Harpacticoid copepod communities of floating seaweed: controlling factors and implications for dispersal

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Key words: Copepoda, Harpacticoida, floating seaweed, community structure, colonisation, dispersal

Abstract

The structure of harpacticoid copepod communities of floating detached intertidal algae was studied by surveys and experiments. Seaweed clumps were sampled from Faxaflói, western Iceland, at various distances from the shore (0.2–14 km). Altogether 20 species of harpacticoids were found in these clumps, most of them typical phytal species. Multidimensional scaling ordination (MDS) separated the samples into three distinct clusters in which the communities were significantly different from each other. The distance from shore did not seem to affect the community structure. However, diversity and abundance of harpacticoids increased with size and complexity of the clumps. Experimental *Ascophyllum nodosum* fronds placed 300–600 m offshore were rapidly colonised by harpacticoids. Density and species diversity were, after 20 days afloat, higher than in the free-floating clumps. Species of the genus *Harpacticus* were successful colonisers, in particular *Harpacticus chelifer* and *Harpacticus uniremis*. In a survey of macrofauna (0.5-mm sieve) on floating algae clumps from various locations around Iceland, *H. chelifer* was present in all clumps studied, up to 117 km offshore. Its sex ratio was skewed towards females, often with a high ratio of ovigerous females. There was, however, no evidence that this species is using the algal clumps as a platform for reproduction.

Introduction

Harpacticoid copepods are among the most abundant and species-rich invertebrate groups associated with rocky shore algae (see Coull et al., 1983; Hicks, 1985 for review). They occupy several sub-habitats: interstices of finely divided epiphytes or other algal structures, the surfaces of the fronds themselves and the sediment accumulated at the bases of fronds (Moore, 1973; Hicks, 1977; Pallares & Hall, 1974). Harpacticoids generally lack planktonic larval stages but many are good swimmers, in particular the phytal ones (e.g. Hicks & Coull, 1983; Hicks, 1985; Palmer, 1988).

Floating drift algae are commonly encountered in near- and offshore waters of the world's oceans. They are of various kinds including unattached macro- and micro-algae species and detached intertidal or shallow water species (Kingsford, 1992; Ingólfsson, 1995; Castillo Arenas & Drekman, 1995; Sundbäck et al., 1996). These aggregates, normally of variable size, can include several species and travel long distances (Ingólfsson, 1995; Kingsford, 1995). Floating macroalgae clumps may hold a rich marine fauna including a number of fish (Mitchell & Hunter, 1970; Kingsford & Choat, 1985; Tully & Ó Cedigh, 1989; Safran & Omori, 1990; Kingsford, 1992; Davenport & Reeves, 1993; Druce & Kingsford, 1995) and invertebrate species (Yeatman, 1962; Highsmith, 1985; Tully & Ó Cedigh, 1986; Edgar, 1987; Locke & Corey, 1989; Ingólfsson, 1995, 1998; Ingólfsson & Ólafsson, 1997). These animals either colonise the drift algae at sea or are carried by detached intertidal seaweed from the shore. Recent studies of macrofauna on floating uprooted seaweed originated from the intertidal around Iceland have shown that many pelagic and benthic species rapidly colonise these clumps, and there are strong indications that rafting on the floating seaweed facilitates long distance dispersal of intertidal macrofauna species (Ingólfsson, 1995, 1998). The widespread pelagic species *Parathalestris croni* is

closely associated with floating seaweed around Iceland, where ovigerous females dominate the population and clearly use the macroalgal clumps as nests for their non-swimming nauplii (Ingólfsson & Ólafsson, 1997).

Yeatman (1966) investigated six clumps of drifting *Sargassum* algae in the Gulf Stream to determine if they were able to carry littoral harpacticoids and cyclopoids across the Atlantic Ocean. Yeatman gave few details, but he found five species of harpacticoids and one cyclopoid species in the clumps and concluded that the drift algae was an important vehicle for littoral copepod transport when such algae reach distant shores via ocean currents. As far as we know, no other studies have been reported on harpacticoid assemblages of drift algae.

In the present study, we examine the harpacticoid copepod communities of floating algal clumps sampled at various distances from the shore, in order to determine the structure of these communities and throw light on their regulating factors (distance from shore, size of clump, composition of the seaweed community, etc). Secondly, we studied the colonisation patterns of the harpacticoids by use of experimental clumps in near-shore waters. Thirdly, we wanted to assess the possibility of long-distance dispersal of harpacticoids by means of floating algae. Finally, preliminary observations indicated that the species *Harpacticus chelifer* had a skewed sex ratio towards females in off-shore clumps, and we aimed to determine if the clumps served a nest function for this species, as was found in the case of *Parathalestris croni* (Ingólfsson & Ólafsson, 1997).

Materials and methods

Free-floating clumps, composed mostly of the species *Ascophyllum nodosum* and/or *Fucus vesiculosus*, were collected along a 90 km long transect in the Bay of Faxaflói on 7 July and 6 August 1993 (Fig. 1). The clumps were retrieved with a plankton net (diameter: 0.465 m, mesh: 0.1 mm) and preserved in 4% buffered formaldehyde. A total of 35 clumps was obtained on 7 July, and 40 clumps on 6 August. Thirteen clumps from July and eight from August were selected at random for the detailed analysis of harpacticoids. Some samples dried out during storage and we were unable to process them.

Fronds of the brown vesiculated seaweed *Ascophyllum nodosum* (L.) Le Jol. of approximately equal size, sometimes with the red epiphyte alga *Polysiphonia lanosa* (L.) attached to it, were cut while emersed from a small area on the shore at Seltjarnarnes near Reykjavík, carefully placed in plastic bags, and weighed. Some bags were then randomly selected as controls and the algae immediately preserved with buffered formaldehyde. The remaining fronds were taken directly to sea to the small bay of Eidsvík east of Reykjavík (Fig. 1). There they were carefully removed from the bags, placed on the surface of the sea and tethered to anchored buoys, two to each, with a 4 and an 8 m thin nylon string, respectively. The buoys were about 300–600 m from land where the depth was from 7 to 14 m below mean low level of spring tides. The fronds were retrieved after some time with the plankton net described above. Two experiments were done, both in 1993. In the first, ten fronds were set afloat on 22 June and collected 8 days later, while nine fronds were used as controls. The mean wet weight of the fronds was 347 g (range: 200–640, SD: 125). Five control fronds and five fronds that had been set afloat were selected at random for harpacticoid analysis. In the second experiment, 16 fronds were set afloat on 14 July and half (randomly selected) collected 9 days and the other half 20 days later. Ten fronds were used as controls. The mean weight of the fronds was 243 g (range: 180–380, SD: 50.0). Three control fronds, three fronds afloat for 9 days, and six fronds afloat for 20 days were selected at random for harpacticoid analysis (all fronds analysed where samples had not dried out).

All preserved algal samples were rinsed in the laboratory through two sets of sieves, 0.5 and 0.063 mm, and the harpacticoids from each sieve counted and identified. The algae were weighed wet and identified.

In a study of the ecology of fry of the lumpsucker (*Cyclopterus lumpus*), about 26 fronds of *A. nodosum* taken from the Seltjarnarnes shore were placed afloat in Eidsvik approximately monthly, for about 10 days, from May 1995 to November 1996. The fronds were then retrieved and treated as before. Also, clumps were collected from the 90 km transect in the Bay of Faxaflói approximately monthly from June 1995 to January 1997 (Ingólfsson & Kristjánsson, 1997). Two to three of the retrieved fronds from Eidsvik and from the Faxaflói transect were selected each month from June 1995 to May 1996 to study life history patterns of *Harpacticus chelifer*. In addition, samples from 1990 to 1992 (described by Ingólfsson 1995) were
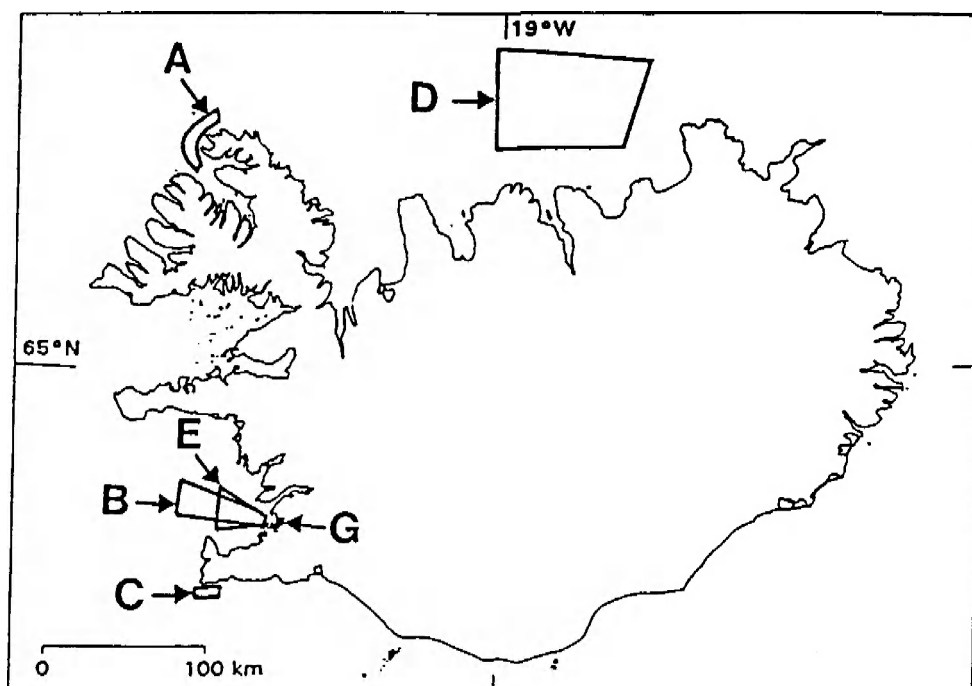
Figure 1. Sampling areas of seaweed clumps around Iceland. Reykjavík and Seltjarnarnes are situated in the vicinity of map designation G. Additional information on sampling locations are given in Table 4.

used to calculate sex ratios of *H. chelifer*, but here only animals retained by a 0.5-mm sieve were available.

Differences in faunal density and environmental variables among habitats were investigated by means of 1-way analysis of variance (ANOVA). Paired *a posteriori* comparisons of density estimates were carried out with a Tukey test, using 95% confidence limits. Prior to the analysis of variance all data were $\log_{10}$-transformed and Cochran's *C*-test used to check the assumption of homoscedasticity. When conditions for the use of parametric test was not fulfilled, Kruskal-Wallis and Mann-Whitney *U* tests were employed. Species diversity was assessed using the Shannon-Wiener information function (H′). Regression analysis was used to investigate the relationship between meiofaunal densities and the measured environmental variables. Species abundance data (the full data set available from the first author upon request) were double square root transformed and subjected to non-metric multidimensional scaling ordination (MDS) and cluster analysis using the Bray-Curtis similarity measure. The ANOSIM randomisation test (Warwick et al., 1990) was used to test for significant differences in harpacticoid community structure and the dissimilarity percentage program (SIMPER, Warwick et al., 1990) used to identify the species making the greatest

contribution to differences between clusters observed in the MDS plot.

Results

Altogether 38 species, plus *Tisbe* spp., were found in the floating algal clumps studied (Table 1). About half of these were found in one or two clumps only and always in low numbers. *Harpacticus chelifer* was found in all floating clumps and was usually the dominant species. Other species having relatively high frequencies were *Harpacticus uniremis* (57%), *Ameira longipes* (54%), *Diarthrodes major* (43%), *Tisbe* spp. (43%), *Heterolaophonte longisetiger* (40%) and *Amphiascus minutus* (29%). *Parathalestris croni* was recorded in over 70% of the July samples, in 7% of the August samples from the Faxaflói transect, and never in the experimental clumps. We will not elaborate more on the distribution of this large harpacticoid because such information is already available in the literature (Ingólfsson & Ólafsson, 1997).

Faxaflói survey

The MDS ordination showed three significantly different assemblages in the free-floating algal clumps in

Table 1. List of species found in the present study, and their respective frequency (F) and average numbers (AV) recorded in Faxaflói survey and Eidsvík experiments

Species	Faxaflói transect		Eidsvík experiments									
			June				July					
			Control		8 days		Control		9 days		20 days	
	F	AV	F	AV	F	AV	F	AV	F	AV	F	AV
Ambunguipedidae												
Ambungipes aff. *rufocinta*					1/5	<1						
Ameiridae												
Ameira longipes	7/21	8			3/5	3	1/3	1	3/3	61	6/6	51
Nitokra typica	2/21	<1										
Canthocamptidae												
Mesochra pygmaea							1/3	2			2/6	1
Itunella sp.	4/21	<1										
Diosaccidae												
Diosaccus aff. *varicolor*											1/6	2
Diosaccus sp.											1/6	<1
Robertsonia sp.							1/3	1				
Amphiascus minutus	5/21	2									5/6	4
Amphiascoides debilis	7/21	2									1/6	<1
Amphiascoides nana					1/5	1						
Amonardia arctica					1/5	<1					1/6	<1
Paramphiascopsis giesbrechti					1/5	<1						
Paramphiascella hispida					1/5	<1						
Ectinosomatidae												
Ectinosoma sp.	1/21	<1					1/3	1			1/6	<1
Microsetella norvegica							2/3	3				
Harpacticidae												
Harpacticus chelifer	21/21	105			5/5	8	1/3	<1	3/3	43	6/6	281
Harpacticus flexus											1/6	<1
Harpacticus septentrionalis					3/5	<1					3/6	<1
Harpacticus uniremis	7/21	1			5/5	87			3/3	4	5/6	65
Harpacticus obscurus	2/21	5									3/6	4
Zaus aurelii	1/21	<1										
Laophontidae												
Laophonte setosa					1/5	<1	1/3	3	1/3	1		
Pseudonychocamptus koreni	2/21	<1										
Heterolaophonte littoralis									1/3	4		
Heterolaophonte strömi	2/21	<1							1/3	2	6/6	7
Heterolaophonte longisetigera	10/21	3			1/5	<1			1/3	2	2/6	34
Paronychocamptus curticaudatus					1/5	<1						
Paralaophonte perplexa					1/5	<1			2/3	5	3/3	3
Parastenheliidae												
Parastenhelia spinosa	8/21	24										

Table 1. Continued

Species	Faxaflói transect		Eidsvík experiments									
			June				July					
			Control		8 days		Control		9 days		20 days	
	F	AV	F	AV	F	AV	F	AV	F	AV	F	AV
Thalestridae												
Thalestris longimana					1/5	<1						
Parathalestris clausi	6/21	2	1/5	1	2/5	1	1/3	<1				
Parathalestris croni	*											
Parathalestris intermedia					1/5	<1						
Rhynchothalestris helgolandica									1/3	1		
Diarthrodes major	7/21	4			1/5	<1			2/3	9	5/6	11
Diarthrodes nobilis									1/3	1		
Dactylopusia vulgaris	2/21	<1	1/5	<1					1/3	3	4/6	33
Tisbidae												
Tisbe spp.	13/21	10	4/5	12	2/5	17						
Number of species		18		3		18		5		15		18

*See Ingólfsson & Ólafsson 1997.
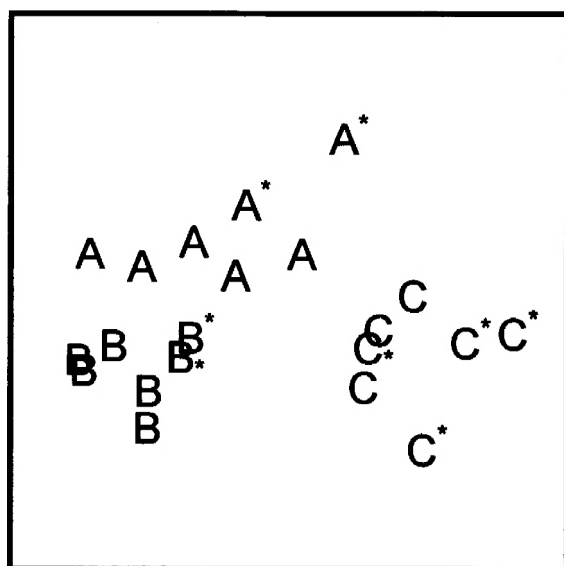
Figure 2. Two-dimensional configuration (non-metric multidimensional scaling ordination) of harpacticoid species abundance data in floating seaweed clumps from Faxaflói in July and August (*) 1993 (stress value=0.14). Symbols A, B and C refer to the three significantly different assemblages of harpacticoid copepods (ANOSIM, $P<0.001$).

Table 2. Results of 1-way ANOVA on physical and biological parameters of algal clumps harbouring the three harpacticoid assemblages

	ANOVA	Tukey
Distance from shore	NS	
Size of clumps	$P<0.01$	B>C
Fucus vesiculosus	$P<0.01$	B>A,C
Ascophyllum nodosum	NS	
Chorda filum	$P<0.001$	B>A,C
Clump diversity	$P<0.001$	A,B>C
Number of Harpacticoid species	$P<0.001$	A,B>C
Harpacticoid diversity	$P<0.001$	A,B>C

Faxaflói 1993 (Fig. 2) (ANOSIM, $P<0.001$). There was no indication that distance from shore or the amount of *Ascophyllum nodosum* affected the assemblage structure (Table 2). The size and composition of the clumps may, however, affect the assemblage structure, as algal diversity of clumps, size of clumps, amount of *Fucus vesiculosus* and *Chorda filum* varied significantly among the three types of assemblages (Table 2). There was no significant difference in the assemblage structure of harpacticoids from samples taken in July and August (Fig. 2, ANOSIM, $p>0.05$). According to SIMPER analysis, three species and one genus contributed mostly to the variance among clumps. *Parastenhelia spinosa* was found almost solely in the B clumps (ANOVA, $P<0.001$, Tukey test) and its density was significantly correlated with diversity and size of the clumps (r^2:0.27, $p<0.01$; r^2:0.38, $p<0.01$, respectively). *Tisbe* spp., not re-

corded in the C clumps, were in significantly higher numbers in A clumps compared with B (ANOVA, $P<0.001$), and their density significantly correlated with the diversity of the clumps (r^2:0.30, $p<0.01$). *Ameira longipes* was almost exclusively found in B clumps (ANOVA, $P<0.001$, Tukey test) and its density significantly correlated with diversity and size of the clumps (r^2:0.18, $p<0.05$; r^2:0.2, $p<0.05$, respectively). Finally, *Harpacticus chelifer* was on average twice as abundant in A and B clumps than in C clumps, though this difference was not significant (ANOVA, $P>0.05$) and its density was not significantly correlated with distance from shore, diversity or size of the clumps. Numbers of harpacticoid species in the samples were significantly correlated with the size of the clumps, the algal diversity of the clumps, and the amount of *Fucus vesiculosus* (r^2:0.37, $p<0.01$; r^2:0.29, $p<0.01$; r^2:0.18, $p<0.05$, respectively), but not to distance from shore, or to the amount of *Ascophyllum nodosum*. Density of harpacticoids was significantly correlated with algal diversity of the clumps (r^2:0.25, $p<0.05$), but not to size of clumps or distance from shore. There was a significant correlation between size of clumps and diversity of clumps (r^2:0.25, $p<0.05$).

Experiments

There was a clear increase in the numbers of harpacticoids in the clumps after 8 or 9 days afloat in both experiments (ANOVA, $p<0.05$), while nauplii larvae did not significantly increase (ANOVA, $p>0.05$) (Fig. 3). In the July experiment, numbers of harpacticoids were also significantly higher after 20 days, but the increase from day 9 to day 20 was not statistically significant (ANOVA, Tukey test $p>0.05$).

For both June and July experiments, the control fronds (taken directly from the shore to the laboratory) contained significantly fewer harpacticoid species than fronds left afloat for 8, 9 or 20 days (Table 1, for June Mann-Whitney U test, $p<0.05$, for July, Kruskal-Wallis, $p<0.05$). In the June experiment only *Tisbe* spp. were found in similar numbers in control and 8 days afloat fronds (Table 3). The most important colonisers were *Harpacticus chelifer, H. uniremis* and *Ameira longipes*. In the July experiment, *Ameira longipes* was found in all floating experimental fronds and was the dominant species after 9 days. There was no significant difference in its abundance between day 9 and 20 (Mann-Whitney U test, $p>0.05$). Other important colonisers, *Harpacticus chelifer, H. uniremis*,
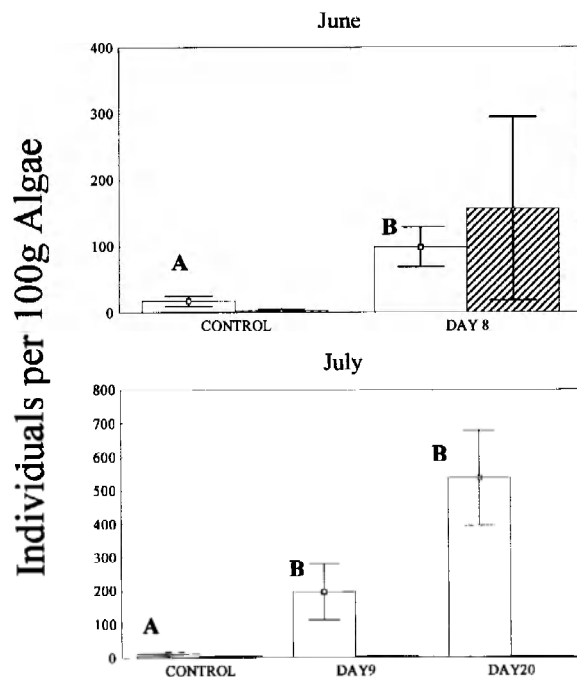

Figure 3. Average numbers (± 1 SE) of harpacticoids in experimental fronds in June and July 1993 (open bars=adults and copepodites, hatched bars=nauplii). Common letter codes indicate no significant differences (Tukey test).

Dactylopusia vulgaris and *Heterolaophonte longisetiger*, showed significant increases in numbers between day 9 and 20 (Mann-Whitney U test, $p<0.005$).

Altogether, 29 species were found in the experimental clumps, and of these 18 were not found in the free-floating clumps from Faxaflói. Apart from the pelagic *Microsetella norvegica* and the sediment dwelling *Paranychocamptus curticaudatus*, the rest of the species have been found to be associated with algae of some sort (e.g. Colman, 1940; Hicks, 1980; Johnson & Scheibling, 1987; Huys et al., 1996; Jarvis & Seed, 1996; pers. obs.). However, of these 18 species, 15 were only found in one or two of the 14 experimental clumps and always in very low numbers, normally as singletons (Table 1).

Distribution of Harpacticus chelifer

Of all the harpacticoid species found in the algal clumps *Harpacticus chelifer* was by far the most abundant. It was found in virtually all drifting fronds taken over several years, from different areas around Iceland, from summer to late autumn and from near-shore up to 117 km offshore (Table 4). The experimental fronds put afloat monthly at Eidsvik 1995–

Table 3. Mean densities and standard errors (SE) (no. 100 g algae^{-1}) of the five most abundant harpacticoid species in experimental fronds in June and July 1993

	Mean	SE	Mean	SE	Mean	SE
	Control (*N*=5)		8 days afloat (*N*=5)			
June experiment						
Tisbe sp.	10	5	17	16		
Harpacticus chelifer	0	0	8	2		
Harpacticus uniremis	0	0	87	24		
Ameira longipes	0	0	3	2		
Paratalestris clausi	0	0	1	1		
	Control (*N*=3)		9 days afloat (*N*=3)		20 days afloat (*N*=6)	
July experiment						
Harpacticus chelifer	0	0	43	8	281	104
Harpacticus uniremis	0	0	4	1	65	27
Ameira longipes	1	1	61	39	51	16
Dactylopusia vulgaris	0	0	3	3	33	29
Heterolaophonte longisetigera	0	0	2	2	34	33

Table 4. Percentage of females, ovigerous females and males of *Harpacticus chelifer* in floating algae clumps from various areas around Iceland. Symbols for sieve mesh aperture: 1=0.5 mm, 2=0.063 mm

Area	Map symbol	Distance from shore (km)	Date	Sampling design	Mesh size (mm)	Total females	Ovigerous females	Total males	*N*
Faxaflói	B	0.9–16.7	Jun 1991	Transect	1	85	30	15	402
Faxaflói	E	0.2–14.2	Jul 1993	Transect	1 & 2	92	61	8	1844
Faxaflói	E	4.1–8.9	Aug 1993	Transect	1 & 2	79	40	21	1037
Faxaflói	E	0.5–31	Jun 1995	Transect	1 & 2	94	40	6	982
Faxaflói	E	0.5–32	Jul 1995	Transect	1 & 2	83	55	17	1414
Faxaflói	E	0.5–33	Aug 1995	Transect	1 & 2	64	10	36	181
Eidsvík	G	0.3–0.6	Jun 1995	Experiment	1 & 2	52	7	48	60
Eidsvík	G	0.3–0.6	Jul 1995	Experiment	1 & 2	52	19	48	58
Eidsvík	G	0.3–0.6	Aug 1995	Experiment	1 & 2	88	39	12	139
Eidsvík	G	0.3-0.6	Sept 1995	Experiment	1 & 2	73	20	27	188
Eidsvík	G	0.3–0.6	Oct 1995	Experiment	1 & 2	79	18	21	39
Eidsvík	G	0.3–0.6	Dec 1995	Experiment	1 & 2	92	0	8	12
Eidsvík	G	0.3–0.6	Jan 1996	Experiment	1 & 2	100	0	0	8
Eidsvík	G	0.3–0.6	Jun 1993, 8 d	Experiment	1 & 2	80	52	20	54
Eidsvík	G	0.3–0.6	Jul 1993, 9 d	Experiment	1 & 2	67	30	33	67
Eidsvík	G	0.3–0.6	Aug 1993, 20 d	Experiment	1 & 2	59	30	41	1316
North	D	58–117	Jul 1992	Survey	1	90	38	10	94
North-west	A	4.1–5.9	Jul 1990	Survey	1	100	45	0	42
South-west	C	0.9–18	Jun 1991	Survey	1	98	32	2	59

196

Individuals / 100g algae

CI

CII

CIII

CIV

CV

1995   1996

Individuals / 100g algae

Juveniles

Non-ovigerous
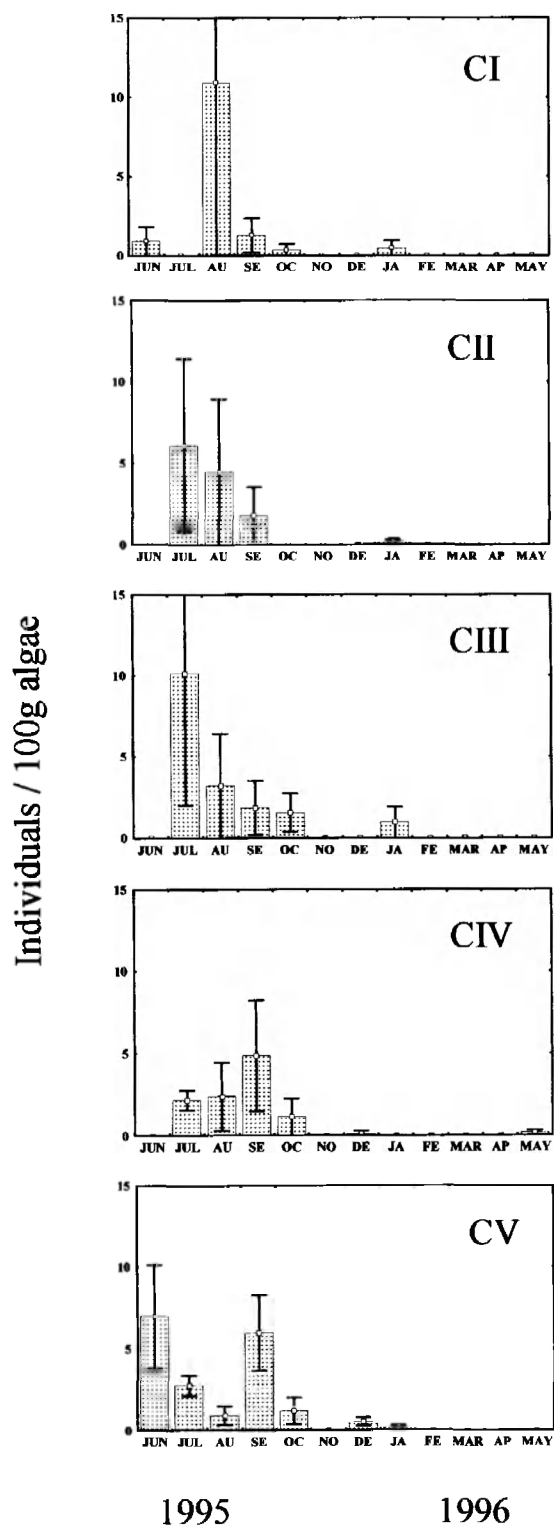Females

Ovigerous females

Males

1995   1996

Figure 4. Average number of juveniles, ovigerous and non-ovigerous females and males of *Harpacticus chelifer* ($n=3$ for June and July; $n=2$ for other occasions) per 100 g of algae in fronds left for 10 days, on approximately monthly intervals (1995–1996). in Eidsvík, Iceland.
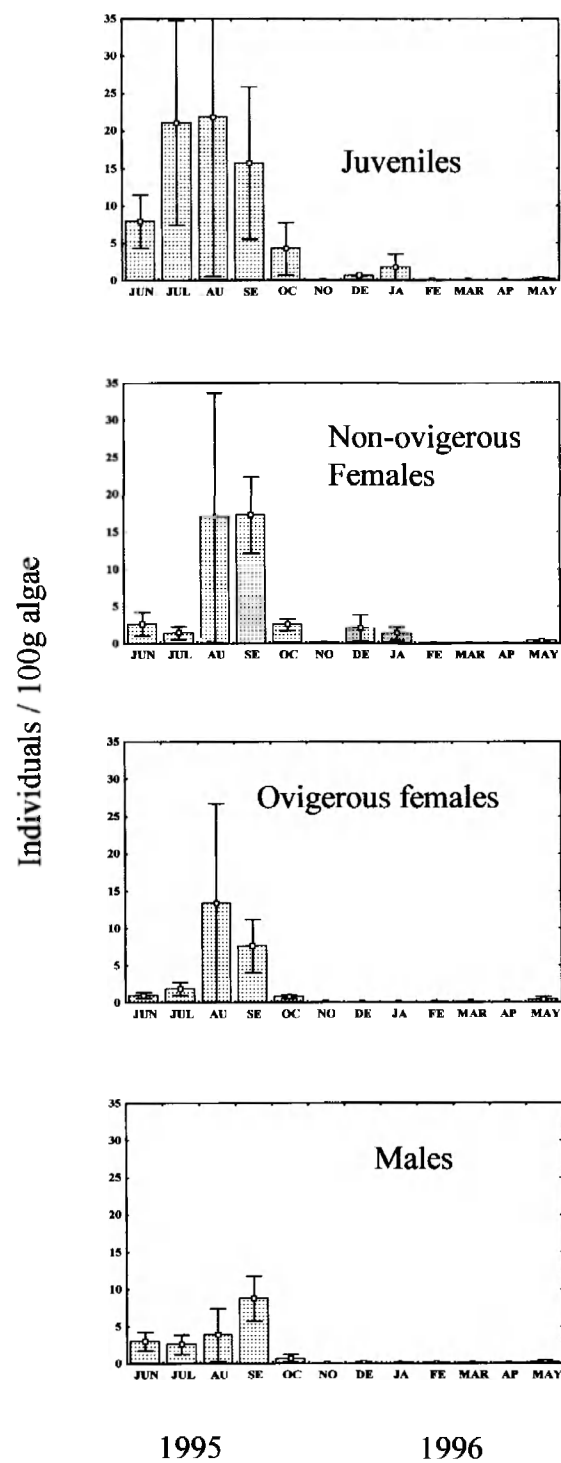
Figure 5. Average number of *Harpacticus chelifer* copepodite stages ($n=3$ for June and July; $n=2$ for other occasions) per 100 g of algae in fronds left for 10 days, on approximately monthly intervals (1995–1996), in Eidsvík, Iceland.

1996 yielded highest numbers of *H. chelifer* from July to September (Fig. 4), while densities were very low during winter, and the species was absent from February to April (Fig. 4). The clumps were colonised by juveniles (all copepodite stages) as well as adult animals, including ovigerous females (Figs. 4 and 5). Juvenile stages were common from June to September, while females were particularly abundant in August and September. *Harpacticus chelifer* was only common in June, July and August in the free-floating clumps collected monthly from the Faxaflói transect 1995–1996 (Fig. 6). Females and copepodites 1–3 were particularly abundant in June. Of ca 8000 adults of *H. chelifer* examined from floating algae, the female/male ratio was 4–1. This ratio was, however, quite variable both within and between years, and between areas (Table 4).

Discussion

Previous studies of the fauna of floating algae in Iceland showed that non-planktonic harpacticoid copepods were an important element of the clump communities, as regards both frequency and abundance (Ingólfsson, 1998). The present study showed that most of these belonged to the genus *Harpacticus*, though many other species were encountered, and some of these were common. The majority of the benthic harpacticoids found in floating algae have been regarded as of phytal habits, and this we had expected. The species composition was indeed quite similar to that found in studies made in the Northern Atlantic intertidal fucoid environment (e.g. Colman, 1940; Hicks, 1980; Johnson & Scheibling, 1987; Jarvis & Seed, 1996). Practically all species found in the current study have been recorded from an intertidal alga, *Chondrus crispus*, in Seltjarnarnes (María B. Steinarsdóttir, unpublished data). Some of the common species have, however, also been found associated with sandy or muddy bottoms, e.g. *Ameira longipes*, *Parastenhelia spinosa* and *Harpacticus uniremis* (Lang, 1948; Sabater, 1986; Huys et al., 1996). However, no species restricted to muddy or sandy habitat were found, apart perhaps from the species belonging to the genera *Itunella* and *Ectinosoma*, recorded only in a few clumps in very low numbers. Only four of these 39 species have been recorded from intertidal mudflats in the Faxaflói area, i.e. *Harpacticus flexus, Parathalestris interme-*

dia, Paramphiascopsis giesbrechti and *Amphiascoides nana* (Emil Ólafsson, unpublished data).

There was high variability among the clumps in harpacticoid assemblages. It seems that the major factors influencing the assemblage structure were the size and the algal diversity of the clumps. Several phytal harpacticoid species have evolved specific morphological features adapted to different kinds of algal surfaces, and are therefore associated with certain types of algae (e.g. Hicks, 1980, 1985). A gradient of habitat complexities generated by different species of intertidal algal communities has been shown to allow for significant linearly related increases in harpacticoid species number and diversity (Hicks, 1980). Even though there was a significant correlation between size of the clumps and their diversity, only 25% of the variance was explained. Size of the clumps may be important, especially when the clumps are at the lower size range, where the fauna are proportionately more exposed to the open sea, which may lead to a relatively higher loss of animals with time. Distance from shore did not apparently influence the assemblage structure, and distance was not linked to density variations of the total harpacticoid fauna or the major species. Neither did Ingólfsson (1995) find any clear-cut pattern in diversity and density of intertidal macrofauna in floating algal clumps in near-shore waters (<17 km from shore) of Iceland. It is not unlikely that time afloat is a major factor structuring the clump assemblages, as suggested by the results from the experimental fronds. One can expect that phytal harpacticoids with good swimming abilities leave the clumps now and again, and some will be lost, unable to find clumps again. Others with poorer swimming capabilities may become dislodged and fall off the clumps. With time, only those that are highly adapted (or pre-adapted) to this unstable environment remain in the clumps. The relationship between distance of clumps from shore and time afloat in near-shore water is undoubtedly not linear. Both local currents and wind conditions may distribute the clumps in random or haphazard manner (cf. Ingólfsson, 1998). One way of assessing the importance of time in structuring harpacticoid assemblages in near-shore water, in addition to experiments similar to those done here, is to set afloat algae clumps equipped with radio senders and retrieve them at certain time intervals. This would also overcome the unnaturalness of tethered fronds, which may act as traps (cf. Ingólfsson, 1998). Our experimental results did not show a decline in species richness with time, as we would predict in offshore areas, presumably be-
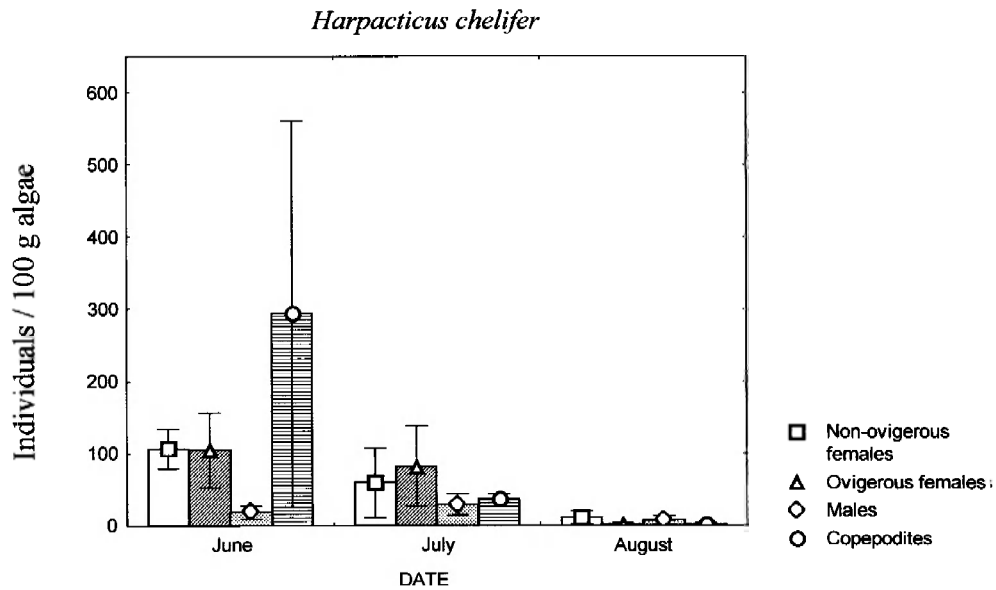
Harpacticus chelifer

Figure 6. Average number of juveniles, ovigerous and non-ovigerous females and males, of *Harpacticus chelifer* (n=2) per 100 g of algae in free-floating fronds, in Faxaflói (1995).

cause of the closeness to land and that the tethered fronds acted as traps. This may also explain that the experimental clumps were colonised by a different suite of harpacticoid species as compared to natural clumps.

The colonisation experiments clearly show that harpacticoids are able to quickly colonise floating algal clumps close to the shore, and attain similar densities after 8 and 9 days as in the free-floating clumps. The harpacticoids may have used several modes in reaching the experimental clumps. Firstly, we noted frequent entanglements of small algal pieces with the experimental fronds. These are likely to carry at least some of the intertidal species, and unquestionably this mode best explained the colonisation of certain macrofauna species of the fronds, e.g. some gastropods (Ingólfsson, 1998). Other species undoubtedly arrived via the water-column. Harpacticoids are commonly found free in the water-mass (e.g. Hicks, 1986; Palmer, 1988; Walters & Bell, 1994) and can for instance disperse through the water and colonise plants >20 m from the entering point (Bell & Hicks, 1991; Kurdziel & Bell, 1992). We encountered harpacticoids in a few control plankton samples free of seaweed, including, amongst others, specimens of *Harpacticus chelifer* and *Tisbe* sp. This further demonstrates that at least some of the harpacticoid species move outside the clumps. Those harpacticoids colonising drift algae at sea do not necessarily have to swim all the

way from the shore, but may use both drift material or aggregates in the water column as resting or feeding stations on their way. Recent observations indicate for instance that harpacticoids are associated with marine snow (organic aggregates ca. 0.5 mm diameter), and that they are able to spend several hours per day visiting or residing on these formations (Walters & Shanks, 1996; Shanks & Walters, 1997).

The association of *Harpacticus chelifer* with the floating seaweed clumps is of particular interest because of its abundance. This species has been found on algae on rocks, from slightly above low-water spring-tide level to approximately 10 m depth close inshore, and is found on most north-west European mainland and island coasts (Huys et al., 1996). It has also been recorded in several areas of the east coast of North America (Lang, 1948). In the Bay of Fundy, the fry of the lumpsucker feeds on these animals, presumably in drift algae (Daborn & Gregory, 1982), and in Eidsvik and Faxaflói, the lumpsucker fry feeds extensively on them and on other members of the genus *Harpacticus* in algal clumps (M. B. Steinarsdóttir, pers. obs.). Johnson & Scheibling (1987) found that unidentified *Harpacticus* species in Nova Scotia disappeared from intertidal algae during winter months and reappeared during spring. It is plausible that the species, i.e. ovigerous females, moves towards the intertidal in summer for breeding purposes. While seeking intertidal areas, the copepodites and females may then

accidentally home in on floating algal clumps. This could explain the skewed sex ratio towards females in practically all clumps, the high number of colonising copepodites both in experimental clumps and free floating clumps, and the absence in clumps during winter.

The vast majority of harpacticoid copepods have direct benthic development, therefore lack planktonic larval stages (e.g. Hicks, 1985). Several studies have shown that adult harpacticoids swim actively (see Palmer, 1988, for review) and this is definitely important for short distance dispersal. However, long distance dispersal (tens and hundreds of kilometres) must be accomplished by other means. We find it likely that the algal rafting by the harpacticoids facilitates dispersal between distant populations when clumps are carried by wind or currents to shores far from the original entering point. Long distance dispersal by algal rafting has been suggested for several macrofaunal species (e.g. Highsmith, 1985; Ingólfsson, 1992, 1995). All the species frequently found in the floating algal clumps in the current study (i.e. *Ameira longipes, Amphiascoides debilis, Amphiascus minutus, Dactylopusia vulgaris, Diarthrodes major, Harpacticus chelifer, H. uniremis, Heterolaophonte strömi, H. longisetigera, Parastenhelia spinosa* and *Parathalestris clausi*) are found on both sides of the Atlantic. Although we have no evidence for transoceanic dispersal of harpacticoids by algal rafting, we are inclined to agree with Yeatman (1962) that this is conceivable, especially in the light of the frequency of clumps in off-shore waters which may, contrary to Hicks' (1977) opinion, remain floating and healthy at sea for months (Ingólfsson, 1998); and of the predominance of harpacticoids in algal clumps. Transoceanic dispersal may be envisioned from America to Europe via the fast-flowing Gulf Stream at relatively low latitudes (cf. Yeatman, 1962), while in regions of cooler waters, such as are found around Iceland the dispersal may well be rather from Europe to America (cf. Ingólfsson, 1992). Single dispersal events may suffice to extend the range of species, e.g. from Europe to America or *vice versa*, but algal rafting may well result in regular gene flow between relatively distant locations, especially in species that are most abundant and frequent in drifting clumps, like *Harpacticus chelifer*.

Acknowledgements

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