

# Distribution and growth of benthic macroinvertebrates among different patch types of the littoral zones of two arctic lakes

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## SUMMARY

1. To evaluate the effect of habitat patch heterogeneity on abundance and growth of macroinvertebrates in arctic lakes, macroinvertebrate abundance, individual biomass, and potential food resources were studied in three patch types in two arctic lakes on the Alaskan North Slope near the Toolik Lake Field Station. An experiment was conducted to determine which sediment patch type supported higher growth rates for *Chironomus* sp., a commonly occurring macroinvertebrate.

2. Potential organic matter (OM) resources were significantly higher in both rock and macrophyte patches than in open-mud patches. Total macroinvertebrate densities in both lakes were highest in rock patches, intermediate in macrophytes and lowest in open-mud. The open-mud patches also had lower species richness compared with other patch types. Additionally, individual biomass for one clam species and two chironomid species was significantly greater in rock patches than in open-mud.

3. In a laboratory experiment, *Chironomus* showed two to three times greater mass increase in sediments from macrophyte and rock patches than from open-mud patches. Rock and macrophyte experimental sediments had at least 1.5 × the percentage OM as open-mud sediments.

4. Chlorophyll *a* appeared to be the best predictor for invertebrate abundances across all patch types measured, whereas OM content appeared to be the variable most closely associated with *Chironomus* growth.

5. Our results combined with previous studies show that the relationships between macroinvertebrate community structure, individual growth, and habitat heterogeneity are complex, reflecting the interaction of multiple resources, and biotic interactions, such as the presence or absence of a selective vertebrate predator (lake trout, *Salvelinus namaycush*).

*Keywords:* *Chironomus* growth, chlorophyll *a*, littoral zone, organic matter resources, *Pisidium* individual biomass

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## Introduction

Benthic macroinvertebrates in lake sediments exhibit heterogeneous spatial patterns which coincide with heterogeneity in both abiotic (e.g. Dinsmore,

Scrimgeour & Prepas, 1999; Heino, 2000) and biotic factors (Johannsson & Beaver, 1983; Johnson, Boström & van de Bund, 1989; Vos *et al.*, 2000). Organic matter (OM) resources in lake sediments are heterogeneous because of the presence or absence of macrophytes, localised currents, pelagic primary production, wave action, or degree of allochthonous inputs (Håkanson, 1977; McGarrigle, 1980). Macrophytes can enhance sedimentation (Håkanson, 1977), contribute directly to the particulate organic pool used by invertebrate populations as a food source (Smock & Stoneburner, 1980; Bowen, 1987; James *et al.*, 1998), or contribute indirectly through leaching of dissolved OM, which is processed by the microbiota, converted to particulate OM and then utilised as food by sediment-dwelling macroinvertebrates (Wetzel & Manny, 1972; Paerl, 1978; Bowen, 1987).

Macroinvertebrates use a variety of OM resources. Algae are an important food source for chironomids (Johannsson & Beaver, 1983; Rasmussen, 1985) as are bacteria (Johnson *et al.*, 1989; Yeager, Foreman & Sinsabaugh, 2001). Although commonly considered grazers and filter feeders, gastropods and fingernail clams often commonly feed on detritus (Krezoski, Mozley & Robbins, 1978; Hamill, Qadri & Mackie, 1979; Holopainen & Jónasson, 1983) and therefore may benefit nutritionally from macrophyte detritus and associated algae and bacteria. Cole & Weigmann (1983) found that the size and abundance of the benthos was significantly associated with the percentage of OM in the sediments. Laboratory experiments have shown that chironomids grow faster on sediments with higher OM content, providing evidence that chironomids can be food limited (Rasmussen, 1985; Vos *et al.*, 2002).

Habitat heterogeneity in lake sediments also alters predator–prey interactions (e.g. Crowder & Cooper, 1982). The importance of predation in structuring lake benthos has been a major focus in aquatic research (e.g. Diehl, 1992; Crowl *et al.*, 1997). Macrophyte beds often harbour high densities of macroinvertebrates by providing refuge from predatory fish (Crowder & Cooper, 1982; Gilinsky, 1984; Hershey, 1985). Fish generally feed selectively on larger macroinvertebrates (Merrick, Hershey & McDonald, 1992), which can result in an indirect effect on smaller taxa because of release from competitive pressure (Hershey, 1990).

The objectives of this study were to identify differences in sediment resource heterogeneity of

different patch types and to investigate effects of these differences on benthic invertebrate distribution, abundance and growth. Sampling of different patch types was performed at one depth within the littoral zone of an arctic lake to isolate resource effects by eliminating depth-related factors such as temperature or oxygen concentrations. An experiment was also conducted to evaluate *Chironomus* sp. growth response to sediments from different patch types. Three hypotheses were tested: (i) species composition and abundance varies among patches; (ii) resources vary among patches; and (iii) species composition, abundance and growth are affected by patch resource availability.

## Methods

### Study area

This study was conducted at Toolik Lake Field Station (68°38'N, 149°43'W) located in the foothills of the North Slope of the Brooks Mountain Range in arctic Alaska (Fig. 1). Benthic macroinvertebrates in lakes of the region are dominated by larval chironomids, a few species of molluscs and a small variety of other taxa (Hershey *et al.*, 1999). Two small oligotrophic lakes near Toolik Lake, E-1 (surface area 6.2 m, max depth 8 m) and I-4 (surface area 8.2 ha, max depth 8 m), were selected for sampling based on size and accessibility. Two fish species occur in E-1, arctic grayling (*Thymallus arcticus*) and slimy sculpin (*Cottus cognatus*). Lake I-4 contains grayling and sculpin as well as lake trout (*Salvelinus namaycush*), round whitefish (*Prosopium cylindraceum*), and burbot (*Lota lota*).

The lake bottoms are characterised by low physical heterogeneity and contain only three distinct patch types: macrophyte beds, rock and bare sediments. Littoral areas have all patch types while profundal areas consist of soft open-mud only. Macrophyte beds (composed mainly of mosses and *Nitella*) are common although they have little vertical structure (Hershey, 1985). Lake sediments in the region are characterised by high concentrations of iron and manganese in the sediments (Sugai & Kipphut, 1992) and open water is distinguished by low nutrient availability (Whalen & Cornwell, 1985). Additionally, oxygen is generally near saturation (O'Brien *et al.*, 1992) because of low water temperatures and low productivity.



Fig. 1 Location of study lakes, E-1 and I-4, near Toolik Lake on the North Slope of the Brooks Mountains, Alaska, U.S.A.

### Mapping

The physical structure of the benthic surface was mapped for identification of patch types present and to locate suitable sampling points. Four longitudinal transect lines were placed along the bottom of each lake. The transects were composed of coloured weighted rope of 1 cm diameter and 75 m long, marked off in 1 and 5 m increments. A 250 m transect was positioned along the shore to select random starting points for transects placed into the lake. The benthic transects were placed at the shoreline, anchored, drawn out perpendicularly into the lake and fixed into place. The transects were used as guides to map the sediment surface and to locate patches from the surface of the lake. A remotely operated vehicle (VideoRay<sup>®</sup> 2002 model, VideoRay LLC, Phoenixville, PA, U.S.A.) was used to record the physical appearance of the sediment surface along these transects. From the resultant video, patches >1 m<sup>2</sup> were characterised as rock, macrophyte or open-mud. Patch type, depth and distance from shore were then estimated.

Dissolved oxygen concentration, pH and temperature in both lakes have been monitored approximately three times per summer since 2000 by the Arctic

Tundra Long-Term Ecological Research Program (LTER). Data are available at [http://ecosystems.mbl.edu/ARC/data\\_doc/lakes/lakedefault.htm](http://ecosystems.mbl.edu/ARC/data_doc/lakes/lakedefault.htm). Example values for these parameters collected during the current study at the 2 m depth where macroinvertebrate and OM resources were evaluated were 9.2 mg L<sup>-1</sup>, 7.5 and 8.6 °C, respectively, on 18 July 2003 in Lake E-1 and 10.49 mg L<sup>-1</sup>, 7.1, and 8.8 °C, respectively, in Lake I-4 on 5 August 2003. Secchi depth in E-1 was 4.1 m. Secchi depth was not measured in Lake I-4 on 5 August 2003.

### Benthic invertebrate and resource sampling

Sampling was conducted at 2 m on 25 July in Lake E-1 and 26 July in Lake I-4. This depth was selected because the objective was to evaluate the effect of patch type on macroinvertebrates independently of depth, and all patches were represented and easily accessible at 2 m. Three replicate samples for macroinvertebrates and three replicates for sediment resources were collected from each of the patch types in Lakes E-1 and I-4 by a means dependent on the patch substrate type. Macrophyte-covered and open mud sediment patches were sampled by snorkelling using an acrylic core tube with an inside diameter of 9.3 cm

and an area of 68 cm<sup>2</sup> (Goyke & Hershey, 1992). Previous studies in Toolik Lake (Hershey, 1985; Goyke & Hershey, 1992) showed that this method permits precise sampling of habitats with relatively low variability. Sediments covering rock were sampled by using a remote bilge-like pump adapted to vacuum water and sediments. The area sampled was visually estimated to equal the cross-sectional area of the diver core used to sample macrophyte and open mud patches. Soft sediment macroinvertebrate samples were processed in the field by washing the cores through a 200 µm net and preserved in 95% ethanol. Note that to fully characterise the macroinvertebrate community in these lakes, many more samples would be required. However, as our objective was to evaluate resource and macroinvertebrate differences between habitat types, we focused effort on precise sampling at the depth where patch types were most variable and evaluated sediment resources as well as macroinvertebrate communities.

Sediment resource samples were transported to the laboratory for further processing. Overlying water from the cores was siphoned off the surficial sediments. Two aliquots were removed from the cores by a syringe subsampler (4.9 cm<sup>2</sup>) for subsequent OM (top 5 cm) and chlorophyll *a* (top 2 cm) analyses. To process sediments sampled from rock patches, the total volume of sediment gathered in the field was measured in a 1 L volumetric beaker. One-fourteenth of sediment (ratio of the subsampler area to the area of a diver core) was removed from the beaker for later chlorophyll *a* analysis and the remaining sediment was saved for OM analysis.

Subsamples for OM resource analyses were processed on a Thermoquest® EA1000 (Thermo Electron Corporation, Waltham, MA, U.S.A.) to determine TN, TC, and C : N ratio. In addition, sediment samples for per cent OM were dried at 105 °C to a constant weight, combusted at 550 °C, rewet and redried at 105 °C. Per cent OM was calculated according to Wetzel & Likens, 2000. Benthic chlorophyll *a* was measured in the laboratory using a fluorometer (after Steinman & Lamberti, 1996). Chlorophyll *a* concentrations were reported in gram per square metre.

Macroinvertebrates were sorted from preserved samples, enumerated and identified to the lowest taxonomic level possible. Species richness, evenness and Shannon–Wiener diversity index were calculated in order to compare aspects of species diversity

between patch types. Organisms were separated into cohorts, if possible, by visual inspection of length-frequency histograms. Mean individual biomass of each cohort of each taxon that was common to all patch types was calculated from length measurements using the following equations (Chironomidae, Tany-  
podinae: Smock, 1980; molluscs: A. E. Hershey, unpublished data).

Chironomidae –

$$\ln \text{ dry wt (mg)} = -5.279 + 2.32 \ln(\text{length, mm})$$

Tany-  
podinae –

$$\ln \text{ dry wt (mg)} = -5.573 + 2.41 \ln(\text{length, mm})$$

$$\text{Valvata} - \ln \text{ dry wt (mg)} = -8.724 + 0.78 (\text{length, mm})$$

Sphaeriidae –

$$\ln \text{ dry wt (mg)} = -9.784 + 3.18 \ln(\text{length, mm})$$

Larval chironomid length was measured using a Wild dissecting microscope coupled to a camera lucida, a Numonics GridMaster digitizer (Montgomeryville, PA, U.S.A.) and an Easydij v. 8.8. image analysis system (GeoComp, Ltd. Golden, CO, U.S.A.). Lengths for Chironomidae were computed as the distance (mm) from the anterior end of the head capsule to the posterior end of the abdomen. Lengths (mm) for molluscs were computed as the maximum shell dimension.

#### *Growth experiment*

Sediments from different patch types were gathered to serve as chironomid growth substrata. The sediments used for the first three treatments were unconsolidated sediments collected from rock surfaces and interstitial spaces, unconsolidated sediments beneath macrophytes and open-mud sediments from Lake E-1. The fourth treatment was open-mud obtained from Lake E-5, a lake experimentally fertilised by the arctic LTER program to increase ambient loading of N and P by approximately fivefold. Sediments for all treatments were sieved (500 µm) to remove large macroinvertebrates and then homogenised. Prior to adding the sediments to growth chambers, subsamples of each sediment type were dried and stored for later sediment analysis. Treatments were randomly added to 1 L plastic growth chambers to a depth of 4–5 cm (2.5 cm for rock) and topped off with lake water that had been sieved to remove zooplankton.

*Chironomus* sp. was selected as an experimental organism to evaluate the effect of resource quality on

macroinvertebrate growth because it is widespread in lakes in this region (Hershey *et al.*, 2006), although it typically is not abundant in the littoral zones (e.g. Hershey, 1985). *Chironomus* larvae were collected from Lake GTH-112, which is easily accessible by road from the Toolik Lake station and was known to support a high density of *Chironomus* (Hershey *et al.*, 2006). Larvae were separated into size classes/instars. Only third instar larvae were chosen for this experiment to provide a uniform starting size and still allow for measurable growth. Twenty chironomids were randomly selected and weighed to provide an initial estimate of mass. Larvae were sorted into groups of 10 and then introduced to a randomly selected treatment.

Six replicates of each of the four treatments were arranged into six arrays, which were attached in a circular arrangement. The arrays were randomly placed in two small plastic pools (approximately 1.8 m diameter, approximately 0.3 m depth) on the shore of Toolik Lake on 3 July 2003. Water flow into the pools was introduced via a pump submerged in Toolik Lake to ensure stable water temperatures consistent with temperatures of the surface waters of Toolik Lake. Three light level readings at 2 m depth were taken by a Licor® meter (Licor Biosciences, Lincoln, Nebraska, U.S.A.) and averaged. Shade cloth covered the top of the pools to simulate the light levels found at 2 m depth and to prevent excess heating of the chambers. Water temperatures were monitored daily during the experiment.

*Chironomus* larvae from three randomly chosen arrays were harvested on 23 July, 3 weeks after the start of the experiment. Larvae were sieved from sediment, measured and weighed wet, then dried at 50 °C for 48 h to determine dry mass. The remaining three arrays of replicates were harvested on 8 August (week 5) in the same manner. Samples for sediment resource analysis, as described above, were obtained from each container following each harvest.

### Data analyses

Two-way analysis of variance (ANOVA) with lake, patch type, and lake by patch type as effects was performed on macroinvertebrate abundances, resource variables and diversity indices. Tukey's Honestly Significant Difference (HSD) was used to test for differences among patch types at a significance level of 0.05. Abundances in the two lakes were pooled together only when a patch effect was significant and no other effects (lake or interaction) were noted. Otherwise, all patch types were analysed individually.

Principal component analysis (PCA) was conducted on %TN, %TC, %OM, C : N and chlorophyll *a* to eliminate multicollinearity effects when conducting multiple regression analyses with correlated variables; most resource variables were highly correlated. The procedure resulted in formulation of new uncorrelated variables. Each variable was specified to belong primarily to the principal component on which it had the highest loading. Multiple regression was then performed on the principal components generated.

ANOVA was used to analyse for differences in mean individual biomass of taxa common to all patch types. Patch means were compared with Tukey's HSD. Biomass response to treatment and date, and treatment by date interaction in the growth experiment was analysed using two-way ANOVA.

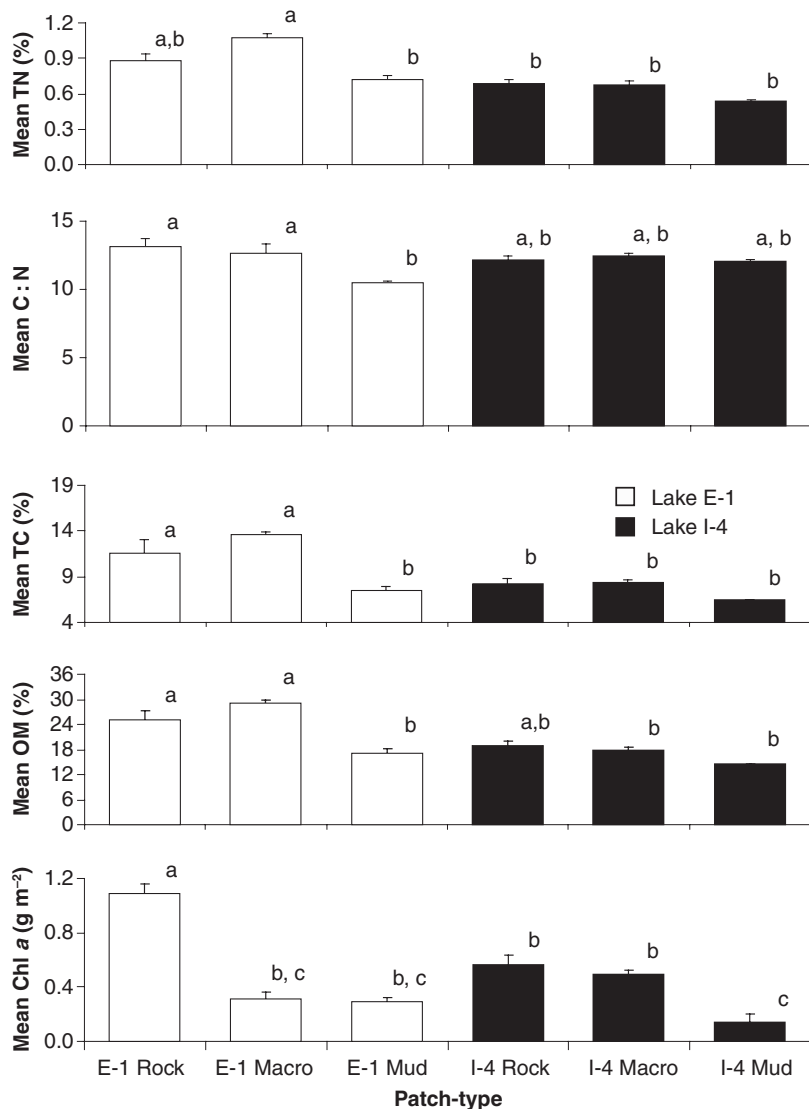
## Results

### Mapping results

The mean bottom areas covered by rock, open-mud sediments and macrophytes were  $6.5 \pm 4.27\%$ ,  $80 \pm 4.73\%$  and  $13.5 \pm 2.04\%$ , respectively, in Lake E-1, and  $6 \pm 1.25\%$ ,  $75 \pm 3.23\%$ ,  $17.5 \pm 3.15\%$ , respectively, in Lake I-4 (Table 1). Note that these transects represent nearshore areas only. Offshore areas were

**Table 1** Approximate percentage of transect surface area for each patch-type in lakes E-1 and I-4

Lake	Patch type	Transect 1	Transect 2	Transect 3	Transect 4	Mean (SE)
E-1	Rock	1	1	5	19	6.5 (4.27)
	Macrophyte	24	14	15	1	13.5 (4.73)
	Mud	75	85	80	80	80 (2.04)
I-4	Rock	10	5	5	5	6.25 (1.25)
	Macrophyte	15	20	10	25	17.5 (3.23)
	Mud	75	75	85	70	75 (3.15)



**Fig. 2** Resource differences by patch-type in lakes E-1 and I-4. Patches that share a letter are not statistically different. Error bars are 1 SE.

deeper and predominantly open-mud habitat in both lakes.

#### *Resource variation among patches*

Because of interaction effects, patch combinations were analysed separately. In general, E-1 rock and macrophyte patches had higher resource abundance than did other patch types for most resources (Fig. 2). Chlorophyll *a* was most variable among patch types and lakes, and the only OM resource that was significantly less abundant in E-1 macrophytes than on E-1 rocks. However, in Lake I-4, rock and macrophyte chlorophyll *a* was similar and significantly higher than mud (Fig. 2).

#### *Macroinvertebrate density and diversity variation among patches*

There was no significant lake by patch type interaction or lake effect for total invertebrate density versus patch type. Rock patches supported significantly more total macroinvertebrates than macrophytes, which supported more than open mud (Table 2). Lake by patch interaction and a patch effect were observed for 'other' macroinvertebrates, which included all taxa except molluscs and chironomids. E-1 rock had significantly higher density of 'other' macroinvertebrates than all other patches in both lakes. This effect was primarily because of a high density of oligochaetes in sediments from E-1

**Table 2** Community composition of patch types in lakes E-1 and I-4. Numbers are calculated mean densities per square metre (SE). 'Effects' refers to the presence of statistical significance in a two way ANOVA ( $\alpha = 0.05$ ) with interaction between patch and lake. An asterisk under 'Int.' signifies the presence an interaction. Entries under 'Patch' and 'Lake' are results of *post hoc* one-way ANOVA analyses with multiple comparisons (Tukey's HSD,  $\alpha = 0.05$ ). Statistical differences between patch types are indicated by a > sign. R, rocky sediment; Mp, macrophyte sediment; M, open mud.

Taxon	Lake E-1			Lake I-4			Effects		
	Rock	Macrophyte	Mud	Rock	Macrophyte	Mud	Int.	Patch	Lake
Other taxa	5691 (1221)	539 (49)	490 (130)	1963 (932)	1472 (517)	221 (221)	*	E-1 R > all others	
Hydracarina	294 (170)			294 (225)					
Oligochaeta	5152 (1336)	196 (130)	294 (85)	1472 (1178)	883 (170)	221 (220)	*	E-1 R > E-1 Mp, M, I-4 Mp, M	
Nematoda		147 (49)		49 (49)	490 (419)				
<i>Grenisia praeterita</i>	245 (98)	196 (130)	196 (98)	147 (147)	98 (98)				
Gastropoda	491 (214)	442 (170)	98 (49)	5054 (1545)	1619 (225)	147 (220)	*	I-4 R > E-1 M, I-4 Mp > E-1 M	I-4 > E-1
<i>Valvata</i> sp.	49 (49)	49 (49)		3434 (1076)	1275 (273)	147 (220)	*	I-4 R > I-4 M, all E-1 I-4 Mp > all E-1	I-4 > E-1
<i>Gyraulus</i> sp.				638 (354)			*	I-4 R > all others	I-4 > E-1
<i>Lymnaea elodes</i>	442 (255)	392 (130)	98 (49)	981 (468)	343 (98)			R > M	
Sphaeriidae	4367 (817)	1717 (649)	2110 (260)	8931 (3237)	2552 (177)	1619 (588)		R > Mp, M	
<i>Pisidium</i> sp.	4073 (553)	1423 (553)	2110 (260)	7066 (2988)	2306 (343)	1619 (588)		R > Mp, M	
<i>Sphaerium</i> sp.	294 (294)	294 (170)		1864 (932)	245 (177)				
Chironomidae	7459 (1524)	5152 (2618)	1472 (294)	4952 (1160)	4514 (1076)	1914 (147)		R, Mp > M	
Tanytopodinae	1325 (473)	1423 (428)	393 (322)	1325 (170)	245 (245)			R > M	
<i>Ablabesmyia</i> sp. 1	49 (49)	147 (147)		981 (49)	147 (147)		*	I-4 R > all others	I-4 > E-1
<i>Arctopolopia</i> sp.		49 (49)			49 (49)				
<i>Procladius</i> sp.	1276 (248)	1226 (260)	393 (322)	245 (177)	49 (49)				E-1 > I-4
Orthocladinae	2601 (1215)	3140 (2089)	98 (98)	1963 (626)	687 (49)	810 (221)			E-1 > I-4
<i>Corynoneura</i> sp.	147 (85)	98 (49)	49 (49)						I-4 > E-1
<i>Heterotrissocladius hirtapex</i>	245 (177)		49 (49)	736 (306)	638 (98)	515 (588)			
<i>Paracladius</i> sp.	49 (49)								
<i>Parakiefferiella</i> sp. 4	98 (98)			49 (49)					
<i>Pseudomithia</i> sp.		147 (147)		736 (306)					
<i>Zalutschia tatrica</i>		2895 (1816)		294 (147)					
<i>Zalutschia trigonacis</i>	2600 (1002)								
<i>Zalutschia zalutschicola</i>									
Chironominae	3385 (85)	589 (225)	539 (130)	1668 (603)	3582 (803)	294 (294)	*	E-1 R > E-1 Mp, M I-4 Mp > I-4 M, E-1 Mp, M	E-1 > I-4
Chironomini	2159 (177)	343 (214)	539 (130)	638 (638)	3485 (872)	1030 (442)	*		I-4 > E-1
<i>Pagastiella ostanta</i>				343 (343)	196 (49)	294 (294)			
<i>Sergentia</i> sp.				49 (49)					
<i>Stictochironomus rosenscholdti</i>	2159 (177)	343 (214)	539 (130)	245 (245)	3288 (825)	736 (147)	*	R > Mp, M	
Tanytarsini	1226 (260)	246 (130)	1030 (225)	1030 (225)	98 (98)			R > M	
<i>Micropsectra</i> sp.	785 (245)	147 (85)	147 (85)	147 (85)	49 (49)				
<i>Paratanytarsus</i> sp.	147 (85)	98 (98)		98 (49)					
<i>Stempellinella</i> sp.	147 (147)			392 (130)	49 (49)			R > Mp, M	

Table 2 (Continued)

Taxon	Lake E-1			Lake I-4			Effects		
	Rock	Macrophyte	Mud	Rock	Macrophyte	Mud	Int.	Patch	Lake
	<i>Tanytarsus</i> sp.	147 (147)			98 (98)				
Prodiamesinae	98 (49)		245 (130)						
<i>Monodiamesa bathyphila</i>	49 (49)		196 (98)			74 (74)			
Diamesinae	18 008 (3253)	7850 (2832)	4170 (512)	20 900 (5373)	10 157 (895)	3901 (957)		R > Mp > M	
Total macroinvertebrates									

Note: Chironomids not identifiable to the genus level but identifiable to the subfamily level are included in subfamily totals.

rock. Gastropod density differed significantly between lakes, patch types, and, except for *Lymnaea*, showed a significant lake by patch interaction. In general, rocks and macrophytes supported more gastropods than mud patches and gastropods were most abundant on rocks in Lake I-4 compared with other patches. Both Sphaeriidae and Chironomidae were more abundant in rock than open-mud patches overall. Sphaeriids density was similar in macrophyte and open-mud patches, whereas chironomids were more abundant in macrophytes than mud. Tanytarsinae were more abundant in rock compared with open-mud patches; tanytarsinae were not detected in I-4 open-mud patches. Orthoclads did not show any significant effects of lake, patch type, or lake × patch interaction overall, although there were some significant effects for individual taxa (Table 2). Chironominae showed significant lake and interaction effects, which were attributable to higher densities of Chironominae in Lake I-4 macrophyte and Lake E-1 rock patches than other patch types. The density of Tanytarsinae was higher in rock compared with macrophyte patches and Tanytarsinae were not detected in open-mud patches in either lake.

Rock patches supported significantly higher species richness ( $14.8 \pm 0.9$ ) than macrophyte patches ( $10.3 \pm 0.8$ ) which had significantly more species than open-mud ( $6.5 \pm 0.2$ ; Fig. 3). Evenness did not differ among the patch types. Lake and interaction effects on species richness were not significant. Rock and macrophyte patches ( $2.1 \pm 0.1$  and  $1.9 \pm 0.2$ , respectively) were not different with respect to H' diversity, but both of these patch types had significantly higher H' diversity than open mud ( $1.5 \pm 0.02$ ; Fig. 3).

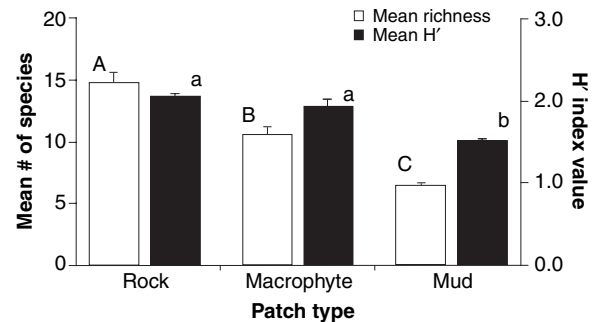


Fig. 3 Species richness and Shannon–Wiener diversity values (H') by patch type for lakes E-1 and I-4. Patches that share a letter are not statistically different. Error bars are 1 SE.

**Table 3** Loadings of Lake E-1 and Lake I-4 resource parameters from principal components analysis. Eigenvectors range from 1 to -1. The magnitude indicates their relative influence on the principal component.

Resource	Lake E-1		Lake I-4	
	PC-1	PC-2	PC-1	PC-2
TN	0.55	0.04	0.49	-0.22
TC	0.53	0.23	0.50	0.02
C : N	0.35	-0.58	0.09	0.97
OM	0.53	0.22	0.51	-0.05
Chl <i>a</i>	0.07	0.75	0.48	0.07

**Table 4** Significant  $R^2$  values of principal components (PC-1, 2). Univariate analysis of each principal component versus taxa group resulted in the below  $R^2$  values. Asterisks indicate which principal component was significant in multivariate models with each taxa group density as the dependent variable.

Taxa group	Lake E-1		Lake I-4	
	PC-1 $R^2$	PC-2 $R^2$	PC-1 $R^2$	PC-2 $R^2$
Other	0.02	0.80*	0.67*	0.19
Gastropoda	0.09	0.15	0.83*	0.00
Sphaeriidae	0.10	0.37	0.58*	0.00
Chironomidae	0.17	0.55*	0.27	0.02
Total invertebrates	0.01	0.73*	0.62*	0.02

#### Resource effects on macroinvertebrate densities

The PCA produced two new, uncorrelated variables for use in multivariate regression models for each lake. For Lake E-1, principal component 1 (pc-1) was composed primarily of TN, TC and %OM, while principal component 2 (pc-2) was chiefly a combination of chlorophyll *a* and C : N (Table 3). In Lake E-1, only pc-2 was significant with respect to distribution among patches for total invertebrates, explaining 55–80% of the variation in total macroinvertebrates, chironomids and 'other' taxa (Table 4). Little of the variation in clam and gastropod density in Lake E-1 was explained by either pc variable. In Lake I-4, pc-1 was a primarily a combination of TN, TC, %OM and chlorophyll *a* while pc-2 was mainly C : N (Table 3). Only pc-1 was significant, explaining 58–83% of the variation in total macroinvertebrates, 'other' macroinvertebrates, clams and gastropods. Neither pc variable significantly explained chironomid distribution among patch types in Lake I-4 (Table 4).

#### Individual biomass variation in patches

In Lake E-1, *Pisidium* sp. cohort 1 (of two cohorts) and *Stictochironomus rosenschoeldi* cohort 1 (of three cohorts) were the only common taxa that showed observable differences in mean individual biomass among patches (Table 5). Macrophytes supported two times higher individual biomass of *Pisidium* sp. than rock and 1.3 times that of open-mud. Individual *S. rosenschoeldi* were approximately 1.3 times heavier in sediments overlying rock than in open-mud and 1.2 times larger than in macrophyte-covered sediment patches.

In Lake I-4, differences in mean individual biomass among patch types were observed for *Valvata* sp. (one cohort), *Pisidium* sp. cohort 1, *S. rosenschoeldi* cohort 1 (of three cohorts) and *Heterotrissocladius hirtapex* (one cohort; Table 5). For each of these taxa, individual biomass was greatest in rock patches. Individual biomass was also greater in macrophyte compared with open-mud patches for *Pisidium*, *Stictochironomus* and *Heterotrissocladius*.

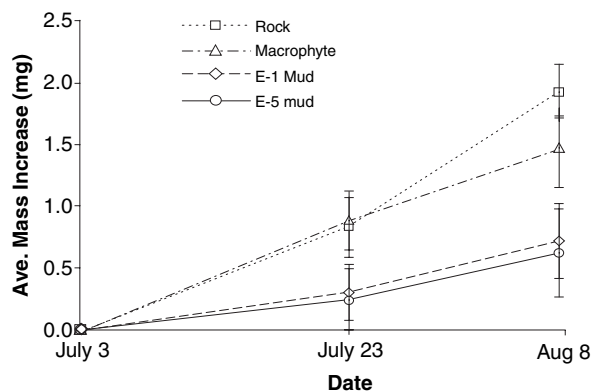
#### Chironomus growth

The mean mass of larval *Chironomus* sp. used in the growth experiment at time zero was  $0.78 \pm 0.08$  mg ( $n = 20$ ). Both treatment and date  $\times$  treatment interaction significantly affected *Chironomus* mass ( $F_{\text{Treatment}} = 10.42_{(3,3)}$   $P < 0.0001$ ,  $F_{\text{Date} \times \text{treatment}} = 4.10_{(6,6)}$ ,  $P = 0.0007$ ; Fig. 4). At week 3, the mass of *Chironomus* at 3 weeks in both rock and macrophyte treatments was approximately three times that of *Chironomus* in E-1 and E-5 mud treatments, respectively. At 5 weeks, *Chironomus* in rock treatments had gained about three times the mass as chironomids in either E-5 mud or E-1 mud treatments. Chironomids in macrophyte treatments gained more than two times the mass after 5 weeks as those in E-5 and E-1 mud (Fig. 4).

Resources differed between treatments (Fig. 5). Both rock and macrophyte treatments had significantly higher %TN and %TC than either open-mud treatment at each harvest. C : N ratios were significantly higher in macrophyte-derived sediments than the other treatments, but C : N ratios among the rock or mud treatments did not differ significantly. Sediments from macrophytes had significantly higher %OM than from rock treatments and sediments

**Table 5** Mean individual biomass of common taxa in  $\mu\text{g}$  (SE) by patch type in lakes E-1 and I-4. In 'multiple comparisons' patches with significantly higher mean values are depicted with a '>'. No difference between mean values is depicted with an '='. R, rocky sediment; Mp, macrophyte sediment; M, open-mud. Analysis is one-way ANOVA with multiple comparisons (Tukey's HSD,  $\alpha = 0.05$ ).

Lake	Taxon	Patch-type	Mean individual biomass (SE) in $\mu\text{g}$	<i>n</i>	Multiple comparisons	<i>F</i> -value	<i>P</i> -value
E-1	<i>Pisidium</i> sp. (cohort 1)	Rock	0.35 (0.02)	73	Mp > R	10.54 <sub>(2,133)</sub>	<0.0001
		Macrophyte	0.70 (0.10)	23			
		Mud	0.55 (0.06)	40			
	<i>Stictochironomus rosenschoeldi</i> (cohort 1)	Rock	90.0 (3.5)	42	R > Mp = M	4.40 <sub>(2,55)</sub>	0.0168
		Macrophyte	74.3 (11.9)	6			
		Mud	68.5 (4.7)	10			
	<i>Procladius</i> sp. (cohort 1 ?)	Rock	42.8 (7.1)	10	R = Mp = M	1.90 <sub>(2,19)</sub>	0.1762
		Macrophyte	63.2 (18.3)	7			
		Mud	81.9 (20.2)	5			
I-4	<i>Valvata</i> sp.	Rock	3.1 (0.3)	61	R > Mp	12.57 <sub>(2,95)</sub>	<0.0001
		Macrophyte	1.4 (0.2)	26			
		Mud	2.3 (0.5)	11			
	<i>Pisidium</i> sp. (cohort 1)	Rock	0.64 (0.04)	133	R = Mp > M	5.37 <sub>(2,191)</sub>	0.0054
		Macrophyte	0.47 (0.06)	40			
		Mud	0.33 (0.07)	21			
	<i>Stictochironomus rosenschoeldi</i> (cohort 1)	Rock	118.2 (9.4)	7	R = Mp > M	16.61 <sub>(2,30)</sub>	<0.0001
		Macrophyte	101.8 (4.6)	22			
		Mud	41.1 (9.2)	4			
	<i>Heterotrissocladius hirtapex</i>	Rock	409.5 (15.7)	13	R > Mp > M	15.33 <sub>(2,30)</sub>	<0.0001
		Macrophyte	325.4 (19.5)	13			
		Mud	245.7 (25.5)	7			
	<i>Pagastiella ostansa</i>	Rock	117.1 (12.6)	3	R = Mp = M	0.97 <sub>(2,30)</sub>	0.4209
		Macrophyte	118.9 (27.4)	4			
		Mud	81.9 (18.1)	4			



**Fig. 4** Average mass increase of *Chironomus* sp. in different patch-type sediments during a 5-week growth experiment. The experiment was conducted during the summer of 2003 and started on 3 July with a mid-experiment collection on 23 July and a final collection on 8 August. Error bars are  $\pm 1$  SE.

from both of these patch types had significantly greater %OM than mud. Chlorophyll *a* was significantly higher in macrophytes than all other treatments, which did not differ significantly from each other.

## Discussion

Resource availability, macroinvertebrate abundance and diversity, and individual biomass varied among patch types of the same depth in two arctic lakes. Experimental evidence revealed that resource differences among patches affect *Chironomus* growth. We suggest that resources may also explain differences in individual biomass between patch types for other taxa. The most important resource supporting growth was %OM. Previous work elsewhere has also shown that resource availability limits macroinvertebrate communities (e.g. Ward & Cummins, 1979; Vos *et al.*, 2000, 2002). However, predation also affects macroinvertebrate abundance between patch types (e.g. Crowder & Cooper, 1982; Gilinsky, 1984; Hershey, 1985). Here, we discuss the effect of resource variability among patch types on macroinvertebrate communities and consider these results in light of predation effects in these same communities (Merrick, Hershey & McDonald, 1991; Cuker, McDonald & Mozley, 1992; Hershey *et al.*, 1999).

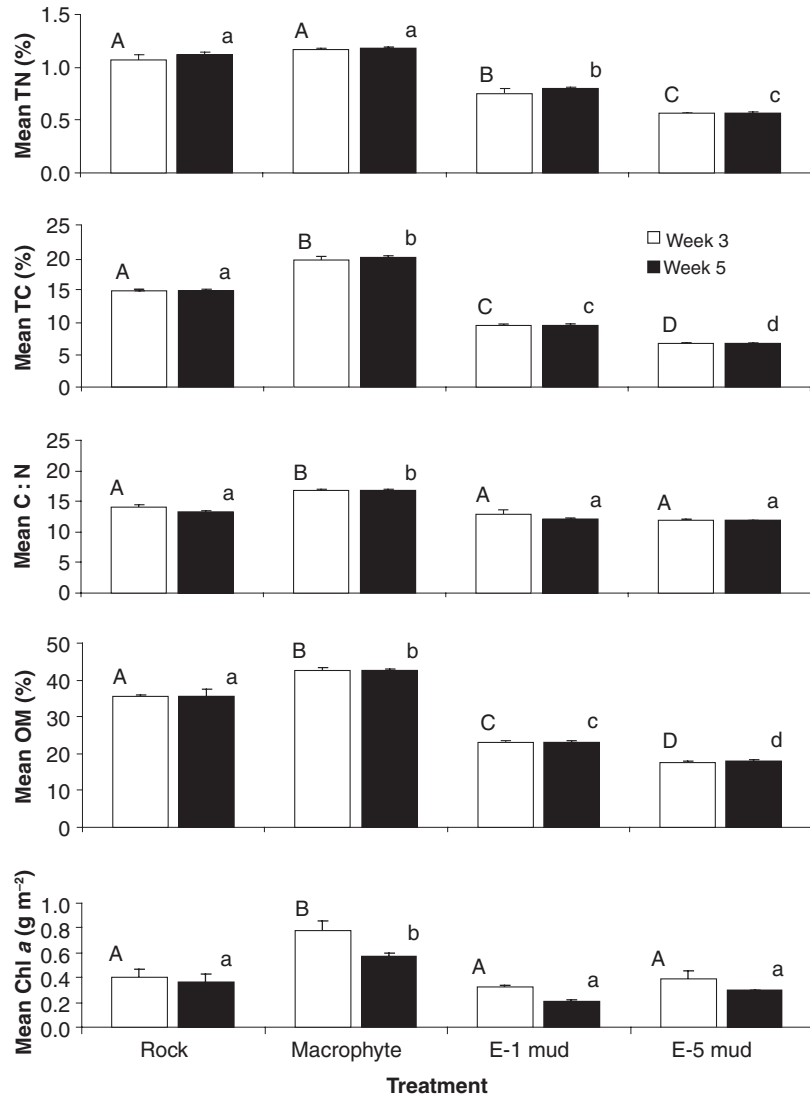


Fig. 5 Resource differences by patch-type in growth experiment. Patches that share a letter are not statistically different. Error bars are 1 SE.

Resource variability between patch types

Percent TC, TN and OM reflect detrital, and microbial biomass in sediments. Rocks were covered with a flocculent matrix, similar to that observed in Toolik Lake (Cuker, 1983). Flocculent sediments have higher respiration rates compared with sediments of other types, indicating greater benthic microbial activity (Sweerts, Rudd & Kelly, 1986). Lake I-4 rocks had less flocculent matrix (<1 cm) than Lake E-1 rocks (2–3 cm) (S. R. Beaty, personal observation) and correspondingly lower %OM. Sediment dissolved and particulate organic matter (DOM and POM, respectively) increase with macrophyte decomposition (Wetzel & Manny, 1972; Landers, 1982; Bowen, 1987).

Thus, high%OM in sediments from macrophytes to open-mud reflects more input of detritus. We would expect %TN to behave similarly. However, %TN was highest in macrophyte patches only in Lake E-1. Unfortunately, we have no data that provide a clear explanation the uneven pattern of %TN between patch types in the two lakes.

Algae are also a significant component in the diets of many benthic invertebrates, although their importance varies considerably. Chironomids in a Polish lake fed primarily on benthic algae (Kajak & Warda, 1968). However, Johannsson & Beaver (1983) estimated that algae accounted for only 15–34% of the energy requirements of *Chironomus semireductus*. In tundra ponds, available algae composed <1% of

chironomid organic carbon demands (Butler, Miller & Mozley, 1980). We noted that many chironomids (especially Orthocladinae, although not Chironomini) from both E-1 and I-4 had diatoms along with detritus and mineral particles in their guts. Chlorophyll *a* concentrations were high in some areas of high macroinvertebrate densities, consistent with the result that pc-1 in Lake I-4 and pc-2 in Lake E-1, on which chlorophyll *a* was most highly loaded, explained the most variation in macroinvertebrate abundances. Algae also leach DOM, which fuels sediment microbes (Paerl, 1978). Thus, even if invertebrates do not feed heavily on algae, they may indirectly benefit from high algal biomass through the microbial loop.

#### *Macroinvertebrate responses to patch type*

Density differences that existed between patch types were due primarily to chironomids, sphaeriid clams and gastropods. In most cases, these taxa were most abundant in rock patches and more abundant in macrophytes than open-mud. Clearly rock and macrophyte habitats offer more surface area per square metre of lake bottom than does open mud. However, when sampling macrophyte patches, the macrophytes themselves were removed and only underlying sediments were included in samples. Thus, macrophytes and open-mud samples had the same habitat surface area per square metre of lake bottom. Rock sampling involved removing sediments from a larger surface than the bottom area intersected by the sampling device aperture and we have no way of estimating this area. Thus, higher densities on rock substrate may have been due, in part, to greater surface heterogeneity per unit area of lake bottom.

However, differences in individual biomass between patches can only be accounted for by resource quality. Macroinvertebrate size differences have previously been observed in sediments of differing resource availability (Cole & Weigmann, 1983; Gresens, 1997; Sagova-Mareckova & Kvet, 2002). For most of the taxa that showed differences in individual biomass, either rock habitat supported greatest individual biomass or rock and macrophyte habitat had similar individual biomass, and both were greater than in open mud. This pattern is similar to that observed for abundances. *Stictochironomus rosenscholdi*, the dominant Chironomini showing this pattern, is trophically very similar to *Chironomus*

(Hershey *et al.*, 2006). Furthermore, the *Chironomus* growth experiment, where habitat heterogeneity was uniform across treatments, showed that rocks and macrophytes supported faster growth than open mud. Other studies have also shown that OM can limit chironomid growth (Cole & Weigmann, 1983; Rasmussen, 1985; Vos *et al.*, 2000, 2002). The open-mud treatment from the fertilised lake did not result in a significant effect on chironomid growth compared with unfertilised treatments. However, resources in E-5 sediments were not enhanced (Fig. 5). Similarly, sediment nutrient concentrations did not significantly change after 2 years of experimental nutrient addition to two other arctic lakes (McCoy, 1983) and experimental fertilisation in limnocorrals in Toolik Lake did not result in a growth effect on chironomids (O'Brien *et al.*, 1992). Thus, the transfer of water column nutrients to the sediments is very slow or insignificant.

High Chironomini abundance in macrophyte patches compared with open-mud was also observed in Toolik Lake and an experiment showed that density was reduced in open mud compared with macrophyte patches by sculpin predation (Hershey, 1985). However, high Chironomini density in rock patches observed in Lake E-1 is more likely related to higher quality resources. At very high densities, sculpin can effectively reduce some taxa on rocks (Cuker *et al.*, 1992). However, sculpin predation pressure is much greater in open-mud compared with rock habitats in lakes where lake trout are not present, such as Lake E-1 (Hanson, Hershey & McDonald, 1992).

There is little ecological literature on sphaeriid clams. Jónasson (1972) and Lopez & Holopainen (1987) found that *Pisidium* sp. is adapted to burrowing and filtering of sediment pore water, but *Sphaerium* sp. is primarily a suspension feeder (Mackie, 1979). In this study, *Pisidium* was two- to threefold more abundant in rock than in either open-mud or macrophyte patches. Although occurrence on rock patches may not seem consistent with a burrowing behaviour, all *Pisidium* collected were only a few to several millimetre in length, such that burrowing could easily be supported in the 1–3 cm of sediment overlying rocks. The flocculent nature of these sediments may also facilitate filtering of sediment pore water. Sphaeriid clams have not been found in guts of sculpin or grayling, which occur in Lake E-1, although they are preyed upon by lake trout and round whitefish (Hershey, 1985; Merrick *et al.*, 1992), which occur in

Lake I-4 but not Lake E-1. It seems unlikely that fish predation was important in determining their relative abundance between lakes or habitats because sphaeriids appeared to be slightly more abundant in Lake I-4. Thus, although we observed significant patch effects on sphaeriids, we cannot attribute these to predation and could not explain variation in their abundance using PCA. Further research is needed to understand factors affecting the distribution of this macroinvertebrate group.

Gastropod distribution is affected by resources, competition and predation. Gastropods were dominated by *Lymnaea* in Lake E-1 and by *Valvata* in Lake I-4. In Lake E-1, *Valvata* densities were low in rock and macrophyte habitats and undetectable in open-mud. In other lakes near Toolik Lake, *Lymnaea* out-competes *Valvata* by reducing its fecundity when lake trout are absent, but when lake trout are present, *Lymnaea* are reduced by lake trout predation, resulting in high *Valvata* density (Hershey, 1990). Elsewhere, *Lymnaea* reduces the fecundity of *Physa* (Brown, 1982). Therefore, low *Valvata* density in Lake E-1, where lake trout are absent, was likely a result of competition with *Lymnaea*. Likewise, in Lake I-4, where lake trout are present, *Lymnaea* density was low because of predation, which resulted in high density of *Valvata*. Resources were also important in determining gastropod distribution among patches in Lake I-4, where pc-1 explained 83% of the variation, but not in Lake E-1, where none of the variation in gastropod densities was explained by PCA.

Lakes E-1 and I-4 both had higher species richness in rock than macrophyte patches, while macrophytes supported higher richness than open-mud. These findings are consistent with the hypotheses that richness is positively correlated with density and habitat physical complexity (Gray, 1974; Pielou, 1975). Lack of differences in species evenness among patch types indicates that differences seen in  $H'$  were driven by species richness.

## Conclusions

Few studies have compared macroinvertebrate abundance and growth between rocky and soft sediment patch types in littoral areas of lakes, while also controlling for effects of depth and measuring patch OM resources. We found that rock and macrophyte patches in arctic lakes generally had higher resources,

supported higher macroinvertebrate density and richness, and had greater individual biomass of common taxa. Experimental evaluation of *Chironomus* growth clearly demonstrated that resources associated with sediments from rock and macrophyte patches supported more growth than those from open-mud patches. Sediment OM appeared to be the most important resource for supporting growth. We suggest that patch resources may also explain differences in individual biomass between patch types for other taxa. *Chironomus* incubated in sediments from a lake that had been experimentally fertilised for two summers did not show enhanced growth, but those sediments also did not show enhancement in any of the resources measured in this study, suggesting that transfer of water-column resources to the sediments is slow or not significant. Rock and macrophyte patches comprised a small percentage of the surface area of the littoral zone. However, higher diversity and abundance, and growth of dominant taxa in these habitats suggest that these relatively rare patch types may be disproportionately important to lake productivity compared with their abundance. Other studies in these and other lakes in the region show that differences in predator regime between lakes, predator effectiveness between patch types, and competitive interactions between gastropod species can also affect macroinvertebrate abundances. Thus, relationships between macroinvertebrate community structure, individual growth and habitat heterogeneity reflect the interaction of multiple resources as well as interspecific interactions.

## Acknowledgments

Our grateful thanks go to Matthew Keyes, Amber Ulseth, Angela Detweiler, Thomas McDonald, Ryan Barile, and the Toolik Lake staff for their assistance on this project and two anonymous reviewers for critical comments and reviews of the manuscript. This work was supported by the National Science Foundation through grants NSF/DEB-0090202 and NSF/DEB 0516043 to A. E. Hershey.

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(Manuscript accepted 21 September 2006)