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Distribution, abundance, and ecological importance of marine sympagic fauna in the Arctic

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Sympagic (under-ice) fauna is important to the food web of the northern ice-covered oceans, and it functions as a link in the energy transfer from primary production (ice algae, phytoplankton) to seabirds and marine mammals. The most conspicuous sympagic organisms are one- to two-year-old polar cod (*Boreogadus saida*) and amphipods belonging to the species *Gammarus wilkitzkii, Apherusa glacialis, Onisimus nanseni,* and *Onisimus glacialis,* but other crustaceans (copepods, mysids, isopods, amphipods), foraminifers, rotatorians, nematodes, polychaetes, chaetognaths, pteropods, and appendicularians have also been found. Biomass values up to 20–40 g (wet weight) m^{-2} of ice undersurface have been recorded, but values of 0.1–10 g m^{-2} are more common, and the mean value in Arctic multi-year ice is probably of this order. Both grazers and predators are present in the sympagic fauna.

Autochthonous sympagic animals of both sexes and in all developmental stages (juveniles, immature individuals, mature individuals) occur in the ice habitat. They are not normally benthic or pelagic, and may be adapted physiologically (e.g., with high tolerance to brine) and morphologically (e.g., with spiny appendages enabling the animals to cling to the ice). Examples of autochthonous animals are *G. wilkitzkii* and the mysid *Mysis polaris.*

Allochthonous sympagic animals are found temporarily in the ice, and may occur as nekton, plankton, or benthos. They may actively seek out the ice habitat for shelter or food, or may be passively transported by hydrodynamic action. Examples of allochthonous animals are *A. glacialis, Parathemisto libellula,* calanoid copepods, and *B. saida.*

The composition and abundance of the sympagic fauna are especially dependent upon the age, structure, and history of the ice habitat; water depth; and origin of surrounding water masses. Generally, old, stable drift ice from the Polar Basin contains more autochthonous sympagic animals than does newly frozen ice on the margins of the Arctic. Ice above shallow water usually contains more animals than does ice above deep water.

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Introduction

It is now generally recognized that the sea ice in the Arctic harbours a specialized flora and fauna. It is also generally believed that sea-ice organisms form a link in the transfer of energy between primary production (ice algae, phytoplankton) and fish, seabirds, and marine mammals. The main questions we want to answer are:

1. What are the composition and abundance of the sympagic (under-ice) fauna and how are they related to the physical environment?
2. What is the role of sympagic organisms in Arctic food chains? What do they eat and who are their predators?

Nomenclature

Several different designations have been used for organisms found in the sea ice or near the ice undersurface. Among these are "anakatobenthos" (Mohr and Tibbs, 1963), "under-ice benthos" (George and Paul, 1970), "epontic fauna" (Bradstreet and Cross, 1982), "cryopelagic fauna" (Andriashev, 1968), "under-ice fauna" (Gulliksen, 1984), "ice fauna"/"sub-ice fauna" (Andriashev, 1968), and "sympagic fauna" (Carey, 1985). In this connection we shall refer to the review by A. G. Carey, Jr (Carey, 1985), who has discussed the different terms used and concluded that *sympagic,* meaning "with ice", seems to be the most appropriate.

Ice as a habitat

When discussing the ice as a habitat, it must be stressed that "sea ice" is not a homogeneous substrate. The age of each ice floe, its morphology, and its chemical composition, combined with the oceanographic regime surrounding it (salinity, temperature, water currents, depth), are of the utmost importance for the sympagic organisms recorded.

Among the terms describing the morphology of ice are *frazil ice, platelet ice, congelation ice (= columnar ice),* and *anchor ice.* (Martin, 1981; Maykut, 1985; Sugden, 1982). Frazil ice consists of needles or thin discs 1–4 mm in diameter that form in turbulent, slightly supercooled water. Larger discs are called platelets, measure about 2–15 cm across, and are about 2 mm thick. Such platelets may attach themselves to permanent structures or may form a sponge-like layer called the "platelet-layer", which may accumulate to a thickness of 2–4 m beneath congelation ice (Dayton *et al.*, 1969). Congelation ice is a coherent layer of ice which forms at the ice/water interface. It makes up most polar pack ice (Maykut, 1985). Anchor ice is composed of submerged platelets or frazil ice attached to the sea bottom (Dayton *et al.*, 1969).

Platelet ice and anchor ice are generally less common in the Arctic than in the Antarctic (Sugden, 1982). More important for the composition of the sympagic fauna in the Arctic are the desalinization process that takes place when sea water freezes and the influence this has on the morphology of the ice. Salt occurs as brine pockets in the ice (Weeks, 1968). The pockets may interconnect and form brine channels with as many as 50 to 300 channel openings m^{-2} of ice (Lake and Lewis, 1970; Eide and Martin, 1975; Niedrauer and Martin, 1979). The congelation ice may actually be a "sponge-like" structure with submerged ridges, holes, burrows, channels, and crevices.

The salinity of melted ice typically decreases from 10–20 to 3–8 as the ice gets thicker (Malmgren, 1927; Cox and Weeks, 1974). An ice sheet may have a salinity gradient, from "freshwater conditions" at the upper surface to those of sea water with a very high salinity and density near the undersurface, offering euryhaline conditions to the animals. Brine may actually be seen draining through small holes in the undersurface or through stalactites. Stalactites may reach lengths up to 6.0 m (Dayton and Martin, 1971), but those from 5 to 20 cm are more common in the Arctic and leave holes with a diameter of 2–3 cm in the undersurface when they break off (own obs.).

Fauna

Species composition

A variety of organisms belonging to several different taxa have now been reported as sympagic fauna. Forty-seven species belonging to the following groups: Foraminifera, Rotatoria, Nematoda, Polychaeta, Chaetognatha, Copepoda, Mysidacea, Isopoda, Amphipoda, Decapoda, Pteropoda, and Appendicularia, were recorded near the surface of old pack ice close to the Soviet drift station NP-23 (Melnikov and Kulikov, 1980). A species list can be extended considerably by including species recorded in other investigations, especially from ice above the continental shelf. However, many of these species are undoubtedly temporary immigrants to the ice undersurface. It is therefore necessary to concentrate on singling out the organisms which are permanent residents of the ice habitat. The sympagic fauna should be separated into an *autochthonous* group and an *allochthonous* group (Melnikov and Kulikov, 1980). Autochthonous sympagic animals of both sexes and in all developmental stages (juveniles, immature individuals, mature individuals) occur in the ice habitat, while allochthonous sympagic animals are found temporarily in the ice, and also occur as nekton, plankton, or benthos at other times of the year.

The sympagic *macrofauna* (> 0.5 mm) is dominated by amphipods (Cross, 1982; Carey, 1985); and five to ten different species, among them *Apherusa glacialis, Onisimus glacialis,* and *Gammarus wilkitzkii,* are reported most frequently in investigations from the Arctic. However, only one of these, *G. wilkitzkii,* is known to be autochthonous. Another autochthonous macrofaunal species is probably the mysid *Mysis polaris.*

The sympagic *meiofauna* (62 μm–500 μm) is more diverse than the macrofauna, and includes nematodes; rotifers; and harpactoid, cyclopoid, and calanoid copepods (Cross, 1982; Carey and Montagna, 1982; Kern and Carey, 1983). Larvae of benthic polychaetes, pelecypods, gastropods, tunicates, turbellarians, and cirripeds become more frequent above shallow water (Grainger and Hsiao, 1982; Pett *et al.*, 1983; Horner, 1977).

Little is known about sympagic *microfauna* (< 62 μm), but ciliates, heliozoans, and unpigmented flagellates have been reported (Nansen, 1906; Usachev, 1949; Grainger and Hsiao, 1982; Horner, 1976).

There are thus relatively few autochthonous species. Melnikov and Kulikov (1980) identified *Gammarus wilkitzkii, Mysis polaris, Derjuginia* af. *tolli, Tisbe furcata,* and *Harpacticus superflexus* as autochthonous animals from the central Arctic Basin, and the list is probably not much longer.

By definition, autochthonous animals are dependent on a permanent ice cover throughout the year. The ice cover of the Arctic Ocean has been repeatedly destroyed over the last 0.7 million years (Herman and Hopkins, 1980), and the last period with an ice-free Arctic Ocean was probably about 11 000 years ago (Olausson and Jonassen, 1969). However, 11 000 years is short in evolutionary terms, and it is thus not surprising that there are so few autochthonous sympagic species.

Adaptation to a life associated with ice is observed in autochthonous animals. *Gammarus wilkitzkii* and *Mysis polaris* are both bad swimmers, and *M. polaris* moves around at the ice undersurface in a "saltatory" way (Melnikov and Kulikov, 1980). *G. wilkitzkii* has spiny appendages with which it attaches itself to the ice (own obs.). As a euryhaline osmoregulator, it is also physiologically adapted to staying in the vicinity of the ice by conforming to the ambient brine with a salinity from about 34 to 60 (Aarset and Aunaas, 1987).

The list of allochthonous animals is long, and there may be hydrodynamic, geographical, or biological reasons for the occurrence of these animals in the ice.

Most interesting from an ecological viewpoint are those animals which have predominantly biological reasons for occurring in the ice, for instance those which actively seek out the ice for food, shelter, or reproduction. Many of the frequent and conspicuous sympagic macrofaunal amphipods belong to this group. For example, during the summer *Apherusa glacialis* is quite common at the ice undersurface, where it feeds and grows, but the lack of mature individuals at the surface during the winter (Barnard, 1959; George and Paul, 1970) and spring (Melnikov and Kulikov, 1980) suggests that this amphipod descends into deeper water at the beginning of the dark winter period to reproduce (Melnikov and Kulikov, 1980).

Three other conspicuous amphipods, *Onisimus nanseni, Onisimus glacialis,* and *Gammarus loricatus,* may exhibit reverse behaviour. They occur less frequently in the summer, and more frequently in spring and autumn, and it is likely that all three species occupy the niche vacated by *Apherusa glacialis* (Melnikov and Kulikov, 1980). However, the information available about the life strategies of these four species is not consistent. For instance, there are indications that *Onisimus glacialis* is autochthonous (own obs.). The scanty and somewhat inconsistent information available emphasizes the need for intensified studies of life strategies based upon data from investigations of both zooplankton and sympagic fauna.

Another example of an allochthonous sympagic organism is the polar cod (*Boreogadus saida*). Young polar cod find refuge and food on or near the undersurface of ice. However, when sexually mature at an age of about two to three years, they descend to deeper waters. Older specimens of polar cod are rare in the ice.

An example of shorter-term occurrences near the ice sub-surface is that of the amphipod *Parathemisto libellula,* which may occur in swarms below the ice during the night, especially where most light penetrates the ice (Gulliksen, 1984).

Water depth is especially important for the composition of the sympagic communities of the continental shelf (Carey, 1985). Benthic organisms may migrate to the ice undersurface to feed or release their young (Carey, 1985), or small organisms may be carried up to the overlying ice ceiling by advection. For example, few or no benthic species were found on the ice undersurface overlying depths greater than 70 m in the vicinity of Resolute in the Canadian High Arctic. (D. Pike, pers. comm.).

The question of whether an animal is autochthonous or allochthonous, is interesting when comparing the sympagic faunas in the Antarctic and the Arctic. Only about 15 % of Antarctic pack ice is more than one year old, and ice older than two to three years is rare (Sugden, 1982). Antarctic pack ice is mostly seasonal, surviving the summer in only a few areas such as the western Weddell Sea. Most Arctic ice is, however, more than one year old, and much of it is considerably older than Antarctic ice (Sugden, 1982). Autochthonous sympagic animals are therefore probably very rare or absent in the Antarctic compared with the Arctic, undoubtedly owing to the small amount of multi-year ice in the Antarctic. Another difference is related to the more frequent occurrence of anchor ice in the Antarctic; records of animals brought up to the ice undersurface in the Arctic are rare.

It is also believed that there is a greater potential for production of frazil ice and platelet layers in the Antarctic than in the Arctic. Platelet layers, which may become several metres thick in the Antarctic, increase the ice surface and available substrate for ice algae and other microorganisms, increase the room available for sympagic invertebrates and fish, and offer better protection from predation by birds and marine mammals.

Abundance and biomass

Quantitative estimates of sympagic fauna are scarce. This is attributable both to the inaccessibility of the ice undersurface and to the difficulties caused by the unevenness of the substrate. Most estimates are based upon investigations using SCUBA equipment, and the techniques, which are dependent upon the morphology of the undersurface, include direct counts within randomly placed quadrats below the ice, photography of defined areas, scraping with plankton nets along defined distances, or combinations of these techniques.

Golikov and Scarlato (1973) were pioneers in their studies of sympagic fauna in the Franz Josef Land archipelago, and reported a biocoenosis of twelve species in the autumn with a total biomass of 36 g m^{-2} (wet weight) to which *Apherusa glacialis* contributed 24 g

m^{-2}. Cross (1982) reported a maximum value of 1.24 g m^{-2} for any single sample in communities dominated by either *A. glacialis* or *Ischyrocerus anguipes*. Barnard (1959) gave a rough calculation for amphipods of about 1 g m^{-2}.

From our own diving investigations in the Barents Sea, north of Svalbard and in the Fram Strait, biomass values ranged from large areas with no animals to local values of 25.2 g m^{-2} during the period 1982 to 1987. The biomass values were generally higher in multi-year ice than in first-year ice, and the highest values were recorded in multi-year ice in July–August 1986, ranging from 1.6 to 25.2 g m^{-2}, with an overall mean of 9.6 g m^{-2} for sympagic organisms. Values within small areas showed wide variation, depending upon the morphology of the sub-surface of the floe.

A locality in multi-year ice investigated in 1986 was dominated by *Apherusa glacialis,* with ca. 2500 individuals m^{-2} and with a mean wet weight of ca. 0.01 g per individual. *Gammarus wilkitzkii* are generally larger, and at least four year classes may be found in multi-year ice. The highest density recorded for this species was nearly 200 individuals m^{-2}, with a mean individual weight of 0.12 g, but single individuals weighing about 1 g have also been recorded (Lønne and Gulliksen, in prep.).

First-year ice distant from multi-year ice had no or very few animals, indicating that colonization takes place from multi-year ice. *A. glacialis* and *Onisimus* spp. colonized new ice faster than *G. wilkitzkii.* Sympagic animals may, however, find a refuge in drifting ice from glaciers during the summer, and first-year ice may be colonized locally by such animals (Gulliksen, 1985).

Nematodes and copepods usually rank as first and second in meiofaunal abundance in sympagic communities. In Stefanson Sound, off the northern coast of Alaska, meiofaunal densities ranged from 4500 to 8000 individuals m^{-2}, while offshore in the fast ice the range was 36 000 to 320 000 individuals m^{-2} (Carey, 1985).

In addition to age, the morphology and type of ice are also important for the sympagic fauna. Hard congelation ice with a flat undersurface and few holes usually has fewer animals than that with an undersurface perforated by brine channels. This is partly owing to the microdistribution of the different species. *Gammarus wilkitzkii* and *Onisimus glacialis,* for instance, occur in holes caused by salt drainage (own obs.).

With minimum ice cover, the ice in the Arctic Ocean covers about 7 × 10^6 km^2 (Maykut, 1985). With an average value of 1 g m^{-2} this gives 7 million tonnes of sympagic fauna in the Arctic. The main export of ice from the Arctic Basin is through the Fram Strait. On an annual basis, about 10 % of the ice drifts southwards through this strait between Greenland and Spitsbergen. This means that there may be a yearly loss of 0.7 million tonnes of sympagic organisms from the surface to deeper layers.

Diet

A natural question to ask when discussing the diet of sympagic animals is: "What is available as food?"

The presence of algae in the ice has been known and studied since the mid-1800s. Taxonomic studies were predominant during the first hundred years, but more ecological knowledge has been gained during the past two to three decades (e.g., Horner, 1976 and 1985; Hsiao, 1980).

Most Arctic studies of ice organisms have been made in areas of land-fast ice in the spring. A general pattern has emerged for Arctic regions with seasonal ice cover; and the ice algae may start growing as early as February and represent a primary production of 0.015–0.020 g C m^{-2} per day (McRoy and Goering, 1974). An annual production of 5 g C m^{-2} has been reported (Clasby *et al.*, 1976). Limited growth may also take place in the water column below the ice without exhausting the nutrients, but a bloom in the water does not really start until the ice melts (Alexander, 1980; Horner and Schrader, 1982; Rey and Loeng, 1984).

In the spring, the ice algae in the Arctic, which are composed primarily of pennate diatoms, develop in a layer of unconsolidated ice crystals on the underside of the ice (e.g., Horner and Schrader, 1982; Apollonio, 1985). During the summer, the centric diatom *Melosira arctica* becomes more conspicuous, and may form long featherlike threads below the ice (own obs.).

Many authors have suggested that the ice-algal bloom is an important food source (Carey, 1985), but diet studies are relatively scarce, especially concerning the smaller sympagic organisms. An investigation from the Canadian High Arctic revealed that four sympagic amphipod species and three copepod species all consumed ice microalgae, and that these algae were present both on the undersurface of the ice and in the water column (Bradstreet and Cross, 1982). In addition, crustacean parts were present in the gut contents of *Gammarus wilkitzkii* and *Parathemisto* spp. Sympagic amphipods are probably the major grazers in all Arctic sympagic environments, but some of them are also scavengers and predators (Cross, 1982; Carey, 1985). Trophic links to sympagic amphipods via meiofauna and microfauna should be studied more intensively as should trophic relationships between zooplankton and sympagic organisms. We have for instance observed *G. wilkitzkii* feeding on pteropods.

Some of the allochthonous species undoubtedly migrate to the ice undersurface to feed. In McMurdo Sound in the Antarctic, field experiments showed that the allochthonous amphipod *Paramoera walkeri* swam to an area where production of ice algae was enhanced by clearing snow off an area of ice. Chlorophyll *a* analysis of gut contents from freshly collected animals and laboratory feeding experiments showed that both *P. walkeri* and another amphipod, *Cheirimedon fougneri,* include microalgae in their diets (Kottmeier *et al.*, 1985).

We know that sympagic animals eat sympagic flora but have not determined the quantitative importance of this feeding. Important for the herbivores is the fact that the ice algae are produced earlier in the year than phytoplankton, and thus extend the period of available food (Carey, 1985).

The polar cod, *Boreogadus saida,* is an opportunistic feeder, and a wide variety of food items has been recorded in its diet. In open water, it generally eats copepods (Hognestad, 1968). The diet of fish from under "first-year" ice consisted mainly of copepods (*Calanus finmarchicus, C. glacialis*) and the hyperiid amphipod *Parathemisto libellula.* Fish from "multi-year" ice had a more diverse diet, with the sympagic amphipods *P. libellula* and *Apherusa glacialis* as the most common food items (Lønne and Gulliksen, in press). *Gammarus wilkitzkii* was, however, not eaten, even if it contributed to more than 80 % of the biomass of the sympagic fauna where the fish were collected. The avoidance is probably related to the "spiny" morphology of *G. wilkitzkii.* According to Alexander (1980), the mouth morphology of *Boreogadus* is adapted for feeding on an overlying surface.

Predators

The trophodynamical importance of the sympagic organisms when they sink down through the water column is little known. What is, for instance, the fate of the about 0.7 million tonnes of sympagic organisms released annually when about 10 % of the polar pack ice melts in the Greenland Strait?

Although quantitative data are scarce, we have some qualitative information about the role of sympagic organisms as food for seabirds and marine mammals. The polar cod has a key function in this transport of energy (Klumov, 1937), and it is reported as the main food item for a number of different vertebrates in the ice-covered parts of the Arctic. In an investigation from land-fast ice in the Canadian High Arctic, polar cod were of major importance to five of the six bird and mammal species studied (Bradstreet and Cross, 1982). Other important taxa were calanoid copepods and *Parathemisto.* If cod are absent, birds and mammals can turn to lower levels in the food chain for alternative food (Bradstreet, 1982).

In the pack ice, seabirds take whatever is available in open water between the floes. However, the size of prey seems to be important. A small bird like the little auk (*Alle alle*) feeds on smaller prey (copepods and other small crustaceans), while larger birds like the black guillemot (*Cepphus grylle*) and Brünnich's guillemot (*Uria lomvia*) feed on larger specimens like *Gammarus wilkitzkii* and polar cod. A general observation is that when the sympagic organisms are abundant they become major elements in the diet of seabirds, especially alcids.

The ringed seal (*Phoca hispida*) is the Arctic mammal most often reported as including sympagic fauna in its diet (Dunbar, 1941; Bradstreet and Cross, 1982), but the diet varies widely with the food available (Gjertz and Lydersen, 1986). The ringed seal is usually reported to be a pelagic feeder, but it has been observed that the species may feed on benthos if pelagic or sympagic fauna is absent (Gulliksen, 1985). Polar cod is usually reported as the most common prey item for marine mammals feeding in the pelagic zone. Invertebrate sympagic fauna may, however, be important for young marine mammals, as has been reported for the harp seal (*Phoca groenlandica*) (Sivertsen, 1941).

Arctic vertebrates are generally quite opportunistic in their feeding strategy: a requisite for survival in the harsh Arctic environment. The diet of Arctic vertebrates often reflects what is available within their respective habitats, and inventories of food available should therefore always be included in diet studies of marine mammals.

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