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Amphipods and isopods in the rocky intertidal: dispersal and movements during high tide

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Abstract Animals in the intertidal, both mobile and sessile, generally exhibit some zonation pattern, in which each species shows a preference for, or is confined to, some height levels. The study of zonation patterns is, however, almost exclusively based on surveys made during low tide, when many animals are relatively inactive. We studied zonation patterns of amphipods and isopods on rocky shores in southwestern Iceland, both by traditional sampling at low tide as well as by sampling during high tide. The distributional patterns seen at high tide differed significantly from that at low tide. One amphipod, *Anonyx sarsi*, was common around baits at all levels at high tide but absent from the intertidal at low tide. Several other species were either relatively more common or tended to be recorded higher, or in one instance, lower on the shore when the tide was in than at low tide. There was also evidence of some species changing habitats within the intertidal with the tidal cycle. Many species, however, moved little away from their respective zones occupied at low tide, and for some species, including some capable of rapid swimming, very limited mobility was indicated. We conclude that low-tide surveys of the intertidal give an incomplete picture of the community structure, and even key species may be missed in such surveys.

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Introduction

The vertical zonation patterns of sessile or slowly moving algae and animals in the rocky intertidal have been much studied in the past, both by observation and experiments (for recent reviews, see Little and Kitching 1996; Raffaelli and Hawkins 1996). The distributional patterns of more mobile animals have received less attention. The few available studies, however, have shown that mobile species show a characteristic abundance distribution along the environmental gradient of the shore (e.g. Ingólfsson 1977), although typically less distinct than that of sessile or slow-moving species. These studies have mostly been conducted by surveys of the shore during low tide (and in daylight), when many mobile species can be expected to be relatively inactive.

The compositions of intertidal communities often change with the tides. Migrations of fishes and decapod crustaceans into the intertidal on the rising tide are well documented, especially on muddy and sandy shores (e.g. Brown and McLachlan 1990; Gibson 2003). A number of studies on the tidal migrations of fishes and decapod crustaceans have also been carried out on rocky shores (Black and Miller 1991; Warman et al. 1993; Rangley and Kramer 1995a, b). These tidal migrations are evidently often related to feeding (e.g. Raffaelli et al. 1990; Hunter and Naylor 1993; Rangeley and Kramer 1995a; Gibson 2003), as are the conspicuous migrations of numerous birds into the intertidal on the falling tide (e.g. Alerstam et al. 1992). Although less studied, some smaller invertebrates, for example amphipods, are also known to make extensive tidal migrations, both on sandy and muddy shores (Watkin 1941; Hager and Croker 1980; Armonies 1994) and on rocky shores (Ingólfsson and Agnarsson 1999). In some instances, these are also clearly related to feeding (Ingólfsson and Agnarsson 1999).

The aim of this study is to compare the distributional patterns of small mobile invertebrates on the rocky shore at high and low tide. We ask: does the vertical distributional pattern apparent in the intertidal at low tide remain unaltered at high tide? We focus on 16 common peracarids (12 amphipods and 4 isopods), almost all of which are known to be present in the intertidal at low tide. Their feeding habits are in general rather poorly known and may be quite plastic. *Anonyx sarsi* is a voracious scavenger and predator (Ingólfsson and Agnarsson 1999). *Calliopius laeviusculus* feeds both on small animals and algae (Pederson and Capuzzo 1984). Grazers on macroalgae include *Idotea* spp. (e.g. Jormalainen et al 2001), *Hyale nilssoni* (e.g. McBane and Croker 1983), and probably also *Amphithoe rubricata* (Dahl 1973; cf. Cruz-Rivera and Hay 2000), while *Jaera* spp. graze on microalgae (Sjöberg 1967). *Caprella septentrionalis* is possibly primarily a filter feeder (cf. Takeuchi and Hirano 1995), as is *Ischyrocerus anguipes* (Dahl 1973), while *Corophium bonelli* is probably a detrivore (cf. Osterling and Pihl 2001). *Gammarus* spp. appear omnivorous or detrivorous (e.g. Dahl 1973). The feeding habits of *Dexamine thea* have not been described, to our knowledge.

Materials and methods

Data obtained in the spring and summer months of 1975–1996 from 29 transects from sheltered to fairly sheltered rocky shores of southwestern Iceland, sampled at spring tides, were used to establish the low-tide vertical distribution of common amphipods and isopods in the area. Fucoids (principally *Ascophyllum nodosum*, *Fucus vesiculosus*, and *F. serratus*) dominate these shores; their slope is gentle and the substratum consists of boulders with some bedrock. Stations were spaced at vertical intervals of 0.5 m along the transects, and at each station two quadrats (20 × 20 cm) were sampled. All animals and algae were removed from the quadrats and taken to the laboratory, where animals were rinsed from the algae over a 0.5-mm sieve. The total number of stations sampled was 227. Some transects near Seltjörn (see below) sampled in 1996 were close to transects studied in 1975. No conspicuous differences were noted between the two periods.

The main study site for high-tide distributions was Seltjörn, a small bay near Reykjavík, southwestern Iceland (64° 9.350′ N, 22° 1.875′ W). Seltjörn lies within the area covered by the above transects, and can be considered a typical rocky shore of the area. The tidal difference at spring tide is approx. 4 m; the mean low water of springs (MLWS) is 0.2 m above chart datum (CD) and the mean high water of springs is 4.0 m above CD. The width of the tidal zone is about 100 m. A tidal current is not noticeable at this site.

Three stations were placed on a transect, at 0.6 m (station 1), 1.6 m (station 2), and 2.2 m (station 3) above CD, respectively. The horizontal distance was 59.0 m between stations 1 and 2, and 35 m between stations 2 and 3. Traps designed to catch small moving animals were deployed at these stations. The traps were of cylindrical Plexiglas, 25.5 cm long and had an outside diameter of 12 cm. A removable funnel with a 9-mm hole was fitted at one end [see Ingólfsson and Agnarsson (1999) for details]. Two traps spaced approx. 10 m apart horizontally were set at each station, each trap bolted to a rock with the funnel facing landwards. They were put in place at low tide in the early afternoon near the time of spring tides, one trap at each level baited with fresh haddock fillet weighing 50–70 g, while the other trap was unbaited. Traps were emptied after approx. 25 h, after two high-tide periods (one in the evening and one the following morning), and then left for another 25 h, with the previously baited trap now unbaited, and vice versa. Except for *Anonyx sarsi*, which was almost exclusively caught in baited traps, species did not show significant differences in numbers caught in baited and unbaited traps. We therefore assume the animals to have entered the traps accidentally while swimming.

Traps were deployed in this manner twice monthly, when possible, from February to November 1995, and then monthly to December 1996. Here we use data obtained from spring to autumn, March–October (26 trapping sessions in all, involving 322 trap-days), since adverse weather in mid-winter obviously affected the efficiency of the traps. Also, the low-tide distribution of some species may change with season (e.g. Leifsson 1998). At spring tides from March to October both the evening and morning high tides at Reykjavík (but not always the falling and rising tides) occur mostly in daylight, although in March and October these tides would be at twilight.

Similar traps were deployed monthly at Geldinganes near Reykjavík (64° 9.675′ N, 22° 48.125′ W) from July to December 1996 (7 trapping sessions). Here we use data from July to October (5 trapping sessions, involving 60 trap-days). The stations were located at 0.7 m (station 1), 1.6 m (station 2), and 2.4 m (station 3) above CD. The shore is quite similar to that of Seltjörn, but much steeper, the distance between stations 1 and 2 being 6.5 m, and that between stations 2 and 3 about 5.0 m.

On 3 March 1995 samples were taken at low tide from five 20×20 cm quadrats at each of the three trapping stations on the Seltjörn transect, and, in addition, at two stations located midway between stations 1 and 2 and between stations 2 and 3. Samples were treated as described above. The sampling was repeated during low tide on 24 May 1995. In addition, at these dates, amphipods and isopods were collected qualitatively from under stones at stations 1, 2, and 3.

On 13 July 1995 a wire was laid along the Seltjörn transect, and six stations were located at vertical intervals of 0.5 m along it, the lowest station being 0.4 m above CD, the highest 2.9 m above CD. Small buoys were attached to the wire with strings to mark the stations. Two bunches of the brown seaweed *Ascophyllum nodosum* were collected from each station, each bunch weighing approximately 1.5–2.0 kg, wet weight (a 10-l bucket was used in the field to standardize weight). Animals were rinsed from the algae in the laboratory over a 0.5-mm mesh. A diver repeated the sampling the following day at high tide. The diver used a bag with a mesh of 0.2 mm to enclose two bunches of *A. nodosum*, each approximately 1.5 kg, at each station before cutting the plants loose.

The ratio of the number of a species caught in traps over the number taken during low tide, multiplied by 10, is taken as a rough measure of mobility of the species, here termed "mobility index". In order to ascertain whether the species being studied were able to swim sufficiently fast to move appreciable distances in the intertidal during high tide, we measured swimming speeds in the laboratory. Freshly caught animals were released at one end of a 73 cm long aquarium (at 30 ppt salinity and 12–13°C) illuminated by a light shining sideways along the tank, and the duration of the swimming spurts, which lasted until the animals reached the other end of the aquarium or settled on the bottom, were measured with a stopwatch.

Results

All peracarids tested were capable of rapid swimming (Table 1). Most animals clearly swam at variable speeds, and their top speeds were generally well above the averages over the measured course.

▶

Fig. 1 Vertical distribution of some amphipods and isopods of rocky shores in southwestern Iceland, based on 29 transects sampled 1975–1996. The species are arranged approximately from upper left to lower right according to their vertical distribution; zero values are not visible on the graphs. The lines are fitted by distance-weighted least squares by SYSTAT (tension = 0.45). About 95% of identified males of the genus *Jaera* belonged to *J. prehirsuta*, the remainder to *J. albifrons*. *MHWN* mean high water of neaps, *MTL* mean tide level, *MLWN* mean low water of neaps, *MLWS* mean low water of springs

Most amphipods and isopods that were common in 1975–1996 transects were also found at Seltjörn. Here we consider 12 amphipod and 4 isopod species (or taxa). A few additional rare peracarids found are not considered. The transect data show a variety of distributional patterns (Fig. 1). The amphipods *Gammarus*

Table 1 Swimming speeds of individuals of six amphipod and one isopod species, measured in a 73-cm-long aquarium (salinity ca 30 ppt, temperature 12–13°C). Measurements were made on freshly caught animals on 11 and 12 June and 25 July 2002. A bright light shone at the release point. Each animal was timed once

Species	Distance (cm)	Time (sec)	Speed (cm/sec)	Time (min) for 100 m
Gammarus marinus	60	9.0	6.7	25
G. marinus	71	9.1	7.8	21
G. marinus	40	6.0	6.7	25
G. marinus	73	7.6	9.6	17
G. marinus	73	7.8	9.4	18
G. marinus	43	11.3	3.8	44
G. marinus	71	8.6	8.3	20
G. marinus	52	5.9	8.9	19
G. obtusatus	46	7.7	6.0	28
G. obtusatus	58	11.0	5.3	32
G. obtusatus	29	6.2	4.7	36
G. obtusatus	57	13.9	4.1	41
G. finmarchicus	62	12.1	5.1	33
G. oceanicus	61	10.7	5.7	29
Calliopius laeviusculus	69	6.9	10.0	17
C. laeviusculus	70	11.1	6.3	26
Hyale nilssoni	43	4.0	10.8	16
H. nilssoni	60	9.0	6.7	25
Idotea granulosa	40	10.2	3.9	42
I. granulosa	42	4.3	9.8	17

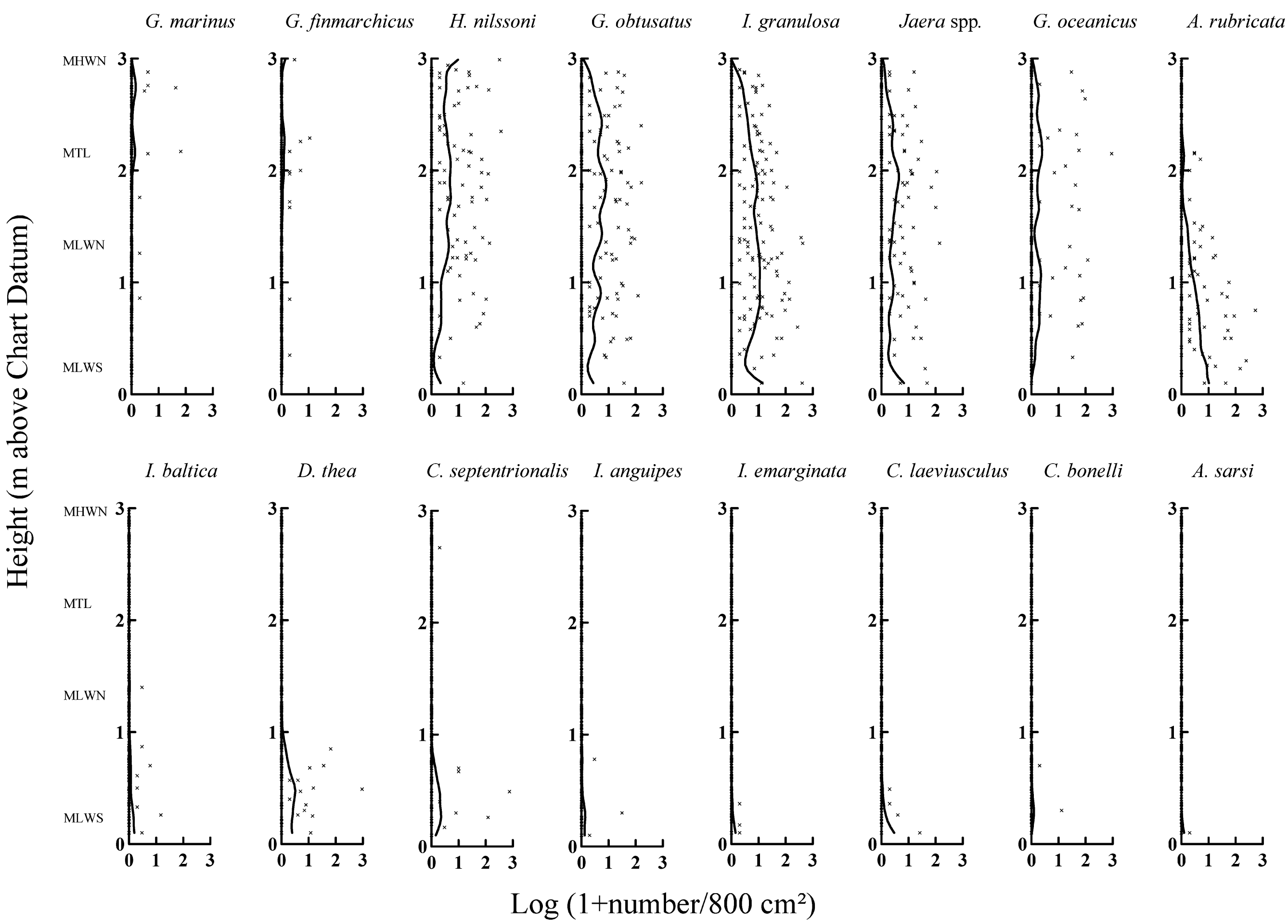

Table 2 Animals collected near trapping stations at Seltjörn on 3 March and 15 May 1995

Height (m) above chart datum	*Hyale nilsoni*		*Gammarus marinus*		*G. obtusatus*		*G. finmarchicus*		*G. oceanicus*		*Amphithoe rubricata*		*Dexamine thea*		*Idotea granulosa*		*I. emarginata*		*I. baltica*		*Jaera spp.*		*Caprella septentrionalis*	
	Quadrats[a]	Stones[b]	Quadrats[a]	Stones[b]	Quadrats[a]	Stones[b]	Quadrats[a]	Stones[b]	Quadrats[a]	Stones[b]	Quadrats[a]	Stones[b]	Quadrats[a]	Stones[b]	Quadrats[a]	Stones[b]	Quadrats[a]	Stones[b]	Quadrats[a]	Stones[b]	Quadrats[a]	Stones[b]	Quadrats[a]	Stones[b]
2.2	1	0	0	19	4	266	1	0	0	0	0	0	0	0	1	0	0	0	0	0	22	0	0	0
1.9	0	–	0	–	5	–	0	–	0	–	0	–	0	–	0	–	0	–	1	–	30	–	0	–
1.6	0	0	0	0	17	236	0	70	0	0	0	0	1	0	3	0	0	0	0	0	37	0	0	0
1.1	0	–	0	–	7	–	0	–	0	–	2	–	6	–	9	–	0	–	2	–	24	–	0	–
0.6	0	0	0	0	0	18	0	0	0	9	4	0	2	0	1	3	103	301	10	0	1	0	1	0

[a]Number collected from 10 quadrats, each 20×20 cm (5 on each date), at 5 height levels
[b]Number collected from under stones at 3 height levels

finmarchicus and *G. marinus* are most common in the upper shore, above mean tide level (MTL), although there are records from lower down. The amphipod *Hyale nilssoni* occurs throughout the intertidal, although less commonly below the level of mean low water of neaps (MLWN). The amphipods *G. obtusatus* and *G. oceanicus*, the isopods *Jaera* spp. (94% of 142 identifiable males belonged to *J. prehirsuta*, the remainder to *J. albifrons*), and *Idotea granulosa* appear common throughout the part of the intertidal here considered. The amphipod *Amphithoe rubricata* appears at MTL and becomes increasingly common towards lower levels. The isopod *I. baltica* and the amphipods *Dexamine thea* and *Caprella septentrionalis* are virtually confined to the levels below MLWN. The amphipod *Calliopius laeviusculus* occurs still lower. There are few records of the isopod *I. emarginata*, and the amphipods *Ischyrocerus anguipes, Corophium bonelli,* and *Anonyx sarsi*, but those all stem from the lowest part of the shore.

The data obtained at low tide at Seltjörn from traditional transects and by searching under stones (Table 2), and by rinsing *Ascophyllum* (Fig. 2) agree well with the patterns described above with the following exceptions: the amphipod *G. oceanicus* at Seltjörn appeared to be restricted to the lowermost levels while the amphipod *H. nilssoni* was rare and only found above the MTL.

In all 1,648 individual peracarids (omitting a few very rare species not considered further here) were caught in the traps from March to October, while 5,524 were obtained in the low-tide surveys at Seltjörn (Table 3). The mobility index was quite variable among species. One species considered, *Anonyx sarsi*, was only caught in traps and constituted some 45% of the total catch of peracarids. Several species had a relatively high mobility index (around 10 or more), but for most species this index was much lower, indicating limited movement at high tide.

The amphipods *G. finmarchicus* and *H. nilssoni* and the isopod *Jaera spp.*, were limited to the traps at the two topmost stations (Fig. 3). *G. obtusatus* was considerably more common at the topmost two stations than at the lowermost one. *G. marinus* and *G. oceanicus* appeared equally common at all stations. *Idotea emarginata* was only caught at the lowermost station, while the amphipod *Calliopius laeviusculus* and *Caprella septentrionalis* were confined to the two lowermost stations. The isopods *I. baltica* and *I. granulosa*, and the amphipods *D. thea*, *Ischyrocerus anguipes*, and *A. sarsi* were found at all stations, though generally more commonly at the lower ones. The amphipods *Amphithoe rubricata* and *Corophium bonelli* were caught rarely, but only at the topmost and the lowermost stations. The Geldinganes trap data are mostly too meagre to present a reasonable picture, and are therefore not shown here. The observed patterns were, in general, in agreement with those from Seltjörn, although *Anonyx sarsi* was more evenly distributed along the transect at Geldinganes than at Seltjörn (see Ingólfsson and Agnarsson 1999).

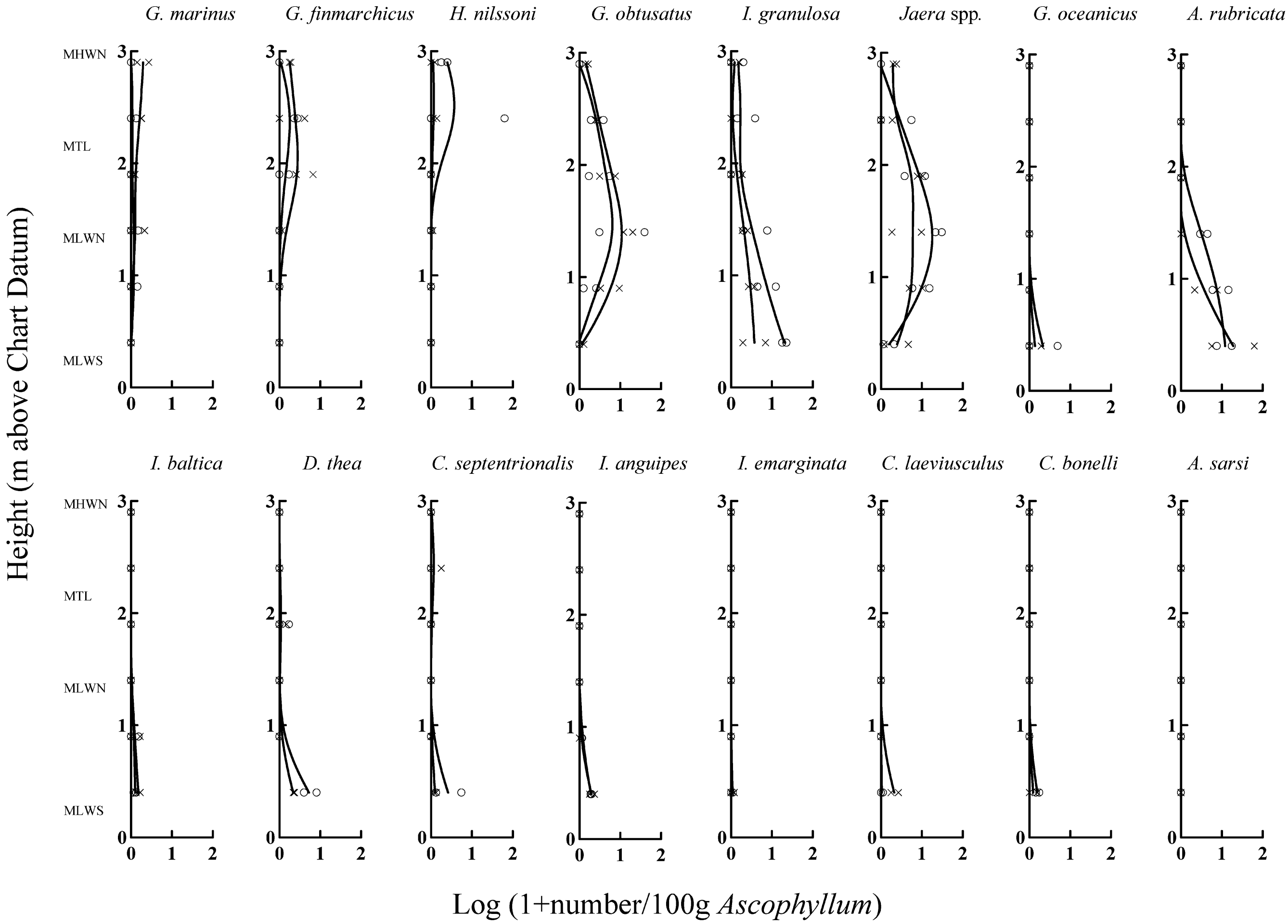

Fig. 2 Densities of amphipods and isopods in samples of the brown seaweed *Ascophyllum nodosum* taken along a transect at Seltjörn at high (*crosses*) and low (*circles*) tide in July 1995. The species are arranged in the same order as in Fig. 1. The lines are fitted by distance-weighted least squares by SYSTAT (tension = 0.5). Abbreviations on the height axis are as in Fig. 1

There was no significant difference in the vertical distribution of peracarids in *Ascophyllum nodosum* at high and low tide (Fig. 2). However, the density (numbers/100 g algae, wet weight) of *Idotea granulosa* in the algae was significantly lower at high than at low tide; the values for two-way analysis of variance (ANOVA) were $F = 11.3$, $df = 1$, $P < 0.01$. Amphipods of the genus *Gammarus* appeared to show the opposite trend, although this was not significant even when all species of the genus were lumped (values for two-way ANOVA were $F = 3.84$, $df = 1$, $P = 0.07$).

Discussion and conclusions

The measured swimming speeds suggest that most peracarid species studied here are capable of swimming considerable distances at high tide, even the entire width of a 100 m tidal zone within hours or less. Several studies show that species of the genus *Gammarus* sensu stricto are good swimmers (e.g. Fincham 1972; Dieleman 1977), although their mobility index here recorded is comparatively low. It is also indicative of

Table 3 "Mobility index" of common amphipods and isopods at the Seltjörn intertidal. The table shows total number of animals obtained at Seltjörn in low tide surveys and in traps deployed in March–October. The "mobility index" is the ratio of the number of animals caught in traps over the number obtained in low-tide surveys, multiplied by 10

Species	Low-tide surveys	Traps	"Mobility index"
Anonyx sarsi	0	815	TO[a]
Calliopius laeviusculus	1	23	230.0
Corophium bonelli	9	34	37.8
Dexamine thea	84	146	17.4
Ischyrocerus anguipes	18	19	10.6
Gammarus oceanicus	35	33	9.4
Idotea baltica	18	13	7.2
G. marinus	29	19	6.6
G. finmarchicus	118	57	4.8
Caprella septentrionalis	34	9	2.6
G. obtusatus	1,646	358	2.2
I. emarginata	405	40	1.0
I. granulosa	746	48	0.6
Hyale nilssoni	61	2	0.3
Amphithoe rubricata	586	7	0.1
Jaera prehirsuta	1,725	18	0.1
Total	5,524	1,648	

[a]Only obtained in traps

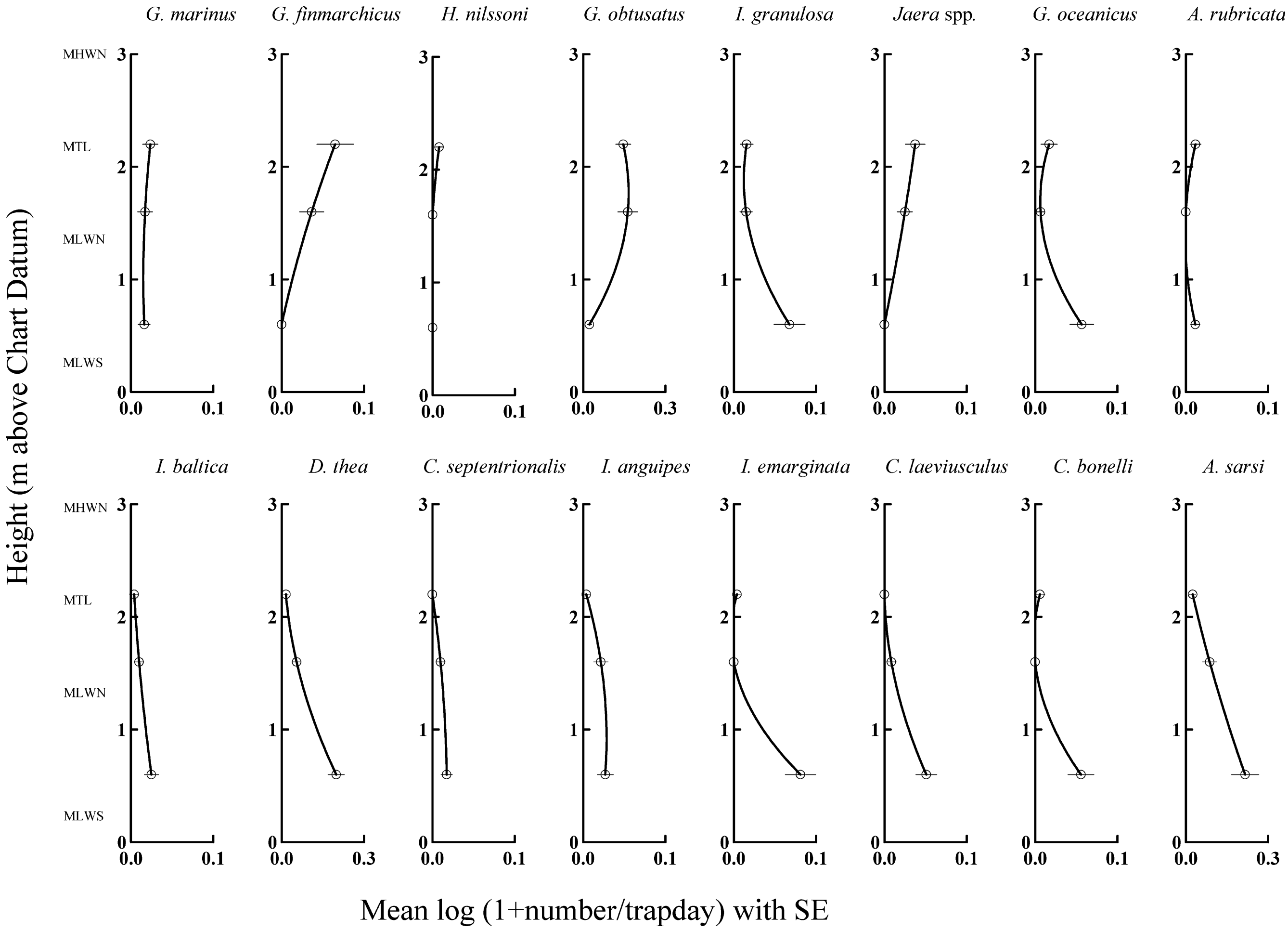

Fig. 3 Catches of amphipods and isopods in funnel traps at three different levels on the transect at Seltjörn, from March to October in 1995 and 1996. The number of trapping sessions was 26. The number of trap-days was 104 for the lowermost station, 112 for the middle station and 106 for the uppermost station. Numbers for the upper two levels have been adjusted for reduced potential catching time (i.e. submergence). The species are arranged in the same order as in Fig. 1. Abbreviations on the height axis are as in Fig. 1

the swimming potential that many of the species here studied have been reported to colonize experimental floating algae located between 300 and 600 m from the shore at a depth of 7–14 m below MLWS (Ingólfsson 1998, 2000). Some did so in appreciable numbers; these included species with high "mobility indices" (*Calliopius laeviusculus*, *Dexamine thea*, *Ischyrocerus anguipes*) as well as species with much lower indices (*Idotea granulosa*, *Gammarus* sp. juveniles). *Anonyx sarsi* has not been recorded from floating algae, to which it is apparently not attracted.

The Seltjörn trap data for several species showed patterns quite at variance with the low-tide distributions. The most pronounced differences are shown in Fig. 4. The most notable was the amphipod *A. sarsi*, which was trapped in abundance at all trapping levels, but not recorded at all at low tide at Seltjörn, while the transect data showed a single record from near the level of MLWS. This involves an upward migration on the rising tide in excess of 80 m for some individuals, and a similar downward migration on the receding tide. The amphipods *D. thea* and *Ischyrocerus anguipes* clearly occur higher up on the shore at high tide than at low tide. *C. laeviusculus*, *Caprella septentrionalis*, and *Idotea baltica*, were also caught higher on the shore then expected from low-tide records, although the data for these species are somewhat meagre. Several specimens of the amphipod *Amphithoe rubricata* were taken in the topmost traps, lying higher on the shore than any previous records of the species in southwestern Iceland. Several specimens of the amphipod *Gammarus marinus*, on the other hand, were caught in the lowermost traps, situated lower than any previous record of the species. Although the distribution by *G. oceanicus* in traps agrees well with the "normal" low-tide pattern in southwestern Iceland, conditions at Seltjörn appeared unusual in that all 35 individuals obtained at low tide were from the lower shore, below MLWN. However, 8 of the 33 animals trapped were from above this level (Yates corrected $\chi^2 = 7.4$, $P = 0.002$). The net result of the observed movements is that the invertebrate species diversity of the shore increases at high tide.

There have been earlier reports of tidal movements or migrations of some of the species studied here. Sars

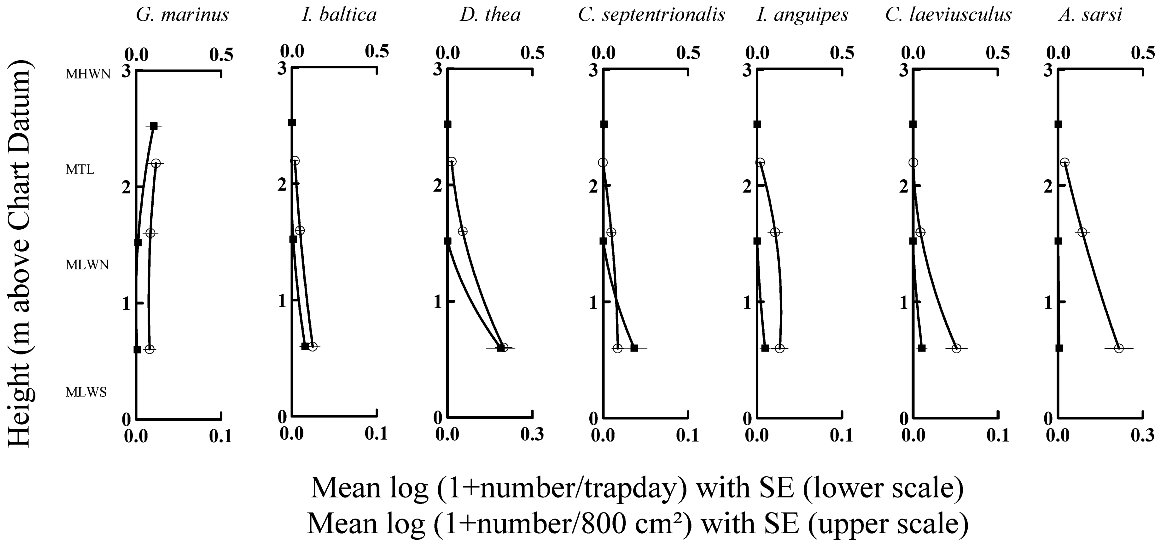

Fig. 4 Main differences in the intertidal distribution of common amphipods and isopods between high tide and low tide in southwestern Iceland. *Open circles* (*lower scale*) indicate catches of traps at high tide at three height levels at Seltjörn near Reykjavik (cf. Fig. 3) while *filled squares* (*upper scale*) are based on 29 low-tide transects from southwestern Iceland (cf. Fig. 1), with means calculated for three height intervals: 0.1–1.0, 1.1–2.0, and 2.1–3.0 m above chart datum. At high tide *Gammarus marinus* was found lower in the intertidal than any previous record during low tide. The remaining species shown were found at higher elevation at high tide, often migrating more than 1 m up the intertidal, equivalent to a horizontal distance in excess of 25 m. Abbreviations on the height axis are as in Fig. 1

(1890–1895) and Watkin (1941) found *Calliopius laeviusculus* (syn. *C. rathkei*) ascending beaches on the rising tide in Norway and Britain, respectively, and Watkin (1941) also report this for *D. thea*.

It is quite likely that physical factors, such as lack of moisture, are important in setting the upper limits to the distribution of peracarids on the shore at low tide (e.g. Dorgelo 1977). Drawing also on references from studies on sessile and slow-moving organisms (review in Raffaelli and Hawkins 1996), one could expect these highly mobile animals to spread widely through the intertidal at high tide. The results presented here show that several species extend their range upwards at high tide (and downwards in a the case of a single species). Nevertheless, many species appeared to move little, and showed similar distributions at high tide and low tide. Why this is so is unclear. At present it is difficult to associate these migrations with feeding, except in the case of *Anonyx sarsi*. It seems certain, however, that swimming power can hardly be limiting for most of the studied species. Distance per se nevertheless appeared to play a role in the dispersal of the very strong swimmer *A. sarsi* up the shore at high tide, as it distributed itself more evenly vertically on a steep and narrow shore at Geldinganes than at the wide Seltjörn shore (Ingólfsson and Agnarsson 1999), although this was not the case for the amphipods *D. thea* and *C. laeviusculus*.

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