

The annual organic carbon budget of Young Sound, NE Greenland

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Abstract

On the basis of data presented in the previous chapters a carbon budget for the respective compartments of the outer region of Young Sound (76 km²) was established. The average and maximum water depth of the region was 76 m and 177 m, respectively. Primary production was mainly related to the activity of phytoplankton (65%), benthic macrophytes (21%) and benthic microphytes (13%), while the contribution sea-ice algae and corallines was negligible (<1%). The pelagic grazing community was completely dominated by copepods, which were capable of consuming 87% of the pelagic primary production.

The benthic carbon demand was almost balanced by the measured sedimentation of POC and the benthic primary production. The organic carbon collected in the sediment traps was estimated to consist of 40% terrestrial carbon, 20% fecal pellets, while the rest was poorly defined marine detritus. The benthic sink for settling organic material was dominated by microbial respiration (59%) and only to a minor extent related to macrofauna respiration (15%) and carbon preservation (26%).

The total primary production in the region (1119 t C yr⁻¹) only sustained c. 40% the estimated organic carbon demand (2850 t C yr⁻¹). Thus, the independently determined input of TOC (990 t C yr⁻¹) imported to Region 1 from land via freshwater runoff and the TOC import of 1446 t C yr⁻¹ from the Greenland Sea are required to balance the carbon sinks of the net heterotrophic region. A complete balance between the respective compartments cannot be expected, as the various components of the carbon budget are determined independently. The microbial and viral loops remain poorly constrained, as does the carbon demand of the top-predators. Only the importance of walrus was quantitatively assessed.

11.1 Introduction

Only very few interdisciplinary studies exist that quantitatively assess annual carbon flow through entire marine ecosystems (Walsh et al., 1989; Jørgensen, 1996; Nixon, 1995). The obvious reason is the massive effort required to measure all relevant

biogeochemical and hydrographic processes during a seasonal cycle. Nevertheless, to gain fundamental quantitative insight into the functioning of ecosystems, and to evaluate how they will respond to changes in environmental controls like climate or

anthropogenic inputs, such integrated efforts are essential. Performing ecosystem studies in remote areas like the high Arctic is especially challenging – and performing all measurements simultaneously is almost impossible.

To fulfill the original ambition of resolving and investigating the carbon flow through a representative High Arctic ecosystem, various components had to be investigated in successive years. The results of those efforts are summarized in the previous chapters. The present chapter will compile the insights obtained and will establish a carbon budget for a well-defined region of outer Young Sound (Region 1, see Chapter 3). The budget is used to evaluate the importance of various processes and the link between the respective compartments of the system. Specific questions include:

- What is the relative importance of the different organic carbon sources?
- What is the relative importance of the different organic carbon sinks?
- Is the region net heterotrophic or net autotrophic?
- And which central aspects are missing in our present understanding of the system?

To perform this evaluation it was necessary to interpolate and extrapolate measurements performed at different points in time over a 10-year period and to upscale measurements performed at single sites or along depth transects. We chose to extrapolate the findings of the respective stations to the bathymetry of Region 1, which encloses a total area of 76 km² and a water volume of 5.8 km³ (Chapter 3). The average water depth in Region 1 is 76 m and the maximum depth of 177 m is reached along the Northwestern boundary. Twenty one percent of the seafloor area lies at water depths from 0 to 40 m, which roughly defines the depth interval of the photic zone, while 25% of the area lies at depths below 100 m (Fig 11.1).

The data presented in the preceding chapters was collected during a period with large interannual variations in sea-ice cover, downwelling irradiance, precipitation and freshwater input. To constrain the present task and to combine investigations from different years we defined a standard year. This year has an open-water period of 86 days (i.e. 18 July–12 October), which represents the average conditions for the period 1990–2000. In order to define a representative irradiance, we chose to use the light data com-

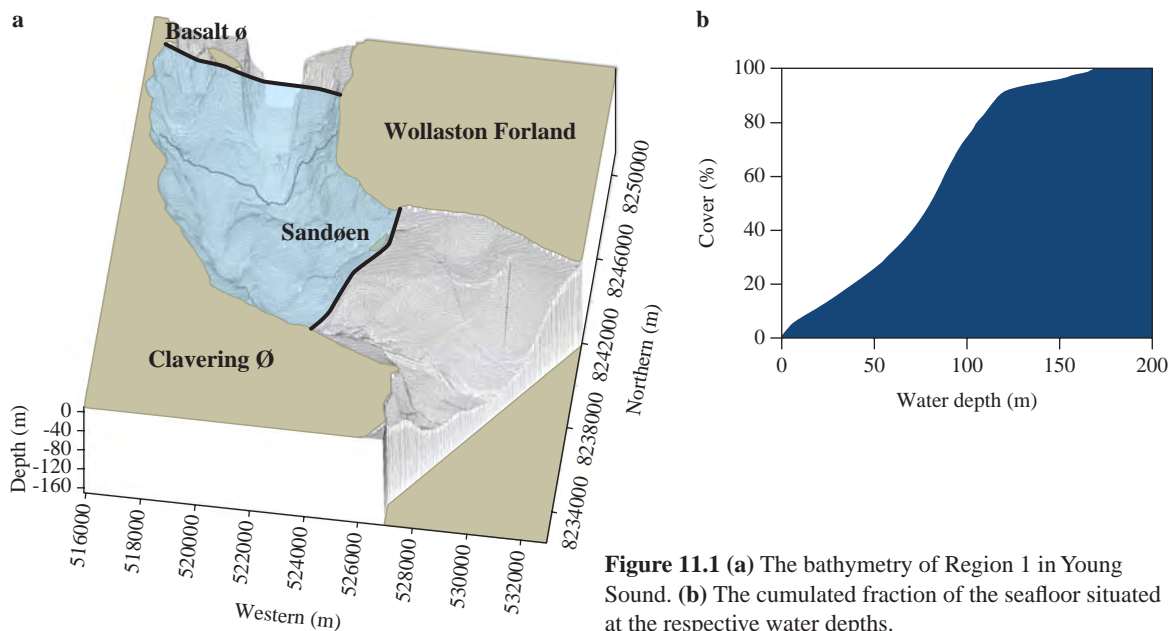


Figure 11.1 (a) The bathymetry of Region 1 in Young Sound. (b) The cumulated fraction of the seafloor situated at the respective water depths.

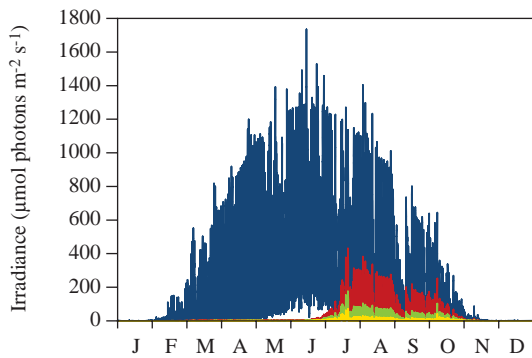


Figure 11.2 Downwelling irradiance measured during 1999 (blue), and the inferred light availability at 10 m (red), 20 m (green) and 30 m (yellow) water depth, taking into account the measured light extinction in the snow and sea-ice cover and in the water column during the same year.

piled during 1999, the snow and sea-ice thickness, and the light extinction coefficients for snow, sea ice and water measured during the same year (Chapter 4). We thereby calculated the irradiance available within the water column and at the sediment surface at the respective water depths (Fig 11.2). These data are used to estimate the annual carbon production of the respective primary producers.

Collecting CTD data from the deeper inner part of the fjord.



Photo: Søren Rysgaard

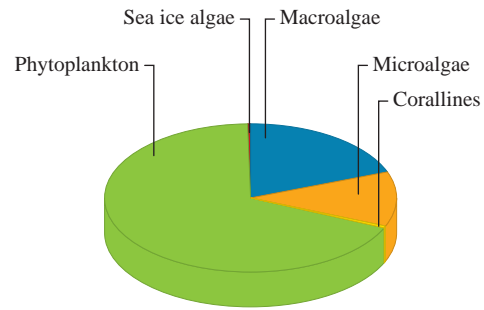


Figure 11.3 The relative contribution of the respective primary producers to the ecosystem production in Region 1 of Young Sound. Phytoplankton 65%, benthic macroalgae 21%, benthic microphytes 13%, sea-ice algae and benthic corallines < 1%. Total primary production in Region 1 is 1119 t C yr⁻¹.

11.2 Results & discussion

11.2.1 Primary production

The net primary production of benthic microalgae, corallines and *Laminaria saccharina* in Region 1 during a standard year as defined above can be calculated from the information provided in Fig. 9.3 & Table 9.3, Chapter 9. *Laminaria saccharina* only accounts for a few percent of the macroalgae biomass in Region 1, but assuming that the remaining foliose biomass (*Fucus*, *desmarestia*) has a P-E relation similar to that of *Laminaria*, the total benthic net primary production amounts to 391 t C yr⁻¹ (Fig 11.3). The corresponding gross primary production of the pelagic community and the sea-ice algae as measured by ¹⁴C incubations equals 728 t C yr⁻¹ as calculated on the basis of information provided in Chapters 4 and 5 (Fig 11.3).

It is remarkable that, despite the average water depth of 76 m the benthic community is responsible for 35% of the ecosystem production of 1119 t C yr⁻¹ in Region 1 (Fig. 11.3). This calculation even compares the net activity of the benthic community with the gross activity of the pelagic community. There is no simple way to convert the net production of the benthic community to gross production, but a number of microsensor studies have concluded that the gross rates of benthic microphytes are 3–6 times higher than the net production (Fenchel & Glud, 2000 and references therein). One might argue that the benthic microphytic contribution should be increased correspondingly. Most of the labile organic

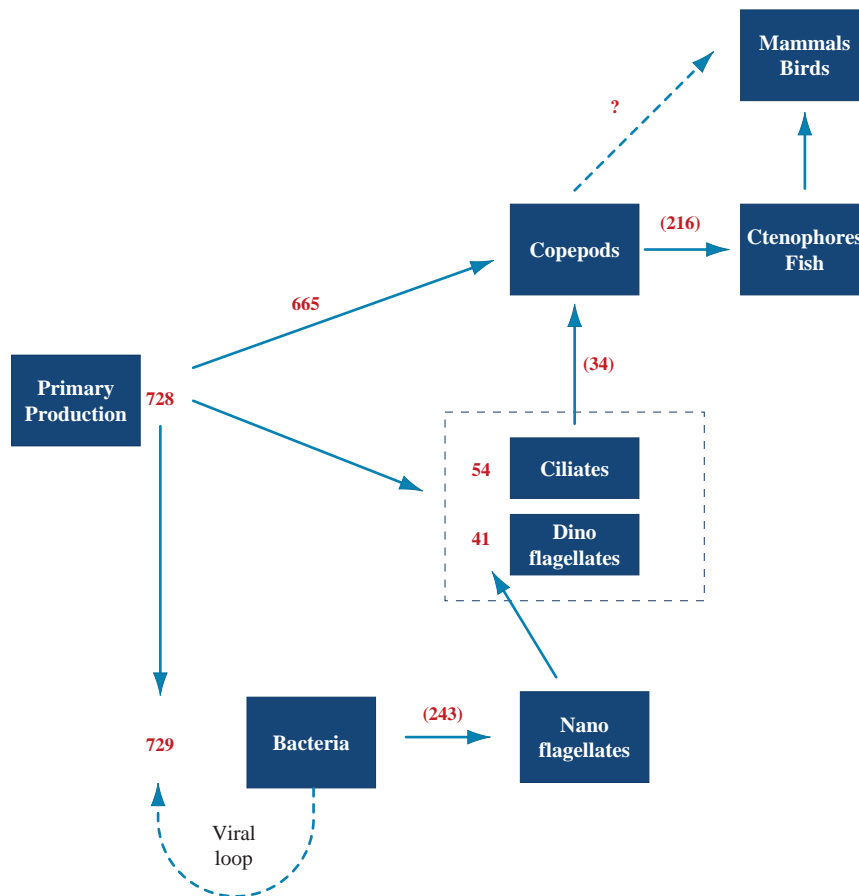
material is, however, quickly recycled through a close autotrophic-heterotrophic coupling within the diatom cover. Likewise, the net production of the macrophytes only represents a minor fraction of the gross production, but, again, most of this difference is respired within the plant itself. Nevertheless, the data strongly emphasize the relative importance of benthic primary production for the carbon flow in Arctic fjord systems. Given the low inclination of the topographic relief surrounding Greenland, one may speculate that benthic primary production is also quantitatively important for the carbon cycling in the coastal waters outside the fjord systems. Considering the high sea-ice algae productivity measured in other locations (e.g. Horner & Schrader, 1982; McMinn et al., 2000) it is surprising that the contribution of sea-ice algae is negligible, an observation confirmed by several investigations performed in successive

years. We ascribe this to light impedance by the snow cover during early spring, and the dynamic nature of the sea-ice matrix during late spring due to massive freshwater intrusion, which inhibits sea-ice algal blooms.

11.2.2 A carbon budget for the pelagic food web

The annual pelagic gross primary production in Region 1 as derived from measurements performed during the ice-covered period, 11–27 June 1999, and the open-water period of 87 days in 1996 amounts to 728 t C yr⁻¹ (Fig. 11.4; see also Chapter 5). Any contributions during the rest of the season can be ignored due to the fjord being covered by snow and sea-ice in the remaining period. The pelagic primary production is primarily related to the activity of diatoms (Chapter 5). This production can either be grazed by the metazoan or the protozoan communities, but it

Figure 11.4 The pelagic food web of Young Sound extrapolated from information provided in Chapter 5. The carbon requirement of the respective compartments are written next to the boxes and values next to the arrow represent the amount of organic carbon that potentially can be transferred to the next trophic level. See text for details on the calculations. Units: t C yr⁻¹.





Midnight at Sandøen – an evening off.

also supports the bacterial production through leakage of photosynthetates and sloppy feeding. Finally, a fraction of the phytoplankton production could also sink ungrazed to the sea floor and contribute to covering the benthic carbon demand.

The grazing community of Region 1 is dominated by the copepods *Calanus glacialis* and *C. hyperboreus*. When the metazoan grazing potential estimated for Station A (Chapter 5, Table 5.6) is extrapolated to Region 1, their annual carbon requirement amounts to 665 t C yr⁻¹, accounting for 90% of the pelagic primary production (Chapter 5; Rysgaard et al. 1999). The copepods could, however, also complement their carbon demand by grazing on the protozoan grazers. Assuming that the entire protozoan production (Chapter 5, Table 5.6) is grazed by copepods, this corresponds to a potential food source of 34 t C yr⁻¹ (Fig 11.4). Sustaining the observed biomass of protozoan grazers represented by ciliates and heterotrophic dinoflagellates (Chapter 5) requires a basin-wide carbon source of 54 and 41 t C yr⁻¹, respectively (Fig 11.4). The estimated copepod production (Chapter 5, Table 5.6) represents the main food supply for the higher trophic levels and represents a basin-wide carbon supply of 216 t C yr⁻¹. Minor carbon pools and turnover by larvae plankton and *appendicularia* accounting for 4% of the zooplankton biomass were ignored in the present budget.

The lower trophic levels and the microbial loop of Young Sound are very poorly constrained. However, when the estimated annual prokaryotic carbon demand at Station A (Chapter 5) is extrapolated to Region 1, it corresponds to a carbon request of 729 t C yr⁻¹. Given that the pelagic primary producers in Young Sound are dominated by larger specimens, bacteria in principle represent the only food source for nanoflagellates, which in turn are grazed by the larger protozoan zooplankton (Fig. 11.4). If the nanoflagellates consume the entire bacteria production (Chapter 5, Table 5.6) it corresponds to a carbon food source of 243 t C yr⁻¹, which is channeled further up through the trophic system (Fig 11.4). However, a significant fraction of the bacterial production could represent internal DOC cycling mediated by viral lysis. It is generally assumed that 10–40% of the bacterial carbon demand in pelagic environments is covered by virus-induced bacterial lysis (Wilhelm & Suttle, 1999; Middelboe, 2007). However, the viral loop of Young Sound still remains to be investigated, and to give a quantitative estimate of this pathway would be pure guesswork. Resolving the importance of the lower trophic grazing levels and the microbial and viral loops has high priority in the future research plans for Young Sound.

The pelagic primary production of Region 1 (728 t C yr⁻¹) balanced the carbon demand of the meta-

and protozoan grazing communities ($665 + 54 + 41 - 34 = 726 \text{ t C yr}^{-1}$) (Fig 11.4). This leaves very little room for the poorly investigated microbial loop (or a direct vertical export of algae material from the photic zone), and the water column thus appears to be net heterotrophic. However, as discussed in Chapter 6, $2436 \text{ t TOC yr}^{-1}$ is imported to Region 1, of which $990 \text{ t TOC yr}^{-1}$ is of terrestrial origin, while $1446 \text{ t TOC yr}^{-1}$ originates from the Greenland Sea. This material more than balances the carbon demand of the net heterotrophic water column and contributes to the vertical transport of organic material required by the benthic community (see below).

11.2.3 Vertical export of organic material and potential sources of sedimenting POC

The net import of particulate material to Region 1 that is not recycled in the water column, ultimately settles at the sediment surface where it is mineralized by benthic animals or microbes, or buried in the sediment record. A sediment trap placed at 65 m water depth in Region 1 revealed vertical POC fluxes of 17, 19 and $25 \text{ g C m}^{-2} \text{ yr}^{-1}$ during the years 2003, 2004 and 2005, respectively (Chapter 6; Rysgaard et al., unpub). Assuming that these values represent the average benthic sedimentation rate of organic material, they correspond to an annual POC sedimentation of $1548 \pm 317 \text{ t C yr}^{-1}$. Isotopic analysis of the material collected in the sediment traps suggested that roughly 40% of the material was of terrestrial origin and discharged into the sound via freshwater runoff (Chapter 6). Based on the sediment trap data, this corresponds to an import of $517 \text{ t POC yr}^{-1}$ to Region 1 from terrestrial sources during 2003, very close to the independent mass balance studies of $495 \text{ t POC yr}^{-1}$ (Chapter 6; Rysgaard et al., 2003). When the average POC sedimentation rate measured during 2003–2005 is applied, this fraction amounts to 619 t C yr^{-1} . The material presumably represents a relatively refractory carbon pool and the POC contribution from land almost balances the benthic carbon preservation (see below). The net import of DOC to Region 1 from land-based sources was estimated at 503 t C yr^{-1} and is in principle available to the planktonic food web, even though it presumably represents a relatively refractory carbon pool (Chapter 6). The remaining POC collected in the sediment traps ($1548 - 619 = 929 \text{ t C yr}^{-1}$), must either be produced within the region, be advected into the system from the

Greenland Sea, or represent resettling of resuspended material (the latter can presumably be ignored due to the position of the sediment trap c. 40 m above the sediment; Chapter 6). Visual inspection of the trap material revealed intact algae cells (mainly diatoms), but copepod pellets represented an important and distinct fraction of the collected material. Assuming that an average of 40% of the carbon ingested by copepods is released as fecal pellets (Møller et al., 2003), the pellet production in Region 1 can be estimated at 266 t C yr^{-1} . The remaining material in the traps ($929 - 266 = 663 \text{ t C yr}^{-1}$) must represent other sources of marine detritus, of which a significant fraction presumably is advected into the region from the Greenland Sea. This can be especially important during late spring prior to sea-ice break-up when a productive polynya develops off the fjord and probably feeds the outer regions of Young Sound with labile organic carbon via estuarine and tidal circulation (Chapters 3 & 5). The total TOC import to Region 1 from the Greenland Sea was estimated at 1446 t C yr^{-1} ; Chapter 6), but, unfortunately, the relative fractions of DOC and POC remain unknown.

11.2.4 Benthic carbon demand

The POC settling at the seafloor is either preserved in the sediment record or mineralized by fauna and microbes. Based on the information in Table 8.2, Chapter 8, the annual benthic carbon preservation of Region 1 can be calculated at 564 t C yr^{-1} , while the microbial carbon mineralization (including polychaetes, see below) equaled 1320 t C yr^{-1} (Fig. 11.5). The latter value was derived from core incubations excluding most of the benthic macro and megafauna. The carbon requirement of the most prominent macrofauna groups i.e. brittle stars, bivalves and sea urchins was calculated at 53, 151 and 2 t C yr^{-1} , respectively, using the recommendations in Chapter 7 & 8. A recent study does, however, suggest that the carbon requirement of the sea-urchin community in Region 1 may be as high as 36 t C yr^{-1} (Blicher et al., *in press*). Polychaetes were presumably reasonably well represented during the core incubations and their carbon demand has previously been estimated at 72 t C yr^{-1} (Glud et al., 2000). Hence, microbial respiration accounted for 1248 t C yr^{-1} ($1320 - 72 \text{ t C yr}^{-1}$) and benthic animals for 312 t C yr^{-1} ($53 + 151 + 36 + 72 \text{ t C yr}^{-1}$) of the degradation in the sediment. For bivalves it has been estimated that 20% of the

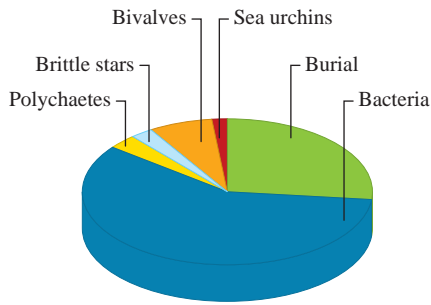


Figure 11.5 The relative contribution to the benthic carbon requirement in Region 1 of Young Sound. The total requirement is 2124 t C yr⁻¹. Bacteria accounts for 59%, burial for 26%, brittle stars for 3%, bivalves for 7%, sea urchins for 2% and polychaetes for 3% of the requirements.

assimilated organic carbon is excreted and thus made available to the benthic microbial community (Sejr et al., 2004). Assuming that this value is representative of all benthic fauna groups, faunal excreta would sustain 5% (62 t C yr⁻¹) of the microbial carbon demand. When all these values are compiled, the total benthic carbon requirement of Region 1 amounts to 2124 t C yr⁻¹ (Fig. 11.5 & Fig. 11.6). The net benthic exchange of DOC is marginal (Chapter 8) and is ignored in the established benthic carbon budget. It follows that the benthic heterotrophic activity (i.e. 1560 t C yr⁻¹) is larger than the entire primary production of the region and that external carbon sources (i.e. from land and the Greenland Sea) are required to balance the budget.

The microbial carbon requirement, dominated by the oxygen and sulfate respiring bacteria, accounts



Photo: Søren Rysgaard

for 59% of the annual benthic carbon demand. This value is extrapolated from 79 sediment core incubations performed in 1994 (6), 1996 (67) and 1997 (6) (numbers in brackets represent the respective number of incubations). The extent to which the value represents average conditions in Young Sound is open to discussion, and we have no means of directly evaluating the interannual variability of the benthic microbial carbon mineralization. However, 1996 had an open-water period of 87 days, which is similar to the value for the standard year defined above, and the precipitation of 223 mm during 1996 was close to the annual mean of 198 mm for the period 1996–2003, (Rasch & Caning, 2005). Thus, the light availability in, and the freshwater input to Young Sound during 1996 presumably reflect the average conditions reasonably well. The remaining components of the ben-

thic carbon demand all integrate time scales greater than one year, and as such they presumably provide a relatively robust average value for the area.

The enhanced O₂ uptake following settling of the summer bloom only represents c. 10% of the annual respiration, and on an annual basis most of the benthic activity is presumably sustained by a slowly-degrading carbon pool with a decay rate constant of 76 yr⁻¹ (Chapter 8). The benthic macro- and megafauna only accounts for 15% of the total benthic carbon requirement and 25% of the microbial activity (Fig. 11.5). This confirms the general observation that fauna metabolism on its own only has a minor role in carbon mineralization in marine environments (e.g. Glud et al., 1998, 2003). The impact of benthic fauna on benthic mineralization is mainly indirect through bioturbation and bioirrigation activities that stimulate microbial

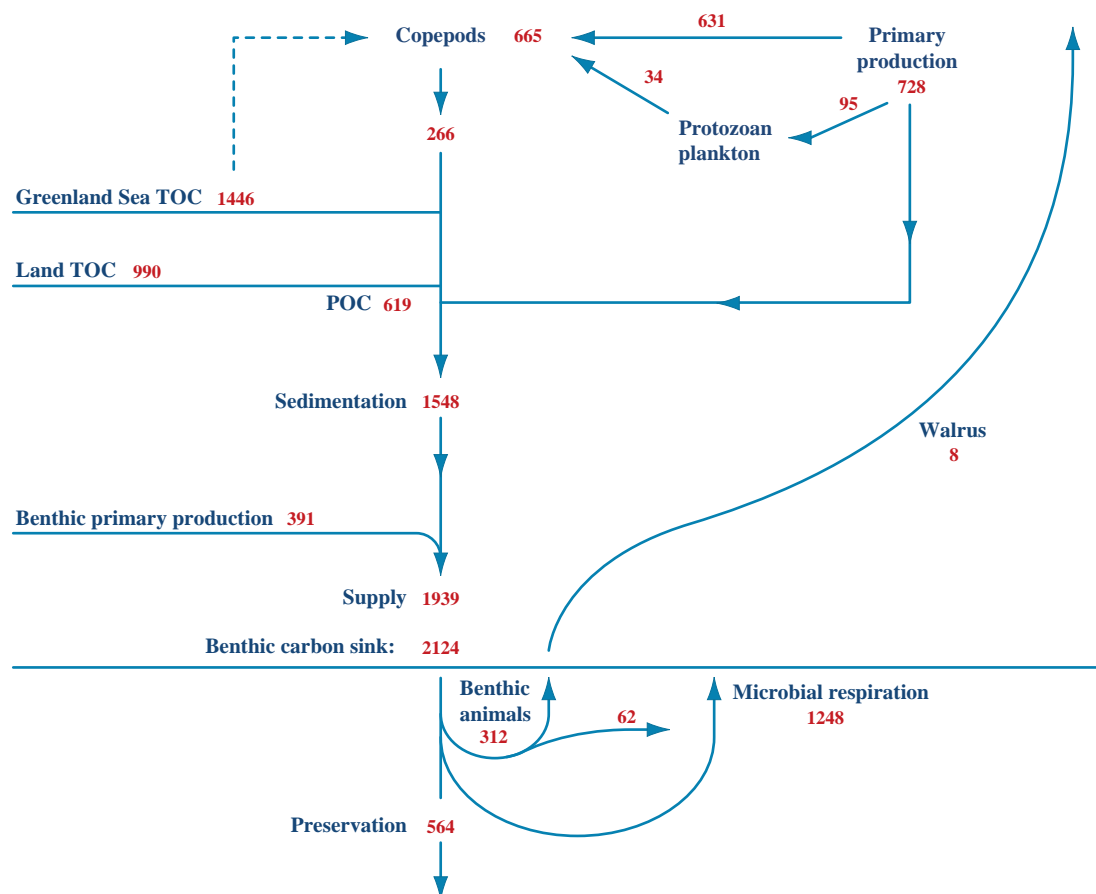


Figure 11.6 Annual carbon budget for Region 1 in Young Sound, Units: t C yr⁻¹. See text for details on the calculations.

and chemical oxidation processes. In total, 26% of the benthic POC demand is preserved in the sediment.

The benthic carbon requirement must be balanced by the POC flux from the overlying water column. Taken together, the annual vertical POC transport measured during 2003–2005, and the benthic primary production as estimated for a normalized standard year (see above), sustained $92 \pm 16\%$ (1949 ± 317 t C yr⁻¹) of the benthic carbon requirement. Thus, a good agreement between the supply and demand of organic material for the benthic community can be observed when all the independent measurements are considered (Fig. 11.6).

11.2.5 Higher trophic levels

Most of the higher trophic levels in Region 1 have not been studied in any detail. No reliable estimates exist of the biomass or carbon requirement of fish, seals, birds or whales that occasionally visit the sound. Likewise, we have no information on the quantitative importance of ctenophores and euphausiids that occasionally exhibit mass occurrence within the sound and thus could represent an important grazing potential.

The only top predator to receive attention is the walrus, which has colonized the island Sandøen, and it was concluded that the population consumes 85 tons of shell-free bivalves, corresponding to 25 t C yr⁻¹ in outer Young Sound (Regions 0, 1, 2 & 3) (Born et al., 2003; Chapter 10). Assuming that the foraging of walruses is evenly distributed, this leads to carbon consumption in Region 1 of 8 t C yr⁻¹ (Fig. 11.6), representing a negligible amount of the standing stock of bivalves (Chapters 7 & 10)

11.2.6 Concluding remarks

Young Sound represents one of numerous High Arctic sill fjords, and the interdisciplinary study summarized in the previous chapter offers a unique opportunity to establish a carbon budget for Region 1 in this generally rarely studied type of ecosystem (Fig 11.6). The exercise of establishing such a budget does, however, also reveal that several components are poorly constrained, especially the microbial and viral loops, which could potentially represent a significant sink for organic material in the system. Likewise, the coupling from the invertebrate fauna to the top consumers (fish, seals, whales, birds) – with the exception of the walrus – remains unresolved. The

microbial loops and the top consumers deserve more attention in the future (see Chapter 12).

Nevertheless, the present understanding of the system allows us to draw some general conclusions. Even excluding the microbial loop, it follows that the total carbon demand of the benthos and the pelagic grazing community (i.e. 2850 t C yr⁻¹) by far exceeds the primary production of the system (i.e. 1119 t C yr⁻¹) i.e. the net heterotrophic system is in deficit of 1731 t C yr⁻¹. Independent measurements coupled to a hydrodynamic model estimated that the region has a net import of organic material amounting to 2436 t C yr⁻¹ with 60% being delivered from the Greenland Sea and the rest from land. This material thus supports the carbon demand of the region. A full balance between these two components cannot be expected, as the advective carbon import is very dependent on the estimated freshwater input. A sensitivity analysis revealed an estimated net import bracketed by a minimum and maximum value of 1300 and 4400 t C yr⁻¹, respectively. The annual freshwater input varied by a factor of 2.5 during 1996–2004 (from 132 to 338 10⁶ m³) (Rasch & Caning, 2005; Chapter 2), and is an important factor in regulating the net carbon import to the region.

11.3 Acknowledgments

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11.4 References

- Born, E. W., Rysgaard, S., Ehlme, G., Sejr, M., Acquarone, M. & Levermann, N. 2003. Underwater observations of foraging free-living Atlantic walruses (*Odobenus rosmarus rosmarus*) and estimates of their food consumption. *Polar Biol.* 26: 348-357.
- Blicher, M. E., Rysgaard, S. & Sejr M. K. *in press*. Growth and production of the sea urchin, *Strongylocentrotus droebachiensis*, in a high-arctic fjord, and growth along a climatic gradient (64-77°N). *Mar. Ecol. Prog. Ser.*
- Fenchel, T. & Glud, R. N. 2000. Benthic Primary production and O₂-CO₂ dynamics in a shallow water sediment: Spatial and temporal heterogeneity. *Ophelia* 53: 159-171.
- Glud, R.N., Holby, O., Hofmann, F. & Canfield D. E. 1998. Benthic mineralization in Arctic sediments (Svalbard). *Mar. Ecol. Prog. Ser.* 173: 237-251.
- Glud, R. N., Risgaard-Petersen, N., Thamdrup, B., Fossing, H. & Rysgaard S. 2000. Benthic carbon mineralization in a high-arctic sound. *Mar. Ecol. Prog. Ser.* 206: 59-71.
- Hansen, P. J., Hansen, B. W. & Bjørnsen, P. K. 1997. Zooplankton grazing and growth: Scaling within the size range 2 µm to 2000 µm. *Limnol. Oceanogr.* 42: 687-704.
- Horner, R. A. & Schrader, G. C. 1982. Relative contribution of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of the Beaufort Sea. *Arctic* 35: 485-503.
- Jørgensen, B. B. 1996. Case study - Aarhus Bay. In: Jørgensen, B. B. & Richardson, K (eds.). *Eutrophication in Coastal Marine Ecosystems*. Coastal and Estuarine Studies. American Geophysical Union, Washington: 137-154.
- McMinn, A., Ashworth, C. & Ryan, K. -G. 2000. *In situ* net primary productivity of an Antarctic fast ice bottom algal community. *Aquat. Microb. Ecol.* 21: 177-185.
- Middelboe, M. (2007): Microbial disease in the sea: Effects of viruses on marine carbon and nutrient cycling". In Eviner, V. et al. (eds.). *Ecology of infectious diseases: Interactions between disease and ecosystem*. Princeton University Press.
- Møller E. F., Thor, P. & Nielsen, T. G. 2003. Production of DOC by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* through sloppy feeding and leakage from fecal pellets. *Mar. Ecol. Prog. Ser.* 262: 185-191.
- Nixon, S. W., Granger, S. L. & Nowicki, B. L. 1995. An assessment of the annual mass balance of carbon, nitrogen, and phosphorous in Narragansett Bay. *Biogeochemistry* 31: 15-61.
- Rasch, M. & Caning, K. (eds.) 2004. ZERO - Zackenberg Ecological Research Operations. 10th Annual Report, 2005. Danish Polar Center, Ministry of Science, technology and Innovation. Copenhagen, 85 pp.
- Rysgaard, S., Nielsen, T. G. & Hansen, B. W. 1999. Seasonal variation in nutrients, pelagic primary production and grazing in a high-Arctic coastal marine ecosystem, Young Sound, Northeast Greenland. *Mar. Ecol. Prog. Ser.* 179: 13-25.
- Rysgaard, S., Glud, R. N., Sejr, M. K., Bendtsen, J. & Christensen, P. B. *in press*. Inorganic carbon transport during sea ice growth and decay: A carbon pump in polar seas. *Journal of Geophysical research Ocean.* 2006JC003572
- Sejr, M. K., Petersen, J. K., Jensen K. T. & Rysgaard, S. 2004. Effect of food concentration on clearance rate and energy budget of the Arctic bivalve *Hiatella arctica* (L) at subzero temperature. *J. Exp. Mar. Biol. Ecol.* 311: 171-183.
- Walsh, J. J., McRoy, C. P., Coachman, L. K., Goering, J. J., Nihoul, J. J., Whitley, T. E., Blackburn, T. H., Parker, P. L., Wirick, C. D. Shuert, P. G., Grebmeier J. M., Springer, A. M., Tripp R. D., Hansell, D. A., Djenidi, S., Deleersnijder, E., Henriksen, K., Lund, B. A., Andersen P., Müller-Krager, F. E. & Dean, K. 1989. Carbon and nitrogen cycling within the Bering/Chukchi Seas: Sources regions for organic matter effecting AOU demands of the Arctic Ocean. *Prog. Oceanogr.* 22. 277-359.
- Wilhelm, S. W & Suttle, C. R. 1999. Viruses and nutrient cycles in the sea. *Bioscience* 49: 781-788.