3. Bacteria

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Background/Data Sources

In the past two decades numerous studies have reported on the quantitative significance of energy and matter flows through the "microbial loop", particularly studies by biological oceanographers interested in nutrient cycling (Pomeroy 2004). While there have been numerous surveys and studies of the phytoplankton primary producers in the NEUS Ecosystem, spatially and temporally comprehensive surveys of the distribution, abundance and metabolic rates of heterotrophic bacterioplankton have not been conducted. Consequently, our estimates of bacterioplankton metabolic rates must be based on indirect methods and on studies and knowledge derived from comparable ecosystems. The primary grazers of bacterioplankton, the microzooplankton, are also poorly characterized for this shelf ecosystem. Together, the bacterioplankton and microzooplankton feeding guilds link dissolved primary production and detritus (particulate organic carbon) to the mesozooplankton. Subsequently, it is available to the living marine resources at higher trophic levels.

Network models such as Ecopath frequently use the detritus compartment to accumulate heterotrophic egestion/excretion energy and sedimented primary production not utilized in the surface mixed layer. In order to process this accumulation of detritus, we added bacteria and microzooplankton guilds (consumption followed by respiration) and transferred a component (secondary production of microzooplankton) to the grazing food chain via mesozooplankton ingestion (mesozooplankton are assumed to be omnivores).

In the EMAX network models the detritus node is particulate organic carbon (POC) processed by vertebrate/invertebrate detritivores which consume the POC and attached bacteria/protozoa. Since bacteria utilize labile and semilabile dissolved organic carbon (DOC), the tacit assumption is that bacterial extracellular enzymes convert the POC to DOC before it is taken up by the bacteria. Even though DOC represents a large nonliving organic carbon pool in the water column, much of it is refractory, and since we do not know its bioavailability to bacteria, the EMAX network models did not explicitly model a node for DOC. Moreover, the operational definition of DOC is the organic matter which passes through a 0.7 μm glass fiber filter, and includes small particles and colloidal organic carbon, making it difficult to distinguish POC and DOC assimilation efficiencies.

In the EMAX networks, bacteria utilize and respire POC. The photoassimilated dissolved organic carbon released by phytoplankton and bacterioplankton are fed upon by microzooplankton prior to a transfer pathway to mesozooplankton. This is obviously a simplification of what occurs in the "microbial loop" which has multiple transfer steps between different size classes of phytoplankton and a variety of microbial heterotrophs (Calvet and Saiz 2005). There is a debate in the literature about whether the "microbial loop" is a sink for POC and DOC (respiration of primary production and storage of carbon in inactive microbial cells) or a source of carbon to the grazing food chain through mesozooplankton acting as omnivores (Ducklow 1994). The assimilation efficiency of bacteria for DOC and POC is often assumed to be 50%, but it may be lower due to the refractory nature of much of the DOC and components of the POC (Pomeroy 2001).

Quantitative Approach for Estimates

Since we had estimates of the phytoplankton biomass and primary production from satellite data for the four subregions of the NEUS Ecosystem, it was assumed that bacterial secondary production (BP) should be roughly 10% of the primary production (PP). We adjusted the consumption of the bacterioplankton node so that the BP:PP ratio = 0.10 (Table 3.1). This is lower than the commonly assumed BP:PP range of 0.15 to 0.30 (Pomeroy 1979; Cole *et al.* 1988; Pomeroy 2001). The outcome of this adjustment was that bacterial consumption was roughly 40% of the net production (PP). This is similar to the value reported in Calbet (2001) for the consumption of primary production by micro- and mesozooplankton in coastal waters. Bacterioplankton have a critical role in processing the excretion (DOC) and egestion (POC) from the other living nodes in the EMAX network. The resultant transfer of recycled carbon from the microbial loop to the grazing food chain improves the overall transfer efficiency of the network energy flow. Given this important trophic role for bacterioplankton, the fact that they might consume 40% of PP via either direct or indirect energy pathways in the EMAX model is not unreasonable.

The other key assumptions were: bacterial gross growth efficiency (GGE) = 0.24; growth rate (P:B) = 0.25 per day; Assimilation Efficiency (AE) = 0.80 and carbon x 10 = wet weight (Bratbak and Dundas, 1984). These assumptions permitted the estimate of the bacterial biomass from BP and growth rate, while the various energy flow ratios (C:B, R:B, R:P, etc.) can be computed using the GGE and AE values. Ducklow (2000) reported an average bacterial growth rate of 0.3 d^{-1} for the eastern North Atlantic spring phytoplankton bloom, and lower rates (0.05-0.25 d^{-1}) for other open sea regions. Reinthaler and Herndl (2005) reported a mean bacterioplankton growth rate of 0.2 ± 0.3 d^{-1} for the southern North Sea. Assuming an average bacterial growth rate of 0.25 d^{-1} applies to the NEUS Ecosystem, then the standing stocks of bacterioplankton biomass in the GOM would be estimated at 0.345g C m^{-2}. This equates to approximately 17% of the phytoplankton standing stock (2.011 g C m^{-2}), based on an average vertically integrated chlorophyll value of 52.73 mg Chl m^{-2} and a phytoplankton carbon:chlorophyll ratio of 40:1.

Del Giorgio and Cole (2000) summarize estimates of bacterial net growth efficiency for a variety of marine systems, reporting a mean value of 0.27. This net growth efficiency (NGE) is slightly lower than our value of 0.30. The growth rate assumption yields an annual P:B = 91.2 which is slightly lower than the value of 100 for bacteria given in Pomeroy (2001). EMAX doesn't use DOC as a food source for bacterioplankton, but Ducklow and Shia (1992) estimate a bacterial conversion efficiency of 20% for DOC and 50% of bioavailable organic matter (like algal exudate). Since the continental shelves have a greater percentage of bacteria attached to particles (POC) than the free living bacteria which dominate the open ocean, we assumed that bacterial enzymes convert the POC to DOC which is consumed by the bacterioplankton. Since EMAX has the bacterioplankton consuming detritus from egestion by the other living nodes, algal exudate and the phytoplankton that sediment out of the euphotic zone, we assumed that the AE = 0.80. The quality of the available POC and DOC seems to determine the AE value and the assimilation efficiency differs between the carbon (used for respiration) and nitrogen (used for growth and cell division). Thus the literature had a broad range of values for AE. The AE for the different heterotrophic nodes determines the rates at which this POC flows into detritus and is shown by the Lindeman Spine in the network output. Our balanced network flow models had high AE values which minimized this POC production.

The resulting biomass of bacterioplankton was 0.345 g C m^{-2} with a production of 0.0863g C m^{-2} d^{-1} for the Gulf of Maine (GOM). The carbon values were converted to wet weight (see Table 3.2) based on the following conversion factors: carbon x 0.5 = dry weight; and dry weight x 0. 20 = wet weight (or carbon wt. x 10 = wet weight). The estimated wet weight biomass is 3.452 g m^{-2} and annual production is 315.026 g m^{-2} y^{-1}. This implies that the annual P:B ratio = 91.3 (which lies between the 163 for phytoplankton and 72 for microzooplankton). Given the GGE and AE assumptions, the net growth efficiency (NGE) is 0.30 which implies that respiration is 70% of the assimilated energy, with the other 30% going to secondary production. NGE values in the literature generally lie between 0.20 and 0.40 (Reinthaler and Herndl, 2005). The choice of the NGE value has a major role in determining whether the microbial loop is a sink for primary production or a link to the grazing food chain. The bacterioplankton consumption was 0.360 g C m^{-2} d^{-1} with respiration representing 0.201 g C m^{-2} d^{-1} and production 0.086 g C m^{-2} d^{-1}. The energetic ratios were: C:B = 1.042; P:B = 0.250 (assumption); R:B = 0.583; and P:R = 0.429. Table 3.1 provides values reported for some other oceanic systems: coastal embayment (Narragansett Bay, NB) and open ocean (North Atlantic Bloom Experiment, NABE). Most of the information on the structure/function of the bacterioplankton community is from studies in estuaries and the open ocean. We assumed that the metabolic activity of bacterioplankton in continental shelf water lies somewhere between the extremes of this gradient. Table 3.1 provides an overview of the underlying assumptions used to estimate bacterial production and biomass, plus the diagnostic energy flow ratios used in the EMAX network model.

In NB the reported gross primary production is 1.49 g C m^{-2} d^{-1} and phytoplankton biomass is 3.8 g C m^{-2}. NB net primary production (0.87 g C m^{-2} d^{-1}) is comparable to our estimate for GOM (0.9 g C m^{-2} d^{-1}), while the standing crop biomass is higher than our estimate for the GOM (2.01 g C m^{-2} d^{-1}). The NABE model is based on values averaged over a 20 day spring bloom/post-bloom period, and we presume that these daily values do not represent the yearly average which is lower in the open ocean than on continental shelves. In NB the standing crops (g C m^{-2}) are 1.2 for pelagic bacteria and 0.5 for microzooplankton, compared to NABE values of 0.1 for bacteria and 0.5 for microzooplankton. The bacterioplankton biomass in the GOM is 0.345 g C m^{-2} which lies along the gradient between NB and the NABE.

In EMAX we partitioned assimilated energy 70% to respiration and 30% to secondary production, which is much different than that reported for the open ocean where respiration is 90% and secondary production is 10% (Ducklow and Carlson, 1992). Our values were chosen to have the bacterioplankton be a link through microzooplankton to the grazing food chain, while the oceanic values assume that the microbial loop is a sink for DOC with most of the carbon being respired. In order to eliminate POC accumulation from the egestion emanating from the other living nodes in EMAX, we assumed that the 70% respiration component would remove this detritus. The secondary production component (30%) provides the link to the grazing food chain.

Del Giorgio and Cole (2000) summarized measurements of bacterial growth efficiency (BGE) for a number of marine systems. In their work, BGE is the ratio of bacterial production to bacterial respiration plus production (BGE = BP/[BR+BP]), and they reported a mean BGE value of 0.27 for coastal areas. This value implies that 73% of the carbon uptake is respired and 27% is retained as organic carbon production, yielding a respiration:production ratio of 2.7 and a consumption:production ratio of 3.7. The bacterial carbon demand (BCD) is BP:BGE and provides an estimate of the heterotrophic consumption in relation to the net primary production.

Since we ignored the DOC component of bacterial consumption, our BCD estimates will be biased high. An exception is bacterial uptake of phytoplankton dissolved production, for which we assumed 100% assimilation efficiency.

Only a portion of the POC is bioavailable to bacteria, but we assumed that all the dissolved primary production was utilized by them. Since we did not know the percentage of POC bioavailability, we adjusted the bacterial respiration rate in order to consume the "apparent detritus production" to prevent it from accumulating or having to export a large faction out of our system boundaries. Since the network models we used balance the flows through the detritus component, one has to develop a way to consume the "apparent detritus production". We decided not to explicitly incorporate the DOC pool in the energy flow pathway, even though it represents a large non-living carbon pool (15 times the POC and 75 times the phytoplankton carbon) of unknown bioavailability in the "microbial loop". We incorporated POC in the EMAX energy flow, since it was a component of the diet matrix for a number of feeding guilds (or nodes) in the network. All of the material egested in the different heterotrophic nodes contributes to the POC pool.

Results

The GOM data in Table 3.1 shows the estimates that were used in EMAX. We assumed a gross growth efficiency of 24% for EMAX (Table 3.2), noting that Del Giorgio and Cole (2000) reported 20%. The ratio of heterotrophic secondary production:primary production in EMAX is 0.10 (assumption), whereas Ducklow (2000) and Reinthaler *et al.* (2005) report a value of 0.15 and Cole *et al.* (1988) report a range between 0.20-0.30.

As shown in Table 3.2, EMAX used fairly high values of Assimilation Efficiency (AE, 80%) and Gross Growth Efficiency (GGE, 24%) since we wanted to prevent the accumulation of detritus or its export out of the system. We assumed that net primary production is approximately balanced by the heterotrophic community respiration on the NEUS Continental Shelf Ecosystem. If one used the values suggested in the literature (AE < 50% and GGE = 20%), then the bacterioplankton would consume the net primary production and none would be available for transfer to the grazing food chain that supports living marine resources (LMRs). EMAX assumed that the microbial food web was a link to the grazing food chain. Using these lower values for AE and GGE would lead to the ecosystem being net heterotrophic (P<<R) and runs counter to field observations, but supports the notion of the "microbial loop" being a carbon sink. This issue is discussed at greater length by Williams (2000) who estimated that bacteria provide 40% of the heterotrophic community respiration. The implications of bacterial GGE values on bacterial consumption of DOC is explored by Ducklow (2000) and Del Giorgio and Cole (2000). Nagata (2000) estimated that bacterial consumption of DOC corresponded to 42% of net primary production, while Williams (2000) estimated that this value was 50%. The issue of the P versus R balance in the water column is discussed by Del Giorgio and Williams (2005).

The EMAX bacteria/phytoplankton biomass and productivity ratios listed in Table 3.1 are similar to those in the literature. Therefore, even if there are some problems with our carbon to wet weight conversions, our scaling between bacteria and phytoplankton seems to be reasonable. Since a significant fraction of the bacterial biomass in oligotrophic, oceanic areas is metabolically inactive, there is much variation in the C:B, R:B, and P:B ratios in the literature, with a wide range of values as one moves from estuarine to open ocean regions. We did not have

the regional data necessary to estimate the metabolically active bacterial biomass, so we used an approach based on literature values to bound the bacterial biomass and rates.

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Table 3.1. Comparison of biomass and rate parameters reported for phytoplankton and bacterioplankton in Narragansett Bay (NB) and North Atlantic Bloom Experiment (NABE) with estimates derived for the Gulf of Maine (GOM).

Parameter	Units	NABE	NB	GOM EMAX
Phytoplankton Biomass	g C m^{-2}		3.8	2.011
Net Primary Production	g C m^{-2} d^{-1}	0.87	0.87	0.90
Gross Primary Production	g C m^{-2} d^{-1}		1.49	1.124
Phytoplankton Production:Biomass				0.447
Bacteria Biomass	g C m^{-2}	0.1	1.2	0.345
Bacteria Consumption – detritus	g C m^{-2} d^{-1}		1.32	0.360
Bacteria Consumption – DOC	g C m^{-2} d^{-1}		0.035	
Bacteria Consumption – total	g C m^{-2} d^{-1}		1.35	0.360
Bacteria Respiration	g C m^{-2} d^{-1}	10.6	0.0863	0.201
Bacteria Production	g C m^{-2} d^{-1}	2.2	0.482	0.0863
Bacteria Production:Biomass			0.40	0.25
Bacteria Production:Respiration			5.59	0.429
Bacteria Consumption:Production				4.166
Microzooplankton Standing Crop	g C m^{-2}	0.5	0.5	0.261

Table 3.2. Bacterioplankton conversions/comparisons.

Parameter	GOM EMAX	Reported Values	Reference
Assimilation Efficiency	80%	50%	Pomeroy & Wiebe 1993
		25-30% (on natural DOC)	Pomeroy & Wiebe 1993
Gross Growth Efficiency	24%	20%	Del Giorgio & Cole 2000
g C: Wet Weight	1:10	1:10	Bratbak & Dundas 1984
mg C:mg dry	0.5	0.5	Bratbak & Dundas 1984
mg dry:mg wet	0.2	0.2	Bratbak & Dundas 1984
mg C:mg wet	10	10	Bratbak & Dundas 1984
Heterotrophic:Primary Production	0.10	0.15	Ducklow 2000
		0.15	Reinthaler *et al.* 2005
		0.20-0.30	Cole *et al.* 1988
Bacteria:Phytoplankton Biomass	0.17	01-0.6	Ducklow 2000
		0.16	Pomeroy 1979
		0.27	Pomeroy 2001