FOREST GROUND BEETLES (COLEOPTERA: CARABIDAE) ON A BOREAL ISLAND: HABITAT PREFERENCES AND THE EFFECT OF EXPERIMENTAL REMOVALS

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The Canadian Entomologist **132**: 627 – 634 (2000)

Abstract

We used pitfall trapping to measure the species richness and relative abundance of ground beetles (Coleoptera: Carabidae) in four forest habitats on Kent Island, a 80-ha island in the Bay of Fundy, New Brunswick, Canada. Sixteen species of ground beetles representing 11 genera were identified in the forested habitats on Kent Island; the relative paucity of ground beetle species may be a result of the island's harsh climate, dense colonies of breeding seabirds, and isolation from the mainland. Estimates of ground beetle population densities on Kent Island ranged from 50 000 to 250 000/ha. Most ground beetle species were trapped in all habitats and appeared to be habitat generalists. In a series of experiments in which we removed all ground beetles trapped daily over a 3-week period in two experimental plots, ground beetle densities remained as high as in a control plot; other ground beetles quickly moved into the experimental plots to replace beetles that had been removed. The density of ground beetles was highest in intact forest and large forest patches; in contrast, the density of invertebrates other than ground beetles (*i.e.*, possible prey or competitors of ground beetles) was highest in open habitats and isolated forest patches, where ground beetles were less common. Removing ground beetles from experimental plots did not result in an increase in the density of other invertebrates.

Apigian K, Wheelwright NT. 2000. Les carabes (Coleoptera : Carabidae) d'une forêt insulaire boréale : préférences d'habitat et effet de retraits expérimentaux. *The Canadian Entomologist* **132** : 627–634.

Résumé

Nous avons utilisé des pièges à fosses pour mesurer la richesse en espèces et l'abondance relative des carabes (Coleoptera : Carabidae) dans quatre habitats forestiers de l'île Kent, une île de 80 ha dans la baie de Fundy, Nouveau-Brunswick, Canada. Seize espèces appartenant à 11 genres ont été capturées dans ces habitats; la pauvreté relative des carabes résulte probablement des conditions climatiques rigoureuses de l'île, de la présence de colonies importantes d'oiseaux de rivage reproducteurs et de l'isolement loin du continent. Des estimations des densités des populations de carabes dans l'île ont donné des chiffres allant de 50 000 à 250 000/ha. La plupart des espèces ont été capturées dans tous les habitats et semblent être des généralistes quant à l'habitat. Au cours d'une série d'expériences, nous avons procédé au retrait de tous les carabes recueillis chaque jour pendant 3 semaines dans deux parcelles; après le retrait, les densités de carabes étaient tout aussi élevées que dans une parcelle témoin car d'autres carabes sont venus remplacer les carabes retirés. La densité des carabes était maximale dans les forêts intactes et les grands boisés; en revanche, les invertébrés autres que les carabes (*i.e.*, des proies ou des compétiteurs potentiels des carabes) abondaient dans les habitats ouverts ou les petits boisés isolés où les carabes étaient moins communs. Le retrait des carabes n'a pas entraîné d'augmentation de densité des autres invertébrés.

[Traduit par la Rédaction]

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Introduction

We measured the abundance of ground beetles (Coleoptera: Carabidae) in various forest habitats on Kent Island, New Brunswick, Canada, using pitfall trapping. Few data exist on the ground beetle faunas of islands, particularly of boreal islands such as Kent Island. The aim of this study was to gain a better perspective on the effect of isolation on ground beetle faunas by surveying ground beetles, particularly in forested habitats, and describing the number of species, their occurrence in different forest habitats, and their population densities. We also report seasonal trends in ground beetle capture rates and the results of a removal experiment designed to determine the impact of ground beetles on densities of other invertebrates, including possible prey or competitors of ground beetles.

Kent Island is a difficult environment for the colonization and establishment of ground beetle populations for several reasons. The island lies more than 20 km from the mainland. It is limited in area and topographical range, depauperate in terms of plant species and habitat types, and subjected year-round to cold temperatures, fog, salt spray, and strong winds. The island is also unusual because it supports dense colonies of breeding seabirds that prey on beetles and physically alter habitats by plucking and trampling vegetation (Cannell and Maddox 1983; NT Wheelwright, personal observation). Based on models of island biogeography, we predicted that the ground beetle fauna of Kent Island would be relatively impoverished and generalized in habitat use compared with ground beetle faunas on larger islands or in mainland habitats.

Methods

Study Site. Our study was conducted at the Bowdoin Scientific Station on Kent Island (44°35′N, 66°45′W) during June and July 1997. Kent Island, the outermost island in the Grand Manan Archipelago, is 80 ha in area, 3 km long, and about 0.5 km wide at the widest point. The northern third of the island is forested; the remainder of the island is largely open habitat dominated by various species of grasses (McCain 1975). The island is located 9 km south of Grand Manan Island and more than 20 km from the nearest mainland in Maine or Nova Scotia.

We sampled beetles in the island's four principal forest habitats: (1) dense 30- to 40-year-old monospecific stands of white spruce, *Picea glauca* (Moench) Voss (Pinaceae), bordering abandoned pastures; (2) relatively open monospecific stands of American mountain ash, *Sorbus americana* Marsh. (Rosaceae), that were established after a fire 50 years ago; (3) dense monospecific stands of balsam fir, *Abies balsamea* (L.) P. Mill. (Pinaceae), on sites logged 55 years ago; and (4) undisturbed mixed forests consisting of red spruce, *Picea rubens* Sarg., balsam fir, mountain ash, heartleaf birch, *Betula cordifolia* Regel (Betulaceae), and yellow birch, *Betula alleghaniensis* Britt., in which trees were up to 120 years old [vascular plant nomenclature follows Gleason and Cronquist (1991)]. The heavily shaded understory of the white spruce stands was covered almost entirely with needles, with almost no herbaceous cover and few mosses. The understory beneath the mountain ash was relatively dense and consisted mainly of whorled aster, *Oclemena (Aster) acuminata* (Michx.) Nelson (Asteraceae), and mountain wood fern, *Dryopterus campyloptera* (Kunze) Clarkson (Polypodiaceae). The wet heavily shaded balsam fir understory was largely moss-covered (Futamura and Wheelwright 2000). The understory beneath the mixed forest was composed of various boreal herbaceous species (McCain 1975). We selected two study sites representing each of the four forest types; each of the eight study sites was separated from the remaining sites by at least 100 m. Although this study concentrated on forest habitats, we also sampled beetles in fields and other habitats around the island, using pitfall traps and visual censuses, using the following methods.

Sampling Methods. We used pitfall traps to quantify ground beetle abundance and richness [for a discussion of the limitations of the technique, see Halsall and Wratten (1988)]. Traps consisted of plastic cups (6 cm in diameter and 8 cm deep) set in the ground, with plastic funnels to prevent beetles and other invertebrates from escaping and small plastic lids suspended by wires 3–5 cm above the cup to act as rain guards. In each habitat, traps were set in grids of 10 traps (each grid a 3 × 3 array in an area 100 m^2, with one outlier trap). Each trap was separated by at least 5 m from the nearest trap and was located in representative microhabitats at least 20 m from the edge of the habitat or any path. General pitfall sampling was carried out throughout June and July. To compare the abundance of ground beetles among the four forest types described above, trap contents were collected each morning between 14 and 17 June and again between 16 and 18 July.

Individual beetles were identified to species using reference collections (voucher specimens deposited at the Bowdoin Scientific Station); identifications were verified by R Nelson (Colby College, Waterville, Maine). *Pterostichus adstrictus* and *Pterostichus pensylvanicus*, two species that were difficult to distinguish in the field (although see Bousquet 1986; Larson *et al.* 1999), both occurred on Kent Island but were combined as a single taxon in our censuses, as were the similar species *Calathus ingratus* and *Calathus gregarius* (see Table 1 for taxonomic authorities). To supplement our trapping surveys and gain a fuller picture of the ground beetle fauna, we searched haphazardly for ground beetles in forested and open habitats whenever we walked around the island in June and July.

Removal Experiment. To gain a better estimate of the density of the beetles and to assess the impact of the predatory beetles on other invertebrates (including possible prey and competitors of ground beetles), we removed all ground beetles captured in two experimental plots within one of our study areas. Three trap grids (two removal grids and one control, each with 81 traps in a 9 × 9 array in an area of 625 m^2) were set up in a monospecific stand of white spruce. Traps were similar to those described above; however, to increase trapping success, we added four pieces of aluminum flashing (20 cm long and 4 cm high) radiating away from each trap at 90° angles to act as baffles. Each trap was checked daily between 4 and 24 July (n = 21 trapping periods, each one 24 h long), and the numbers of each ground beetle species and other invertebrates (identified to family) were noted. In the control plot, beetles were released 2.5 m away. In the two experimental plots, beetles were released several hundred metres away.

Statistical Analyses. Two-way analyses of variance (ANOVA) were used to test for differences in the abundance of ground beetles in different habitats, using Statview 4.01 (Abacus Concepts 1992). Descriptive data are given as means ± SD.

Results

Species Richness and Relative Abundance. Sixteen species of ground beetles representing 11 genera were identified in the forested habitats on Kent Island (Table 1). Densities of all ground beetles combined varied between habitats, and seven of nine individual species showed significant differences between habitats (Table 1). Ground beetles were abundant in the white spruce stands, where the understory was densely shaded, devoid of vegetation, and covered thickly with dead needles. On the other hand,

TABLE 1. Mean daily abundance of ground beetles (Coleoptera: Carabidae) (number/trap) within 100-m^2 trapping grids.

	Forest type				Statistics	
Species*	Mixed	Balsam fir	Mountain ash	White spruce	$F_{3,474}$	P
Agonum retractum Lec.	0.01	0.1	0.5	0.03	38.2	<0.001
Bembidion wingatei Bland	0.01	0.01	—	0.03	2.0	0.11
Calathus ingratus Dej. – *C. gregarius* Say†	0.01		0.02	0.03	1.1	0.33
Calathus opaculus Lec.	1.5	1.6	0.6	2.7	14.8	<0.001
Carabus granulatus L.			0.1	—	7.8	<0.001
Platynus decentis Say	0.6	0.6	0.1	0.5	4.2	<0.01
Pterostichus adstrictus Eschz. – *P. pensylvanicus* Lec.†	3.6	2.1	1.0	1.1	30.4	<0.001
Pterostichus coracinus Newm.	0.9	0.5		0.3	16.7	<0.001
Sphaeroderus stenostomus Web.	0.1				10.5	<0.001
Mean no. of individuals/trap	6.3	4.6	3.5	4.7	11.3	<0.001
Mean no. of species/trap	2.3	1.9	2.1	2	2.5	0.06
Total no. of individuals	757	495	415	559		
Total no. of species‡	9	7	8	8		

NOTE: Dashes indicate that the species was not trapped in a particular forest type. The total number of beetles counted and identified in the forest-habitat study was 2226. F and P values represent the results of one-way ANOVAs testing for differences in abundance between the four habitat types (df = 3,474).

*Four other ground beetle species (*Calosoma frigidum* Kby., *C. nemoralis* Mul., *Chlaenius sericeus* For., and *H. rufipes* DeG.) were present on Kent Island but were not included in the analysis of habitat use.

†This species pair was not distinguished in the field (see Methods).

‡Includes *N. biguttatus* F., which was present in each habitat at low densities.

mountain ash stands, with their relatively lush understory, had the lowest density of ground beetles. *Pterostichus adstrictus – P. pensylvanicus* and *Calathus opaculus* were the most abundant species on the island and were commonly found in all forest habitats. *Platynus decentis* occurred at low densities in all habitats. Overall, 9 of the 16 species appeared to be generalists and were found in most forest habitats. Several species were more specialized in their habitat use, notably *Sphaeroderus stenostomus* (exclusively in mixed forest) and *Carabus granulatus hibernicus* (exclusively in mountain ash stands) (Table 1). The mean number of ground beetle species per trap did not vary significantly between habitats, but habitats did vary in the mean number of individuals per trap, with ground beetles being most dense in mixed forest and least dense in mountain ash stands (Table 1). There was no difference in the number of individual ground beetles captured per trap for 14–17 June (5.0 ± 3.5, n = 240 trap-days) versus 16–18 July (4.8 ± 5.3, n = 238 trap-days) (t_{476} = 0.45, P = 0.65). Likewise, the number of species of ground beetles per trap did not differ between sampling periods (2.2 ± 1.1 versus 2.0 ± 1.1; t_{476} = 1.61, P = 0.11).

Removal Experiment. We removed a mean of 172.1 ± 70.7 ground beetles in total every day from each of the two 25 × 25 m experimental plots between 4 and 24 July. Despite the removal of thousands of ground beetles from experimental plots over the course of 3 weeks, and a decline in capture rates in all plots between 4 and 24 July (Spearman's rank test, ρ = –0.08, n = 1080, P = 0.005), daily capture rates in the experimental plots did not differ from those in the control plot (Fig. 1; ANOVA, $F_{2,537}$ =

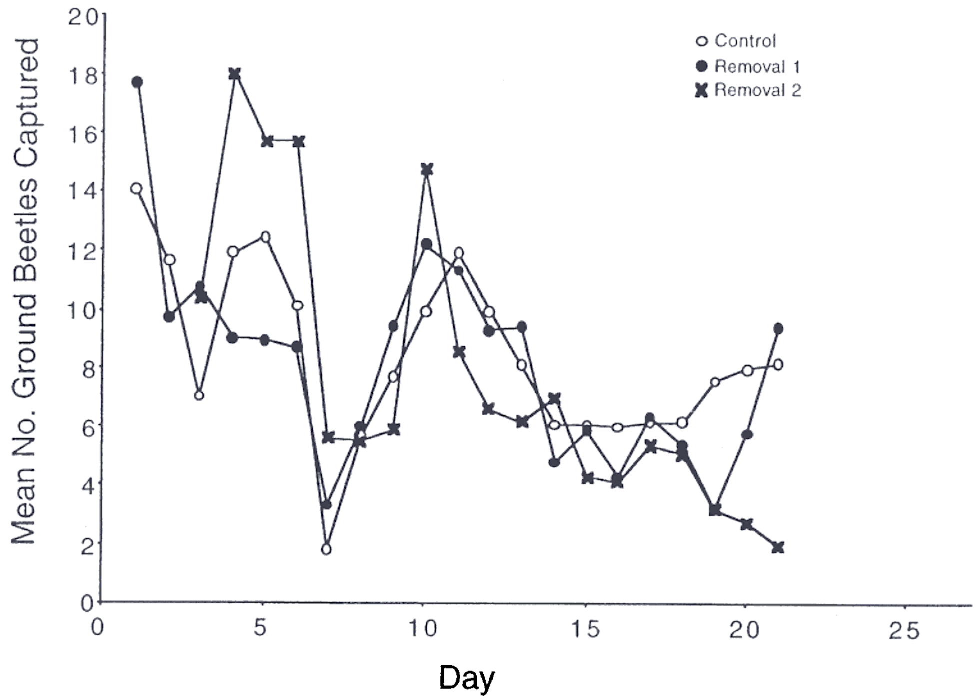

FIGURE 1. Mean number of ground beetles captured per pitfall trap in a control plot and in two experimental plots (Removal 1 and Removal 2) from which all ground beetles captured in traps were removed daily and released several hundred metres away.

0.26, $P = 0.77$). The mean daily capture rate over the 3-week period was 8.1 ± 5.9 beetles/trap ($n = 189$ trap-days) and 7.9 ± 6.8 beetles/trap ($n = 163$ trap-days) in the two experimental plots and 8.4 ± 5.6 beetles/trap ($n = 188$ trap-days) in the control plot. Presumably, ground beetles that were removed from the experimental plots were quickly replaced by beetles from nearby sites. Preliminary homing experiments (see below) indicated that few, if any, of the beetles that were displaced in the removal experiment returned to the experimental plots.

We examined the impact of ground beetle removal on the densities of other invertebrates that may act as prey for, or competitors of, ground beetles. The mean daily capture rates of invertebrates other than ground beetles [chiefly harvestmen (Phalangida), spiders (Araneida), pillbugs (Isopoda), other beetles (Coleoptera: Staphylinidae, Curcurlionidae, Byrrhidae, and Scarabidae), and ants (Hymenoptera: Formicidae)] were actually significantly higher in the control plot (3.4 ± 3.6 individuals/trap) than in the two plots where ground beetles had been removed (3.0 ± 3.3, first experimental plot; 1.5 ± 1.5, second experimental plot) (ANOVA, $F_{2,537} = 20.40$, $P < 0.0001$). However, there was no significant difference in capture rates between the control plot and the first experimental plot alone (*i.e.*, excluding the second experimental plot; ANOVA, $F_{1,349} = 1.13$, $P = 0.29$). Collectively, these results do not provide support for the prediction that removing large numbers of ground beetles leads to an increase in the number of other invertebrates.

Other Observations. We compared ground beetle densities in white spruce stands of different sizes and in grassy habitats ($n = 2$ sites/habitat type) (Fig. 2). Daily capture rates of ground beetles in traps located in large (1 ha or larger) stands of white spruce ("forest") were similar to those in smaller (less than 400 m^2) spruce stands surrounded by abandoned pasture ("fragments") (6.2 ± 0.6 beetles/trap and 5.8 ± 0.6 beetles/trap, respectively). Daily capture rates were lowest under small isolated clumps of white spruces

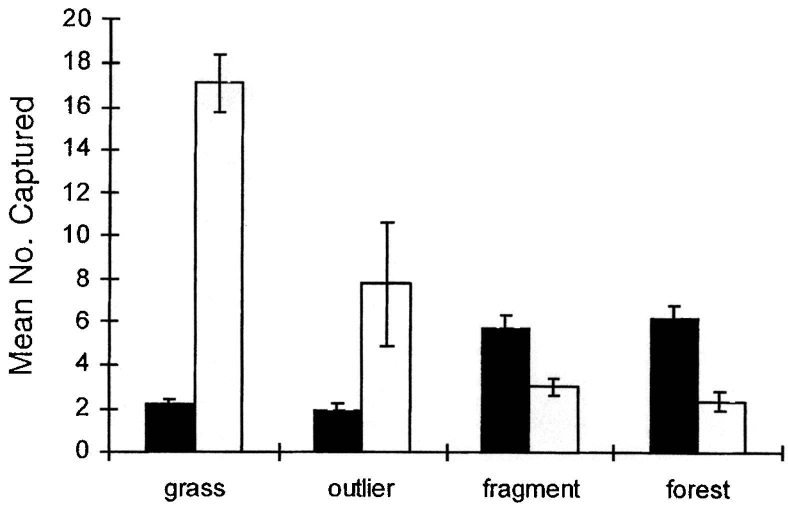

FIGURE 2. Mean (± SD) number of ground beetles (filled bars) and other invertebrates (open bars) captured in pitfall traps in grassy habitats, beneath single outlying white spruce, in small forest fragments, and in dense white spruce forest. Ground beetles were more common in forest habitats, whereas the invertebrates on which they prey or that act as competitors were more common in open habitats.

("outliers") and in adjacent open grassy habitats ("grass") (2.0 ± 0.2 beetles/trap and 2.2 ± 0.2 beetles/trap, respectively). Differences in capture rates between patches of various sizes were significant (Fig. 2; ANOVA, $F_{3,495} = 26.99$, $P < 0.0001$). Invertebrates other than ground beetles showed the opposite trend, with capture rates inversely related to the size of forest patches (Fig. 2). Densities of ground beetles in open habitats on Kent Island may be limited, in part, by Herring Gulls, *Larus argentatus* Pontoppidan (Charadriiformes: Laridae). Gulls, which nest and forage in open habitats throughout the island, prey heavily on ground beetles, as indicated by direct observations of the birds' feeding behavior and examination of regurgitated pellets composed almost entirely of beetle elytra (NT Wheelwright, personal observation).

Based on two preliminary mark–recapture experiments, the densities of ground beetles were estimated at 50 000 – 250 000/ha (n = 307 individuals marked, with 4 marked individuals recaptured). Ground beetles did not show a tendency to return to their site of capture when released even a short distance away. Of 446 individuals captured in one of four trapping grids, each grid located 15 m from a central site, only 3 were recaptured in their original site after being released at the central site (0.7%).

Discussion

Only 16 species of Carabidae were recorded on 80-ha Kent Island. In general, small isolated islands and habitat patches tend to have depauperate ground beetle faunas (Bengtson 1980; Niemelä *et al.* 1987; Nilsson *et al.* 1988; Bauer 1989). Previous studies suggest that the ground beetle fauna of Kent Island is comparable with that of other similarly sized boreal islands. For example, Bengston (1980) found six species of ground beetles on Stora Dimun (270 ha) in the Faroe Islands, whereas Niemelä *et al.* (1987) found 12 species on Rodloga (81 ha) and 10 species on Norrora (160 ha). Both of these islands are located within 40 km of mainland Sweden. Nilsson *et al.* (1988) listed 25 species on Goton in Lake Malaren, Sweden. On much larger Brunette Island ($20\ km^2$), located 15 km off the coast of Newfoundland, Larson *et al.* (1999) identified 36 species of ground beetle, including 8 species shared with Kent Island. On Brunette

Island, as on Kent Island, *P. adstrictus* was the most abundant species captured in pitfall traps. Niemelä *et al.* (1992) found this species to be abundant in central Alberta as well. At least 3 of the 16 species of ground beetles found on Kent Island are of European origin (*Carabus nemoralis*, *Harpalus rufipes*, *Notiophilus biguttatus*; Larson *et al.* 1999). Their presence on Kent Island is difficult to explain, especially that of *C. nemoralis*, which is flightless. Evidently they are effective dispersers and colonizers of new sites. They may have become established during the nineteenth century, when Kent Island was home to an active fishing trade and sheep were raised and agricultural crops cultivated (Gross 1936).

On Kent Island, pitfall samples were dominated by relatively few species, as has been found in studies in other areas of Canada and the United States (Holliday 1991; Niemelä 1992; Clark *et al.* 1997). More than 90% of the individual beetles captured were represented by five species (*Pterostichus. adstrictus*, *P. pensylvanicus*, *P. coracinus*, *C. opaculus*, and *Platynus decentis*). These species, relatively general in their habitat distribution on Kent Island, are well known from elsewhere in Canada to be habitat generalists (*P. adstrictus*) or forest generalists [the other two *Pterostichus* spp. (*P. pensylvanicus* and *P. coracinus*) and *P. decentis*] (Lindroth 1966; Niemelä *et al.* 1992). The widespread distribution of *C. opaculus* on Kent Island was unusual because elsewhere it is usually confined to areas of sandy substrate (Lindroth 1966). Conceivably, the island's depauperate ground beetle fauna results in reduced competition and allows *C. opaculus* to be a habitat generalist. On the other hand, two other ground beetle species were confined to a single habitat type on Kent Island. *Carabus granulatus hibernicus* occurred only in the mountain ash stands and *S. stenostomus* only in mixed forest, which is consistent with Lindroth's (1961) classification of both species as habitat specialists. A comparative study of the same species on the New Brunswick mainland and nearby islands would be valuable for determining the influence of interspecific competition on habitat selection in ground beetles.

Our results on seasonal patterns in ground beetle abundances were equivocal. We found no difference in capture rates during two 3-day sampling periods conducted a month apart (in mid-June and again in mid-July). On the other hand, capture rates clearly declined over a 3-week period during July in control and experimental plots in our removal experiments (Fig. 2). Capture rates in the removal experiments during mid-July were similar to those of the independent 3-day mid-July sample (*i.e.*, about 5 beetles/trap), but much higher than those at the beginning of July. Together, these results suggest that ground beetle densities on Kent Island rise between mid-June and early July and then fall back to mid-June levels by mid-July.

Although ground beetle densities on Kent Island were estimated at 50 000 – 250 000/ha, the removal of thousands of beetles over a 3-week period did not result in an increase in the density of invertebrates. This was unexpected, because of numerous observations of ground beetles preying on a variety of invertebrates, and because trapping in spruce stands of different sizes revealed a negative correlation between the abundance of ground beetles and the abundance of other invertebrates. Because beetles relocated in our experiments were apparently quickly replaced by others moving into the removal plots, actual ground beetle densities were hardly altered by the experiments. Alternatively, factors other than ground beetle densities may be responsible for determining the abundance of other invertebrates.

In conclusion, we found that Kent Island, a small isolated island in the Bay of Fundy, has a relatively low species richness of ground beetles (Lindroth 1961, 1966) and that most species occurred in all forest types, despite substantial differences in the structure, physical conditions, and plant composition of the habitats. Ground beetle densities are very high on Kent Island, especially in mixed forest and larger forest stands.

Acknowledgements

We thank R Nelson (Colby College), for identifying the ground beetles, and J Spence, for helpful comments on the manuscript. Our research was supported by grants from the National Science Foundation. This represents contribution No. 140 from the Bowdoin Scientific Station.

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(Date received: 12 October 1999; date accepted: 02 August 2000)