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Ciliated epibionts on the Arctic sympagic amphipod *Gammarus wilkitzkii* as indicators for sympago–benthic coupling

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Abstract In September 2003 specimens of the sympagic amphipod *Gammarus wilkitzkii* were sampled in drifting pack ice above 50 m water depth and in the pelagic/benthic environment beneath in the coastal waters off Svalbard (Norway). Abundance values ranged between 1.5 and 8 individuals m^{-2} for the pelagic/benthic and the sympagic environments, respectively, and showed corresponding sex ratios of 1:1.4, favoring males. In the ice a significantly higher number of juveniles prevailed. In contrast, ovigerous females were more abundant among pelagic/benthic living specimens. Approximately 25% of the individuals hosted ciliated epibionts of the genera *Ephelota*, *Cryptacineta*, *Acineta*, *Podophrya* (all suctoria), and *Epistylis* (peritrichia). *Cryptacineta* and *Ephelota* were the most abundant epibionts on this amphipod species. Female specimens of *G. wilkitzkii* showed the highest degree of infestation ($>2,100$ individual epibionts per amphipod specimen: indE/A) followed by juveniles ($>1,200$ indE/A) and males (>220 indE/A). Highest densities of epibionts were found on anterior body parts with the antennae bearing up to 130 individuals. This is the first sighting of epibionts on crustacea from the sympagic environment. We interpret them as biomarkers that indicate the existence of sympago–benthic coupling processes between the ice and the underlying waters and the seafloor. The population structure and the proportion of infested specimens are equal for the amphipods sampled from both the sympagic and the pelagic/benthic environment, indicating

the existence of exchange (coupling) processes between the two habitats. Considering the annual ice cycle, local ice drift patterns, and the shallow water depth in the sampling area, we hypothesize that ice amphipods spend ice-free periods near the seafloor where they may serve as basibionts for protozoans and eventually re-colonize the ice with the onset of ice formation. Our observations strongly emphasize that shallow coastal areas serve as both retention (rather than sink) areas for ice fauna during ice-free periods, and as stepping-stones for re-colonizing the ice when the ice is formed in winter.

Introduction

The Arctic sea ice is a dynamic habitat to live in because of the seasonality in freeze and melt processes. A diverse flora and fauna, however, has adapted to the unstable nature of this environment (e.g. Aarset 1991). *Gammarus wilkitzkii* Birula is often considered the most abundant gammarid amphipod species in Arctic sea ice. In the northern Barents Sea this species reaches mean abundance values of 60 individuals m^{-2} sea ice for multiyear ice and up to 35 individuals m^{-2} in seasonal ice, corresponding to biomass values between 6 and 2 g wet mass, respectively (recalculated from Arndt and Lønne 2002, based on data from, for example, Gulliksen 1984; Lønne and Gulliksen 1991; Poltermann 1997; Hop et al. 2000). Because *G. wilkitzkii* is a long-living species reaching a size of up to 5 cm total body length, its individual biomass is highest among the ice-amphipod community (Beuchel and Lønne 2002). In the Arctic ice pack this species is generally the most dominant in terms of total sympagic biomass (Arndt and Lønne 2002).

In contrast to various pelagic and benthic organisms that spend only parts of their life cycle in sea ice and are often enriched in ice above shallow waters, the permanent residents within the sympagic community are

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strongly associated with sea ice during all stages of their life (autochthonous species) (Melnikov and Kulikov 1980; Gulliksen and Lønne 1989). One of the major problems for autochthonous sympagic organisms is believed to be the loss of their habitat when the ice melts. In seasonally covered fjords that are open to drift ice, pelagic occurrence of ice fauna is regularly observed (Steele and Steele 1974; Weslawski 1994; Poltermann 1997; personal observation). Furthermore, sympagic fauna is regularly released to the water column along the marginal ice zone when the ice retreats during summer melt (Werner et al. 1999; Arndt and Pavlova 2005). The archipelago of Svalbard is located in the shear zone of the perennial and the seasonal ice pack as well as the Atlantic and Polar water regime. In Svalbard waters, *G. wilkitzkii* was the most abundant ice-amphipod species with not only sympagic but also pelagic occurrence (Arndt and Pavlova 2005). By morphology and life-style sympagic amphipods are considered benthic species that are adapted to the ice as an “upside-down benthic” habitat (Mohr and Tibbs 1963). It has been stated earlier that the ice amphipod’s swimming capability is limited to short distances (Lønne and Gulliksen 1991). However, there is evidence that *G. wilkitzkii* can afford the costs of swimming in the water column when this species loses contact with the ice surface (Werner et al. 1999). It has recently been suggested (Arndt and Pavlova 2005) that shelf areas, and in particular fjords and bays, which are regularly impacted by drifting multiyear ice, are retention (rather than sink) areas for dislodged ice amphipods. In this article we present observations that support the hypothesis that *G. wilkitzkii* is capable of surviving in ice-free waters, and that it eventually recolonizes sea ice above shallow waters. We discuss whether these vertical movements are migratory, which is typical for allochthonous sympagic species, or a casual event in the life cycle of the defined autochthonous species *G. wilkitzkii* (Melnikov and Kulikov 1980; Gulliksen and Lønne 1989).

Materials and methods

Sampling site and sampling procedures

The area of investigation is located east of Spitsbergen (Norway) in the crossway of Hinlopen Strait, Erik-Eriksen Strait, and Heleysund/Storfjord (Fig. 1). Specimens of *G. wilkitzkii* were collected in loose drift ice and open water in the last week of September 2003. Thick, old drift ice of 2- to 3-m thickness prevailed at the shallow ice station (50 m water depth). Quantitative under-ice sampling was performed using a diver-operated suction sampler (Lønne 1988) that collected all specimens of *G. wilkitzkii* in a defined area irrespective of body length. A diver-held plankton-net sampled qualitatively. Due to the heavy ice conditions trawling was conducted 24 nautical miles further to the east by means of pelagic (Harstad and Tucker) and bottom

trawls (mesh size variable from ≥ 1 cm depending on speed of towing). This station was well situated on the shelf and had a water depth of about 130 m. Semi-quantitative values were retrieved from information on the trawled water volume based on trawl time, speed of net towing, and trawl opening. For Harstad and bottom trawls the mouth opening was assumed to be ellipsoid in shape (134 and 156 m², respectively); for the Tucker trawl the opening was 1 m². The data from the pelagic and benthic samples were pooled and not treated separately to account for the variability in mesh sizes used to get the complete spectrum of life stages of *G. wilkitzkii* in the water column.

Sea ice conditions at the sampling site vary significantly in the course of a year (see simplified ice chart in Fig. 2 for September 2002 to October 2003). Open water was only observed from July until September. The area

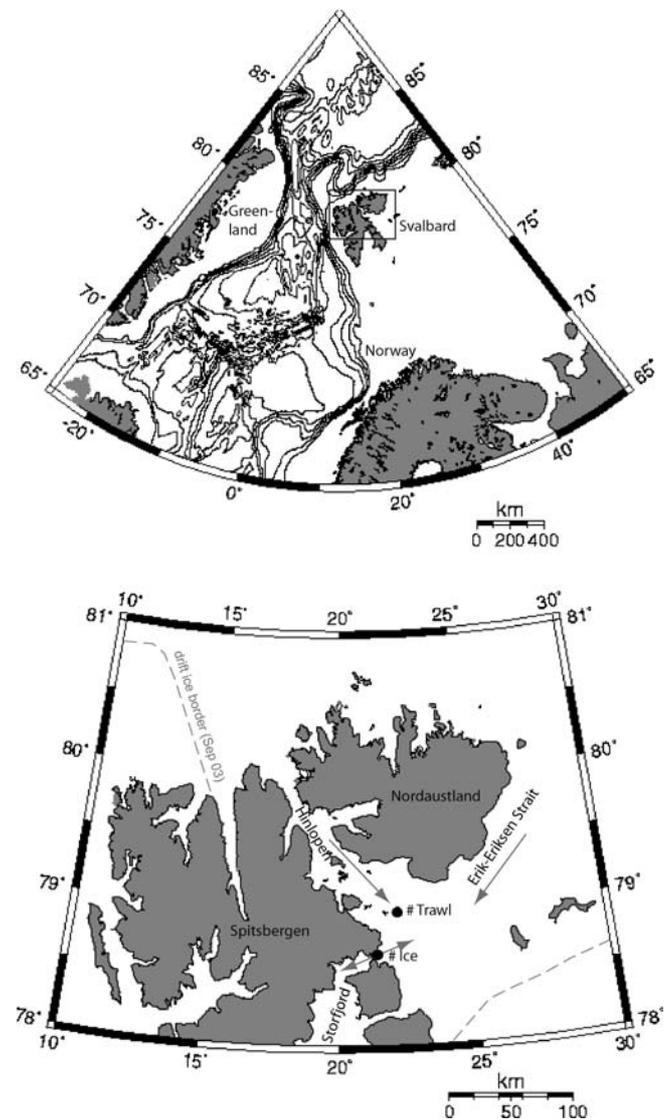


Fig. 1 Map of sampling locations on Svalbard; scope also denotes borderline of the ice pack in September 2003 and direction of ice drift

of interest is impacted by drift ice that originates from the central Arctic and enters the area mainly through Erik-Eriksen Strait but also Hinlopen Strait. A minor exchange of sea ice takes place via strong tidal currents ($4\text{--}5\text{ m s}^{-1}$, Haarpaintner et al. 2001) through Heleysundet originating from the Storfjord. In addition, sea ice forms in situ during fall/winter. Ice motion characteristics and land mass distribution in the study area illustrate that there is a great chance for drifting sea ice to move over or into shallow waters. According to the ice charts provided by the Sea Ice Service from the Norwegian Meteorological Institute (Fig. 2), most of July, August, and September show no ice coverage for the area of investigation. The impact of drift ice commences in late September/October. In situ observations confirm that vast open water areas with only loose drift ice prevailed during the sampling period (ice concentration approximately 40%).

Post-sampling procedures

All ice amphipods were counted, examined for epibionts, and sexed. Individuals of *G. wilkitzkii* with fully developed oostegites were considered as females; males were determined by the presence of genital papillae. All individuals without visible genitals were interpreted as juveniles.

For the analysis of epibiotic infestation 30 specimens of *G. wilkitzkii* (16 females, 3 males, 11 juveniles) preserved in 10% formalin were used. The individuals were dissected and each anatomical unit was examined under a dissecting microscope to evaluate densities of individual epibionts per amphipod specimen (indE/A) and densities of individual epibionts per “anatomical unit” (i.e. body parts and appendages) of the amphipod (indE/unitA). The epibionts were isolated and treated using the silver carbonate technique described by Fernandez-Galinao (1976) and the procedures described by Fernandez-Leborans and Castro de Zaldumbide (1986). In addition, the slides were treated with neutral red and methyl green. Different body parts of the epibionts were measured using an ocular micrometer. Light microscope images were obtained by means of image analysis (KS300 Zeiss).

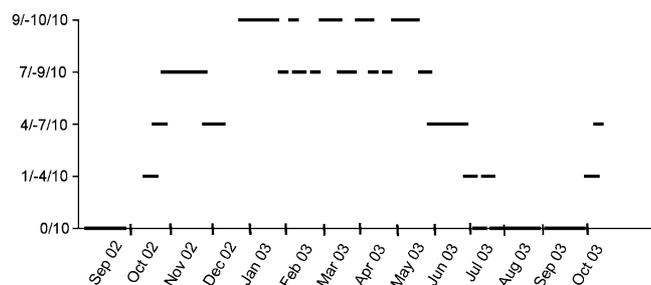


Fig. 2 Ice coverage at the sampling site in the course of a year ranging from open water (0/10), to very open drift ice (1/-4/10), open drift ice (4/-7/10), close drift ice (7/-9/10), and very close drift ice (9/-10/10). Ice charts provided three or four times a week by the Sea Ice Service of the Norwegian Meteorological Institute

Statistical analysis of the distribution of the different epibionts on the “anatomical units” of *G. wilkitzkii* was conducted using a Statgraphics program. A detailed description of morphological features and morphometry can be found in Fernandez-Leborans et al. (submitted).

Results

In total, 359 individuals of *G. wilkitzkii* were sampled (quantitatively and qualitatively) underneath the sea ice, and 53 individuals were found in the different pelagic and benthic trawls. Abundance values ranged between 8 individuals m^{-2} for the sympagic environment and 11 individuals 10^3 m^{-3} (or 1.5 individuals m^{-2} integrated for the entire water column of 130 m) for the pelagic/benthic realm.

The analysis of the population structure showed a comparable female:male ratio of 1:1.4 for both the sympagic and pelagic/benthic environments. Only in the sympagic did a significantly higher percentage of juveniles (19%, $\chi^2 = 10.04$, $P \leq 0.01$) prevail. The fraction of ovigerous (egg-carrying) females was twice as high in the pelagic/benthic (27% of all females) compared to the sympagic (11%) environment ($\chi^2 = 4.26$, $P \leq 0.05$). However, females carrying well-developed hatch in their brood pouch occurred only in the ice. The proportion of individuals infested by dense epibionts was equal in the two realms (between 25 and 26% of the total, Fig. 3). In general, infestation affected more males than females or juveniles but was observed on all size classes; the smallest specimen that hosted epibionts was a juvenile of approximately 15 mm in total body length (equivalent to age 1+; Beuchel and Lønne 2002).

Epibiotic protozoans found on *G. wilkitzkii*

The epibionts studied on *G. wilkitzkii* were four types of suctorian and one type of peritrich ciliate belonging to the following genera: *Ephelota*, *Cryptacineta*, *Acineta*, and *Podophrya* (all subclass Suctorina Claparède and Lachmann) and *Epistylis* (subclass Peritrichia Stein; for taxonomical classification see Lynn and Small 2000). Representatives of these ciliates were disposed on the antennae, antennulae, pereopods, pleopods, and telson and on the surface of the body, mainly on the abdomen of the basibiont. A detailed review on genus and species descriptions as well as their taxonomic position and statistical distribution on the host is given in Fernandez-Leborans et al. (submitted).

Ephelota

Ciliates of the suctorian *Ephelota* are characterized by a truncated cone-like body shape (Fig. 4, parts 1, 2). At the apical end a concave cavity was visible. Two types of

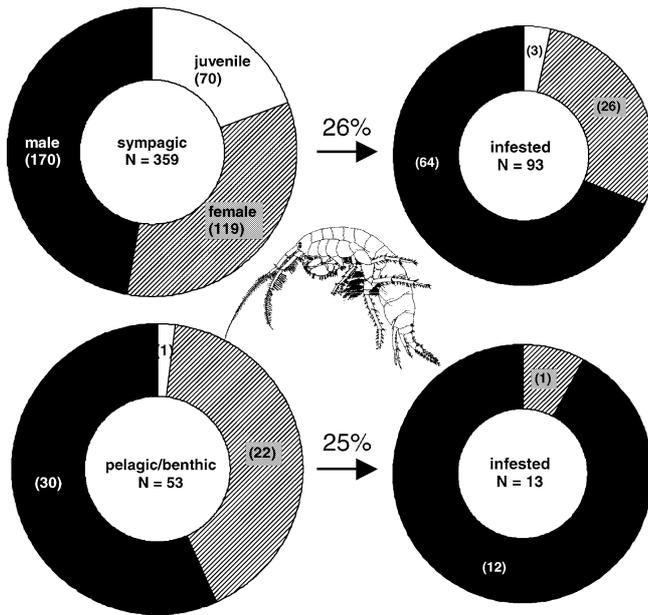


Fig. 3 Population structure of the specimens of *Gammarus wilkitzkii* sampled in the sea ice (sympagic) and in the water column or near the sea floor (pelagic/benthic) and percentage of individuals infested by epibionts; absolute numbers given in parentheses

tentacles aligned this cavity: prehensile tentacles and capitate (feeding) tentacles, both with haptocysts.

The macronucleus was large and highly ramified, lobate, and surrounded by numerous spherical micronuclei. A contractile vacuole was located laterally displaced in the apical region of the body. The stalk length was approximately four times longer than the body and showed fibrillar structures and transversal striations. Its apical (suprastylar) end was amplified and joined the cellular body in a conspicuous funnel-shaped widening.

Up to 10% of the ciliates present were resting stages. This stage is characterized by stalked individuals with a spherical, encapsulated body. The macronucleus was present as dense and ramified nodes. At the apical pole, tentacles were aligned in a spiral.

Different stages of reproduction were found on *G. wilkitzkii*. Some specimens showed exogenous, oval buds of similar size that were projecting out of the apical cavity of the body. The buds had a horseshoe-shaped ciliar field. The set of traits described for this type of *Ephelota* ciliate make us believe that the species studied on *G. wilkitzkii* is *E. plana* Wailes

Cryptacineta

Representatives of the genus *Cryptacineta* are spherical and laterally flattened and bear a thick transparent, mucilaginous layer (Fig. 4, part 3). Anteriorly, two fascicles composed of 8–26 capitate tentacles were visible. The spheroid macronucleus was located centrally and accompanied by a small spherical micronucleus. A contractile vacuole was placed above the macronucleus.

The long, longitudinally striped stalk had a curved spatulate end, which was embedded in the posterior end of the lorica.

Individuals examined of this genus on *G. wilkitzkii* were in the process of reproduction. Endogenous buds (pyriform in shape and limited in number) were visible in the apical end of the body.

This suctorian genus is characterized by a thick mucoid lorica, which completely envelops the stalked, tulip-shaped body. Anteriorly, two fascicles of tentacles project through the lorica, and posteriorly the stalk also penetrates the surrounding lorica (Curds 1985).

Acineta

Ciliates of the suctorian *Acineta* were characterized by the presence of a triangular or bell-shaped, laterally compressed lorica (Figs. 4, part 4). Two fascicles of 14–20 capitate tentacles each were located at the anterior end of the body. The spherical macronucleus was located centrally along with a contractile vacuole placed above. The long stalk joined the lorica in a definite collar-like region. The set of traits described for the specimens found on *G. wilkitzkii* make us believe that they belong to the species *Acineta compressa* Claparède and Lachmann.

Podophrya

The individuals of the genus *Podophrya* are miniature in size and have a characteristic spheroid or ovoid body shape (Fig. 4, part 5). In comparison to the body the stalk can reach a considerable length. Between 20 and 28 capitate tentacles were spread randomly over the body surface. The rounded macronucleus was located eccentrically. A spherical micronucleus was disposed close to the macronucleus. A contractile vacuole was placed above the macronucleus near the apical end of the body.

Size of body, shape of tentacles, and the presence of only one contractile vacuole and a micronucleus make the *Podophrya*-types found in this study most alike with *P. fixa* Ehrenberg (Curds 1986; Matthes et al. 1988).

Epistylis

These peritrich ciliates were colonial with colonies generally composed of two oval zooids (Fig. 4, part 6). At the apical end of the body a peristomial lip protruded outward. The macronucleus was crescent shaped; the micronucleus was spherical and located close to the macronucleus. Above the macronucleus a contractile vacuole was visible. The stalk was robust, non-contractile, and characterized by numerous longitudinal striations.

The genus *Epistylis* comprises a large number of species but species determination is difficult. We there-

fore consider this species as *Epistylis* sp. (Lynn and Small 2000).

Distribution of the protozoan epibionts on *G. wilkitzkii*

The number of epibionts per amphipod fluctuated between 499 and 3,346 individuals. The genus *Cryptacineta* showed the highest densities (215–2,571 indE/A), followed by *Ephelota* (2–1,302 indE/A), and in lesser pro-

portion the other three genera, *Acineta*, *Podophrya*, and *Epistylis*, which did not surpass 240 indE/A (Table 1).

Epibionts colonized 37 anatomical units of the *G. wilkitzkii*, including left and right appendages (antennulae, antennae, maxillae, maxillipeds, gnathopods, pereiopods, pleopods, uropods, telson, and abdomen). With regard to the means of epibionts per anatomical unit, females showed the highest value (2,172.5 indE/A, $n=16$), followed by the juveniles (1,202.00 indE/A, $n=11$), and the males (222.80 indE/A, $n=3$).

Fig. 4 Microscopic images of protozoan epibionts found on *G. wilkitzkii*; 1 *Ephelota plana* ($\times 140$), 2 *E. plana* ($\times 328$), 3 *Cryptacineta* ($\times 430$), 4 *Acineta* ($\times 320$), 5 *Podophrya* ($\times 604$), 6 *Epistylis* ($\times 810$)

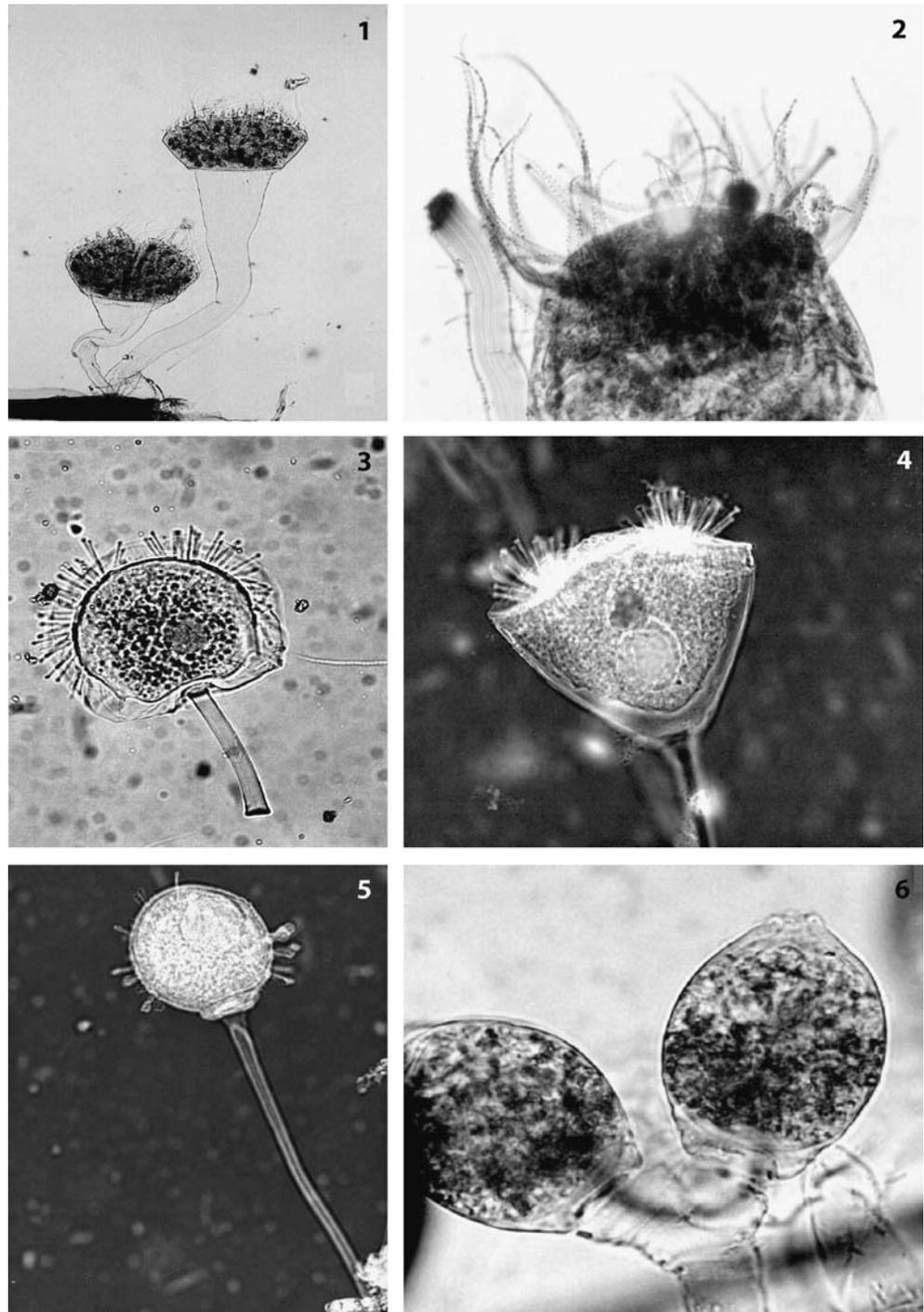


Table 1 Biometric values of the basibiont (in centimeters) and number of individual epibionts on *Gammarus wilkitzkii* (sorted by genus)

	Mean	Standard deviation	Minimum	Maximum
Length (cm)	2.90	0.88	1.30	4.00
Width (cm)	0.48	0.11	0.30	0.60
Total no. of epibionts per amphipod	1,723.27	855.81	499.00	3,346.00
<i>Ephelota</i>	399.82	408.04	2.00	1,302.00
<i>Cryptacineta</i>	1,209.36	725.97	215.00	2,571.00
<i>Acineta</i>	26.64	71.98	0.00	240.00
<i>Podophrya</i>	36.18	31.97	2.00	112.00
<i>Epistylis</i>	51.27	51.02	0.00	158.00

Ephelota and *Cryptacineta* were present on all these anatomical units; *Acineta* was found on 24 units, *Podophrya* on 32, and *Epistylis* on 30. In general *Acineta* was present mainly on the posterior parts of the crustacean body (abdomen, uropods, and telson), whereas *Podophrya* and *Epistylis* were restricted to the anterior body parts. A positive relationship was found between epibiont burden and host size for *Ephelota* (Pearson $r=0.73$, $P \leq 0.05$), *Podophrya* ($r=0.65$, $P \leq 0.05$), and *Epistylis* ($r=0.68$, $P \leq 0.05$).

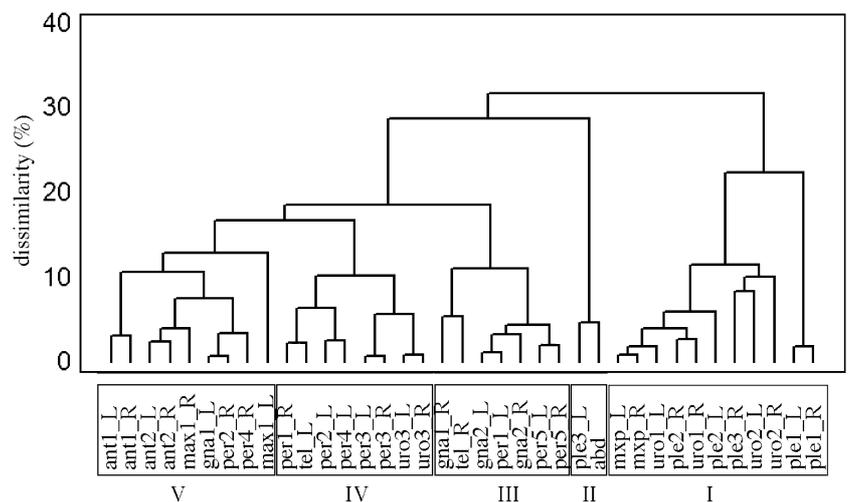
With regard to the total number of epibionts on each anatomical unit including appendages, there was no significant difference between the right and the left side of the gammarid (Pearson $r=0.95$, $P \leq 0.05$). This holds true for the genera *Ephelota* ($r=0.98$, $P \leq 0.05$), *Cryptacineta* ($r=0.95$, $P \leq 0.05$), *Acineta* ($r=0.99$, $P \leq 0.05$), and *Podophrya* ($r=0.76$, $P \leq 0.05$), but not for *Epistylis*.

In comparison, *Cryptacineta* showed the highest mean densities on most infested units (84.09 indE/unitA), followed by *Ephelota* (23.73 indE/unitA) and *Acineta* (13.45 indE/unitA). In contrast, *Podophrya* and *Epistylis* appeared in much lower numbers (2.36 and 4.03 indE/unitA, respectively).

The dendrogram in Fig. 5 shows the results of a cluster analysis of the epibiont assemblage on each of the specified anatomical units based on 30 examined speci-

mens of *G. wilkitzkii*. In general, separation of body parts by degree of infestation is not well distinguishable by clusters. However, the majority of posterior units are grouped in clusters I and II, whereas most anterior appendages are aligned in cluster V. Cluster I is separated from the remaining body parts on the highest dissimilarity level (32.4%). This group comprises the posterior body parts and appendages (uropods 1–2, most pleopods) but also the paired maxillipeds. The mean density per unit was approximately 24 individual epibionts. The abdomen, which hosts the highest numbers of epibionts on the posterior body end (mean: approximately 40 indE/unitA), is part of cluster II. A high degree of infestation (approximately 91 indE/unitA) is found on both pairs of gnathopods (between approximately 82 and 113 indE/unitA) and pereopods 1 and 5; these are combined in cluster III. The anterior appendages such as antennulae, antennae, maxillae 1 but also some pereopods are grouped in cluster V and have an average density of approximately 61 indE/unitA. Highest densities of epibionts were found on the antennae (107–130 indE/unitA). As in some other appendages the infestation of left and right antennulae and antennae are grouped in “nearest neighbor” clusters. The cluster with the lowest mean densities (cluster IV: 9.64 indE/unitA) comprises the majority of the pereopods, uropod 3, and parts of the telson.

Fig. 5 Dendrogram of the hierarchical cluster analysis using the densities of epibionts on each anatomical unit of all the specimens analyzed of *G. wilkitzkii*. I–V: clusters, *ant1* antennulae, *ant2* antennae, *max* maxillae, *mxp* maxilliped, *gna* gnathopods, *per* pereopods, *ple* pleopods, *uro* uropods, *tel* telson, *abd* abdomen, *L* left, *R* right



Discussion

Gulliksen and Lønne (personal communication) observed epibiotic ciliates on benthic living specimens of *G. wilkitzkii* earlier but a systematic description of species composition, distribution, and degree of infestation has been missing so far. We herein give the first sighting of epibiota on crustacea sampled in the sympagic environment. In earlier studies in the Svalbard area, sampling was restricted to ice that derived from the polar basin or to young ice that had formed over deep water (Gulliksen and Lønne 1989; Lønne and Gulliksen 1991). In this study we focused not only on drift ice but also on the underlying water body and the seafloor in shallow, coastal areas.

The ice amphipod *G. wilkitzkii* is released to the water column with the onset of summer melt and ice break-up and descends to the seafloor (Steele and Steele 1974; Arndt and Pavlova 2005; this study). The female:male ratio and the proportion of individuals infested with epibionts are the same for both groups, sympagic and pelagic/benthic living specimens of *G. wilkitzkii*. The analogy in population structure indicates the tight coupling between the two realms in shallow coastal areas. We therefore suggest that coupling processes exist both ways between sea ice and the underlying waters and the seafloor.

As stated earlier, the shallow pelagic/benthic realm serves as a retention (rather than a sink) area for sympagic fauna (Arndt and Pavlova 2005). Sampling occurred in fall, a period of ice manifestation after 3 months of open water at the study site. A relatively high percentage of pelagic and benthic living specimens hosting epibionts may indicate that the amphipod has spent the ice-free period in the water column and the benthos without molting. In *G. wilkitzkii*, egg development takes between 6 and 7 months (Poltermann et al. 2000) and during this period ovigerous females do not molt. The high degree of infestation with epibionts supports the reduced molting rate of ovigerous females. The molt cycle is not known for *G. wilkitzkii* but earlier studies indicate a slowed molting rate in cold (polar) waters along with a slow growth rate and longevity (Clarke 1982; Arntz et al. 1994). For freshwater gammarids Pöckl (1992) found a strong temperature dependency of the molt rate, which ranged between 50 and 84 days at 4°C for mature individuals. For *G. wilkitzkii* intermolt phases are assumed to be even longer. Specimens of *G. wilkitzkii* therefore provide a relatively persistent habitat for epibionts. Crustaceans act as a semi-permanent substrate for epibionts since molting, grooming, and the potential for abrasion (such as when moving in the narrow channels of the ice matrix) often dislodge the protozoan burden. Obligate epibiotic ciliates have evolved various forms of dispersal stages and rapid multiplication procedures to facilitate new settling on the new exoskeleton after ecdysis (Fenchel 1965; Threlkeld et al. 1993; Cook et al. 1998). The suctoria

Ephelota sp. (this study), peritrich and chonotrich ciliates perform exogenous budding by external protrusion of the parental cell whereas other suctoria of the genera *Cryptacineta* and *Acineta* produce endogenous buds by plasma invagination (Hausmann et al. 2003). The suctorians are ciliated only as dispersal stage (exo- or endogenous bud) before they settle. On new, mostly species-specific substrates and by morphogenesis they develop to sessile mother cells (Hausmann et al. 2003). The “mature” stage bears tentacles that catch prey such as the dispersal stages of sessile epibionts and motile protozoan epizotes (Cook et al. 1998). The majority of suctorian species live in fresh water (Hausmann et al. 2003) and show no or little site specification (Cook et al. 1998; Fernandez-Leborans and Tato-Porto 2000b). Predation success of suctorians is, however, facilitated if either the substrate (host) or the medium (ambient water circulation, respiratory current) moves.

The stages involved in food uptake in peritrich ciliates are normally sessile (stalked zooids) and live on various substrates. They prey on protozoans and bacteria (Gilbert and Schröder 2003). Colonial societies are widely distributed. The nonfeeding dispersal stage is a motile telotroch. It may transform into a swimming, “feeding” zooid, which is capable of reproducing itself or of transforming back into a telotroch (Gilbert and Schröder 2003). Growth and reproduction of peritrich ciliates can be very rapid (Gilbert and Schröder 2003) and involve longitudinal fission or budding (Hausmann et al. 2003). On crustaceans, peritrich ciliates often infest the buccal area and anterior body part (including gills; Fernandez-Leborans and Tato-Porto 2000a) or the postabdominal region (Cook et al. 1998) where they take advantage of either the respiratory or filter-feeding current (Clamp 1993; Cook et al. 1998) or the particle-rich efflux from the cloaca (Cook et al. 1998; Gilbert and Schröder 2003). Whether the process of multiplication and dispersion is slowed in polar waters is not known.

In sea ice ciliates are regularly part of a diverse microbial community (Lizotte 2003) but are only represented by motile species of different genera from those found in this study (e.g. *Peritromus*, *Euplotes*, Friedrich and Hendelberg 2001). Epibiotic ciliates affect feeding, swimming, respiration, reproduction, and survival (Threlkeld et al. 1993). The specimens of *G. wilkitzkii* we sampled in the pelagic/benthic were, however, in good physical shape, had filled guts, and were in a state of reproduction and mating (“prae-copula”). Because amphipods are the only macrofaunal crustacea that permanently inhabit sea ice, and sessile ciliates have not been observed earlier in the ice ecosystem but are common on pelagic and benthic-living crustacea and other invertebrates (e.g. Threlkeld et al. 1993; Fernandez-Leborans 2000; Fernandez-Leborans and Tato-Porto 2000a, 2000b; Gilbert and Schröder 2003), the only way infestation with epibionts could occur on *G. wilkitzkii* is when this species is released to the water column at ice melt. Once settled on *G. wilkitzkii* rapid growth and

multiplication rates of the various ciliate species facilitate effective dispersion. In addition, transmission from one specimen to the other is enabled during mate guarding (prae-copula), copulation, and embryo–female contact (Cook et al. 1998). The appendages showing highest densities of epibionts are the gnathopods and antennae. Their diverse utilization in food uptake, intraspecific communication, and grooming make these appendages susceptible to infestation. Because ciliates are known to actively seek the best conditions for settling they may prefer the anterior end of the amphipod because of the strong water movements due to the respiratory current (Arndt 2002). *Podophrya* and *Epistylis* concentrated on the anterior body units of *G. wilkitzkii*, *Acineta* was mostly found posteriorly, and in *Ephelota* and *Cryptacineta* there was no obvious site specification on the host (this study). Even though probably slowed in polar waters, a high potential for dispersion and effective transmission processes along with a low site specification may compensate for the relatively low host abundance in the pelagic/benthic environment.

During winter and spring the onset of ice formation and the increased impact of drift ice in shallow areas may enable the amphipod to re-colonize the ice. In Fig. 6 we illustrate the “closed-cycle hypothesis” for ice amphipods in a simplified scheme, which becomes valid in shallow areas (shelves, sea mountains). The ice amphipods may reach the ice surface either by swimming upward or by hovering along the seafloor. The re-colonized ice eventually leaves the shelf and moves into deeper waters. This means that infested ice amphipods can be found in sea ice over deep water if the ice has formed or traveled over shallow waters. The correspondence in the rate of infested specimens from the pelagic/benthic with the sympagic environment confirms the origin of the sympagic specimens from the pelagic/benthic realm. Abrasion while moving in the interior of sea ice and molting may successively liberate the amphipod from epibiontic burden and may explain why infested *G. wilkitzkii* have not been observed earlier in drift ice over deep water.

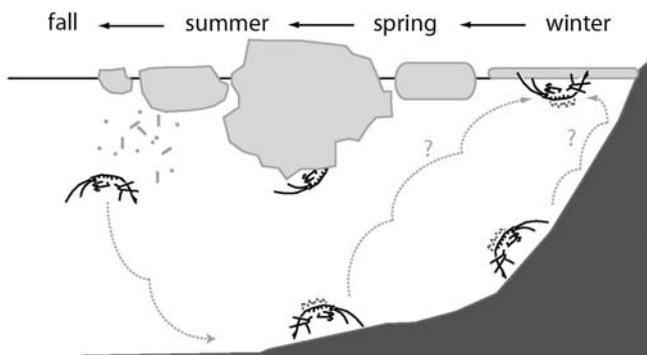


Fig. 6 Schematic illustration showing the presumed cycling of *G. wilkitzkii*; infestation with epibionts is indicated on the dorsal part of benthic-living specimens; for explanation see text

Colonization of new ice regularly occurs by those organisms exploring the vicinity of older ice (Arndt and Lønne 2002) and—in shallow (coastal) areas—by benthic organisms or benthic living “immigrants” such as *G. wilkitzkii*. The occurrence of the benthic decapod *Eualus gaimardii* in the ice at our sampling site is a good indicator for the existence of benthos–sympagic coupling processes (personal observation). The coupling is weakened with distance from coastline and increasing water depth; benthos–sympagic organisms are frequently found within the 10-m depth contour (Steele and Steele 1974; Cross 1982). At our sampling site water depth was greater (50 m) but sampling occurred in drift ice that moved off shore.

When entering the pelagic/benthic environment *G. wilkitzkii* provides a substrate for a diverse epibiontic ciliate community, which has not been described in earlier studies (Morado and Small 1995; Fernandez-Leborans 2000; Fernandez-Leborans and Tato-Porto 2000a; 2000b). Suctorian ciliates of the genus *Ephelota* have been found as epibionts on various taxa of crustacea: copepods, decapods, euphausiids, and on the caprellid amphipod *Caprella acutifrons* (Fernandez-Leborans and Tato-Porto 2000b). However, in this study we give the first recording of this genus on a gammarid amphipod. The genus *Cryptacineta* and its only species *C. operta* have been found on two gammarid species sampled in Lake Baikal, *Carinogammarus seidlizi* and *C. wagneri* (Swarzewsky 1928) and, therefore, we present herein the first recording of this ciliate in the marine environment. Ciliates of the genus *Acineta* have been described as epibionts on decapods, cladocerans, copepods, ostracods, isopods, and in numerous amphipod species (Fernandez-Leborans and Tato-Porto 2000b). The majority of these amphipod species belong to the family Gammaridea and were sampled in Lake Baikal. Only a few species have been attributed as epibionts in the marine environment (e.g. the corophoid amphipod *Corophium volutator* is basibiont for *Acineta corophii*, the amphipod *Talorchestia* for *A. talitrus*; Fernandez-Leborans and Tato-Porto 2000b). Ciliates of the genus *Podophrya* have been found on decapods (*P. sandi* on *Cambarellus patzcuarensis*) and copepods (*P. flexilis* on *Cyclops*; Curds 1986). The epibiontic species *P. niphargi* was described for the gammarid *Niphargus strouhali* (Fernandez-Leborans and Tato-Porto 2000b). The peritrich ciliate *Epistylis* has been observed as epibiont on many taxa of crustacea (copepods, decapods, cladocerans, branchiopods, and amphipods). Among the amphipods, *Gammarus tigrinus* showed a high diversity of epibiontic *Epistylis* species: *E. gammari*, *E. nitocrae*, *E. ovalis*, *E. thienemanni*, and *E. zschokkei*. Species of *Epistylis* have also been described on *G. oceanicus*, *G. salinus*, *G. pulex* (Fernandez-Leborans and Tato-Porto 2000a), and *G. duebeni* (Dunn and Dick 1998).

The correspondence in population structure and the proportion of infested amphipod specimens in both the sympagic and the pelagic/benthic environment along with the annual ice cycle in the sampling area give high

evidence for the existence of sympagic–benthic coupling processes in *both* ways between the ice environment and the underlying waters in shallow ice-covered seas. Recently, the sympagic occurrence of the benthic amphipod *Anonyx sarsi* in the ice pack of the western Barents Sea has been interpreted as a vertical migration in search of food (Werner et al. 2004). In allochthonous species vertical migration can be part of the life-cycle or life strategy (Melnikov and Kulikov 1980). Being an autochthonous sympagic species *G. wilkitzkii* does not perform vertical migration but shows only pelagic occurrence along the marginal ice zone (Werner et al. 1999; Arndt and Pavlova 2005) and near shore (Steele and Steele 1974; Weslawski 1994; Poltermann 1997; Arndt and Pavlova 2005) during ice break-up and summer melt. In this study we have demonstrated that epibiota may serve as external markers that illustrate the capability of *G. wilkitzkii* to survive ice-free periods as a pelagic/benthic-living species in coastal retention areas and to eventually return to the ice environment using near-shore ice as a stepping-stone for re-colonization.

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