

Mass mortality in two common soft-bottom invertebrates, *Hydrobia ulvae* and *Corophium volutator* – the possible role of trematodes

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ABSTRACT: Two littoral macrofaunal invertebrates, *Hydrobia ulvae* (Prosobranchia) and *Corophium volutator* (Amphipoda) suffered mass mortality on an intertidal mudflat in the Danish Wadden Sea in May–June 1990. Dissection of collected *H. ulvae* individuals revealed a considerable increase from March to May in numbers of infected individuals by microphallid trematodes that use *H. ulvae* and *C. volutator* as first and second intermediate host, respectively. The numbers of infested snails were hereafter reduced by an amount equal to the observed mortality rate of snails. At the same time, the *C. volutator* population became extinct. Since other conceivable mortality factors could be ruled out, parasites are suspected to be the causative agent. Apart from the expected effects on potential predators by the decline in the two invertebrate populations, the benthic community changed and destabilization of the substratum occurred probably because of the die-off in *C. volutator*. Meteorological data suggest high temperatures as a triggering factor of the mass-development of the studied trematodes.

INTRODUCTION

Unexplained fluctuations in abundance are a characteristic feature of *Corophium volutator* populations (Watkin, 1941; Reise, 1978; Ólafsson & Persson, 1986). In order to understand the factors causing temporal variability, we studied the population dynamics of *C. volutator* and other co-occurring macrofaunal invertebrates on a "*Corophium*-bed" (Reise, 1978). During this study we observed mass mortalities in *Hydrobia ulvae* and *C. volutator* in spring 1990 without any obvious triggering factor. The failure to explain the incident by means of the most common mortality factors made us focus on the possibility of diseases. Parasites have previously been suggested as an important factor influencing *Corophium* populations (Lauckner, 1987a). Some of these parasites use *H. ulvae* and *C. volutator* as first and second intermediate host, respectively. To test the hypothesis that the co-occurrent decline in *H. ulvae* and *C. volutator* was caused by digenean trematodes, we examined individuals of *H. ulvae* and *C. volutator* collected before the incidence for parasites. Here we report on data of macrobenthic populations from our study area during spring 1990 and present data on parasite infections in *H. ulvae* and *C. volutator*. The possible impact of other conceivable mortality agents are discussed.

MATERIAL AND METHODS

The sampling site was located in the upper intertidal zone (600 m from the mean high water line, MHWL) in the Danish Wadden Sea (54°56' N: 8°39' E) (Jensen & Kristensen, 1990). The distance between the MHWL and the MLWL is about 1.5 km on this mudflat. Silty-trenches for coastal protection, each about 200 × 250 m², are established along the shoreline. The *Corophium*-bed occurred in front of such silty-trenches to about 800 m from the MHWL covering an area of about 80 ha. At low tide, the bed was composed of a mosaic of elevated plateaus and pools, covering 56 % and 44 % of the area, respectively. The plateaus, which were inhabited by high numbers of *Corophium volutator*, had a siltier and softer substratum (17.9 % silt) when compared with the pools (9.6 % silt) (Mouritsen, 1991). *C. volutator* occurred only sporadically in the pools. Data reported here refer only to sampling on the plateaus in March, May and June 1990. However, the sampling programme on this locality was continued after June 1990 and we report on some further trends in the faunal development.

Ten core samples (each 50 cm²) were collected on each sampling occasion and sieved through a 500 µm mesh. Retained animals were preserved in neutralized formaldehyde (4 %). The body length of *C. volutator* and the shell height of *Hydrobia ulvae* were measured, and length-weight regressions (Möller & Rosenberg, 1982; Bachelet & Yacine-Kassab, 1987) were used to calculate biomass. The weight of *C. volutator* individuals in May was used to estimate the biomass lost between May and June. In *H. ulvae* the weight of parasitized individuals in May was used. Adult individuals (>3.3 mm) of *C. volutator* were sexed. Unbiased samples (all individuals from one to three cores) of *H. ulvae* (≈ 220 individuals) and *C. volutator* (≈ 150 individuals) from each sampling occasion were dissected and examined for parasites using a binocular microscope. Identification of trematodes was performed using a light microscope and published descriptions (Deblock, 1980; Lauckner, 1987a).

RESULTS

Corophium volutator and *Hydrobia ulvae* were the most abundant organisms on the *Corophium*-bed during March through May 1990, contributing more than 80 % of all macrobenthic specimens (Table 1). The size distributions of the two populations in May are shown in Figures 1 and 2. The *C. volutator* population was dominated by adults (68 %) of which egg-carrying females constituted 38.5 %. Between May 5th and June 12th, however, all *C. volutator* individuals vanished (≈ 14 000 ind m⁻²), while the *H. ulvae* population was reduced by 40 % (≈ 10 000 ind m⁻², Table 1 and Fig. 3). In terms of biomass, ≈ 13 g ashfree-dry-weight m⁻² was eliminated. Examination of sediment samples in the field in June indicated that *C. volutator* actually had been exterminated from the entire 80 ha bed-area. The presence of *C. volutator* is easily evidenced by the presence of burrow holes on the sediment surface. During sampling in June, the characteristic topography of the bed (see Materials and Methods) was unaltered compared with its appearance in May, but in July it had disintegrated although soft and less soft areas still could be distinguished. Its former heterogeneous structure had disappeared completely by August. *C. volutator* was not registered on the former bed area until after nine months (April 1991), whereas the *H. ulvae* population regained its

Table 1. Species composition on the "Corophium-bed" (Højer, 1990) (numbers m^{-2}). Pairwise comparisons were made using Mann-Whitney non-parametric tests. (*: $0.01 < p < 0.05$; **: $0.001 < p < 0.01$; ***: $p < 0.001$; n.s.: $p > 0.05$). O: Oligochaeta; N: Nemertinea; P: Polychaeta; G: Gastropoda; L: Lamellibranchia; C: Crustacea

Species	March		May		June
<i>Tubificoides benedeni</i> (O)	1340	***	4240	ns	4960
<i>Lineus ruber</i> (N)	0	**	360	**	0
<i>Eteone longa</i> (P)	20	ns	100	ns	260
<i>Heteromastus filiformis</i> (P)	600	**	180	ns	330
<i>Nereis diversicolor</i> (P)	300	**	600	*	300
<i>Pygospio elegans</i> (P)	1460	*	2380	**	3400
<i>Hydrobia ulvae</i> (G)	26860	ns	24460	***	14560
<i>Retusa obtusa</i> (G)	0	*	140	ns	334
<i>Macoma balthica</i> (L)	220	ns	240	***	1360
<i>Mya arenaria</i> (L)	200	ns	140	ns	60
<i>Corophium volutator</i> (C)	18620	ns	14080	***	0
<i>Corophium arenarium</i> (C)	0	ns	0	*	200

abundance within two months. However, a population of *C. volutator* (mean \pm S.E.: $151.1 \text{ ind } 50 \text{ cm}^{-2} \pm 37.2$ corresponding to $30\,200 \text{ ind } m^{-2}$), established within an artificial silty trench landward to the bed (400 m from the study site), persisted in July. Here, *H. ulvae* occurred in low numbers (mean \pm S.E.: $4.6 \text{ ind } 50 \text{ cm}^{-2} \pm 1.0$ corresponding to $920 \text{ ind } m^{-2}$).

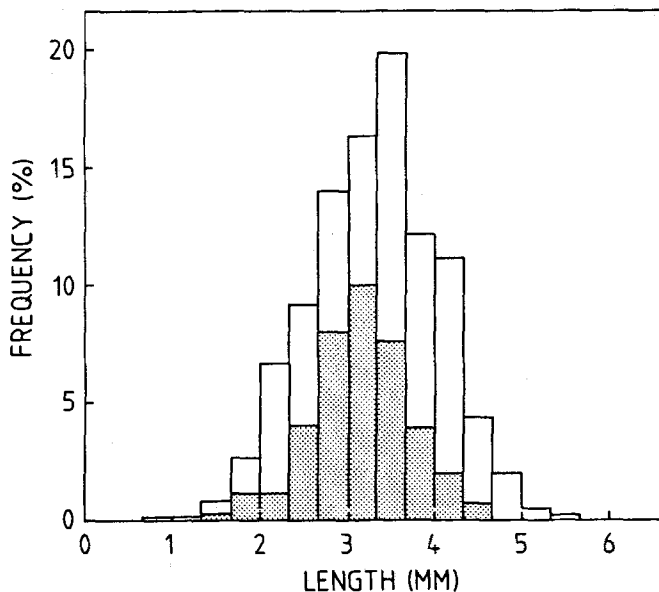


Fig. 1. Length-frequency distribution of *Hydrobia ulvae* on May 5th ($n = 990$). The length-frequency distribution of *H. ulvae* individuals parasitized with microphallid trematodes is also indicated (shaded area)

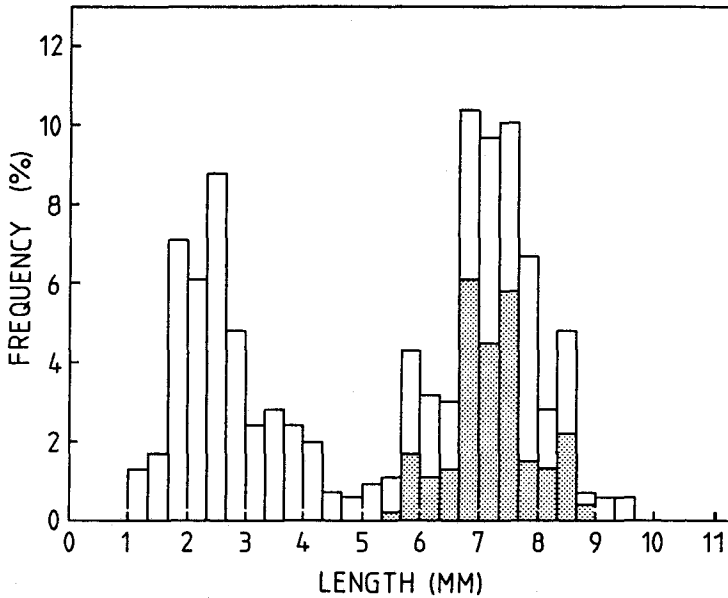


Fig. 2. Length-frequency distribution of *Corophium volutator* on May 5th ($n = 537$). The percentage of egg-carrying females is indicated by the shaded area. The adult population (> 3.3 mm) consisted of 20.8% males, 38.5% egg-carrying females and 40.7% females without eggs

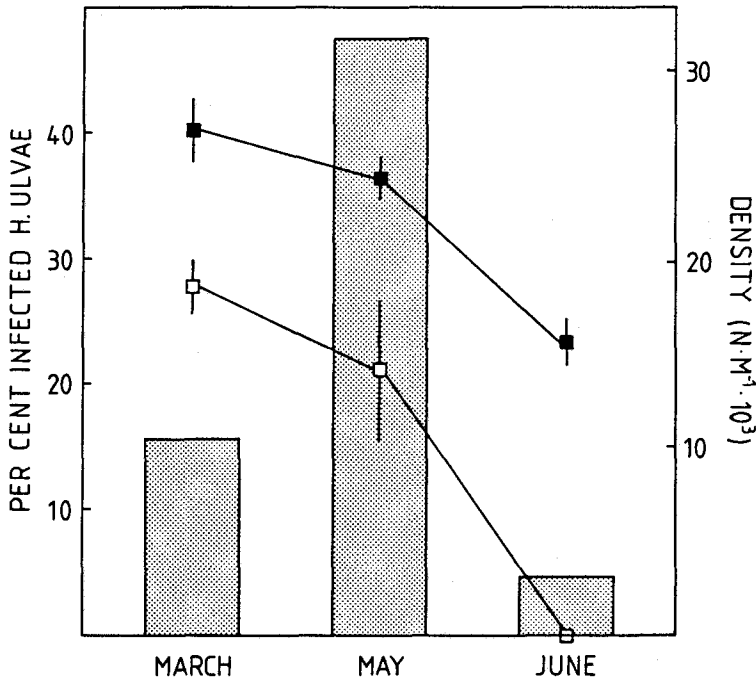


Fig. 3. Abundance of *Hydrobia ulvae* (■) and *Corophium volutator* (□) (mean numbers $m^{-2} \pm 95\%$ C.L.) and percentage of microphallid infected *H. ulvae* (bars) on the *Corophium*-bed during spring 1990

To examine whether parasites were possibly involved in the mortality of *C. volutator* and *H. ulvae*, we dissected individuals collected before the event. *H. ulvae* individuals revealed a peak in infection rate by trematodes in May (Fig. 3). At this time, 47% of the individuals were heavily parasitized by microphallid trematodes (Table 2) (*Microphallus claviformis*, 95%, and *Maritrema subdolum*, 5%), which use *H. ulvae* and *C. volutator* as

Table 2. Frequency of *Hydrobia ulvae* host to different numbers of cercariae during spring 1990

Number of cercariae per individual	March	May	June
0	40.0	5.3	—
0–10	8.7	6.2	10.0
10–10 ²	37.2	22.1	20.0
10 ² –10 ³	14.3	63.7	30.0
10 ³ –10 ⁴	—	2.7	40.0
Number of infected <i>H. ulvae</i> m ⁻²	4110	11521	720

intermediate hosts and shorebirds as primary hosts (Lauckner, 1987a). Dissected specimens of *H. ulvae* showed a considerable increase in the density of cercariae within snails between March and May as a result of the maturation process of the larval trematodes (Table 2). The decline in numbers of infected *H. ulvae* from May to June corresponds well with the reduction in *H. ulvae* density (Fig. 3). Examination of *C. volutator* individuals collected in May indicated that 53.8% ($n = 52$) of adult *C. volutator* contained metacercariae, whereas only 2.9% ($n = 70$) of the juveniles were parasitized. On average, the parasitized adults carried only 3.8 ± 0.6 (S.E.) metacercariae. Judging by their sizes ($\approx 160 \mu\text{m}$), these metacercariae could belong to either of the two microphallid species observed in *H. ulvae*. Since the trematode infestation in the *H. ulvae* population peaked on May 5th, intensive transmission of cercariae to *C. volutator* should occur after this date. For this reason it is not surprising that each *C. volutator* individual contained only few metacercaria on May 5th.

DISCUSSION

Several factors could in principle cause high mortality in benthic invertebrates during a short period. Conceivable factors include: (1) extreme weather conditions, (2) oxygen depletion or pollutants, (3) predation and (4) diseases. However, as only two species (*Hydrobia ulvae* and *Corophium volutator*) responded to any large extent, the causative factor (or factors) acted selectively. It (or they) should provide an explanation of the differential survival of the two invertebrate populations during May to June, as well as the persistence of a *C. volutator* population in the silty trench.

Ad 1. Possible meteorological conditions that could influence the survival of *C. volutator* and *H. ulvae* populations include high temperatures, prolonged desiccation due to off-shore winds or strong on-shore winds that could destroy the bed (through erosion). The survival of a *C. volutator* population within the silty trench precludes that air-temperature or desiccation per se could have caused mortality in *C. volutator*. Strong on-

shore winds ($> 18 \text{ m s}^{-1}$) (data from Danish Meteorological Institute) occurred three days in the period from mid-March to early May, whereas the wind velocities were below 18 m s^{-1} throughout the period from early May until mid-June. In addition, the bed persisted during a hurricane force storm in January 1990. Furthermore, as the bed was present in June the extermination of *C. volutator* preceded the disintegration of the bed and not vice versa.

To *H. ulvae*, desiccation could still be a problem. However, off-shore winds ($> 10 \text{ m s}^{-1}$) that might cause desiccation on the upper shore (pers. obs.) occurred during 10 days in the period from March 12th to May 5th, but only during two days in the period from May 5th to June 12th. Even if temperatures were higher during the latter period, desiccation lasting a few days could not kill *H. ulvae*. Experiments have indicated high survival rates in *H. ulvae* specimens subjected to desiccation at temperatures reaching 39°C (Lassen & Kristensen, 1978). In conclusion, the meteorological conditions during the period from early May until mid-June could not per se be responsible for the high mortality rates in the two invertebrates.

Ad. 2. Oxygen depletion or pollutants are also unlikely mortality factors in the present case. The study area is a homogeneous mudflat without macrovegetation, and signs of anoxic conditions on the sediment surface have never been observed in the area (pers. obs.). Moreover, the presence of oxygen depletion and pollutants high in the intertidal zone, away from terrestrial runoffs, is unlikely and would undoubtedly have affected other species as well as the population of *C. volutator* in the silty trench. Since both the bivalve *Macoma balthica* and the polychaete *Pygospio elegans* showed increased numbers due to recruitment during May to June (Table 1), it is highly unlikely that environmental factors per se should have caused the observed die-off in *C. volutator* and *H. ulvae*.

Ad. 3. Selective predation by migratory shorebirds, which forage at the study site in large numbers during spring and autumn, could be a factor of importance. The dunlin, *Calidris alpina*, is quantitatively the most important species in the Danish Wadden Sea during spring and autumn migration (exceeding 400 000 in autumn; Laursen & Frikke, 1984) that feeds on *C. volutator* and *H. ulvae* (Boere & Smit, 1981; Mouritsen, 1991). However, we maintain that they could not have caused the present declines in numbers of *H. ulvae* and *C. volutator*. Regular counts of dunlins at Langli Field Station in the northern part of the Danish Wadden Sea in spring 1990 show a typical phenology of dunlins in the Danish Wadden Sea (sensu Laursen & Frikke, 1984), with peak numbers of feeding birds during the end of April to beginning of May (Fig. 4). From these counts, an estimate of bird-days between March 12th and June 12th by interpolated counts amounts to $5.3 \cdot 10^5$ bird-days. Of those, only 36.1% occurred between May 5th and June 12th. The dunlin population had actually left the Danish Wadden Sea before June 1st. Consequently, the predation pressure from dunlins on benthic invertebrates was higher during the period between March and May than during May–June. However, shorebirds usually exhibit a patchy distribution and concentrate their feeding efforts on particularly food-rich areas, as for example *Corophium*-beds. On the *Corophium*-bed in question, the density of foraging dunlins observed during a bird survey in autumn 1989 was $141 \pm 26 \text{ ind ha}^{-1}$ (mean \pm S.E. of counts during 13 low tides; Mouritsen, unpubl. data). Considering that the numbers of dunlins in the Danish Wadden Sea is almost twice as high in autumn as in spring (Laursen & Frikke, 1984), we may assume much lower foraging

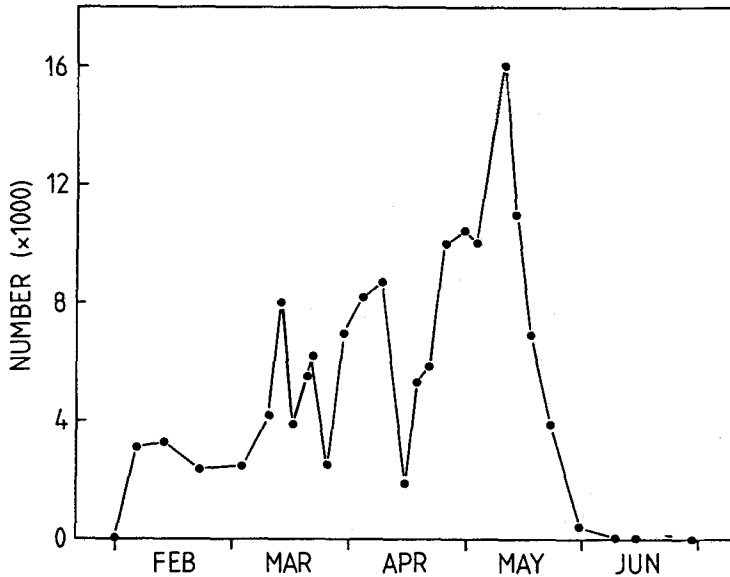


Fig. 4. Phenology of dunlins, *Calidris alpina*, at Langli (northern part of the Danish Wadden Sea) in spring 1990. The bird counts are performed by staff members at Langli Field Station, The National Forest and Nature Agency, and represent total counts according to standard methods. -: no birds registered

intensity in spring 1990. To calculate the energy demand of a population of dunlins we used a conservative estimate of their individual requirements at 4 times their basic metabolic rate ($4 \text{ times } 9 \text{ kcal day}^{-1} \text{ ind}^{-1}$; Evans et al., 1979; Pienkowski et al., 1984). To meet the energy requirement of the foraging dunlin population in the period from May 5th to June 1st – using a population density of 141 ind ha^{-1} – $3.5 \text{ g ashfree-dry-weight m}^{-2}$ is needed. This corresponds to 26 % of the *C. volutator* population (if the same high numbers of dunlins persisted on the bed until June 12th, their potential consumption would have been 37 % of the *C. volutator* population). The potential consumption of 26 % of the *C. volutator* population would be diminished by the use of other food items by dunlins (e.g. *H. ulvae* and other species). In view of the optimal foraging theory (e.g. Stephens & Krebs, 1986), it is highly unlikely that the dunlins should have eaten the entire *C. volutator* population; they would have left the area long before the amphipods became scarce. It would also be difficult to understand the persistence within the silty trenches of a *C. volutator* population that is exposed to shorebird predation for a longer time than those at our main study site due to longer emersion time on the upper shore. In conclusion, shorebird predation could not on its own have caused the die-off in the two invertebrate populations.

Possible marine predators include flat-fish, gobies, sticklebacks, crabs and shrimps. Except shrimps (Jensen & Jensen, 1985), the 0-groups of these predators do not migrate into this area before early summer (June/July; Reise, 1978). Juvenile shrimps ($< 2 \text{ cm}$) occurred in high numbers on the flat in June, but due to their small size they would not be significant predators on *C. volutator* and *H. ulvae* (Evans, 1983). Furthermore, the impact

of marine predators on prey organisms is limited by the short submersion time on the upper shore (Reise, 1978).

Ad. 4. The possibility that parasites were involved in the present mass mortalities is supported both by data on the frequency of parasitized snails and by the observed parasite species in *H. ulvae*. Observations of local extinctions of *C. volutator* populations have previously been suspected to involve parasites (Muus, 1967; Ólafsson & Persson, 1986; Lauckner, 1987a). Laboratory experiments have also demonstrated the death of *C. volutator* individuals exposed to microphallid infested *H. ulvae* (Lauckner, 1987a). Chitinolytic and proteolytic enzymes released by the penetrating and migrating cercariae, in addition to growth of these larvae, may result in severe damage of *C. volutator* tissue and finally cause the death of infested specimens (Lauckner, 1987a). However, mass mortality in *H. ulvae* caused by parasites has not been reported earlier, but in other snails, hosts to digeneans, increased mortality has been demonstrated (Lauckner, 1987b). Overexploitation of the host's resources by parasites, and tissue damage during their release are considered to be the main causes (Dobson, 1988).

High densities of co-existing intermediate hosts may be an important feature characterizing events of parasite-mediated mass mortality. Because of the short longevity of cercariae when free-living (Smyth & Halton, 1983), a short distance between intermediate hosts is of crucial importance for their successful transmission. Such conditions prevailed in May at the study site. In the silty trench, in contrast, the microphallid trematodes probably had little impact on the *C. volutator* population due to the low numbers of *H. ulvae* and, in turn, a low total cercariae production.

In summary, the hypothesis of parasite-mediated mass mortality provides a coherent explanation of all observations. No data seem to produce contraevidence against this hypothesis, and for this reason it is the simplest explanation. In contrast, the other suggested mechanisms could not offer a sufficient explanation of the data. In addition, we would have serious problems inventing some further mechanism that could explain both the mortality of *H. ulvae* and *C. volutator*, and the differential survival of *C. volutator* on the bed and within the silty trench.

The incident had widespread effects besides its influence on benthic populations. Considerably less food would be available to predators later in the season (shrimps, crabs, fishes and birds), as the eliminated biomass corresponds to 76% of the annual secondary production in a *Corophium*-bed (Asmus & Asmus, 1985). The topographic structure of the bed changed probably as a consequence of the decline in *C. volutator*. It happened during a period of calm weather, whereas the bed persisted during a hurricane force storm in January 1990 (Maddox, 1990). Thus, wave action could not be responsible for the topographic alterations. Instead, we suggest that the absence of *C. volutator* caused sediment destabilization. Recently, Meadows et al. (1990) have shown that absence/presence of *C. volutator* may have significant impact on coastal erosion/sedimentation. Reise (1978) also observed that a decline of a *C. volutator* population caused alterations in the sediment topography.

Parasite-induced mass mortality in *C. volutator* is not an annual event, as high densities of *C. volutator* occurred at the study site during summer and autumn in 1989 and 1991 (unpubl. data). In an attempt to assess the possible impact of meteorological characteristics on the present parasite incidence, we collected data on spring temperatures for the last decade. Temperatures were considerably higher in spring 1990 than

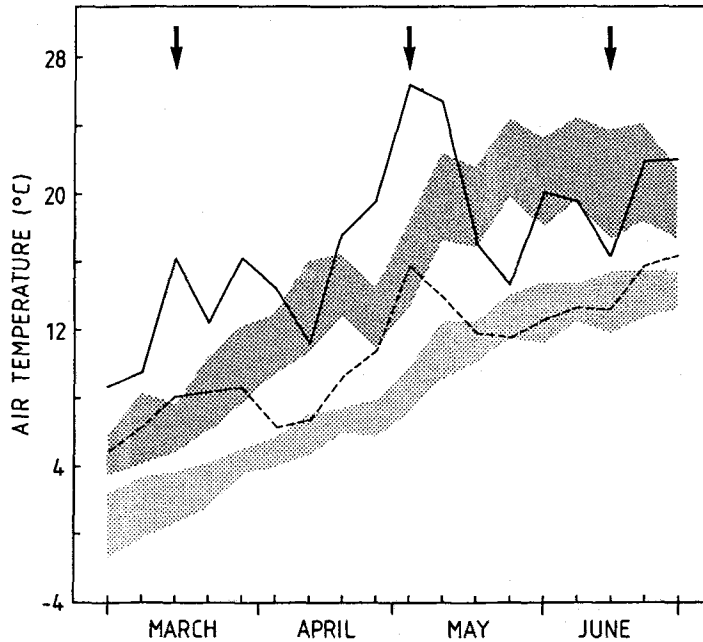


Fig. 5. Air temperatures near the study site during spring. The shaded areas show 95% C.I. of 10-year normals (1980–89) of weekly mean (light shaded area) and maximum (dark shaded area) temperatures. Dashed and fully drawn lines indicate the weekly mean and maximum temperatures during spring 1990, respectively. Arrows denote sampling occasions. In 1990, both the mean and the maximum temperatures were unusually high before the die-off in *C. volutator* during May–June. Data was acquired from the Danish Meteorological Institute, Copenhagen

is normal during this season (Fig. 5). Laboratory studies have demonstrated that temperature may be an important factor influencing life-history traits of larval trematodes within their poikilotherm intermediate hosts (Rees, 1948; Stirewalt, 1954; Gumble et al., 1957; Watertor, 1968; Shostak & Esch, 1990). The generally reported positive relationship between temperature and production of cercariae suggests that the high temperatures during spring 1990 were an important factor causing the present mass development of trematode larvae in *H. ulvae* and, in turn, their successful transmission to *C. volutator*. This possibility is further supported by Ginetsinskaya (1988) with respect to *Maritrema subdolum*. He reports that cercariae of this species emerge from *H. ulvae* only when the temperature rises to 20–30°C. On intertidal flats, this may happen during low-tide on the upper shore.

Recent studies indicate that parasites may play an important role in controlling populations and even community structure (Holmes & Price, 1986; Harwood & Hall, 1990; Minchella & Scott, 1991). The present study suggests that marine ecologists should pay more attention to the role of parasites and to elucidating conditions under which parasitism becomes an important process regulating the population dynamics of marine organisms.

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