# Chapter 11 Ecological Drivers of and Responses by Arctic Benthic Communities, with an Emphasis on Kongsfjorden, Svalbard



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Abstract Knowledge on the causes and consequences that structure benthic communities is essential to understand and conserve Arctic ecosystems. This review aims to summarize the current knowledge on the effects of abiotic and biotic factors on species interactions and community traits, i.e. diversity, structure, and functioning of Arctic coastal hard- and soft-bottom habitats, with emphasis on Kongsfjorden (Svalbard). Current evidence indicates that descriptive and mensurative studies on the distribution of species prevail and few studies allow inferences on the underlying processes generating observed patterns. Furthermore, Arctic hard- and softbottom communities show some fundamental differences in their ecology. The recovery in hard-bottom communities from disturbance, for instance, takes exceptionally long (i.e. > decadal) due to slow growth and/or sporadic recruitment, while it is considerably shorter in soft-bottom communities. Also, Arctic hard-bottom communities display strong competitive hierarchies that appear negligible in communities populating sedimentary shores. This review concludes with a suggestion to shift the focus in Arctic benthos research from pattern to processes and the identification of major research gaps. These include (i) the apparent demarcation of studies

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© Springer Nature Switzerland AG 2019 H. Hop, C. Wiencke (eds.), *The Ecosystem of Kongsfjorden, Svalbard*, Advances in Polar Ecology 2, https://doi.org/10.1007/978-3-319-46425-1\_11 being devoted to either rocky or to sedimentary shores, which hamper studies on habitat connectivity, (ii) the lack of studies addressing the effects of pathogens and diseases on community ecology, and (iii) the incomplete assessment of potentially significant drivers of community ecology, such as trophic interactions, recruitment success, and competition.

**Keywords** Arctic ecosystems · Biotic interactions · Climate change · Disturbance · Polar biota · Rocky habitats · Sedimentary habitats · Succession

# 11.1 Introduction

One goal of ecology is to identify the factors and underlying processes by which the distribution of species and ultimately the structure of ecological communities are controlled in space and time. Such knowledge is particularly sought for polar ecosystems because global change is expected to be strongest at high latitudes (IPCC 2013). Predictions about, for instance, the future heat budget of the Arctic ocean indicate that its warming will be significantly above that of the global average (Serreze et al. 2009). The predicted ecological consequences of global change may be dramatic for Arctic ecosystems (IPCC 2014), which are connected by ocean currents, e.g. the West Spitsbergen Current, to the temperate zone. This connection will likely spur a warming-induced introduction of non-indigenous, cold-temperate biota to the Arctic (Krause-Jensen and Duarte 2014). As a consequence, the type and frequency of species interactions might increase and change food web structure in marine Arctic ecosystems (Kortsch et al. 2015). This will include benthic habitats because the dispersal ability of many benthic species, including sessile forms, by pelagic propagules may be sufficiently high to reach Arctic shorelines under favourable oceanographic conditions (e.g. Sirenko and Gagaev 2007; Alvsvåg et al. 2009; Matishov et al. 2012; reviewed in Renaud et al. 2015a).

While the northward extension of species ranges may affect frequency and type of species interactions in coastal, benthic communities, a warmer Arctic may also affect the interactions among species that are currently present. At higher seawater temperature, the physiological responses and demands of species will generally change, with variations among species (Doney et al. 2012). As a consequence, it can be assumed that the direction and/or intensity of interactions between resident competitors, consumers and their prey, or the effectiveness of pathogens will change. Furthermore, global warming will reduce the extent and thickness of sea ice, enhance glacial retreat, and increase riverine discharge (Polyakov et al. 2010; Sahade et al. 2015). All of these indirect effects of warming will affect the abiotic environment and disturbance regimes in which Arctic benthic communities thrive and will ultimately alter community organisation (see Grebmeier 2012 for the Arctic; Sahade et al. 2015 as an example for Antarctica).

As a prerequisite for the conservation of coastal Arctic ecosystems and the development of management strategies, it will be necessary to understand the underlying processes that modify coastal Arctic ecosystems. Their protection should be a prime interest of human society because near-shore benthic organisms provide significant services to (a) sustain coastal ecosystems, (b) protect coastlines, and (c) attenuate the effects of global climate through (i) retention of senescent matter and fixation of external energy, fueling higher trophic levels, including humans, (ii) the reduction in coastal erosion by sea-floor consolidation (Fig. 2 in Wang et al. 2012), and (iii) as a carbon sink, respectively. The major goal of this review is to provide an overview on benthic research conducted in Kongsfjorden since the synopsis by Hop et al. (2002), who collated the achievements of the initial research period preceding the year 2000. Until the review by Hop et al. (2002), the state-of-the-art for benthos research in Kongsfjorden comprised qualitative rather than quantitative information about the vertical and horizontal distribution of species. Furthermore, descriptive studies with a trophic perspective prevailed, providing fundamental information sought for the construction of quantitative ecosystem and carbon flow models for Kongsfjorden. Hop et al. (2002) also identified major research gaps. However, basic information on primary production, the role of biological factors in shaping ecological communities, and the effects of seasonal variation in abiotic and biotic conditions, especially during winter, had not been gathered by then.

The scope of this review is on the ecology of species assemblages that populate coastal rocky and sedimentary substrata in the Arctic with an emphasis on Kongsfjorden (Fig. 11.1), a flagship site of marine ecological research in the Arctic. Unless stated otherwise, we use the term coastal to refer to hard-bottom habitats from intertidal down to a depth of 30 m, i.e. within the operating range of SCUBA divers and to soft-bottom habitats down to 400 m, as this is within the typical depth range of Arctic fjords, including Kongsfjorden. Subjects with very limited or lacking information on the ecology of Kongsfjorden benthos will be supplemented by knowledge obtained in studies conducted in other Svalbard regions or, if applicable, other regions of the Arctic. Differences in research foci of rocky and sedimentary habitats entail an unbalanced presentation of research topics between both habitats in this review. Facilitation, for instance, had been studied in Arctic hard-bottom, but not in soft-bottom communities. Regarding the taxonomic scope of this review, we considered algae and invertebrates >0.5 mm in size (for micro-phytobenthos see review by Karsten et al., Chap. 8). Besides the temporal dynamics in the assemblage of benthic species, we summarize the results of studies assessing the processes that structure benthic communities rather than the spatial patterns in community structure and diversity. We present the available knowledge about the role of abiotic factors separately for rocky and sedimentary habitats, followed by studies addressing the influence of biotic factors on (i) species interactions, (ii) diversity, (iii) structure, and (iv) function of benthic communities. As a final consideration, we propose perspectives for future research on Arctic marine ecosystems.



**Fig. 11.1** Map indicating sampling sites referred to in this review from outside (**a**) and within (**b**) the Svalbard archipelago and different zones in Kongsfjorden (**c**, adopted from Hop et al. 2002): 1 =outer, 2 = middle, 3 = transitional, and 4 = inner. *HB* hard-bottom, *SB* soft-bottom

# **11.2 Rocky Habitats**

The proportion of hard-bottom habitats in Kongsfjorden is much lower than that of sedimentary habitats. Nevertheless, rocky shores are algae-dominated ecosystems with significant functions such as sites of high primary production and a sink for carbon. As bioengineers (Krause-Jensen and Duarte 2014), algae provide habitat and nursery grounds and function as a food source that sustains a diverse suite of associated fauna (e.g. Christie et al. 2003; reviewed in Bartsch et al. 2008). Much sampled study sites of hard-bottom communities in Kongsfjorden include Kvadehuken (78°58.6'N; 11°30.1'E), Kongsfjordneset (78°58.37'N; 11°29.35'E), and Hansneset (78°59.1'N; 11°57.8'E) (Fig. 11.1c). At these locations, observational and experimental long-term studies on the succession of species and temporal shifts in biodiversity have been conducted (Table 11.1).

## 11.2.1 Species Succession

The non-seasonal, continuous, and directional sequence of species replacement in newly exposed areas is referred to as primary succession while secondary succession comprises the recolonization of previously populated areas that were cleared by a disturbance (Ricklefs 1990). Overall, information on the succession of species in polar marine hard-bottom communities is extremely scarce (Dunton et al. 1982; Newell et al. 1998; Barnes and Conlan 2007) and lacking for the underlying processes. Information about research on the succession of benthic species in the Arctic is summarized in Table 11.1, but presently misses, to the best of our knowledge, intertidal rocky shores and hard-bottom areas >20 m water depth. Polar hard-bottom benthos is considered to have relatively slow rates of growth, reproduction, and, hence, low rates of colonization and recolonization (Bowden et al. 2006; Konar 2007; Zacher et al. 2007; Fricke et al. 2008). Methods for studying species succession of hard-bottom communities include placement of settlement panels (i.e. primary succession) and experimental clearing of natural substrata (i.e. secondary succession) followed by non-destructive monitoring of species abundances through (i) *in-situ* observation or (ii) underwater photography (e.g. Barnes and Kukliński 2005b; Beuchel and Gulliksen 2008; Fig. 11.2).

## 11.2.1.1 Primary Succession

The primary succession of species has been studied in subtidal hard-bottom habitats of Kongsfjorden through manipulative field experiments in conjunction with potential drivers of community structure and diversity (Fricke et al. 2008). They followed the initial 8 weeks of primary species succession on newly deployed (i.e. empty) ceramic settlement panels at 0.5 m water depth close to Ny-Ålesund harbour. During

Table 11.1	Summarizir	informa	tion about environ	mental conditions ar	lu-təs br	p of studies or	n successio	on of species	of hard-botto	m assemblages	
Studied factor	Authors	Year	Study site	Sampling method	Depth [m]	Start of experiment	Duration [y]	Seasonal timing	Temperature [°C]	Primary colonisers	Response variables
Primary succession	Schmiing	2005	Kongsfjordneset (KF)	Polyethylene tiles (ø 40 cm)	20	2002	ŝ	June– August	~ 3.6	Bryozoa, algae, polycheats	Species abundance, biomass, cover
Secondary succession	Beuchel and Gulliksen	2008	Kvadehuken (KF)	Photo quadrats $(50 \times 50 \text{ cm})$	15	1980	23	August– September	3–5	Sea anemones, tunicates, algae	Species abundance, cover
Primary and secondary succession	Fricke et al.	2008	Near Ny Ålesund harbour (KF)	Ceramic tiles (9.6 × 9.6 cm)	0.5-8	2004, 2005	1.75	August, May	0.6–6.2	Algae (Bacillariophyta), polycheats	Species abundance, cover
Primary succession	Streicher	2014	Kongsfjordneset (KF)	Polyethylene tiles (ø 40 cm)	20	2002	10	June– August	~ 3.6	Bryozoa, algae, polycheats	Species abundance, biomass, cover
Primary succession	Barnes and Kukliński	2005a, b	Southern Isfjord (IF)	Acrylic panels (15 × 15 cm)	12	2002	1	August	-1.8 to 4	Bryozoans, polychaets	Species abundance, cover
Primary succession	Kukliński et al.	2013	Adventfjorden, 3 locations (IF)	Acrylic panels (15 × 15 cm)	9	2007	1	January	-1.5 to 8.3	Bryozoans	Species abundance, cover

KF = Kongsfjorden, IF = Isfjorden



Fig. 11.2 SCUBA divers taking photo samples at a monitoring site. (Courtesy of Erling Svensen)

the first 4 weeks, opportunistic groups such as Bacillariophyta and filamentous green algae, including Urospora sp. and Ulothrix implexa, monopolized the substratum. In the course of the next 4 weeks, an additional green alga of the family Acrosiphoniaceae appeared. These pioneering species have inhibitory and/or facilitating effects on the succession of species (Fricke et al. 2008; Zacher and Campana 2008). From temperate regions it is known that, for instance, mat-forming Bacillariophyta precondition the substrate by providing UV-free space (Vinebrooke and Leavitt 1999) or by the production of extracellular polymers (Lam et al. 2005), thereby facilitating the colonization by propagules of certain algal species. In contrast, Bacillariophyta may preempt the substrate, inhibiting the settlement of e.g. red algal propagules (Huang and Boney 1985; Zacher and Campana 2008). In Kongsfjorden, primary succession of species was also followed beyond the initial phase for communities developing on ceramic settlement panels at 8 m depth. After 12 months, communities were dominated by members of the Ectocarpales (Phaeophyceae), such as Pylaiella littoralis, P. varia, and Ectocarpus siliculosus and the green alga U. implexa. Furthermore, the first sessile invertebrates were encountered at that time. After 21 months of panel deployment, communities showed a higher cover in members of the green algal class Ulvophyceae, the brown alga Dermatocelis laminariae, and invertebrates, particularly the polychaete Cireis spirillum, than 12 month old communities (Fricke et al. 2008). Despite differences in species composition, there was no significant difference in species richness between the 12 and 21 months old communities, suggesting slow assemblage of species.

To the south of Kongsfjorden, in Isfjorden (Fig. 11.1b), Barnes and Kukliński (2005b) followed the initial colonization by animals on settlement panels (225 cm<sup>2</sup>) immersed at 12 m depth. Colonists were absent during the first 3 days, but one bryozoan and several specimens of polychaetes had settled by the end of the first

week. After a year of immersion, panels were 3-11% covered with, on average, 250 individual colonists. This is at least an order of magnitude lower than the coverage on most non-polar rocky shores (Barnes and Kukliński 2005b), but higher than what has been recorded for an Antarctic locality (Pearse and Pearse 1991). Most individual colonists (80–93%) were sessile tube-dwelling polychaetes (Spirorbis tridentatus), but bryozoans constituted the most speciose group of colonizers. According to Barnes and Kukliński (2005b), species richness (i.e. 20 taxa) was as high as or higher than in many similar colonization studies along the north Pacific or north Atlantic coasts. Using a similar set-up, Kukliński et al. (2013) followed species succession in Adventfjorden on settlement panels deployed in January (i.e. during the polar night) for 1 year. A total of 22 taxa of primary colonizers were recorded. The first settlers were mainly polychaetes, while the last settlers comprised hydroids, cheilostome bryozoans, and spirorbid polychaetes, appearing in February and November, respectively. The settlement and rapid increase in the density of some groups of organisms (e.g. polychaetes and cirripeds) were positively correlated to the timing of blooming phytoplankton.

Later stages of primary succession of hard-bottom communities were studied near Kongsfjordneset in the middle zone of Kongsfjorden (Fig. 11.1c) at 20 m depth from 2002 to 2004, using polyethylene panels (Schmiing 2005). Highest densities of recruits were recorded after 1 year (up to 20,600 ind. m<sup>-2</sup>) with strongly declining density during the second year (2-4,000 ind. m<sup>-2</sup>) and an increase to an average of about 7,700 ind. m<sup>-2</sup> after the third year of panel incubation. A different pattern was observed in biomass, which was lowest after the first year (4.2 g dry mass  $m^{-2}$ ) and increased to 8.3 and 8.7 g dry mass m<sup>-2</sup> after the second and third year, respectively. The differences in recruit density between years could be explained by the gradual decline in the abundance of juvenile barnacles and mobile species over time during which the density of bryozoans and algae increased. Bryozoans (24 species) dominated the community in abundance and biomass towards the end of the monitoring. Schmiing (2005) concluded that, at least initially, communities developed comparatively slowly. Using the same set-up, Streicher (2014) analyzed annual photos taken between 2002 and 2012 (Fig. 11.3a-f). He found 32 taxa on the panels, indicating relatively species-poor communities compared to the 75 taxa encountered by Schmiing (2005). This difference in taxon richness may be partly due to different sampling methods (in-situ observation vs. photography) (Jørgensen and Gulliksen 2001). Streicher (2014) reported on a significant change in species composition of the coralline algae-dominated community in the course of the 10-year study (Fig. 11.3a-f). Some taxa showed a monotonical increase in abundance (i.e. algae, anthozoans, polychaetes, and chitons), while the abundance of other taxa (bryozoans, echinoderms, gastropods, and crustaceans) was without trend and highly variable between years. Colonization by sponges and hydrozoans did not occur until several years after panel deployment. The findings by Streicher (2014) principally corroborate results of studies indicating a slow succession of Arctic hard-bottom communities (Fig. 11.3g-l; Beuchel and Gulliksen 2008; Konar 2013). The extremely low abundance of presumably competitive superior species such as the sea anemones Urticina eques and Hormathia nodosa on 10-year-old settlement panels indicates that succession had most likely not reached a climax stage by then.



**Fig. 11.3** Species succession on hard-substrates. Primary species succession on white polyethylene panels (40 cm  $\emptyset$  = 1256 cm<sup>2</sup> surface area) deployed at Kongsfjordneset for 2 (**a**), 4 (**b**), 7 (**c**), 9 (**d**), 10 (**e**), and 12 years (**f**) of exposure (Streicher 2014). Secondary succession on 2500 cm<sup>2</sup> submerged rock face at Kvadehuken after 1 (**g**), 3 (**h**), 4 (**i**), 5 (**j**), 7 (**k**), and 10 years (**l**) of initial clearing (Beuchel and Gulliksen 2008)

#### 11.2.1.2 Secondary Succession

We are aware of only two studies addressing the secondary succession of species on hard substrata in Kongsfjorden. Fricke et al. (2008) recorded the initial period of secondary succession (i.e. 8 weeks) of benthic communities developing for 12 or 21 months at 8 m water depth on ceramic settlement panels after their transplantation to 0.5 m water depth. Panel transplantation simulated an environmental disturbance related to the break-up of sea ice cover. The species composition of

transplanted communities changed significantly, but some effects were dependent on community age. Four weeks after transplantation of the 12 months old communities, Bacillariophyta abundance increased, while brown algae had disappeared and the abundance of green algae was strongly reduced. These significant changes in species composition resulted also in a significant reduction in species richness. During the next 4 weeks, macrobenthic biota started to recover. For instance, the abundance of sessile invertebrates, mainly the hydroid *Obelia dichotoma*, increased greatly. At the same time, the abundance of Bacillariophyta declined significantly. While transplantation did not affect species richness of 21 months old communities, their species composition was similarly affected by this treatment as was that of 12 months old communities. A species-specific acclimation potential and capacity to recover from stress were regarded as structuring mechanisms of species composition. Bacillariophyta, for instance, seemed to be more tolerant than algae to the near surface conditions in this experiment (Fricke et al. 2008).

In a long-term study on secondary species succession, most visible organisms were scraped off the subtidal bedrock at Kvadehuken (Fig. 11.1c) at the start of the study in 1980 (Beuchel and Gulliksen 2008). Subsequently, the succession of species was documented through annual photographic surveys on cleared (Fig. 11.3g-l) and untreated plots (Fig. 11.2). At the species level, the conspicuous sea anemones U. eques and H. nodosa recovered from the disturbance after 8 to 10 years. At the community level, where 23 taxa of epifauna were recorded, significant differences between cleared and untreated areas prevailed for the first 13 post-disturbance years (Beuchel and Gulliksen 2008). Their study suggests that different recolonization patterns for individual species were related to differences in their longevity, rate of maturity, predation pressure, and recruitment success. No climax stage was reached by the benthic community at Kvadehuken, which may be explained by frequent disturbance events (e.g. ice-scour and storm events), which could keep the community at an early to intermediate successional stage (sensu Huston 1979, this review Sect. 11.2.3.4 Disturbance). The length of time required to recolonize cleared bedrock at Kvadehuken indicates that recovery from disturbance takes longer in Arctic communities than in those from lower latitudes (e.g. Sousa 1979). This notion is corroborated by Konar (2013) who studied secondary species succession of experimentally turned boulders on the coastal Beaufort Sea of Alaska. She showed in her experiment that <10% of completely cleared boulder surfaces were recolonized after 7 years. Partial clearings, however, recovered substantially within 4 years due to vegetative regrowth of sponges and encrusting coralline algae.

In conclusion, a very limited number of studies on the succession of species have been conducted in Arctic hard-bottom habitats. As an incipient trend, species succession of Arctic benthic communities appeared to be much slower than in temperate areas (Dunton et al. 1982). In addition, coastal Arctic benthos experiences high levels of disturbance (Dayton 1990; Grebmeier and Barry 1991) due to increased physical (e.g. ice-scour), biological (e.g. consumer activities), and anthropogenic disturbances (Jewett et al. 1999). Consequently, Arctic communities are recurrently set back to earlier successional stages. The slow succession in combination with frequent disturbances results in a low recovery potential of Arctic benthos, which should heighten the vulnerability of coastal Arctic ecosystems to anthropogenic disturbances, such as effluent discharge (Krumhansl et al. 2015). Current knowledge on the succession of species on Arctic rocky shores is, however, insufficient to draw strong conclusions. Future research on species succession will benefit from placing clearance studies into a larger context. The performance of clearance studies at different water depths or distances to sites affected by anthropogenic stress (e.g. melting glaciers resulting from industry-related global warming), will improve our ability to predict the consequences of climate change on coastal Arctic ecosystems and unravel the underlying processes of species succession.

# 11.2.2 Long-Term Change

Comparative and monitoring studies were used to assess historic changes in Kongsfjorden hard-bottom communities. Repeating the 1996–1998 benthos survey at Hansneset (Hop et al. 2012; Voronkov et al. 2013, Fig. 11.1c) in 2012–2014 aimed to unravel changes along a depth gradient (Fredriksen et al. 2014; Bartsch et al. 2016; Paar et al. 2016). For documentation of gradual changes, species abundance has been recorded annually at Kvadehuken since 1980 (Beuchel and Gulliksen 2008) and at Kongsfjordneset since 2002 (Streicher 2014).

## 11.2.2.1 Comparative Studies

Overall, growth (only algal species), total biomass, and species richness (only fauna) was higher in 2012–2014 and species composition had changed considerably between surveys conducted in the periods 1996-1998 and 2012-2014. Algal biomass peaked in the 1996–1998 survey at greater depth (i.e. 5 m) than in the 2012– 2014 survey (i.e. 2.5 m), when it had increased almost fivefold (Bartsch et al. 2016). There was a general upward shift in the lower depth limit of most dominant brown algal species by ca. 2–3 m (Fredriksen et al. 2014; Bartsch et al. 2016). Across the entire depth gradient, algal biomass increased by 70% since 1996–1998, although the biomass of annual species declined during this period (Bartsch et al. 2016). The total number of species of algae was comparable between 1996-1998 (i.e. 62) and 2012-2014 (i.e. 58), but not the composition of species as only 42 species were present in both investigations. Four species of red algae that were commonly found in 1996–1998 were absent at Hansneset in 2012–2014, while two red algal species were newly recorded (Fredriksen et al. 2014). In the upper littoral zone (intertidal down to 1.5 m water depth), the number of algal species increased from 20 to 45 between both surveys, including two and seven new records of green and brown algae, respectively (Fredriksen et al. 2014). Similarly to algae, faunal biomass and secondary production increased tenfold at shallow water depth (2.5-5 m) between 1996-1998 and 2012-2014 (Paar et al. 2016). Moreover, animal biomass and secondary production increased with increasing water depth in 1996-1998, but decreased along the depth gradient in 2012–2014. These trends in temporal change of biomass and diversity of Kongsfjorden hard-bottom benthos were corroborated by Węsławski et al. (2010) for intertidal communities sampled in southern Spitsbergen (i.e. Hornsund Fjord and the adjacent Sørkappland coast, Fig. 11.1b) in 1988 and in 2007–2008. Their study revealed "a two-fold increase in species numbers, a three-fold increase in the biomass of macroalgae, and an upward shift in algal occurrence (mainly *Fucus distichus*) on the coast." However, new species records were not reported by Węsławski et al. (2010). The authors concluded that the relatively higher stability in intertidal community structure in Hornsund Fjord than in Kongsfjorden was a result of the isolation of the former from warm Atlantic waters (Węsławski et al. 2010).

The authors of the above-mentioned comparative studies suggest that the warming of the Arctic is most likely the ultimate cause for the observed changes in biomass maxima, species distribution and composition of hard-bottom communities. The reduction in ice-scour was considered as the proximate reason for an increase in biomass at shallow water depth, as Kongsfjorden has been free of fast ice during most of the last decade (Pavlova et al., Chap. 4). The upward shift in the vertical distribution of many types of algae, including kelp species, was also attributed to warming, as the glacial meltdown is expected to lead to higher loads of terrigenous particles and hence, reduced solar irradiance at depth in coastal waters. The upward shift of kelp may have indirectly caused the increase in secondary production and animal biomass at shallow water depth because kelps are an attractive habitat for a large number of associated fauna in Kongsfjorden and other Svalbard fjords (Lippert et al. 2001; Włodarska-Kowalczuk et al. 2009, this review Sect. 11.2.4.3 *Epibiosis*).

#### 11.2.2.2 Monitoring Studies

The hard-bottom communities at Kvadehuken, Kongsfjorden and further north in Smeerenburgfjorden, Svalbard (Fig. 11.1b,c) have been monitored for more than 30 years. In both fjords, community structure was relatively stable during the 1980s and early 1990s. After this period, however, biodiversity increased and this was accompanied by a decline in the abundance of actinarians and increase in density of the sea urchin *Strongylocentrotus droebachiensis* in combination with the abrupt and substantial formation of dense carpets of brown algae (mainly *Desmarestia* spp. in Kongsfjorden). As a consequence of this regime shift, average algal cover increased from 8% to 40% in Kongsfjorden and from 3% to 26% in Smeerenburgfjorden (Kortsch et al. 2012).

# 11.2.3 Abiotic Factors in Hard-Bottom Habitats

The effects of solar irradiance on community traits were studied most thoroughly in hard-bottom habitats. This bias in research effort may be due to the strong dependency of algal growth and survival to the available quality and quantity of photosynthetic active radiation (PAR). Algae function as bioengineers by attracting invertebrates through the provision of food, shelter, and settlement substratum and ultimately the predators of these invertebrates (Christie et al. 2003; Watt and Scrosati 2013; Krause-Jensen and Duarte 2014). The exponential attenuation of PAR with water depth may explain why water depth was the most important environmental driver in the species composition of hard-bottom fauna (Voronkov et al. 2013) or sea-ice break-up for the regime shift in marine benthos (Kortsch et al. 2012). Compared with the research effort on Arctic sedimentary habitats (see below), it seems that less experimental evidence has been accumulated on the disturbance effects of icebergs and sedimentation stress on the structure and diversity of Arctic hard-bottom communities.

#### 11.2.3.1 Temperature

Many long-term studies reported on the relation between macrobenthos change and indicators of climate change. In these studies, temperature is considered one of the most important environmental drivers of ecological change. Even though most of the species observed in Arctic waters thrive at a relatively wide temperature range (Wesławski et al. 1993), a change of less than 2 °C in sea surface temperature may trigger a significant reorganization of benthic community structure (Mueter and Litzow 2008; Kortsch et al. 2015; Renaud et al. 2015b). Temperature may be also one of the major factors affecting hard-bottom communities in Kongsfjorden because a missing sill facilitates the inflow of the relatively warm Atlantic water transported by the West Spitsbergen Current into Kongsfjorden. A documented strengthening of the West Spitsbergen Current (Saloranta and Haugan 2001) is considered as one of the main reasons of the above mentioned faunal and floristic changes in Kongsfjorden benthos (Beuchel et al. 2006; Fredriksen et al. 2014; Paar et al. 2016). During the winter of 2005-2006 for instance, substantial inflow of warmer water of the West Spitsbergen Current changed the hydrographic situation to a "warm mode" with year-round water temperatures >0 °C (Cottier et al. 2007). While direct evidence on the effects of altered temperature regimes on Kongsfjorden hard-bottom benthos is missing, Beuchel et al. (2006) showed that species diversity was negatively correlated to shifts in the North Atlantic Oscillation (NAO). An increase in biodiversity of hard-bottom communities, for instance, was observed in Kongsfjorden as well as Smeerenburgfjorden between 1994 and 1996 at a time when the NAO shifted to a negative mode (i.e. an increase in seawater temperature). Besides the possible direct effects of higher seawater temperature on algal and animal physiology, warming results in reduction of sea ice cover, and glacial retreat that indirectly frees up colonization areas and alters salinity, irradiance, disturbance, and sedimentation regimes. In the course of global warming, cold-temperate biota may succeed Arctic species (Węsławski et al. 2010, 2011), as distribution ranges of the former are expected to shift northward (Müller et al. 2009; Krause-Jensen and Duarte 2014; Kortsch et al. 2015).

## 11.2.3.2 Salinity

During the polar summer, large amounts of freshwater enter Kongsfjorden through glacial and river drainage, generating vertical and horizontal salinity gradients. While studies on species-specific salinity tolerances exist e.g. for kelps (Karsten 2007), studies explicitly assessing the influence of salinity on hard-bottom communities are to our knowledge missing. Kukliński et al. (2013) argued that low salinity reduced survival of polychaete larvae in Adventfjorden (Fig. 11.1b), which is highly influenced by ice and freshwater discharge from rivers. Since the response of this and other studies that advocate salinity effects (e.g. Fricke et al. 2008) were confounded by concomitantly changing environmental factors such as irradiance or sedimentation rate, it is impossible to conclude on the magnitude and direction of salinity effects at the community level.

#### 11.2.3.3 Irradiance

Polar organisms encounter unique, extreme seasonal changes in light conditions. In particular photoautotrophic organisms have to cope with long periods of either complete lack or continuous supply of light as an essential resource, which is why polar algae are low-light adapted, yet tolerant to high light (Zacher et al. 2009). While physiological adaptions of algae to minimum light conditions have been well described (reviewed in Gómez et al. 2009; Bischof et al., Chap. 10), information about seasonal irradiance effects at higher levels of ecological organization is missing. Existing evidence suggests, however, three environmental factors that mainly affect light regimes in the Arctic with consequences on the structure of benthic communities.

Firstly, physical processes alter the quality and quantity of solar radiation with water depth, resulting in an exponential gradient in the available photon density and energy. Algae are confined to live on PAR-exposed hard substrata, including bedrock, scattered stones in sedimentary habitats, and biological or anthropogenic structures. Herein, different groups of algae deploy different photosystems to capture solar radiation with different efficacy at a given depth, which causes vertical bands that are dominated by different algal assemblages and associated fauna. This light-mediated vertical zonation of hard-bottom communities and temporal changes in zonation patterns have been documented for Kongsfjorden (Hop et al. 2002, this review Sect. 11.2.2 Long-Term Change).

Secondly, tidal glaciers and river discharge in Arctic fjords have a strong influence on light attenuation due to the release of terrigenous particles (Zacher et al. 2009). This generates strong spatial gradients in water transparency, along which turbidity decreases with increasing distance from tidal glaciers and river mouths. In addition, temporal changes in the concentration of dissolved and particulate matter lead to variation in water transparency through time (Hanelt et al. 2004). In Kongsfjorden, for instance, the depth of the euphotic zone (>1% of surface PAR) decreases at Hansneset from 18–24 m in spring to 6–7 m in summer (Hanelt et al. 2004; Hop et al. 2012). In the Stefansson Sound Boulder Patch site (Beaufort Sea, Alaska), kelp grows slower at shallower sites because these are closer to the mouth of a major river delta, which carries considerable amounts of turbid water to the boulder patch compared to sites at greater depth, which are further away from the river delta and are characterized by clearer water (Aumack et al. 2007). The presence of kelp and other canopy-forming algae may alter the physical environment for the benthic sub-canopy community in terms of irradiance, although empirical evidence for this is missing for polar systems (Bischof et al., Chap. 10). Therefore, changes in the light regime are likely to be reflected at the community level, affecting function (e.g. productivity) or structure of the understory benthos. Observational evidence for light-driven community responses on Arctic rocky shores comes from the study by Kortsch et al. (2012). The authors report on an abrupt five to eight-fold increase in algal abundance in two Arctic fjords (Kongsfjorden and Smeerenburgfjorden) during a 30 y period in which ice-cover (i.e. the third major factor affecting light regimes in polar waters) got gradually reduced. Their study suggested that reduced ice cover will increase PAR, hence supporting algal growth and abundance (this review Sect. 11.2.2 Long-Term Change). This interpretation is corroborated by Clark et al. (2013). According to their models, the interaction of relative small changes in a seasonally variable factor (i.e. solar irradiance) with step-change events (i.e. sea-ice break-up) are likely to induce tipping points, by which shallow polar benthic communities may shift from a heterotrophic to an autotrophic state (Clark et al. 2013).

Kelp species were reported to grow mainly during the dark winter period, by mobilization of carbohydrate deposits from summer photosynthesis (Dunton et al. 1982). Some animal species in the Alaskan Arctic showed that during winter there are shifts in the dependency of carbon from phytoplankton to kelp sources (Dunton and Schell 1987). Hence, kelp growth may fuel benthic food webs with carbon during the polar night, though empirical support on this and potentially other ecological consequences of winter-grown kelp tissues are missing (Berge et al. 2015b). Experimental evidence of irradiance effects on Arctic benthic communities from manipulative experiments is scarce. Fricke et al. (2008) showed that algae bleached and died within 4 weeks after transplantation from 8 to 0.5 m water depth in Kongsfjorden. The effects of near-surface conditions were different for 1-year than for 2-year old assemblages, indicating that the timing of altered irradiance levels may be important for the magnitude of light effects. In this transplantation experiment, however, several factors changed besides irradiance levels (e.g. wave exposure), which may also affect the species composition, making conclusions about irradiance effects at the community level difficult. The only experiment manipulating light conditions for field-grown benthic assemblages in the Arctic is the study by Fricke et al. (2011). In contrast to the many reported detrimental UV-effects at the physiological level (reviewed in e.g. Häder et al. 2015), their study revealed few UV-effects on community structure. Younger communities were more sensitive to UV-B radiation than older ones, which may be due to the protective function of some community members, e.g. diatoms, for UV-sensitive taxa. Despite the limited experimental evidence, it becomes apparent that irradiance can affect the structure of benthic communities, but these effects are dependent on other factors (e.g. successional age) and will not affect all community members in the same way.

#### 11.2.3.4 Disturbance

Sea Ice

The near-shore is one of the most disturbed marine habitats worldwide. As a disruptive force, ice-scour is an important structuring factor for Arctic coastal benthic communities (Wesławski et al. 1993; Barnes 1999; Gulliksen and Svensen 2004; Sahade et al. 2004). During winter, only the zone of the coast above the high water line freezes solidly, forming an ice-foot (Ellis 1955). While the latter may physically protect freezing-resistant algae, it also makes colonization of hard substrates by algae and macrofauna extremely difficult (Svendsen 1959; Keats et al. 1989; Barnes 1999; Zacher et al. 2009). Estimates indicate that the total number of macrozoobenthic species in the hard-bottom intertidal of Svalbard (Wesławski et al. 1993; Szymelfenig et al. 1995), Baffin Island (Ellis 1955), Bjørnøya (Wesławski et al. 1997), and Greenland (Sparck 1933; Madsen 1936; Ellis 1955) does not exceed 100 species (Wesławski et al. 2011). On rocky shores (down to depths of a few metres), ice-scour impedes persistent macrobenthos colonization and limits organisms to ice-protected areas, such as crevices and small rock pools (Ellis and Wilce 1961; Zacher et al. 2009; Hop et al. 2012). As a result, biomass is considerably reduced on the exposed coastline (Svendsen 1959; Wilce 1959; Krapp 2002). At ice-disturbed locations (down to 2.5 m water depth), annual and pseudo-perennial algae (in the latter, parts of the thallus are cast off every year) survive the winter as microscopic stages or rhizoidal cushions, which are characterized by high growth rates and short resilience times (Keats et al. 1985; Wiencke et al. 2007; Zacher et al. 2009; Hop et al. 2012). Locations sheltered from drifting ice, such as Hansneset (Fig. 11.1c), are characterised by higher macroalgal species richness in the upper sublittoral zone than ice-exposed sites (Wiencke et al. 2004; Włodarska-Kowalczuk et al. 2009; Hop et al. 2012). The climate-induced reduction of fast ice (e.g. Pavlova et al., Chap. 4) and ice-scouring have also been proposed as the most likely causes for the observed increase in algal biomass and species richness in Kongsfjorden during the last 15 years (Fredriksen et al. 2014; Bartsch et al. 2016).

In Kongsfjorden, icebergs and smaller pieces of ice (i.e. bergy bits, *sensu* Armstrong et al. 1966) calve from five tidewater glaciers (e.g. Dowdeswell and Forsberg 1992), including Kongsbreen (Fig. 11.1c), which is the most active glacier in the Svalbard archipelago (Lefauconnier et al. 1994). Principally, scouring frequency is negatively correlated with water depth, i.e. shallow zones are more frequently disturbed by ice-scour than deeper areas (Dowdeswell and Forsberg 1992; Laudien et al. 2004, 2007).

Studies on the effect of ice on sublittoral hard-bottom communities below 5 m water depth are still lacking from Kongsfjorden. In this fjord, signs of ice-scour on

rocky shores are mainly found at Hansneset (J. Laudien pers. obs.), where icebergs scour small, horizontal areas of bedrock. Experimental removal of benthos from rocky shores, simulating the effects of a physical disturbance like ice-scour indicates that complete recovery of these communities may take more than a decade (this review Sect. 11.2.1.2 Secondary Succession).

#### Wave-Exposure

Qualitative and quantitative information about the effects of waves on hard-bottom benthos is missing. Kukliński et al. (2006) recorded more diverse and species-rich bryozoan assemblages on large rather than on small boulders. As a possible explanation for this pattern, they proposed a higher wave-induced turnover rate of small boulders, thereby resetting the colonization process more frequently on small than on large boulders.

## Submarine Rock Avalanches

Knowledge on the impact of substrate movements on benthic communities below the low-salinity surface water layer is scarce and mainly covers ecological effects on soft-bottom communities (e.g. Okey 1997). However, substrate sliding is a common event not only in the Arctic (e.g. Hjelstuen et al. 2007), but also in all coastal and continental slopes including a large range of types and scales of seafloor disturbances (e.g. Schuster and Highland 2007). These range from the movement of a few grains to movements of hundreds of square kilometres and disturbances may be very variable in intensity, as well as in their temporal and spatial range (Okey 1997). Submarine rock avalanches destroy biota, but they also open up new space, which may be colonized subsequently by benthic communities. Timing and size of the disturbed area are important factors modulating the colonization process and diversity patterns (e.g. Gutt and Piepenburg 2003).

Near Kvadehuken (Fig. 11.1c), the scour of a submarine rock avalanche was discovered during an investigation using a remotely operated vehicle (ROV) in 2009 (J. Laudien unpubl. data). In a 20 m wide area, the sessile fauna was destroyed from 75 m water depth down to at least 200 m, i.e. at the depth where the ROV transect ended. Only mobile macrofauna was observed in the impacted zone, the green sea urchin *S. droebachiensis* being, by far, the numerically dominant species. No algae were recorded on the disturbed barren ground, in contrast to the surrounding zone (Laudien and Orchard 2012). To the best of our knowledge, no further information on the impacts of rock falls or avalanches in Kongsfjorden exists. Using information on geological characteristics of the sea floor (e.g. lithology, faults, slope, or topography) and coast (e.g. morphology and rivers) may facilitate detection of rock-fall impacted benthos (e.g. Kamp et al. 2008) and spur research about the ecological effects of this type of disturbance.

#### Sedimentation

Global warming causes glacial retreat and increased river drainage that result in higher sedimentation loads that affect hard-bottom organisms. Sedimentation reduces access of sessile organisms to their resources by, for instance, clogging mouth parts of suspension feeders (Torre et al. 2014), covering photosynthetic active surfaces of algae (Chapman and Fletcher 2002), or increased light attenuation (this review Sect. 11.2.3.3 *Irradiance*). The distance to tidal glaciers should generate a gradient in sedimentation rate, along which sedimentation impact diminishes with increasing distance from a glacier (Holte et al. 1996; Voronkov et al. 2013). We found no studies assessing the effects of sedimentation on entire rocky shore communities. Ronowicz et al. (2008) reported on lower diversity, frequency of occurrence, and sexual output of hydroid assemblages growing epiphytically on kelps near-by than further apart from a tidal glacier in Hornsund Fjord (Fig. 11.1b).

# 11.2.4 Biotic Factors in Hard-Bottom Habitats

## 11.2.4.1 Consumers

Grazers and predators strongly alter benthic community structure and functioning in non-polar ecosystems (e.g. Paine 2002; Estes et al. 2011). For Arctic hard-bottom habitats, however, little information exists on consumer feeding preferences and community responses to consumption.

## Primary Consumption

The study by Wessels et al. (2006) is to our knowledge the only systematic assessment of feeding preferences for herbivores living in Arctic habitats. This study suggests that only two species of the algae-associated fauna, i.e. the amphipod Gammarellus homari and the green sea urchin S. droebachiensis significantly feed on algae. While G. homari preferred delicate red algae, S. droebachiensis preferably consumed leathery kelps (Fig. 11.4). These feeding preferences were, however, not reflected by fatty acid trophic markers, which may be due to low lipid content in grazers or strong fatty-acid modification during algal digestion (Wessels et al. 2012). In contrast to seaweeds in Antarctica (Amsler et al. 2009), Wessels et al. (2006) found few Arctic species of algae (e.g. Ptilota gunneri and Desmarestia viridis) to be chemically defended against herbivores and that G. homari, but not S. droebachiensis consumption appeared to be deterred by morphological as well as tissue-specific algal traits. In the middle zone of Kongsfjorden (Fig. 11.1c), lush algal communities dominate the shallow rocky shores (Hop et al. 2016), suggesting that herbivores are unable to control algal biomass throughout the fjord. The notion of negligible grazer effects on Arctic benthos is corroborated by the study of Konar



**Fig. 11.4** Rocky shores. Main forms of documented (solid line) and hypothesized/scarcely observed (stippled line) biotic drivers of coastal (<30 m) Arctic hard-bottom communities. Consumption by (1) avian predators on benthic invertebrates, (2) benthic grazers on seaweeds, and (3) scavengers such as the crab *Hyas araneus* or the gastropod *Buccinum undatum* on carrion; (4) interference competition among encrusting species (mainly bryozoans); (5) invertebrate and seaweed epibionts on kelp surfaces; (6) associational defence in trophic interactions; (7) recruitment of seaweeds and invertebrates. Line width indicates relative magnitude of effects

(2007) that demonstrated low recolonization on cleared surfaces of caged and uncaged boulders. Nevertheless, persistence of algae-denuded areas in the presence of urchins in Kongsfjorden (Molis et al. 2008) and other sub-Arctic habitats (e.g. Sivertsen 2006) suggest that *S. droebachiensis* consumption will locally maintain barren grounds. The activity of consumers has also been hypothesised by Beuchel and Gulliksen (2008) and Streicher (2014) to be responsible for slow recolonization of rocky areas, although consumer abundance was not manipulated in these studies to draw thorough inferences.

## Secondary Consumption

Knowledge on predator-prey interactions of Arctic hard-bottom habitats is extremely scarce. The spider crab (*Hyas araneus*) and the whelk *Buccinum* spec. were observed feeding on fish bait (Fig. 11.4; Markowska et al. 2008) and both species are trophically classified as omnivorous (Legeżyńska 2001; Kaczmarek et al. 2005). The field study by Lippert and Iken (2003) assessed the food value of abundant sessile or sluggish invertebrate species for the natural suite of consumers of Kongsfjorden

hard-bottom habitats. Their study showed that the natural assemblage of consumers preferred fish (control food) to invertebrate food. This pattern was principally confirmed in laboratory assays using the non-native sea star *Asterias rubens* as consumer (Lippert and Iken 2003). Lack of preference for the naturally abundant invertebrates may not necessarily result from anti-predator defences, but could also be explained by a relatively high nutritional value of the control food. The study by Lippert et al. (2004) corroborates the notion that anti-predator defences may have been rarely evolved in prey species living on Arctic rocky shores as a result of low predation pressure. Yet, Lippert et al. (2004) only tested the amphipod *Anonyx nugax* as an Arctic predator. Hence, more predatory species need to be tested before generalizations about the frequency of anti-predator defences in and the level of predation pressure on Arctic prey can be inferred.

#### Food Webs

A large research effort has been undertaken to characterize food webs of the Arctic Ocean (reviewed in e.g. Wassmann et al. 2006; Renaud et al. 2008; Kedra et al. 2015). Studies using, for instance, biochemical markers, such as stable isotopes or fatty acids revealed qualitative descriptions of the structure of numerous local Arctic food webs (e.g. Renaud et al. 2011; McMeans et al. 2013). Although >300 food web studies have been conducted, the general processes governing the structure of Arctic food webs are still not well understood (Kedra et al. 2015). To advance from patterns towards a mechanistic understanding of food webs, several limitations in the research of Arctic food webs have to be overcome. Firstly, spatial limitations exist as studies collating large-scale data sets are missing and there is a strong bias in regional research efforts. For instance, more than 20% of benthic food web studies were conducted in the Canadian Arctic (Kedra et al. 2015). Secondly, taxonomic limitations occur as the number of species considered in food web studies may represent a relatively small fraction of the total species pool. The study by McMeans et al. (2013), for instance, included just four benthic species that dwell on rocky shores. Thirdly, temporal limitations are clearly apparent as few food web studies were conducted during the polar night (but see Berge et al. 2015b; Morata et al. 2015). Fourthly, methodological limitations exist as consistent food web data are vet missing (Kedra et al. 2015). Last but not least, there are conceptual limitations as empirical manipulations in the laboratory and in the field are required to elicit basic (e.g. feeding preferences and consumption rates) and more advanced information (e.g. density-dependent or indirect consumer effects) that drive consumer-prey interactions. The structuring role of the non-consumptive effects of predators (i.e. predation risk) and particle consumption of plants/seaweeds by grazers for benthic food webs, which receive growing attention in non-polar ecological research (Peckarsky et al. 2008), has been thus far neglected in Arctic community ecology research.

#### 11.2.4.2 Facilitation

Facilitation denotes a biological interaction, which is, directly or indirectly, beneficial to at least one participant without being detrimental to the other organism (Bruno et al. 2003). Until recently, facilitative processes have been largely unanticipated and neglected by ecological theory, though necessary for a more integrative understanding of the drivers of community structure and function (Bruno et al. 2003). Positive interactions between Arctic species are known from observational and experimental studies. Seaweeds may serve a species-rich associated fauna as shelter against consumers, substrate, or improve access to food sources, e.g. for filter feeders living attached to kelp blades (this review Sect. 11.2.4.3 *Epibiosis*). A temperature-induced increase in algal biomass in two Svalbard fjords, for instance, was accompanied by higher invertebrate abundance (Kortsch et al. 2012), suggesting that algae facilitated invertebrate subsistence. Teichert et al. (2012) observed that the sheet-like coralline red algae seem to host 55% of the organisms observed in their study sites at Nordkappbukta, Svalbard (see also Chenelot et al. 2008, 2011 for detailed descriptions on corraline algae ecology from the Aleutian Islands). The associated fauna seeks refuge by either living in the gaps between or inside hollow parts of the rhodoliths. By their provision of microhabitats, rhodoliths may enhance diversity in areas of low complexity and, thus, act as ecosystem engineers (Teichert et al. 2014). The rhodoliths themselves profit from giving shelter to grazers such as the chiton Tonicella rubra because grazers remove the algal epibionts from the surface of rhodoliths (Teichert et al. 2012). Moreover, associational defences have been documented in Kongsfjorden. There, multi-year persistence of species-rich patches dominated by the kelp A. esculenta on an urchin-barren was mediated by the presence of the brown alga D. viridis (Molis et al. 2008). Evidence from field experiments suggests that the presence of the chemically defended D. viridis reduced the density of S. droebachiensis, which has been shown to readily consume A. esculenta (Wessels et al. 2006). High concentration of sulphuric acid inside D. viridis vacuoles generate pH levels as low as 0.7 (Pelletreau and Muller-Parker 2002) affecting the direction and speed of urchin movements (Molis et al. 2008). Facilitation may also occur across Arctic ecosystems when coastal benthic food chains receive seabird-mediated support from pelagic production. Zmudczyńska-Skarbek et al. (2015) reported that seabirds may fertilize the coastal benthos in the vicinity of a mixed colony of Brünnich's guillemots (Uria lomvia) and black-legged kittiwakes (Rissa tridactyla) in Isfjorden (Fig. 11.1b). However, seabird-derived nutrient enrichment did not affect algal production directly. Rather seabirds indirectly enhanced, at least partly, the supply of food for benthic secondary consumers such as the hermit crab Pagurus pubescens via fertilization of phytoplankton, which is consumed by suspension feeders, which are preyed upon by P. pubescens.

#### 11.2.4.3 Epibiosis

Epibiosis is the facultative association between two organisms, in which one, i.e. the epibiont, lives attached to the surface of the other organism, i.e. the basibiont (Wahl 1989). Epibiosis is a typical, though not exclusive phenomenon in aquatic environments that incurs a tight interaction between organisms due to spatially close bonds, which may has neutral, positive, or negative effects on the performance of at least one of the associates (Wahl 1989; Karez et al. 2000). There is anecdotal information on epibiosis from the rocky intertidal of Kongsfjorden (Hansen and Haugen 1989; Kukliński et al. 2006). Almost all studies about epibiosis on Arctic rocky shores looked at subtidal algae, mainly kelps (Fig. 11.4), fouled by bryozoans as the most speciose group of epibionts, followed by polychaetes and hydroids (Rozycki and Gruszczyski 1986; Lippert et al. 2001; Carlsen et al. 2007; Włodarska-Kowalczuk et al. 2009). In Hornsund Fjord (Fig. 11.1b), a total of up to 308 animal species may live on kelps, at a mean of 11.5 and a maximum of 47 species on individual kelps (Włodarska-Kowalczuk et al. 2009). Neither species richness nor composition of (i) the total epifauna (Lippert et al. 2001; Włodarska-Kowalczuk et al. 2009), (ii) bryozoans (Carlsen et al. 2007), or (iii) hydroids (Ronowicz et al. 2013) varied significantly between different algal species, suggesting low host-specificity of the algal-attached macrofauna. The richness of epibiotic animal species depended on algal morphology, was variable among kelp parts (Lippert et al. 2001), but independent of algal age (Ronowicz et al. 2008). More animals exist on- and inside the holdfast of kelps than on the lamina or stipe, presumably as a consequence of habitat persistence and superior protection by a holdfast against consumers and wave action (e.g. Włodarska-Kowalczuk et al. 2009).

## 11.2.4.4 Pathogens and Parasites

The presence of pathogens and parasites are a fundamental and ubiquitous component of ecological systems that helps keeping the abundance of interacting species balanced (Wilson et al. 2013). Despite the occurrence of, for example, parasitic trematodes throughout the Palearctic, comprehensive parasitological research is thus far missing for the coastal habitats around Svalbard (Rokicki 2009). Several intermediate hosts of parasites, including molluscs, crustaceans, and echinoderms live on Arctic rocky shores (Scheibling and Stephenson 1984; Rokicki 2009; Wilson et al. 2013), suggesting that the biotic conditions for the existence of parasites are given. While parasite-induced mass mortalities in the sea urchin *S. droebachiensis* have been reported from sub-Arctic shores (e.g. Skadsheim et al. 1995), this has not been yet recorded for Svalbard coastal waters. The extent of a mass mortality in urchins is correlated with seawater temperature and the transmission of pathogenic agents is effective at  $\geq 8$  °C (Scheibling and Stephenson 1984), i.e. above the maximum sea water temperature in west Spitsbergen fjords during the last century (Pavlov et al. 2013), but this may change in a warming Arctic.

#### 11.2.4.5 Competition

The few studies that assessed the role of competition in structuring Arctic hardbottom communities exclusively considered encrusting species, usually dominated by bryozoans that assembled on boulders (Fig. 11.4). Space is a limiting resource for these species (Konar 2007), which they deplete by spreading over hard substrata and eventually growing over and killing neighbouring species, i.e. interference competition (Barnes and Kukliński 2003). Ecological theory suggests a negligible role of competition under high environmental stress (Menge and Sutherland 1987), which is partly supported empirically by Barnes (2000), who reported of decreasing importance of interspecific competition with increasing latitude in the southern hemisphere. It is also corroborated by the absence of interspecific competition in encrusting Arctic communities growing on boulders in the intertidal (Barnes and Kukliński 2004b), where ice-scour is most intense. However, in subtidal boulder fields (e.g. at Stefansson Sound, Beaufort Sea) and rhodolith beds (e.g. at Nordkappbukta, Fig. 11.1b) interspecific competition was apparent (Dunton et al. 1982; Konar and Iken 2005; Chenelot et al. 2008; Teichert et al. 2012, 2014). Moreover, Barnes and Kukliński (2004a, b) reported on interspecific competition between bryozoans growing on stones in the shallow waters of two Svalbard fjords (Hornsund Fjord and Kongsfjorden, Fig. 11.1b), but also that different aspects of competition (e.g. intensity, transitivity) varied significantly at different spatial scales. The effects of interspecific competition may also explain the temperaturemediated shift from a sea anemone-dominated community to a state, in which filamentous and canopy-forming algae prevail in Kongsfjorden and Smeerenburgfjorden (Kortsch et al. 2012). Presumably, the sea anemone U. eques pre-empted the substrate, thereby precluding successful recruitment of inferior competitors such as filamentous algae, which are typical pioneering species in coastal benthic habitats (Connell and Slatyer 1977).

Barnes and Kukliński (2003) found an exceptionally strong, consistent competitive hierarchy among encrusting species (mainly bryozoans) in boulder communities of Hornsund Fjord (Fig. 11.1b). Superior competitors were superior everywhere and inferior competitors were inferior everywhere. Only species with intermediate competitive abilities varied in dominance between sites at the local, but less so at the regional scale (Barnes and Kukliński 2004b). This infers that patterns in species succession can vary between sites, although the end result of this succession will be similar at all locations. Higher taxonomic membership (i.e. phylum affiliation) of encrusting Arctic species was an appropriate predictor for their competitive performance, which decreased from the rare demosponges and ascidians, via the common cheilostome and rare cyclostome bryozoans to the common hydroids, polychaetes, and cirriped crustaceans (Barnes and Kukliński 2004a). Similarly, Konar and Iken (2005) showed that sponges, bryozoans, and tunicates were superior space competitors compared to crustose corallines, while hydroids were the least competitive group in an Alaskan boulder community. As the amount of available space for settlement rather than recruit density determined the level of intensity of competition

(Barnes and Kukliński 2004b), colony size and thus growth rates of the encrusting species are important drivers of competition. Therefore, interspecific competition may be generally low in the Arctic as a result of the relative low growth rates in Arctic encrusting species (Barnes and Kukliński 2005b; Fricke et al. 2008; Konar 2013). In addition, the rare occurrence of competitively superior species (Barnes and Kukliński 2004a) due to, for instance, limited available space for their settlement, favours inferior space competitors such as crustose corallines in an Arctic Alaska boulder community (Konar and Iken 2005). The conclusion that interspecific competition may be generally low in the Arctic is supported by the results of Barnes and Kukliński (2004b) who found that competition intensity varied significantly at the regional scale, i.e. between Arctic and boreal sites. Competitively inferior pioneering species display by and large faster growth rates than superior competitors (Connell and Slatver 1977), which explains, why intraspecific competition prevails in encrusting Arctic communities (Barnes 2000). In Hornsund Fjord, for instance, nearly 80% of all observed competitive interactions involved intraspecific encounters (Barnes and Kukliński 2003), but varied considerably (at a range of 3–79%) at the local scale, indicating (i) strong patchiness in the conditions that promote competition and (ii) that species succession is repeatedly set back and far from reaching a climax state in these subtidal encrusting communities (Barnes and Kukliński 2005a) as well as in more algae-dominated benthos after even 24 years (Beuchel and Gulliksen 2008, this review Sect. 11.2.1 Species Succession). The second notion corroborates the fact that the most inferior space competitor, the bryozoan Hameria scutulata was also the most abundant species, showing an exceptionally high proportion (i.e. 97%) of tied encounters with conspecifics.

#### 11.2.4.6 Recruitment

The vast majority of Arctic recruitment research focuses on fish species. The few studies that addressed recruitment onto hard substrata mainly considered encrusting fauna, but rarely algae (Fig. 11.4). Overall, recruit density of Arctic encrusting fauna is about one order of magnitude lower than in most non-polar studies (Barnes and Kukliński 2005b), but clearly higher than in Antarctica (Barnes 2000). According to the model of Menge and Sutherland (1987), low recruitment should increase the importance of physical disturbance over competition and consumer effects in community regulation (this review Sects. 11.2.3.4 Disturbance and 11.2.4.5 Competition). In terms of taxon richness, recruitment of fauna onto settlement panels deployed in Kongsfjorden, but also in Isfjorden (Figs. 11.1b and 11.3), was comparable (20 taxa) to what has been reported for temperate sites (Barnes and Kukliński 2005b; Schmiing 2005). Yet, apart from the tube dwelling polychaete Spirorbis tridentatus as the dominating recruiting species (80–93% of total recruits), the remaining recruits were all bryozoans, indicating exceptionally low recruit diversity at higher taxonomic (i.e. phylum) levels. Studies including benthic photoautotrophs in their sampling indicate relatively high recruitment success of diatoms

and green, filamentous macroalgae in Kongsfjorden (Fricke et al. 2008). In striking contrast, algal recruitment was negligible even after 7 years in an experiment conducted in Arctic Alaska in the Beaufort Sea (Konar 2013). Grazer activity does not explain this limited recruitment success (this review Sect. 11.2.1 *Species Succession*). Konar (2013) suspects that, in addition to low recruitment intensity, recruitment of at least some Arctic benthic biota may also be infrequent (at a decadal range) compared to that in non-polar habitats. Barnes and Kukliński (2005b) also inferred rarity of recruitment events as an explanation for the absence of sponge, ascidian, and barnacle recruits in areas that were surrounded by reproductive adults. Hence, vegetative, lateral regrowth (e.g. of sponges and coralline algae), rather than larval supply seems to be a faster, i.e. more important and efficient mechanism for recolonization of, for example, boulders (Konar 2013).

To our knowledge, only MacGinitie (1955) and Kukliński et al. (2013) reported on seasonal patterns in larval presence of Arctic benthos, with the latter also studying recruitment. In Adventfjorden (Fig. 11.1b), the meroplanktonic larvae of most species occurred with pronounced abundance for a few weeks in spring or early summer, while larvae were absent during winter (Kukliński et al. 2013). Surprisingly, settlement intensity of most benthic invertebrates peaked in July, i.e. after the phytoplankton bloom. This mismatch decoupled recruits from a major food supply. Probably, alternative food sources such as detritus (Renaud et al. 2015a) may be available for recruits on rocky shores in late summer and autumn. Settlement greatly vanished until and throughout winter. In the Chukchi Sea, larvae of many species were present throughout the winter (MacGinitie 1955).

# **11.3 Sedimentary Habitats**

In contrast to hard-bottom habitats, soft-bottoms offer extensive three-dimensional substrate, in which many inhabitants (infauna) find shelter. The substrate instability of sedimentary shores strongly limits algal recruitment and survival. Hence, the standing stock of autochthonous, photoautotroph biomass is less in soft- than hard-bottom areas and the fauna of the former depends more on pelagic primary production than the latter. For these and other reasons, the soft-bottom communities respond differently to environmental factors and are, in part, structured by different processes than hard-bottom communities. Furthermore, different methods are used to sample hard- and soft-bottom communities, due to differences in substrate characteristics. This may be one reason why hard- and soft-bottom communities are frequently studied separately (Table 11.2), despite their frequent spatial proximity in coastal environments (Voronkov et al. 2016). Similar to studies on hard-bottoms, mensurative approaches prevail, but manipulative experiments have been very scarcely applied in studying the structure and diversity of soft-bottom benthos in Svalbard (Table 11.2).

in hard- (H) and soft	-bottom (	S) habitats in Kongsfjor	den		
Studied factor	Habitat	Location	Study type	Target organisms	References
Succession	Н	KF	Mensurative	Epifauna	Schmiing (2005)
	Н	KF	Mensurative	Epifauna	Beuchel and Gulliksen (2008)
	Н	KF	Mensurative	Epifauna	Fricke et al. (2008)
	Н	KF	Mensurative	Epifauna	Streicher (2014)
	Н	KF	Mensurative	Epifauna, macroalgae	Schwalfenberg (2011)
Long-term change	Н	IF	Observational	Mytilus edulis	Berge et al. (2005)
	Н	KF	Mensurative	Epifauna, macroalgae	Beuchel et al. (2006)
	Н	HSF	Observational	Epifauna, macroalgae	Węsławski et al. (2010)
	Η	KF,SBF	Mensurative	Epifauna, macroalgae	Kortsch et al. (2012)
	Н	KF	Observational	Seaweeds	Fredriksen et al. (2014)
	Η	KF	Mensurative	Epifauna	Paar et al. (2016)
	Н	KF	Mensurative	Macroalgae	Bartsch et al. (2016)
	H,S	BF,IF,GF,BB,YB,YH	Mensurative	Decapod fauna	Berge et al. (2009)
	S	MF	Mensurative	Macrofauna	Renaud et al. (2007)
	S	KF	Mensurative	Macrofauna	Kędra et al. (2010a, b)
	S	KF	Mensurative	Macrofauna	Węsławski et al. (2011)
Zonation	Н	IF to WF	Mensurative	Epifauna	Hansen and Haugen (1989)
	Η	KF	Mensurative	Epifauna	Sahade et al. (2004)
	Η	KF	Observational	Macroalgae	Hop et al. (2012)
	Н	KF	Mensurative	Epifauna	Laudien and Orchard (2012)
	Η	KF	Mensurative	Epifauna	Voronkov et al. (2013)
	S	KF	Mensurative	Macrofauna	Kaczmarek et al. (2005)
	S	KF	Observational	Meio-, macrofauna	Bick and Arlt (2005)
Irradiance	Η	KF	Manipulative	Epifauna, macroalgae	Fricke et al. (2011)
Disturbance	Η	Alaska	Manipulative	Epifauna, macroalgae	Konar (2007, 2013)

Table 11.2 List of publications published since Hop et al. (2002) that report on the effects of abiotic and biotic factors on the ecology of species assemblages

	S	KF	Mensurative	Macrobenthos, infauna	Laudien et al. (2007), Nowak et al. (2016)
	s	KF	Mensurative	Meiofauna	Veit-Köhler et al. (2008)
	s	KF	Manipulative	Macrobenthos	Petrowski et al. (2016b)
Bioturbation	s	KF	Manipulative	Macrofauna	Petrowski et al. (2016a)
Sedimentation consumption	Н	HSF	Mensurative	Epiphytic hydroids	Ronowicz et al. (2008)
	S	KF	Mensurative	Macrozoobenthos	Włodarska-Kowalczuk and Pearson (2004)
	s	KF	Mensurative	Infauna	Włodarska-Kowalczuk et al. (2005, 2012), Kędra et al. (2010a), Kendal et al. (2003), and Włodarska-Kowalczuk and Kędra (2007)
	s	HSF	Mensurative	Infauna	Włodarska-Kowalczuk and Węsławski (2008), and Włodarska-Kowalczuk et al. (2013)
	S	IF	Mensurative	Infauna	Włodarska-Kowalczuk et al. (2007)
	Н	KF	Manipulative	Natural suite of predators	Lippert and Iken (2003)
	н	KF	Manipulative, lab	Anonyx nugax	Lippert et al. (2004)
	н	KF	Manipulative, lab	19 seaweeds, 2 grazer species	Wessels et al. (2006)
	Η	Greenland	Observational	Eider prey items	Merkel et al. (2007a, b)
	Н	GF	Observational	Hyas araneas, Buccinum sp.	Markowska et al. (2008)
	Н	KF	Manipulative, lab	9 seaweeds, 2 grazer species	Wessels et al. (2012)
	Н	Nunavut	Observational	Species of 4 functional groups	McMeans et al. (2013)
	S	KF	Mensurative	Amphipods	Legeżyńska (2001)
	S	KF	Mensurative	Seals	Lydersen et al. (2001)
					(continued)

Table 11.2 (continuity)	ied)				
Studied factor	Habitat	Location	Study type	Target organisms	References
	S	KF	Mensurative	Macrofauna	McMahon et al. (2006)
	S	KF	Mensurative	Amphipods	Legeżyńska (2008)
	S	KF	Manipulative	Macrofauna	Petrowski et al. (2016a)
Competition	Η	HSF	Observational	Bryozoans	Barnes and Kukliński (2003)
	Н	KF & HSF	Observational	Encrusting taxa	Barnes and Kukliński (2004a)
	Η	KF & HSF	Observational	Encrusting taxa	Barnes and Kukliński (2004b)
	Η	KF & HSF	Observational	Encrusting taxa	Barnes and Kukliński (2005a)
	Η	KF	Observational	Bryozoans	Kukliński et al. (2006)
Recruitment	Η	IF	Observational	Encrusting taxa	Barnes and Kukliński (2005b)
	Η	KF	Manipulative	Kelp	Wiencke et al. (2006)
	Н	KF	Manipulative, lab	Kelp	Müller et al. (2008)
	Η	AF	Observational	Encrusting species	Kukliński et al. (2013)
Facilitation	Η	KF	Manipulative	Epifauna	Molis et al. (2008)
	Η	Svalbard	Observational	Epifauna	Teichert et al. (2012)
	Н	IF	Mensurative	Selected fauna of trophic levels	Zmudczyńska-Skarbek et al. (2015)
Epibiosis	Η	KF	Mensurative	Seaweed epibionts	Lippert et al. (2001)
	Η	KF	Mensurative	Seaweed epibionts	Carlsen et al. (2007)
	Η	HSF	Mensurative	Seaweed epibionts	Włodarska-Kowalczuk et al. (2009)
	Η	14 Svalbard sites	Mensurative	Hydroids	Ronowicz et al. (2013)
	Η	Svalbard	Mensurative	Epibiontic hydroids	Ronowicz et al. (2013)
	Η	HSF	Mensurative	Epibiontic hydroids	Ronowicz et al. (2013)
Exemplary studies fr	om Svalba	ard and if annronriate	elsewhere in the	Arctic were only include	d if no study from Konøsfiorden was found

Abbreviation of locations: KF Kongsfjorden, HSF Hornsund Fjord, SBF Smeerenburgfjorden, IF Isfjorden, AF Adventfjorden, GF Grønfjorden, WF Wijdefjorden, MF van Mijenfjord, MGF Magdalenefjorden

# 11.3.1 Species Succession

Generally, very few studies have addressed the succession of species in Arctic softbottoms. This is particularly so for research on primary succession, while several studies have investigated the recolonization of disturbed sedimentary habitats. Here, most attention has been given to the recolonization of ice-scours.

#### 11.3.1.1 Primary Succession

In Kongsfjorden, the initial colonization of soft-bottom meiofauna was studied by Veit-Köhler et al. (2008) and that of the macrofauna by Nowak (2012) and Nowak et al. (2016). At a depth of 20 m, Veit-Köhler et al. (2008) deployed containers filled with organism-free sediments to follow the succession of species and to compare the species composition of experimental communities to that of ambient communities. While the total number of meiofauna individuals reached levels of ambient communities within 1 year, the composition of meiofauna species remained different between experimental and ambient communities throughout the period. In the succession of macrofauna a shift was observed from pioneering species (e.g. the cumacean Lamprops fuscatus) to more specialised taxa, as well as from surface detritivores towards subsurface detritivores (Alvsvåg et al. 2009). Species composition of experimental and unmanipulated macrofauna communities was comparable after 3 years, but changed in subsequent years, probably due to elevated water temperature, which kept the fjord ice-free. Several species of naturally abundant macrofauna, e.g. the polychaete *Dipolydora quadrilobata*, did not settle in experimental plots. The studies by Veit-Köhler et al. (2008) and Nowak et al. (2016) demonstrate that neither meio- nor macrofauna develop mature communities within 3 years, indicating the possibility of long-lasting disturbance effects on Arctic soft-bottom benthos.

#### 11.3.1.2 Secondary Succession

In Arctic Canada, the recolonization of disturbed, i.e. ice-scoured, soft-bottoms is characterized by a clear disturbance-associated fauna that shows a distinct species composition compared to communities of unscoured areas (Conlan et al. 1998). As a result, soft-bottom communities at a depth of 5 m, which get frequently ice-scoured, feature a more disturbance-associated fauna than communities at greater depth. This pattern has also been observed in Kongsfjorden (Laudien et al. 2007). Recently ice-scoured soft-bottoms host pioneering species, such as cumaceans and polychaetes (e.g. Capitellidae and Spionidae) (Conlan and Kvitek 2005). The abundance and biomass of the scour-associated fauna increased with scour age, but did not exceed that of unscoured areas. Species composition of scour-associated communities was, however, different for many years compared to that of communities

inhabiting unscoured areas (Conlan and Kvitek 2005). Recovery of ice-scoured soft-bottom communities had reached about 75% of pre-scour conditions after 8–9 years, indicating slow recolonization.

# 11.3.2 Long-Term Change

Each summer since 1997, the soft-bottom macrofauna of Kongsfjorden has been sampled by the Institute of Oceanology PAN (IOPAN, Sopot, Poland) with a van Veen grab (sediments sieved on 0.5 mm sieve) at three stations: (i) Kongsbreen glacial bay (N78.89 E12.47) in the inner zone at 90 m, (ii) close to Blomstrandøya (N78.99 E11.98) in the transitional zone at 80 m, and (iii) in the middle zone (N78.99 E11.57) at 270 m (Figs. 11.1c). The three stations represent the gradual change in benthic community composition along the fjord axis (from the taxonomically and functionally impoverished communities of the glacier-impacted inner basin to the more diverse communities inhabiting the stable sediments at the entrance of the fjord) as documented by Włodarska-Kowalczuk and Pearson (2004). Although the stations are located at different depths, this should not affect the comparison of communities between stations. Włodarska-Kowalczuk et al. (2005) showed that density and biomass of macrozoobenthos in Kongsfjorden were not significantly correlated with depth between 40 and 380 m, while there was no or a very weak relationship between diversity and depth. The other two benthic monitoring programs in Svalbard waters comprise (i) the Hausgarten program, in which 15 stations off Kongsfjorden at depths from 1,000 to 5,500 m have been sampled since 1999 by the Alfred Wegener Institute Helmholtz Centre of Polar and Marine Research (described in Soltwedel et al. 2005), and (ii) three stations along the fjord axis of Hornsund at depths from 80 to 230 m (sampled since 2001 by the IOPAN, JM Wesławski unpubl. data) (Fig. 11.1b). The first published results from the Kongsfjorden monitoring show the temporal stability of benthic species richness at the station located in the inner zone, in Kongsbreen glacial bay (Fig. 11.1c). Species richness remained at the level of about 20 species (with very little variation among the replicate samples) throughout the period from 1997 to 2008 (Węsławski et al. 2011). The number of species recorded in the middle zone of Kongsfjorden was much more variable and strongly varied inter-annually with a general trend of increase - from below 60 species per sample in 1997 to almost 80 species per sample in 2008. Węsławski et al. (2011) attributed the temporal stability of the fauna in the inner zone to a much lower interannual variability in hydrological conditions as these parts of Kongsfjorden are isolated by sills or shallows (as Lovénøyane shallows) from the influence of oceanic water masses. The decade-long stability in diversity and species composition within the inner basins, isolated from the open sea, was also shown in van Mijenfjorden (Fig. 11.1b) where stations studied in 1980 were revisited in 2000–2001 (Renaud et al. 2007). A similar study in Kongsfjorden compared fauna sampled at the same stations in 1997-1998 and 2006 (Kedra et al. 2010b). They studied 31 stations located throughout the fjord at depths ranging from 27 to 365 m. The basic separation of the fauna into the communities - the one inhabiting the inner zone and the one in the central basin (including the Hop et al. [2002] transitional, middle and outer zones) was clearly visible in both sampling periods. In the inner zone, the macrobenthic density, biomass, species richness, and diversity did not differ significantly between the two sampling periods and species composition differed little between 1997–1998 and 2006. In the central basin, some changes in the attributes of benthic communities were observed. Firstly, the separation of the fauna into the two associations (transitional and middle zones) documented in 1997–1998 was not visible in samples collected in 2006. Species richness, diversity, and total biomass increased significantly between the two sampling periods. Also, an increase in relative density of annelids and a decrease in the relative density of molluscs were noted. Within the annelid group, an increase in the number of tube-dwelling species such as the polychaetes Maldane sarsi and Laene ebranchiata was observed. The warming of fjord water in the central basin may have resulted in increased pelagic primary productivity, further reflected in the higher concentrations of organic matter in sediment and the increase in benthic biomass as documented by Kędra et al. (2010b).

For epifauna, the extensive study by Berge et al. (2009) of decapod fauna in Isfjorden compared the communities sampled in 1908, 1958, and 2007. Their study showed that the species composition remained stable, but the relative proportion of dominant taxa changed over the years. They related the observed change from specialized shrimp predators towards more opportunistic, scavenging crabs to increased levels of disturbance from more trawling activities and climate fluctuations.

## 11.3.3 Abiotic Factors in Soft-Bottom Habitats

Substrate stability in sedimentary habitats is greatly affected by a number of abiotic factors, of which several have been carefully studied, especially scouring by icebergs. Interestingly, the more direct effects of temperature, salinity, and waveexposure, typically studied with regard to ecology of communities of the temperate zone, and to a certain degree of Arctic hard-bottom habitats, have achieved less attention in the research of Arctic sedimentary habitats.

## 11.3.3.1 Irradiance

To the northeast of Spitsbergen, i.e. between 79° and 81°, light conditions are insufficient for primary production by late September (Eilertsen et al. 1989) and a seasonal peak in pelagic biomass production has been reported for several Arctic locations (for an overview see Węsławski et al. 1991). Consequently, the supply of fresh food from the water column to the benthos is highly seasonal. This, together with lower water temperature during the following winter months may reduce growth of some (e.g. Iceland cockle *Clinocardium ciliatum*), but not all filterfeeding species (e.g. Greenland smoothcockle *Serripes groenlandicus*), as the study by Ambrose et al. (2012) suggests. An *in vitro* experiment with intact sediment cores sampled during the polar night revealed that infauna activities quickly increased after experimental addition of fresh food (Morata et al. 2015).

#### 11.3.3.2 Disturbance

Icebergs

Scouring by icebergs is among the most significant disturbances that coastal polar ecosystems experience (Gutt and Starmans 2001). For Brandal, a soft-bottom site in the middle zone of Kongsfjorden (Fig. 11.1c), empirical data suggest that 17, 4, and 0.5% of icebergs plough the ground at 5, 10, and 21 m depth, respectively (Dowdeswell and Forsberg 1992; Laudien et al. 2007). Large scratches, where the benthos is disturbed by grounded ice, can commonly be observed at shallow sublittoral areas in the inner zone of Kongsfjorden (Laudien et al. 2007). Besides causing high benthic faunal mortality, ice-scour also changes sediment characteristics, bottom topography, and near-bottom current regimes, resulting in resuspension and transport of sediments (Woodworth-Lynas et al. 1991; Gutt 2001; Barnes and Conlan 2007). In addition, scour depressions may be affected by winter infill of brine, which causes local hypoxia (Kvitek et al. 1998; Barnes and Conlan 2007). Overall, the impact of ice-scour causes changes in the abundance, diversity, biomass, and species composition of soft-bottom communities and presumably shifts in ecosystem processes (e.g. bioturbation intensity, resource use) and function (e.g. in primary productivity or nutrient cycling) (Conlan et al. 1998; Gutt 2001; Conlan and Kvitek 2005; Laudien et al. 2007).

The 'Intermediate Disturbance Hypothesis' (IDH) (Connell 1978; Huston 1979) states that biotopes affected by moderate disturbance are characterized by higher diversity. In contrast, frequently disturbed habitats are only colonized by pioneer communities, while mature and less diverse assemblages dominate zones with low disturbance impact. Laudien et al. (2007) provide evidence that the soft-bottom communities of Kongsfjorden at 30 m water depth, which are rarely affected by icescour, are characterized by lower species richness (species richness of a number of sampling units from a site of defined area, i.e. SR<sub>s</sub> sensu Gray 2000). Knowledge on intra- and interspecific competition of soft-bottom fauna from this ecosystem is scarce. The pattern of SR<sub>s</sub> observed may, however, be explained by competitive exclusion of species. With moderately increasing rate and intensity of ice-scouring at intermediate water depth, the potential competition for space and food (Wilson 1990) of dominating species would be mitigated by the disturbance, reducing the abundance of competitively superior species. Thus, inferior competitors co-occur, resulting in higher species richness and manifold life strategies (Węsławski et al. 2011). At shallow water depth, ice-scour is frequent and intense, and may locally result in low diversity and biomass. Results from benthic assemblages of a moderately scoured (yearly 1–7 times) habitat at Barrow Strait (Conlan and Kvitek 2005) also support the IDH. They found that macrofaunal recolonization of Arctic icescours progressed as a linear increase in resemblance from the scoured relative to the unscoured community. The significant correlation of the community parameters with the scour age also supports the IDH. Species succession upon ice impact results in a variety of simultaneous stages of recolonization, which characterise the impacted grounds and thus beta-diversity increases on a larger scale (Conlan and Kvitek 2005).

Global warming and resulting higher calving activities of glaciers will increase the level of physical disturbance caused by ice scouring for high-latitude, near-shore benthic communities in the coming decades. In the long term, however, physical impact will be reduced as retreating glaciers will become disconnected from the sea (Węsławski et al. 2011). At present, five tidewater glaciers calve into Kongsfjorden and the icebergs drift through the fjord. As a result of their fast diminishment, >75% of the icebergs are likely to melt in less than 2 days (Dowdeswell and Forsberg 1992), with the effects on the benthos varying along the fjord axis.

#### Whiplash

Besides icebergs, though on a smaller spatial scale, movements of individual kelp thalli feature another source of physical disturbance for soft-bottom communities. A field experiment conducted by Petrowski et al. (2016a) revealed that disturbance by movements of a *Saccharina latissima* thallus reduced the number of individuals and species in a soft-bottom community in Kongsfjorden by as much as 49% and 36%, respectively. Hence, detached algae may promote small-scale patchiness in coastal sedimentary areas.

#### Sedimentation

Sediment input of terrigenous material through river drainage and glacial inflow is a major structuring force of Arctic soft-bottom communities (e. g. Feder and Jewett 1988; Blanchard et al. 2010). For Kongsfjorden, fluxes of particulate inorganic matter of up to 800 g m<sup>-2</sup> day<sup>-1</sup> have been reported in front of Kongsbreen glacier (Svendsen et al. 2002). Sediment load decreased gradually with distance from glaciers (Paar 2012) and was <25 g  $m^{-2}$  day<sup>-1</sup> in the outer zone of Kongsfjorden (Zajączkowski 2008). Sedimentation of inorganic material is particularly stressful and energetically expensive to most filter feeders, which have to remove mineral particles to minimize clogging of feeding and respiration organs (Moore 1977). Additionally, the proportion of organic material decreases with increasing turbidity, which results in more intensive feeding efforts. Likewise, phytoplankton and benthic primary production are depressed in highly turbid surface waters, lowering feeding efficacy of filter feeders (Moore 1977). The deposition of inorganic material also hinders settlement of larvae and stresses benthic species, which need to maintain contact with the sediment surface (Rhoads and Young 1970; Fetzer et al. 2002). Thus, sedimentation strongly modulates the community structure of Arctic fjord communities.

In zones with high sedimentation impact, infaunal organisms are smaller, more mobile, less abundant, and do not penetrate as deeply into the substrate as conspecifics of less impacted zones (Hop et al. 2002; Włodarska-Kowalczuk and Pearson 2004; Blanchard et al. 2010). Consequently, infaunal communities near glaciers tend to be less complex and diverse than those in the outer zone of Kongsfjorden (Fig. 11.1c), where sedimentation impact is less strong (Kaczmarek et al. 2005; Włodarska-Kowalczuk et al. 2005, 2012). The pattern of decreased diversity in the glacial-impacted inner basin of Kongsfjorden is apparent at the species level and higher taxonomic levels of macrobenthos, as well as major taxonomic groups comprising the soft-bottom macrobenthic community (Wlodarska-Kowalczuk et al. 2007). Declining biodiversity was also reported with decreasing distance to glaciers or glacial outflows in other Arctic fjords for soft- and hard-bottom communities (Kendall 1994; Holte et al. 1996; Włodarska-Kowalczuk and Wesławski 1996; Włodarska-Kowalczuk et al. 2007, 2013). The physically-controlled communities in glacial bays were less diverse and more homogenous in terms of spatial variability compared to the benthic communities in outer basins (Kendall et al. 2003; Włodarska-Kowalczuk and Wesławski 2008).

Close to the glacier margin in Kongsfjorden, small mobile bivalves such as *Thyasira dunbarii*, *Yoldiella lenticula*, and *Y. solidula* dominate the assemblage (Włodarska-Kowalczuk and Pearson 2004; Kędra et al. 2010b). The latter are mobile deposit-feeding bivalves, which are able to maintain their vertical position in the uppermost layers of unstable, rapidly depositing sediment (Ockelmann 1958). The small, mobile polychaete *Chone* cf. *paucibranchiata*, which can feed on suspended and deposited organic particles (Cochrane 2003), is numerically dominating in this habitat.

Moderate levels of sedimentation in the middle zone of Kongsfjorden allow coexistence of sessile tube-building (e.g. *Maldane sarsi, L. ebranchiata*) and motile polychaetes (e.g. *Cossura longocirrata*), together with mobile detritus-feeding bivalves (Wlodarska-Kowalczuk and Pearson 2004; Wlodarska-Kowalczuk et al. 2005, 2012; Kędra et al. 2010b). The progressive increase in less mobile, larger organisms that also penetrate deeper into the sediment, as well as the increasing fraction of bioturbators and suspension feeding fauna, and concomitant increase in complexity in physical community structure, taxonomic and functional diversity, characterize the soft-bottom community down fjord (Elverhøi et al. 1993; Włodarska-Kowalczuk and Pearson 2004; Włodarska-Kowalczuk et al. 2005, 2012; Kędra et al. 2010b). This is accompanied by reduced turbidity and sedimentation (Zajaczkowski 2008; Paar 2012).

While surface deposit-feeders and sub-surface detritivores dominate the Kongsfjorden inner zone, their contribution diminishes in the middle zone of the fjord (Fig. 11.1c), where the abundance of suspension feeders increases (Włodarska-Kowalczuk et al. 2005; Laudien et al. 2007). This pattern reflects the general trend that deposit-feeders are of greater importance towards glacier margins and with intensified glacier activity (Syvitski et al. 1989; Włodarska-Kowalczuk and Pearson 2004).

The biomass of soft-bottom communities decreases toward glacial sediment sources, i.e. rivers and glacier margins (Feder and Matheke 1980; Włodarska-Kowalczuk et al. 2005; 2007; Laudien et al. 2007; Blanchard et al. 2010). The high concentration of suspended inorganic matter in front of glaciers proximately reduces irradiance and ultimately depresses primary production. This is reflected in a scarcity of food accessible to sub-surface detritivo-rous fauna (Gorlich et al. 1987). However, a relationship between microphytoben-thic biomass and turbidity at 5 m water depth along the longitudinal axis of Kongsfjorden (excluding areas in front of the glaciers) was not detected (Woelfel et al. 2010).

Ongoing warming of the coastal waters around Svalbard is predicted to increase the natural glacial disturbance in the inner zone of Kongsfjorden (Kedra et al. 2010b). This will increase glacial run-off and river discharge into the fjord leading to increased siltation, lower salinity, and a reduction in the depth of the euphotic zone. As a result, Wesławski et al. (2011) assume that coastal habitats will become more homogenous with biodiversity subsequently decreasing. By comparing softbottom community data from 1997 to 1998 with the one from 2006, changes in structure, diversity, and species composition are already evident in the central basin of Kongsfjorden (Kedra et al. 2010b). Blomstrandbreen glacier (Fig. 11.1c) significantly retreated within the last two decades. This has increased river run-off (Nowak and Hodson 2013) and changed the input of sediment (Lantuit et al. 2012). Kędra et al. (2010b) suggest that a decreased impact of sedimentation on the benthic fauna may be the reason for the reduced abundance of species typical for glacial bays in the central part of the fjord. In the long-term, glaciers may retreat extensively or disappear, which should improve water transparency. This should restructure Arctic coastal habitats and communities adjacent to fjords and force them into a new state (Wesławski et al. 2011).

## 11.3.4 Biotic Factors in Soft-Bottom Habitats

Numerous studies assessed species distribution patterns of Kongsfjorden softbottom benthos and considered mainly the role of abiotic factors for the generation of these patterns (e.g. Włodarska-Kowalczuk and Pearson 2004; Włodarska-Kowalczuk et al. 2005; Laudien et al. 2007; Kędra et al. 2010b; Węsławski et al. 2011). Little information is available, however, on the role of biotic factors affecting soft-bottom species assemblages at higher latitude (Table 11.2). We found no information on whether and how facilitation, epibionts, pathogens or parasites, and recruitment affect the structure and diversity of soft-bottom species assemblages. Therefore, this part of the review focuses on those biotic factors that are generally assumed to be important for sedimentary marine ecosystems, i.e. consumption, competition, and bioturbation (Woodin 1999), and potentially so for the coastal soft-bottom areas in Kongsfjorden (Fig. 11.5).



**Fig. 11.5** Sedimentary shores. Main forms of documented (solid line) and hypothesized/scarcely observed (stippled line) biotic drivers of Arctic soft-bottom communities (coastal to 400 m water depth). (1) Competition for space among infauna species; Disturbance by (2a) movements of detached kelps, (2b) foraging mammals, and (3) burrowing of bioturbators such as the lugworm *Arenicola marina*; Consumption by (4) scavengers such as amphipods, *Buccinum undatum*, and *Hyas araneus* on carrion, (5a) benthic predators such as *H. araneus* (presumably density-dependent), and (5b) carnivorous mammals. Line width indicates relative magnitude of effects

## 11.3.4.1 Consumers

Arctic soft-bottom communities depend on the deposition of organic material as food that originates from pelagic (e.g. Grebmeier and Barry 1991), benthic (e.g. Renaud et al. 2015a), or sympagic (e.g. Sun et al. 2009) production.

## Primary Consumption

Besides the input of organic matter from the outer shelf, i.e. outside Kongsfjorden, the sedimentation of phytoplankton and ice-algae produced inside Kongsfjorden offers additional large amounts of food for benthic organisms (McMahon et al. 2006; Sun et al. 2007; Kim et al. 2011; Kuliński et al. 2014; Morata et al. 2015). Furthermore, macroalgae may also contribute to the input of organic material into soft-bottom areas down to 900 m after their detachment from rocky shores (Krumhansl and Scheibling 2012). In Kongsfjorden, Petrowski et al. (2016a) documented that detached kelp covered, on average, 11% of the seafloor at a shallow sedimentary site (Fig. 11.6), although spatial dynamics were high (Buschbaum et al. unpubl. data). The accumulation rate of detached macroalgae at deeper parts



Fig. 11.6 Natural accumulation of detached seaweeds (mainly *Saccharina latissima*) at Brandal, Kongsfjorden. (Photo: C. Buschbaum)

of Kongsfjorden is unknown as is the consumption rate of macroalgal detritus by soft-bottom fauna and how this may affect food web structure. Using stable isotopes, however, Renaud et al. (2015a) have shown that in another Svalbard fjord, in Isfjorden (Fig. 11.1c), organic carbon originating from kelp may contribute >50% to the diet of several suspension-feeding bivalves. Future availability of kelp as a food source for benthic fauna will presumably increase as a result of a warming-induced expansion of vegetated coastal habitats (Kortsch et al. 2012; Krause-Jensen and Duarte 2014) and the projected intensification of storms (Young et al. 2011). Arctic subtidal shallow soft-bottom areas down to 30 m water depth can also show high microphytobenthos productivity, which may exceed pelagic primary production (Glud et al. 2009; reviewed in Karsten et al., Chap. 8). Sevilgen et al. (2014), for instance, found that the summer primary production of benthic microalgae in a subtidal nearshore area of Kongsfjorden is similar to that of temperate sedimentary sites and constitutes an additional important food source for the densely populated benthic animal community.

The concentration of particulate organic carbon (POC) in sediments decreases from about 10–12 mg POC g<sup>-1</sup> sediment in the outer zone to 2 mg g<sup>-1</sup> in the inner zone of Kongsfjorden (Fig. 11.1c; Kuliński et al. 2014), similar to other Svalbard fjords (Winkelmann and Knies 2005). That trend is at least partly explained by the presence of three retreating tidal glaciers in the inner zone of Kongsfjorden. The glacial meltdown increases water turbidity in the inner zone through the release of terrigenous material, which ultimately lowers pelagic primary production and the concentration of organic matter on the seafloor (Włodarska-Kowalczuk and Pearson 2004). Kim et al. (2011) documented also a significant decrease of marine organic matter contribution from 55% in the outer zone to 9% in the inner zone (based on  $\Delta^{14}$ C data and the concentration of retene, i.e. a compound formed upon maturation of higher plant triterpenoids). The lower quantity of organic matter and the glacier-induced disturbance (i.e. high water turbidity, high sedimentation rate of mineral matter, unstable sediment, and ice-scour) result in decreased benthic biomass and diversity in the Kongsfjorden glacial bays (Włodarska-Kowalczuk et al. 2005; Kędra et al. 2010b).

Despite the pronounced seasonality in Arctic primary production, benthic foodweb structure appears to be quite stable in Kongsfjorden between winter and summer (Kędra et al. 2012). Additionally, sediment respiration did not vary seasonally at greater depth (Berge et al. 2015b). Likewise, standing stock and diversity of softbottom organisms remained similar at shallow (Kedra et al. 2011) and greater depth (Włodarska-Kowalczuk et al. 2016). This evidence indicates that food reserves of labile POC may be stored in Kongsfjorden sediment year-round to support benthic standing stocks and activity (see also the 'Food Bank Theory' developed for the Antarctic shelf, Mincks et al. 2005; Glover et al. 2008; McClintic et al. 2008; Smith and DeMaster 2008). The seasonal stability of Kongsfjorden in May-June and September can be ascribed to two phytoplankton blooms occurring near the mouth of the fjord (Hegseth et al., Chap. 6). These blooms cause multiple input of fresh organic material to the area. This can be quickly used by benthic organisms, but may also serve as more continuous food source for polar deposit- and suspension-feeders, which are quite flexible in their food choice and are also able to use older, resuspended organic matter (Gili et al. 2001; Renaud et al. 2011; Kedra et al. 2012). Berge et al. (2015a) and Włodarska-Kowalczuk et al. (2016) suggest that the insensitivity of benthic biota to the strong variability in pelagic productivity in Kongsfjorden may also be related to the large contribution of benthic macroalgaederived materials. The latter is part of the diet of benthic consumers, as recently reported from Isfjorden by Renaud et al. (2015a). Thus, the lack of seasonal effects in biomass and diversity of benthic communities in Kongsfjorden may strongly differ from other, less productive fjords. For example in Rijpfjorden (Fig. 11.1b), Morata et al. (2015) documented lower benthic biomass in winter than in summer, but a strong, quick increase in activity of benthic organisms (collected during polar night) in response to experimentally added food to the sediment.

#### Secondary Consumption

Modes of consumption in Arctic soft-bottom fauna comprise suspension- and deposit-feeding, grazing, predation, and scavenging (Feder et al. 2005, 2007; Kaczmarek et al. 2005; Tamelander et al. 2006; Berge et al. 2009; Kędra et al. 2010a, 2012; Pabis et al. 2015). All these feeding modes are well represented in high latitude soft-bottom communities and many species deploy multiple feeding modes depending upon food availability (Fig. 11.5). Several species of amphipods, decapod crabs, and whelks, for example, can switch between predation and

scavenging (Legeżyńska et al. 2000; Thompson 2002; Legeżyńska 2008; Markowska et al. 2008) and a high flexibility in feeding modes is also reported for many other soft-bottom organisms in Kongsfjorden (Renaud et al. 2011; Kędra et al. 2012; Legeżyńska et al. 2014). Thus, many organisms show an opportunistic feeding behaviour.

Predation is considered as a key factor affecting species occurrence and population dynamics in marine sedimentary systems from the tropics to temperate regions (e.g. Ambrose 1984; Reise 1985; Wilson 1990; Ouijon and Snelgrove 2005). Arctic marine mammals such as walrus (Odobenus rosmarus) feed by rooting in the sediment on the bottom with their muzzles up to a depth of 0.2 m (Johnson and Nelson 1987). The diet of walrus consists of various soft-bodied species such as polychaete and echiurid worms (Sheffield and Grebmeier 2009) as well as larger endobenthic invertebrates, including the bivalves Mya truncata and S. groenlandicus (e.g. Wijg et al. 1993; Born and Acquarone 2007) (Fig. 11.5). This feeding behaviour affects the structure of soft-bottom communities directly through the removal of prey and indirectly through regeneration of nutrients in and bioturbation of the sediment (Ray et al. 2006). Feeding behaviour that scours the sediment is also described for ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) by which especially the latter species intensively forages for soft-bottom invertebrates (Lowry et al. 1980a, b; Lydersen et al. 2001). However, abundances of predatory mammals are comparatively low in Kongsfjorden and, due to their high spatial and temporal variability, the overall consequences of their activity for the entire soft-bottom system are difficult to assess (Hop et al. 2002). Besides information on predatory mammals, knowledge on predator-prey interactions is relatively scarce for Arctic soft-bottom systems and it has been suggested that predation plays a minor role as a structuring factor for soft-bottom communities in high Arctic regions (Gulliksen et al. 1999; Quijon and Snelgrove 2005). Berge et al. (2009) intensively investigated the species composition of the decapod fauna from Isfjorden (Fig. 11.1b) where they found, in addition to eight shrimp species, only two crab species (the brachyuran spider crab H. araneus and the anomuran hermit crab P. pubescens). These two crab species were also exclusively found in coastal waters of southern Svalbard (Węsławski 1987) and at a shallow soft-bottom site in Kongsfjorden (Legeżyńska 2001; Petrowski et al. 2016b). However, reports on high numbers of predatory crabs (e.g. snow crab Chionoecetes opilio), sea stars, and the brittle star Ophiura sarsii exist for the Bering, Beaufort, and Chukchi Seas (Feder et al. 2005; Bluhm et al. 2009; Harris et al. 2009) as well as the Barents Sea (Sundet and Bakanev 2014). Although the studies from Svalbard fjords do not provide quantitative data, it can be concluded that the predatory crab fauna there is relatively species-poor compared to the Arctic open shelf systems.

To investigate potential predation effects on a soft-bottom community at a shallow site in Kongsfjorden, Petrowski et al. (2016b) conducted a predator exclusion experiment at Brandal (Fig. 11.1c) using cages ( $0.5 \times 0.5$  cm mesh). They found no differences in species number and density of organisms in areas with and without predator access although the spider crab (*H. araneus*) was regularly observed and predatory fish species such as Atlantic cod (*Gadus morhua*) and shorthorn sculpin (*Myoxocephalus scorpius*) commonly occur at the experimental site (Brand and Fischer 2016). Presumably, natural predator densities were too low to affect the benthic community in this area. This notion is corroborated by Bender (2014), who manipulated in an enclosure study at the same site the abundance of *H. araneus* and detected a significantly reduced species diversity and number of infauna individuals in plots with three-times above ambient crab density. These results indicate that natural predation pressure by epibenthic predators may currently be of minor importance for population dynamics of shallow soft-bottom species assemblages in Kongsfjorden (Fig. 11.5) because predator densities seem to be low and strongly reduced in comparison to many sedimentary environments of temperate regions (e.g. Reise 1985; Beukema 1991). This might change in a warmer Arctic due to the postulated northward expansion of boreal predatory crab species (Woll et al. 2006; Fagerli et al. 2014) and/or an increase in the abundance and activity of resident predators such as *H. araneus* (Berge et al. 2009).

Many marine benthic predators are omnivorous and feed on carrion (Fig. 11.5). This is also true for the predatory benthic invertebrate fauna in the Arctic. The common crab species, H. araneus and P. pubescens, have been sampled with carrionbaited traps and regularly observed feeding on carcasses of dead invertebrates in Kongsfjorden (Legeżyńska 2001, C. Buschbaum pers. obs.). Further examples of necrophagous organisms include the whelk B. undatum, a very abundant gastropod in nearshore soft-bottom areas in Kongsfjorden (Kaczmarek et al. 2005, C Buschbaum pers. obs.) and other Svalbard fjords (Markowska et al. 2008), as well as several scavenging amphipod species such as the lysianassoid amphipods A. sarsi and Onisimus caricus (Legeżyńska et al. 2000; Legeżyńska 2001, 2008; Nygard et al. 2012). Due to the high abundance of short-lived, small-sized organisms in soft-bottom areas of Kongsfjorden and resulting high availability of dead invertebrates (Legeżyńska et al. 2000), it is very likely that many omnivorous consumers favour this readily accessible food source. This feeding behaviour together with the comparatively low densities of predators may explain current missing predatory effects in soft-bottom communities of Kongsfjorden (Petrowski et al. 2016b).

## 11.3.4.2 Competition

In Kongsfjorden, mean density of macrobenthic invertebrates (body size >1 mm) in soft-bottom habitats ranges from 4,000 to 14,000 individuals m<sup>-2</sup>, depending on water depth and proximity to the glacier (Bick and Arlt 2005; Włodarska-Kowalczuk et al. 2005; Laudien et al. 2007). These values are somewhat similar to densities reported from tropical and temperate soft-bottom environments, where mean densities range from 1,000 to 20,000 individuals m<sup>-2</sup> (Petrowski et al. 2016b and references therein). The high individual numbers in Kongsfjorden may cause competition for space in soft-bottom habitats (Bolam and Fernandes 2003). In comparison to rocky shores, however, the role of competition in soft-bottom community organization can be reduced due to the more three-dimensional nature of the substrate and

the resulting opportunity for the organisms to live at different depths within the sediment (Wilson 1990).

Petrowski et al. (2016a, b) reported a density of about 45,000 individuals m<sup>-2</sup> in a shallow subtidal soft-bottom site in Kongsfjorden (i.e. Brandal, Fig. 11.1c), with 98% of the individuals occurring in the top 5 cm of the sediment. Although most of the organisms of that area belong to small-sized species (<1 cm), it is surprising that despite these extremely high densities, sediment layers below 5 cm were relatively scarcely colonized. As the sediment of the study site appeared well oxygenated (e.g. no black anoxic layer) to a depth of at least 10 cm, oxygen depletion seems an unlikely explanation for the aggregation of species to the upper 5 cm of the sediment. The low level of colonisation between the uppermost sediment layer and very deep-burrowing species (up to 30 cm depth), such as the lugworm Arenicola marina and M. truncata (Laudien et al. 2007; Petrowski et al. 2016b), can be a hint that competition for space seems to be of minor importance as a structuring factor for soft-bottom assemblages at least for specific sites in Kongsfjorden. Otherwise, the organisms would more intensively use deeper sediment layers, especially in areas or at water depths with low physical disturbance by e.g. icebergs (this review Sect. 11.3.3.2 Disturbance). However, experimental evidence for this assumption does not exist and more detailed studies are needed to test whether competition may be generally of minor importance in the regulation of softbottom community structure in Kongsfjorden and other Arctic regions.

Like competition for space, competition for food may also be of minor importance for the existing sedimentary assemblages in Kongsfjorden because, otherwise, densities of several 10,000 individuals m<sup>-2</sup> of the same feeding mode (especially suspension- and deposit-feeding) would not be reachable. Low competition for food among epibenthic predators and scavengers is assumed, too. As mentioned above, their comparatively low abundance and opportunistic feeding behaviour (e.g. in amphipods) as well as the high availability of carcasses of relatively small-sized benthic and pelagic organisms may diminish food shortage (Legeżyńska 2008). Missing food competition is reflected, for example, by widely absent intra- and interspecific aggression behaviour of crabs and whelks (*H. araneus, B. undatum*) at experimentally offered carrion baits (Legeżyńska et al. 2000; Legeżyńska 2001; Markowska et al. 2008).

Clear patterns of succession after disturbance with opportunistic species as first recruiting organisms followed by species that are more competitive suggest potential competition effects in soft-bottom communities of Kongsfjorden. However, a disturbance experiment at a near-shore area in Kongsfjorden revealed that the macroinvertebrate species community of physically disturbed areas (digging of sediment) may reach the pre-disturbance condition within 7 days (Petrowski et al. 2016b). Thus, recovery that included direct competition between the species happened very rapidly after the physical disturbance. These results, obtained from a small-scale experiment performed at one site in the shallow subtidal zone of Kongsfjorden, thus indicate that competition between soft-bottom macrobenthic organisms is presently not a strong factor for structuring communities in Kongsfjorden.

In contrast to macrobenthos, the benthic meiofauna community shows succession patterns in soft sediments of Kongsfjorden. Veit-Köhler et al. (2008) deter-

mined experimentally that primary succession of meiofauna takes about 3 years, i.e. the period when species composition of previously animal-free plots was similar to that of natural control plots. However, whether this is a consequence of competition or rather of different temporal colonisation by the species remains unclear.

#### 11.3.4.3 Bioturbation and Ecosystem Engineering

The sedimentary habitats of Kongsfjorden are inhabited by a variety of invertebrate species, which use the soft-bottom as habitat, but may also alter its characteristics through their bioturbating and engineering activities. Włodarska-Kowalczuk and Pearson (2004), for example, mention that mobile organisms, e.g. protobranch bivalves, may decrease the stability of the uppermost sediment layers. On the other hand, a high density of sedentary tube-dwelling invertebrates can increase the sediment integrity in the middle and outer zone of Kongsfjorden. Thus, different kinds of sediment reworking by numerically dominant species differently modify the properties of the bottom and may cause indirect sediment-mediated inhibition or facilitation for other organisms (Bouma et al. 2009).

At shallow subtidal sites of Kongsfjorden, Bick and Arlt (2005) and Petrowski et al. (2016b) identified the tube-dwelling polychaetes *Euchone analis* and *Pygospio* elegans as dominating species. Both species use sand particles to construct their tubes and form aggregations of several square meters with densities >4,000 individuals m<sup>-2</sup>. In the temperate zone, dense polychaete mats may suppress other species by hampering, for example, movements of burrowing species (Wilson 1990), yet, their potential effects on Arctic species assemblages have not been studied. Włodarska-Kowalczuk and Pearson (2004) and Włodarska-Kowalczuk et al. (2005) showed that also deeper areas of Kongsfjorden may be densely populated with ecosystem engineering and bioturbating organisms, but consequences for other organisms are largely unknown. However, the recent study by Petrowski et al. (2016b) provides experimental evidence that bioturbators cause structuring effects on Arctic soft-bottom communities. At a shallow sedimentary site (Brandal, Fig. 11.1c), they found aggregations of large-sized (up to 23 cm in length) and deep-burrowing lugworms A. marina with a mean abundance of 12 individuals  $m^{-2}$  (Fig. 11.7). Experimental exclusion of lugworms modified the species composition and increased species richness, number of individuals, and dry mass of the benthic community in comparison to control plots where lugworms were present. Thus, the intensive burrowing activity by A. marina seems to hamper the establishment of other species, which are sensitive to sediment disturbances. These results reveal that sediment-mediated species interactions may be an important biotic driver of softbottom community structure in at least specific areas of Kongsfjorden and possibly elsewhere in the Arctic if bioturbating organisms occur in high abundances or have a large size.



**Fig. 11.7** Natural density of mounds formed by the bioturbating activity of the lugworm *Arenicola marina* at Brandal, Kongsfjorden. (Photo: C. Buschbaum)

# 11.4 Synopsis and Outlook

The structure of our review exemplifies the rather artificial separation into studies addressing either hard- or soft-bottom communities. This research divide is not unique to ecological studies of Arctic benthos, but seems common in benthic ecology. This habitat classification is, however, a mediocre reflection of the natural situation, which is characterized by a plethora of connections between both habitat types. The mobility of larger macrozoobenthos (e.g. crabs, molluscs), and demersal fishes, for instance, allows migrations between sedimentary and rocky shores. In Kongsfjorden, spider crabs crossed several hundreds of metres of soft-bottom area in a few days to get from one rocky area to another (A. Bender unpubl. data). Another example of habitat connectivity involves soft-bottom communities that benefit from storm-induced detachment and subsequent dislocation of large algal species (e.g. kelp) from rocky shores as food subsidies (Renaud et al. 2015a), but soft-bottom communities also suffer from disturbances mediated through thallus movements (Petrowski et al. 2016a). In a warmer Arctic, the frequency of ecological links between rocky and sedimentary areas may increase due to sea ice retreataccompanied intensification of storm effects, species additions in the course of a borealization of Arctic shores, or temperature-mediated increase in consumer activity levels. Hence, to gain a more comprehensive understanding on the ecology of benthic communities and to stress its role as a flagship site for Arctic marine research, future studies in Kongsfjorden should focus on connectivity among hardand soft-bottom habitats.

Since the review by Hop et al. (2002), research in Kongsfjorden has changed from mainly qualitative species inventories to quantitative description of patterns of the distribution of species in space and time. These observational studies revealed, for example, changes in community structure and diversity along vertical (Laudien et al. 2007; Laudien and Orchard 2012; Bartsch et al. 2016) or horizontal gradients (e.g. Włodarska-Kowalczuk and Pearson 2004). In addition, monitoring and comparative studies at different times helped to elicit successional and historical changes in the species composition of benthic communities (e.g. Beuchel and Gulliksen 2008; Berge et al. 2009; Kedra et al. 2010b). During the last 15 years, a considerable number of studies related changes in community traits to the effects of environmental factors, for example, ice-scour (e.g. Laudien et al. 2007), sea ice retreat (e.g. Kortsch et al. 2012), climate variability (Beuchel et al. 2006), and melting glaciers (e.g. Ronowicz et al. 2008). These mensurative studies provide valuable hints for the possible drivers of patterns of species distributions and organisation of ecological communities. A mensurative approach, however, is conducted at the risk of missing the influence of unknown, simultaneously acting factors, by which the interpretation of patterns may be confounded. For instance, patterns of species distributions along a depth gradient, which were related to changes in the frequency of iceberg-mediated disturbance, may be confounded by additional environmental factors that also change with water depth such as substrate composition, wave-exposure, or light attenuation. To increase certainty in the causality between environmental factors and community responses, manipulative experiments turn out to be a powerful tool in studying benthic ecology in the temperate zone. In benthic systems, multiple factors commonly act simultaneously, causing additive or multiplicative effects. The simultaneous manipulation of multiple factors offers insight into the relative contribution and interactive effects of the environmental factors under investigation. Manipulative experiments are, however, usually restricted in space and time. Consequently, the combination of mensurative, monitoring, and manipulative field experiments represents a useful approach to (i) identify the factors that drive benthic community traits, (ii) rank factors by their importance, and (iii) unravel the underlying processes that generate community change. Moreover, future investigations could intensify the assessment of functional community responses such as productivity, respiration rates, or filtration rates to estimate the capacity of Arctic benthos in the provision of ecosystem services.

Research on Kongsfjorden benthos, and probably in other parts of the Arctic as well, displays at several instances prioritization, which likely obscure general conclusions. Firstly, there is an apparent taxonomic bias in ecological studies. Studies on epibiosis, for instance, in some regions largely focused on kelp-associated organisms. Likewise, competitive interactions were mainly addressed through studies with encrusting animal species, which seem to be overwhelmingly dominated by cheilostome bryozoans. Secondly, there is a habitat-specific research bias. The succession of species has been mainly investigated for rocky shore communities (but see Veit-Köhler et al. 2008 and Nowak et al. 2016 for exceptions), while facilitation has been exclusively studied in hard-bottom communities. Similarly, competition studies appear restricted to rocky shore communities. Whether competition plays an inferior role in sedimentary areas is unknown, although possible, as soft-bottom communities were shown to be densely populated (e.g. Petrowski et al. 2016b). This situation may be amplified through the postulated arrival of boreal species (e.g. Müller et al. 2009). Presently, the biogeographic range of marine species expands at a rate of 50 to 70 km per decade poleward (Krause-Jensen and Duarte 2014) and first reports of the reappearance of boreal species on Arctic shores exist (e.g. Berge et al. 2005; Sirenko and Gagaev 2007), but see Feder et al. (2003) and Norton and Feder (2006). Thirdly, there is a methodological bias. For the construction of food web models, many studies use stable isotopes to elicit trophic interactions (e.g. Iken et al. 2005; Feder et al. 2011; Kedra et al. 2012; McMeans et al. 2013; Renaud et al. 2015a). While stable isotope studies help to establish trophic links, this method provides limited information on e.g. feeding preferences, feeding rates, diet switch and resulting consumer fitness and performance. Furthermore, the prevalence of omnivory may exacerbate the interpretation of results obtained from stable isotope analyses. An improved knowledge of consumer effects on benthic communities could be achieved by direct observational and experimental investigations.

Last, but not least, there is a topical bias in Arctic benthos research. Very few Arctic studies have considered recruitment. This is surprising because ecological theory predicts that the relative importance of the major drivers of community regulation is modulated through the intensity of recruitment (Menge and Sutherland 1987). For most of the benthic species in Kongsfjorden it is neither clear when, how often, and on which spatial scales settlement happens, nor what kind of post-settlement processes affect recruitment success. For example, Petrowski et al. (2016b) encountered adult lugworms (A. marina) in high abundances at a shallow soft-bottom site in Kongsfjorden, but were unable to find juveniles. Laudien et al. (2007) did not detect any. This may be a consequence of, for instance, irregular recruitment events or spatial segregation between juvenile and adult lugworms. Similar uncertainties exist for other, ecologically key species at higher latitudes such as the Greenland smoothcockle, which is the prime food source for Arctic marine mammals. Recruitment success may be also altered as a result of climate change. Arctic kelp, for instance, germinate less successfully in a warmer, more UV-exposed Arctic Ocean (Wiencke et al. 2006; Müller et al. 2008), which may also have effects at the community level (Bischof et al. 2006). Furthermore, successful recruitment to Arctic habitats by cold-temperate species with a relatively long pelagic phase may be supported by warmer surface waters

and altered current patterns. As the Arctic Ocean is surrounded by land masses inhabited by cold-temperate biota, the future Arctic may experience the arrival of those biota that are able to cross the sea and recruit onto the rocky shores further north (Müller et al. 2009; Krause-Jensen and Duarte 2014; Kortsch et al. 2015). For this migration process, the island of Bjørnøya (Fig. 11.1a) has been suggested as a potential stepping stone (Węsławski et al. 1997). Without a better understanding of recruitment patterns, their natural dynamics as well as the factors affecting recruitment success of Arctic benthic species, it will be difficult to distinguish between the effects of global change and natural variability in recruitment success.

Another topic which has been thus far unjustifiably neglected in Arctic benthos research is the role of symbionts (but see Hoberg et al. 1980, 1982), pathogens, and diseases. As there is clear evidence that global warming will increase disease risk (Altizer et al. 2013), polar regions are among the particularly sensitive areas of future parasitic impact (Kutz et al. 2009). Besides pole-ward range extensions of parasites and potential hosts (Post et al. 2013), increased temperatures may reduce the immune competence in host species (Rokicki 2009). Thus, the benthos may be more adversely affected by parasites and diseases in a warmer Arctic, with yet unknown implications on community structure and function.

Undoubtedly, coastal Arctic ecosystems are challenged by global warming. Besides the direct, physiological effects of higher temperatures, glacial and sea ice retreat will initially amplify sedimentation and freshwater impact and in the long run storm-induced effects, all of which will indirectly affect the ecology of Arctic benthic communities as it has been already documented for an Antarctic coastal benthic ecosystem (Sahade et al. 2015). Moreover, the expected changes resulting from the arrival of boreal species on Arctic shores will alter species interactions. This may be particularly momentous for consumer-prey interactions because consumers play a fundamental role in shaping benthic communities of the temperate zone, while consumer impact in the Arctic seem to be presently of minor importance.

Acknowledgements We are grateful to Tobias Dolch who kindly supplied maps displayed in Fig. 11.1. We thank one anonymous reviewer, H.M. Feder, and H. Hop for their constructive comments, which greatly improved the quality of this review. MWK was supported by the Polish-Norwegian Research Programme operated by the National Centre for Research and Development under the Norwegian Financial Mechanism 2009–2014 in the frame of Project Contract No Pol-Nor/201992/93/2014 (DWARF) and by the National Science Centre grant based on a decision No DEC-2012/05/B/NZ8/02654 (BIOSIZE).

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