

The marine ecosystem of Kongsfjorden, Svalbard

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Kongsfjorden is a glacial fjord in the Arctic (Svalbard) that is influenced by both Atlantic and Arctic water masses and harbours a mixture of boreal and Arctic flora and fauna. Inputs from large tidal glaciers create steep environmental gradients in sedimentation and salinity along the length of this fjord. The glacial inputs cause reduced biomass and diversity in the benthic community in the inner fjord. Zooplankton suffers direct mortality from the glacial outflow and primary production is reduced because of limited light levels in the turbid, mixed inner waters. The magnitude of the glacial effects diminishes towards the outer fjord. Kongsfjorden is an important feeding ground for marine mammals and seabirds. Even though the fjord contains some boreal fauna, the prey consumed by upper trophic levels is mainly Arctic organisms. Marine mammals constitute the largest top-predator biomass, but seabirds have the largest energy intake and also export nutrients and energy out of the marine environment. Kongsfjorden has received a lot of research attention in the recent past. The current interest in the fjord is primarily based on the fact that Kongsfjorden is particularly suitable as a site for exploring the impacts of possible climate changes, with Atlantic water influx and melting of tidal glaciers both being linked to climate variability. The pelagic ecosystem is likely to be most sensitive to the Atlantic versus Arctic influence, whereas the benthic ecosystem is more affected by long-term changes in hydrography as well as changes in glacial runoff and sedimentation. Kongsfjorden will be an important Arctic monitoring site over the coming decades and a review of the current knowledge, and a gap analysis, are therefore warranted. Important knowledge gaps include a lack of quantitative data on production, abundance of key prey species, and the role of advection on the biological communities in the fjord.

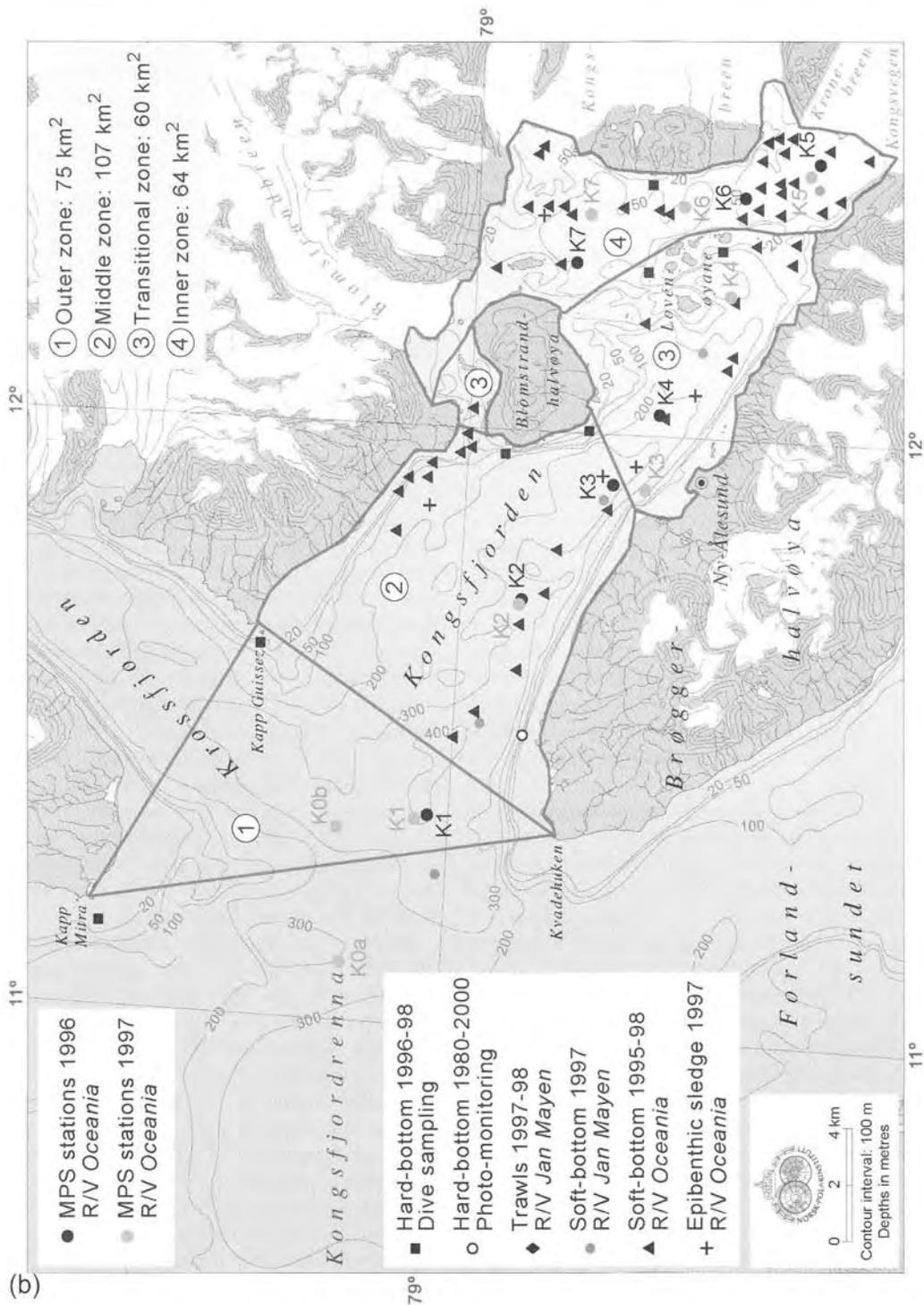
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Kongsfjorden, a glacial fjord in the Arctic, is located on the west coast of Svalbard at 79°N, 12°E (Fig. 1). Because it is an open fjord with no sill at the entrance, the exchange across the shelf-fjord boundary has a large impact on both the physical and biological variation in this fjord system (Svendsen et al. 2002 [this issue]). The Atlantic influence makes this fjord sub-Arctic rather than Arctic, as might be expected at this high latitude. Western Svalbard coastal waters are influenced by the northernmost extension of the warm North Atlantic Current, which carries

relatively warm and salty water into the West Spitsbergen Current (Loeng 1991; Svendsen et al. 2002). The strength of this current is likely linked to climatic variability represented by the North Atlantic Oscillation (e.g. Hurrell 1995), which is correlated with variations in sea ice extent in the Nordic seas (e.g. Vinje 2001). Differences between “cold” and “warm” years have been noted for coastal marine ecosystems in Svalbard (Wesławski & Adamski 1987). Climate change will most likely influence the partially closed water body of Kongsfjorden from both



Fig. 1. (a) The Svalbard Archipelago; Bjørnøya not shown (left). (b) Bathymetric map of Kongsfjorden, showing pelagic and benthic sampling stations (opposite page). Based on species distribution, substrate and the overriding environmental gradient, Kongsfjorden is divided into four zones. Pelagic samples were collected by Multi Plankton Sampler (MPS stations K0–K7), plus WP-2, WP-3 nets and Tucker Trawl (locations not indicated). Benthic hard-bottom samples were collected at 0–30 m by divers (quantitative frames and hand collection or suction sampling), and photo-monitoring was performed by stereo-photography on marked sites at 15 m depth. Soft-bottom samples were collected by van Veen grab and Karstengreifer box corer, and macrobenthos by epibenthic sledge. (Caption continues opposite page, bottom.)



(b)

Fishes were caught in a Campelen 1800 bottom trawl. The land and glaciers on the map were extracted from the Norwegian Polar Institute's digital map series 250 (original scale was 1:250 000). The bathymetry was digitized from Arctic Chart number 522 (Norwegian Polar Institute 1974; original scale 1:100 000). The map can be downloaded from the Internet at: <ftp://npolar.no/Out/anne/KongsfjordenGIS/web/index.html>.

ends: the outer fjord influenced by oceanographic conditions and the inner fjord influenced by large tidal glaciers (Svendsen et al. 2002).

Kongsfjorden represents a border area between Atlantic and Arctic biogeographic zones, and the biodiversity and animal populations in this fjord are strongly structured by the different physical factors that influence the fjord from both ends. An increased influx of Atlantic Water into the Kongsfjorden system would alter the species composition towards boreal species, whereas glacial input and distance from the coast would tend to make the inner part of the fjord more Arctic. In addition, the glacial input of freshwater and sediments create steep environmental gradients in the fjord system. The gradual reduction in the magnitude of glacial effects with distance from the glaciers provides a system well suited to a study of structural and functional biodiversity. The strong environmental gradients in sedimentation and freshwater input induce large changes in community composition and abundance from inner to outer fjord, particularly for the benthos (e.g. Holte et al. 1996; Holte & Gulliksen 1998). Seabirds and marine mammals that utilize benthic or pelagic food sources are also affected by such changes in the community composition, since their foraging sites are predominantly located where suitable prey species are abundant.

Production in Kongsfjorden is dependent on light as well as on stratification and mixing. The depth of the euphotic layer decreases from 30 m at the fjord entrance to 0.3 m in the turbid waters close to the glacier fronts. Another factor that reduces available light in the water column is the ice cover, particularly when the ice is snow-covered. This condition exists for five to seven months in the inner fjord basin and about one month in the central basin (Svendsen et al. 2002). An extended presence of ice cover has a limiting effect on primary production during early spring. However, the fjords on the west coast of Svalbard are relatively productive, being comparable with production levels estimated for the Barents Sea (Sakshaug et al. 1994; Hegseth 1998).

This overview presents the "state of the art" for existing knowledge about the glacially influenced marine ecosystem of Kongsfjorden. The presence of the international research community in Ny-Ålesund, which is a European Union funded Large Scale Facility, has further increased the importance of Kongsfjorden as a focus for

fjordic and coastal research. Kongsfjorden will be an important Arctic monitoring site over the coming decades, since this fjord has become a key European site for Arctic marine studies. A review of the current status of knowledge and a gap analysis is therefore warranted. This paper emphasizes the marine ecosystem, mainly with regard to organisms and their abundance and distribution patterns in the fjord. The physical factors are identified, but these are described much more completely in Svendsen et al. (2002).

Pelagic and sympagic communities

Phytoplankton

Sampling of phytoplankton has generally been performed in the middle of the fjord without regard to the recently observed differences in physical conditions on the two sides of the fjord (Svendsen et al. 2002). The investigations have focused on discrete measurements of biomass and species distribution and a few primary production studies. A total of 148 phytoplankton taxa have been recorded from Kongsfjorden to date; 67 of these taxa belong to the Bacillariophyta and 46 to the Dinophyta (Eilertsen et al. 1989; Hasle & Heimdal 1998; Keck et al. 1999; Wiktor 1999; S.-Å. Wängberg, pers. comm.). Most of the species are either of Atlantic or cosmopolitan origin. Only 31 (21%) of the phytoplankton species in Kongsfjorden are considered to be Arctic or boreal-Arctic species based on the classification by Hasle & von Quillfeldt (1996).

There is a pronounced seasonal signal in phytoplankton growth and distribution in Kongsfjorden. The long polar night (116 days) stops production by autotrophic organisms. A single winter investigation from Svalbard fjords confirms that only flagellates, presumably heterotrophic, survive in the water column during this time (Wiktor 1999). Autotrophic algae probably survive as resting stages in sediments in Svalbard, similar to the situation in northern Norwegian fjords (Eilertsen et al. 1995; Hegseth et al. 1995). Resting spores of the main species of diatoms that bloom in spring have been found in Kongsfjorden after the bloom (Hasle & Heimdal 1998).

In spring, more than 60 phytoplankton taxa have been identified, most of which are diatoms. Common species in open water

during May include the haptophyte *Phaeocystis pouchetii* (max. cell no. 12 mill. l⁻¹) and diatoms like *Chaetoceros socialis* (max. cell no. 4.7 mill. l⁻¹) and *Thalassiosira nordenskiöldii*, whereas *Fragilariopsis* species are less numerous. Among the dinoflagellates, a few *Proto-peridinium* and *Gymnodinium* species have been found (Eilertsen et al. 1989; Wiktor 1999). The phytoplankton distribution in the inner and transitional zones (Fig. 1b) is strongly related to the presence of ice cover within the fjord. Small diatoms and flagellates dominate at the ice edge zone, whereas flagellates dominate below the ice (Wiktor 1999).

During the early spring (March), the transparency in the water is quite high, with a euphotic zone (Photosynthetically Active Radiation [PAR] >1% of surface values) >30 m. Presence of diatoms indicates the start of the phytoplankton growth season (Wiktor 1999). The spring bloom is the only predictable phytoplankton production peak in the fjord. Commencing in late April, a considerable increase in phytoplankton biomass has been observed, from 20–25 mg Chl-*a* m⁻² in ice edge zones or under the ice to about 250 mg m⁻² in open water during mid-May. The timing of the bloom coincides with similar blooms along the northern Norwegian coast, indicating a strong light or day length control (Eilertsen et al. 1989). The magnitude of phytoplankton biomass is likely to be higher than indicated by the available data (Table 1), which do not cover the peak of the bloom or the outer part of the fjord (J. Wiktor, pers. comm.). The few available data on sedimentation indicate that only a minor component (1.4 mg C m⁻² d⁻¹) of the diatom-dominated spring bloom sinks from the

water column (Wiktor 1999). This corresponds to observations of a longer lasting bloom than along the Norwegian coast where it usually culminates in less than a month and sinks out of the euphotic zone (Eilertsen & Taasen 1984). The spring bloom in Kongsfjorden is subsequently slowed down by heavy grazing (Eilertsen et al. 1989), yielding a low sedimentation signal. Thus, the spring bloom seems to be controlled by light at its onset and grazing during its later phase.

The summer season in Kongsfjorden is characterized by very diverse phytoplankton communities, with >130 taxa recorded. In the inner part of the fjord, dinoflagellates (*Proto-peridinium* spp., *Gymnodinium* spp. and *Gyrodinium* spp.; max. cell no. 0.6 mill. l⁻¹) and small, unidentified flagellates dominate. In the middle part of the fjord, the chrysophyte *Dinobryon balticum* (max. cell no. 3.5 mill. l⁻¹), in addition to dinoflagellates are numerous. Diatoms (*Thalassiosira antarctica* var. *borealis*, *Cylindrotheca closterium* and *Chaetoceros* spp.) occasionally occur in the middle and outer part of the fjord (max. cell no. 0.2 mill. l⁻¹), together with *Phaeocystis pouchetii*, *Dinobryon balticum* and dinoflagellates (Halldal & Halldal 1973; Eilertsen et al. 1989; Hasle & Heimdal 1998; Keck et al. 1999; Okolodkov et al. 2000). Occasional observations of coccolithophorids (*Coccolithus pelagicus* f. *hyalinus* and f. *pelagicus*), sometimes in high amounts (max. 130 000 cells l⁻¹), indicate that inflow of Atlantic Water takes place in the fjord at irregular intervals (Halldal & Halldal 1973; Hasle & Heimdal 1998). However, the effect of this inflow to the overall phytoplankton composition and production is unknown.

Light conditions largely determine the level

Table 1. Kongsfjorden: phytoplankton biomass (mean integrated data 0–50 m) as chlorophyll, carbon and cell numbers in outer and inner part of the fjord at different times of the year.

Season Part of fjord	Winter	Early spring	Spring bloom	Summer		Autumn		References
	Inner	Inner	Inner	Inner	Outer	Inner	Outer	
Chl (mg m ⁻²)		19.6–24.4	176–260	32.6–53.8 6.9	58.6–158	24.1	42.4–46.1	Halldal & Halldal (1973), Eilertsen et al. (1989), Wiktor (1999), Hegseth (unpubl.)
C (g m ⁻²)	1.7–2.5	5.0	15.0	0.78–2.20	0.35–5.3	1.2 ^a	2.1–2.3 ^a	Wiktor (1999, unpubl.)
Cells (10 ⁶ m ⁻²)	108 ^b	18–67	115–278		32–64			Halldal & Halldal (1973), Wiktor (1999)

^a Calculated from C/Chl=50.

^b Heterotrophic flagellates.

of primary production. The long days during summer give high daily doses of PAR even though the highest intensity ($1300 \mu\text{mol m}^{-2}\text{s}^{-1}$) is low compared to that at lower latitudes (Svendsen et al. 2002). Water transparency decreases dramatically in early June when the rivers thaw and the ice and snow melt increase. This is especially important in the inner part of the fjord where the euphotic zone can be as little as 0.3 m (Keck et al. 1999) and may reduce the growth of photosynthetic algae (Eilertsen et al. 1989). In the central part of the fjord, water transparency during summer is largely dependent on water currents and tides. Near Lovénøyane, the euphotic zone may vary between 6 and 25 m (Svendsen et al. 2002) and in the inner part of zone 2 (Fig. 1b) the transparency can be reduced by 50% within 10 h (S.-Å. Wängberg and K. Gustavson, pers. comm.). Maximum biomass in the inner part of the fjord has been registered in the surface 0-15 m layer, with the shallowest maxima closest to the glaciers (Halldal & Halldal 1973; Okolodkov et al. 2000). Blooms occur irregularly, and both bloom and non-bloom conditions have been observed during summer (e.g. Keck et al. 1999). A surface mixed layer of 30-40 m (Svendsen et al. 2002) is prominent in Kongsfjorden. Nutrients in this layer may be reduced to about half the winter values, and biomass may be reduced to almost winter values (6-7 mg Chl-*a* m^{-2} ; Eilertsen et al. 1989) (Tables 1, 2). However, considerably higher values ($>150 \text{ mg m}^{-2}$) have been found in some years (Halldal & Halldal 1973).

Grazing may be a dominant factor controlling phytoplankton growth in the outer part of the fjord where summer sedimentation rates are low, particularly in comparison with the inner basin. The outer part of the fjord has the highest zooplankton biomass, dominated by copepods, and the greatest amount of sinking faecal pellets. In the inner part of the fjord, particulate organic material is primarily composed of degraded

detritus rather than phytoplankton (Keck 1999).

Primary production has only been measured in summer in the transitional zone (Fig. 1b). Integrated rates measured in July 1979 and 1980 were between 7.0 and 1.3 $\text{mg C m}^{-2} \text{ h}^{-1}$, respectively (Eilertsen et al. 1989); in July 1997 rates varied between 0.3-4.2 $\text{mg C m}^{-2} \text{ h}^{-1}$ (S.-Å. Wängberg and K. Gustavson, pers. comm.). A considerably higher carbon production, with daytime values in the range of 45-92 $\text{mg C m}^{-2} \text{ h}^{-1}$ for the upper 30 m, was measured in July 1996 (R. Hapter, pers. comm.) The variability in these data reflects real summer variance in phytoplankton abundance. Clear sunny days with low attenuation in the water column may yield similar production rates in the upper 10 m, whereas cloudy days with high attenuation result in production rates at 8-10 m depth of only 20% of the surface values (S.-Å. Wängberg and K. Gustavson, pers. comm.). Calculations based on these measurements show that primary production in Kongsfjorden in summer is light saturated, in the range of 50-70 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. These values are in the low end of the range of irradiances supporting maximum photosynthesis in the Barents Sea (Rey 1991).

Daily primary production is relatively high during the summer due to the 24-hour daylight (Table 3). In the upper 2 m, the mean production rate over 24 hours was found to be 76% of the rate at noon (S.-Å. Wängberg and K. Gustavson, pers. comm.). Eilertsen et al. (1989) found that the production at night was 50% of the noon production in Smeerenburgfjorden, a fjord in north-western Spitsbergen. Using 76% of the noon rate as a mean, the Kongsfjorden data from Eilertsen et al. (1989) give daily, integrated primary production rates of 0.024 and 0.128 $\text{g C m}^{-2} \text{ d}^{-1}$ (in 1980 and 1979, respectively). These rates are within the range for early spring production in the Barents Sea, but they are substantially lower than the summer values for the Barents Sea (Rey 1993). A higher daily production of 0.8-1.4 g C m^{-2} was measured in Kongsfjorden in July 1996 (R. Hapter, pers. comm.), which is comparable to spring bloom production values from the Barents Sea (Rey 1993). The night production was about 32% of the daytime production, in the upper 30 m of the water column (R. Hapter, pers. comm.). Rysgaard et al. (1999) explored correlations between annual production and open water (i.e. productive) periods in Arctic and sub-Arctic locations.

Table 2. Concentrations of nitrate, phosphate and silicate ($\mu\text{mol l}^{-1}$) for Kongsfjorden in different seasons. Data are means for the upper 20 m (autumn concentrations are similar down to 50 m).

Season Part of fjord	Winter	Summer	Autumn	
	All	Outer	Inner	Outer
Nitrate	10-12	1.6-3.3	0.6-0.7	0.2-0.3
Phosphate	0.7-0.8	0.5	0.15-0.16	0.1
Silicate	4-6	1.4-1.5	1.6-2	1.2-1.3

Based on that correlation ($0.29 \text{ g C m}^{-2} \text{ d}^{-1}$) and 4-6 productive moths per year in Kongsfjorden, the annual primary production in Kongsfjorden would be 35-50 $\text{g C m}^{-2} \text{ y}^{-1}$, which is comparable with production estimates from the northern Barents Sea (Sakshaug et al. 1994; Hegseth 1998). An estimate based on the lowest summer values would yield an annual production between 4 and 23 $\text{g C m}^{-2} \text{ y}^{-1}$ (Eilertsen et al. 1989), whereas the highest summer values yield 120-180 $\text{g C m}^{-2} \text{ y}^{-1}$ (R. Hapter, pers. comm.). The latter value is comparable to previous estimates for Spitsbergen fjords (Eilertsen et al. 1989), the southern Barents Sea (Sakshaug et al. 1992) and fjords in northern Norway (Eilertsen & Taasen 1984). However, estimates ranging from 4 to 180 $\text{g C m}^{-2} \text{ y}^{-1}$ (Table 3) indicate large temporal variability in Kongsfjorden.

In the late summer and early autumn, phytoplankton biomass decreases (Table 1). This could be a consequence of heavy grazing since heterotrophic dinoflagellates, ciliates, nauplii, and small and larger copepods are found to be common, particularly in the central and outer parts of the fjord (E. N. Hegseth, pers. comm.). Diatoms appear to be rare at this time, and nutrient concentrations, particularly nitrate (Table 2), are low in the surface mixed layer. These conditions might favour motile dinoflagellates that are capable of swimming from the surface to the pycnocline. The inner part of the fjord still suffers from a poor light regime due to glacial run-off, and small flagellates dominate the plankton. The outer part can also be heavily influenced by the sediment-loaded glacial water, and it has been estimated (assuming a C/Chl ratio of 50; J. Wiktor, pers. comm.) that phytoplankton may comprise as little as 15-20% of the particulate organic carbon in the water masses (E. N.

Hegseth, pers. comm.). The rapidly decreasing day length finally terminates the growth season; no further growth occurs once the polar night starts (October 25).

Pelagic microbial heterotrophs

Heterotrophic micro-organisms play a key role in most pelagic ecosystems and are likely to be of considerable importance in Kongsfjorden. Bacterioplankton biomass in Kongsfjorden is unknown, but in Hornsund, a similar Svalbard fjord, bacterioplankton abundance ranged from 0.8 to 1.3×10^8 cells l^{-1} , equivalent to about $2 \mu\text{g l}^{-1}$ or 1.1% of total planktonic biomass in summer (Zajaczkowska & Zajaczkowski 1988). Bacterioplankton production ranging from 7 to 29 $\mu\text{g C l}^{-1} \text{ d}^{-1}$ was measured in the upper 8 m of Kongsfjorden in July 1997 (S.-Å. Wängberg and K. Gustavson, pers. comm.). These values are relatively high compared to estimates of 0 to 13 $\mu\text{g C l}^{-1} \text{ d}^{-1}$ recorded during summer from other Arctic coastal locations (Pomeroy et al. 1990; Nielsen & Hansen 1995, 1999; Møller-Niklas & Herndl 1996; E. F. Møller & Nielsen 2000).

Incidental reports on protozooplankton such as choanoflagellates, dinoflagellates and ciliates from Kongsfjorden have been made by Hasle & Heimdal (1998), Keck et al. (1999), and Wiktor (1999), whereas Keck et al. (1999) and Okolodkov et al. (2000) give some quantitative information on the mixotrophic *Dinobryon balticum* and heterotrophic dinoflagellates. Planktonic foraminifera, including *Globoquadri-rinapachyderma*, *Globigerinita bradyi* and *Globigerina quinqueloba*, have also been recorded from sediments within the fjord's inner zone, indicating influx of Atlantic Water (Elverhøi et al. 1980).

Table 3. Daily primary production from phytoplankton measured during summer in Kongsfjorden, and calculations of annual production based on 4-6 productive months per year.

Time (year)	Primary production		Comments	Reference
	Daily (July) ($\text{g C m}^{-2} \text{ d}^{-1}$)	Annual ($\text{g C m}^{-2} \text{ y}^{-1}$)		
1979	0.128	23	Daily mean production rate 76% of noon rates, based on measurements by S.-Å. Wängberg and K. Gustavson (unpubl. data)	Calculated from Eilertsen et al. (1989)
1980	0.024	4		
	0.29	35-50	Annual values are calculated for Kongsfjorden, based on values for Arctic and sub-Arctic seas	Calculated from Rysgaard et al. (1999)
1996 data)	0.8-1.4	120-180	Night production 32% of daytime production	R. Hapter (unpubl.

Sympagic biota

The pelagic ecosystem in Kongsfjorden is influenced by seasonal variations in insolation and temperature, resulting in sea ice formation during the winter. Apart from frozen-in blocks of glacier ice, the ice cover has a relatively flat underside (Gerland et al. 1999). The maximum ice thickness (0.7 m) is much less than that of seasonal ice-covered areas in the Canadian Arctic (about 2 m; R. D. Brown & Cote 1992). The fjord ice supports a sympagic (ice-associated) community that includes both ice algae and ice fauna. The presence of snow on top of the sea ice affects both the biomass (Welch & Bergman 1989) and the primary production rates of ice algae (Grossi et al. 1987). Ice algae start to grow on the underside of the ice during early spring. Algae have been found at least 20 cm into the ice, at progressively lower concentrations away from the underside of the ice (E. N. Hegseth and S. Gerland, pers. comm.).

Visual examination of approximately 10 ice cores each from spring 1997 and spring 1998 indicated that the algae on the underside of the ice are patchily distributed, and that the period of maximum concentration occurs in late May (S. Gerland and J. Wiktor, pers. comm.). An ice core taken in the inner fjord in late May 1998 revealed that diatoms, principally *Nitzschia* spp. such as *N. frigida*, dominate. The species diversity can be high, but the community is mainly composed of diatom species: *Pleurosigma stuxbergii*, *Cylindrotheca closterium*, *Navicula* spp. (particularly *N. pelagica*), *Entomoneis* spp., *Cocconeis* spp. and *Thalassiosira* spp. However, dinoflagellates (*Dinophysis acuta*, *Gyrodinium* spp., *Protoperidinium* spp.), vegetative cells and cysts have also been observed. Further into the ice, the diversity diminishes and communities are dominated by *Navicula* species. Since the sampling has been qualitative, cell numbers are not available.

Ice fauna has been sampled occasionally in Kongsfjorden (Weslawski et al. 1993; M. Poltermann, pers. comm.). The amphipod *Gammarus setosus*, which is often associated with ice, was the most common species (3000 ind. m⁻² in some patches) in shallow locations (2 m) off the eastern coast of Blomstrandhalvøya (June 1997). Single polar cod (*Boreogadus saida*) and the autochthonous sympagic amphipod *Gammarus wilkitzkii* were also collected from

ice holes in May 1998. Another ice amphipod, *Apherusa glacialis*, has been reported in benthic suction pump samples (summer 1998; A. Y. Voronkov, pers. comm.). The copepods *Pseudocalanus acuspes*/*P. minutus* were the dominant zooplankton component (290 ind. m⁻³) in under-ice net samples (Weslawski et al. 1993). Cirripedia nauplii, an important meroplanktonic link between pelagic and benthic realms, were found in high concentrations along the edge of fast ice during spring 2000 (S. Gerland and M. Poltermann, pers. comm.).

Zooplankton

The zooplankton community in Kongsfjorden is similar to that of other sub-Arctic fjords with respect to the complexity of its taxonomic structure. Patterns of distribution in terms of abundance and biomass indicate strong variability related, most likely, to bottom topography, advection of Atlantic water masses and factors associated with glacial activity. The estimated biomass (dry mass) in Kongsfjorden was relatively high (8.8±5.1 g m⁻²), especially in the fjord's outer basin (11.5±4.3 g m⁻²). The mean dry biomass was only 30% lower than that of the Greenland and Norwegian seas (13.5 g m⁻² and 12.1 g m⁻², respectively) (Richter 1994). However, it was higher than the dry biomass in the West Spitsbergen Current north-west of Kongsfjorden (8.4±2.2 g m⁻²) and in the southern Nansen Basin (4.6±1.3 g m⁻²) (Mumm et al. 1998). The most important feature of the zooplankton in Kongsfjorden is the co-occurrence of boreal and Arctic taxa. *Calanus finmarchicus* or *Metridia lucens* belong to the Atlantic biogeographic province (Wiborg 1954; Hirche & Mumm 1992), whereas *Calanus glacialis* and *Limacina helicina* are inhabitants of the Arctic biogeographic province (Kobayashi 1974; Conover 1988; Grainger 1989).

The characterization of Kongsfjorden's zooplankton presented here is based on samples collected in July (1996, 1997) and in September 1997 at eight stations (Fig. 1b). Samples were collected in vertical, stratified hauls with a Multi Plankton Sampler (opening area 0.25 m⁻², mesh size 0.180 mm), and the subsequent laboratory analysis followed standard procedures (Omori & Ikeda 1984). The zooplankton community in Kongsfjorden comprised representatives from most major marine zooplankton groups (Table

4), with the highest number of species/genera identified among Copepoda (20), followed by Amphipoda (4) and Euphausiacea (4). All taxa found in Kongsfjorden have been recorded previously in other Spitsbergen fjords (Stott 1936; Digby 1961; Koszteyn & Kwasniewski 1989; Kwasniewski 1990; Weslawski et al. 1990; Weslawski, Jankowski et al. 1991; Weslawski, Krasniewski et al. 1991; Sywula et al. 1993). In addition, a few species that are known from Nordic waters or other fjord environments were recorded in Kongsfjorden. They include the copepods *Metridia lucens*, *Gaidius tenuispinus*, *Bradydium similis* and *Xanthocalanus* sp., and a species of Monstrilloidea as well as the euphausiids *Thysanoessa raschii* and *T. longicaudata* and a mysid *Boreomysis arctica*.

In Kongsfjorden, the most abundant zooplankton species were Copepoda: *Oithona similis*, *Calanus finmarchicus*, *C. glacialis* and *Pseudocalanus acuspes/P. minutus* (Table 5). These were accompanied by other taxa such as *Bivalvia veligers*, *Limacina helicina* juveniles and *Fritillaria borealis*. However, it must be noted that relative abundance varied markedly between observations. The most notable difference observed between the zooplankton sampled in summer 1996 and in summer and autumn 1997 was a decrease in the number of *C. glacialis*. The absolute abundance of this species varied from 2600 to 63300 ind. m⁻² in 1996, whereas it varied from 5900 to 15500 ind. m⁻² and from 4600 to 12800 ind. m⁻² in summer and autumn of 1997, respectively. This suggests that there were pronounced differences in environmental conditions between these two years, possibly related to influx of Atlantic

Table 4. Major zooplankton taxa in Kongsfjorden.

Taxon	No. of species or genera identified
Hydrozoa	2
Ctenophora	2
Gastropoda	2
Polychaeta	1
Copepda	20
Euphausiacea	4
Decapoda	1
Mysidacea	2
Cumacea	1
Amphipoda	4
Appendicularia	2
Chaetognatha	2

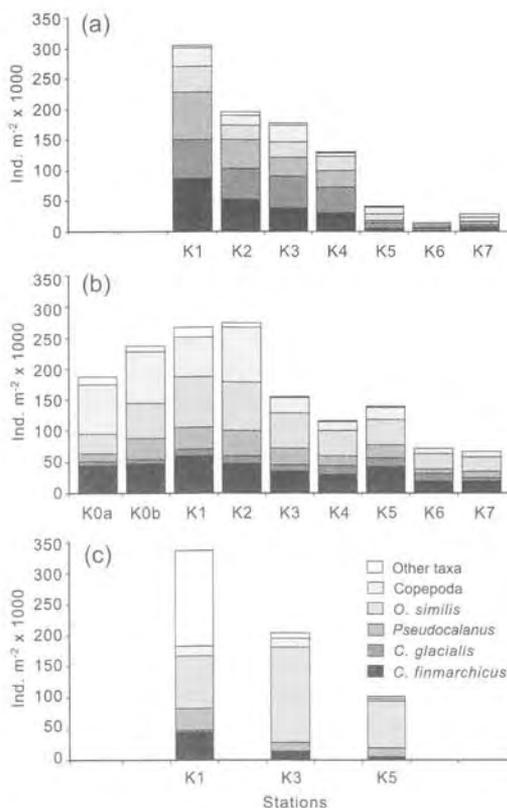


Fig. 2. Integrated zooplankton abundance (ind. m⁻²) in Kongsfjorden: (a) July 1996; (b) July 1997; (c) September 1997.

Water from the West Spitsbergen Current with associated changes in temperature and salinity (Svendsen et al. 2002). A remarkable difference between July (1996, 1997) and September (1997) was an increased abundance of *Bivalvia veligers* (0-130 versus 2000-336600 ind. m⁻²) and *Limacina helicina* juveniles (0-900 versus 5800-98600 ind. m⁻²). Thus, seasonal changes in Kongsfjorden's zooplankton community are related not only to the life cycle and growth of holoplankton but also to peaks in meroplankton. Similar observations have been made for fjords in south-west Greenland (Smidt 1979).

Abundance of zooplankton in Kongsfjorden differed between locations within the fjord as well as between years and months (Fig. 2). For example, the mean abundance of *C. finmarchicus* in July 1996 varied between the basins by an order of magnitude: 31200-87000 ind. m⁻² at outer stations K1-K4 versus 2300-6600 ind. m⁻² at inner stations K5-K7 (Fig. 2a). The abundance

was lower in July 1997, but showed the same basic pattern: 30 400–59 500 ind. m⁻² in the outer part versus 18 600–41 800 ind. m⁻² in the inner part (Fig. 2b). The difference between outer and inner basins was even more pronounced in September 1997: 126 500 ind. m⁻² at station K1 versus 11 300 ind. m⁻² at station K5 (Fig. 2c). This pattern indicates a highly dynamic pelagic system as well as the presence of strong environmental gradients in the fjord. The bottom-living copepod, *Neoscolecithrix farrani*, was found in low abundance at stations in the outer basin. Its abundance was highest (180 ind. m⁻²) in winter cooled water (station K5). The abundance of *Metridia longa* varied with depth, and its distribution is likely affected by advection. At stations with bottom depth <100 m, *M. longa* ranged from 22 to 272 ind. m⁻², whereas at deeper stations it varied from 1400 to 34 600 m ind. m⁻². A low number of *M. longa* (180 ind. m⁻²) at a 200 m deep station K4, in July 1996, might have been due to the presence of cold water of local origin at this site.

The larger zooplankton forms, such as euphausiids (*Thysanoessa inermis*, *T. raschii* and *T. longicaudata*), amphipods (*Themisto libellula*, *T. abyssorum*), pteropods (*Limacina helicina*, *Clione limacina*) and ctenophores (*Mertensia ovum*, *Beröe cucumis*), are also prominent members of the Kongsfjorden zooplankton community (Weslawski et al. 2000; Falk-Petersen et al. 2002; J. M. Weslawski, pers. comm.). Earlier studies

indicate that *Themisto* (12 ind. m⁻³), *L. helicina* (8 ind. m⁻³) and euphausiids (2 ind. m⁻³) are numerically dominant (Weslawski et al. 2000). Deep living and fast swimming macroplankton such as *Meganyctiphanes norvegica* and *Boreomysis arctica* have also been caught (S. Kwasniewski, pers. comm.).

The zooplankton biomass in Kongsfjorden has been estimated using mean individual dry mass values derived from the literature for Copepoda (Hay et al. 1991; Mumm 1991; Richter 1994; Hanssen 1997; Scott et al. 2000) and individual dry mass for *Bivalvia veligers* and *L. helicina* juveniles (formalin preserved). However, the estimates do not include larger species, since they have not been sampled representatively for this purpose. The calculated dry mass of zooplankton in Kongsfjorden for summer and early autumn varied from 1.4 to 20.1 g m⁻² for the entire water column (Table 6). It was always higher at stations in the outer than in the inner fjord basin. The three *Calanus* species contributed the most to the zooplankton dry mass and accounted for approximately 90% of the biomass in July. In September, the proportion of *Calanus* never exceeded 80% due to the high abundance of the small-size taxa, such as *Pseudocalanus*, *Oithona similis*, *Bivalvia veligers* or *L. helicina* juveniles. The boreal species *C. finmarchicus* constituted 41%, 36% and 33% of the dry mass in July 1996, July 1997 and September 1997, respectively. The Arctic species *C. glacialis* made up 50%, 35% and 29% and *C. hyperboreus* contributed 7%, 22% and 13% to the zooplankton biomass in the respective years. Generally, the proportion of *C. finmarchicus* decreased while *C. glacialis* increased with distance from the fjord's entrance. This can most likely be attributed to the amount of cold water present, cold water providing a refugium for the Arctic *C. glacialis*.

Table 5. The most abundant zooplankton taxa in Kongsfjorden.

Taxon	Relative abundance		
	July 1996	July 1997	Sept. 1997
<i>Calanus finmarchicus</i>	25.0	22.8	9.3
<i>Calanus glacialis</i>	25.2	6.3	1.3
<i>Calanus hyperboreus</i>	0.6	1.4	0.3
<i>Pseudocalanus acuspes</i> , <i>P. minutus</i>	21.6	13.3	9.5
<i>Microcalanus pusillus</i> , <i>M. pygmaeus</i>	2.1	3.8	1.5
<i>Metridia longa</i>	1.0	6.9	1.3
<i>Bradydium similis</i> , <i>Neoscolecithrix farrani</i>	0.9	0.5	0.4
<i>Oithona similis</i>	15.3	28.8	48.9
<i>Oncaea borealis</i>	0.6	2.4	0.6
Copepoda nauplii	5.7	10.3	0.4
<i>Bivalvia veliger</i>	0.01	0.03	18.6
<i>Limacina helicina</i>	0.1	0.2	6.3
<i>Fritillaria borealis</i>	0.03	2.1	0.3

Pelagic–benthic coupling

Pelagic–benthic coupling encompasses various processes, of which the most important is the sinking of organic, bio-available matter through the water column to the benthic system (i.e. particle flux), where it can be grazed, buried or advected. Organic matter is produced in the euphotic layer of the fjord, advected in from the outer shelf or added from allochthonous sources such as glacial meltwater. Sedimentation

is dependent on the density gradient of surface waters and is controlled by physical forces such as light regime, meteorological conditions, turbulence, advection (Wassmann et al. 1996), freshwater run-off (Keck 1999) and biological processes such as organic flocculation (Eisima 1986; K. R. Dyer 1989; Syvitski & Shaw 1995) or pelletization of particulate material (Levis & Syvitski 1983). Zooplankton grazing is perhaps the single most important factor regulating the amount of organic material sinking to the bottom of Kongsfjorden (Syvitski 1980; Conover et al. 1986; Wassmann & Slagstad 1993; Wassmann et al. 1996). At present, the overall amount of organic matter during the growth season is unknown, but there is some scattered information on the different sources contributing to the sedimentation. The rate of sedimentation of total particulate matter (TPM) under the euphotic zone ranges from 7.8 g m⁻² d⁻¹ in May to 107 g m⁻² d⁻¹ in July, of which particulate organic matter is 1.5 g m⁻² d⁻¹ to 7.4 g m⁻² d⁻¹, respectively (Svendsen et al. 2002). Relatively low flux of organic matter under the euphotic zone in May is likely to be partly dependent on advection in the upper part of the water column, buoyancy of algae in growth phase and density stratification caused by melting of glacial and fast ice (Wassmann 1985). A high percentage of inorganic matter in the flux of TPM in July is caused by seasonal maximum of glacier ablation.

Sinking phytoplankton biomass is an important component of organic matter and has been found to range from 0.0013 g C m⁻² d⁻¹ during spring to 0.005 g C m⁻² d⁻¹ during summer in Kongsfjorden (Table 7). Estimates of the phytoplankton daily

loss rate range from 2 to 5% of carbon biomass during spring (Wiktor 1999) and 3.5 to 5% of chlorophyll in late summer (Keck 1999). Another source of sinking organic matter is faecal pellets. Their sedimentation is higher in summer than in spring, and may increase to 0.75 g C m⁻² d⁻¹ in the outer part of the fjord (Table 7), presumably because of high grazing activity.

The glacier outflow enhances the advection of high amounts of organic material into the inner fjord where it sinks rapidly to the bottom in shallow areas (most of the inner part of the fjord is < 100 m deep). The organic material consists of highly degraded macrophytes as well as zooplankton, phytoplankton and faecal pellets. The high rate of sedimentation of mineral and organic solids in the inner part of fjord in summer could be connected with flocculation and reflocculation of fine suspensions at the front of the glaciers (Eisima 1986; K. R. Dyer 1989). Limited light conditions in the turbid waters of the inner fjord may enhance phytoplankton mortality. Advected zooplankton become moribund when they come into contact with the near-glacial freshwater (Weslawski & Legezyska 1998). The discharge of Kongsbreen's main outflow channel in the peak of the season was 139 m³ s⁻¹ and copepods die within 15 min of being exposed to salinities below 9 psu (Zajaczkowski & Legezyska 2001). During the melting season (100 days), as much as 85 tonnes of zooplankton may be removed from the water column due to osmotic shock, constituting 15% of the zooplankton biomass in the fjord (Zajaczkowski & Legezyska 2001). The glacial run-off thus provides an important mechanism for pelagic-benthic coupling in the

Table 6. Total dry mass (g m⁻²) of zooplankton in the water column of Kongsfjorden and percent dry mass of the main taxa.

Date Station	July 1996								July 1997							September 1997				
	K1	K2	K3	K4	K5	K6	K7	K0a	K0b	K1	K2	K3	K4	K5	K6	K7	K1	K3	K5	
Total DM (g m ⁻²)	17.0	10.4	13.5	7.9	5.4	1.4	2.8	9.9	11.9	14.9	9.9	6.6	5.8	8.0	4.7	3.0	20.1	10.3	4.5	
Percent DM of total:																				
<i>Calanus hyperboreus</i>	10.4	3.3	5.8	6.4	6.2	4.9	3.8	27.3	25.4	30.6	12.1	21.7	13.9	17.1	17.7	15.6	9.6	23.2	5.6	
<i>C. glacialis</i>	35.4	47.8	56.6	58.3	70.6	55.2	39.4	28.1	21.8	26.0	38.1	36.1	52.5	52.1	49.1	47.0	26.0	29.1	42.7	
<i>C. finmarchicus</i>	50.8	46.0	35.5	33.2	20.8	36.3	53.8	36.8	43.7	36.3	37.1	35.9	29.6	27.2	28.8	32.9	37.4	26.8	24.9	
<i>Metridia longa</i>	0.5	0.3	0.3	0.1	0.0	0.1	0.1	3.8	4.2	2.6	5.5	0.7	0.0	0.1	0.1	0.1	2.9	3.0	0.4	
<i>Pseudocalanus</i>	1.5	1.0	0.5	0.4	0.2	2.5	2.9	0.8	1.5	1.3	2.3	1.5	1.2	1.4	1.6	1.7	2.4	1.7	4.8	
<i>Oithona similis</i>	0.7	0.7	0.6	0.9	0.6	0.9	0.8	1.0	1.5	1.6	2.3	2.6	2.2	1.5	1.9	2.3	3.6	12.9	17.2	
<i>Bivalvia veliger</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.7	0.5	0.4	
<i>Limacina helicina</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	5.3	1.4	1.7	
Other Copepoda	0.7	0.5	0.5	0.2	1.2	1.7	0.9	2.1	1.8	1.6	2.6	1.3	0.5	0.6	0.4	0.4	1.1	1.6	2.4	

inner part of the fjord by increasing the advection and sinking of organic matter. Much of the dead zooplankton becomes food for necrophagic amphipods, such as *Onisimus caricus*, which constitute more than 99% of the scavenging macrofauna in the inner part of Kongsfjorden (Zajaczkowski & Legezynska 2001).

Benthic communities

Benthic microalgae

Thick mats of microalgae are reported to grow on nearly all surfaces in shallow areas along the margins of Kongsfjorden, as well as epiphytically on macroalgae (C. Wiencke, pers. comm.). No studies of benthic microalgae in Kongsfjorden have been undertaken, but the microalgal community probably resembles that found at Bjørnøya (Metzeltin & Witkowski 1996), the southernmost island of the Svalbard Archipelago. At Bjørnøya, diatoms dominated and the species diversity was high. Cosmopolitan species were most numerous, whereas ice-related Arctic species were rare.

Benthic microbial heterotrophs

Marine sediments, with their steep redox potentials, provide niches for a wide variety of metabolically diverse heterotrophic micro-organisms (bacteria and protozoa). These aerobic and anaerobic micro-organisms are often responsible for the bulk of remineralization of organic matter in sediments and provide a source of food for higher trophic levels within the benthos. Sulphate-reducing bacteria dominate anaerobic remineralization, which can be the most important process of organic material degradation on the continental shelves (Canfield 1993). Such anoxic processes can account for 60–90% of organic matter remineralization in some Svalbard fjords (Kostka et al. 1999).

Benthic bacteria have received little attention in Kongsfjorden, but have been examined in some of the other fjords in Svalbard and on the west coast shelf (Blackburn et al. 1996; Arnosti et al. 1998; Glud et al. 1998; Sahm & Berninger 1998; Thamdrup & Fleischer 1998; Knoblauch, Jørgensen 1999; Knoblauch, Sahm et al. 1999; Ravensschlag et al. 1999; Sahm et al. 1999). These studies, along with studies conducted elsewhere

Table 7. Observed suspended and sedimented organic matter in Kongsfjorden during spring and summer (inner and outer part of the fjord).

Season, part of fjord	Suspended matter (g C m ⁻³)	Sedimented matter (g C m ⁻² d ⁻¹)	References
Spring, inner part			
Carbon content (POC)			
(excluding mesozooplankton)	0.7	0.08	Zajaczkowski (unpubl.)
Phytoplankton cells	0.1	0.0013	Wiktor (1999)
Heterotrophic microplankton	0.03	0	Wiktor (1999)
Faecal pellets	0.00035	0.0011	Zajaczkowski (unpubl.)
Mesozooplankton (copepods)	0.012 ^a	<i>n.a.</i>	Kwasniewski (this paper)
Summer, inner part			
Carbon content (POC)			
(excluding mesozooplankton)	1.22	8.6	Zajaczkowski (unpubl.)
Phytoplankton cells	0.06	0.0027 ^b	Keck (1999), Keck et al. (1999)
Heterotrophic microplankton	0.004	<i>n.a.</i>	Keck et al. (1999)
Faecal pellets	0.0026	0.64	Zajaczkowski (unpubl.)
Mesozooplankton (copepods)	0.03 ^a	<i>n.a.</i>	Kwasniewski (this paper)
Summer, outer part			
Carbon content (POC)			
Excluding mesozooplankton	1.46	2.45	Zajaczkowski, (unpubl.)
Phytoplankton cells	0.11	0.005 ^b	Keck (1999), Keck et al. (1999)
Heterotrophic microplankton	0.004	<i>n.a.</i>	Keck et al. (1999)
Faecal pellets	0.0086	0.75	Zajaczkowski, (unpubl.)
Mesozooplankton (copepods)	0.02 ^c	no data	Kwasniewski (this paper)

^a 75 m water column

^b calculated from a loss rate of 4.5% of suspended phytoplankton biomass (Keck 1999)

^c 250 m water column

in the Arctic (e.g. Rysgaard et al. 1996), have revealed the presence of microbial communities which are well adapted to a cold environment and which can degrade organic matter as efficiently as those in warmer environments. The heterotrophic microbial community in Kongsfjorden can be expected to be similar, and the supply of organic matter, rather than temperature, probably controls the benthic microbial production.

Benthic protozoa have been studied in Kongsfjorden; all studies have focused on foraminifera. Rouvillois (1966) recorded 33 species of foraminifera from the inner part of the fjord, whereas Elverhøi et al. (1980) recorded 41 species from the same area, of which only three were planktonic forms. Most of the benthic species recorded in the latter study were Arctic forms, but a few boreal species were also present. The low diversity was attributed to high turbidity of the bottom water and to the very soft substratum (Elverhøi et al. 1980). More recently, 123 species of foraminifera have been recorded from the inner part of the fjord, with up to 169 ind. g⁻¹ sediment. The diversity was greatest in deeper waters, probably due to a more stable environment (Slinning 1995).

Macrobenthos

Benthic invertebrates and macroalgae have been sampled extensively in Kongsfjorden (Fig. 1b).

Macroalgae grow in the littoral and sublittoral zone of the fjord, mainly from 0 to 20 m (N. A. Kovaltchouk and B. Vögele, pers. comm.), although some red algae may grow down to 40 m (Klekowski & Weslawski 1990). Benthic fauna is found at all depths, but the diversity and abundance/biomass of individual species varies with depth and substratum (Włodarska-Kowalczyk et al. 1998; Jørgensen & Gulliksen 2001) (Table 8).

Intertidal zone.—The intertidal zone, between maximum spring and minimum neap tides, is subject to wave action, drying, freezing and ice scouring from both sea ice and smaller icebergs. Sediments (fine mud to sand) are present on level ground, often near freshwater outflows. Organisms in such localities must therefore be able to tolerate osmotic stress, sediment accumulation and displacement. Rocky substrata are most common in areas with steep angles that are exposed to strong hydrodynamic activity.

Intertidal hard substrata include bedrock and stable rocks, or large boulders. Level or sloping bedrock surfaces are usually overgrown by macroalgae, which are dominated in the central and inner areas by *Fucus distichus* and *Pylaiella littoralis* and in the exposed outer areas by *Chordaria flagelliformis*. The cirripede *Semibalanus balanoides* and the gastropod *Littorina saxatilis* occur in sheltered places. Detri-

Table 8. Basic fauna characteristics of benthic habitats in Kongsfjorden: *n* = number of samples taken in the habitat; tot N = total number of species found within the habitat; Number = species per sample; H = Shannon-Wiener index of diversity (log *e*); Abundance = ind. 0.1 m⁻²; Biomass = g w.w. 0.1 m⁻². Range of mean ± s.d. is listed.

Habitat	Depth (m)	<i>n</i>	tot. N	Number	H	Abundance	Biomass
Intertidal rock and stone substrata	0-5	32	42	10		50-8000	1-27
Intertidal soft substrata	0-5		<20			<300	<10
Subtidal macrophytes on stony grounds in the euphotic zone							
Algae	2-30		44				200-21 000
Fauna			100	10-51		32-16 277 ^b	200-20 000
Subtidal rock without kelp ^a	2.5-30	32-42	29-396	2-138		48-116 448	0.7-105 445
Subtidal gravel substrata	2.5-30	10	174	46-91		916-4144	88-681
Infauna of subtidal soft sediments in inner basin	40-83	24	85	24±6	1.98±0.23	442±233	2.7±1.5
Infauna of subtidal soft sediments in outer basin	72-380	76	210	39±9	2.63±0.26	464±235	6.9±8.6

^a Four variants of this type of community were recorded.

^b Ind. per 100 g wet biomass for macrophytic epifauna.

tivorous and omnivorous gammarid and caprellid amphipods are abundant. In the inner parts of the fjord, *Ischyroceros anguipes* and *Gammarus setosus* dominate, whereas *Gammarellus homari* occurs in lower numbers. In the middle and transitional zone of Kongsfjorden (Fig. 1b), *G. homari* and *I. anguipes* are most abundant. Fewer than 50 animal species have been collected, but total density of up to 8000 ind. m⁻² and total wet biomass up to 30 g m⁻² have been recorded (J. M. Weslawski, pers. comm.).

The *intertidal sediments* are inhabited by the amphipod *Onisimus littoralis* and an abundant meiofauna dominated by Nematoda. The macrofauna generally consists of fewer than 20 species, with total density up to 300 ind. m⁻² and total wet biomass up to 10 g m⁻² (J. M. Weslawski, pers. comm.).

Subtidal zone.—The subtidal zone extends from the minimum neap tide line down to the shelf break, but quantitative information on hard bottom substrata is generally limited to 30 m depth (i.e. the limit for SCUBA diving surveys). This is also the lower depth distribution limit for most macroalgae in the fjord. Large macroalgae are typically absent from shallow areas in Kongsfjorden, except for locations sheltered from the outward moving ice stream.

Subtidal hard-bottom includes bedrock and boulders on bedrock or sedimentary substrata and may cover extensive areas between 2 and 30 m depth in all zones of the fjord. Several physical factors may determine the composition of fauna and macroalgae on such substrata in Kongsfjorden, such as water depth, substratum surface angle, current velocity and silt settling rates.

The upper sublittoral zone down to 2.5 m is characterized by a belt of annual or pseudo-perennial macroalgal species, such as *Chordaria flagelliformis*, *Pylaiella littoralis* and *Acosiphonia* sp. These species are well adapted to ice scouring because they can survive the winter as microscopic stages or as rhizoidal cushions. These species also tolerate UV radiation relatively well. Below this belt, down to 5–15 m, there is a kelp forest mainly structured by the perennial canopy species *Alaria esculenta*, *Laminaria saccharina* and *L. digitata*, the annual *Saccorhiza dermatodea* and—in the inner and in the transitional zone—the endemic Arctic species *L. solidungula*. The pseudoperen-

nial and perennial species *Phycodrys rubens*, *Ptilota gunneri*, *Fimbrifolium dichotomum*, *Desmarestia aculeata*, *Palmaria palmata*, *Devaleraea ramentacea* are typical undergrowth species in the middle zone, whereas these are replaced by *Turnerella pennyi* and *Desmarestia viridis* in the outer zone. Crustose coralline algae often cover hard substrata. The lower limit of macroalgal distribution is determined by the metabolic carbon balance under the low light conditions at that depth (Gómez et al. 1997). Seventy algal species with total wet biomass of 0.02–21 kg m⁻² have been recorded in Kongsfjorden (N. A. Kovaltchouk and B. Vögele, pers. comm.). Generally, the benthic marine macroalgal flora is a depauperate North Atlantic flora, supplemented by four of the five known endemic Arctic species. The ecologically important endemic Arctic brown alga *Laminaria solidungula* occurs in the zones 3 and 4 only, indicating Arctic conditions in the inner part of the fjord (Fig. 1b).

The fauna associated with macroalgae comprise about 100 species of motile and sessile invertebrates, with bryozoans and amphipods being the most abundant taxa (Lippert et al. 2001). Abundances ranged from 32 (on *Laminaria digitata*) to 16277 individuals (on *Ptilota gunneri*) per 100 g wet algal biomass and species number from 10 (on *Acosiphonia* sp.) to 51 (on *Alaria esculenta*). Patterns of dominating animal taxa and their distribution among algal groups are similar to those of the North Sea and the British Isles, but epifauna associated with Arctic macroalgae appears to be less diverse (Rozycki & Gruszczynski 1986; Lippert et al. 2001).

More than 450 taxa of invertebrates have been recorded on hard substrata in Kongsfjorden (A. Y. Voronkov and H. Hop, pers. comm.). Bryozoans, polychaetes and crustaceans had the highest species diversity. Bryozoa is a diverse group in Kongsfjorden, having a wide distribution on hard substrata and even on soft bottoms. The bryozoan diversity of Kongsfjorden includes 147 species and 23 varieties, which constitutes more than half of all known bryozoans in Svalbard waters (Gontar et al. 2001). In samples from the outer, middle and inner part of the fjord, more than 60% of the invertebrates were widespread boreal–Arctic species, 11% were boreal species, and 14% were true Arctic species. About 54% of the invertebrates in samples from

hard substrata were suspension feeders, 23% were deposit feeders and 14% were carnivores. Hard substrata sometimes contain pockets of sediments on horizontal surfaces, and infaunal organisms that occur in these soft substrata were included in these numbers. An investigation using suction sampling between 20 and 30 m depth near Kvadehukken (Fig. 1b) revealed 73 taxa from this type of bottom (Jørgensen & Gulliksen 2001). The total wet biomass ranged from 380 to 2200 g m⁻². Vertical and overhanging rocky faces even contained organisms often regarded as "soft-bottom species", but such animals were most abundant on horizontal surfaces where sedimentation and ice-rafted pebbles had created heterogeneous habitats with pockets of sediments overlying hard substrata.

A key organism on rocky ground within the euphotic zone in Kongsfjorden is the green sea urchin *Strongylocentrotus droebachiensis*. The morphologically similar species *S. pallidus* also occurs in such areas, but it is less abundant. The sea urchins at Kvadehukken in outer Kongsfjorden have showed a slow increase in abundance since 1980, and a rapid increase since 1998 to densities of 80 ind. m⁻² in 1999–2000 (F. Beuchel and B. Gulliksen, pers. comm.). The total coverage of brown macroalgae, their major food supply, has fluctuated widely, but there has been a general increase in algal cover from 30% before 1994 to 70–90% cover in recent years. However, large grazed areas devoid of kelp but with high densities of *S. droebachiensis* are common. Such areas are also populated by sessile organisms such as the actinarian *Urticina eques*, barnacles (*Balanus balanus*) and bryozoans (Gontar et al. 2001). The abundance of *U. eques* at Kvadehukken increased from 1982 until 1990, with a maximum of 300 ind. m⁻², and then declined to 50 ind. m⁻² or less in 1996–2000 (F. Beuchel and B. Gulliksen, pers. comm.).

Subtidal rocky habitats below depths influenced by sea urchin grazing (15–20 m) are heavily populated by sessile filter-feeders in Kongsfjorden. These animals can represent 90% of the standing biomass at these depths. The barnacle *Balanus balanus* dominates overall community biomass, but other sessile organisms can also be abundant, especially poriferans (mainly *Haliclona* sp.), actinarians (*Hormathia nodosa*), sedentary polychaetes (*Thelepus cincinnatus*, Spirorbidae), molluscs (*Chlamys islandica*, *Hiatella arctica*, *Tonicella marmorea* and

T. rubra) and ascidians (*Didemnum albidum*, *Botrylloides aureum*, *Styela rustica* and *Halocynthia pyriformis*). The semi-sessile brittle star *Ophiopholis aculeata* is very common, as are several species of amphipods, decapods (*Lebbeus polaris*) and isopods (*Janira maculosa*, *Munna minuta*). The often large and conspicuous octocoral *Gersemia rubiformis* is most common in the outer part of the fjord.

Our knowledge of the fauna below diving depths is based on qualitative dredge hauls. Motile animals and fragments of sessile organisms predominate in such samples, which frequently include megafaunal organisms such as the sea-stars *Crossaster papposus*, *Henricia* sp. and *Pteraster* sp. and sponges (*Myxilla* sp., *Haliclona* sp. and *Polymastia* sp.) in addition to the species mentioned above.

Subtidal soft-bottom includes gravel, silt, clay and mud. Ice-rafted drop stones are common throughout the fjord (Whittington et al. 1997) and they provide a substratum for the development of islands of hard ground communities in sedimentary areas. Gravel habitats occur in patches throughout the fjord, usually on level or slightly sloping substrata exposed to strong bottom currents. Such bottom types are common, for example, near Kapp Mitra and Kapp Guisnez (Fig. 1b). The low abundance of sessile epifauna in these areas is mainly due to strong bottom currents grinding the rocks and making them unsuitable for settlement. Such bottom types often have gravel overlaying firm clay, containing thick-shelled molluscs such as *Mya truncata*, *Hiatella arctica* and *Astarte* sp. Relatively high densities of filter-feeding brittle stars (*Ophiopholis aculeata*) and other ophiurids may occur there. Detritivorous amphipods may also be conspicuous elements in the gravel epifauna. Motile organisms such as gastropods (*Buccinum* spp., *Neptunea* spp.) and hermit crabs (*Eupagurus* spp.) are often found crawling on such substrata.

Finer sediments cover the deeper parts (> 50 m depth) of Kongsfjorden, particularly the inner basin where the sea floor below 5–10 m depth is composed of poorly consolidated soft mud deposited from the outflow of the adjacent glaciers. The fauna includes the protobranch molluscs *Portlandia arctica*, *Yoldiella lenticulata*, *Y. nana/solidula* and *Y. fraterna*, the lucinid bivalve *Thyasira dunbari*, the polychaete *Chone paucibranchiata* and a suite of tanaid crustaceans

dominated by *Sphyrapus anomalus*. All of these are motile surface-deposit feeding species of small body size. Throughout the basin, cirratulid polychaetes, principally *Chaetozone setosa* are also abundant and the nephtyid polychaete *Aglaothamum malmgreni* occurs frequently. There is a high degree of similarity in the species composition of samples taken throughout the basin although patterns of dominance are different near the glacial fronts (M. Kendall and S. Cochrane, pers. comm.). Eighty-five macrofaunal species have been recorded from the inner basin; densities vary from 210 to 620 ind. m⁻² and wet biomass from 1.2 to 4.2 g m⁻².

The deeper areas (>100 m depth) of the outer zones of Kongsfjorden are comprised of soft mud, which tends to become sandier towards the open sea. In general, sediments are far more consolidated than in the inner fjord. The fauna is characterized by the large tube-dwelling polychaetes *Maldane sarsi*, *Laonice cirrata* and *Spiochaetopterus typicus*. The smaller tubicolous polychaete *Prionospio cirrata*, the motile polychaete *Lumbrineris mixochaeta* and the suspension-feeding bivalve *Batharca glacialis* are also typical inhabitants in these regions.

Changing patterns in the identity of the dominant fauna help define three faunal zones in the fjord (Fig. 1b). The polychaetes *Terebellides stroemi* and *M. sarsi* dominate the transitional zone south of Blomstrandhalvøya (zone 3). The deeper reaches of the fjord (250–400 m, zone 2) are dominated by *S. typicus* and *P. cirrata*, and the outer zone close to the open sea (zone 1) is dominated by numerous *L. cirrata* and the burrowing polychaete *Leitoscoloplos* sp. The burrowing polychaete *Lumbrineris mixochaeta* and the surface deposit feeding *Myriochele oculata* are common throughout the fjord.

A total of 201 macrofaunal soft-bottom species have been recorded from the middle to outer fjord, with total density of 230–500 ind. m⁻² and total wet biomass between 1 and 15.5 g m⁻² (Włodarska-Kowalczyk 2001). The soft-bottom fauna of zones 2 and 3 (Fig. 1b) mainly represents a widespread boreal–Arctic deep shelf association in areas of mixed Arctic and Atlantic water (e.g. Dahle et al. 1998). The outer zone 1 exemplifies deep fine sediment areas influenced by Atlantic water and the soft-benthic community is more similar to that of Kongsfjordrenna (Kendall 1996) and northern Norwegian fjords (e.g. Larsen 1997; Holte & Gulliksen 1998).

Infaunal functional groups

Grouping the species within faunal assemblages according to their functions can improve our understanding of community ecology and the influence of changing environmental conditions. New insights into the relative importance of differing environmental variables in structuring benthic communities may also be obtained (Bonsdorff & Pearson 1999; Pearson 2001). In Kongsfjorden, the comparative distribution of functional groups was assessed based on feeding habits, relative mobility and bioturbatory activity (M. Włodarska-Kowalczyk, C. Cochrane and T. Pearson, pers. comm.).

Organisms were categorized into five types depending on their feeding habits: carnivores, suspension feeders, surface deposit feeders, subsurface deposit feeders and omnivores (Fig. 3). Surface deposit feeders comprised over 90% of the populations of the inner basin. This proportion declined progressively through the three outer zones, to less than 30% in the entrance area (zone 1). Conversely, subsurface deposit feeders increased from 4% of the population in the inner basin to just below 40% in the outer fjord.

Three motility groups were identified: motile, semi-motile (moving only intermittently), or sessile (Fig. 3). Motile organisms predominated in all areas of the fjord, making up just over 50% of the population in the central area and around 80% in the other three areas. Sessile organisms comprised between 10 and 15% of the populations present in the three outer regions of the fjord but were rare in the inner basin. Semi-motile animals were secondarily important in the inner basin and central areas but sparse in the transitional and entrance areas.

Four categories of bioturbatory activity were defined (Dauwe et al. 1998; Pearson 2001) (Fig. 3). Diffusive mixing describes vertical bioturbation as a diffusive transport process resulting from the activities of e.g. free-living polychaetes, subsurface deposit feeders and carnivores and burrow excavating crustaceans. Surface deposition includes the defecation (egestion) of particles at the sediment surface by e.g. filter and surface deposit feeding tubicolous polychaetes and sedentary bivalves. Conveyor belt transport describes the translocation of sediments, from depths within the sediments to the surface during subsurface deposit feeding or burrow evacuation.

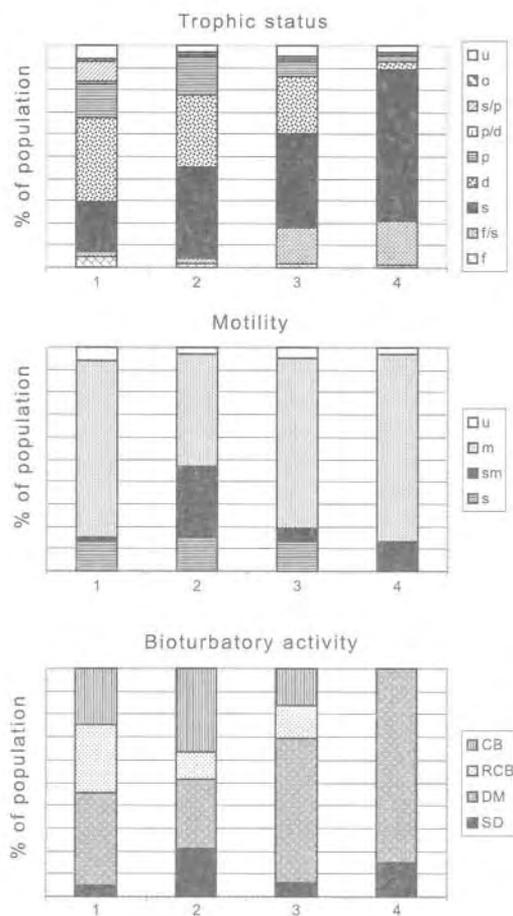


Fig. 3. Functional group analyses of the infaunal sedimentary benthos for Kongsfjorden: outer (1); middle (2); transitional zone (3); and inner basin (4) (Fig. 1b). The changing proportions for functional groups, based on abundance, are presented for: trophic status (top): suspensivores (f), surface detritivores (s), sub-surface detritivores (b), carnivores (c), omnivores (o), unknown (u); Motility (middle): sessile (s), semi-motile (d), motile (m), and unknown (u). Bioturbatory activity (bottom): surface deposition (SD), diffusive mixing (DM), conveyance (CB), reverse conveyance (RCB).

Finally, reverse conveyor belt transport describes the subduction of particles from the surface to some depth by feeding or defecation.

The populations in the inner basin completely lack the conveyor belt group as well as the reverse conveyor belt group and are heavily dominated (> 80%) by organisms that cause diffusive mixing. Surface depositors were scarce in the inner basin and the transitional zone but comprised over 20% of the organisms in the central and outer areas of the fjord. Conveyor belt bioturbators reached

their highest numbers (>20%) in the central area of the fjord whereas reverse conveyor belt activity was highest in the outer fjord. Diffusive mixing remained important in all three down-fjord areas but did not predominate in the two outer zones.

The inner fjord is dominated by populations of small, motile suspensivores and surface detritivores that, for the most part, bioturbate the surface sediments by diffusive mixing and surface deposition. Such organisms are well adapted to survive in areas of high sedimentation and intermittent physical disturbance. As distance from the glaciers increases, the proportion of sessile and semi-motile organisms increases progressively, as does the proportion of conveyor and reverse conveyor animals. These changes reflect the increasing sedimentary stability down-fjord as glacial disturbance levels diminish and the concomitant increase in the complexity and diversity of the infaunal benthic system. The changing ratios between these functional groups may be used as useful proxies for modelling relative community disturbance levels in relation to other indicators of environmental change.

Shrimp and fishes

Pandalus borealis is the most common shrimp in Kongsfjorden. The population mainly consists of small individuals, but not necessarily young individuals since cohort analyses have shown that there are seven to eight year-classes of males in fjords in Svalbard (Hansen & Aschan 2001). The shrimp change sex from male to female at age 4 along the Norwegian coast, but further north in the Arctic sexual maturation occurs later, at age 5 to 6 (Teigsmark 1983; Aschan 2001). Although shrimp spawn annually off the coast of Norway and in the Barents Sea, spawning might only occur in alternate years further north in the Arctic, particularly during cold periods. The proportion of female shrimp near the coast of Svalbard is low, suggesting that the fjords mainly function as growth areas for part of the population (M. Aschan, pers. comm.). The Svalbard fjords do not seem to have resident populations (Drengstig et al. 2000).

Shrimp are commercially caught in Kongsfjorden using bottom trawls. Trawling generally occurs in deep water (>120 m depth) on soft sediments, and the highest densities are found at 200-300 m depth. There are generally between

200–500 ind. kg⁻¹ in each haul (M. Aschan, pers. comm.).

Catch statistics exist for the shrimp fishery in Kongsfjorden and Krossfjorden for the last 20 years. Total catches have fluctuated widely, with peaks in 1985, 1990, 1995 and 1998 (Fig. 4). Around Spitsbergen, catches increased in the early 1980s, as more ships entered the fishery (Aschan et al. 2000), but dropped after 1986 due to declining shrimp stocks. Shrimp surveys have been performed annually in the Spitsbergen area since 1984 (Aschan & Sunnanå 1997). These have shown some fluctuations in the biomass index for the Spitsbergen area, with a slight recovery in the late 1990s (Fig. 4).

There are several other shrimp species in Kongsfjorden. The most abundant are *Sabinea septemcarinata*, *Lebbeus polaris*, *Sclerocrangon boreas* and *Spirontocaris spinus* (Gulliksen et

al. 1999). However, they are much less abundant than *Pandalus borealis* and are not caught commercially in Kongsfjorden. *Lebbeus polaris* is a member of the hard-bottom community in shallow waters (H. Hop, diving obs.).

Fishes in the Arctic have developed special adaptations to life in cold water. These include physiological adaptations such as tolerance and bioenergetic adjustments to low ambient temperatures (e.g. Hop et al. 1997), but also molecular adaptations in the oxygen transport system (haemoglobin) and cold adapted enzymes (e.g. di Prisco 2000). Only a few fish species, such as polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*), are found in the pelagic realm. However, some benthic species, such as daubed shanny (*Leptoclinius maculatus*), snailfishes (*Liparis* spp.) and Greenland halibut (*Reinhardtius hippoglossoides*) have pelagic larvae that are often caught in pelagic plankton trawls. Polar cod is a dominant species in the Kongsfjorden ecosystem based on their abundance in pelagic and benthic trawl catches (Ihalainen & Storemark 2000) (Table 9). The 0+ age group dominate in pelagic hauls, whereas fish from benthic hauls were up to age 5+. Both inside and outside Kongsfjorden (i.e. Isfjorden)

Table 9. Shrimp and fish biomass caught in 20-min trawl hauls with a Campelen 1800 bottom trawl deployed from R/V *Jan Mayen* in Kongsfjorden, August 1997–98.

Fjord zone Depth range (m) Trawl hauls	Transitional 109–300 <i>n</i> = 3 (kg)	Mid./outer 230–346 <i>n</i> = 2 (kg)
Shrimp		
Shrimp (<i>Pandalus borealis</i>)	75.32	48.13
<i>Sabinea septemcarinata</i>	0.68	0.79
Fishes		
Polar cod (<i>Boreogadus saida</i>)	106.71	48.79
Atlantic cod (<i>Gadus morhua</i>)	22.53	
Greenland halibut (<i>Reinhardtius hippoglossoides</i>)	12.77	1.94
Long rough dab (<i>Hippoglossoides platessoides</i>)	3.75	1.17
Eelpouts (<i>Lycodes</i> spp.)	1.53	0.93
Deepwater redfish (<i>Sebastes mentella</i>)	1.22	1.39
Sea-snail (<i>Liparis liparis</i>)	0.50	
Stout eelblenny (<i>Anisarchus medius</i>)	0.45	
Snake blenny (<i>Lumpenus lampretaeformis</i>)	0.22	
Atlantic poacher (<i>Leptagonus decagonus</i>)	0.19	0.14
Daubed shanny (<i>Leptoclinius maculatus</i>)	0.16	0.20
Gelatinous snailfish (<i>Liparis fabricii</i>)	0.14	
European sculpin (<i>Artediiellus europaeus</i>)	0.11	
Sea tadpole (<i>Careproctus reinhardtii</i>)	0.10	0.15
Redfish (<i>Sebastes marinus</i>)	0.09	
Capelin (<i>Mallotus villosus</i>)	0.02	
Snailfishes (<i>Liparis</i> spp.)		0.07
Leatherfin lump sucker (<i>Eumicrotremus derjugini</i>)		0.08
Thornback ray (<i>Raja clavata</i>)		0.40

Table 10. Species collected by divers using hand nets, from different shallow water locations in Kongsfjorden: outer fjord (Kapp Mitra and Kapp Guisnez); middle zone (Kvadehuken and Hansneset); and transitional zone (old dock in Ny-Ålesund and Juttaholmen), in August 1997.

Fjord zone Locations Depth range (m) Sample size	Outer 2 2.5–20 13 (%)	Middle 2 5–30 28 (%)	Transitional 2 2.5–15 71 (%)
Shorthorn sculpin (<i>Myoxocephalus scorpius</i>)			
	69.2	17.9	19.7
Sea-snail (<i>Liparis liparis</i>)			
	15.4	3.6	
Leatherfin lump sucker (<i>Eumicrotremus derjugini</i>)			
	7.7	57.1	
Atlantic wolffish (<i>Anarhichas lupus</i>)			
	7.7	10.7	
Arctic staghorn sculpin (<i>Gymnacanthus tricuspidis</i>)			
		10.7	70.4
Snake blenny (<i>Lumpenus lampretaeformis</i>)			
			4.2
Daubed shanny (<i>Leptoclinius maculatus</i>)			
			2.8
Stout eelblenny (<i>Anisarchus medius</i>)			
			2.8

Fig. 4. Annual total shrimp trawl catches (tonnes wet weight), 1980–1999, for management areas in Kongsfjorden: location 12, southern part of outer Kongsfjorden, inner Kongsfjorden and the northern part of Forlandsundet; and location 19, northern part of outer Kongsfjorden and Krossfjorden. (Data provided by the Directorate of Fisheries and the Norwegian Trade Council, Tromsø.) Estimated indices of biomass (in 100 tonnes) for shrimp in the Spitsbergen area (west and north-west), 1984–1999, are included (Torensen 2000).

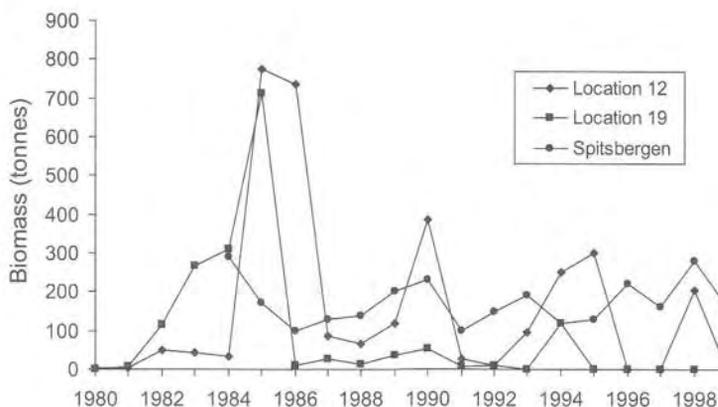
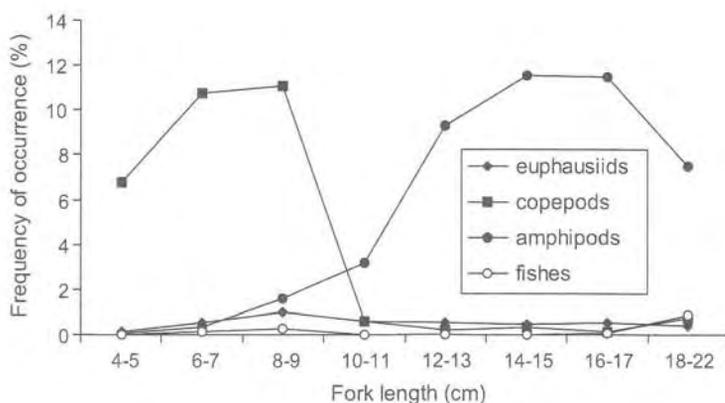


Fig. 5. The diet of polar cod in Kongsfjorden/Isfjorden, as indicated by percent occurrence of four main prey groups for different cod size classes.



there is a significant shift from a diet dominated by copepods to a diet dominated by amphipods when polar cod reach a size of 8–10 cm (Fig. 5). This shift coincides with a change from pelagic to benthic distribution, and may reflect availability of suitably sized prey. A similar tendency is found in polar cod associated with sea ice (Lønne & Gulliksen 1989).

Most fishes in Kongsfjorden are benthic, and ecological information on some is available from Spitsbergen waters (e.g. Haug & Gulliksen 1982; Falk-Petersen et al. 1988; Vollen 1998). In addition to the trawl samples from 1997–98 (Table 9) (H. Hop, pers. comm.), trawling has been performed annually since 1994 as part of the UNIS marine biology course (O. J. Lønne, pers. comm.). The benthic fish community in Kongsfjorden probably consists of about 30 species. However, the taxonomy of some genera such as the eelpouts (*Lycodes* spp.) and snailfishes

(*Liparis* spp.) are not well resolved, primarily because of wide morphological variation in these groups (Able & McAllister 1980; P. R. Møller & Jørgensen 2000).

Both Arctic and boreal fish species are present in Kongsfjorden. Arctic species are represented by polar cod, Greenland halibut as well as smaller species such as sculpins, blennies, snailfishes and eelpouts (Tables 9 and 10). Boreal species, such as Atlantic cod (*Gadus morhua*), long rough dab (*Hippoglossoides platessoides*) and deepwater redfish (*Sebastes mentella*), are also common in the deep water in Kongsfjorden, and haddock (*Melanogrammus aeglefinus*) have been caught in the outer fjord. Polar cod is the most common species, but larger species such as the Greenland halibut and Atlantic cod may contribute more to total fish biomass in the fjord. The largest fish in Kongsfjorden is the Greenland shark (*Somniosus microcephalus*), caught regularly by shrimp

trawlers and also in nets near Ny-Ålesund (C. Lydersen, pers. comm.).

The shallow water (<30 m) fish community mainly consists of Arctic species such as the shorthorn sculpin (*Myoxocephalus scorpius*) and the smaller Arctic staghorn sculpin (*Gymnancanthus tricuspis*), juvenile stages of the leatherfin lump sucker (*Eumicrotremus derjugini*) and snailfishes (*Liparis* spp.) (Table 10). Boreal species are also present, such as Atlantic wolffish (*Anarhichas lupus*) and Atlantic cod, which reside in caves at 20–30 m near Kvadehuken. Small schools of juvenile Atlantic cod have also been observed at 10–15 m depth at this location (H. Hop, diving obs.).

Marine mammals and seabirds

Kongsfjorden has diverse, abundant marine mammal and seabird communities. Marine mammals are represented by pinnipeds (seals and walrus), cetaceans (whales) and the polar bear (*Ursus maritimus*). Seabirds include fulmars, marine ducks, alcids, gulls, terns and some shorebirds. The number and biomass of upper trophic level animals has a marked seasonal peak in the spring–summer season. This is largely attributable to migratory species that are regular, transient inhabitants in the fjord. However, there are also a few resident species within this community that remain in the vicinity of Kongsfjorden throughout the year.

Within and between seasons there are important changes in food availability in various parts of the fjord that, in part, determine the spatial and temporal distribution of foraging by the top predators. The retreating ice edge normally forms a highly productive area with an extensive phytoplankton bloom in spring that results in prey organisms being concentrated in the upper water layers. These animals act as an attractant that concentrates both marine mammals and birds in these areas. When the shore-fast ice has melted, glacier fronts, which act as up-welling areas for zooplankton due to freshwater discharge from the bottom of the glacier (Svendsen et al. 2002), become prime feeding areas for marine mammals and birds during late summer and early autumn. The phenomenon of “freshwater shocked” zooplankton appears to be an added attraction of these areas to fishes, and mammalian and avian predators are attracted to

both food types (Weslawski & Legezynska 1998). River outflows also serve to concentrate foraging birds, but their shallow depths likely limits the utility of these areas for seals and whales. The avian and mammalian marine predators in Kongsfjorden are sufficiently diverse, and enough generalist feeders are present, to ensure that many sympagic, pelagic and benthic marine organisms (above some minimal size) are eaten in large quantities by mammals and seabirds.

Pinnipeds

Ringed seals (*Phoca hispida*) are distributed throughout the circumpolar Arctic and they are the most abundant Arctic seal. Kongsfjorden is an important breeding site for this species in Svalbard (Lydersen & Ryg 1991), and the ringed seal is the most numerous pinniped species in the area (Table 11). This small phocid breeds in land-fast ice areas within the fjord. Ringed seals build lairs in this habitat to protect themselves and their young from harsh, winter weather and predators (Gjertz & Lydersen 1986; Lydersen & Gjertz 1986; Lydersen & Smith 1989). Snow depth is a limiting factor for the location of lairs in Kongsfjorden, because the average snow depth of 20 cm (Svendsen et al. 2002) does not permit subnivian lair construction. Hence, the prime habitat for ringed seals in Kongsfjorden occurs in the inner fjord area that contains glacier-ice pieces frozen into the annual ice and zones containing pressure ridges (Lydersen & Gjertz 1986; Smith & Lydersen 1991). These ice structures tend to cause accumulation of drifting snow, which provides sufficient snow depth for ringed seal lairs. Some 50–100 pups are born annually in March–April in Kongsfjorden (Lydersen & Gjertz 1986) (Table 11). Lactation lasts approximately 6 weeks and breeding takes place toward the end of the maternal care period (Lydersen & Kovacs 1999). As the spring melt proceeds ringed seals are increasingly visible in the fjord because they haul out to rest and sun themselves on the ice surface. Young of the year disperse from the natal areas shortly after nursing has terminated. During several weeks in June, adults and sub-adults spend most of their time out of the water while they undergo their annual moult. At this time ringed seals can occur at very high densities on the limited remaining sea ice in Kongsfjorden. After moulting, many ringed seals leave the fjord and move along the coast or move

northward to the pack ice (Gjertz et al. 2000a). Breeding-aged animals return in the early winter to Kongsfjorden and maintain holes in the ice as the inner fjord once again becomes ice-covered (Svendsen et al. 2002).

The bearded seal (*Erignathus barbatus*) also breeds in Kongsfjorden, but this species prefers the drifting pack ice as its breeding habitat (Kovacs et al. 1996). Its large body size (M. Andersen et al. 1999) affords it thermal protection and predators are avoided to a large degree by its extremely aquatic nature. Bearded seals are rarely found even a metre away from the water, and their young swim and dive within hours of their birth (Lydersen et al. 1996; Lydersen & Kovacs 1999). Throughout their range, including Kongsfjorden, bearded seals are found at quite low densities. Approximately 25 pups are born annually in the Kongsfjorden–Krossfjorden area (Table 11) (K. Kovacs and C. Lydersen, pers. comm.) during late April–May (Hammill et al. 1994; Lydersen et al. 1996). Pups remain with their mother 3–4 weeks and then females mate with males that have managed to attract them via their elaborate

“singing” behaviour (Van Parijs et al. 2001). Similar to ringed seals, bearded seals moult in Svalbard in June. They can often be found on the land-fast ice in clusters, together with ringed seals at this time of year in Kongsfjorden.

Harbour seals (*Phoca vitulina*) also occur in small numbers within Kongsfjorden (Table 11). Currently, this species does not breed in the fjord; all birthing takes place on small islands west of Prins Karls Forland and along the west coast of this island, just south of the mouth of Kongsfjorden (Prestrud & Gjertz 1990; Gjertz & Børseth 1992). Some juvenile harbour seals routinely haul out on small rocks and ledges near Lovénøyane during the spring and summer, and a small mixed juvenile and adult group is habitually present around the south-west corner of Kongsfjorden, at Kvadehuken. The year-round ice-free conditions that occur due to the West Spitsbergen Current (Svendsen et al. 2002), are undoubtedly an important factor in harbour seals being located at Svalbard’s high latitude.

Walrus (*Odobenus rosmarus*) found in Svalbard are part of a population that breeds

Table 11. Marine mammal and seabird abundance, residency patterns and factors relevant to the calculation of their energy consumption in Kongsfjorden. Seabird abundance values are based on averages of annual counts that have been made for over a decade in Kongsfjorden (Norwegian Polar Institute seabird database). Details regarding abundance estimates and energy calculations for marine mammals and sea birds are described in the text.

Species	Abundance estimate	Residency period	Mean body size (kg)	Birds’ clutch size	% of feeding within the fjord
Ringed seal, adults	160	1 Dec.–30 June	70		100
Ringed seal, pups	80	1 April–30 June	20		100
Ringed seal, subadults	100	1 April–30 June	40		100
Ringed seal, adults	20	1 July–30 Nov.	70		100
Ringed seal, subadults	20	1 July–30 Nov.	40		100
Bearded seal, adults	50	Year round	325		100
Bearded seal, subadults	25	Year round	200		100
Bearded seal, pups	25	1 May–15 June	100		100
Harbour seal	15	Year round	70		100
Walrus	5	15 April–15 July	800		100
White whale	50	15 April–15 July	800		100
Minke whale	5	1 May–31 July	5000		100
Common eider	4000 prs.	15 May–1 Aug.	1.800	3.5	100
Little auk	1000 prs.	1 June–15 Aug.	0.160	1	50
Black guillemot	100 prs.	1 June–1 Sept.	0.360	1.5	100
Atlantic puffin	50 prs.	1 June–1 Sept.	0.460	1	100
Brünnich’s guillemot	1700 prs.	15 May–10 Aug.	0.820	1	70
Northern fulmar	1000 prs.	14 April–1 Oct.	0.650	1	10
Black-legged kittiwake	5200 prs.	15 April–1 Sept.	0.370	1.5	30
Glaucous gull	100 prs.	15 April–1 Oct.	1.800	2	100
Arctic tern	1500 prs.	1 June–1 Sept.	0.110	1.5	100

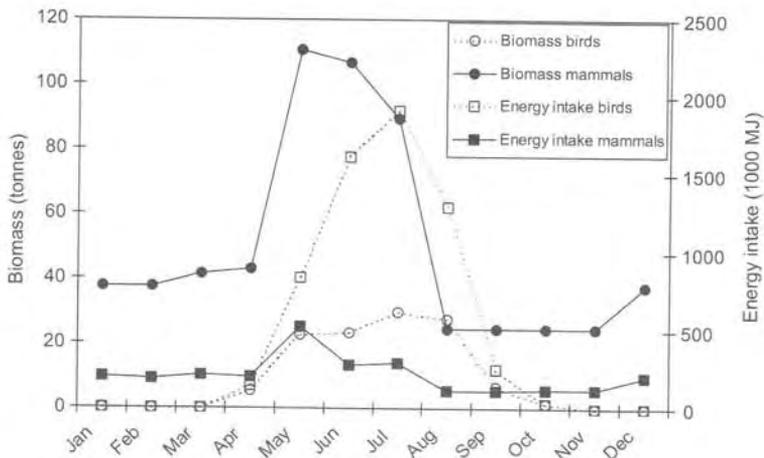


Fig. 6. Seasonal patterns in biomass of, and energy consumption by, marine mammals and seabirds in Kongsfjorden. See text and Table 11 for details regarding calculation of biomass and energy intake

primarily in the Franz Josef Land area (Gjertz & Wiig 1994a, 1995; Wiig & Gjertz 1996; Wiig et al. 1996; L. W. Andersen et al. 1998). They spend the winter on pack ice in southern parts of Svalbard and in north-eastern Svalbard and eastward toward Russian territories. During the spring, particularly when heavy multiyear ice is carried in toward the coast, walrus begin to appear in Kongsfjorden. The vast majority of walrus in Svalbard waters are males, although recent sightings of females with calves have been made (K. Kovacs and C. Lydersen, pers. comm.). Walrus are regularly seen in the Kongsfjorden area from early spring until late summer. Walrus are routinely hauled out at Sarstangen in spring and on haul-out areas on the east side of Prins Karls Forland during summer.

Harp (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) are also seen sporadically in small numbers in Kongsfjorden during spring. Their residency times in the fjord are very short.

Cetaceans

White whales (*Dephinapterus leucas*) are the most commonly sighted cetacean in the Kongsfjorden area and they are the most numerous whale species in Svalbard (Gjertz & Wiig 1994b; Lydersen, Martin et al. 2001). Pods of white whales are seen in the area for days at the time, from the early spring through the summer months. Ice edges are a favoured site in spring, and glacier fronts are a prime feeding area in summer. Group size is highly variable, and no specific studies have been conducted to document

the use of Kongsfjorden by this species.

Minke whales (*Balaenoptera acutorostrata*) are also seen regularly, particularly in the outer part of Kongsfjorden, through the late spring and summer months (Table 11). Occasionally, they also come into the inner fjord area.

Fin whales (*Balaenoptera physalus*) also forage on occasion in Kongsfjorden, but these and other large baleen and odontocete whales that frequent Svalbard waters tend to remain in coastal and offshore waters as opposed to inside the fjords.

Polar bears

Polar bears are occasionally present in Kongsfjorden, and represent the top predator in the ecosystem. They hunt both ringed and bearded seals, particularly young of the year. However, Kongsfjorden is not highly frequented by polar bears and since there are no systematic records of their occurrence and predation rates, it is not possible to estimate their impact on the system.

Seabirds

It is estimated that ca. 15 000 pairs of nine species of seabirds breed in significant numbers (>50 breeding pairs) in Kongsfjorden (Table 11). The common eider (*Somateria mollissima*) is the largest contributor to the total bird biomass, followed by black-legged kittiwake (*Rissa tridactyla*) and Brünnich's guillemot (*Uria lomvia*) (Table 11). Virtually all of the birds are migratory, leaving Kongsfjorden during the winter months. Their arrival time in the spring

and departure in autumn varies among species. Thus, the peak in total biomass by adult birds inhabiting the area is reached during a 3-month period, ca. 15 May to 15 August (Fig. 6).

Several other seabird species breed in the Kongsfjorden area, including Arctic skua (*Stercorarius parasiticus*), long-tailed skua (*S. longicaudus*), great skua (*S. skua*), greater black-backed gull (*Larus marinus*), long-tailed duck (*Clangula hyemalis*) and red-throated diver (*Gavia stellata*). However, these are so few in numbers that they contribute little to the avian biomass in the area and are excluded from our biomass and food consumption estimates (below).

The seabirds can be divided into two groups according to their foraging strategies. The alcids—Brünnich's guillemot, black guillemot (*Cepphus grylle*) and little auk (*Alle alle*)—and Atlantic puffin (*Fratercula arctica*) are pursuit divers that catch zooplankton and small fish while diving at sea. The diving depth capacity in these birds is related to body size. The largest of these species, the Brünnich's guillemot, makes the deepest dives (>200 m; Croll et al. 1992), whereas the smallest, the little auk (zooplankton feeder), dives to rather shallow (<30 m) depths (Falk et al. 2000). Mehlum et al. (2001) found that Brünnich's guillemots in Kongsfjorden dive as deeply as 136 m, although mean dive depth was 45 m. The common eider is mainly a benthic feeder that forages in shallow waters, down to depths of 15 m (Frimer 1995). The other group consists of surface feeders or near-surface feeders, and is represented in Kongsfjorden by the northern fulmar (*Fulmarus glacialis*), kittiwake, glaucous gull (*Larus hyperboreus*) and Arctic tern (*Sterna paradisaea*). The first three normally feed on zooplankton and pelagic fish from the sea surface, whereas the Arctic tern and sometimes also the kittiwake plunge into the water to catch prey. Glaucous gulls employ various foraging habits while feeding on carrion along the shores and other seabirds, including eggs, chicks and adult birds.

The largest food consumption rate by the seabird community is reached during the chick rearing period, when the adults provision chicks in addition to themselves. The amount of food needed to raise nestlings depends on the length of the nestling period and the clutch size. Common eider ducklings leave their nests at the age of one day, whereas the other eight species have nestling periods varying from 20 to 55 days.

Consumption estimates

Marine mammals and seabirds are consumers of significant quantities of fish and invertebrate biomass in Kongsfjorden. To assess their impact on the lower trophic levels, as well as potential limits to the abundances of these upper trophic level animals, crude energy budgets were constructed for the Kongsfjorden system (Table 11; Fig. 6). Although individual marine mammal and seabird species do exhibit prey preferences that fall into various segments of the community, such as pelagic or benthic food webs, the distinctions are not sufficiently clear to calculate impacts on subsections of the Kongsfjorden ecosystem. For example, bearded seals are usually described as being benthic predators, but in the Kongsfjorden area they eat a wide variety of prey types including pelagic fauna (e.g. Hjelset et al. 1999). The energetics of marine mammals in Kongsfjorden is reviewed by Lydersen & Kovacs (1999), and of seabirds by Mehlum & Gabrielsen (1993) and Ellis & Gabrielsen (2001).

Marine mammals

The energy budget calculations for various marine mammals are based on a combination of species-specific doubly labelled water experiments and studies of mass loss, some of which are seasonal (Ryg et al. 1990; Lydersen & Hammill 1993a; Lydersen 1995; Lydersen & Kovacs 1999; Lydersen et al. 1996). Additional information needed for estimates of energetic requirements is from the broader literature on marine mammal metabolism and energy use (Kleiber 1975; Lavigne et al. 1986). When specific knowledge for a particular age group or season is lacking, a field metabolic rate (FMR) of $2 \times$ basal metabolic rate (BMR) was utilized (Lavigne et al. 1986). The annual energy intake for marine mammals is the monthly sum total for the species present in Kongsfjorden (Fig. 6).

Ringed seal abundance is based on the density of breeding lairs in different ice types (Smith & Lydersen 1991) and a sex ratio of 1:1 (Lydersen & Gjertz 1987). This species is an opportunistic feeder that consumes a wide variety of prey types, including cephalopods, crustaceans, tunicates and fish (e.g. Gjertz & Lydersen 1986; Weslawski et al. 1994). They feed on sympagic ice fauna as well as on pelagic and benthic invertebrates and fish. The water depths within Kongsfjorden

do not present a barrier to ringed seals; even pups a few weeks old dive to the bottom in the inner areas of the fjord (Lydersen & Hammill 1993b; Gjertz et al. 2000a). The food intake is zero during moulting in June, and thereafter most ringed seals leave the area. The ringed seals in Kongsfjorden require an annual energy consumption of approximately 703 350 MJ. This is equivalent to about 121 tonnes of polar cod, caught in autumn (5.8 MJ kg⁻¹) or 185 tonnes of relatively fat-rich invertebrates, such as *Themisto libellula* in early winter (3.8 MJ kg⁻¹).

Bearded seal numbers are based on the mean number of pups born in the area over a 6-year period and an adult sex ratio of 1:1. Bearded seals eat a highly variable diet that contains fish as well as many invertebrate species, most of which are taken from the bottom (Lydersen et al. 1996; Hjelset et al. 1999; Krafft et al. 2000; Lydersen, Kovacs et al. 2001). Their benthic feeding and shallow diving habits tend to limit their movement patterns. However, young animals have been documented to disperse broadly after weaning, and dive depths much deeper than the maximum depths recorded for adult animals have been documented for pups that were only a few months old (Gjertz et al. 2000b). Bearded seals fast during the moulting period and the food intake is reduced during breeding, but an increased energy intake occurs later in the season, from the Kongsfjorden ecosystem, to compensate for this energy loss. Bearded seals consume approximately 1162 240 MJ of food energy annually from the Kongsfjorden system.

Harbour seals, walruses, white whales and minke whales are regular visitors in the Kongsfjorden area. Their numbers and periods of visitation are based on unpublished data and educated guesses (K. Kovacs and C. Lydersen, pers. comm.). Harbour seals diet analyses suggest that polar cod and Atlantic cod are the most important prey species, but that they also eat many other fish species. Invertebrates appear to be a minor component of the diet. Cephalopod beaks and shrimp parts are only occasionally recovered in scats (M. Andersen, C. Lydersen and K. Kovacs, pers. comm.). Harbour seals require an estimated 77 955 MJ of energy annually to support the small group that frequents Kongsfjorden. Walruses are shallow divers that feed mainly on benthic invertebrates including *Mya truncata*, *Buccinum* spp. and also

perhaps *Serripes groenlandicus* in Svalbard (Gjertz & Wiig 1992; Wiig et al. 1993). A crude estimate of their possible energy consumption in the Kongsfjorden area is 40 600 MJ. White whales infrequently visit Kongsfjorden, but the duration of their stays and their group sizes are highly variable so the estimate of their energy consumption in this fjord is crude. Fatty-acid analyses of the blubber of white whales from Svalbard suggest that polar cod and capelin dominate their diet and that they might also consume zooplankton and shrimp (Dahl et al. 2000). They dive to the bottom of the fjords in Svalbard routinely and are likely to feed on benthic organisms (Lydersen, Martin et al. 2001). Energy consumption by white whales in the Kongsfjorden area is estimated to be 405 700 MJ. The minke whale's diet consists of a wide variety of crustaceans and fish (e.g. Lydersen et al. 1991). Although this species is solitary, and occurs at low densities, its sheer body size means that an individual animal requires hundreds of kilograms of food daily (Markussen et al. 1992). Minke whales likely account for approximately 160 300 MJ of energy consumed from Kongsfjorden.

Harp seals and hooded seals were not included in the consumption estimates because they have low abundances and occur so infrequently that they would have minor impact on the system. Polar bears were also not included in the energetics calculations because they occur at low densities in the area and there is a lack of information regarding their residency in the Kongsfjorden area.

Seabirds

Seabirds are important consumers in the Kongsfjorden ecosystem. The approach by Mehlum & Gabrielsen (1995), estimating the energy expenditure and food consumption of the seabirds in the Barents Sea region, is followed here to estimate the energy intake for the seabird community (or biomass of seabirds) breeding in Kongsfjorden (Fig. 6). The daily energy expenditure (expressed as the field metabolic rate, FMR) by free-living seabirds is estimated by the use of the doubly labelled water technique (Gabrielsen 1994; Ellis & Gabrielsen 2001). We used literature values for FMR for adult birds of the actual species in calculations of food consumption. We assumed that the FMR

is constant throughout the time period when the birds are present in Kongsfjorden. From the FMR's we calculated the daily gross energy intake (GEI) by applying an assimilation coefficient of 75% (Brekke & Gabrielsen 1994) to all species and the food demand by using an average energy density of the prey of 5 kJ g⁻¹ wet mass (Mehlum & Gabrielsen 1995). The daily food consumption was multiplied with the residence time and breeding population size to obtain the total annual food consumption for adult birds. Seabirds breeding in Svalbard may travel far out at sea to find food for their young (Mehlum & Gabrielsen 1993; Mehlum et al. 1998). Individuals of the same species may forage close to the shore, whereas others travel out of the fjords to forage. For species that spend some of their time feeding outside Kongsfjorden, we corrected the consumption estimates by taking into account the estimated percentage of feeding conducted inside the fjord, subjectively (F. Mehlum and G. W. Gabrielsen, pers. comm.).

Estimates of GEI of chicks of different ages were obtained from measurements of FMR in chicks from little auk, kittiwake, black guillemot, Brunnich's guillemot, puffin and Arctic tern (Klaassen et al. 1989; Gabrielsen et al. 1992; Konarzewski et al. 1993; G. W. Gabrielsen, pers. comm.). FMR in chicks of common eider, glaucous gull and fulmar were estimated from growth curves and FMR measurements from other species. For all species, an assimilation coefficient of 70% was used for the first 15 days of growth, whereas a coefficient of 75% was used after 15 days (Breivik 1991).

We used estimates of daily GEI at 5-day intervals and integrated these over the whole nestling period to obtain the total GEI for the whole nestling period. It was assumed that all chicks left Kongsfjorden just after fledging. The exception was the common eider. We assumed that the eider ducklings resided within Kongsfjorden for 14 days after hatching. The chicks consume only 52.8 t (or 7.3%) of the total food demand of the seabird community (720.1 t). Approximately 484.6 t (or 67.3%) of this is taken from Kongsfjorden.

Food consumption estimates can be used to estimate fluxes of nitrogen, phosphorous and carbon from prey through the seabird community. In accordance with Brekke & Gabrielsen (1994), the excrement production by seabirds was estimated as 10.2% (dry mass) of the food con-

sumption (wet mass), and the nitrogen production as 21% of the dry mass of excrement. The production of phosphorous was calculated as 40% of the nitrogen production (Sendstad 1978). The carbon flux was estimated from the food consumption, assuming a dry mass/wet mass ratio of 1/3 and a carbon content of 40% of the dry mass (Sakshaug et al. 1994).

The annual nitrogen and phosphorous production by the seabird community from prey taken in Kongsfjorden was estimated to be 10.4 and 4.2 tonnes, respectively. These values amount to 0.03 and 0.01 g m⁻² y⁻¹ of the deposited material. The total annual carbon flux from prey taken in Kongsfjorden through the seabirds was estimated to be 0.21 g C m⁻² y⁻¹. Most of the nutrients produced by the seabird community are recirculated into the marine ecosystem, but significant quantities are also exported to the terrestrial ecosystem adjacent to Kongsfjorden. The chicks, while in the breeding colonies, produce 7.3% of the nutrients, or 760 kg nitrogen and 304 kg phosphorous. The contribution from adult birds to the fertilization of the terrestrial ecosystem is harder to estimate and depends on the proportion of the time spent in the colonies. Faeces account for most of the nutrient transport from sea to land by seabirds, but other sources are birds taken by terrestrial predators, carcasses, shed feathers and lost eggs.

Our estimate of the annual carbon flux through the seabird community in Kongsfjorden is similar to the flux obtained in a similar calculation for the seabird community around Bjørnøya (0.18 g C m⁻² y⁻¹). This is comparable to the fluxes in seabird communities in productive shelf regions elsewhere (Mehlum & Gabrielsen 1995). Since the production of seabird prey in Kongsfjorden is unknown, the consumption can currently only be related to primary production. The annual amount of carbon consumed by the seabird community in Kongsfjorden equals 0.91-5.25% of the phytoplankton carbon production in the fjord, calculated from the lowest production estimate, and only 0.12-0.18% based on the highest estimate. Even the lowest values for consumption are considerably higher than the corresponding mean value (0.076%) obtained from 11 previous studies in northern shelf waters (reviewed by Mehlum & Gabrielsen 1995). This may indicate that a considerable part of the biomass consumed in Kongsfjorden is based on advected carbon.

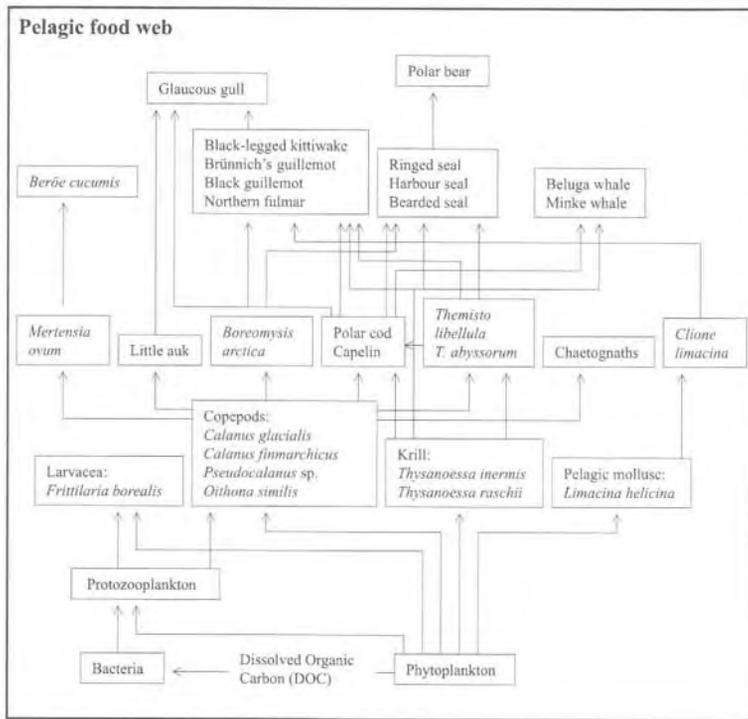


Fig. 7. Conceptual model outlining the main compartments and pathways in the pelagic food web in Kongsfjorden. Boxes denote taxa that are important for the energy flow (arrows), with some abundant representatives from Kongsfjorden listed by species. Each row in the diagram represents a trophic level (although some boxes may have overlapping trophic levels).

Pelagic food web

The pelagic food web in Kongsfjorden (Fig. 7) consists of primary producers and four trophic consumer levels: grazers and first- to third-order consumers. The degree to which the pelagic grazers in the fjord are sustained by advected phytoplankton and protozooplankton production is not known, but it is most likely large.

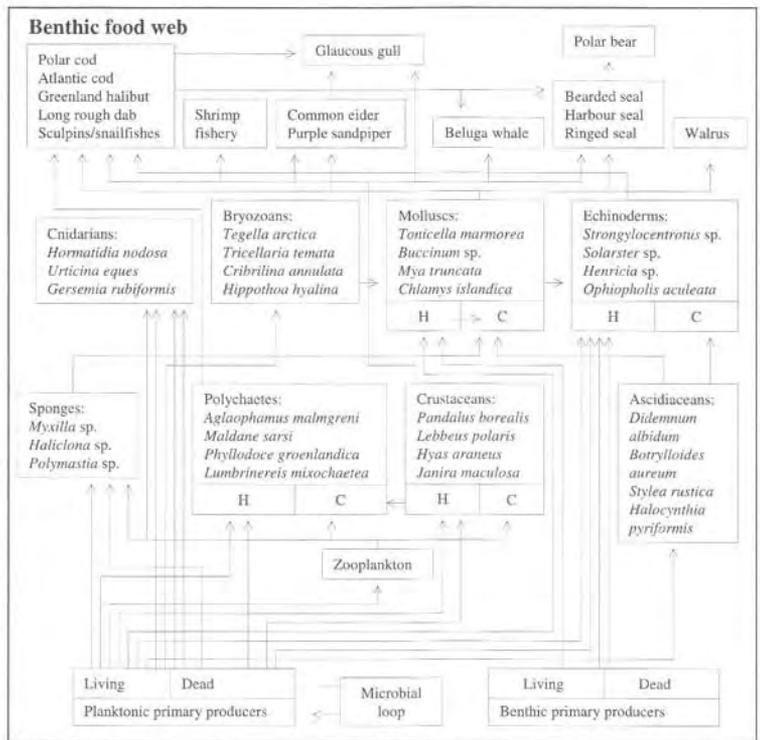
The most abundant first-order consumers in the water column in Kongsfjorden are copepods (primarily *C. finmarchicus*, *C. glacialis* and *Pseudocalanus* spp.), krill (*Thysanoessa inermis*, *T. raschii*), larvaceans (*Fritillaria borealis*) and the pelagic mollusc *Limacina helicina*. Numerically, the copepods dominate completely. This diverse group also contains omnivorous or carnivorous species, such as *Oithona similis* and *Metridia longa*, which occasionally become numerous components of the zooplankton community.

The main second-order consumers in Kongsfjorden are pelagic fishes, the pelagic amphipod *Themisto libellula*, chaetognaths, the mysid *Boreomysis arctica*, the pelagic mollusc *Clione limacina*, the ctenophore *Mertensia ovum* and some seabird species such as the little auk. Among the planktivorous fish found in the fjord,

juvenile polar cod are probably the most important predator on copepods, but the migratory capelin may be periodically encountered in high numbers. *Clione limacina* rely for the most part on *Limacina helicina* as a prey (Falk-Petersen et al. 2001). Another ctenophore *Berøe cucumis* is the only main predator on *Mertensia ovum* (Falk-Petersen et al. 2002).

Marine mammals and seabirds dominate the higher trophic levels in Kongsfjorden. Among the whales, the beluga or white whale, and the minke whale are of greatest importance as predators on fish and zooplankton (Lydersen et al. 1991; Dahl et al. 2000). The ringed seal is the most abundant seal in the fjord and is believed to forage extensively on a wide range of zooplankton and fish from sympagic, pelagic and benthic communities (Gjertz & Lydersen 1986). Other seals, such as bearded and harbour seals, also prey on pelagic and benthic fishes as well as zooplankton (Hjelset et al. 1999). During their periods of residency in the fjord, kittiwakes, guillemots and fulmars are important predators of zooplankton and fish. The glaucous gull preying on seabirds and the polar bear preying on seals represent the top predators in the pelagic food web.

Fig. 8. Conceptual model outlining the main compartments and pathways in the benthic food web in Kongsfjorden. Boxes denote taxa that are important for the energy flow (arrows), with some abundant representatives from Kongsfjorden listed by species. Primary producers are divided into living and dead to signify the difference between predators and detritivores. Lower sections on some boxes denote herbivorous (H) and carnivorous (C) members of that organism group.



Benthic food web

Benthic macroalgae and phytoplankton are important primary producers for benthic animals in Kongsfjorden (Fig. 8). Herbivores feeding on living benthic algae are primarily grazing molluscs (Polyplacophorans: *Tonicella marmorea*, *T. rubra*; Prosobranchs: *Margarites* spp.) and the sea urchin *Strongylocentrotus droebachiensis*. However, water currents may also transport dead macroalgae from the shore to deeper waters where they function as direct food for larger macroinvertebrates (e.g. sea urchins and snails). Current-exposed surfaces with less accumulation have revealed a diverse fauna of filter feeders, especially within the taxa Porifera (sponges), Hydrozoa, Bryozoa, and Ascidiacea.

Benthic production is based on living phytoplankton or sedimented organic material derived from phytoplankton production (via the pelagic-benthic coupling). The vertical flux results in accumulation of material on the horizontal surfaces. Dredge and trawl hauls have revealed a diverse epifauna, with the shrimp *Pandalus borealis* being the most abundant species.

Carnivorous invertebrates represent several

phyla/classes, but the most conspicuous ones are prosobranch snails (Mollusca) and sea stars (Echinodermata). Examples of snails are the *Buccinum* spp., *Neptunea despecta* and *Polynices pallidus*. Examples of sea stars are *Solaster* sp., *Henricia* sp. and *Pteraster* sp. Carnivorous polychaetes are also common, for example *Phyllodoce groenlandica*, *P. citrina*, *Aphelochaeta malmgreni*, *Nothria conchylega*, *Glycera* sp. and members of the Lumbrineridae.

Several benthic fish species find their food at the bottom. The two most abundant flatfishes are the Greenland halibut and the long rough dab (*Hippoglossoides platessoides*), the first being more pelagic than the latter (Haug & Gulliksen 1982). The Greenland halibut feed on other fish, *Pandalus borealis* and amphipods (Vollen 1998), whereas food items such as polychaetes, sea urchins, brittle stars and benthic crustaceans (amphipods, decapods) are commonly recorded in the stomachs of long rough dabs (Klemetsen 1993). Atlantic cod and red fish are common in deep water of Kongsfjorden, preferring crustaceans (amphipods, decapods) and fish. Sculpins mainly occur in shallow water where they feed on a variety of organisms, including

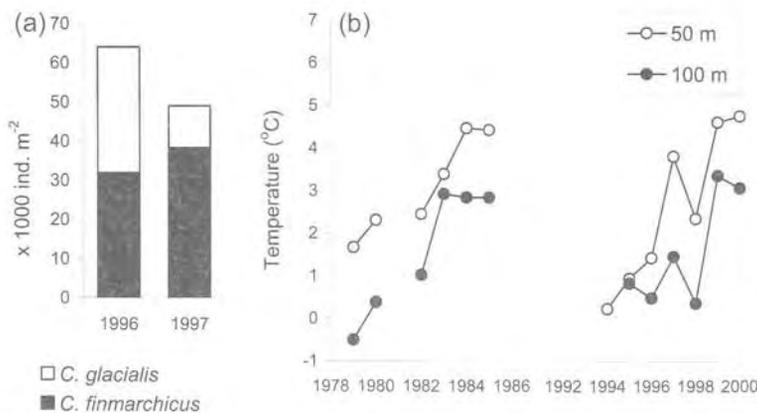


Fig. 9. (a) Historical variability in ocean climate (summer sea temperatures) in Kongsfjorden (Normann & Pettersen 1984; Normann 1986; A. Beszczynska-Møller, pers. comm.). (b) Abundance of Arctic *Calanus glacialis* and boreal *C. finmarchicus* in Kongsfjorden in a "cold" (1996) and "warm" (1997) year (Kwasniewski et al. unpubl. ms).

crustaceans and fish. Snailfishes are found both in shallow and deep waters where they feed on benthic and pelagic crustaceans (decapods and amphipods) (Falk-Petersen et al. 1988).

Generally, birds are less dependent on benthic food sources, but the common eider is usually regarded as a benthic feeder on sea urchins and mussels (Bustnes & Lønne 1995). Shorebirds, such as the purple sandpiper (*Calidris maritima*), are also commonly observed feeding on benthos, especially crustaceans, in the intertidal zone (Leinaas & Ambrose 1999).

The most important mammal feeding on benthos in Kongsfjorden is the bearded seal, but the other seal species also utilize benthic food sources. The walrus feeds on soft and gravel bottom surfaces mainly consuming bivalves such as *Mya truncata* (Gjertz & Wiig 1992). The glaucous gull preys on birds but also eat benthic organisms such as spider crabs (*Hyas araneus*), if they become available.

Environmental impacts

Climatic influences

Seasonal and annual climatic variation that alters the distribution of water masses in the Arctic will influence Kongsfjorden. The Atlantic influence is expected to become stronger under conditions of climate warming. The warming of Svalbard waters may have started as early as in the 1920s (Blacker 1957), but still seems to be ongoing according to more recent temperature records for Kongsfjorden (Fig. 9a). Because aquatic organisms are often associated with particular

water masses, climatically induced changes in the proportions of the various water masses will most likely be reflected by changes in the taxa present in Svalbard waters (e.g. Blacker 1957; M. F. Dyer et al. 1984; Galkin 1998; Kwasniewski et al. unpubl. ms). The pelagic community is probably the most sensitive to interannual variability, as indicated by a shift in community composition of species between "cold" and "warm" years. The Arctic *Calanus glacialis* was abundant in the cold year of 1996, whereas the boreal *C. finmarchicus* dominated in the warmer year of 1997 (Fig. 9b). An increased influx of Atlantic water will probably also result in the establishment of other boreal species in Kongsfjorden, including benthic organisms with pelagic life stages. Blacker (1957) showed that benthic species associated with Atlantic water had extended their range northwards from 75° to 78° N by the early 1950s and displaced those animals associated with Arctic conditions, which were common to the west of Spitsbergen in early surveys (1878–1931). However, Dyer et al. (1984) found no large changes in a more recent survey (1978–1981), but rather a considerable overlap in the distribution and temperature ranges for Atlantic and Arctic species. Expected fauna additions to Kongsfjorden may include the blue mussel (*Mytilus edulis*), since it has recently become established on Bjørnøya (Weslawski et al. 1997). The macroalga *Laminaria hyperborea*, which has been recorded from Isfjorden (Gulliksen et al. 1999), is another likely candidate for range expansion.

There is a large interannual variation in the extent of sea ice in Kongsfjorden (Svendsen et al. 2002). Little ice would favour pelagic and

benthic production in spring, whereas extensive ice cover would reduce production and delay the onset of plankton blooms. The cover of brown macroalgae at Kvadehukken was very low in 1998, after a cold winter with prolonged ice cover during spring (F. Beuchel and B. Gulliksen, pers. comm.). The variability in ice cover also affects the population of ringed seals in Kongsfjorden, since they use the ice and snow lairs on the ice in inner Kongsfjorden for breeding purposes (Smith & Lydersen 1991).

Changes in glacier action—either an increase or decrease in meltwater run-off or calving—will result in changes in the temperature, salinity and turbidity of the nearby water masses (Elverhoi et al. 1980). Higher precipitation and glacial melt rates are expected because of climate warming, and the transfer of water from land to the fjord will increase. The tidal glaciers in inner Kongsfjorden are already in a state of retreat (150 m y^{-1} ; Svendsen et al. 2002). Glacial sedimentation, with its influx of fine-grained inorganic particles, and ice-scouring have a profound effect on the benthic fauna, producing low species diversity and a dominance of opportunistic taxa (Holte et al. 1996; Pugh & Davenport 1997). Increased siltation may reduce biodiversity, as shown in a Franz Josef Land-Svalbard comparison (Wlodarska-Kowalczyk & Weslawski 2001). Because many organisms are limited in their physical tolerance ranges (e.g. Wiencke et al. 1994), changes in salinity can affect the taxonomic composition of marine biological communities and cause mortality in zooplankton populations (Zajaczkowski & Legezynska 2001). The physical disturbance of the sediments caused by extensive ploughing by glacier calving affects mainly the benthic communities in the shallow inner basin, outside the tidal glaciers. Changes in the position of the glacier fronts (Lefauconnier et al. 1999) will alter the area of seafloor disturbance, but glacial retreats will also open up new habitats for colonization by benthic organisms.

Stratospheric ozone depletion: enhanced UV radiation

Because of its detrimental effect on many biological processes, the increase of UV-B radiation on the Earth's surface due to stratospheric ozone depletion (Shindell et al. 1998) represents a major threat to life (Bothwell et al. 1994; Wängberg

et al. 1996). Numerous biological processes are impaired during exposure to UV-B radiation, especially photosynthesis (Bornman 1989; Vass 1997), as has been shown for Kongsfjorden macroalgae (Hanelt et al. 1997; Brouwer et al. 2000; Bischof et al. 2001; Karsten et al. 2001). One target of UV-B is the CO_2 fixing enzyme RubisCO (Bischof, Hanelt et al. 2000; Bischof, Kräbs et al. 2000).

Despite the damaging effects of UV radiation, the photosynthetic abilities of species from the upper and mid-sublittoral zones appear to be able to acclimate to it (Bischof et al. 1998; Bischof et al. 1999). One physiological basis of acclimation may be the accumulation of UV-absorbing mycosporine-like amino acids (MAAs), which are thought to function as natural UV sunscreens (Dunlap & Shick 1998). A survey revealed that all red algae from the eulittoral/upper sublittoral of Kongsfjorden contained several MAAs (Karsten et al. 1998). Exposure to the full solar spectrum leads to a strong accumulation of these compounds (Karsten et al. 1999; Karsten & Wiencke 1999; Bischof, Hanelt et al. 2000; Bischof, Kräbs et al. 2000), which, in turn, partly protects against UV-induced inhibition of photosynthesis.

At the level of the organism, growth is significantly inhibited by UV-B radiation in upper and mid-sublittoral species (Aguilera et al. 1999). Shade adapted species from the lower sublittoral such as *Phycodrys rubens* do not survive when exposed to surface UV levels. On the other hand, no UV-induced inhibition of growth or photosynthesis was found in the eulittoral *Fucus distichus*. The life-history stages of brown algae that are most sensitive to UV-B radiation are the zoospores, and the depth distribution of these species reflects the light requirements of the unicellular stages (Wiencke et al. 2000). Besides abrasion, UV-B radiation determines the upper distribution limit of the studied species (Fig. 10). Changes in the zonation of individual species and the community structure may be expected in species in which growth or the viability of microscopic stages is affected by UV-B radiation. This applies especially to species from the eulittoral (intertidal zone) and upper sublittoral (subtidal zone). The macrothalli of species in deep waters are extremely susceptible to UV stress, but they are not affected because of the high attenuation of UV-B in the water column. UV-B radiation has a greater influence in the

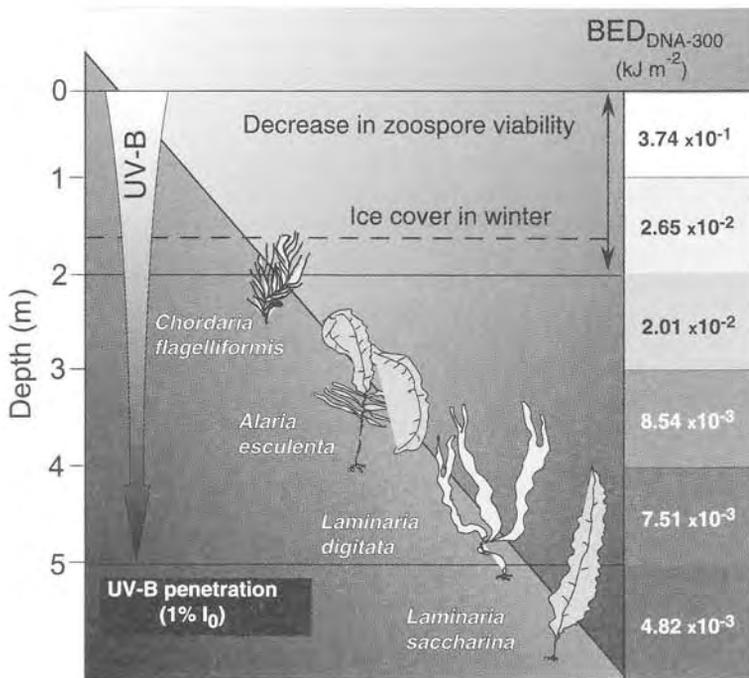


Fig. 10. Hypothetical scenario relating the present UV-B regime in Kongsfjorden (expressed as biologically effective doses [BED] for DNA damage) to zoospore viability of brown algae and the macroalgal zonation (modified from Wiencke et al. 2000; printed with permission of the publisher, Inter-Research Science Publisher).

outer than the inner part of the fjord because of differences in water transparency (Svendsen et al. 2002).

The effects of UV-B radiation on two animals occurring in Kongsfjorden, the sea urchin *Strongylocentrotus droebachiensis* and the copepod *Calanus finmarchicus*, have been studied in Canada. As in macroalgae, MAAs also serve as UV sunscreens in *S. droebachiensis*. The sea urchin accumulates MAAs from their diet of macroalgae, which reduce UV-B-induced damage to its eggs and embryos (Adams & Shick 2001). In contrast, eggs of *C. finmarchicus* exhibit a high mortality after UV exposure, probably as a direct result of DNA damage (Kouwenberg et al. 1999). A model that included meteorological and hydrographic conditions and ozone depletion showed that mortality could be as high as 32.5% in the Gulf of St. Lawrence (Browman et al. 2000).

Human influences

Marine ecosystems in the Arctic are sensitive to human impacts. The intensity of local impacts in Svalbard is generally lower than along the Norwegian coast, but the environment may be more sensitive to perturbations, due to the low

temperatures, periodic ice cover and glacial sedimentation. Human impacts in Svalbard and Kongsfjorden are reviewed by Kovacs (1996) and Shears et al. (1998), but there is currently no environmental assessment criteria specifically aimed at Svalbard. While local sources of contamination can be identified and remedied, the Arctic is also subjected to continuous long-distance transport of contaminants, which represents a long-term threat to its marine ecosystems.

Ny-Ålesund, on the southern shore of Kongsfjorden (Fig. 1b), is one of the world's northernmost human settlements. Coal mining was carried out there from 1917 until 1962, and in recent years (after 1990) Ny-Ålesund has developed into a small, but active, international research community. A strict environmental policy has resulted in minimal impacts from the current settlement, but some residual environmental contaminants exist in the immediate vicinity of the mining sites. Organic enrichment of the sea floor by hydrocarbon input may influence the benthic faunal assemblages (Steichen et al. 1996), although the benthic fauna in the middle zone shows no signs of such enrichment (S. Cochrane, pers. comm.). Poly-aromatic hydrocarbon (PAH) levels may be relatively high near point sources

(Skei 1993), but in Kongsfjorden sediments the PAH levels are generally low to moderate (Olsson et al. 1998). Levels of polychlorinated biphenyls (PCBs) and heavy metals were generally low (Skei 1993; Shears et al. 1998), except near landfills where elevated PCB levels have been found.

Indications of atmospheric long-range transport events of semi-volatile organic compounds have been described for the Svalbard region (Oehme 1991; Oehme, Haugen et al. 1996; Oehme, Schlabach et al. 1996). Elevated concentrations of PCBs and the cyclodiene insecticide chlordane, originating from the North American continent, have been found in air masses over Kongsfjorden. Every year, several atmospheric long-range transport events are reported, and under certain meteorological conditions transport of large amounts of pollutants from central Europe into the Arctic can take place within a few days (AMAP 1998). Traces of pesticides and dioxins, indicating long-range transport, have been found in marine sediments in Kongsfjorden (Skei 1993).

The Svalbard area is also affected by long-distance transport of artificial radionuclides from the global fallout of past nuclear test explosions and other sources (Aarkrog 1993). Measurements on glacial ice cores show that fallout from the Chernobyl accident reached the Kongsfjorden area (Pinglot et al. 1994). In addition, radionuclides from European nuclear reprocessing plants have been found in seawater samples from Arctic areas (e.g. Dahlgaard 1995; Kershaw et al. 1999) including Kongsfjorden (Gerland et al. 2002a, Gerland et al. 2002b). The levels of ⁹⁹Tc in seawater in Kongsfjorden in 2000 are similar to those measured in the south-western Barents Sea (J. E. Brown et al. 2002; Gerland et al. 2002b). Radionuclides are trapped in the sediments of the inner part of the fjord, which acts as a temporary reservoir (Papucci et al. 1998).

Anthropogenic contaminants, both of local and distant origins, may accumulate in body tissues of organisms and become biomagnified in the marine food web (e.g. Hop et al. in press). Levels of organochlorines (OCs) were generally low in invertebrates from Kongsfjorden (Hop et al. 2001). Both OCs and heavy metals have been measured in ringed seals and seabirds in the Kongsfjorden area (Norheim 1987; Savinova et al. 1995; Henriksen et al. 1998; Severinsen

et al. 2000). In Svalbard, the highest OC levels have been reported for top predators (polar bears, glaucous gulls and ringed seals), but still generally lower than those found in eastern parts of the Russian Arctic Sea (Savinova et al. 2000; Muir et al. 2000). In contrast, Hg and Cd levels in birds from Kongsfjorden were higher than in other parts of the Barents Sea, indicating a possible local source of these metals (Savinov et al. 2000).

Human induced, physical disturbances are seen in sonar imageries of soft sediments in the deeper outer parts of Kongsfjorden, which are subject to shrimp trawling (Shears et al. 1998). This activity disturbs the stratigraphy of marine sediments in the area and influences the faunal communities (Freese et al. 1999). Bringing both ships and people, tourism can also cause disturbance to birds and marine mammals in the Kongsfjorden area.

Is Kongsfjorden a representative or a unique Arctic marine fjord system?

Kongsfjorden is an open fjord in the Arctic with both Atlantic and glacial influences. In these regards it is similar to most other fjords along the western coast of Svalbard. Further north slightly different conditions are encountered, probably because of the greater influence of Arctic water masses and the presence of sills (e.g. Raudfjorden and Woodfjorden, on the northern coast of Spitsbergen) (Eilertsen et al. 1989; Keck 1999). Different bottom currents, with stronger influences on sediments and the benthic ecosystem, have been seen in the north-west corner of Spitsbergen (Magdalenafjorden) (Keck 1999).

The fjords of Spitsbergen are characterized by very low populations of heterotrophic flagellates during the winter (Wiktor 1999). These conditions prevail until light levels increase in spring and freshwater from the glaciers and melting of sea ice become prominent. The timing of the spring bloom will depend upon the creation of a surface mixed layer, which confines the phytoplankton mainly within the euphotic zone. Most fjords studied in Svalbard show peaks in biomass during summer, and this biomass is comparable among fjords on the western coast (Halldal & Halldal 1973; Eilertsen et al. 1989; Keck 1999). Dinoflagellates, cryptophytes and

other autotrophic flagellates dominate the phytoplankton communities during the summer. The primary production rates in west coast fjords appear to be similar, although there is considerable interannual variation (Eilertsen et al. 1989). Conditions for phytoplankton growth seem to be of poorer quality in summer for fjords on the northern coast (e.g. Raudfjorden, Woodfjorden) due to deeper mixed layers (Eilertsen et al. 1989). Nutrients in fjords in the north of Svalbard are also lower than for the west coast fjords, indicating that the spring bloom may have consumed more or, possibly, that the blooms are more extensive. Low sedimentation rates, with a dominance of faecal pellets, suggest that these systems are heavily grazed (Keck 1999).

Since Kongsfjorden is an open fjord, the role of advection is probably substantial. In Lindåpollene (near Bergen, western Norway) the ratio of fjord cross-sectional area to the total fjord volume is approximately 10^{-7} m^{-1} (Aksnes & Magnesen 1983). The biological system in this mainland fjord is believed to be influenced predominately by internal (fjordic) processes. In Kongsfjorden this ratio is on the order of 10^{-2} m^{-1} . We therefore presume that the role of advection in Kongsfjorden is high based on the fjord topography and the presence of advective driving forces (Svendsen et al. 2002). The abundance of *Calanus finmarchicus* is most likely influenced significantly by "advective production" (Aksnes et al. 1989). Changes in zooplankton distribution (i.e. different population structure in different parts of the fjord) and community composition (e.g. lack of *M. longa* when Transformed Atlantic Water is absent) also indicate that advection processes are important (Kwasniewski et al. unpubl. ms). Kongsfjorden is likely similar to other fjords without sills on west Spitsbergen with regard to the influence of advection. Isfjorden is a much larger system with many side arms and may be less suitable for monitoring changes on a local scale. Hornsund (near Sørkapp) being a glacially influenced, open fjord of comparable size, is probably the most suitable fjord for comparisons with Kongsfjorden. However, even though Hornsund is located further south, it is more influenced by Arctic water from the current around Sørkapp ("Sørkappstrømmen" Loeng 1991), and the benthic fauna is more Arctic than in Kongsfjorden (Włodarska-Kowalczyk et al. 1998).

The benthic macrofauna of Kongsfjorden is

broadly representative of other fjords and coastal areas of west Spitsbergen. In the inner basin, in front of the Kongsbreen glacier, the benthic fauna is similar to that found at similar depths in the glacial outflow in Sassenfjorden, a side arm of Isfjorden (Kendall & Aschan 1993; Kendall 1996). Both fjords are numerically dominated by small-bodied polychaetes (particularly cirratulids, paraonids and sabellids), tanaid crustaceans and both protobranch and Thyasirid bivalves. Holthe et al. (1996) noted the dominance of small-bodied polychaetes among the fauna of Adventfjorden, a side arm of Isfjorden. On a slightly broader scale, Włodarska-Kowalczyk et al. (1998) showed a clear difference between the fauna of glacial bays in the east and west of Svalbard. They also recorded differences between inner and outer fjord basins, clearly detectable in Kongsfjorden as well.

Some food web models have been made for Arctic marine ecosystems, particularly for the eastern Canadian Arctic (Welch et al. 1992) and the Barents Sea (Sakshaug et al. 1994), although these may not be directly applicable to fjords. The majority of fjordic biological studies have been undertaken in boreal or sub-Arctic fjords undisturbed by recent glacial activity (e.g. Balsfjorden and Masfjorden in northern Norway; Aksnes et al. 1989; Falk-Petersen et al. 1990). Boreal species, such as *Calanus finmarchicus*, euphausiids (*Thysanoessa* spp.) and capelin, tend to dominate the pelagic food webs in these fjords. These boreal groups are also present in Kongsfjorden, but the dominant species of the system are Arctic species, such as *Calanus glacialis*, *Themisto libellula* and polar cod. Even though the boreal part of the pelagic system is similar to that of north Norwegian fjords, the dominating Arctic part of the system is similar to that of a high Arctic marine food web, such as the marine ecosystem of Lancaster Sound, Arctic Canada (Welch et al. 1992).

One unique attribute of Kongsfjorden is the presence of both boreal and Arctic species. Their balance is influenced by oceanographic conditions (Atlantic versus Arctic) and glacial inputs, both of which are sensitive to climate changes. Because Kongsfjorden receives variable climatic signals between years, it functions as a climate indicator on a local scale. The presence of both boreal and Arctic fauna in Kongsfjorden expands the food availability for secondary consumers (fish larvae, ctenophores,

shrimp larvae) and abundant marine mammal and seabird populations, but advection is also important for sustaining upper trophic level predators in this area.

Gaps in knowledge

Kongsfjorden has received a considerable amount of research attention for a fjord at such high latitude. This is partly due to the presence of the town of Ny-Ålesund, which has served as an infrastructure base for decades. Recently (since 1996), the level of scientific activity has been enhanced by interdisciplinary collaboration within the international Ny-Ålesund Large Scale Facility. The fact that Kongsfjorden is suitable as a site for exploring the impacts of possible climate changes, which are currently topical, also serves as an addition impetus to scientific activity in the area. Svendsen et al. (2002) describe the general climate-driven forces (i.e. Atlantic influx and melting of tidal glaciers) that affect the physical environment in Kongsfjorden from both ends, but there is a need to assess the interannual variability and climate signals that might be reflected in the Kongsfjorden ecosystem. We have demonstrated the effects of different water masses on zooplankton distribution, and the effects of glacially induced environmental gradients (i.e. sedimentation and freshwater runoff) on both pelagic and benthic communities. The structure of the pelagic and benthic food webs in Kongsfjorden is generally known, but quantitative data on production, biomass and consumption are often lacking. It is not yet possible to construct adequate carbon flow models for the fjord or to quantify feeding by upper trophic level organisms separately for the pelagic and benthic systems.

Basic information on primary production within the fjord is lacking, including information on the physical and chemical factors controlling the rate of production (e.g. light, nutrients, mixing and advection) as well as biological factors (grazing, sedimentation). Because primary production drives the pelagic system, it is critical for future modelling to couple production levels to higher trophic levels. The heterotrophic micro-organisms, important in the system, are also poorly described in Kongsfjorden. The zooplankton community is relatively well known, and a zooplankton transect down the middle of the fjord (Fig. 1b) is now

sampled annually to create a time series, which can be linked to the variability in physical factors (e.g. the North Atlantic Oscillation). However, seasonal data (i.e. winter and spring) are needed for determination of zooplankton dynamics and secondary production. There is also little information on the larger zooplankton such as krill and pelagic amphipods, which represent important food sources for some of the seabirds and marine mammals. There is a need to assess the coupling between fjord and shelf processes in order to determine the potentially large role of advection in plankton ecology.

Pelagic–benthic coupling has been estimated, using sedimentation rates for both organic and inorganic sediments. However, the advection of biomass into Kongsfjorden has not been estimated. Its contribution to the pelagic–benthic coupling and the extent to which increased glacial run-off influence the sinking of organic matter advected from the shelf remain unknown.

The benthic ecosystem is relatively well known, particularly with regard to the macroflora and fauna, but this knowledge is mainly based on data collected during the summer. Data from all seasons are needed to determine benthic production, as well as seasonal changes in community composition. A 20-year time series (F. Beuchel and B. Gulliksen, pers. comm.) indicates that there are large interannual fluctuations in macroalgae as well as longer cycles in both macroalgae and benthic fauna. There are some indications that this variability is related to climate change, but the causal relationships still need to be established. The benthic microalgal communities remain a largely unknown part of the autotrophic system, and the benthic microbial community is also poorly studied. The larger benthic organisms (i.e. megafauna, hyperbenthos and benthic fish), which are an important food source for many of the seabirds and marine mammals, are comparatively well studied, but there are still gaps in our knowledge of their abundance, biomass and production in the fjord, and little is known about the effects of changing physical factors on their distribution.

Fishes are a central part of the marine food web, and contain some key species such as the polar cod. Capelin and Atlantic cod are probably more abundant during years with large influxes of Atlantic water, but this needs to be further explored. We lack estimates of standing stocks for any of the second order consumers in the

fjord. Such data would be of great importance for food web models involving both lower and upper trophic levels. Information on the physiology of the fish fauna is essential to understand their life style and ecological constraints. Because of the sensitivity to variations in hydrographic conditions, the Arctic and boreal fish fauna in Kongsfjorden may be particularly suitable for studies of ecological effects of climate warming, but also for studies of biological, physiological and molecular adaptations to extreme environmental conditions. The knowledge available on Antarctic fishes will be useful to establish a framework for detailed studies of physiological and biochemical adaptive strategies in Arctic fishes.

For the upper trophic levels, there is a need for greater resolution in our knowledge of the temporal and spatial patterns of use of the fjord for the different species (e.g. foraging site locations and seasonal diet patterns). Updated abundance estimates for primary residents of the fjord, such as the ringed seal, are needed. The densities and distributions of prey species are poorly known for some of the important taxa, such as the polar cod and large zooplankton, and the seasonal quality of prey also needs further attention. The coupling between population dynamics and physical parameters, such as seasonal and annual variability in ice cover, needs to be better established in order to evaluate long-term fluctuations. Winter ecology studies of seabirds are also needed since it is likely that their durations of residency in the Kongsfjorden have been underestimated in this study and previously.

Concluding remarks

Kongsfjorden is already an established reference site for Arctic marine studies, and it is important to extend the current ecosystem knowledge via comprehensive long-term biological and hydrographical observations. The existing high level of understanding of Kongsfjorden and the plans for future research that are already in place make the fjord an important site for the study of climate change on high latitude marine ecosystems. As more information is assembled, and the gaps identified are filled, quantitative models for the pelagic and benthic ecosystems will be linked. The resulting whole ecosystem model can then be joined to models of climate to

make predictions concerning the effects of global warming on the Arctic marine biota. Existing evidence suggests that the response to climate change will be most rapid in the pelagic system as individuals within both the phyto- and zooplankton are short-lived. Responses in the benthos will take place more slowly, reflecting their longer lifespan, slower growth and less frequent reproduction of these larger species. With the depth of knowledge that already exists underpinning future research, there is considerable potential for Kongsfjorden to stand as a sentinel for the effects of climate change on the biota of northern Eurasian seas as well as being a key reference site for pan-European studies of biodiversity.

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