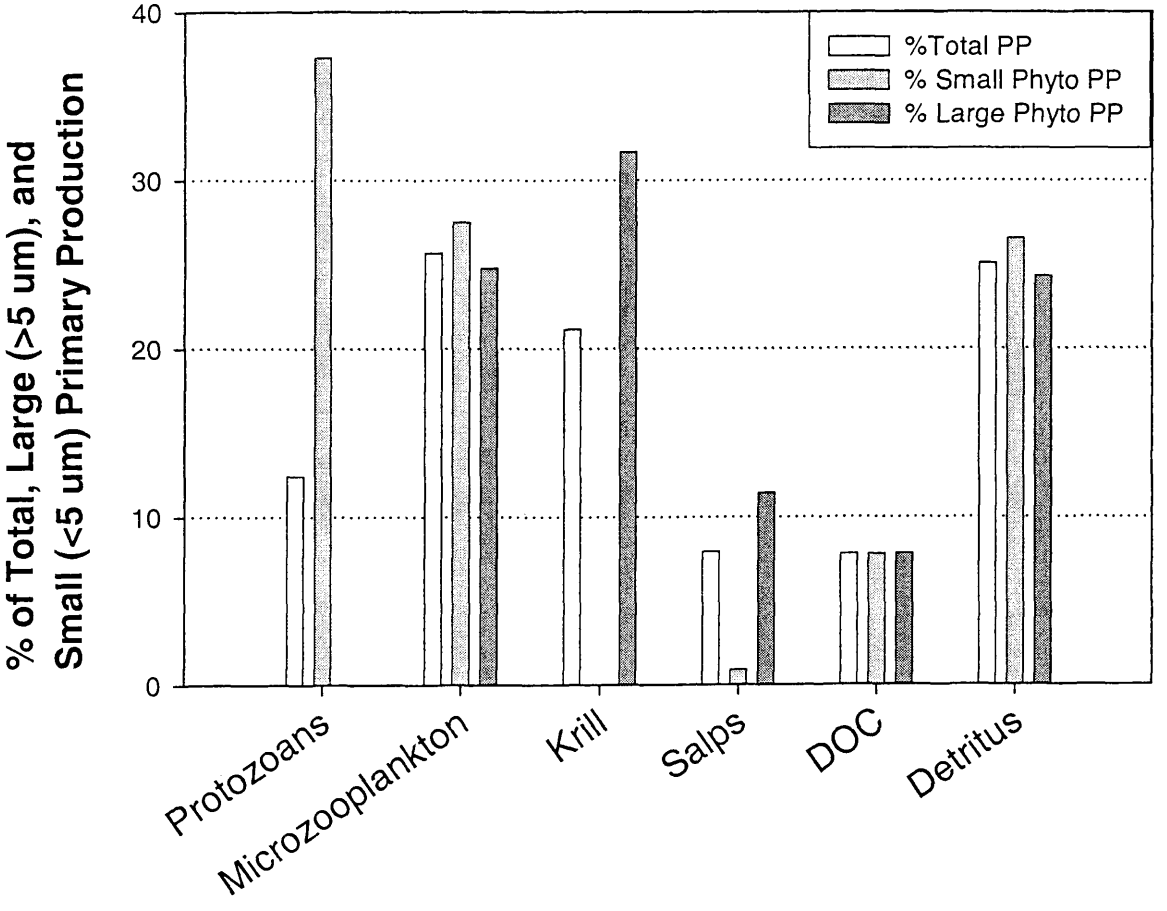


Figure 33. The fate of the carbon primary production for the western Antarctic Peninsula in January, 1999. The primary production is expressed as total, large (>5 μm), and small (<5 μm) primary production that is consumed by protozoans, microzooplankton, or krill, goes to detritus, or is released as DOC.

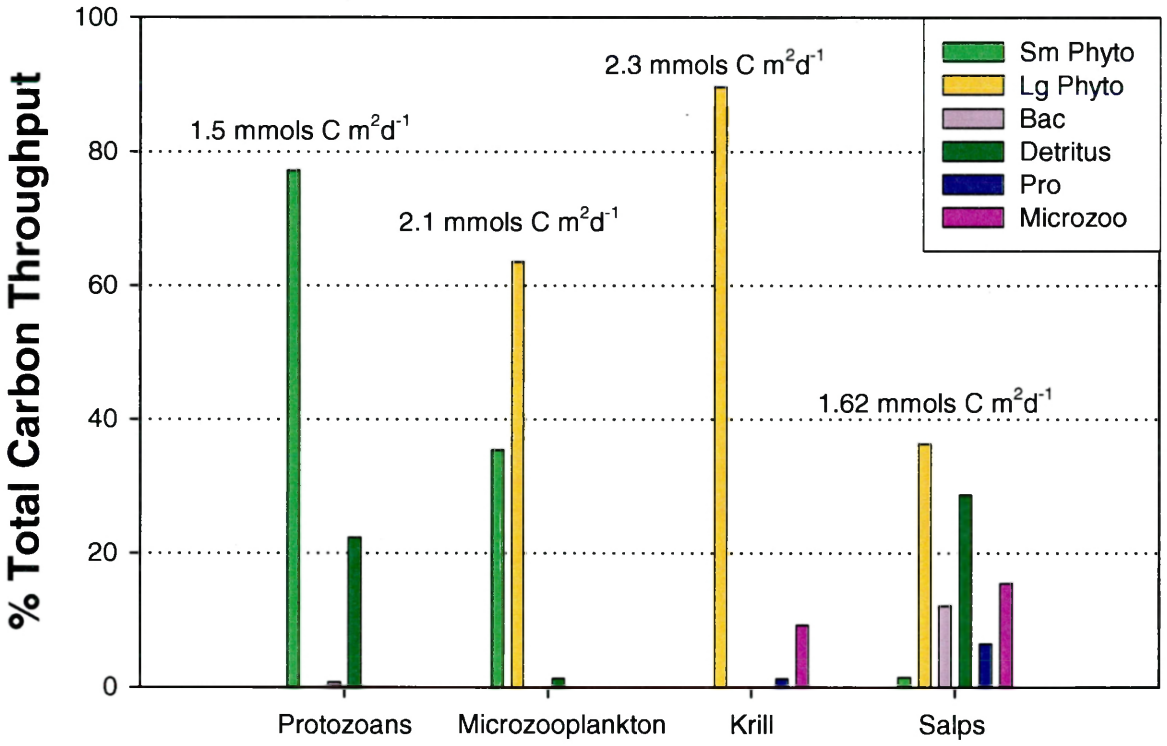


Figure 34. Zooplankton diet composition for the carbon solution for the western Antarctic Peninsula in January, 1999. The percentage of the diet contents for each zooplankton size class and salps is shown. The total input in mmols Cm^{-2} d^{-1} for each consumer is also shown.

(Table 30). It is possible that some of these flows are consumed as detritus by other organisms before sinking. The sum of detrital consumption by protozoans, microzooplankton, krill, and salps is 15% of the primary production (Table 31). The model structure assumes that all of the large phytoplankton and fecal pellets going to detritus sink. However, the high consumption of detritus suggests that some of these particles were consumed, explaining the difference of 4% between the sum of large sinking particles and the realized sinking shown in Table 30.

Large phytoplankton supply 30% of the carbon to the DOC pool and krill supply 16.5%, 10% less than they contributed in 1996 (Figure 35). The salps contribute 12%, a significant contribution to the DOC pool.

Network Analysis (1999 Carbon Model)

The index of recycling, ***L*** revealed that the average carbon atom is cycled through the food web 1.7 times before leaving through respiration, sinking detritus, or fecal pellets (Table 32). The **Total ingestion/ pp** of 1.3 indicates that 30% of the carbon ingestion comes from recycling in the food web (Table 32). The bacterial production was still very low, just 2.6% of the net primary production as shown by ***Fbac.*** The krill processed the most carbon (***Fkri*** = 28%), followed by the microzooplankton (***Fmic*** = 26%) and protozoans (***Fpro*** = 17%).

Salps, microzooplankton, and krill indirectly provide between 13 and 20% of the bacterial uptake of carbon (Table 33). Krill depend on large phytoplankton for 90% of their diet and small phytoplankton for 10%, which comes through indirect pathways (Table 33). The salps depend strongly on large phytoplankton for 74% of their diet. The

Table 30. Export flows from the upper 35 m in the 1999 WAP carbon model. The sinking of large phytoplankton, and fecal pellets from krill, salps, and myctophids account for more than 122 % of the sinking detrital export flow.

	% of Net PP exported
Sinking of Large Phytoplankton	16
Krill Fecal Pellets	2
Salp Fecal Pellets	2
Myctophid Fecal Pellets	2
Sum of Large sinking particles	22
Sinking Detrital Export	18

Table 31. Outputs from the detritus pool as a % of the primary production. The consumption of detritus by protozoans, microzooplankton, and salps adds up to 14.8 % of the primary production, more than enough to explain the 4 % difference between large particles and realized sinking shown in Table 37.

	Outputs as % of PP
Sinking Detrital export	18.2
Protozoan consumption	3.6
Microzooplankton consumption	0.3
Salp consumption	6.0
Krill consumption	4.9
Detritus to DOC	0.0

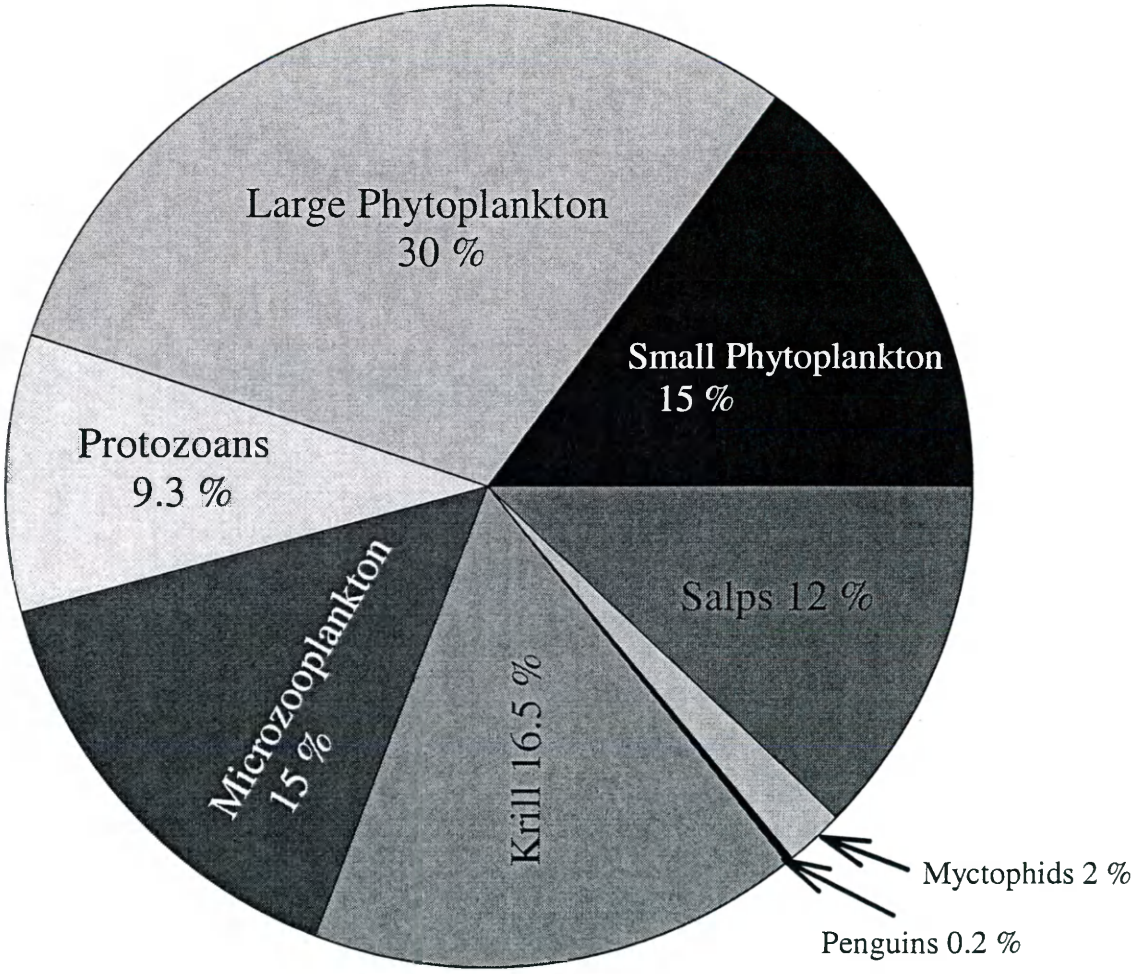


Figure 35. Contributions to the DOC pool in the 1999 western Antarctic Peninsula carbon inverse solution as a % of total flows entering pool.

Table 32. Network analysis indices for the WAP 1999 carbon inverse solution.
L is the index of recycling equal to the number of times a carbon atom cycles through the food web before leaving through respiration, sinking, or predation by higher trophic levels.
The **Total ingestion/ PP** is the total ingestion of all animal components plus the ingestion of DOC by bacteria divided by the net primary production.
Fbac is the ratio of bacterial production to net primary production.
Fpro, Fmic, and Fmes, Fmyc, Fsal and **Fpen** are the ratios of the total flows through each compartment to the total flows through all six animal compartments.

Index	
L	1.7
Total Ingestion/ PP	1.3
Fbac (%)	0.1
Fpro (%)	17.0
Fmic (%)	26.1
Fmes (%)	28.4
Fmyc (%)	3.9
Fsal (%)	24.1
Fpen (%)	0.4

Table 33. Dependency coefficients for the WAP 1999 carbon inverse solution. The fraction of the total ingestion by a component j (column designation) that passes through a component i (row designation) on its way to component j. For example, 36 % of the input to microzooplankton is mediated by small phytoplankton. Network Analysis program, NETWRK.exe by Ulanowicz (1986) provided the values shown.

	Entering									
Leaving	Small Phytoplankton	Large Phytoplankton	Bacteria	Protozoans	Microzooplankton	Krill	Myctophids	Penguins	Salps	DOC
Small Phytoplankton	0.00	0.00	0.33	0.85	0.36	0.10	0.10	0.10	0.26	0.33
Large Phytoplankton	0.00	0.00	0.67	0.15	0.64	0.90	0.90	0.90	0.74	0.67
Bacteria	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.12	0.02
Protozoans	0.00	0.00	0.11	0.01	0.00	0.02	0.02	0.02	0.09	0.11
Microzooplankton	0.00	0.00	0.19	0.02	0.00	0.09	0.09	0.09	0.21	0.19
Krill	0.00	0.00	0.20	0.02	0.00	0.02	1.00	1.00	0.05	0.20
Myctophids	0.00	0.00	0.02	0.01	0.00	0.01	0.01	0.01	0.01	0.02
Penguins	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Salps	0.00	0.00	0.13	0.01	0.00	0.01	0.01	0.01	0.03	0.13
DOC	0.00	0.00	1.00	0.01	0.00	0.00	0.00	0.00	0.12	0.02

salps depend on all other components except for myctophids and penguins for at least 5% contributions to their diet. The DOC pool depends on krill, microzooplankton, protozoans, and salps for between 11 and 20% of its carbon input.

The effective trophic levels for the 1999 carbon inverse solution are very similar to the 1996 trophic levels (Table 34). The protozoans, with a trophic level of 2.01, act almost entirely as grazers on small phytoplankton and consume only a relatively small amount of bacteria. Microzooplankton act entirely as grazers on small and large phytoplankton, and consumers of detritus giving resulting in a trophic level of 2. Krill act chiefly as grazers of plankton resulting in a trophic level of 2.09. Myctophids and penguins have trophic levels exactly 1.0 greater than the krill trophic level, because they both depend on krill for 100% of their diets. Salps feed at a trophic level of 2.34, reflecting their varied diet.

Sensitivity Analysis

In the 1996 inverse solution, the input parameters that brought about the most changes in the food web flows, were the large and small net primary production. The +/- 10% changes in the large net primary production, caused between 20 (-10% change) and 25 (+10% change) of the flows to change by more than 10% (Figure 36, Tables 35 and 36). The +/- 10% changes in the small net primary production, triggered changes of greater than 10% in between 25 (-10% change) and 30 (+10% change) of the 46 total flows (Figure 36, Tables 35 and 36).

The flow that was most sensitive to changes in the input parameters was the krill consumption of detritus. The 10% increase in the large phytoplankton primary

Table 34. Effective trophic level of the components in the WAP 1999 carbon model, found using the network analysis program, NETWRK.exe by Ulanawicz (1986). The nonliving components, DOC and Detritus are assigned trophic levels of 1.

Component	Effective Trophic Level
Small Phytoplankton	1
Large Phytoplankton	1
Bacteria	2
Protozoans	2.01
Microzooplankton	2
Krill	2.09
Myctophids	3.09
Penguins	3.09
Salps	2.34
DOC	1
Detritus	1

production, increased the consumption of detritus by krill by 12 X and the decrease of 10% decreased the consumption to zero (Figure 36, Tables 35 and 36). The 10% increase in the small phytoplankton primary production, increased the consumption of detritus by krill by 24 X and the decrease of 10% also decreased the consumption to zero (Figure 36, Tables 35 and 36). Other flows that showed large changes to manipulations of the input parameters were the release of DOC by large and small phytoplankton. The large phytoplankton release of DOC increased by about 2 X with 10% increases in large phytoplankton primary production and minimum bacterial production (Figure 37, Tables 35 and 36). The small phytoplankton release of DOC increased 4.6 X with the increase in minimum bacterial production (Figure 37, Tables 35 and 36).

The input parameters that had the greatest effects on the flows in the 1999 inverse solution, as seen in the 1996 model, were the large and small primary production. The +/- 10% changes in the large phytoplankton production, brought about changes greater than 10% in between 35 (+10% change) and 41 (-10% change) of the total 56 flows (Figure 38, Tables 37 and 38). The +/- 10% changes in the small primary production, triggered changes greater than 10% in between 24 (-10% change) and 27 (+10% change) of the flows (Figure 38, Tables 37 and 38). The increase in minimum bacterial production changed 34 of the 56 flows by more than 10% (Figure 39, Tables 37 and 38). Changes in penguin feeding and in salp maximum feeding brought about changes of greater than 10% in 7 or fewer flows (Tables 37 and 38).

There wasn't one flow that stood out as being the most sensitive in the 1999 solution. Many of the flows were altered by more than 10% by changes in 3 of the input

parameters. The microzooplankton consumption of bacteria, bacteria to detritus, and bacterial release of DOC were zero in the original solution and made positive by the increase in the minimum bacterial production (Figure 39, Tables 37 and 38). The minimum bacterial production was zero in the original solution, so the increase forced positive bacterial production.

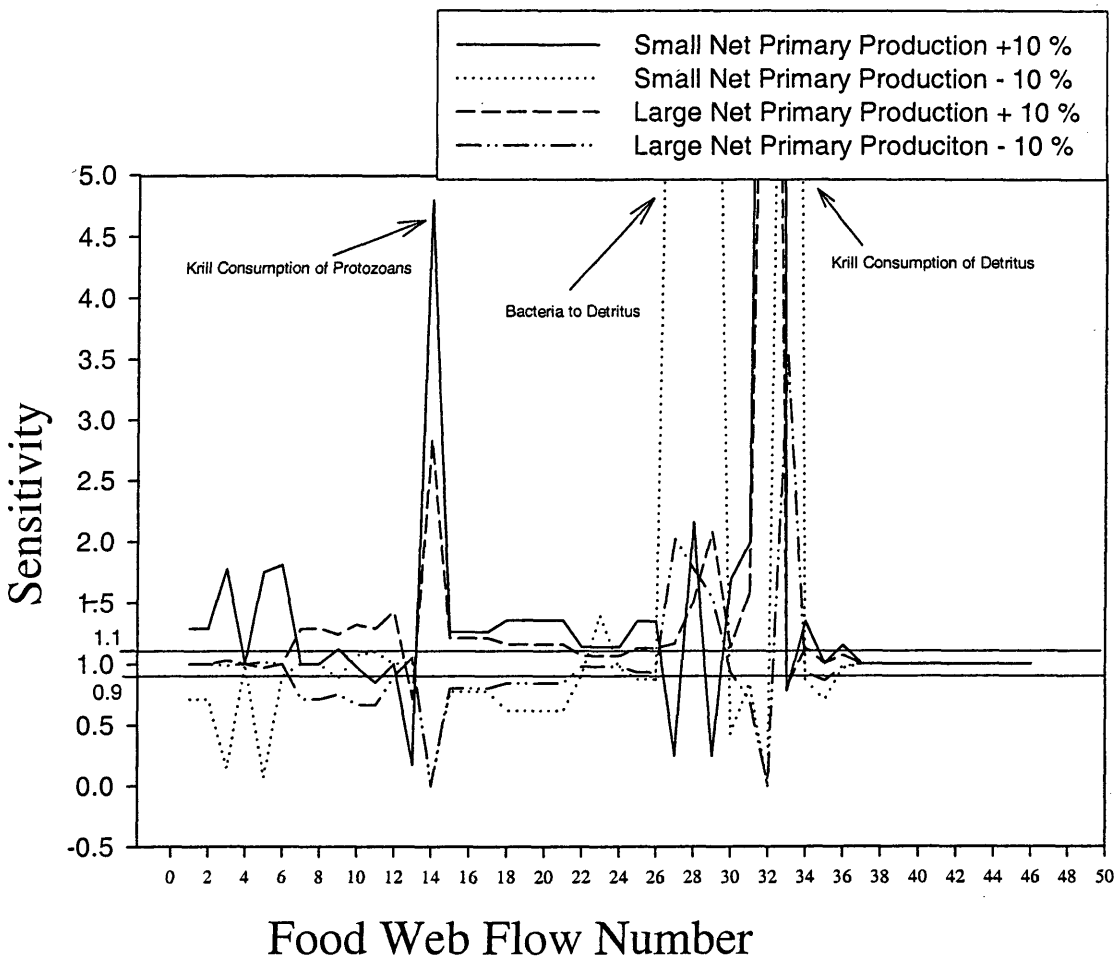


Figure 36. Sensitivity analysis for changes in the input parameters: large and small net primary production in the western Antarctic Peninsula, 1996 carbon model. The input parameters, representing measurements, were varied by + and - 10 %, individually. The response of the food web flow is the new value resulting from the +/- 10 % change in the input parameter divided by the original value of the flow. Food web flow numbers are described in Tables 34 and 35.

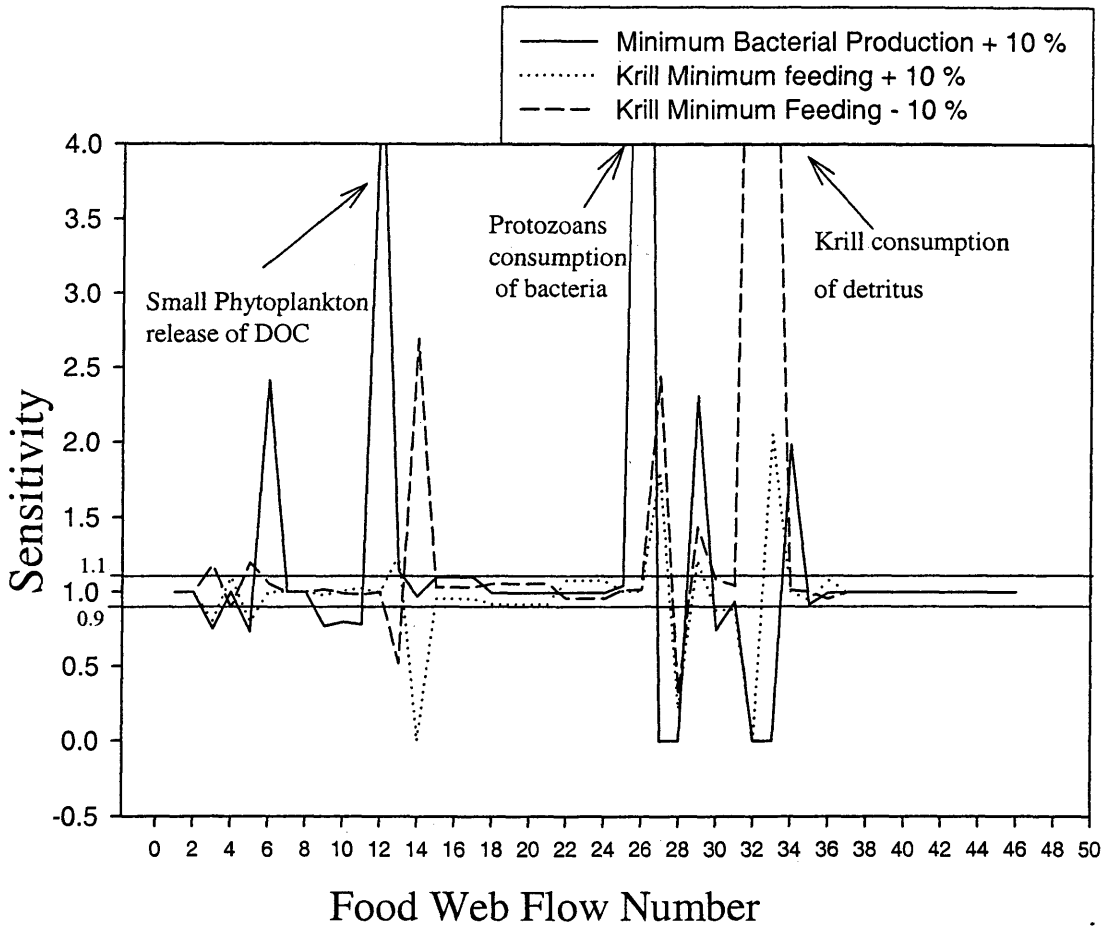


Figure 37. Sensitivity analysis for changes in the input parameters: minimum bacterial production and krill minimum feeding in the western Antarctic Peninsula, 1996 carbon model. The input parameters, representing measurements, were varied by + and - 10 %, individually. The response of the food web flow is the new value resulting from the +/- 10 % change in the input parameter divided by the original value of the flow. Food web flow numbers are described in Tables 34 and 35.

Table 35. Sensitivity Analysis with change in input parameters by + 10 % for the WAP 1996 carbon model.
The ratio shown is the model flow resulting from the 10 % change in the input parameter divided by the original model flow.
A '+' before a value indicates the value was 0 in original solution and increased to the # mmols C $m^{-2}d^{-1}$ shown.

Flow #	Flow	Small Net Primary Production	Large Net Primary Production	Export	Minimum Bacterial Production	Maximum Bacterial Production	Bacterial Biomass	Mininimum Microzooplankton Feeding	Maximum Microzooplankton Feeding	Temp	Krill minimum feeding	Krill maximum feeding	Krill Biomass	Penguin Feeding	Myctophid Minimum Feeding	Myctophid Maximum Feeding	Myctophid Biomass
1	Large phytoplankton gross primary production	1.29	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
2	Large phytoplankton respiration	1.29	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
3	Microzooplankton grazing of large phytoplankton	1.77	1.03	1.00	0.75	1.00	1.00	1.00	1.00	1.00	0.81	1.00	1.00	1.00	1.00	1.00	1.00
4	krill grazing of large phytoplankton	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00	1.00	1.00	1.00	1.00	1.00
5	Large phytoplankton sinking	1.75	0.97	1.00	0.73	1.00	1.00	1.00	1.00	1.00	0.80	1.00	1.00	1.00	1.00	1.00	1.00
6	Large phytoplankton release of DOC	1.81	1.00	1.00	2.41	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
7	Small phytoplankton gross primary production	1.00	1.29	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
8	Small phytoplankton respiration	1.00	1.29	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
9	Protozoan grazing of small phytoplankton	1.12	1.24	1.00	0.77	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00	1.00	1.00	1.00	1.00
10	Microzooplankton grazing of small phytoplankton	0.98	1.32	1.00	0.80	1.00	1.00	1.00	1.00	1.00	1.01	1.00	1.00	1.00	1.00	1.00	1.00
11	Small phytoplankton to detritus	0.85	1.29	1.00	0.78	1.00	1.00	1.00	1.00	1.00	1.02	1.00	1.00	1.00	1.00	1.00	1.00
12	Small phytoplankton release of DOC	1.00	1.43	1.00	4.56	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
13	Microzooplankton consumption of protozoans	0.17	0.71	1.00	1.14	1.00	1.00	1.00	1.00	1.00	1.25	1.00	1.00	1.00	1.00	0.99	1.00
14	krill consumption of protozoans	4.79	2.83	1.00	0.97	1.00	1.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	1.00	1.03	1.00
15	Protozoan respiration	1.26	1.21	1.00	1.10	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00
16	Protozoans to detritus	1.26	1.21	1.00	1.10	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00
17	Protozoans to DOC	1.26	1.21	1.00	1.10	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00
18	Microzooplankton respiration	1.36	1.16	1.00	0.99	1.00	1.00	1.00	1.00	1.00	0.92	1.00	1.00	1.00	1.00	1.00	1.00
19	Mesozooplantkton consumption of microzooplankton	1.36	1.16	1.00	0.99	1.00	1.00	1.00	1.00	1.00	0.92	1.00	1.00	1.00	1.00	1.00	1.00
20	Microzooplankton to detritus	1.36	1.16	1.00	0.99	1.00	1.00	1.00	1.00	1.00	0.92	1.00	1.00	1.00	1.00	1.00	1.00
21	Microzooplankton to DOC	1.36	1.16	1.00	0.99	1.00	1.00	1.00	1.00	1.00	0.92	1.00	1.00	1.00	1.00	1.00	1.00
22	krill respiration	1.14	1.07	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.08	1.00	1.00	1.00	1.00	1.00	1.00
23	krill to detritus (Faecal pellets)	1.14	1.07	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.08	1.00	1.00	1.00	1.00	1.00	1.00
24	krill to DOC	1.14	1.07	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.08	1.00	1.00	1.00	1.00	1.00	1.00
25	Bacterial respiration	1.35	1.13	1.00	1.05	1.00	1.00	1.00	1.00	1.00	1.01	1.00	1.00	1.00	1.00	1.00	1.00
26	Bacteria to protozoans	1.35	1.13	1.00	9.01	1.00	1.00	1.00	1.00	1.00	1.01	1.00	1.00	1.00	1.00	1.00	1.00
27	Bacteria to microzooplankton	0.25	1.17	1.00	0.00	1.00	1.00	1.00	1.00	1.00	1.81	1.00	1.00	2.08	1.00	1.51	1.00
28	Bacteria to detritus	2.16	1.51	1.00	0.00	1.00	1.00	1.00	1.00	1.00	0.21	1.00	1.00	2.10	1.00	1.35	1.00
29	Bacteria to DOC	0.25	2.08	1.00	2.31	1.00	1.00	1.00	1.00	1.00	1.21	1.00	1.00	1.24	1.00	1.82	1.00
30	Protozoan consumption of detritus	1.69	1.14	1.00	0.75	1.00	1.00	1.00	1.00	1.00	0.88	1.00	1.00	1.00	1.00	1.00	1.00
31	Microzooplankton consumption of detritus	1.99	1.58	1.00	0.94	1.00	1.00	1.00	1.00	1.00	0.88	1.00	1.00	1.00	1.00	1.00	1.00
32	krill consumption of detritus	24.36	12.09	1.00	0.00	1.00	1.00	1.00	1.00	1.00	0.00	1.00	1.00	1.01	1.00	1.14	1.00
33	Detritus to DOC	0.78	0.81	1.00	0.00	1.00	1.00	1.00	1.00	1.00	2.06	1.00	1.00	3.37	1.00	6.37	1.00
34	Bacterial ingestion of DOC	1.35	1.13	1.00	1.99	1.00	1.00	1.00	1.00	1.00	1.01	1.00	1.00	1.00	1.00	1.00	1.00
35	Total Particulate Export out of the top 35 m	1.00	1.00	1.00	0.92	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00
36	Krill to export (Consumption by higher trophic levels or death)	1.15	1.07	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.08	1.00	1.00	1.00	1.00	0.99	1.00
37	Myctophid consumption of krill	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00
38	Penguins consumption of krill	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00	1.00	1.00
39	Penguins to detritus	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00	1.00	1.00
40	Penguins to DOC	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00	1.00	1.00
41	Penguin respiration	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00	1.00	1.00
42	Penguin to export (Consumption by higher trophic levels or death)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00	1.00	1.00
43	Myctophids to detritus	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00
44	Myctophids to DOC	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00
45	Myctophids to respiration	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00
46	Myctophids to export (Consumption by higher trophic levels or death)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00

Table 36. Sensitivity Analysis with change in input parameters by - 10 % for the WAP 1996 carbon model.
The ratio shown is the model flow resulting from the 10 % change in the input parameter divided by the original model flow.
A '+' before a value indicates the value was 0 in original solution and increased to the # mmols C $m^{-2}d^{-1}$ shown.

Flow #	Flow	Small Net Primary Production	Large Net Primary Production	Export	Minimum Bacterial Production	Maximum Bacterial Production	Bacterial Biomass	Mininimum Microzooplankton Feeding	Maximum Microzooplankton Feeding	Temp	Krill minimum feeding	Krill maximum feeding	Krill Biomass	Penguin Feeding	Myctophid Minimum Feeding	Myctophid Maximum Feeding	Myctophid Biomass
1	Large phytoplankton gross primary production	0.71	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
2	Large phytoplankton respiration	0.71	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
3	Microzooplankton grazing of large phytoplankton	0.15	0.99	1.02	1.00	1.00	1.00	1.00	1.00	1.00	1.18	1.00	1.00	1.00	1.00	1.00	1.00
4	krill grazing of large phytoplankton	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00	1.00	1.00	1.00
5	Large phytoplankton sinking	0.07	1.02	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.20	1.00	1.00	1.00	1.00	1.00	1.00
6	Large phytoplankton release of DOC	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.06	1.00	1.00	1.00	1.00	1.00	1.00
7	Small phytoplankton gross primary production	1.00	0.71	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
8	Small phytoplankton respiration	1.00	0.71	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
9	Protozoan grazing of small phytoplankton	0.88	0.75	1.01	1.00	1.00	1.00	1.00	1.00	1.00	1.02	1.00	1.00	1.00	1.00	1.00	1.00
10	Microzooplankton grazing of small phytoplankton	1.07	0.67	1.01	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00
11	Small phytoplankton to detritus	1.10	0.66	0.96	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00	1.00	1.00	1.00	1.00
12	Small phytoplankton release of DOC	1.00	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
13	Microzooplankton consumption of protozoans	1.01	1.05	0.96	1.00	1.00	1.00	1.00	1.00	1.00	0.52	1.00	1.00	1.00	1.00	1.01	1.00
14	krill consumption of protozoans	0.00	0.00	1.29	1.00	1.00	1.00	1.00	1.00	1.00	2.70	1.00	1.00	1.00	1.00	0.97	1.00
15	Protozoan respiration	0.77	0.80	1.04	1.00	1.00	1.00	1.00	1.00	1.00	1.03	1.00	1.00	1.00	1.00	1.00	1.00
16	Protozoans to detritus	0.77	0.80	1.04	1.00	1.00	1.00	1.00	1.00	1.00	1.03	1.00	1.00	1.00	1.00	1.00	1.00
17	Protozoans to DOC	0.77	0.80	1.04	1.00	1.00	1.00	1.00	1.00	1.00	1.03	1.00	1.00	1.00	1.00	1.00	1.00
18	Microzooplankton respiration	0.62	0.84	1.03	1.00	1.00	1.00	1.00	1.00	1.00	1.06	1.00	1.00	1.00	1.00	1.00	1.00
19	Mesozooplantkton consumption of microzooplankton	0.62	0.84	1.03	1.00	1.00	1.00	1.00	1.00	1.00	1.06	1.00	1.00	1.00	1.00	1.00	1.00
20	Microzooplankton to detritus	0.62	0.84	1.03	1.00	1.00	1.00	1.00	1.00	1.00	1.06	1.00	1.00	1.00	1.00	1.00	1.00
21	Microzooplankton to DOC	0.62	0.84	1.03	1.00	1.00	1.00	1.00	1.00	1.00	1.06	1.00	1.00	1.00	1.00	1.00	1.00
22	krill respiration	0.91	0.98	1.02	1.00	1.00	1.00	1.00	1.00	1.00	0.96	1.00	1.00	1.00	1.00	1.00	1.00
23	krill to detritus (Faecal pellets)	1.40	0.98	1.02	1.00	1.00	1.00	1.00	1.00	1.00	0.96	1.00	1.00	1.00	1.00	1.00	1.00
24	krill to DOC	0.97	0.98	1.02	1.00	1.00	1.00	1.00	1.00	1.00	0.96	1.00	1.00	1.00	1.00	1.00	1.00
25	Bacterial respiration	0.87	0.93	1.02	1.00	1.00	1.00	1.00	1.00	1.00	1.01	1.00	1.00	1.00	1.00	1.00	1.00
26	Bacteria to protozoans	0.87	0.93	1.02	1.00	1.00	1.00	1.00	1.00	1.00	1.01	1.00	1.00	1.00	1.00	1.00	1.00
27	Bacteria to microzooplankton	12.11	2.02	1.08	1.00	1.00	1.00	1.00	1.00	1.00	2.44	1.00	1.00	2.25	1.00	1.99	1.00
28	Bacteria to detritus	8.14	1.77	0.49	1.00	1.00	1.00	1.00	1.00	1.00	0.31	1.00	1.00	1.73	1.00	0.94	1.00
29	Bacteria to DOC	7.93	1.54	0.22	1.00	1.00	1.00	1.00	1.00	1.00	1.43	1.00	1.00	1.44	1.00	1.17	1.00
30	Protozoan consumption of detritus	0.43	0.93	1.12	1.00	1.00	1.00	1.00	1.00	1.00	1.09	1.00	1.00	1.00	1.00	1.00	1.00
31	Microzooplankton consumption of detritus	0.84	0.71	1.41	1.00	1.00	1.00	1.00	1.00	1.00	1.04	1.00	1.00	1.00	1.00	1.00	1.00
32	krill consumption of detritus	0.00	0.00	4.89	1.00	1.00	1.00	1.00	1.00	1.00	9.66	1.00	1.00	0.99	1.00	0.86	1.00
33	Detritus to DOC	15.44	3.53	0.00	1.00	1.00	1.00	1.00	1.00	1.00	5.26	1.00	1.00	6.35	1.00	3.78	1.00
34	Bacterial ingestion of DOC	0.87	0.93	1.02	1.00	1.00	1.00	1.00	1.00	1.00	1.01	1.00	1.00	1.00	1.00	1.00	1.00
35	Total Particulate Export out of the top 35 m	0.70	0.86	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
36	Krill to export (Consumption by higher trophic levels or death)	0.96	0.98	1.02	1.00	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.01	1.00
37	Myctophid consumption of krill	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00
38	Penguins consumption of krill	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00
39	Penguins to detritus	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00
40	Penguins to DOC	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00
41	Penguin respiration	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00
42	Penguin to export (Consumption by higher trophic levels or death)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00
43	Myctophids to detritus	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00
44	Myctophids to DOC	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00
45	Myctophids to respiration	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00
46	Myctophids to export (Consumption by higher trophic levels or death)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00

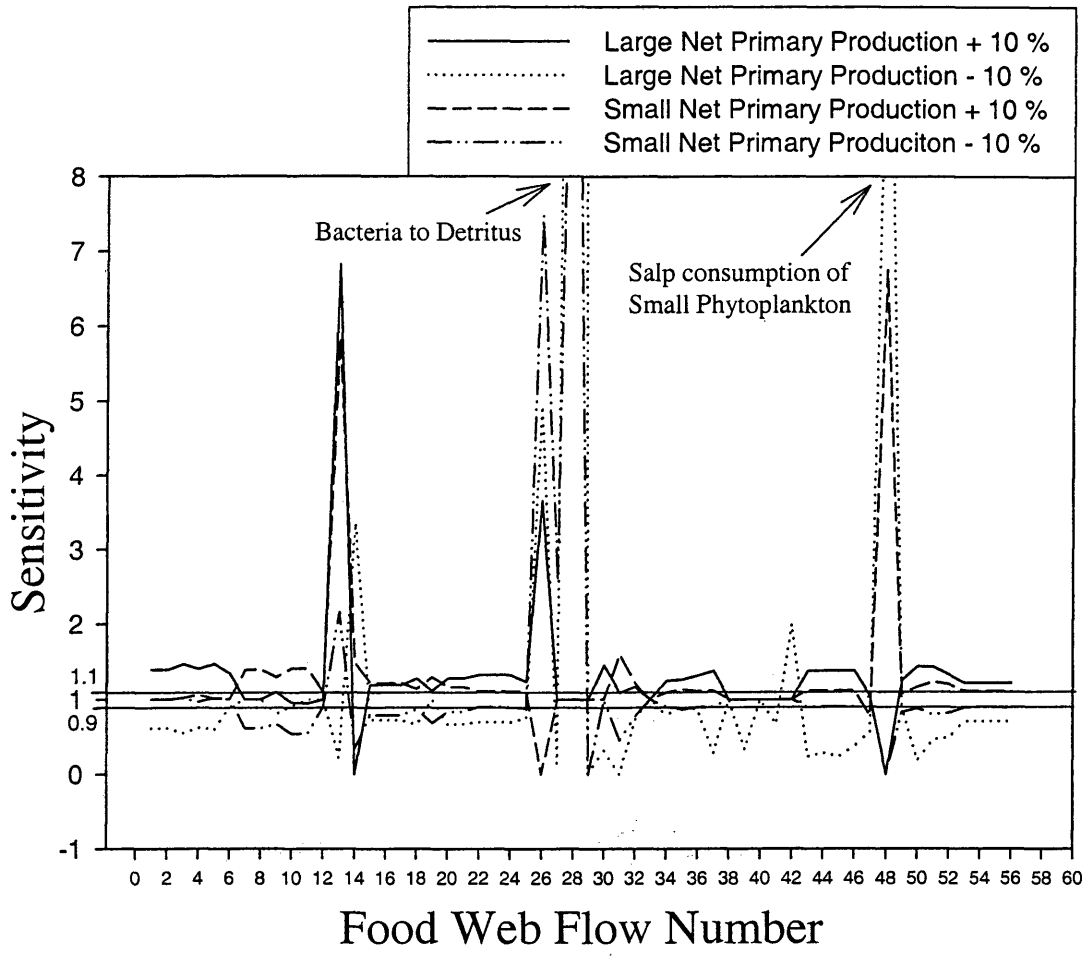


Figure 38. Sensitivity analysis for changes in the input parameters: large and small net primary production in the western Antarctic Peninsula, 1999 carbon model. The input parameters, representing measurements, were varied by + and - 10 %, individually. The response of the food web flow is the new value resulting from the +/- 10 % change in the input parameter divided by the original value of the flow. Food web flow numbers are described in Tables 37 and 38.

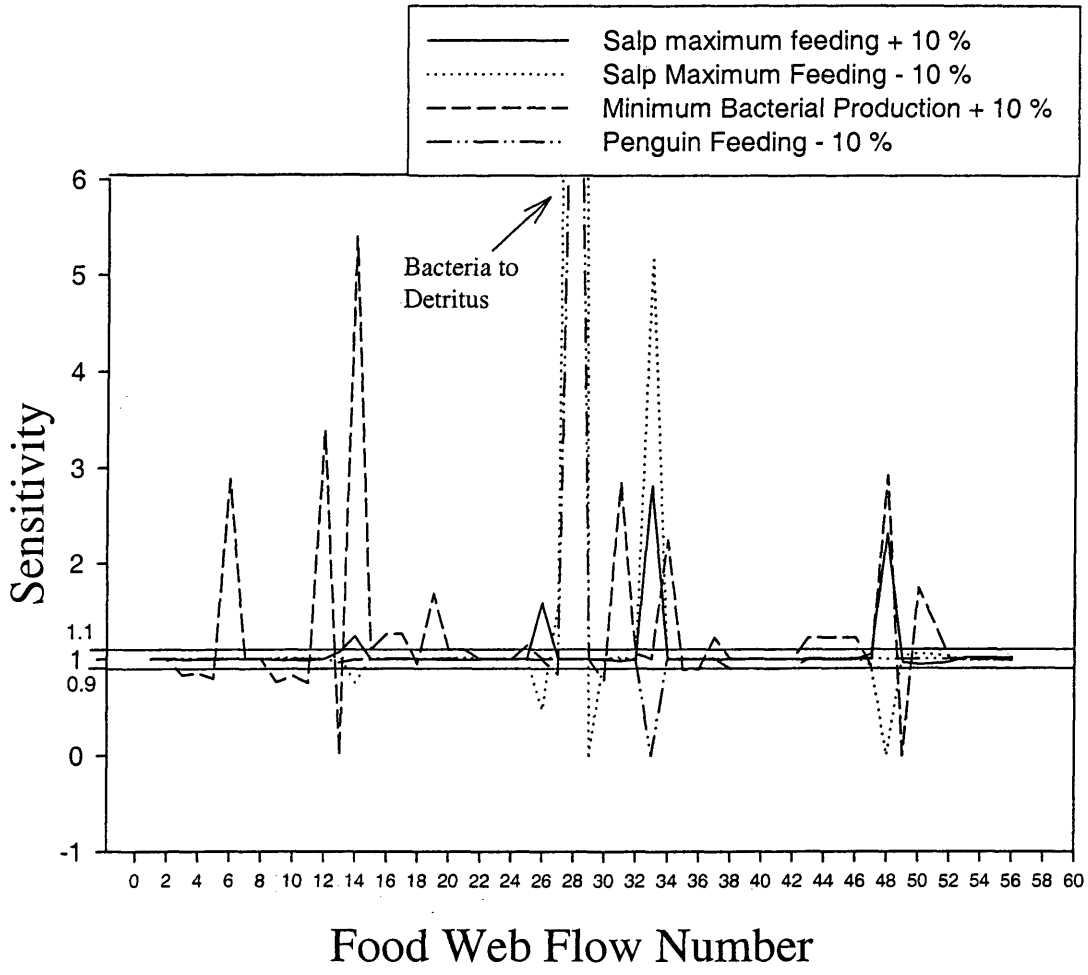


Figure 39. Sensitivity analysis for changes in the input parameters: large and small net primary production in the western Antarctic Peninsula, 1999 carbon model. The input parameters, representing measurements, were varied by + and - 10 %, individually. The response of the food web flow is the new value resulting from the +/- 10 % change in the input parameter divided by the original value of the flow. Food web flow numbers are described in Tables 37 and 38.

Table 37. Sensitivity Analysis with change in input parameters by + 10 % for the WAP 1999 carbon model.
The ratio shown is the model flow resulting from the 10 % change in the input parameter divided by the original model flow.
A '+' before a value indicates the value was 0 in original solution and increased to the # mmols C m-2d-1 shown.

Flow #		Large Net Primary Production	Small Net Primary Production	Export	Minimum Bacterial Production	Maximum Bacterial Production	Bacterial Biomass	Minimum Microzooplankton Feeding	Maximum Microzooplankton Feeding	Temp	Krill minimum feeding	Krill maximum feeding	Krill Biomass	Penguin Feeding	Myctophid Minimum Feeding	Myctophid Maximum Feeding	Myctophid Biomass	Salp minimum feeding	Salp maximum feeding
1	Large phytoplankton gross primary production	1.39	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
2	Large phytoplankton respiration	1.39	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
3	Microzooplankton grazing of large phytoplankton	1.47	1.02	1.00	0.83	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
4	krill grazing of large phytoplankton	1.40	1.06	1.00	0.85	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
5	Large phytoplankton sinking	1.47	1.01	1.00	0.79	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
6	Large phytoplankton release of DOC	1.35	1.00	1.00	2.88	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
7	Small phytoplankton gross primary production	1.00	1.39	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
8	Small phytoplankton respiration	1.00	1.39	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
9	Protozoan grazing of small phytoplankton	1.09	1.29	1.00	0.76	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
10	Microzooplankton grazing of small phytoplankton	0.95	1.41	1.00	0.82	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
11	Small phytoplankton to detritus	0.95	1.41	1.00	0.75	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
12	Small phytoplankton release of DOC	1.00	1.10	1.00	3.40	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
13	Microzooplankton consumption of protozoans	6.82	5.85	1.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.16	1.00	1.00	1.00	1.00	1.07
14	krill consumption of protozoans	0.00	1.48	1.00	5.39	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01	1.00	1.00	1.00	1.00	1.24
15	Protozoan respiration	1.19	1.22	1.00	1.10	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
16	Protozoans to detritus	1.19	1.22	1.00	1.26	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
17	Protozoans to DOC	1.19	1.22	1.00	1.26	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
18	Microzooplankton respiration	1.27	1.14	1.00	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
19	Mesozooplankton consumption of microzooplankton	1.11	1.30	1.00	1.68	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
20	Microzooplankton to detritus	1.28	1.17	1.00	1.09	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
21	Microzooplankton to DOC	1.28	1.17	1.00	1.09	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
22	krill respiration	1.33	1.11	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
23	krill to detritus (Faecal pellets)	1.33	1.11	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
24	krill to DOC	1.33	1.11	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
25	Bacterial respiration	1.23	1.10	1.00	1.14	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
26	Bacteria to protozoans	3.66	0.00	1.00	77.73	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01	1.00	1.00	1.00	1.00	1.58
27	Bacteria to microzooplankton	1.00	1.00	1.00	+0.475	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
28	Bacteria to detritus	1.00	1.00	1.00	+0.404	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
29	Bacteria to DOC	1.00	1.00	1.00	+0.211	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
30	Protozoan consumption of detritus	1.45	1.00	1.00	0.78	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
31	Microzooplankton consumption of detritus	1.09	1.60	1.00	2.86	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98
32	krill consumption of detritus	1.17	1.22	1.00	1.06	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
33	Detritus to DOC	1.00	1.00	1.00	+0.167	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.15	1.00	1.00	1.00	1.00	1.00
34	Bacterial ingestion of DOC	1.25	1.09	1.00	2.25	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
35	Total Particulate Export out of the top 35 m	1.26	1.14	1.00	0.89	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
36	Krill to export (Consumption by higher trophic levels or death)	1.32	1.11	1.00	0.89	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
37	Myctophid consumption of krill	1.38	1.12	1.00	1.22	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
38	Penguins consumption of krill	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00	1.00	1.00	1.00	1.00
39	Penguins to detritus	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00	1.00	1.00	1.00	1.00
40	Penguins to DOC	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00	1.00	1.00	1.00	1.00
41	Penguin respiration	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00	1.00	1.00	1.00	1.00
42	Penguin to export (Consumption by higher trophic levels or death)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.00	1.00	1.00	1.00	1.00
43	Myctophids to detritus	1.38	1.12	1.00	1.22	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
44	Myctophids to DOC	1.38	1.12	1.00	1.22	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
45	Myctophids to respiration	1.38	1.12	1.00	1.22	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
46	Myctophids to export (Consumption by higher trophic levels or death)	1.38	1.12	1.00	1.22	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
47	Salps consumption of large phytoplankton	1.04	0.77	1.00	0.92	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.05
48	Salps consumption of small phytoplankton	0.00	6.75	1.00	2.93	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	2.32
49	Salps consumption of bacteria	1.25	1.07	1.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.96
50	Salps consumption of protozoans	1.43	1.16	1.00	1.74	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.94
51	Salps consumption of microzooplankton	1.43	1.23	1.00	1.39	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95
52	Salps consumption of detritus	1.33	1.19	1.00	1.01	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.97
53	Salp respiration	1.22	1.11	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.02
54	Salps to detritus (Faecal pellets)	1.22	1.11	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.02
55	Salps to DOC	1.22	1.11	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.02
56	Salps to export	1.22	1.11	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.02

Table 38. Sensitivity Analysis with change in input parameters by - 10 % for the WAP 1999 carbon model.
The ratio shown is the model flow resulting from the 10 % change in the input parameter divided by the original model flow.
A '+' before a value indicates the value was 0 in original solution and increased to the # mmols C m-2d-1 shown.

Flow #		Large Net Primary Production	Small Net Primary Production	Export	Minimum Bacterial Production	Maximum Bacterial Production	Bacterial Biomass	Minimum Microzooplankton Feeding	Maximum Microzooplankton Feeding	Temp	Krill minimum feeding	Krill maximum feeding	Krill Biomass	Penguin Feeding	Myctophid Minimum Feeding	Myctophid Maximum Feeding	Myctophid Biomass	Salp minimum feeding	Salp maximum feeding
1	Large phytoplankton gross primary production	0.61	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
2	Large phytoplankton respiration	0.61	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
3	Microzooplankton grazing of large phytoplankton	0.55	1.01	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01
4	krill grazing of large phytoplankton	0.62	0.96	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01
5	Large phytoplankton sinking	0.59	1.02	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01
6	Large phytoplankton release of DOC	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
7	Small phytoplankton gross primary production	1.00	0.61	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
8	Small phytoplankton respiration	1.00	0.61	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
9	Protozoan grazing of small phytoplankton	0.80	0.67	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01
10	Microzooplankton grazing of small phytoplankton	0.91	0.54	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01
11	Small phytoplankton to detritus	1.00	0.54	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01
12	Small phytoplankton release of DOC	1.00	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
13	Microzooplankton consumption of protozoans	0.22	2.16	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.96	1.00	1.00	1.00	1.00	1.03
14	krill consumption of protozoans	3.35	0.34	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	0.75
15	Protozoan respiration	0.72	0.79	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
16	Protozoans to detritus	0.72	0.79	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
17	Protozoans to DOC	0.72	0.79	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
18	Microzooplankton respiration	0.66	0.87	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
19	Mesozooplankton consumption of microzooplankton	1.00	0.68	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
20	Microzooplankton to detritus	0.67	0.84	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01
21	Microzooplankton to DOC	0.67	0.84	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01
22	krill respiration	0.69	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
23	krill to detritus (Faecal pellets)	0.69	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
24	krill to DOC	0.69	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
25	Bacterial respiration	0.75	0.88	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
26	Bacteria to protozoans	4.93	7.48	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	0.47
27	Bacteria to microzooplankton	0.15	2.62	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.84	1.00	1.00	1.00	1.00	1.55
28	Bacteria to detritus	39.96	14.69	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	10.87	1.00	1.00	1.00	1.00	26.51
29	Bacteria to DOC	0.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	28.21	1.00	1.00	1.00	1.00	0.00
30	Protozoan consumption of detritus	0.32	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 38. Continued.

Flow #		Large Net Primary Production	Small Net Primary Production	Export	Minimum Bacterial Production	Maximum Bacterial Production	Bacterial Biomass	Minimum Microzooplankton Feeding	Maximum Microzooplankton Feeding	Temp	Krill minimum feeding	Krill maximum feeding	Krill Biomass	Penguin Feeding	Myctophid Minimum Feeding	Myctophid Maximum Feeding	Myctophid Biomass	Salp minimum feeding	Salp maximum feeding
31	Microzooplankton consumption of detritus	0.00	0.45	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.02
32	krill consumption of detritus	0.73	0.77	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
33	Detritus to DOC	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
34	Bacterial ingestion of DOC	0.79	0.91	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
35	Total Particulate Export out of the top 35 m	0.90	0.86	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
36	by higher trophic levels or death)	0.86	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
37	Myctophid consumption of krill	0.28	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01
38	Penguins consumption of krill	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00	1.00	1.00
39	Penguins to detritus	0.33	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00	1.00	1.00
40	Penguins to DOC	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00	1.00	1.00
41	Penguin respiration	0.67	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00	1.00	1.00
42	Penguin to export (Consumption by higher trophic levels or death)	2.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00	1.00	1.00
43	Myctophids to detritus	0.24	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01
44	Myctophids to DOC	0.28	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01
45	Myctophids to respiration	0.24	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01
46	(Consumption by higher trophic levels or death)	0.38	0.90	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01
47	Salps consumption of large phytoplankton	0.56	1.04	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.94
48	Salps consumption of small phytoplankton	12.05	0.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00
49	Salps consumption of bacteria	0.90	0.83	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.03
50	Salps consumption of protozoans	0.18	0.88	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.06
51	Salps consumption of microzooplankton	0.46	0.79	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.05
52	Salps consumption of detritus	0.48	0.82	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.03
53	Salp respiration	0.71	0.89	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98
54	Salps to detritus (Faecal pellets)	0.71	0.89	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98
55	Salps to DOC	0.71	0.89	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98
56	Salps to export	0.71	0.89	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98

Discussion

There were many similarities between the WAP 1996 and 1999 inverse carbon solutions. Although production was about 10 X greater in the 1996 WAP inverse solution, the sinking particulate flux as a % of the primary production was very similar in 1999, 0.18 vs. 0.20. The e-ratio was also very similar in 1999, 0.35 vs. 0.37 in 1996. Salps made a large contribution to the model export in 1999. Salp fecal pellets exported 2% of the primary production and salp production available for higher trophic levels made up 8% of the primary production. Salps also made a significant contribution to the DOC pool, 12% in 1999, replacing the 14% decrease in the Krill's contribution between 1996 and 1999. Salps have been attributed to consuming more than 100% of the primary production in Antarctic coastal waters (Perissinotto & Pakhomov, 1998). In the 1999 model they consumed 8% of the primary production. The occurrence of salps was very patchy in the area of the western Antarctic Peninsula, ranging from .08 to 1600 salps / 1000 m^3 , with an average of 122 salps / 1000 m^3 . The salps must have had a much more significant effect on the food web on smaller spatial scales, where they were in high abundance.

The amount of recycling was very similar in 1996 and 1999. In 1999, $\boldsymbol{L}$ was slightly higher, 1.5 vs. 1.4. The introduction of salps helped increase recycling in the system by adding more internal flows, but increased recycling due to their relatively significant contributions to export.

The bacterial production was very low in both models, 0.8% of the primary production and 2% for 1999. The constraints used for bacterial production were between

0 and 50% of primary production and the inverse method arrived at solutions close to the minimum constraints for both years. Despite the low productions, the ingestion of DOC by bacteria was equal to 16% for 1996 and 17% for 1999 with almost all of this ingestion being respired by bacteria. The low bacterial production may be a result of the tendency of the inverse method to minimize flows. It also shows that a higher bacterial production was not necessary to satisfy the measurements of the system.

Leak in the carbon pump?

Huntley et al. (1991) presented a model of a coastal Antarctic marine food web, that estimated the amount of carbon reaching sea birds and mammals. They estimated that 20 – 25% of the primary production was respired and introduced to the atmosphere by these air breathing animals. They argue that sea birds and mammals in the Southern Ocean provide a major leak in the biological pump. The Huntley et.al model includes a 3 trophic-level, short food web of phytoplankton to zooplankton to sea birds and mammals. The model presented for the western Antarctic Peninsula is similar but more specific to the local area, and includes the short food web of large phytoplankton (i.e. diatoms) to Antarctic krill (*Euphasia superba*) to Adélie penguins (*Pygoscelis adeliae*). The Huntley et al. model includes only one compartment for the microbial loop. Huntley et al. assign 7/8 of the primary production to the short food web and 1/8 to the microbial loop. The small proportion going to the microbial loop is based on studies in coastal Southern Ocean waters where Huntley et al. state that microbial processes seem to be suppressed (Huntley et al., 1992). Moloney (1992) challenges the findings by Huntley et al. (1992), arguing that the model is over simplified. Moloney argues that the microbial loop should contain more than one compartment, so that the grazing of small

phytoplankton and the trophic transfers within the microbial loop are considered. The 1996 and 1999 models for the western Antarctic Peninsula include bacteria, protozoans, and microzooplankton, which are all represented by one compartment in the Huntley model.

The respiration by the Adélie penguins in the WAP models was just 0.04% of the primary production in 1996 and 0.1% in 1999. The other source of significant production that could have gone to air breathing animals not in the model, such as whales and seals, was the krill export production. Assuming that all of the krill export production did go to whales in 1996, and using the assumptions of Huntley et al. (1991), an estimate of the total loss of carbon to respiration by air breathing animals can be found. Huntley used the estimate from Laws (1985) that 10% of the krill production was consumed by whales. In the WAP models, the total krill production was equal to the sum of the myctophid consumption of krill, penguin consumption of krill, and the krill export production. For 1996 the total krill production was 1% + 0.1% + 17% = 18.1% of the primary production and for 1999 it was 3% + 0.4% + 8% = 11.4% of the primary production. The respiration of mammals and sea birds in the Huntley model was found using the expression:

$$R_x = (a_x - K_{1x})\, I_x$$

where R_x is the respiration of a compartment, a_x is the assimilation efficiency, K_{1x} is the growth gross efficiency, and I_x is the ingestion as a fraction of the primary production. Assuming values of these parameters from Huntley that will maximize the respiration and using the total krill production times the percentage of krill consumed by whales, the 1996 respiration is:

$$R_x = (0.810 - 0.016) * (0.10 * 0.181) = 0.014$$

and for 1999is: $R_x = (0.810 - 0.016) * (0.10 * 0.114) = 0.010$

The total respiration of birds and mammals from the 1996 WAP model is the penguin respiration of 0.04% plus the whale respiration of 1.4%, equal to 1.44% of the primary production. For 1999, the total respiration is the penguin respiration of 0.1% plus the whale respiration of 1% equal to 1.1% of the respiration. These estimates between 1.1 and 1.44% of the primary production are much lower than the estimate of 20 – 25% in Huntley et al. (1991) and are similar to estimates by Moloney (1992) and Banse (1995). Moloney (1992), using the Huntley (1991) model, assumed that 20% of the primary production was consumed by zooplankton and 80% went to the microbial loop and that the microbial loop gross growth efficiency was 0.01 vs. 0.35, assumed by Huntley. Moloney (1992) estimated that birds and mammals respired 5% of the net primary production. Karl Banse (1995), in another response to the Huntley et al. paper, used variations of the Huntley model to argue that <= 3% of the net primary production was respired by birds and mammals. Banse argued that the food web modeled by Huntley was over simplified and that the growth efficiencies used were too high. In response to Moloney's criticism, Huntley et al. (1992) argued that their model was based on measurements from Antarctic coastal systems, where as Moloney used assumptions from the Benguela Current, a low latitude system. Huntley et al. (1992) argued the microbial food web only receives a small portion of the primary production and its activity is suppressed in Antarctic coastal systems. Our models were based on measurements from the western Antarctic Peninsula. They did show a very low bacterial production of less than 2% in both 1996 and 1999, agreeing with Huntley et al.'s

(1991,1992) assumptions. Measurements of bacterial production or microzooplankton grazing were not available for the western Antarctic peninsula, so constraints of 0 – 50% of primary production for bacterial production and 0 – 75% of primary production for microzooplankton grazing were used. Despite the large ranges assumed, the values inferred by the inverse method for bacterial production and microzooplankton grazing are consistent with all of the other measurements used in the model. Although the bacterial production was very low, agreeing with the assumption of a suppressed microbial loop by Huntley et al. (1992), the bacteria consumed 14% of the primary production in 1996 and 17% in 1999. Most of this carbon was respired by the bacteria. The total respiration of the microbial organisms in 1996 was 14% for the bacteria, plus 12% for the protozoans, plus 16% for the microzooplankton, equal to 42% of the primary production. The Huntley model predicted the entire microbial loop respired between 0 and 16% of the primary production, however this model does not consider the many interactions within the microbial loop that lead to the loss of carbon through respiration in the WAP models or the potential of bacteria to be active despite a low production.

Despite a magnitude difference in the primary production and the presence of salps in the food web in 1999, the inverse carbon solutions for 1996 and 1999 showed many similarities. The particulate flux and estimated export ratios were very similar. The throughput of the particulate detritus pool was about twice that of the DOC pool in both years. Bacterial production was very low, but in contrast to the traditional view of the domination of the short food web (Laws, 1985; Huntley; 1991), the microbial food web including bacteria, microzooplankton, and protozoans processed a significant

amount of the primary production. The relative roles of the microbial food web and short food webs will be examined in more detail in the next chapter.

Chapter IV. Synthesis

North Atlantic vs. Western Antarctic Peninsula

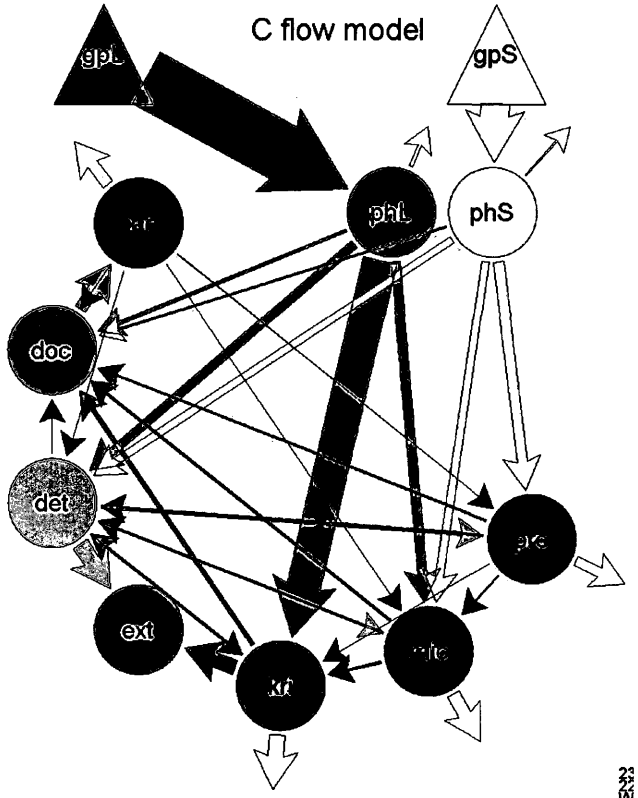
The following chapter is a synthesis of the inverse solution results for the North Atlantic Bloom Experiment (NABE) and the western Antarctic Peninsula (WAP). A direct comparison is made between the WAP 1996 and NABE carbon models in order to find differences in the food web functions expressed in the two regions, as a result of the different food web structures. The results of the NABE and WAP models are classified according to the food web types described by Legendre and Rassoulzadegan (1996), to see where they lie along a continuum of oceanic systems.

A direct comparison between the WAP 1996 carbon inverse solution and the NABE carbon inverse solution is meaningful because the inferred primary production in the models were similar: 63 mmols $Cm^{-2}d^{-1}$ for NABE and 89 mmols $Cm^{-2}d^{-1}$ for the 1996 WAP carbon model. Also, many of the results of the WAP 1996 and 1999 models were similar with respect to the food web flows normalized to the primary production. A new condensed model for the WAP, with the same components as the NABE model, except for krill replacing the mesozooplankton in the WAP, was made for the comparison. The higher trophic levels including myctophids and penguins were not included in the condensed model. The same input measurements and assumptions used for the original WAP 1996 carbon model shown in Table 21, were used in the condensed model, except for the higher trophic level measurements that were not required.

The condensed model inverse solution for the western Antarctic Peninsula is shown in Figure 40. The condensed model flows were almost identical to the flows in the original 1996 carbon model. Only 2 flows changed by more than 1%. The krill consumption of protozoans was 35% smaller in the condensed model, but was less than 1% of the primary production in both models. The krill export flow was 7% larger in the condensed model than the full model, but increased just 1% with respect to the primary production.

Table 39 compares the NABE and WAP 1996 carbon flows from the condensed model, as absolute and normalized flows. The phytoplankton production was divided differently between the small and large phytoplankton for the NABE and WAP models. In the NABE model, the phytoplankton production was split 50/50 in the constraint equations for small and large phytoplankton. In the WAP 1996 model, 2/3 of the production was designated to the large phytoplankton and 1/3 to the small phytoplankton in the constraint equations. The model obeyed these constraints, as can be verified by subtracting the phytoplankton respiration from the corresponding gross production in Table 39 to find the net primary production. The largest flow within the WAP food web was the krill grazing of large phytoplankton, while the largest flow within the NABE food web was bacterial ingestion of DOC. The sum of microzooplankton and protozoan grazing in the NABE model was twice as great as in the WAP model. Krill grazing in the WAP model was 8 times larger as a percentage of the primary production than mesozooplankton grazing in the NABE model.

The DOC release by phytoplankton was equal to 6% of the primary production in the WAP model vs. a much larger portion of 25% in the NABE model. The bacteria



gpS = Gross PP for Small Phytoplankton
gpL = Gross PP for Large Phytoplankton
bac = bacteria
det = detritus
ext = Export
mes = mesozooplankton
mic = microzooplankton
pro = protozoans

Figure 40. WAP 1996 condensed carbon inverse model flow diagram. The myctophids and penguins were excluded from this model for a direct comparison with the NABE carbon model. Grey flows leaving compartments are losses to respiration. Inputs are from gross primary production for small phytoplankton (gps) and large phytoplankton (gpl). Export from the surface ocean enters the ext compartment. Black arrows are flows that were zero in the inverse solution.

Table 39. Comparison of the North Atlantic carbon inverse solution and the 1996 western Antarctic Peninsula condensed inverse solution. Flows are expressed as absolute values and as a % of the primary production for each area.

Food Web Flow	WAP Flows (mmols $Cm^{-2}d^{-1}$)	NABE Flows (mmols $Cm^{-2}d^{-1}$)	WAP 1996 Flows as % of PP	NABE Flows as % of PP
Large phytoplankton gross primary production	62.3	33.2	70	53
Large phytoplankton respiration	3.1	1.7	4	3
Microzooplankton grazing of large phytoplankton	9.8	15.3	11	24
krill or mesozooplankton grazing of large phytoplankton	37.1	2.9	42	5
Large phytoplankton sinking	8.9	3.6	10	6
Large phytoplankton release of DOC	3.4	9.7	4	15
Small phytoplankton gross primary production	31.2	33.2	35	53
Small phytoplankton respiration	1.6	1.7	2	3
Protozoan grazing of small phytoplankton	11.5	13.3	13	21
Microzooplankton grazing of small phytoplankton	8.7	11.9	10	19
Small phytoplankton to detritus	7.7	0.1	9	0
Small phytoplankton release of DOC	1.7	6.2	2	10
Microzooplankton consumption of protozoans	1.3	0.5	2	1
krill or mesozooplankton consumption of protozoans	0.2	1.5	0	2
Protozoan respiration	11.1	9.6	12	15
Protozoans to detritus	1.6	1.9	2	3
Protozoans to DOC	1.6	5.9	2	9
Microzooplankton respiration	14.6	11.3	16	18
krill or mesozooplankton consumption of microzooplankton	2.1	0.9	2	1
Microzooplankton to detritus	2.1	3.2	2	5
Microzooplankton to DOC	2.1	7.7	2	12
krill or mesozooplankton respiration	17.3	1.2	20	2
krill or mesozooplankton to detritus (Faecal pellets)	2.4	0.8	3	1
krill or mesozooplankton to DOC	3.9	1.2	4	2
Bacterial respiration	12.1	13.5	14	21
Bacteria to protozoans	0.6	6.1	1	10
Bacteria to microzooplankton	0.0	4.6	0	7
Bacteria to detritus	0.0	6.3	0	10
Bacteria to DOC	0.0	9.8	0	16
Protozoan consumption of detritus	3.7	0.0	4	0
Microzooplankton consumption of detritus	1.0	0.0	1	0
krill or mesozooplankton consumption of detritus	0.0	0.0	0	0
Detritus to DOC	0.0	6.1	0	10
Bacterial ingestion of DOC	12.7	46.7	14	74
Total Particulate Export out of the top 35 m	17.9	9.8	20	16
krill or mesozooplankton to export (Consumption by higher trophic levels or death)	15.8	2.1	18	3

were much more active in the NABE model. Bacteria ingested 74% of the primary production in the NABE model vs. just 14% in the WAP model.

The particulate export leaving the surface ocean was similar for the two models, 20% for the WAP and 16% for NABE. Krill export production, representing predation of krill by higher trophic levels like Adélies or an increase in the krill biomass, was 18% of the primary production, much higher than the 3% export production from mesozooplankton in the NABE model. The estimated e- ratio from the NABE model is equal to the sum of the sinking particulate matter, and the mesozooplankton export production, both normalized to the primary production:

$$e = 0.16 + 0.03 = 0.19.$$

The estimated e-ratio from the WAP model is equal to the sum of the sinking particulate matter, and the krill export production:

$$e = 0.20 + 0.18 = 0.38.$$

Comparison of short food web vs. microbial food web

The short food web is believed to be the most significant pathway for carbon in coastal waters of the Southern Ocean (Huntley et al., 1991) and the microbial food web is believed to play an active role in the North Atlantic (Ducklow et al., 1993; Harrison et al., 1993; Lochte et al., 1993). The relative activities of the short food web and microbial food webs are given for the WAP 1996 and NABE carbon models in Table 40. All of the flows within the short food web that lead to export out of the surface ocean through sinking or potential transfer to higher trophic levels were summed. The flows within the

Table 40. Comparison of the microbial and short food web flows for the WAP 1996 condensed carbon model and the NABE carbon model. Flows are normalized to the primary production for each model. The ratio of the total microbial food web flows to the total short food web flows is shown at the bottom of the table.

	WAP 1996	NABE
Microbial Food Web Flows	% of PP	% of PP
S Phytoplankton to Detritus	8.7	0.1
S Phytoplankton to DOC	1.9	9.9
Protozoan Grazing of S Phytoplankton	12.9	21.1
Protozoan Grazing of Bacteria	0.7	9.6
Microzooplankton Grazing of Bacteria	0.0	7.3
Microzooplankton Grazing of L Phytoplankton	11.1	24.3
Microzooplankton Grazing of S Phytoplankton	9.8	18.8
Microzooplankton Grazing of Protozoans	14.3	0.7
Bacterial DOC Ingestion	1.8	74.1
Bacterial Release of DOC	0.0	15.6
Bacteria to Detritus	0.0	10.0
Protozoan to Detritus	1.8	3.1
Protozoans to DOC	1.8	9.4
Microzooplankton to DOC	2.4	12.2
Detritus to DOC	0.0	9.8
Detritus to Protozoans	4.2	0.0
Detritus to Microzooplankton	1.1	0.0
Microzooplankton to Detritus	2.4	5.1
Total	74.8	231.2
Short Food Web Flows		
L Phytoplankton Sinking	10.0	5.7
Krill Grazing of L Phytoplankton	41.8	4.6
Other Krill Production	17.8	3.3
Krill Faecal pellets	2.7	1.3
Total	72.2	14.9
Microbial Food Web Flows / Short Food Web Flows	1.0	15.5

microbial food web were also summed, including all flows between the microbial organisms and their interactions with the detritus and DOC pools. The ratio of microbial to short food web flows for the WAP solution was 1.0, with equal activity from each group of flows. In NABE, the microbial food web was 15.5 times more active than the short food web (Table 40). The krill were the main contributor to the short food web flows in the WAP model. Myctophids and Adélie penguins, not included in this condensed model, consumed an amount of krill equal to 1.1% of the primary production in the original model. The other krill production is a significant flow equal to 15.8 mmols $Cm^{-2}d^{-1}$ or 18% of the primary production. This represents krill growth that was not grazed and is available for predation by higher trophic levels.

Comparison of network analysis indices

A comparison of network analysis indices for the 2 models indicates the bacterial production is much greater in NABE, where it accounts for 43% of the primary production vs. 1% in the WAP model (Table 41). The dominance of krill in the western Antarctic Peninsula is evident with the krill processing 52% ($\mathbf{f_{kri}}$ = 52%) of the total carbon passing through all the zooplankton. The dominance of microzooplankton and protozoans in the North Atlantic is obvious with the total throughput of microzooplankton and protozoans equal to 89% ($\mathbf{f_{mic}}$ = 48 , $\mathbf{f_{pro}}$ = 41) of the total carbon passing through all the zooplankton.

The recycling index, **L** and the **Total Ingestion / PP** indicate greater recycling in the North Atlantic than the western Antarctic Peninsula (Table 41). The average carbon atom passes through the North Atlantic food web 2.6 times before exiting through

Table 41. Network analysis indices for the WAP 1996 condensed carbon model and the NABE carbon model.
Fbac is the ratio of bacterial production to net primary production.
L is the index of recycling equal to the number of times a carbon atom cycles through the food web before leaving through respiration, sinking, or predation by higher trophic levels.
The **Total ingestion/ PP** is the total ingestion of all zooplankton components plus the ingestion of DOC by bacteria divided by the net primary production.
Fpro, Fmic, and Fmes are the ratios of the total flows through each compartment to the total flows through all three grazer compartments.

	WAP 1996	NABE
Fbac (%)	1	43
Fpro (%)	21	41
Fmic (%)	27	48
Fkri or Fmes (%)	52	11
L	1.4	2.6
Total Ingestion / PP	1.0	1.6

respiration or sinking, while **L** for the western Antarctic Peninsula is 1.4. The **Total Ingestion / PP** indicates that in the North Atlantic food web, zooplankton and bacteria process 160% of the primary production, indicating a strong reliance on recycled carbon. In the western Antarctic Peninsula food web, the zooplankton and bacteria process 100% of the primary production, indicating no reliance on recycled carbon.

In order to get an indication of the activity of a compartment, all of the flows entering a compartment can be summed and divided by the net primary production. For the North Atlantic model, 74% of the primary production passes through the DOC pool. For the WAP model, 14% of the primary production passes through the DOC pool. For both models 25% of the primary production passes through the detritus pool.

Discussion

Krill were key organisms affecting the flow of carbon in the western Antarctic Peninsula food web and microbial organisms were key in the North Atlantic. The greatest flows within the WAP model were related to krill, while the greatest flows within the NABE model were bacterial ingestion and microzooplankton grazing. The dominance of krill is not too surprising given that krill usually dominate the zooplankton biomass in the western Antarctic Peninsula (Ross et al., 1998). In 1996 krill biomass was 227 mmols Cm^{-2} (Table 16) vs. the mesozooplankton biomass of 7 mmols Cm^{-2} (Table 1) in the North Atlantic in May 1989. The krill biomass was equal to almost 1/3 of the phytoplankton biomass in the western Antarctic Peninsula.

Active recycling was evident in the North Atlantic model, while weak recycling was seen in the western Antarctic Peninsula model. The microbial food web flows

processed 15.5 times more carbon than the short food web flows processed in the NABE model. In the WAP model, the short food web and microbial food web flows processed an equal amount of carbon. A carbon atom cycles through the NABE food web, on average about 2 times more before exiting than in the WAP model. The organisms in the NABE model depend upon recycled carbon to supply a substantial portion of their diet, while the organisms in the WAP rely very little on recycling. The NABE food web is dominated by DOC flows, with 3 more times the amount of carbon passing through the DOC pool than the detritus pool. In the WAP model more carbon passes through the detritus particulate pool than the DOC pool.

Bacterial production was much greater in the NABE model. In the WAP model, bacterial production was just above zero. The Bacterial ingestion of DOC was about 5 times greater in the NABE model, 74% of primary production vs. 14% for the WAP. This result agrees with findings in the area by Karl et al. (1999), who found that the bacteria were uncoupled with phytoplankton during the spring bloom in the Gerlache strait, just north of the western Antarctic Peninsula. Bacterial biomass was lowest where phytoplankton biomass was high and highest where phytoplankton biomass was low in the Gerlache strait in 1989. High grazing rates of bacteria were measured by dilution experiments in areas of high phytoplankton biomass, during the bloom. The WAP model showed very low grazing of bacteria, equal to just 1% of the primary production. The bacteria respired almost all of their carbon intake. Despite the bacterial production of almost zero, the bacteria still played an active role in the food web by ingesting 14% of the primary production. The bacterial production and the microzooplankton grazing inferred by the WAP models give estimates of these unmeasured flows that are consistent

with all the other measurements. Large ranges were assigned to the constraints for bacterial production and microzooplantkon grazing, because these processes are highly variable across the world's oceans and not well understood in the Southern Ocean (Caron et al.,2000; Froneman and Perissinotto, 1996; Becquevort, 1995; Karl, 1999(2)). The microzooplankton grazing inferred by the inverse method was 21% of the primary production in 1996 and 26% in 1999. The power of the inverse method is evident when it provides estimate of microzooplankton grazing that would not have been known otherwise and was constrained between such a large range of 0 and 75% of the primary production.

The estimated e-ratio of 0.38 for the WAP model was twice as high as in the NABE model, e = 0.19. Krill export production was equal to a large portion of the WAP primary production, 18%. In the WAP 1996 full carbon model, penguins and myctophids together just consumed 1.1% of the primary production in the form of krill. This leaves 17% of the primary production that could go to an increase in krill biomass or could be passed up the food web to other predators not modeled. Baleen whales consume an estimated 10% of krill production in the Southern Ocean (Laws, 1985) and could have consumed some of this krill production. The production could have also gone uneaten and increased the krill biomass. The model assumed no change in the krill biomass over the month of the study. The month of January is during the summer bloom and krill biomass is highly variable across seasons with up to an order of magnitude increase from fall/ winter to spring / summer (Lascara et al., 1999), so a significant increase in krill biomass most likely took place.

The model e-ratio of 0.19 for NABE was lower than the estimated f-ratio of 0.45 found by Martin (1993) using sediment trap data. The model verifies other researcher's conclusions (Garside & Garside, 1993) that all of the new production was not realized in export, but remained in the food web. The model did account for a sink for this unrealized export with the inclusion of the observed changes in biomass of bacteria and microzooplankton. The bacterial biomass increase of 6 mmols $Cm^{-2}d^{-1}$ and the microzooplankton increase of 9 mmols $Cm^{-2}d^{-1}$ were included in the model.

Other food web flows that were inferred by the inverse method that are not otherwise known include interactions with the detrital pools. In both the NABE carbon and WAP 1996 models, the total throughput of the detritus pool was 25% of the primary production. In an inverse analysis of a plankton food web off Southern California, Jackson and Eldridge (1992) also found detritus was a key component, receiving large contributions from sinking phytoplankton and making significant contributions to the dissolved organic matter pool. In the NABE carbon solution, the dissolution of detritus made up 13% of the input to the DOC pool. In an inverse analysis of a plankton food web of the Takapoto Atoll in French Polynesia, Niquil et al. (1998) found that detritus played an important role providing food for all of the zooplankton components. In the NABE carbon solution there was no consumption of detritus by zooplankton, however in the nitrogen solution all of the zooplankton components consumed detritus. This discrepancy is not possible in nature and future solutions could use a C:N ratio to force either the carbon or nitrogen solution to be more consistent with the other. In the WAP models, detritus was consumed by almost all of the zooplankton components in 1996 and all except for microzooplankton in 1999.

Food web flows of dissolved organic matter are other flows the inverse solution estimates that were not measured. In the NABE carbon and nitrogen solutions, the throughputs of the DOC and DON pools were a large portion of the primary production, 74% for carbon and 55% for nitrogen. In the NABE models large phytoplankton, bacteria and microzooplankton made the largest contributions to the DOC and DON pools. Bacteria were one of the biggest contributors to their own food source. In the WAP models, krill, and large phytoplankton were the biggest contributors and sizable inputs were received from all the living components except for bacteria.

The differences in food web structure between the North Atlantic and the western Antarctic Peninsula did result in very different food web function in the two regions. Recycling was strong in the North Atlantic, as evident in the carbon solution and especially the nitrogen solution. Dissolved organic matter flows were 2 –3 times greater than particulate detritus. Recycling in the western Antarctic Peninsula was much less pronounced and the short food web flows were just as significant as the microbial food web flows. Particulate detritus flows equaled dissolved organic carbon flows in the western Antarctic Peninsula. Export in the western Antarctic Peninsula was twice as high as the export in the North Atlantic with respect to the primary production. The flow of carbon within the food web of the North Atlantic was dominated by microbial organisms and interactions with the DOC pool. In the western Antarctic Peninsula, carbon flows were dominated by krill.

Classification of Food Webs

Legendre and Rassoulzadegan (1996) described three pathways for carbon to flow through a food web; the sinking of ungrazed phytoplankton, food web transfer, and recycling. They related these three food web functions to the size structure of the phytoplankton and matching of phytoplankton with grazing. Legendre and Rassoulzadegan derived equations to solve for the proportion of the primary production going to each of the three pathways based on the ratio of large phytoplankton to total phytoplankton, $\mathbf{P_L/P_T}$ and the matching between phytoplankton and grazing, **M**. They used values from the literature to estimate the magnitude of these food web functions for 5 different types of food webs. The food web types ranged along a continuum of a decreasing ratio of export to primary production. On one end of the extreme is the sinking of ungrazed cells, representing a food web with high primary production that is not matched by grazing. On the other end of the extreme is the microbial loop, an almost closed system with near zero input of primary production, and consisting of bacteria and protozoans. In between the two extremes in order of decreasing export/ production are the herbivorous, the multivorous, and microbial food webs. The herbivorous food web is dominated by large phytoplankton production and grazing by mesozooplankton, while the microbial food web is dominated by small phytoplankton production and protozoan and microzooplankton grazing. The multivorous food web includes equal roles of large and small phytoplankton and herbivorous and microbial grazing.

Using measurements of the size structure of the phytoplankton, $\mathbf{P_L/P_T}$ and estimates for the degree of matching, **M,** Legendre and Rassoulzadegan solved for the 3 pathways of carbon flow in the 5 different food web systems and compared the results to

estimates from the literature. Legendre and Rassoulzadegan (1996) found good agreement between their derived values of food web function and the estimates from the literature (coeffiecient of determination, $R^2 = 0.83$), supporting their assumption that the size structure of the phytoplankton and degree of matching strongly influence food web function.

Literature estimates for the 3 food web functions from Table 2 in Legendre and Rassoulzadegan (1996) for five different types of food webs, provide a baseline to compare estimates of these functions from the WAP carbon models and NABE carbon model (Table 42). The food web transfer described by Legendre and Rassoulzadegan (1996), $\mathbf{F_T/P_T}$ includes any carbon passed up the food chain that is exported out of the surface ocean by sinking or transfer to higher trophic levels, before being recycled. This includes the fecal pellets and export production of mesozooplankton or krill. In the WAP models it also includes myctophid, and salp (for 1999) fecal pellets and export production. Penguin export production is also included, but not penguin feces, which are mostly left on land. The recycling pathway, $\mathbf{R_T/P_T}$ was found by subtracting the total export equal to the sum of $\mathbf{F_T/P_T}$ and $\mathbf{D_T/P_T}$, from the total net primary production, equal to 1.0.

The NABE carbon model has food web functions lying somewhere between the multivorous food web and the microbial loop, even though the segregation of the primary production P_L/P_T of 0.5 is much higher than assumed for these systems. The recycling pathway consumes a high proportion of the primary production, $R_T/P_T = 0.9$, putting the North Atlantic food web between the microbial food web and the microbial loop. The food web transfer, F_T/P_T of 0.4 is very low, putting the food web close to the microbial

Table 42. Comparison of food web classifications of the Inverse Model results with the 5 different food web types described by Legendre & Rassoulzadegan (1996). P_L/P_T is the ratio of large phytoplankton to the total net phytoplankton production. **M** is the degree of matching between phytoplankton production and zooplankton grazing. R_T/P_T is the ratio of recycled carbon to the net primary production. F_T/P_T is the ratio of carbon passed up the food web and exported out of the surface ocean to the net primary production. D_T/P_T is the ratio of sinking phytoplankton to net primary production. The values for the 5 food web types are from Legendre & Rassoulzadegan (1996) and are based on literature values from areas representing the different food webs. The Inverse model values are calculated from the model results. F_T/P_T and D_T/P_T are calculated directly from the model results and R_T/P_T is calculated by 1 - (F_T/P_T + D_T/P_T). The matching, M was not expressed for the inverse model results because this was an arbitrary value chosen by Legendre & Rassoulzadegan for the 5 different food web types.

Biogenic carbon pathways (Legendre & Rassoulzadegan, 1996)	P_L/P_T	M	R_T/P_T	F_T/P_T	D_T/P_T
(1) Sinking of ungrazed cells	1.00	0.00	0.00	0.00	1.00
(2) Herbivorous food web	0.80	0.55	0.30	0.60	0.10
(3) Multivorous food web	0.35	0.65	0.60	0.30	0.10
(4) Microbial food web	0.10	0.25 or 0.75	0.80	0.20	0.00
(5) Microbial loop	0.00	0 or 1	1.00	0.00	0.00
Inverse Model					
NABE Carbon	0.50		0.90	0.04	0.06
WAP 1996 Carbon	0.67		0.63	0.20	0.17
WaP 1999 Carbon	0.67		0.68	0.22	0.10

loop, while the sinking phytoplankton pathway, D_T/P_T of 0.10 is the same as in Legendre and Rassoulzadegan (1996) multivorous food web. The WAP 1999 and 1996 models show similar results to the Legendre and Rassoulzadegan (1996) analysis. The WAP 1996 carbon model is closest to the multivorous food web, but still leaning towards the microbial food web. The recycling pathway, R_T/P_T of 0.63 is slightly higher than for the multivorous food web. The food web transfer pathway, F_T/P_T of 0.2 is equal to that of the microbial food web. The WAP 1999 model is also close to the multivorous food web with leanings towards the microbial food web. The recycling pathway, $R_T/P_T = 0.68$ is about halfway between the recycling in Legendre's multivorous food web and microbial food web. The food web transfer is close to the microbial food web value, while the sinking phytoplankton pathway is higher than in the multivorous food web.

The inverse solutions give values of the food web functions that are somewhat different than would be expected using Legendre and Rassoulzadegan's (1996) assumptions of size distribution of primary production and matching. The size distribution of primary production for each of the inverse models indicate food webs lying somewhere between the multivorous and herbivorous food web. However, the food web functions calculated from the inverse model results put the North Atlantic food web somewhere between the microbial food web and microbial loop and the western Antarctic Peninsula food web close to a multivorous food web with leanings towards the microbial loop. The matching parameter used by Legendre and Rassoulzadegan is an arbitraty parameter that is not related directly to measurements. For NABE, the matching between grazers and phytoplankton was likely high because the fast growing microzooplankton and protozoans dominated the grazing. This high degree of matching would push the

NABE food web towards higher recycling in the direction of the microbial loop. For the WAP, the dominance of krill grazing would give a lower degree of matching than in NABE because of the relatively slower growth of krill to microzooplankton and push the food web towards the extreme of sinking of ungrazed cells. There is a bias in both of the inverse solutions towards the microbial loop extreme. The assumptions from Legendre are based on only a few food webs, so it is possible that with data from more systems these description of food web types would be different and biased towards higher recycling.

Appendix

The Inverse Method

All of the possible flows in the food web are defined in mass balance equations (Vezina & Platt, 1988). The flows entering each component must equal the flows leaving plus any observed or assumed change in biomass of the component over the period studied (zero for steady state). The observations of flows are used as targets for the solution. The boundary conditions for the model are defined using measured primary production as the input and measured sedimentation as the output for the system (Vezina & Platt, 1988). Observed biomasses are used along with biological constraints, such as respiration and assimilation efficiency to keep the unknown flows within reasonable ecological and physiological boundaries (Jackson & Eldridge, 1992). For example, the biomass of bacteria can be used to find the maximum maintenance respiration for the bacterial community in the system, using the relationship defined by Moloney and Field (1989). The inverse method then provides a solution that satisfies the conservation of mass equations, the boundary conditions, and the biological constraints.

The inverse solution is set up as a matrix problem and solved using least square techniques including the singular value decomposition (Vezina and Platt, 1988; Jackson & Eldridge, 1992). A number of linear equations describing the mass balance, boundary conditions and measured flows of the food web are put into matrix form. For example, if the measured bacterial production was equal to 10 mmols $Cm^{-2}d^{-1}$ then the linear equation might be:

$$1.0*BactoPro + 1.0*BactoMic + 1.0*BactoDOC = 10\ mmols\ Cm^{-2}d^{-1}$$

where ***BactoPro***, ***BactoMic*** and ***BactoDet*** are the consumption of bacteria by protozoans and microzooplankton, and the contribution of bacterial cells to detritus. The coefficients before each term go into the state variable matrix A, an $m \times n$ matrix, where m is equal to the total number of equations and n is equal to the number of unknown flows in the food web. The flows (***BactoPro***,etc.) go into an $n \times 1$ vector, r and the measured value of 50 mmols $Cm^{-2}d^{-1}$ goes into an $n \times 1$ vector, b. The mass balance and boundary conditions are put into matrix form in a similar way to arrive at the continuity equation for the system:

$$Ar = b$$

The number of equations is usually much less than the number of unknowns for foodwebs. For the mass balance equations, the vector b will hold zero values for a situation that is assumed to be in steady state or nonzero values for a system where the changes in components have been measured. The singular value decomposition is used to arrive at a solution to the continuity equation and assigns estimates of the unknown flows to the vector r.

Biological constraints on processes like respiration and assimilation can be used to provide more equations to further constrain and better approximate a solution. For example if the minimum phytoplankton respiration is assumed to be five percent of gross primary production the equation would be:

$$1.0*Phyres \geq .05*Gpp$$

where Phyres and Gpp are the phytoplankton respiration and gross primary production, respectively. The above equation can be rearranged as follows:

$$1.0*Phyres - 0.05*Gpp \geq 0$$

The coefficients of the equation are put into an $n_c \, x \, n$ matrix of inequality coefficients, G, where n_c is equal to the number of inequality equations. The unknown flows are included in the $n \, x \, 1$ vector, r_n and the right hand side of the equation is put into an $n \, x \, 1$ vector of inequality constants, h. The constraint equation for the system is then written as:

$$Gr_n \geq h$$

The vector r_n is the final solution to the unknown flows and contains r, the solution to the continuity equation plus additional information provided by the solution to the constraint equation. A least distance algorithm is used to arrive at an estimate for r_n (Vezina & Platt, 1988). The solution minimizes the sum total of the flows and the differences between the flows (Vezina & Platt, 1988). Conceptually, the solution gives the point that is within a space defined by an infinite number of potential solutions (like a plane in three dimensions) and is the shortest distance from the solution space to the origin (Vezina & Platt, 1988). The solution is then the simplest of an infinite number of potential non-trivial solutions. The inverse solution obeys the parsimony principle that requires that 1) the flows go as directly as possible where required according to all of the equations that constrain them (mass balance, boundary conditions, biological constraints, etc.), 2) when several pathways leaving a component are of equal length the flows are equally divided among them, and 3) the non-necessary matter exits the food web through

the shortest possible pathway (Niquil et al., 1998). Niquil et al. describe some potential problems with using the parsimony principle, such as the number of trophic levels being artificially shortened because direct flows, such as zooplankton grazing on phytoplankton are favored over less direct flows, like the microbial loop. Despite some bias introduced with the parsimony principle, it provides a unique solution and has been widely used (Vezina and Platt, 1988; Ducklow et al., 1989; Jackson and Eldridge, 1992; Niquil et al., 1998;). We employ it here for ease of calculation and for continuity with earlier applications.

The inverse analysis was performed using a MatLab program written by George Jackson of Texas A & M University. The program takes the data input for the model from an Excel spreadsheet that must be formatted with the continuity and constraint equations. The output of the program includes the inferred flows written to the Excel spreadsheet and a flow diagram of the food web model, with flows having widths proportional to their magnitudes (eg. Fig. 1).

Network Analysis and Sensitivity

There are several network analysis techniques that can be used to evaluate the food web structure. The NETWRK software package by Ulanowicz and Kay (1986) supplies several of the following techniques. Fractional outflows can be easily calculated and give the fraction of the total outputs leaving a compartment that enter another compartment of interest, over all direct and indirect pathways (Kay et al., 1989). A more complex technique is determining dependency coefficients that give a measure of how much each component of the food web depends on every other component. The

dependency coefficient is the fraction of the total input to a component that passes through a specific donor component on its way to the recipient. The dependency coefficient allows one to find how much of an organism's diet comes from another component in the food web, over all direct and indirect pathways (Jackson & Eldridge, 1992). This is more useful in complex food webs where organisms feed at several trophic levels.

The Lindeman trophic aggregation can be used to find the effective trophic levels for components in a food web and the tropic efficiency of each trophic level. The effective trophic level gives an idea of the role the component is playing in the food web. For example, Ducklow et al. (1989) found for an open ocean plankton model that mesozooplankton had an effective trophic level of 2.26 for a month when they were feeding extensively on detritus that had an effective trophic level equal to 1. Normally, the mesozooplankton had trophic levels above 3 when they fed primarily on microzooplankton with tropic levels close to 2. The trophic efficiency can be used to compare organisms within the same trophic level and to track an organism's changing role with other changes in the model (Kay, 1989). The trophic efficiency is a measure of the fraction of the total input entering a trophic level that is passed on to the next trophic level (Rhyther, 1969; Pauly and Christensen,1995). The trophic efficiency can give an indication of which trophic level and its respective components are most important in contributing to export from a system.

In addition to network analysis, different techniques can be used to measure the sensitivity of the model generated by the inverse solution. Jackson & Eldridge (1992) varied each input variable to their inverse model solution by +/- 10% and compared the

resulting solutions. Niquil et al. (1998) removed measured flows from the input to their inverse model solution to test the sensitivity of the solution to the inclusion of particular measurements. Niquil et al. also varied the food web structure by removing and adding intercompartmental flows to their model. The inverse solution can give resolutions of the equations used in the continuity equation and also for the calculated flows (Vezina & Platt, 1988). The resolutions are between zero and one and describe how much independent information each equation within the continuity equation provides for the solution. The resolutions for the flows indicate the degree that each flow was calculated independently from all other defined parameters in the model. Another analysis approach is comparing the model of Legendre & Rassoulzadegan (1996) to the inverse model results. Legendre & Rassoulzadegan developed equations that calculate food web functions like downward flux of DOC and food web transfer, depending on the size structure of the phytoplankton and matching of phytoplankton with grazing. These functions of the food web can be calculated from the inverse model results and compared with the classifications of food webs used by Legendre & Rassoulzadegan (1996).

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