

Timing of Ice Algal Grazing by the Arctic Nearshore Benthic Amphipod *Onisimus litoralis*

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ABSTRACT. Sea ice algae have been widely discussed as a potential food source for pelagic and benthic animals in ice-covered waters, specifically in the light of current substantial changes in the Arctic ice regime. Stomach and gut contents of the Arctic nearshore lysianassid amphipod *Onisimus litoralis* sampled from February to May 2003 indicate that Arctic ice algae were dominant food no earlier than the onset of ice melt. Crustaceans, common prey in a previous study, were absent in stomachs and guts during the survey period. Our data support the concept that sea ice-derived organic carbon is of specific relevance for Arctic plankton and benthos during the period of ice melt.

Key words: Arctic, sea ice, Barrow, fast ice, amphipods, *Onisimus litoralis*, ice algae, diatoms

RÉSUMÉ. On a souvent discuté du fait que les algues de glace de mer pourraient être une source d'alimentation pour les animaux pélagiques et benthiques des eaux recouvertes de glace, surtout à la lumière des changements considérables qui caractérisent le régime de glaciation de l'Arctique. Le contenu de l'estomac et des intestins des amphipodes lysianassides *Onisimus litoralis* en proximité des rives de l'Arctique qui a été échantillonné de février à mai 2003 indique que les algues de glace de l'Arctique étaient dominantes pas plus tôt qu'au moment de la fonte des glaces. Les crustacés, qui étaient une proie courante dans le cadre d'une étude antérieure, ne se retrouvaient pas dans les estomacs et les intestins des animaux au cours de la période d'échantillonnage. Nos données viennent soutenir le concept selon lequel le carbone organique dérivé de la glace de mer revêt une importance particulière pour le plancton de l'Arctique et le benthos pendant la période de la fonte des glaces.

Mots clés : Arctique, glace de mer, Barrow, banquise côtière, amphipodes, *Onisimus litoralis*, algues de glace, diatomées

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INTRODUCTION

Sympagic amphipods are the best-studied metazoans living at the ice-water interface in the Arctic (e.g., Werner, 1997; Poltermann, 2000; Gradinger and Bluhm, 2004; Gradinger et al., 2009a). Under-ice amphipods are an important food for arctic cod (*Boreogadus saida*) as well as birds in the Arctic (Bradstreet et al., 1986). While several Arctic amphipod species are endemic to the multi-year sea ice cover of the central Arctic Ocean, benthic species like *Onisimus litoralis* are common in nearshore seasonal ice regimes (Carey and Boudrias, 1987; Weslawski et al., 2000). In addition to benthic amphipods, juvenile and larval stages of benthic invertebrates (e.g., polychaetes) frequent the nearshore fast ice where they feed on the highly abundant algae in early spring (e.g., Gradinger et al., 2009b).

High Arctic ice-endemic species feed directly at the ice-water interface (Werner, 1997), but less is known about the specifics of how nearshore amphipods and pelagic copepods feed on ice algal matter. The most detailed nearshore case study highlights the feeding of *Calanus glacialis* close to the ice-water interface in Hudson Bay during its night vertical migration (Runge et al., 1991), although it was not

resolved whether this species feeds directly at the ice or ingests organic matter released from the ice during periods of ice melt. The nearshore amphipod *O. litoralis* also ingests sea ice algal matter, in addition to crustaceans, in spring and early summer (Carey and Boudrias, 1987). However, again it is unclear whether *O. litoralis* grazes on the diatoms at the ice-water interface (similarly to e.g., *Apherusa glacialis*, Werner, 1997) or ingests ice algae after their release from a melting ice sheet, for example, from the sediment after it sinks to the sea floor.

Algal food concentrations within the fast ice along the Alaskan coast start to increase significantly in March and continue to occur at levels orders of magnitude above phytoplankton concentrations until ice melt (Horner and Schrader, 1982; Manes and Gradinger, 2009). These algal layers are close to the ice-water interface. We wanted to extend Carey and Boudrias' (1987) observations and wanted to know (1) whether *O. litoralis* ingests ice algae already at low late-winter food concentrations, or only later in the season when ice algal material is released from the ice, and (2) what concurrent algal concentrations were during the sampling periods to assess food availability for herbivorous feeding. We therefore studied the seasonal presence of ice

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algae in the guts and stomachs of *Onisimus litoralis* over periods of ice growth (no algal release) well into the ice-melt regime.

METHODS

We conducted our investigation on nearshore fast ice close to Barrow, Alaska at 71°20' N, 156°42' W. The fast ice along the Alaskan coastline forms in November to December and reaches a thickness of 1.5–1.8 m by April (Gradinger et al., 2009b). Breakup usually occurs between late June and mid-July. The ice, attached to the shore and anchored to the sea floor by up to 20–25 m deep keels (Macdonald, 2000; Mahoney et al., 2007a, b), extends several kilometres out onto the Chukchi and Beaufort shelves.

Sampling was conducted on 12–17 February, 1–5 April, and 27–30 May 2003 in water depths less than 6 m. Four replicate sea ice cores per sampling period were taken with an ice corer, cut into 10 cm long sections, and melted directly to determine algal pigment concentration (Gradinger et al., 2009b). Chlorophyll concentrations were also determined from the water column samples collected with a Kemmerer bottle and sediment samples collected with a sediment corer (further methodological details are provided in Gradinger et al., 2009b). Gut and stomach contents analyses were performed on amphipods collected in baited minnow traps lined with mosquito screen, which were deployed immediately under the sea ice for time periods of up to 24 hours. Bait was wrapped in filter paper and screen material to prevent ingestion. Collected animals were fixed in 4% formaldehyde immediately after sampling and transported to the home lab. We randomly selected three animals from each sampling date and dissected stomachs and guts, which were placed on a microscope slide and microscopically examined at a magnification of 400× using a ZEISS Axiovert inverted microscope. For each time period, we determined the occurrence of identifiable particles in 20 randomly chosen fields of view of the stomach and gut region of each animal. As a relative measure of food composition, we calculated the relative frequency (%) at which certain food items were found in these fields of view (100%: item observed in all fields of view). Digital pictures were taken with a Canon Rebel digital camera at highest resolution and were enhanced using GraphicConverter. Sizes of ingested diatoms were measured using ImageJ (vers. 1.36b). We compared the gut and stomach content dynamics with sea ice algal, phytoplankton, and sediment chlorophyll *a* values (data from Gradinger et al., 2009b).

RESULTS AND DISCUSSION

The gut contents of *Onisimus litoralis* clearly shifted in its composition with time (Fig. 1, Table 1). Pennate diatoms typical for sea ice habitat in Alaskan fast ice (Horner and Schrader, 1982; Gradinger et al., 2009b; Manes and

Gradinger, 2009) were observed in 100% of all fields of view of all animals examined in May, while we observed only one single diatom cell in a total of 60 fields of view studied in three animals collected in February (Table 1). February stomach and gut contents were dominated by aggregates consisting of very small particles (< 5 µm in diameter) with no recognizable biological features. The observations of the April animals revealed intermediate conditions, with ice diatoms in the stomachs and guts of one animal, while those of the other two animals were nearly empty, with no diatoms observed (Fig. 1). All diatoms observed within the guts were pennates and completely empty and clean. The length of the diatom frustules varied between 15 and 151 µm, with a mean value of 47 ± 27 µm (Fig. 1).

The results support the observations by Carey and Boudrias (1987) that sea ice algal diatoms are contributing to the nutrition of *O. litoralis* under coastal fast ice in late spring. The relative frequency of diatoms in the guts of this species followed the seasonal increase in ice algal biomass from 7 to 329 µg of chlorophyll per litre in the bottom 10 cm of the fast ice (Gradinger et al., 2009b; Table 1). We exclude phytoplankton and benthic microalgae as nutritional sources for the amphipods because their biomass remained low throughout the period from February to May (< 1 µg chl /l for phytoplankton, ≤ 1 µg chl/g DW for sediment). The size and taxonomic composition of organisms in the amphipod digestive tracts support this exclusion: we observed only pennate diatoms, which are typical for fast ice algal communities, but are not a significant contributor to phytoplankton biomass at that time of the year (Horner and Schrader, 1982; Manes and Gradinger, 2009). In addition, cells of the sizes observed (frustule lengths of 15 to 151 µm) are basically absent from the water column at that time of the year, while they contribute from 53% to 85% of all particles contained within the ice bottom community during the ice algal bloom periods (Manes and Gradinger, 2009). In May, ice melt had started (Gradinger et al., 2009b), which likely widened the brine channels within the ice (Krembs et al., 2000) and probably made algae more easily accessible for *O. litoralis*' mouthparts and also caused flushing of ice algae out of the ice into the ice-water interface region (Gradinger et al., 1991; Michel et al., 2002). Our data indicate that with the onset of ice melt, *O. litoralis* switched from a more benthic detritivorous feeding style (as evidenced by the high sediment load in the guts and stomach) to an ice algae-dominated nutrition. Similarly, Carey and Boudrias (1987) found fecal pellets to be dominated by ice diatom frustules in May, although substantial amounts of crustacean parts were also present. Increased abundance of ice algae alone, as measured in early April (Table 1), did not cause substantial algal ingestion by *O. litoralis*. This result agrees with Carey and Boudrias' (1987) findings of a crustacean-dominated diet in April except in a high-density spot of *O. litoralis* where stomachs and guts had a relatively high diatom content in that month. Although algal concentrations were higher in the ice than in the water column and at the sea floor in February, apparently they were either

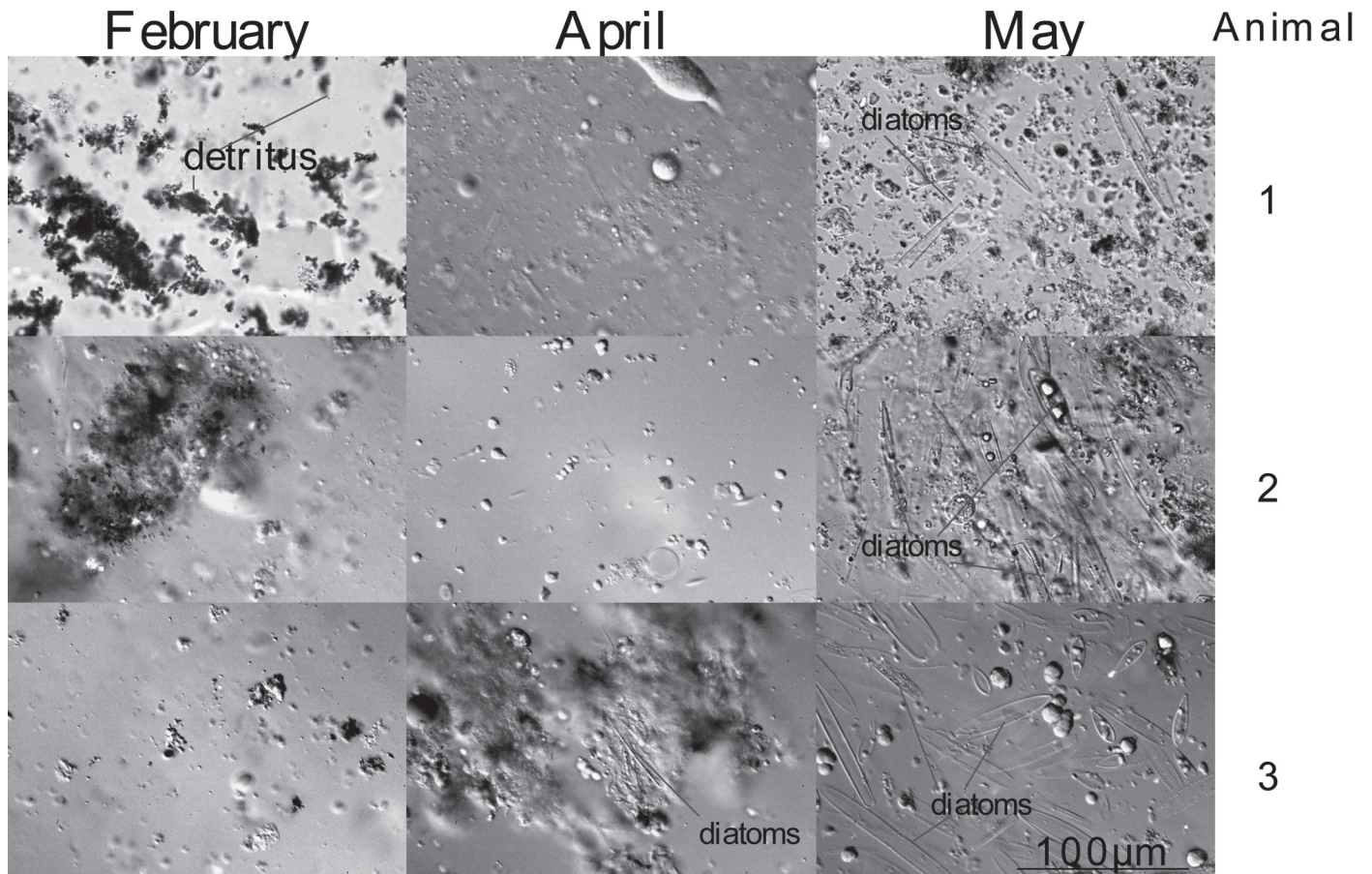


FIG. 1. Stomach and gut contents of three randomly selected amphipods collected in February, April, and May 2003. Note the high relative abundance of pennate diatoms in the May samples. All pictures taken at $400\times$ magnification.

TABLE 1. Composition of stomach and gut content and algal availability for *Onisimus litoralis* in nearshore Arctic waters off Barrow, Alaska. Percent values are the fraction of images that showed a certain group of food item at a given time.

Sampling Event (Month 2003)	Relative Frequency of Particles in Stomach and Guts (% Fields of View)			Chlorophyll <i>a</i> Concentration		
	Sediment Particles ($< 5\mu\text{m}$)	Animal Remains	Pennate Diatoms	Sea Ice ($\mu\text{g/l}$)	Water Column ($\mu\text{g/l}$)	Sediment ($\mu\text{g/g}$ dry weight)
February	83.3	0.0	1.7	7.4 ± 0.7	0.0 ± 0.0	0.5 ± 0.6
April	16.7	0.0	33.3	71.4 ± 16.1	0.1 ± 0.0	0.2 ± 0.4
May	33.3	0.0	100.0	329.3 ± 42.0	0.9 ± 0.0	1.0 ± 0.3

inaccessible or unattractive as a food source (or both) at that time.

The mouthparts of lysianassid amphipods are not typically adapted to algal grazing (Arndt et al., 2005). The two related offshore under-ice amphipod species *O. glacialis* and *O. nanseni*, like other lysianassids, have mouthparts suitable for cutting, crushing, and grinding crustaceans and the like (Arndt et al., 2005), which were frequently found in *O. litoralis* gastrointestinal systems in the Beaufort Sea study (Carey and Boudrias, 1987), though interestingly, not in our study. Information on mouthparts of *O. litoralis* is unavailable to our knowledge, but *O. glacialis* has a forceps-like dactylus on its gnathopod 2 that was interpreted as allowing the species to collect small particles such as diatoms (Arndt et al., 2005). Such a structure, if it also exists in the

evolutionary closely related species *O. litoralis* (Vader et al., 2005), would facilitate the switch to algae-based nutrition in late spring.

Our data narrow the time window over which cryobenthic coupling of *O. litoralis* occurs to the ice melt season. The question remains whether *O. litoralis* ingests the ice algal material at the bottom ice in May, or later, after released ice algal material sinks to the sea floor. Low benthic chlorophyll concentrations throughout the sampling period would support the former, but in that case one would also expect specimens sampled in April to have consumed more diatoms. Possibly, the energetic cost of algal ingestion is worth the effort only when algal concentrations are very high, or algae are accessible only when they melt out of the sea ice. Our observations augment the current widely

used stable isotope approach, which is restricted in its temporal resolution by the low isotopic turnover of *O. littoralis* (Kaufman et al., 2008). These observations also show that gut and stomach analysis provides important information on the relevance of ice diatoms for the nutrition of Arctic amphipods.

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