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Seasonal variation in the vertical migration of *Pontoporeia affinis* (Crustacea, Amphipoda)

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Vertical migration in *Pontoporeia affinis* Lindström was studied during the years 1974–1978 and 1980 on a location north of the Hanko Peninsula, Gulf of Finland, at a depth of 30 metres. The study was carried out using traps standing on the bottom, with a funnel directed upwards to catch animals descending after excursions from the bottom. The traps were used from the beginning of May to the middle of December. With this method, it was found that vertical migration mainly occurs from the middle of July to the beginning of October. The onset corresponds to the time when cessation of growth occurs, and it may thus be related to a depletion of the locally available food supply. During the main period of vertical migration, large week-to-week fluctuations occur that appear related to out- and inward movements of the water caused by changes in the sea level. In many cases, the results indicate that the whole population takes part in the migration.

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1. Introduction

Vertical migration is a widespread form of behaviour in aquatic crustaceans, particularly among planktonic forms, where pelagic movements in relation to the day-night cycle have been described and extensively studied (see e.g. Bainbridge 1961, Segal 1970). In many species of bottom-dwelling crustaceans this behaviour is observed in a modified form where the animals in the night, or as a response to some other environmental stimulus, rise from the bottom to swim around in the overlying body of water.

In the benthic amphipod *Pontoporeia affinis*, occurring in great abundance on soft mud bottoms in the Baltic Sea and in freshwater lakes in northern Europe, this kind of vertical migration has been well demonstrated. Hessle & Vallin (1934) and Segerstråle (1937a) showed that the animals are caught at night in plankton tows at different depths over the bottom. The same is true for the similar North American species *Pontoporeia hoyi* (Lake Michigan: Wells 1960, 1968, Marzolf 1965a, McNaught & Hasler 1966). In some instances pelagic activity of these animals is observed also in daytime, yet only at greater depths (Lake Michigan: McNaught & Hasler 1966, Wells 1968).

Pontoporeia hoyi, described under this name by Smith (1874), is quite similar to the European *Pontoporeia affinis*. Because of this they were considered the same species by almost all earlier workers under the name *affinis* until Segerstråle (1977) presented evidence that *P. hoyi* is the correct name for the North American species.

The predominantly nocturnal occurrence of vertical migration shows that both *P. affinis* (Segerstråle 1937a) and *P. hoyi* (Marzolf 1965a) are negatively phototactic so that the presence of light prevents the animals from rising from the bottom. In *affinis* the effect of light in an L:D regime, under otherwise constant conditions, has been studied by Donner & Lindström (1980) in laboratory experiments using an

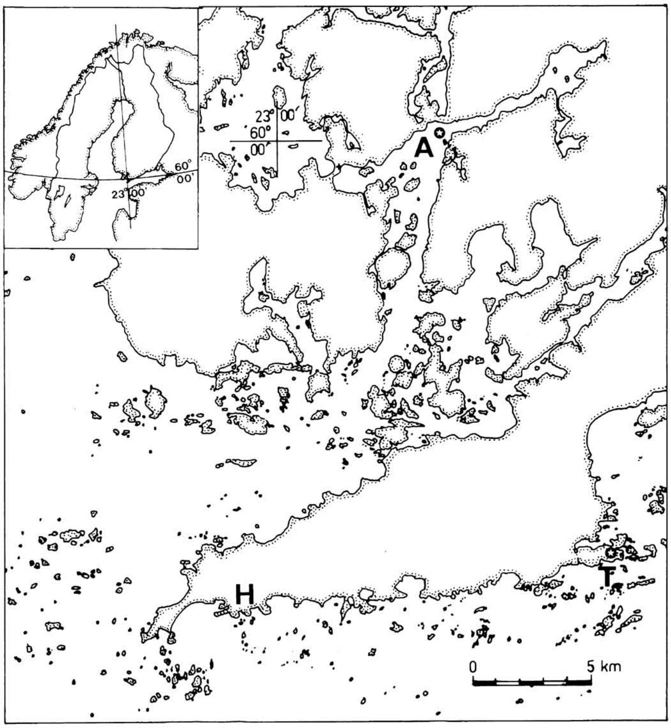

Fig. 1. Map showing the location of the station (A) where the work was carried out. T = Tvärminne Zoological Station. H = the town of Hanko.

infrared recording technique (cf. also Cederwall 1979). According to the results, even weak light strongly reduces the swimming activity (i.e. vertical migration) and at higher intensities completely abolishes it. This is consistent with the very high sensitivity of the eye (Donner 1971). In continuous darkness an endogenous circadian rhythm governs the swimming activity.

The present study was carried out in order to examine the intensity and occurrence of vertical migration in nature during different times of the year and thus to provide a basis for a further analysis of this kind of behaviour in *Pontoporeia*. Aside from light, changes in other environmental parameters may be of importance, considering for example the horizontal migrations that have been described in this species apparently as a response to temperature (Samter & Welter 1904, Wesenberg-Lund 1917, Smith 1972, Grimås 1979). Regarding variations with the time of the year, Lindström & Lindström (1980) showed in laboratory experiments that the intensity of the swimming activity under constant conditions increased regularly from March to December, with a minimum for the period January–March. This result refers to animals of 7–10 mm in size, most of which reach sexual maturity at the end of the year.

Because extensive studies in the field throughout the year are rather laborious to carry out using trawling techniques, a simple method was devised based on the idea of trapping animals descending to the bottom after excursions in the overlying body of water. This paper describes the results obtained using such traps at a site north of the Hanko Peninsula (cf. Fig. 1), in the years 1974–1978 and 1980. The results demonstrate a clear seasonal variation in the pelagic behaviour of *Pontoporeia*.

2. Material and methods

Trapping site and times

The work was carried out at a location about 20 km northeast of the town of Hanko as indicated in Fig. 1 (point marked A). The depth at the site used was 30.5 m, the bottom consisting of soft mud. At this station, trapping was carried out during 14 Aug. to 6 Oct. 1974, 24 May to 19 Oct. 1975, 8 May to 19 Dec. 1976, 1 May to 25 Sept. 1977, 7 May to 22 Oct. 1978 and 9 July to 1 Nov. 1980. In addition, a trap was used through the ice in February and March, in 1975 and 1977, respectively.

On several occasions, bottom samples were taken with an Ekman bottom sampler. The size of the grab was 225 cm^2, in all cases a sieve with 1.5 mm mesh was used.

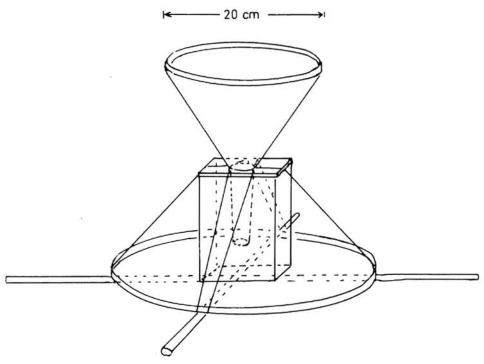

Fig. 2. Trap used in the present study.

Traps used

The traps consisted of a plastic funnel, with an upper diameter of 20 cm (surface area 314 cm^2), attached to a plastic box through its lid as shown in Fig. 2. The inside diameter of the smaller funnel opening was 4.5 cm at the upper, and 1.7 at the lower end. The funnel and the box were attached by strings to a circular metal support provided with four horizontal "legs" to ensure that, when lowered to the bottom, the trap remained standing in an upright position. The whole trap was attached to a line, by which it was lowered to the bottom. At the surface the line was provided with a float. In 1977, 1978 and 1980 a minimum thermometer was attached to the circular support. Since it can be safely assumed that during the summer season, minimum temperatures occur at the bottom, this gave a rough value for the bottom temperature for each trapping period.

The traps were devised to catch pelagic *Pontoporeia* in the funnel at their return to the bottom. From the funnel, they are assumed to slide down in the plastic box and remain there. In the absence of an avoidance reaction, this should give the number of animals returning to the bottom over a surface area corresponding to that of the funnel during the time between two inspections of the trap. The fact that considerable numbers of *Pontoporeia* were caught in this way shows that the principle works. Some kind of avoidance reaction cannot be excluded: it would mean that actually a smaller number of animals were caught than that corresponding to the argument given above. Considering the very high number of *Pontoporeia* caught on many occasions, this effect cannot be great.

The traps were usually inspected once a week, during some periods even once a day. The animals caught in the trap were collected by pouring the contents of the plastic box through a fine sieve (mesh diameter < 0.5 mm), counted and stored in 70 per cent alcohol for later measurements of length, i.e. from the tip of the head to the end of the telson with the animal in its normal swimming position. Most of the catch consisted of *Pontoporeia affinis*, but fairly often, specimens of *Saduria (Mesidothea) entomon.*, *Harmothoe sarsi*, different *Gammarus* species, mysids and more rarely single shrimps (*Leander adspersus*) were caught. However, *Pontoporeia* by far outnumbered all the other species trapped. Of these, at least the polychaet worm *Harmothoe* and the mysids show a light-dependent vertical migration (Sarvela 1971). The *Pontoporeia* caught were usually alive, but particularly the mysids seemed unable to survive when being trapped.

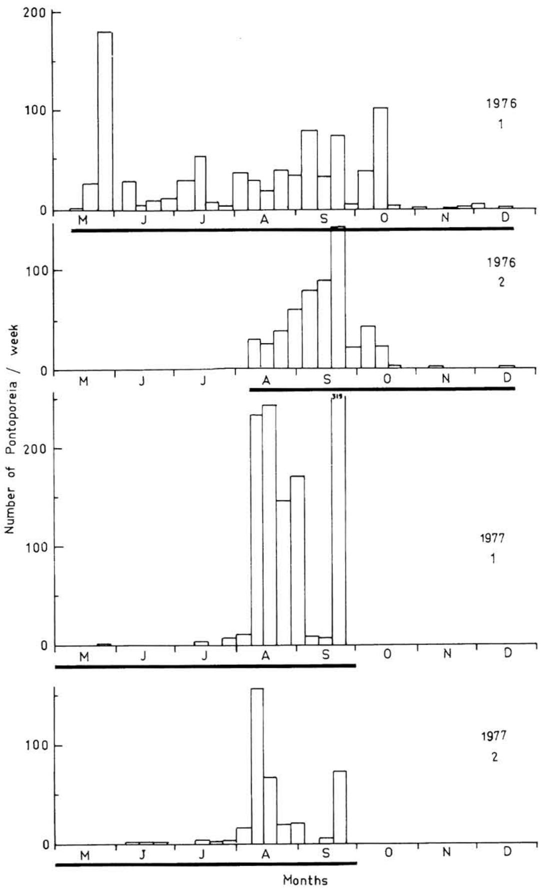

Fig. 3. Weekly catch of *Pontoporeia* in two traps placed at 30 to 40 metres apart from May to December in 1976 and 1977, respectively. A heavy black line indicates the period in which the traps were used. Ordinates: number of *Pontoporeia* caught per week.

3. Results

In order to check the reliability and variability of the trapping method devised, two identical traps were used 30 to 40 metres apart between August and December 1976, and between May and December 1977. The results expressed as weekly catch of *Pontoporeia* are shown in Fig. 3. Generally, the results for both traps reproduce the same pattern, but with a great variation between the traps regarding the catch during single weeks. However, both the onset of the great increase in the weekly catch (in 1977) and the end of the period, when *Pontoporeia* is caught in considerable numbers (in October 1976), are reproduced in the same way by both traps. Also, in August–Sep-

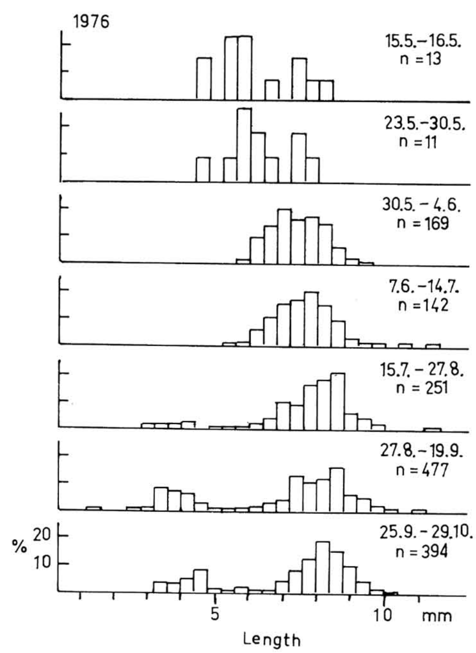

Fig. 4. Length distribution of animals caught during the periods indicated. Ordinates in per cent of the total number in each group. Length classes 0.4 mm.

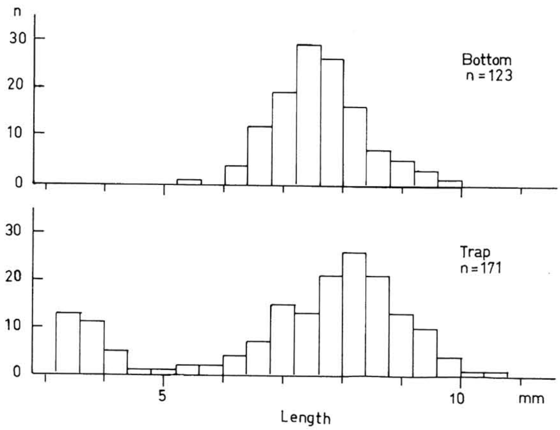

Fig. 5. Comparison between the length distribution of animals obtained by bottom sampling in daytime and animals caught in traps during the same period. Ordinates: number of animals in each 0.4 mm length class. Animals trapped from 9 July to 21 September 1980, bottom samples on 9 July and 6 September 1980.

tember 1977 the same temporal pattern of the catch is reproduced by both traps, although with a smaller number of animals caught in trap No. 2. The reason for this variation is difficult to assess with the restricted material at hand.

Figs. 3 and 6 illustrate the general seasonal distribution observed in the catch of *Pontoporeia* during the period from May to December, for which continuous trapping was carried out. This is also shown in Table 1, which gives the number of *Pontoporeia* caught during consecutive two-week periods during this time. In the total catch of *Pontoporeia* there is considerable variation from year to year, which at least partly is caused by the inherent variability of the trapping method used (Fig. 3). However, a second reason may be the fluctuations known to occur in the abundance of these animals (Segerstråle 1937a, 1960, 1969, Andersin et al. 1978, Grimås 1979, Karjala & Lassig 1985, Sarvala 1986).

An important question is to what extent the animals trapped can be regarded as samples of the same population as that found on the bottom. For this purpose, the size distribution of the animals has been determined as shown in Figs. 4 and 5. The length distribution of the animals trapped in 1976 is shown in Fig. 4, in percentages for the periods indicated. A clear increase in size can be noticed during spring and summer, coming to an end in July–August. From mid-July, a new age class begins to show. The general picture is similar to that described for the growth of *Pontoporeia* in other localities of approximately corresponding depths (Wiederholm 1973, Carlsson 1983, Uitto 1985, Sarvala 1986, *P. hoyi*: Johnson & Brinkhurst 1971, Siegfried 1985), based on material collected by bottom sampling.

In 1980, bottom samples were taken from the same locality as that for the traps on 9 July and 6 September, respectively, and a comparison of the size distribution was made with the animals trapped during the period 9 July to 21 September. The result is shown in Fig. 5. The lack of the smaller stages in the bottom samples is probably explained by the fact that a fairly coarse sieve (1.5 mm) was used for sorting the samples. Considering that the times of the bottom samples are slightly earlier than those of the trapping samples, there is a fair agreement between the size distribution of the daytime population on the bottom and the animals caught in the trap. The results given in Figs. 4 and 5 thus do not contain any indication that the animals caught in the traps represent a special fraction of the population, in agreement with what was already observed by Segerstråle (1937a). This study does not include the situation in late autumn (November–December) where sexually mature males are highly pelagic (Segerstråle 1937a, b).

Table 1. Number of *Pontoporeia* caught in a single trap during successive two-week intervals in different years.

		1975	1976	1977	1978	1980
May	1–15			0	0	
	15–31		207	1	0	
June	1–15		33	0	0	
	16–30	0	9	0	0	
July	1–15	7	106	2	11	25
	16–31	44	14	8	22	34
Aug	1–15	13	71	245	23	41
	16–31	21	85	461	9	29
Sept	1–15	214	99	85	24	31
	16–30	172	88	323	18	117
Oct	1–15		113	0	5	45
	16–31		35	2	0	2
Nov	1–15		1	1		
	16–30		3	2		
Dec	1–15		4			

A special feature observed during all the four years in which the trapping was extended to November–December was that in October, the number of animals caught sank very abruptly, as apparent from Fig. 3 and Table 1. Thereafter, only a few *Pontoporeia* were caught, all of them mature males with their typical long antennae. On 15 October 1978 and 1 November 1980, bottom samples were taken near the traps. In both cases, only a single mature male was obtained in two samples altogether. Accordingly, it is impossible to conclude from the present material that vertical migration comes to a sudden end, an alternative explanation being that horizontal migration and/or predation severely reduce(s) the population on the present site. Also, the fact referred to above, that the sexually mature males are highly pelagic, may mean that they are generally not caught.

In 1975 and 1977, a trap was used through the ice in February–March. No animals were caught. Bottom samples (3 samples each time) did not give any *Pontoporeia* either.

As can be seen from Figs. 3 and 6 the number of animals caught during a single week may sometimes reach fairly high values. Thus in the week 25.8.–31.8.1974 942 *Pontoporeia* were caught, corresponding to 157 animals/night. In 1975, when the trap frequently was inspected daily, the night 20–21.9. gave 140 *Pontoporeia.* Lower numbers, around 40–50 animals/night were often obtained. Knowing the area of the funnel (314 cm^2), the corresponding numbers of animals descending to the bottom per m^2 can be calculated. The maximum number, 157, corresponds to 5000 ind./m^2, a value of 50 equals 1592 ind./m^2. Bottom samples in

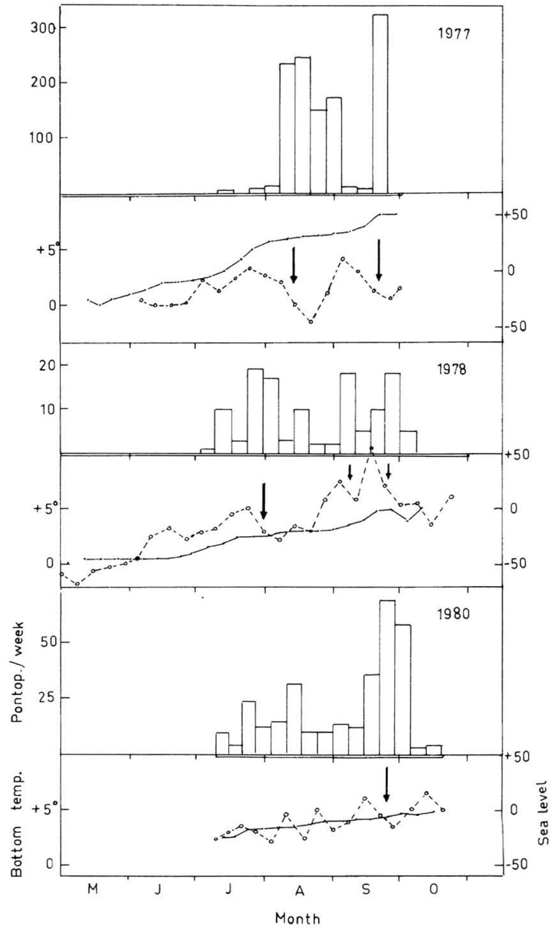

Fig. 6. Weekly catch of *Pontoporeia* in 1977, 1978 and 1980. A double line indicates the period when the traps were used. Ordinates: number of *Pontoporeia* caught per week. Under data for each year, curves for weekly bottom temperatures (line in full, ordinate to the left), and for sea level as recorded by mareograph at the point of Hanko Peninsula (interrupted line, scale to the right in cm). Arrows denote periods with falling sea water level, coincident with large catches of *Pontoporeia.*

August–September, the period of the highest catches in the traps, in 1975, 1978 and 1980 showed that the abundance of *Pontoporeia* on this site never exceeded 1500 ind./m^2. Considering that the smaller stages are missing in the bottom samples (see above, Fig. 5), the maximum value may be 10–20 % too low. Nevertheless, the trapping results indicate that on certain occasions the whole population or a very large majority becomes pelagic at night. This is true assuming that the animals return to the bottom and thus have a chance of being caught in the trap, only once during a single night. However, the chance of being caught may be increased if the animals return to the bottom some or several times during the night. This is consistent with observations in aquaria (M. Lindström, unpublished observations) using an infrared viewer in darkness, where it has been seen that the animals, particularly at the beginning of the dark period, show this kind of behaviour.

Although the variability inherent in the method when only a single trap has been used (cf. Fig. 3) may explain part of the fluctuations in the number of animals caught per week, some additional, external factor or factors affecting the tendency for vertical migration should be looked for. Fig. 6 represents an attempt to elucidate this question in terms of water temperature and changes in sea level. Fig. 6 thus gives the weekly trapping results for the years 1977, 1978 and 1980, together with data for the minimum bottom temperatures during each trapping period, as well as for the changes in sea level as recorded by the mareograph operated by the Institute for Marine Research at the point of the Hanko Peninsula.

Regarding temperatures, there is in all cases a slow and gradual rise from a level slightly above 0°C in May to +5 – +7°C in October. No rapid changes are seen to occur that could be correlated with the fluctuations in the catch of *Pontoporeia*. However, high values in the number of animals trapped appear to be associated with a sinking sea level at Hanko (vertical arrows in Fig. 6). This should result in an outward current in the body of water where the trapping experiments were carried out.

4. Discussion

The present results refer to a single station, at a depth of 30.5 m, situated relatively far inshore, north of the Hanko Peninsula (Fig. 1). In this kind of narrow waters, local conditions may influence the data to a great extent so that the pattern of vertical migration observed is possibly not a general property of the behaviour of this species. Thus, for instance, even variations in depth should modify results of this kind, owing to the strong attenuation of downwelling light in the Baltic Sea. On the other hand, there are features in the results obtained that appear to fit in with data from the work on the seasonal variation in the abundance and growth of *Pontoporeia* (cf. e.g. Wiederholm 1973, Uitto 1985, Sarvala 1986, *P. hoyi*: Siegfried 1985), indicating that the results obtained are not unique for the site used in the present work.

There are three main groups of external, environmental variables that appear to affect vertical migration in *Pontoporeia*, viz. (1) intensity and diurnal variation in the light reaching the bottom; (2) quality of the bottom substrate and the availability of food; and (3) hydrographical factors such as water temperatures, salinity, oxygen, as well as currents. In addition, at least in the laboratory, some internal factors lead to an increase in the off-bottom activity from March–April to the end of the year in pre-adult and adult animals (Lindström & Lindström 1980).

The essentially nocturnal nature of vertical migration in *Pontoporeia* has been well-established in the field (Hessle & Vallin 1934, Segerstråle 1937a, *P. hoyi*: Larkin 1948, Wells 1960, 1968, Marzolf 1965a, McNaught & Hasler 1966). At moderate depths (from 20 to 50 metres) in the Baltic Sea, there is sufficient light at the bottom in daytime to abolish vertical migration (Donner 1971, Donner & Lindström 1980). Considering the present results, an important question is, however, to what extent there is also sufficient light at the bottom at night to depress vertical migration, particularly in June and July as indicated by the data shown in Fig. 3 and Table 1. In the summer months, a relatively high illumination prevails at this latitude (60°N) at the surface all through the night. Furthermore, according to the data published by Niemi (1975) on the vertical transmission of green light (i.e. the spectral region of maximum transmission in these waters), the transmissivity of the water is highest in June and July. His measurements from the Tvärminne region show that the depth at which 1 per cent of the subsurface light remains is 4–8 metres in April–May due to the vernal phytoplankton bloom, whereas in June–July it is 12–18 metres. Again, in August–September, lower values were observed: around 8–10 metres due to large amounts of suspended organic material. It is hence possible, although direct measurements are lacking, that in June–July even at night such a light intensity reaches a depth of 30 metres as may have a depressing effect on the vertical migration of *Pontoporeia*, which at least partly explains the small number of animals trapped in these months. According to the results by Donner & Lindström (1980), weak light intensities, 1–2 log units above the threshold, in the laboratory do not affect the swimming activity (i.e. vertical migration) very strongly.

Pontoporeia affinis is generally considered a detritus feeder and ingests particles smaller than 50–60 µm in diameter (Ankar 1977, *P. hoyi:* Marzolf 1965b). Elmgren (1976) reports finding in one specimen a large number of empty nematode cuticulae and Ankar (1977) assumes that these animals can even masticate organic aggregates larger than 60 µm. Johnson (1987) in a study on the life history, production, and food habits of *Pontoporeia affinis* gives detailed data on the seasonal gut composition in Lake Erken, Sweden, at a depth of 12 metres. Growth at depths around 30 metres mainly occurs from April to July–August (cf. Fig. 4), and it has been related to the material produced by the primary production of the phytoplankton in the spring and the ensuing sedimentation (Wiederholm 1973, Cederwall 1977, Sarvala 1986). Marzolf (1965b) found that in Lake Michigan the distribution of *Pontoporeia hoyi* correlated with the number of bacteria in the sediments and that in the laboratory there was a significant selection of substrates whose surface layers were enriched with organic matter or which were allowed to "condition", assumedly by the growth of bacteria on the substrate surfaces. Related to this may be fact that in the Baltic Sea, *Pontoporeia* is not evenly dispersed but shows a significant degree of aggregation (Cederwall 1978).

How then is this kind of distribution brought about, resulting apparently in a concentration of *Pontoporeia* on parts of the bottom where food is abundant, and also on soft mud bottoms in general? Vertical migration, which also leads to horizontal displacement of the animals, would seem to constitute such a mechanism, but requires the assumption that an unsuitable bottom substrate enhances and a suitable (i.e. rich in ingestible food) substrate reduces the tendency for pelagic movement, which may or may not be combined with a directed horizontal movement in the water. Though detailed studies have not been performed, the fact that in aquaria, under substrateless conditions, swimming activity is much increased (Lindström & Lindström 1980, cf. also Fincham 1970 for *Bathyporeia pelagica*) points to this direction. Considering that at the moderate depth of the present work, the growth of *Pontoporeia* comes to an end in July–August (Fig. 4, cf. also Johnson & Brinkhurst 1971, Cederwall 1977, Carlsson 1983, Uitto 1985), the increased vertical migration observed in August–October can then also be looked upon as resulting from a depletion of the locally available food supply. It should be noted that cessation of growth at this time, or somewhat later, is also observed in the year-class 0 that has not yet reached the final size of these animals (Uitto 1985). This interpretation is supported by results for other benthic crustaceans showing that the degree of emergence from the bottom is increased by starvation (the pink shrimp, *Penaeus duorarum*, Hughes 1968, the isopod, *Eurydice pulchra*, Jones & Naylor 1970). It is also well-known that generally environmental changes, as well as changes in the physiological state of the animal, can induce reversals of the sign of orientation (Creutzberg 1975).

Light (intensity, daylength) and the availability of food are factors changing relatively slowly with the season in the environment of *Pontoporeia*, thus constituting long-term effects in this context. Results such as those shown in Fig. 6, with rapid and large peaks in the number of animals trapped occurring during periods of outflow of water from the water basin, indicate that hydrographical changes act as short-term stimuli for vertical migration during the main season for this activity. The actual nature of these changes cannot be specified at present. Current, as such, cannot constitute the only stimulus since an inward current does not appear to have the same effect as an outward current, unless it is assumed that the animals are able to perceive the direction of flow, which seems rather unlikely. Possibly some difference may exist in the quality of the water flowing out of the basin as compared with the water flowing in. However, in view of the complicated patterns of current recorded in the Archipelago Sea, with frequently opposite directions of current at the surface and at the bottom (cf. Saaristomeren virtaustutkimus 1979), any interpretation of the results shown in Fig. 6 remains highly speculative.

As short-term stimuli, changes in temperature are less likely considering the results in Fig. 6, but temperature may well have a more long-term stimulating effect considering the general rise observed towards autumn. Several authors have noted that *Pontoporeia* performs horizontal movements from warmer to cooler temperatures in the course of the year, consistent with the idea of an increased swimming activity with higher temperatures (Samter & Weltner 1904, Wesenberg-Lund 1917, Grimås 1979, *P. hoyi:* Smith 1972). The horizontal movements of the animals are not in such cases necessarily directed, though they may possibly be so. Horizontal displacement can be brought about passively by water currents, as already discussed in detail by Segerstråle (1937a). Along the coast of the Baltic Sea, current velocities of 10–20 cm sec^{-1} are not uncommon (Laakkonen, Mälkki & Niemi 1981), and even higher values may occur in the relatively narrow waters where the present work was carried out. A current of the velocity of 20 cm sec^{-1} will transfer a freely swimming *Pontoporeia* 720 metres in one hour. Thus also the high number of animals trapped under conditions of a net outflow of water from the basin may be a sign of horizontal transport from the shallower waters of the bay, extending 7–8 km from the trapping site towards NE (Fig. 1).

As pointed out by Donner & Lindström (1980), several fish species that feed on *Pontoporeia* appear to do so mainly in August–November when vertical migration shows the highest intensity according to the present results. Such species are the Baltic herring (Aneer 1975), the smelt (*Osmerus eperlanus*) (Voigt, pers. comm.), and small cod (Axell 1982). In contrast to this, the fourhorn sculpin (*Myoxocephalus quadricornis*), a typical bottomfeeder, feeds on *Pontoporeia* throughout the year, particularly during the summer months when vertical migration is less prominent (Aneer 1975). Vertical migration then involves exposure to considerable predation, for example, in view of the great abundance of the Baltic herring. During the time of intense vertical migration in August–October, the abundance of *Pontoporeia* has been found to decrease strongly (Siegfried 1985, Uitto 1985, Sarvala 1986, Johnson 1987), a fact that probably reflects the significance of off-bottom feeding fish species as predators on *Pontoporeia*.

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