LIFE CYCLES, BREEDING PERIODS AND VERTICAL DISTRIBUTION OF *IDOTEA GRANULOSA* RATHKE AND *I. PELAGICA* LEACH (CRUSTACEA, ISOPODA) ON ICELANDIC SHORES

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The life cycles, breeding periods and vertical distribution of two species of *Idotea* from three intertidal localities in Iceland were investigated over a period of two years. Two of the localities (Straumsvík, Háanef) were in southwestern Iceland while one (Húsavík) was in northern Iceland where sea temperatures are considerably lower. The vertical distribution was widest during the summer for both species. During summer, *I. granulosa* had a wider distribution at Straumsvík than at Húsavík, while the more southern *I. pelagica* was restricted to the lowermost part of the shore. During winter at Straumsvík *I. granulosa* receded to the lowermost part of the shore and disappeared altogether from the intertidal zone at Húsavík. *I. pelagica* at Háanef also disappeared from the shore during winter but for a considerably longer period. Oostegites started to develop on females in late winter and the juveniles were mainly released in the autumn in all cases. Females of *I. granulosa* and *I. pelagica* in the southern region released their broods when one year old and lived to a maximum age of approximately 15 months (*I. pelagica*) or 16-18 months (*I. granulosa*). Females of *I. granulosa* in the North, however, did not release their broods until almost two years old after which they soon disappeared. The present results fit well with observations elsewhere for *Idotea* spp. in that the animals seem to breed less frequently as the temperature decreases. The breeding period also becomes shorter and more confined to the summer at lower temperatures.

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KEYWORDS: *Idotea*; intertidal; distribution; life cycles; breeding period; Iceland.

INTRODUCTION

Isopods of the genus *Idotea* are mostly littoral and sublittoral benthic crawling species with good swimming abilities. They feed mainly on seaweed and other algae and are among the most important algae feeders on the shore (SALEMAA 1987) but also play an important role as scavengers (HEALY & O'NEILL 1984).

Five *Idotea* species have been found in Iceland: *I. granulosa* RATHKE, *I. pelagica* LEACH, *I. emarginata* (FABRICIUS), *I. baltica* (PALLAS) and *I. neglecta* G.O. SARS (INGÓLFSSON 1990). In Iceland the last three species are mainly sublittoral, *I. granulosa* is mainly found in sheltered or semi-exposed intertidal rocky shores where fucoids are dominant, and *I. pelagica* is almost confined to exposed intertidal rocky shores where small species of green and red algae are dominant (INGÓLFSSON 1990). The distribution of the five *Idotea* species around the coast of Iceland is related to sea temperature. All five species are found at the southwest coast where the average temperature at the sea surface in Faxaflói Bay is 5 °C in February and about 10.5 °C in August (STEFÁNSSON 1969). Only *I. granulosa*, however, is found at the east coast where sea temperature is lowest. Until recently *I. pelagica* was believed to reach its distributional limits towards cold waters in Eyjafjörður Bay (INGÓLFSSON 1990 & 1996), but a few specimens were found in July 1996 on a semi-exposed rocky shore near Húsavík (Leifsson, personal observations), where the average temperature at the sea surface is 2.0 °C in February and 8.8 °C in August (STEFÁNSSON 1969).

Numerous studies of *Idotea* spp., including *I. granulosa* and *I. pelagica*, have been carried out along the coast of Europe, ranging from Bergen, Norway (KJENNERUD 1950) and the Baltic (JORMALAINEN & TUOMI 1989; SALEMAA 1979 & 1987) in the north to the southeast coast of Ireland (HEALY & O'NEILL 1984) and the Mediterranean coast of France (KOUWENBERG & PINKSTER 1985; KOUWENBERG & al. 1987) in the south. These, among other studies, include observations of life
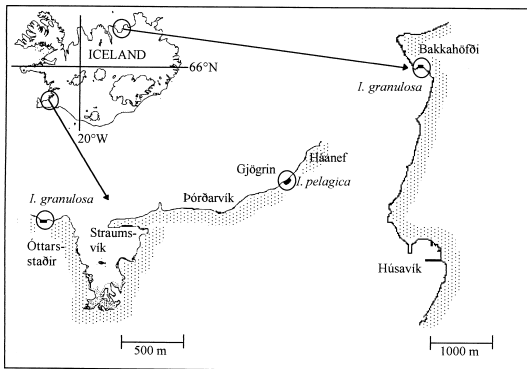
Fig. 1. Sampling localities of *I. granulosa* at Straumsvík and Húsavík and of *I. pelagica* at Háanef. © Iceland Geodetic Survey.
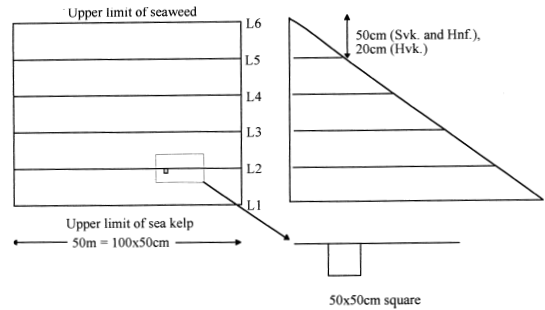

Fig. 2. Organisation of sampling rectangles, height between the 50 m lines and position of the 50 x 50 cm square. Height line 1 (L1) corresponds to 0.2 m above 0.0 m in ANONYMOUS a (1992-1994).

cycles and breeding periods of the animals (e.g. NAYLOR 1955a; SHEADER 1977; SALEMAA 1979 & 1986; HEALY & O'NEILL 1984; KROER 1989) and their vertical and general distribution in the intertidal zone (e.g. NAYLOR 1955b; KROER 1986).

In Iceland two minor investigations on the life cycles and breeding periods of *I. granulosa* and *I. emarginata* have been carried out but no published data exists.

The aim of the present study is to investigate the life cycles, breeding periods and vertical distribution of *I. granulosa* in two localities with different sea temperatures at the coast of Iceland, and of *I. pelagica*, a more southern species reaching distributional limits within Iceland.

MATERIAL AND METHODS

Samples were taken approximately monthly from September 1993 to October 1995 at two localities, Faxaflói Bay (*I. granulosa* and *I. pelagica*) and Skjálfandi Bay (*I. granulosa*) (Fig. 1). *I. granulosa* was taken from a sheltered, rocky shore near Óttarsstaðir west of Straumsvík (Svk) and a rocky shore at Bakkahöfði north of Húsavík (Hvk), while *I. pelagica* was only taken from an exposed rocky shore at Gjögrin between Þórðarvík and Háanef (Hnf).

At each locality a 50 m wide rectangle with upper long

Table 1. Breeding stages of the females.

Breeding stages	Description
b0	No oostegites
b1	Oostegite buds
b2	Marsupium with spherical eggs
b3	Marsupium with elongated eggs
b4	Marsupium with juveniles in embryonic membrane
b5	Marsupium with hatched juveniles
b6	Empty marsupium

side coinciding with the upper limits of seaweed (*Fucus spiralis* L.) and lower long side coinciding with the upper limits of kelp (*Laminaria* spp.) was measured out. The vertical height difference between the rectangle's two long sides was about 1.0 m at Húsavík, 2.5 m at Straumsvík and 2.0 m at Háanef (Fig. 2). The tidal range at spring tide is about 4 m at Straumsvík and Háanef, but about 1.2 m at Húsavík (ANONYMOUS a 1992-1994) and thus the ratio between the height range of the rectangle and the tidal range was 0.63, 0.5 and 0.83 at Straumsvík, Háanef and Húsavík, respectively. The height range was divided into equal parts with six 50 m long lines at Straumsvík and Húsavík (L1-L6) and five lines at Háanef (L1-L5). The height difference between adjacent lines was thus 20 cm at Húsavík and 50 cm at Straumsvík and Háanef. Each 50 m line was divided into one hundred 50 cm long intervals. At each sampling one such interval was chosen randomly at each line of the same predefined rectangle and a 50 x 50 cm square was put down there with its upper side touching the line (Fig. 2).

All algae were cut off each square and put in a plastic bag. The algae were weighed (wet weight) and then rinsed in 70 % isopropanol, after which the liquid was sieved through a 0.5 mm sieve. The animals collected in the sieve were then stored in 70 % isopropanol.

Usually an extra sample of algae, 2-3 kg at Straumsvík and Húsavík and 0.5-1 kg at Háanef, was taken as low down on the shore as possible in an effort to ensure enough material for life cycle studies. During the second year sampling at Háanef was almost only of this kind, as the results for the first year showed that *I. pelagica* is confined to the lowermost part of the intertidal zone during summer and disappears almost altogether from the shore during winter.

Sampling proved impossible on a few occasions due to bad weather conditions and/or high surf, especially at Háanef, and explains some gaps in the results.

In the laboratory the animals were measured to the nearest 0.1 mm from the anterior border of the cephalon to the posterior border of the pleotelson. Individuals of *I. granulosa* longer than 4.9 mm and of *I. pelagica* longer than 3.9 mm were sexed according to NAYLOR (1972).

The reproductive condition of the females was determined

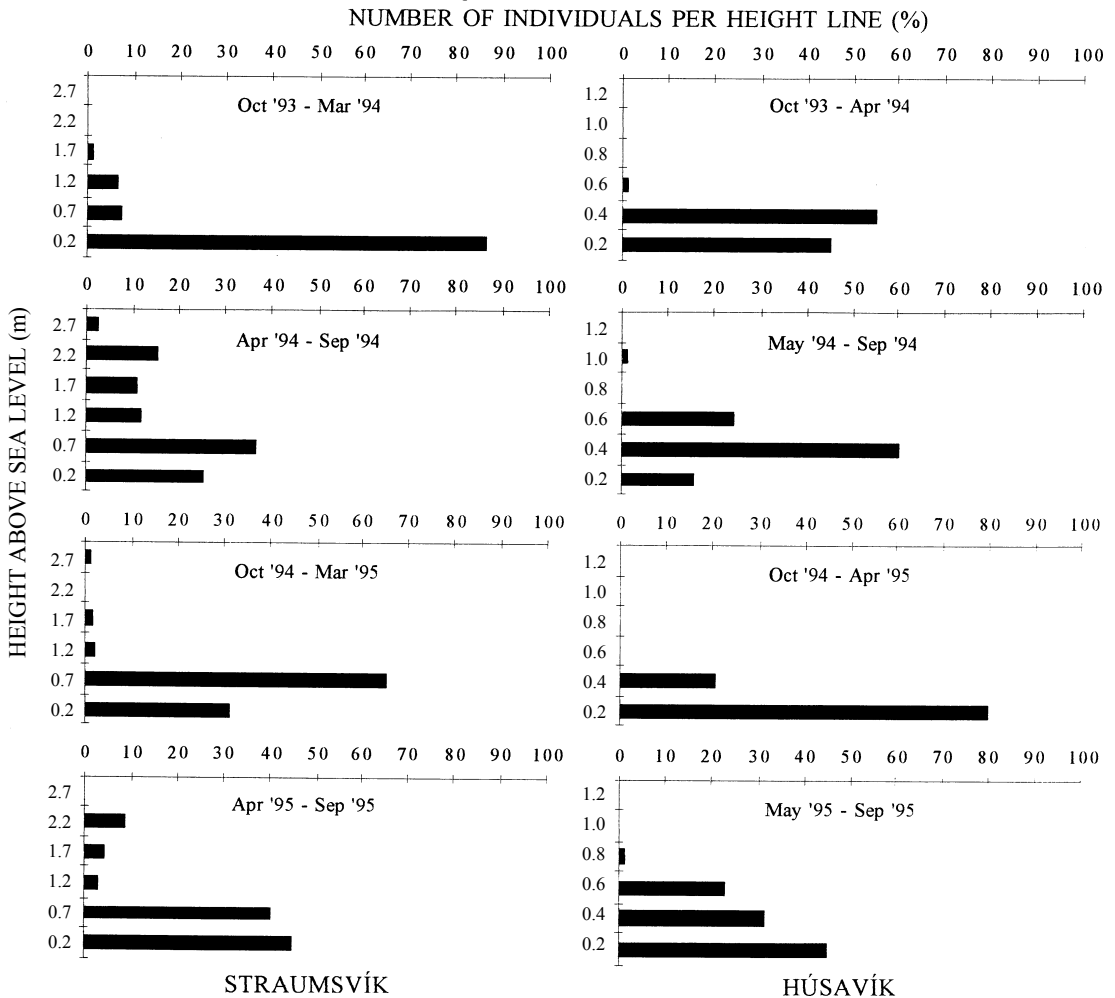NUMBER OF INDIVIDUALS PER HEIGHT LINE (%)

Fig. 3. The seasonal, average vertical distribution of *I. granulosa* at Straumsvík and Húsavík. Height above sea level refers to 0.0 m in ANONYMOUS a (1992-1994).

on the basis of the development of the oostegites. Developmental stage of embryos in the marsupium was further determined and the number of embryos of each stage was counted. Different authors use somewhat different ways in delimiting embryonic stages in *Idotea* spp. (e.g. SHEADER 1977; SALEMAA 1979; KOUWENBERG & PINKSTER 1985; JORMALAINEN & TUOMI 1989). Here seven breeding stages, b0-b6, are used (Table 1). The b0 stage includes many moulting stages, from when the female reaches minimal length for sexing until it grows the oostegite buds (b1); it also includes larger females that have moulted after releasing their young and lost the oostegites. The stage b1 (females with oostegite buds) is a distinct moulting stage but b2-b6 are all within the same moulting stage of the female, which does not moult while carrying brood.

An attempt was made to evaluate the average vertical distribution of *I. granulosa* within the predefined sampling area by calculating an index:

$$\frac{(nL1*1)+(nL2*2)+(nL3*3)+(nL4*4)+(nL5*5)+(nL6*6)}{n \text{ total}}$$

where $nL1$ is the number of animals collected at line 1 (the lowermost line), $nL2$ is the number of animals at line 2, etc. Thus, index value ranges between one and six indicating that all individuals were found at the lower or upper limit of the predefined sampling area, respectively. The index was calculated for each sampling time and for both localities.

The relationship between body length of females carrying brood in the marsupium and the number of eggs or embryos was calculated for both species. The average loss in brood numbers ($\bar{x}$) in marsupium from b2 to b5 was calculated according to the following equation:

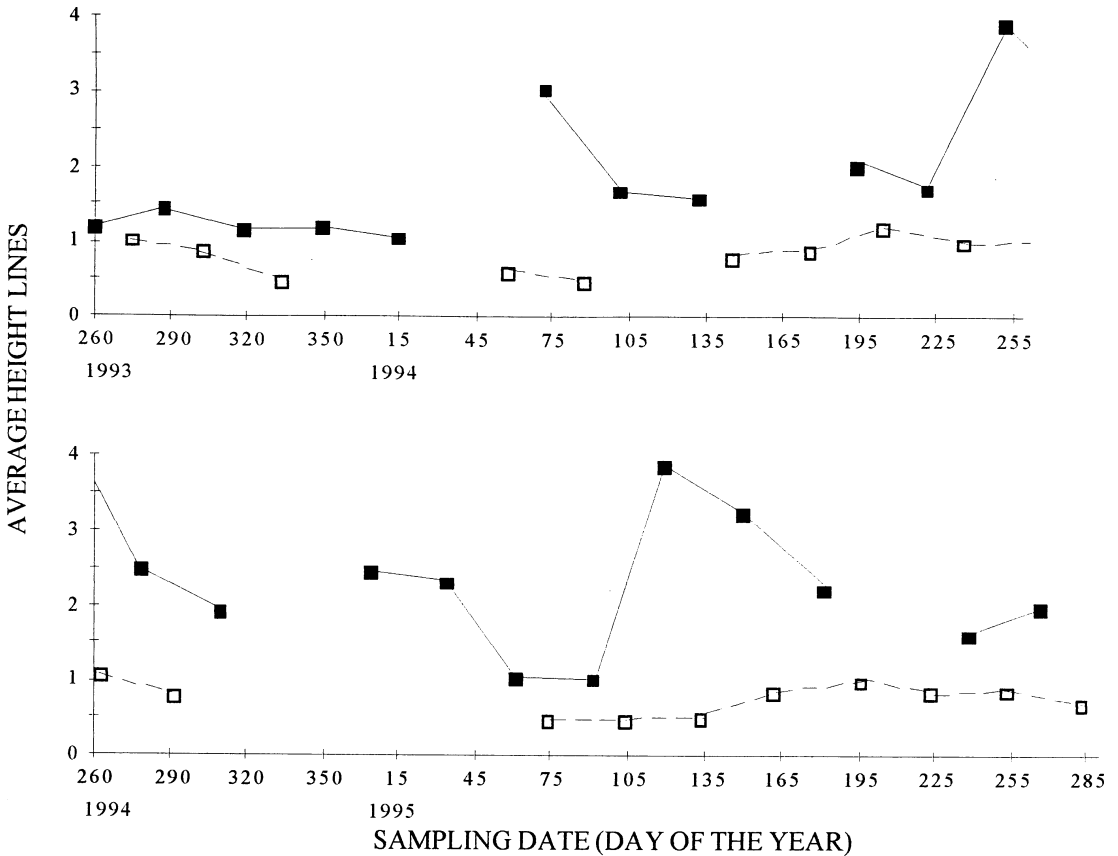$$\frac{\bar{x} \text{ eggs b2} - \bar{x} \text{ embryos b5}}{\bar{x} \text{ eggs b2}} * 100$$

Fig. 4. Average height index for *I. granulosa* at Straumsvík (filled squares) and Húsavík (open squares) from September 1993 to October 1995. Note that height line 1 (L1) corresponds to 0.2 m above 0.0 m in Anonymous a (1992-1994) and that the vertical height between the lines is 0.5 m at Straumsvík but 0.2 m at Húsavík.

The loss was calculated for 10.0-11.9 mm long females of *I. granulosa* at Straumsvík, 12.0-13.9 mm long females of *I. granulosa* at Húsavík and 7.0-8.9 mm long females of *I. pelagica* as females with brood in their marsupium were mainly of these length intervals at the three localities. The average loss between the other breeding stages was not calculated because only a few females at these stages were collected.

Table 2. Some numerical results on the animal length, sexual maturity etc. with SD values when appropriate. Lengths are given in millimeters and age or time in months.

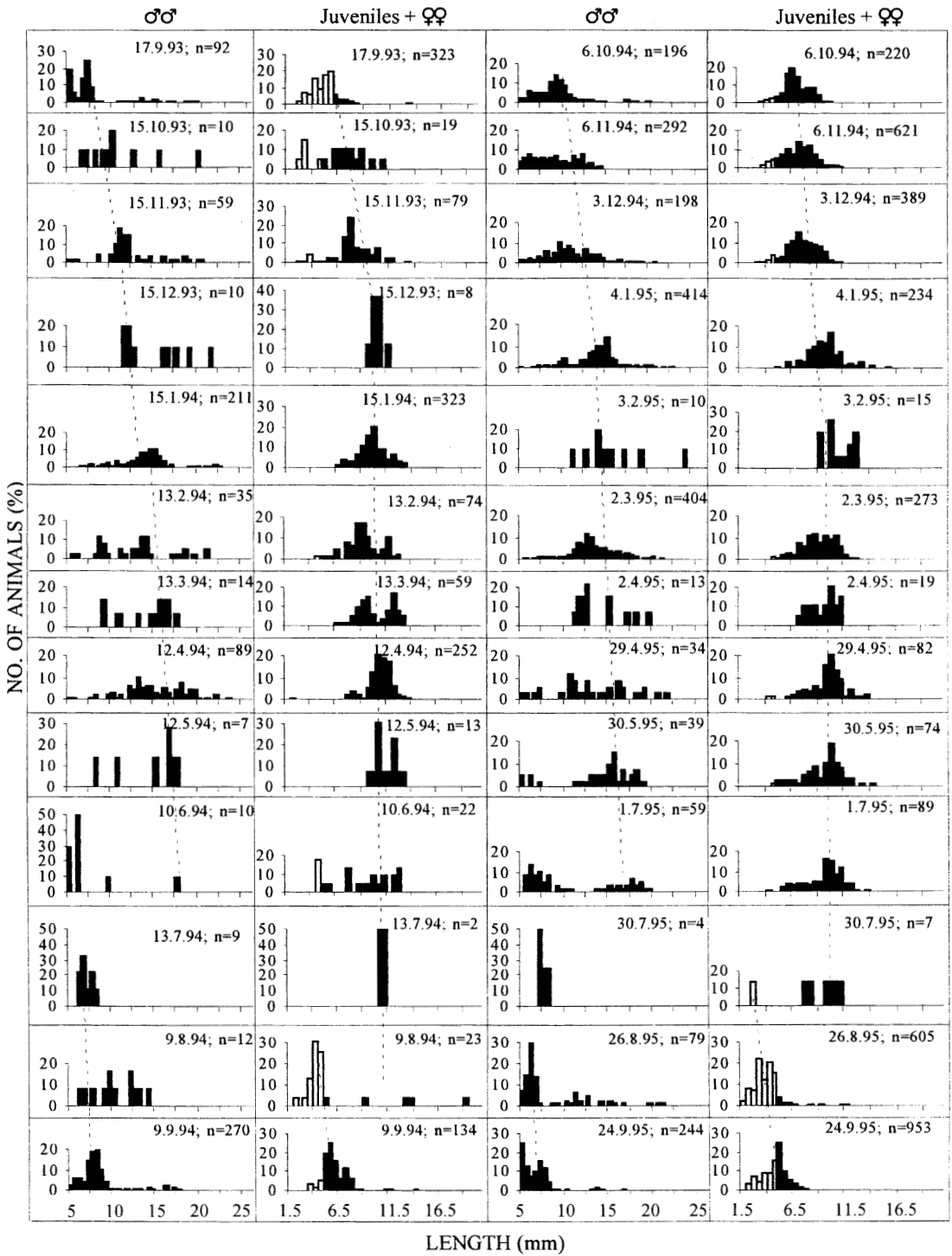| | *I. granulosa* | | | | *I. pelagica* | |
| | Straumsvík | | Húsavík | | Háanef | |
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Max. length	25.8	19.3	26.1	20.9	16.5	11.2
Max. age	18	17	25	26	15	15
Min. length b1		6.5		8.3		5.2
Min. length b2		7.2		9.0		6.3
Average length b2		10.9 ± 1.6		13.1 ± 2.1		8.0 ± 1.0
Maturing age (b2)		8-9		20		10
Max no. of eggs b2		175		277		72
Average no. of eggs b2		82 ± 30.7		119 ± 51.3		36 ± 13.3
Embryo development time		1.5-2		2		1.5-2

Fig. 5. Size frequency distributions of *I. granulosa* at Straumsvík from September 1993 to September 1995. Juveniles white bars, males and females black bars.
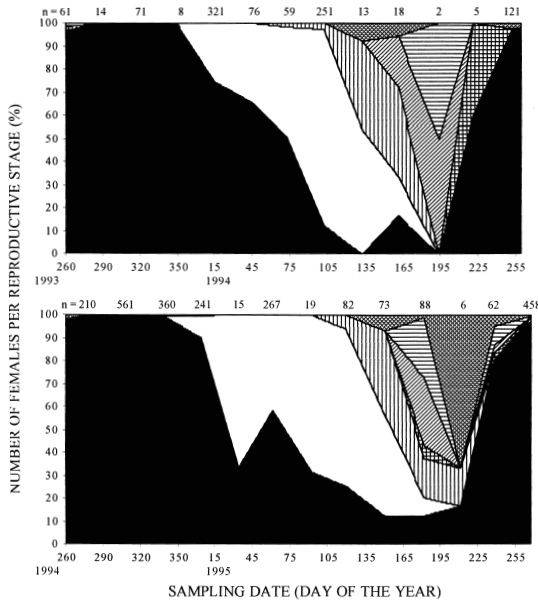
Fig. 6. Breeding stage frequencies of *I. granulosa* females at Straumsvík from September 1993 to September 1995. n = number of females in each sample.

■ b0   □ b1   ▥ b2   ▦ b3   ▨ b4   ▤ b5   ▩ b6

RESULTS

Distribution

Idotea granulosa at both sites was distributed higher up the shore in the summer than in winter (Fig. 3) but this seasonal difference in distribution was not significant (Mann-Whitney U test; $P > 0.05$). While the vertical distribution of the juveniles (< 5.0 mm) along the intertidal at Straumsvík was usually lower than that of the older animals no sexual differences in vertical distribution were observed.

Idotea granulosa at Húsavík was distributed in a lower and narrower zone of the intertidal than at Straumsvík (Fig. 4) and disappeared from the shore from December to February both years. The animals dispersed up the intertidal during summer although not as much as those at Straumsvík. Very few juveniles were found in the intertidal at Húsavík and no differences in the vertical distribution of the juveniles and the older animals were observed, nor were any sexual differences.

I. pelagica at Háanef was found above the lowest line only on two occasions, and in very small quantities. The animals disappeared almost altogether from the intertidal during the winter (December to April) both years.

Life cycles and breeding periods

Most *I. granulosa* females at Straumsvík released their broods in late summer, from late July to September (Fig. 5). The young grew rather rapidly during winter and the fastest growing females had developed oostegite buds (b1) in early January (Fig. 6). Females with spherical eggs in the marsupium (b2) were first observed in April but most females did not reach this stage until late May. This indicates that the duration of the marsupial development is a little over two months. However, some early maturing females apparently release their young already in spring. As females with spherical eggs in marsupium were frequently found in the autumn it is possible that the early maturing females release a second brood in late autumn. The older generation had mostly disappeared from the population in early January both years, and most of the animals, therefore, do not live beyond 16-18 months.

Juveniles of *I. granulosa* at Húsavík were mainly released in autumn. After very little growth the first winter they grew more rapidly the next summer and most of them did not reach maturity until the second summer (Fig. 7). The animals disappeared from the intertidal from December to February both years and when they were observed again in late February some of the one year old females had developed oostegite buds (b1) but most of the females did not develop marsupium with spherical eggs (b2) until the middle of June (Fig. 8). The animals released the broods from the beginning of August to early September, which indicates that the duration of marsupial development is perhaps a little less than two months, and then disappeared from the population. In early autumn there were therefore three generations in the population; newly released juveniles, immature one year olds and mature breeders. The overall growth of *Idotea granulosa* at Húsavík seemed to be rather slow and the longest living animals reached the maximum age of a little more than two years.

The maximum life span of *I. pelagica* in the intertidal at Háanef seemed to be about 15 months (Fig. 9). The animals almost disappeared from the shore in early autumn, while some females were still carrying broods, and did not reappear until the beginning of May the next year. Females with spherical eggs in marsupium (b2) were observed in late May both years (Fig. 10) and the release of broods started in the middle of July, which indicates that the duration of marsupial development is 6-8 weeks.

Brood size increased linearly with the size of females (Fig. 11) and the regression proved to be significant ($P < 0.05$ to $P < 0.001$) for most of the breeding stages b2 to b5 except when very few females of a breeding stage were found. The brood size was usually bigger at
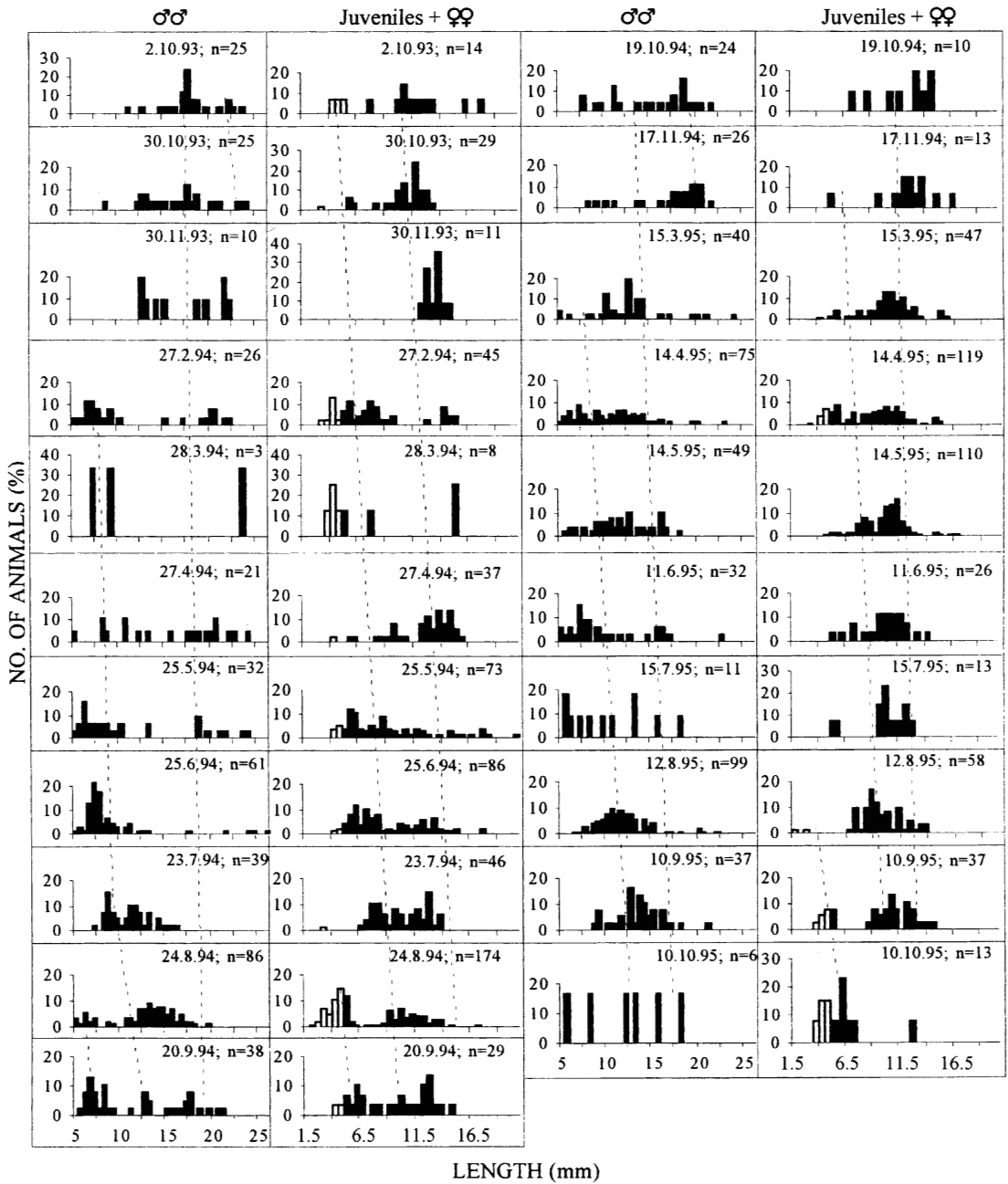
Fig. 7. Size frequency distributions of *I. granulosa* at Húsavík from October 1993 to October 1995. Juveniles white bars, males and females black bars.

Húsavík than at Straumsvík (Fig. 11 and Table 2). Fig. 11 also indicates a brood mortality during the embryonic development. The average reduction in brood size from breeding stage b2 to b5 was about 10 % for *I.*

granulosa at Straumsvík, 19 % for *I. granulosa* at Húsavík and 11 % for *I. pelagica* at Háanef. The reduction was never significant (t-test, d.f. = 96 (Straumsvík), 67 (Húsavík), 35 (Háanef), P > 0.05).
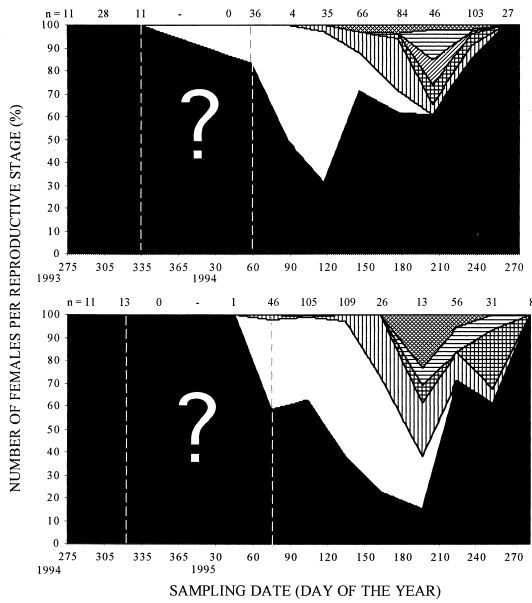
Fig 8. Breeding stage frequencies of *I. granulosa* females at Húsavík from October 1993 to October 1995. n = number of females in each sample, - indicates no sampling, ? indicates interpolated data.

■ b0   □ b1   ▥ b2   ▦ b3   ▨ b4   ▤ b5   ▩ b6

Table 2 shows various results on animal length and size of brood in marsupium. A significant difference in the average length of *I. granulosa* females at breeding stage b2 from Straumsvík and Húsavík, respectively, was observed (t-test, d.f. = 131, P < 0.001) and the same was true for the average number of eggs in marsupium for the same animals (t-test, d.f. = 118, P < 0.001).

DISCUSSION

Distribution

I. granulosa was distributed higher up on the shore in Straumsvík than in Húsavík, where both air and sea temperatures are lower. The animals gathered in the lowermost parts of the intertidal at Straumsvík during winter but migrated into the subtidal at Húsavík from December to February when both the air and sea temperature reach a minimum. Very few juveniles were found on the shore at Húsavík, and those that survive the first days after being released from the marsupium may disperse immediately below the intertidal, or, perhaps, swim away from the shore and temporarily inhabit floating clumps of seaweed. This phenomenon has been observed in the autumn in other localities around

Iceland (Ingólfsson, pers. commn) and has been described from the Galway Bay, western Ireland (TULLY & CÉIDIGH 1986).

The animals seemed to disperse slower up the intertidal at Straumsvík and Húsavík in the spring of 1995 than in 1994. The average air temperature was much lower in February 1995 than in February 1994 (ANONYMOUS b 1994-1995) but almost no difference can be observed in the other first five months of the two years (Fig. 12a). The sea temperature, on the other hand, was much lower at Húsavík in the spring 1995 than in 1994 and somewhat lower at Straumsvík (Fig. 12b) but it was still well above air temperature.

I. pelagica disappeared almost completely from the intertidal from December to April in both years. The juveniles were abundant among the adults during the main breeding period in the autumn and did not seem to disappear from the shore before the adults.

Studies of the vertical distribution of *I. granulosa* along the intertidal of the Isle of Man (NAYLOR 1955b) show that it reaches furthest up the intertidal in the autumn. At that time the juveniles are most abundant, and, as in the Straumsvík intertidal, they do not seem to disperse as much as the larger animals. NAYLOR (1955b) suggests that this is due to their larger ratio of surface to volume, which means that they could suffer more from evaporation during low tide than the adults. The most likely explanation for the retreat of *I. granulosa* to the lowermost part of the intertidal at Straumsvík and the disappearing of *I. granulosa* at Húsavík and of *I. pelagica* at Háanef is that the animals are avoiding cooling and freezing during the lowered air temperature in the winter.

Life cycles and breeding periods

I. granulosa at Húsavík grow slower, become larger and reach maturity later than the animals at Straumsvík (Figs. 5 & 7). In the cold waters at Húsavík, the females apparently need more than one year to reach a minimal size of about 9.5-10.5 mm for full sexual maturity, while this can be accomplished at Straumsvík in less than one year. The brood release period at Húsavík seems to be shorter than at Straumsvík and, unlike Straumsvík, there is little or no evidence of brood release in spring time at Húsavík.

As *I. pelagica* at Háanef disappears from the intertidal for such a long time in winter, its life cycle is hard to follow. Some brood release seems to occur in spring time and the autumn brood release period appears to be similar to that of *I. granulosa* at Straumsvík.

Reviewing studies of life cycles of *Idotea* elsewhere, it appears that, in southern regions, the animals breed more often, produce more generations per year and have the breeding season less confined to the summer than
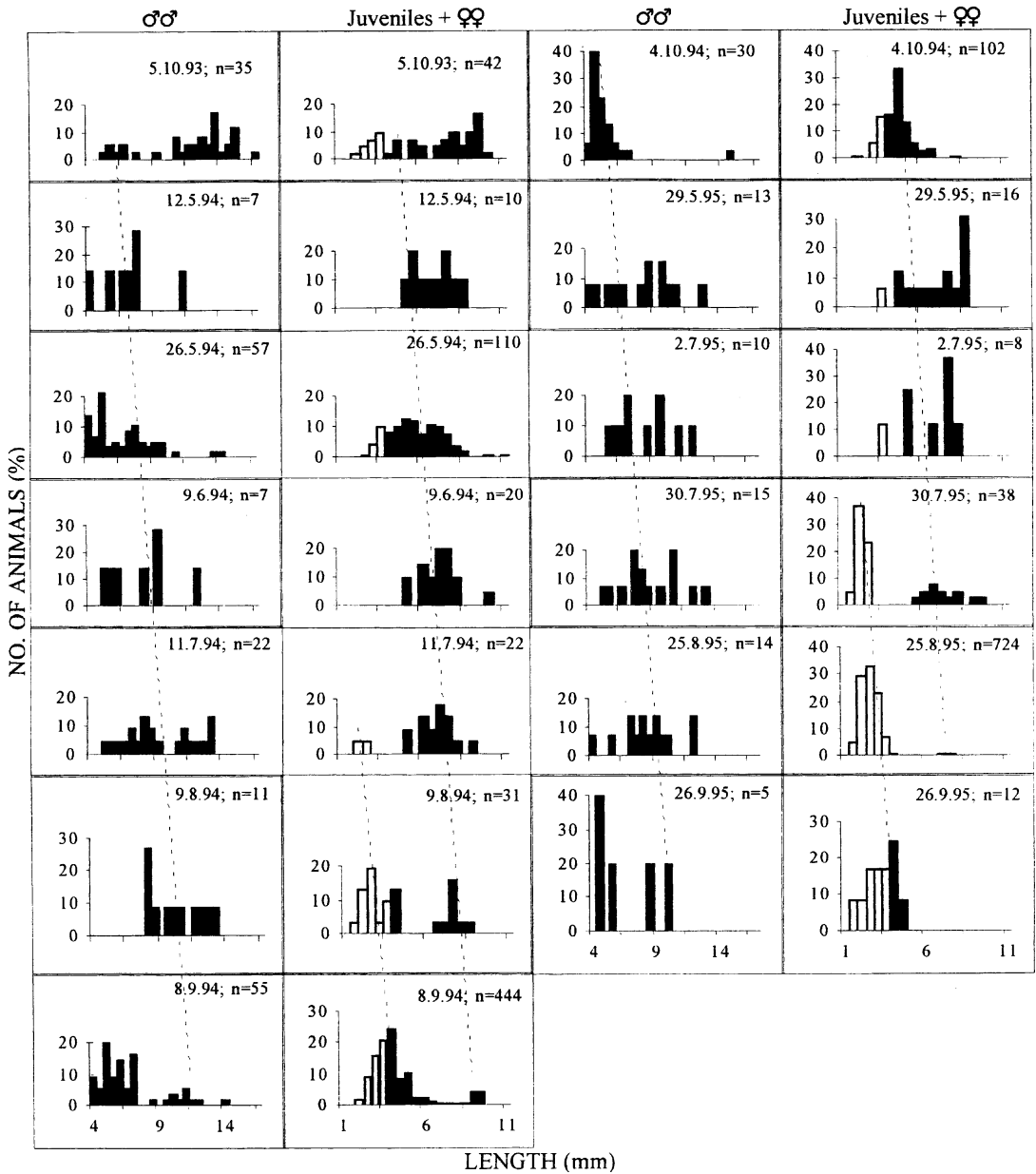
Fig. 9. Size frequency distributions of *I. pelagica* at Háanef from October 1993 to September 1995. Juveniles white bars, males and females black bars.

in northern regions. These trends seem to be both interspecific and intraspecific and have been described by HEALY & O'NEILL (1984) and SALEMAA (1986). Thus two generations of both *I. granulosa* and *I. pelagica* are produced every year at the southeast coast of Ireland (HEALY & O'NEILL 1984) and the populations of *I. granulosa* and *I. baltica* at the Mediterranean coast of France (KOUWENBERG & PINKSTER 1985) breed practi-
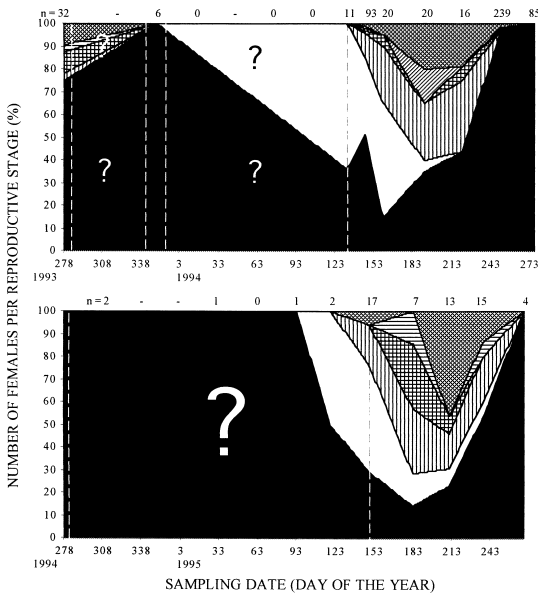
Fig. 10. Breeding stage frequencies of *I. pelagica* females at Háanef from October 1993 to September 1995. n = number of females in each sample, - indicates no sampling, ? indicates interpolated data.

■ b0   □ b1   ▥ b2   ▦ b3   ▧ b4   ▤ b5   ▨ b6

cally throughout the year, while only one generation of *I. neglecta* is produced per year at Bergen (KJENNERUD 1950) and the same is true for *I. granulosa* and *I. chelipes* in the northern Baltic (SALEMAA 1979). In *I. baltica* at least two generations are produced in the southern Baltic, while only one or two in the northern Baltic (KROER 1989; JORMALAINEN & TUOMI 1989). This suggests that breeding periods of *Idotea* species are linked to sea temperature. The results here seem to agree with that pattern. This is not as obvious within Iceland as elsewhere but it must be kept in mind that although more than one generation is in the population at Húsavík at a given time, only one of them is breeding. Furthermore, brood release in spring time is more frequent at Straumsvík than at Húsavík, and even more frequent farther south, like in British waters (HEALY & O'NEILL 1984; SALEMAA 1986), where the sea temperature is higher. This releasing of broods in the spring, however, seems similar to that in the Baltic (SALEMAA 1979), which lies at about the same latitude as Iceland.

If the breeding periods of *Idotea* species are linked to sea temperature, one might expect the breeding of *I. granulosa* at to begin later at Húsavík than at Straumsvík and be of shorter duration. Also, one might expect the breeding period of *I. pelagica* to be more similar to that

of *I. granulosa* at Húsavík than at Straumsvík, as *I. pelagica* reaches its distributional limits towards cold waters at the coasts of Iceland.

The sea temperature at Húsavík was much lower in the spring 1995 than 1994 and somewhat lower at Straumsvík and Háanef the latter spring than the first, although the difference was not as big as at Húsavík. This, however, does not seem to have affected much the beginning of the breeding periods of the animals. This indicates that sea temperature has little direct effect on preparation and beginning of the breeding periods of *I. granulosa* and *I. pelagica*, which is in agreement with conclusions of other authors (e.g. SHEADER 1977; SALEMAA 1979; HEALY & O'NEILL 1984; KOUWENBERG & PINKSTER 1985). It seems more likely that daylength is the timing signal or proximal factor for breeding while sea temperature may be the ultimate factor for the breeding period, i.e. confine it to the summer in colder regions.

The average size of brood in marsupium seems to increase from south to north as the female mean length increases (SALEMAA 1986). This seems to fit well with the results of the present study. The maximum number of spherical eggs in the marsupium of Icelandic female idoteoids seems to be higher than that at the northeast coast of England (SHEADER 1977), at the Isle of Man and in the Baltic (SALEMAA 1979 & 1986). This is probably best explained by the fact that the Icelandic idoteoids usually become longer than their foreign cousins. The average number of spherical eggs in marsupium is much higher at Húsavík than at any other site where *I. granulosa* has been studied and the same seems to apply to *I. pelagica* at Háanef, at least when compared to the results of SHEADER (1977), where the average number of spherical eggs is probably about 30 (see also table 2). The average number of spherical eggs in the marsupium of *I. granulosa* females at Straumsvík is a little higher than that at the Isle of Man (SALEMAA 1986) but a little lower than that in the Baltic (SALEMAA 1979).

The relationship between the number of broods in marsupium and the length of the females has been found to be linear (SALEMAA 1979 & 1986) or logarithmic (SHEADER 1977; KROER 1989). Usually some brood mortality between development stages has been observed (e.g. SHEADER 1977; SALEMAA 1979) as seems to be the case in Icelandic intertidal, but no mortality was observed by KOUWENBERG & PINKSTER (1985). The calculation of the mortality between breeding stages b2 and b5 does not, however, take into account that some of the hatched juveniles at b5 may have left the marsupium.

According to most other authors on *Idotea* spp., the growth of the animals is often suspended during winter (HØRLYCK 1973; SHEADER 1977; SALEMAA 1979 & 1986;
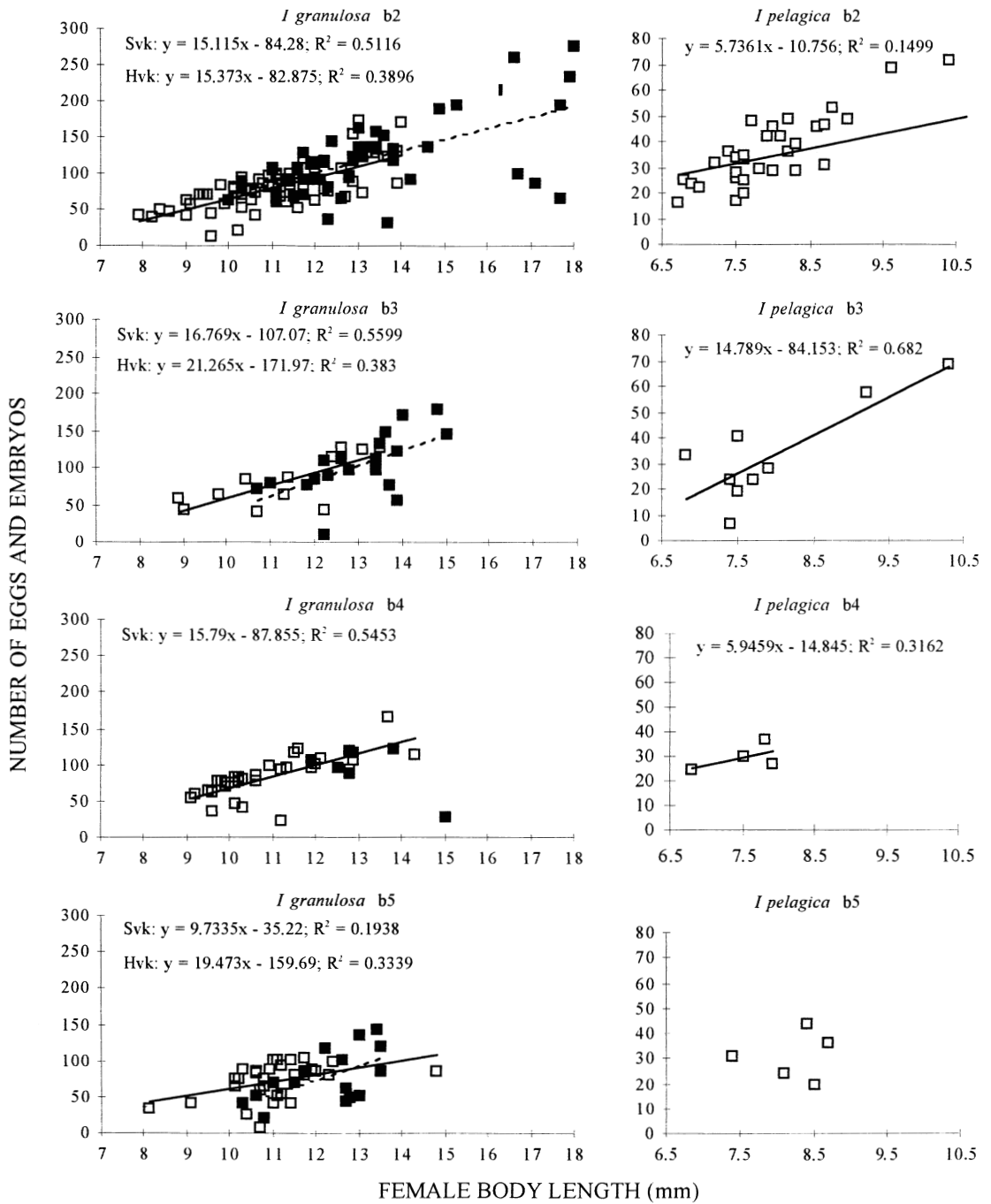
Fig. 11. Relation of length of *Idotea* females to the number of eggs and embryos at development stages b2-b5. In two instances, Húsavík b4 and Háanef b5, there is no apparent regression and the regression was not significant for b4 animals at Háanef. Key to *I. granulosa*: filled squares Straumsvík and open squares Húsavík.
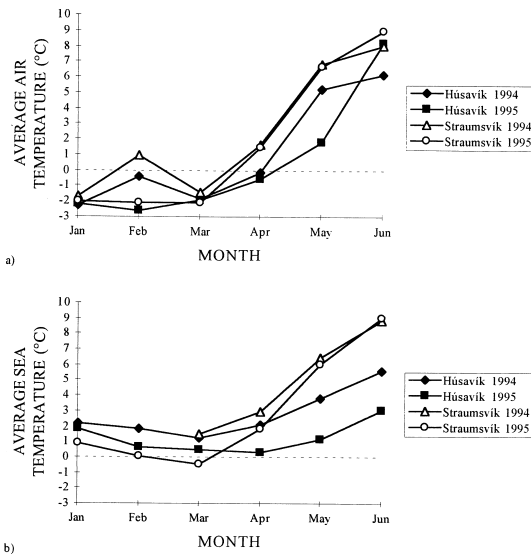
Fig. 12. a) Average air temperature from January to June 1994 and 1995 at Mánárbakki north of Húsavík and at Reykjavík east of Straumsvík. Data from the Icelandic Meteorologic Institute (Anonymous b 1994-1995). b) Average sea temperature from January to June 1994 and 1995 at Grímsey island north of Húsavík and at Reykjavík harbour east of Straumsvík. Data from the Icelandic Marine Research Institute (unpublished).

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Kroer 1989) although not at the southeast coast of Ireland (Healy & O'Neill 1984) and at the Mediterranean coast of France (Kouwenberg & Pinkster 1985). Data on I. pelagica at Háanef are insufficient, but some growth could be observed during winter in I. granulosa at Straumsvík and at least in one year old animals at Húsavík. This winter growth is more rapid, though, in the early winter until December, but it is also discernible in late winter.

The marsupial development time from egg laying to brood release of Icelandic I. granulosa seems similar to that in the Baltic, where it is approximately two months (Salemaa 1979). At the Isle of Man the development time is, however, only about one month (Salemaa 1986) and at the Mediterranean coast of France it is down to 12 (higher temperature) to 27 days (lower temperature) (Kouwenberg & al. 1987). The marsupial development time of I. pelagica at Háanef is 6-8 weeks but at the northeast coast of England it is approximately 5 weeks (Sheader 1977). The development time thus appears to be related to sea temperature, but other factors, for instance food availability for newly released juveniles, may also be involved.

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