4. Microzooplankton

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Background/Data Sources

The microzooplankton group includes holoplankton (protozoa, ciliates, flagellates, copepod nauplii, etc.) and meroplankton (larval stages of benthic invertebrates: trochophores, veligers, etc.). This diverse assemblage has a range of biomass and rate values. For example, in the southeast Bering Sea the protozoan component had a biomass of 10 Mg km^{-2}, a P:B ratio of 72 and a C:B ratio of 144, while the other holoplankton/meroplankton biomass was 13.3 Mg km^{-2}, P:B was 9 and C:B was 27 (Ciannelli *et al.* 2004). In EMAX it was assumed that the microzooplankton were primarily composed of protozoans which have a boom and bust life history strategy that tracks the abundance of their prey (Reid *et al.* 1993). The microzooplankton in the EMAX model feed on bacteria (40% of diet), small phytoplankton (15%), detritus (35%) and other microzooplanton (10%). This diet composition reflects the reality that in nature they consume a wide variety of microautotrophs/heterotrophs (and cannibalize one another). Stimulated by new nitrogen, the spring phytoplankton bloom is often dominated by net plankton (diatoms) which are consumed primarily by mesozooplankton (large and small copepods). Microzooplankton grazing also occurs as a minor component. During the summer stratified period when recycled nitrogen maintains primary productivity, the phytoplankton is dominated by smaller nanoplankton (i.e., dinoflagellates, microflagellates, non-colonial diatoms, etc.) which are grazed by microzooplankton. Microzooplankton grazing of bacteria is the primary link between the microbial loop and grazing food chain.

Quantitative Approach for Estimates

The microzooplankton (MZ) biomass fluctuates seasonally like the phytoplankton biomass, since it is controlled by food resources and grazing. In the EMAX model the food resources are small planktonic autotrophs/heterotrophs and the grazers are mesozooplankton (three nodes). Since we didn't have any independent data on protozoan biomass and rates on the Northeast Continental Shelf, we decided to relate the MZ biomass (in carbon units) to that of phytoplankton (in carbon units) based on Figure 3 in Caron *et al.* (1990) which showed a relationship (log-log) between ciliate and phytoplankton biomass. We assumed that MZ biomass was 0.13 of the phytoplankon biomass, similar to values for unfertilized North Sea mesocosms (Baretta-Bekker, 1994) and Narragansett Bay (Monaco, 1997). Given the boom and bust life history strategy of protozoans, we assumed that their annual biomass would be a relatively small fraction of the annual phytoplankton biomass. As described in the Phytoplankton Section of this document, we had satellite data available to estimate phytoplankton biomass (conversion from chlorophyll *a* to carbon) in the euphotic zone. The phytoplankton biomass was revised to include its distribution throughout the water column, so that it could be used to estimate the MZ biomass. The phytoplankton biomass was 2.0114 g C m^{-2} which resulted in a microzooplankton biomass of 0.2615 g C m^{-2}. These values are shown in Table 4.1. We converted from carbon to dry weight and then to weight wet using the conversion factors in Sherr and Sherr (1984). The dry/wet weight conversion factor was 0.18, while the dry weight/carbon conversion factor was 0.46, yielding a carbon/wet weight conversion factor of 0.0828. Thus the

estimated wet weight biomass for phytoplankton was 20.1144 g m^{-2} and 3.158 g m^{-2} for microzooplankton.

We estimated the ratios of the rates (C:P, P:B, R:P) in carbon units on a daily basis and then converted these to wet weight values on an annual basis. The conversion factors and literature sources for these are shown in Table 4.2. The estimated rates of consumption and respiration shown in Table 4.1 are based on a net growth efficiency of 33% (Straile, 1997; Muren *et al.*, 2005); assimilation efficiency of 90%; and P:B ratio of 72 (Pomeroy, 2001). Using these assumptions, 67% of the assimilated energy goes to respiration and 33% to secondary production. Consumption for the microzooplankton is 0.1737 g C m^{-2} d^{-1} and the assimilation value is 0.1563 g C m^{-2} d^{-1}. Of the assimilated energy, the respiration is 0.1047 and the secondary production is 0.0516. The growth rate (0.197 per day) was based on the assumption that the MZ biomass turns over every 5 days. The growth rate for microzooplankton was assumed to be much slower than that of phytoplankton and slightly slower than that of bacterioplankton. Table 4.1 compares the consumption, respiration and production rates for EMAX GOM (Gulf of Maine) with that of the southeast Bering Sea (BS), North Atlantic Bloom Experiment (NABE), and Narragansett Bay (NB). The NABE values come from a bloom in the open ocean and thus don't represent daily means from a yearly perspective. In theory continental shelf values should fall somewhere along the gradient from inshore waters (NB) to open ocean (BS and NABE). In general the EMAX GOM P:B, P:R, and C:P ratios lie along this inshore/open ocean gradient. Unfortunately most of the literature values that we found came from either inshore waters or the open ocean, so that we had to assume the continental shelf values lies somewhere between the extreme ends of this gradient.

The European Regional Seas Ecosystem Model (ERSEM) lists the assimilation efficiency (AE) for microzooplankton as 50%, even though the value for heterotrophic nanoflagellates is lower at 20% (Baretta-Bekker *et al.* 1995). The bacterial AE is usually assumed to be 50%, even though it can range as low as 25-30% on natural substrates. The AE is related to the mode of feeding, food quality, and the extent of DOC excretion. Protozoa can have significant excretion losses as DOC (Nagata 2000), which explains the range of variation in the AE values. The EMAX AE value was taken as 90% to reflect Protozoa feeding on bacteria attached to detritus (POC), but not DOC, which can be an important pathway (Nagata 2000). The Gross Growth Efficiency (GGE) for microzooplankton is often taken as 40% (McManus 1991), but in EMAX we used 30% (Straile, 1997; Muren *et al.*, 2005). Thus the GGE lies between that of bacteria (24%) and phytoplankton (80%). The microzooplankton secondary production:primary production ratio varies from 7% (ERSEM Model for North Sea, Baretta-Bekker *et al.* 1995) to 14% (English Channel in August, Newell and Linley 1984). The EMAX P:B ratio was assumed to be 72 (Pomeroy, 2001). The EMAX C:B ratio (daily) was assumed to be 0.66 based on an AE of 90%, which is higher than the English Channel C:B value (0.33 per day, Araujo *et al.*, 2005), but is lower than the Baltic Sea value (1.49 per day, Harvey *et al.* 2003). The EMAX R:B ratio was assumed to be 0.40 per day and should lie somewhere between P:B (0.197 per day) and C:B (0.664 per day). Since DOC release can be a significant component for microzooplankton, our R is actually respiration + excretion (where we don't know the magnitude of E). Thus the R:B ratio might differ from 0.40 (58 per yr) if DOC were addressed in the EMAX network model.

The factor for converting microzooplankton carbon weight to wet weight is a multiplier of 12, based on a g C:g dry weight ratio of 0.46 and g dry:wet weight ratio of 0.18 (Table 4.2). As explained in other Sections, we used slightly different carbon to wet weight conversion factors for phytoplankton, bacterioplankton, and detritus (multiplier of 10). Table 4.1 expresses

the P:B, P:R, and C:P ratios on a daily basis, since microzooplankton have a rapid turnover time. We discuss these as yearly values in the text in order to make the values comparable to those reported for other EMAX nodes, which deal with biota with much longer population turnover times.

Results

It is commonly found that when one compares photosynthesis to respiration in the oceanic water column, the ocean appears to be net heterotrophic (P < R; Pomeroy and Wiebe 1993; del Giorgio and Williams 2005). This suggests that either there are methodological problems in measuring primary production and community respiration, or the spatial/temporal coupling is offset and results in biases as one goes from seasonal samples to estimating annual averages. Network analysis balances inputs and outputs from a node so that secondary production of the prey node or food assimilated by the predator node is artificially balanced by respiration, secondary production, net exports/imports, biomass accumulation and harvest removal. Ecopath with Ecosim computes respiration by difference, since it is based on production from the donor node driving the consumption in the receiving node. EcoNetwrk, on the other hand, incorporates respiration as a parameter and is consumption driven. Thus in network models there is a relationship between C:B, R:B, and P:B such that in the balanced models they are different from the input values.

Table 4.2 indicates that the GGE and microzooplankton:phytoplankton biomass (0.13) and productivity (0.07) ratios used in EMAX are similar to those from the literature. This suggests that we got the scaling right in extrapolating from phytoplankton to microzooplankton. We choose a high AE (90%) in EMAX to help transfer the bacterial production efficiently to copepods for transfer up the grazing food chain. Since EMAX did not include DOC as a node, a lot of the bacterial production stems from DOC use beyond just the phytoplankton dissolved production. Therefore, we used higher assimilation efficiencies as compensation to link the microbial food web to the grazing food chain. Our microzooplankton secondary production:phytoplankton production ratio is slightly lower than those reported in the literature.

In EMAX the mesozooplankton biomass (108.4 g wet wet m^{-2}) is much larger than the microzooplankton biomass (3.2 g wet wet m^{-2}), but this is partly compensated for by a higher P:B ratio (72) in microzooplankton compared to the 3 mesozooplankton nodes (P:B range from 20-40). It is assumed that the nauplii and copepodites stages of mesozooplankton reside in the small copepod node and thus the microzooplankton are primarily protozoans. Protozoans can grow almost as rapidly as their bacterial prey which leads to a high P:B ratio, but their boom and bust life history strategy probably results in a much lower average biomass than that of mesozoplankton. Unfortunately traditional zooplankton sampling nets destroy the fragile protozoans, so we lack a monitoring database to evaluate the ecological importance of this microzooplankton group.

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Table 4.1. Comparison of biomass and rate parameters reported for microzooplankton in the southern Bering Sea (BS), North Atlantic Bloom Experiment (NABE) and Narragansett Bay (NB) with estimates derived for the Gulf of Maine (GOM).

Parameter	Units	BS	NABE	NB	GOM
Biomass	g C m^{-2}	1.1	1.2	0.45	0.261
Consumption	g C m^{-2} d^{-1}	2.0	13.9	0.52	0.174
Respiration	g C m^{-2} d^{-1}		7.6	0.19	0.105
Production	G C m^{-2} d^{-1}	0.67	1.9	0.17	0.052
Production:Biomass		0.05	1.6	0.37	0.20
Production:Respiration		0.25	0.89	1.3	0.49
Consumption:Production		2.98	7.3	3.05	3.37

Abbreviations:
BS: Southeastern Bering Sea
NABE: North Atlantic Bloom Experiment
NB: Narragansett Bay
GOM: Initial Gulf of Maine EMAX Input

Table 4.2 Microzooplankton conversions/comparisons.

Parameter	GOM EMAX	Reported Values	Reference
mg dw: mg C		2.2	Sherr & Sherr 1984
mg ww: mg dw		5.56	Sherr & Sherr 1984
mg C: mg wet wt	12.1	12.5	Sherr & Sherr 1984
Assimilation Efficiency	90%	20-50%	Baretta-Bekker *et al.* 1995
Gross Growth Efficiency	30%	40%	McManus 1991
Heterotrophic:Primary Production	0.30	0.07 ERSEM	Baretta-Bekker *et al.* 1995
		0.11 North Sea	Baretta-Bekker *et al.* 1995
		0.14 English Channel	Newell and Linley 1984
Microzoo:Phytoplankton Biomass	0.13	0.11	Baretta-Bekker 1994
		0.12 Narragansett Bay	Monaco *et al.* 1997
		0.99 English Channel	Pomeroy 2001