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# MORTALITY OF BALTIC HERRING (*Clupea harengus* L.) EGGS CAUSED BY SPAWNING SUBSTRATUM ALGAE

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Baltic herring (*Clupea harengus* L.) spawning ground surveys carried out in the northern Baltic proper have shown that, locally, eggs die in very high frequencies (up to 100%). These high mortalities have been shown to be connected to different kind of spawning substratum alge, predominantly filamentous brown algae. Laboratory experiments carried out in 1984, 1987 and 1988 have shown the following algal species to have a significant negative impact on the survival of Baltic herring eggs: *Pilayella littoralis (Ectocarpus siliculosus, Eudesme virescens,* and *Rhodomela confervoides*. The species of the genera *Pilayella) Ectocarpus* and *Rhodomela* displayed the most pronounced negative effects on egg survival in the experiments carried out in 1987 and 1988.The cause of this negative effect is still unknown.

## INTRODUCTION

Observations made during two Baltic herring (*Clupea harengus* L.) spawning ground surveys in 1978 and 1982 revealed high natural mortalities of the eggs (Aneer and Nellbring 1982; Aneer 1985). Locally the mortalities reached 100% compared to $\leq$ 10% which has been considered normal (Hempel 1971). Similar observations have been made in the Finnish archipelagos by Oulasvirta et al.(1985) and also by Rajasilta and Eklund (pers. comm.). In the Finnish and Swedish cases, the egg occurrences were relatively sparse and seldom in denser aggregations. Higher mortalities have been found on European herring spawning grounds but they were normally found in connection with thick deposits of eggs (*e.g.* Baxter 1971; Blaxter and Holliday 1963; Galkina 1968, 1971; Rannak 1971). Similar observations have also been made in other geographical areas (*e.g.* Taylor 1971; Haegele and Schweigert 1985). Elmer (1983), Rannak (1971) and Scabell (1988) have noticed high mortalities in the Baltic area. Rajasilta and colleagues (pers. comm.) observed a probable connection between high mortalities and presence of red algae. This was not confirmed in their follow- up study.

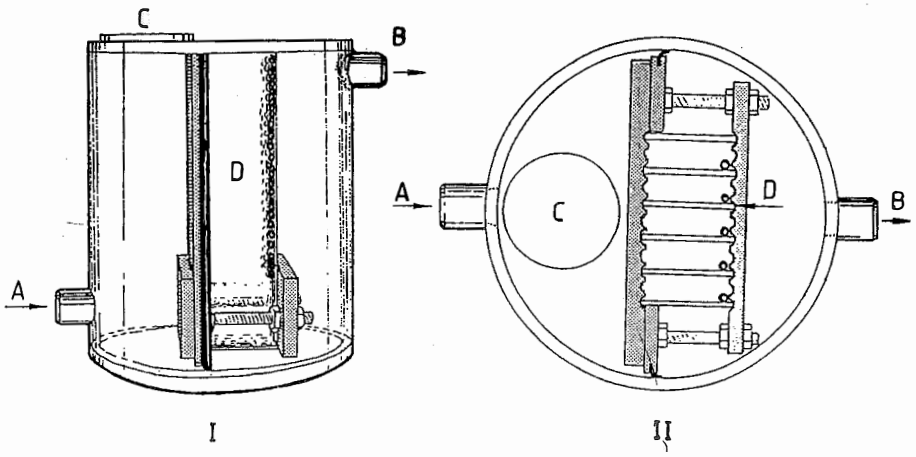
Laboratory experiments carried out by Aneer (1987) ruled out oxygen defficiency as the major cause of death and pointed towards algal exudates as a possible cause. The present paper presents results from laboratory experiments where a) the effect of different amounts of filamentous algae were studied as well as b) the effect of different algal species upon the mortality of Baltic herring eggs. The intention was also to see whether the seasonal mortality pattern observed *in situ* by Aneer (1985) could be reflected in the experiments.

## MATERIAL AND METHODS

Four experiments (June 23 – July 3, 1987 [1–87]; May 25 – June 8, 1988 [1–88]; June 8 – June 20, 1988 [2–88]; June 22 – July 1, 1988 [3–88]) with artificially fertilized Baltic herring eggs were carried out at the Askö Laboratory during the spring spawning season. The eggs were exposed to sea water that had passed a controlled amount of certain algae before reaching the test chambers. In each experiment, fresh eggs were obtained from a single, live, running female Baltic herring (*Clupea harengus* L.) 18.9 – 26.9 cm in length. Adult fish from the area around the laboratory (Lat. 58°49´N; Long. 17°39´E) were caught on hooks on the day of the start of each experiment. The eggs from the females were gently pressed out in a row on 35 wet microscope slides cooled to the temperature of the incoming sea water. On the average, 64.1 ± 22.3 (s.d.) (n = 140 slides) eggs were on each. The slides with eggs were not exposed to air for more than 15 s. After attaching the eggs to the slides, the latter were placed in a tray with fresh sea water cooled to ambient sea water temperature. A mixture of sperm and sea water was added and the water in the tray was gently stirred to ensure that sperm was well spread out over the entire tray. In each experiment the sperm was gently pressed out from 5–6 running, live, males (17.8 – 27.8 cm length range). After a 15- minute exposure to the sperm, the slides were placed in seven test chambers, 5 in each (Fig. 1A).

Fig. 1A. Experimental chamber for study of the survival of Baltic herring eggs subjected to exposure to sea water of different origins. A = water inlet. B = water outlet. C = hole for oxygen/temperature sensor (normally closed by a rubber stopper). D = microscope slide with herring eggs attached. I = lateral view. II = seen from above

Fig. 1B. Experimental set-up for test of influence of algae upon the survival of Baltic herring eggs. A = Filter for removal of particles in the incoming sea water. B = Columns for saturation of the sea water with oxygen (and nitrogen, exp. 1–87). D = container for distribution of saturated sea water to the control chambers (1+2) and to the closed containers with algae from which the sea water enters chambers 3–7. The chambers 1–7 contain the herring eggs (see also Fig. 1A). AF = Amberlit-filter for collection of probable exudates. L = timer-activated light source. ST = Oxygen and temperature meter. U = outlet for sea water. Note: The figure shows only one alga container and one Amberlit-filter. The set-up consists of five similar sets of containers and six filters. The other four/five are only hinted at (at D)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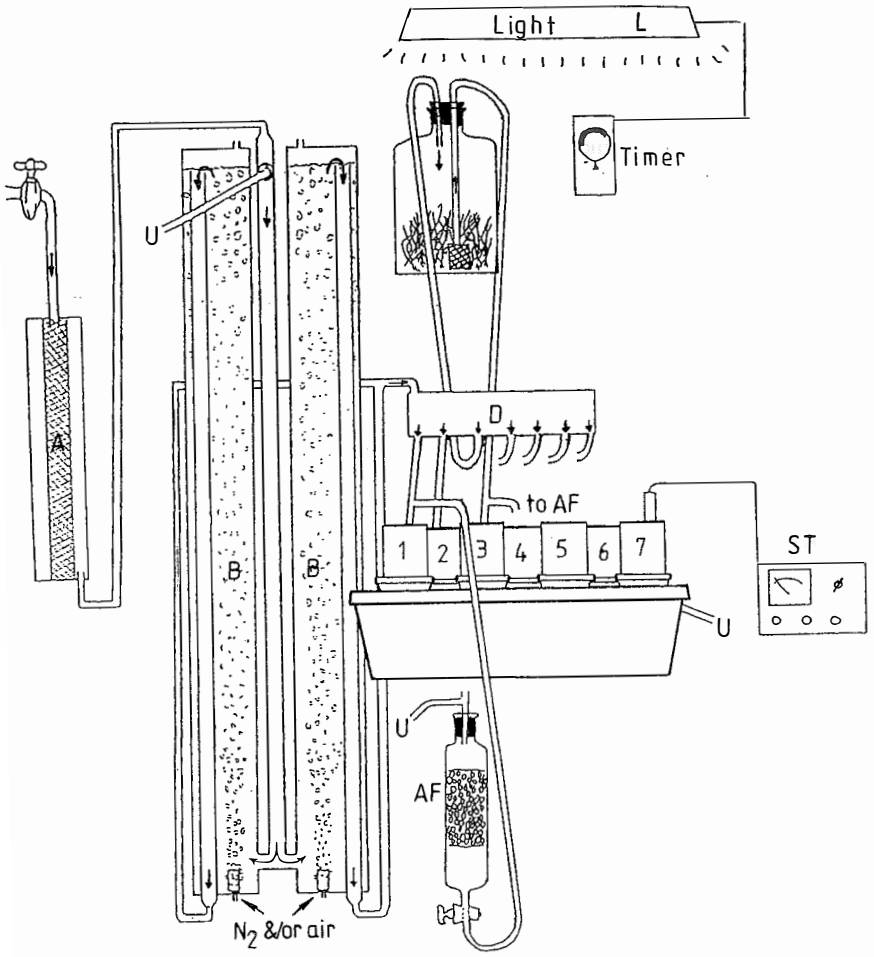
Light
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Figure 1B shows the set-up used in 1988. It was slightly different from that used in 1987 which has been principally described already by Aneer (1987). The test chambers were either controls (n = 2) or connected to a set of 10 $dm^3$ bottles (n = 5) in which freshly collected algae (*Pilayella littoralis/Ectocarpus siliculosus*) in different amounts (100, 300 and 1000 g wet weight) were kept in running sea water of 100% or 50% oxygen saturation (experiment 1–87, Fig. 2) or in which different algal species, collected in the field just prior to the experiments, were kept and through which running sea water passed on down to the test chambers (*Pilayella/Ectocarpus* 300 and 1000 g wet weight respectively, *Rhodomela confervoides, Ceramium tenuicorne,* and *Furcellaria fastigiata* 300 g wet weight respectively (experiments 1 to 3–88). Macrofauna and epiphytes had been removed from the algae as far as possible, but they did not get totally clean from these. Algae that were obviously decaying or under decomposition were not used. The algae were collected by a diver on the day before or on the starting day of each experiment.

Light came from timer-activated fluorescent tubes (2 Philips TL33, 4200°K) simulating the light environment at 4–5 m depth.

Incoming sea water with a salinity of about 6.5‰ was continuously pumped from a depth of about 17 m and not thermoregulated. A volume of about 0.7 $l/dm^3$/min passed the chambers. The incoming water was first filtered through a 300 µm plankton net and then passed on through a 10 $dm^3$ Perlon wool filter before reaching the $N_2$ and/or air saturation columns. Water passing the 10 $dm^3$ bottles was filtered (300 µm) on leaving the bottles. Oxygen content of the water was controlled daily using an YSI Model 57 Oxygen meter. Temperature was measured with a calibrated thermometer.

The flow of water through the experimental chambers was driven by hydrostatic pressure.

With the exception of experiment 1–87, the experiments lasted until all live eggs in the control chamber 1 had hatched (1 live egg remained in chamber 1 in experiment 1–88). Experiment 1–87 had to be terminated before complete hatching due to lack of time for experiments caused by the extremely delayed maturation of herring due to an unusually cold spring 1987.

The development and survival of eggs were generally controlled once a day using a WILD M5 dissecting microscope. The initial mortality was judged to be the sum of malformed, abnormal and undeveloped eggs 24 h after fertilization.

Statistical differences were tested using "differences between two means" (Dixon and Massey 1969, p. 119).

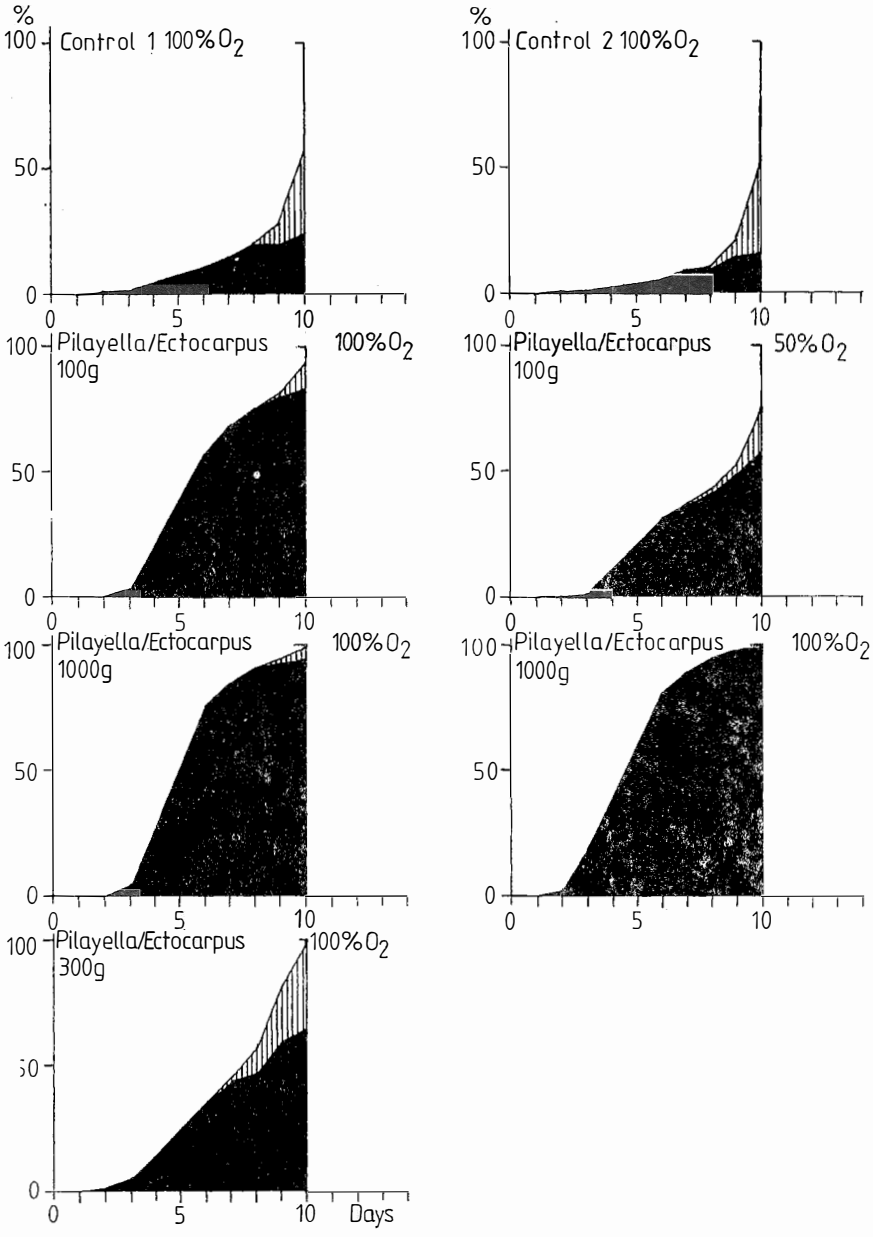


Fig.2. Experiment 1–87. Frequencies of live (white area), hatched (striped area) and malformed/dead (black area) Baltic herring eggs (in per cent of successfully fertilized eggs) which have been subjected to pure, air saturated sea water (controls 1 & 2) and combinations of different amounts of *Pilayella/Ectocarpus* and oxygen saturation levels

**Table 1**

Average temperatures and oxygen saturation levels in per cent of full saturation in the respective experiments together with standard deviations

Experiment 1–87 Temperature: 8.3°C ± 0.8 Range: 6.7°–10.3° (23 June – 3 July)

| | Oxygen saturation (%) |
|---|---|
| Chamber 1 | 97.2 ± 2.2 |
| 2 | 99.1 ± 2.2 |
| 3 | 96.2 ± 1.6 |
| 4 | 38.9 ± 2.8 |
| 5 | 93.7 ± 2.9 |
| 6 | 33.1 ± 12.5 |
| 7 | 91.9 ± 5.0 |

Experiment 1–88 Temperature: 9.3°C ± 1.2 Range: 7.8°–11.6°(25 May – 8 June)

| | Oxygen saturation (%) |
|---|---|
| Chamber 1 | 100.0 ± 1.3 |
| 2 | 101.2 ± 3.0 |
| 3 | 97.9 ± 2.9 |
| 4 | 95.9 ± 1.9 |
| 5 | 96.0 ± 3.3 |
| 6 | 97.4 ± 4.6 |
| 7 | 103.7 ± 4.4 |

Experiment 2–88 Temperature: 10.7°C ± 1.2 Range: 8.9°–12.2°(8 June – 20 June)

| | Oxygen saturation (%) |
|---|---|
| Chamber 1 | 101.1 ± 2.0 |
| 2 | 100.2 ± 2.9 |
| 3 | 97.0 ± 3.6 |
| 4 | 96.6 ± 3.6 |
| 5 | 99.1 ± 2.3 |
| 6 | 96.7 ± 5.3 |
| 7 | 102.1 ± 3.5 |

Experiment 3–88 Temperature: 13.9°C ± 0.6 Range: 12.8°–14.9° (22 June – 1 July)

| | Oxygen saturation (%) |
|---|---|
| Chamber 1 | 99.6 ± 2.0 |
| 2 | 96.2 ± 2.2 |
| 3 | 94.8 ± 1.6 |
| 4 | 89.3 ± 1.6 |
| 5 | 91.9 ± 3.2 |
| 6 | 91.6 ± 5.1 |
| 7 | 97.5 ± 1.9 |

## RESULTS

**Experiment 1–87.** The mortality was significantly higher in all chambers exposed to algal water compared to the controls (Fig. 2) with the exception of chamber 4. Chambers 3, 5, 6, and 7 all differed significantly from the controls at the 99.9% level (Table 2). Initial mean mortality was 8.6% ± 4.2 (s.d.). Temperature and oxygen saturation levels are presented in Table 1.

**Table 2**

Experiment 1–87. Test of the hypothesis that no differences existed between the final results in the different test chambers 1–7 [mortality in per cent of number of successfully fertilized eggs at the start of the experiment (Dixon and Massey 1969, p. 119)]. Table values denote the probability (p) for observed differences between the different treatments. *, **, and *** = significant at the 95%, 99%, and 99.9% level respectively. $\bar{x}$ denotes the respective final mean mortality in each test chamber.

| | 1 | 2 | 1+2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|---|
| $\bar{x}$ | 56.4 | 52.0 | 54.2 | 93.4 | 73.1 | 99.5 | 99.5 | 98.5 |
| s.d. | 7.5 | 25.2 | 17.7 | 4.3 | 18.3 | 1.1 | 1.1 | 1.0 |
| n | 5 | 5 | 10 | 5 | 5 | 5 | 5 | 5 |
| 1 Contr. 1 | – | | | | | | | |
| 2 Contr. 2 | 0.29 *** | – | | | | | | |
| 1+2 Contr. 1+2 | 0.27 *** | 0.14 *** | – | | | | | |
| 3 | 0.999 *** | 0.999 *** | 0.999 *** | – | | | | |
| 4 | 0.94 | 0.87 | 0.94 | 0.98 * | – | | | |
| 5 | 0.999 *** | 0.999 *** | 0.999 *** | 0.997 ** | 0.998 ** | – | | |
| 6 | 0.999 *** | 0.999 *** | 0.999 *** | 0.997 ** | 0.998 ** | 0.00 | – | |
| 7 | 0.999 *** | 0.999 *** | 0.999 *** | 0.990 ** | 0.997 ** | 0.87 | 0.87 | – |

Six days after fertilization, 80.4% of the successfully fertilized eggs were dead in chamber 6 (1000 g *Pilayella/Ectocarpus*, 50% $O_2$ saturation) and 75.8% in chamber 5 (1000 g *Pilayella/Ectocarpus*, 100% $O_2$ saturation). At the same time, the frequency of dead eggs was 58% in chamber 3 but did not exceed 35.2 in any of the other chambers. The oxygen levels were close to the planned levels (Table 1) but dropped to less than 20% (15.9–19.2%) in chamber 6 on day 7 (June 29) and remained low until the end of the experiment.

Table 2 presents the results of the statistical test. All treatment chambers but no. 4 differed significantly (at the 99.9% level) from the controls. Chamber 4 was close to significant at the 95% level.

**Experiment 1–88.** The mortality was considerably lower than in the previous experiment. On average, initial mortality was 8.1% ± 2.3 (s.d.), range 3.0–18.5%. Final mean mortality (of fertilized and normally developing eggs) did not exceed 13.5% (chamber 3, Fig. 3). Temperature and oxygen saturation levels are presented in Table 1.

The differences between the different treatments and the controls were not pronounced (Table 3). Chamber 3 differed significantly from control 2 and the sum of control 1 and 2 at the 99.9% and 99% levels respectively. Chamber 5 was significantly different from chambers 3 and 4.

The weights of the algae used in the experiment decreased due to decomposition/consumption by microfauna and – flora in the following way: *Pilayella/Ectocarpus* 260 to 140 g (–46.2%) and 1000 to 773 g (–22.7%) respectively, *Rhodomela* 270–183 g (–32.2%), *Ceramium* 300 to 170 g (–43.3%) and *Furcellaria* 300 to 253 g (–15.7%). This gives an average decrease in algal biomass (including microfauna) of 32.0% ± 13.1% (s.d.).

**Experiment 2–88.** As in the previous experiment, the mortality was markedly lower than in the 1987 experiment. The oxygen saturation and temperatures are shown in Table 1. Only the treatments with *Rhodomela* and *Pilayella/Ectocarpus* 1000 g differed significantly from the controls. The latter of the two treatments differed significantly from all the other chambers (Table 4). (Fig. 4).

The weight decrease of algae was as follows: Chamber 3 from 300 to 71 g (–76.3%), chamber 4 260 to 200 g (–23.1%), chamber 5 300 to 196 g (–34.7%), chamber 6 1000–532 g (–46.8%) and chamber 7 325 to 252 g (–22.5%). An average decrease was 40.7% ± 22.3% (s.d.).

**Experiment 3–88.** A break in the sea water supply occurred on day 4. It lasted for a couple of hours and left chamber 3 (*Pilayella/Ectocarpus* 300 g) without water but affected also chamber 4. Temperature and oxygen saturation levels are given in Table 1.

Only *Pilayella/Ectocarpus* 300 g and *Rhodomela* were significantly different from both the controls. They were also significantly different from the other treatments. Chambers 5–7 differed significantly from control 1 and chambers 3 and 4 (Table 5).

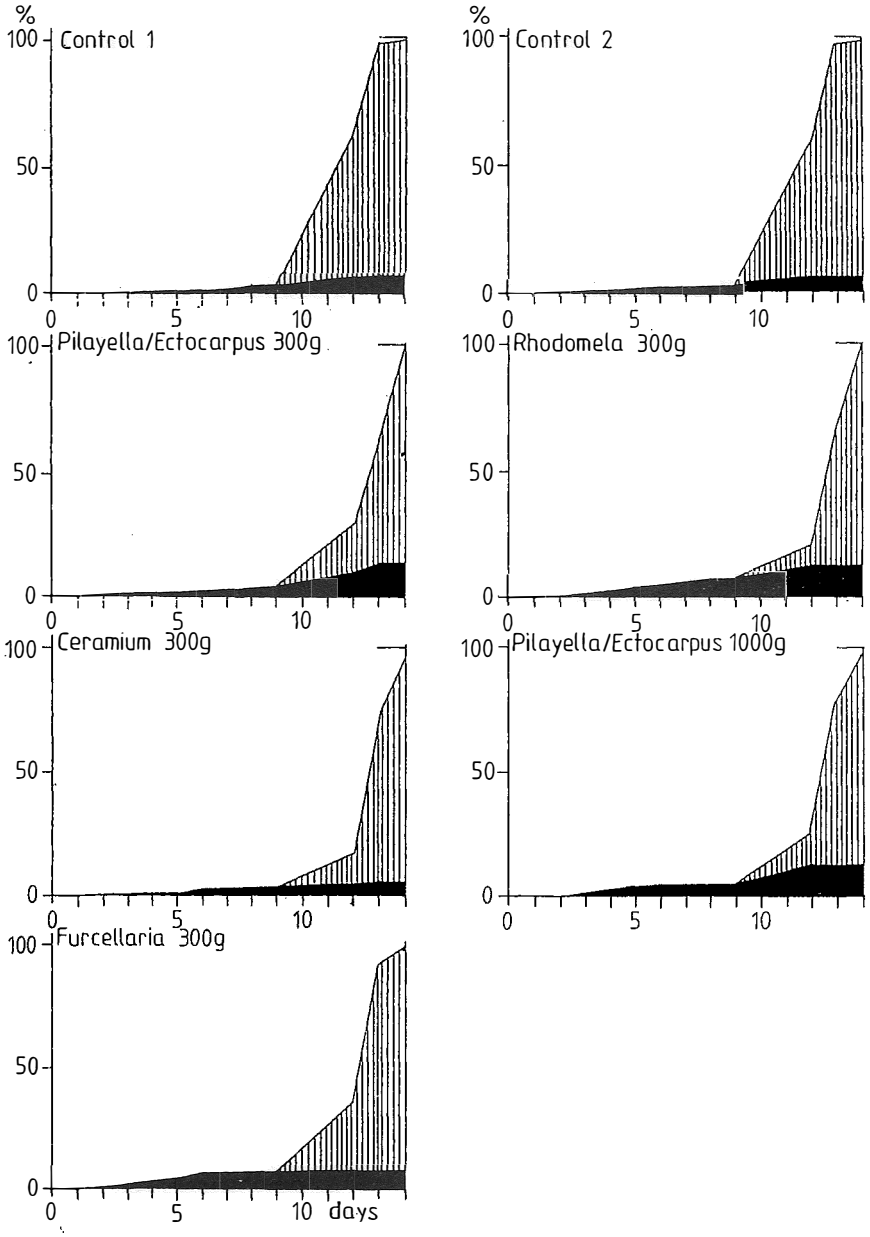


Fig. 3. Experiment 1—88. Frequencies of live (white area), hatched (striped area) and malformed/dead (black area) herring eggs (in per cent of successfully fertilized eggs) in an experiment where the eggs have been subjected to pure, oxygen saturated sea water (controls 1 § 2) or saturated sea water which has passed different species of common spawning substratum algae before reaching the eggs

**Table 3**

Experiment 1–88. Test of the hypothesis that no differences existed between the final results in the different test chambers 1–7 [ mortality in per cent of number of successfully fertilized eggs at the start of the experiment (Dixon and Massey 1969, p. 119) ]. Table values denote the probability (p) for observed differences between the different treatments. *, **, and *** = significant at the 95%, 99%, and 99.9% level respectively. $\bar{x}$ denotes the respective final mean mortality in each test chamber.

| | 1 | 2 | 1+2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|---|
| $\bar{x}$ | 7.0 | 5.3 | 6.2 | 13.5 | 12.5 | 5.9 | 12.5 | 7.4 |
| s.d. | 10.9 | 1.5 | 7.4 | 3.2 | 5.3 | 4.5 | 8.6 | 6.4 |
| n | 5 | 5 | 10 | 5 | 5 | 5 | 5 | 5 |
| 1 Contr. 1 | – | | | | | | | |
| 2 Contr. 2 | 0.27 | – | | | | | | |
| 1+2 Contr. 1+2 | 0.11 | 0.29 | – | | | | | |
| 3 *Pil./Ect.* 300 g | 0.80 | 1.00 *** | 0.99 ** | – | | | | |
| 4 *Rhodomela* | 0.69 | 0.996 ** | 0.94 | 0.28 | – | | | |
| 5 *Ceramium* | 0.16 | 0.22 | 0.07 | 0.997 ** | 0.97 * | – | | |
| 6 *Pil./Ect.* 1000 g | 0.62 | 0.93 | 0.83 | 0.19 | 0.00 | 0.87 | – | |
| 7 *Furcellaria* | 0.05 | 0.52 | 0.25 | 0.94 | 0.83 | 0.33 | 0.71 | – |

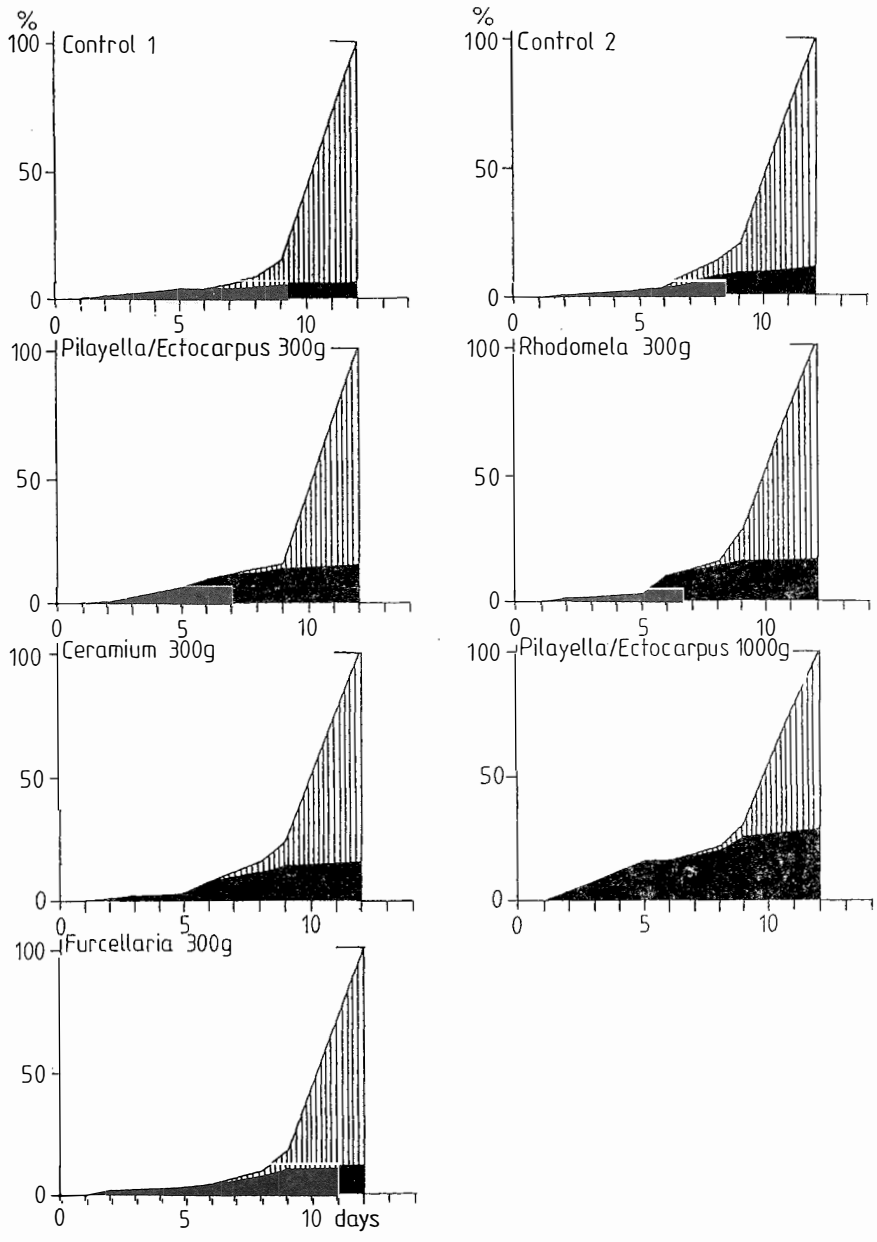


Fig. 4. Experiment 2–88. Frequencies of live (white area), hatched (striped area) and malformed/dead (black area) herring eggs (in per cent of successfully fertilized eggs) in an experiment where the eggs have been subjected to pure, oxygen saturated sea water (controls 1 & 2) or saturated sea water which has passed different species of common spawning substratum algae before reaching the eggs

**Table 4**

Experiment 2–88. Test of the hypothesis that no differences existed between the final results in the different test chambers 1–7 [ mortality in per cent of number of successfully fertilized eggs at the start of the experiment (Dixon and Massey 1969, p. 119)] . Table values denote the probability (p) for observed differences between the different treatments. *, **, and *** = significant at the 95%, 99%, and 99.9% level respectively. $\bar{x}$ denotes the respective final mean mortality in each test chamber

| | 1 | 2 | 1+2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|---|
| $\bar{x}$ | 5.9 | 11.1 | 8.5 | 13.4 | 15.9 | 14.2 | 28.2 | 11.4 |
| s.d. | 5.8 | 9.2 | 7.8 | 8.3 | 2.8 | 6.1 | 10.5 | 8.0 |
| n | 5 | 5 | 10 | 5 | 5 | 5 | 5 | 5 |
| 1 Contr. 1 | – | | | | | | | |
| 2 Contr. 2 | 0.71 | – | | | | | | |
| 1+2 Contr. 1+2 | 0.90 | 0.41 | – | | | | | |
| 3 *Pil/Ect.* 300 g | 0.90 | 0.41 | 0.72 | – | | | | |
| 4 *Rhodomela* | 0.999 *** | 0.73 | 0.992 ** | 0.47 | – | | | |
| 5 *Ceramium* | 0.77 | 0.46 | 0.87 | 0.14 | 0.42 | – | | |
| 6 *Pil./Ect.* 1000 g | 1.00 *** | 0.993 ** | 0.999 *** | 0.986 * | 0.989 * | 0.990 ** | – | |
| 7 *Furcellaria* | 0.787 | 0.04 | 0.78 | 0.30 | 0.765 | 0.466 | 0.995 ** | – |

Generally, the mortality was low with the exception of chambers 3 and 4 which both showed an increased mortality (Fig. 5).

Table 5

Experiment 3–88. Test of the hypothesis that no differences existed between the final results in the different test chambers 1–7 [mortality in per cent of number of successfully fertilized eggs at the start of the experiment (Dixon and Massey 1969, p. 119)]. Table values denote the probability (p) for observed differences between the different treatments. *, **, and *** = significant at the 95%, 99%, and 99.9% level respectively. $\bar{x}$ denotes the respective final mean mortality in each test chamber

| | 1 | 2 | 1+2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|---|
| $\bar{x}$ | 0.3 | 6.8 | 3.5 | 60.0 | 26.7 | 10.0 | 4.5 | 9.2 |
| s.d. | 0.9 | 12.9 | 9.2 | 31.9 | 7.6 | 10.9 | 3.7 | 6.2 |
| n | 5 | 5 | 10 | 5 | 5 | 5 | 5 | 5 |
| 1 Contr. 1 | – | | | | | | | |
| 2 Contr. 2 | 0.74 | – | | | | | | |
| 1+2 Contr. 1+2 | 0.72 | 0.39 | – | | | | | |
| 3 *Pil./Ect.* 300 g | 1.00 *** | 0.999 *** | 0.999 *** | – | | | | |
| 4 *Rhodomela* | 1.00 *** | 0.997 ** | 1.00 *** | 0.97 * | – | | | |
| 5 *Ceramium* | 0.95 * | 0.32 | 0.74 | 0.999 *** | 0.995 ** | – | | |
| 6 *Pil./Ect.* 1000 g | 0.986 * | 0.29 | 0.23 | 1.00 *** | 1.00 *** | 0.714 | – | |
| 7 *Furcellaria* | 0.998 ** | 0.28 | 0.84 | 1.00 *** | 1.00 *** | 0.113 | 0.855 | – |

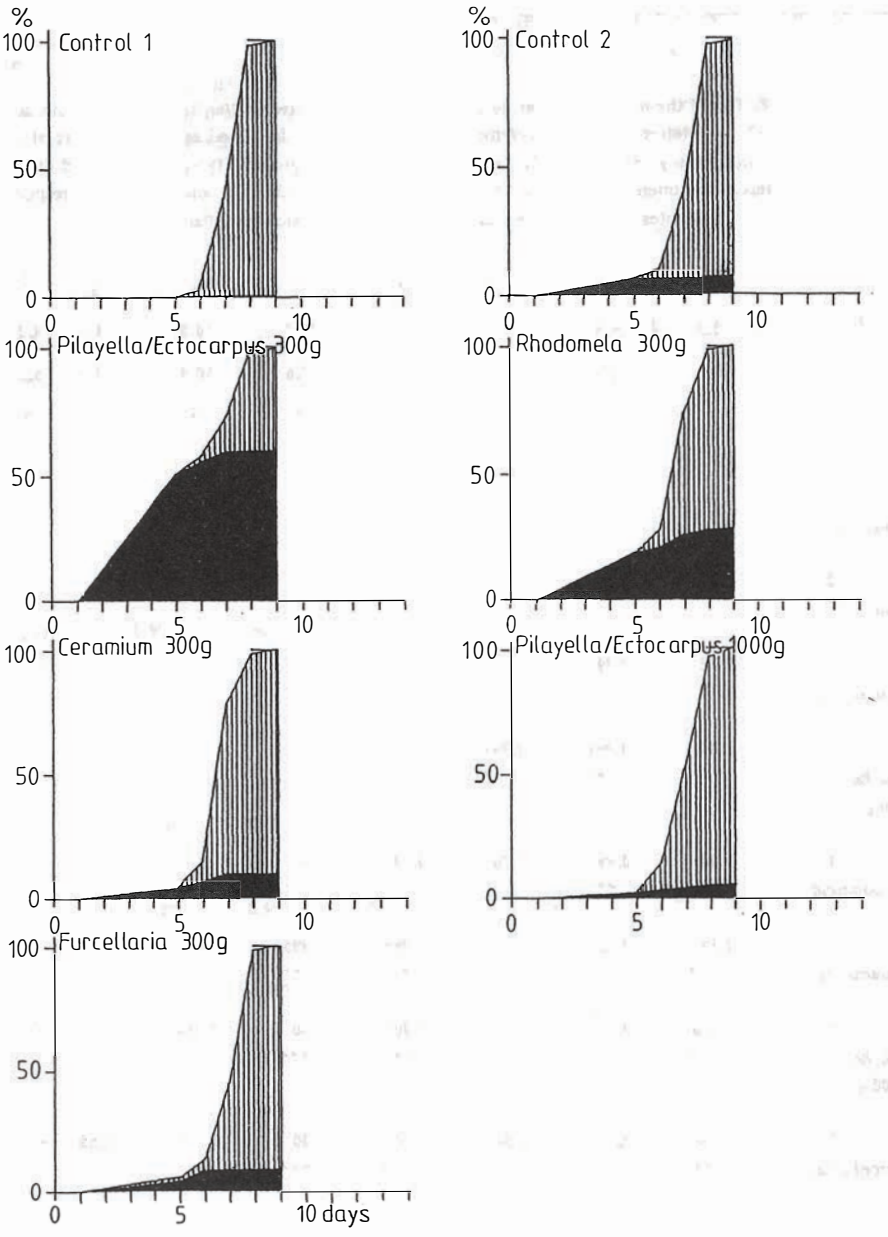


Fig. 5. Experiment 3–88. Frequencies of live (white area), hatched (striped area) and malformed/dead (black area) herring eggs (in per cent of successfully fertilized eggs) in an experiment where the eggs have been subjected to pure, oxygen saturated sea water (controls 1 & 2) or saturated sea water which has passed different species of common spawning substratum algae before reaching the eggs

The algae in the treatment chambers decreased in weight according to the following: chamber 3 300 to 174 g (−42.0%), chamber 4 300 to 260 g (−13.3%), chamber 5 300 to 175 g (−41.7%), chamber 6 1000 to 674 g (−32.6%) and chamber 7 250 to 237 g (−5.2%). This gives an average weight decrease of 27.0% ± 16.8% (s.d.) of the algae.

**Table 6**

Test of the hypothesis that no differences existed in the individual chambers between experiments 1–88, 2–88 and 3–88. The table values denote the probability (p) for observed differences between the three different experiments (Dixon and Massey 1969, p. 119). *, **, and *** = significant at the 95%, 99%, and 99.9% level respectively

| | 1 | 2 | 1+2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|---|
| 1–88/2–88 | 0.16 | 0.84 | 0.50 | 0.02 | 0.80 | 0.986 * | 0.990 ** | 0.62 |
| 1–88/3–88 | 0.83 | 0.20 | 0.53 | 0.999 *** | 0.999 *** | 0.56 | 0.94 | 0.35 |
| 2–88/3–88 | 0.967 * | 0.46 | 0.81 | 1.00 *** | 0.997 ** | 0.55 | 1.00 *** | 0.37 |

Table 6 shows that chambers 5 and 6 differed significantly between experiment 1 and 2 in 1988. It also shows that chambers 3 and 4 were significantly different between experiment 1 and 3 during the same season. When comparing experiments 2 and 3 in 1988 it becomes evident that chambers 3 and 4, as well as chamber 6, differed significantly. The significance for chambers 3 and 4 can be ascribed to the technical disturbance during experiment 3–88. The final mortality in chamber 6 in 1988 was highest during experiment 2.

## DISCUSSION

The experiments presented in this paper, as well as those in Aneer (1987), show that the presence of certain algae has a direct negative impact on the survival of Baltic herring eggs.

The clear differences in mortality rates between the 1987 (very high) and the 1988 experiments (not very high) were probably due to a higher dilution of causative agents during the latter year. When the chemical filters were introduced (Fig. 1B) in 1988 it was necessary to increase the total amount of water flowing through the bottles with algae in order to keep the current speed of water the same in the egg chambers as in previous experiments (Aneer 1987 and experiment 1–87). A presence of exudates or other water transmitted agents (microflora and/or -fauna) in the water from these containers should then have been reduced to about half of the amounts in the 1987 experiment. Such a decrease ought to reduce the negative effects if there is a direct

dose-response relationship. It was evident that the algae had a flora and fauna of microorganisms. Some of these, *e.g.* diatoms but also microfauna passed the 300 µm filters in the algae containers and entered the experimental chambers. This could be seen when the microscope slides with eggs were studied under a dissecting microscope. Effects of the microflora/-fauna on the eggs have not been studied separately and are not known. It is not know either what the effects are of the gradual, but relatively strong (on the average 33%), breakdown of the algae during the experiments. Is the breakdown of the same order of magnitude *in situ*? This has not been studied. *Pilayella* and *Ectocarpus*, at least, are under partial decomposition *in situ* at this time of year (Aneer and Nellbring 1982).

It is unfortunate that the presence of exudates could not be investigated owing to lack of funds.

Besides observations by Aneer and Nellbring (1982) and Aneer (1985, 1987), Oulasvirta et al. (1985) and Rajasilta with colleagues (pers. comm.) have also observed high frequencies of dead Baltic herring eggs in connection with relatively sparse egg occurrencies. In the case of Oulasvirta et al. (1985) they speculated about low oxygen content, "an unfavourable environment for the eggs", and/or a combination of a high temperature and a subsequent rapid drop in temperature in their study area. Low oxygen content was ruled out by Aneer (1987) as the major cause of the observed mortality following results from laboratory experiments and field measurements. Still, it is clear that very low (below 25%), constant oxygen saturation levels definitely also have a marked effect upon malformations and mortality (Braum 1973; Aneer 1987). In this connection temperature also plays a role. Higher temperatures mean that the oxygen saturation levels need to be higher to avoid increased mortality.

Several algae are known to produce a number of more or less toxic compounds in order to affect microorganisms, other plants (Rice 1984) or animals (*e.g.* to prevent herbivores from grazing them too heavily) (Van Alstyne 1988; Hay and Fenical 1988). A study by Hornsey and Hide (1974) on the production of antimicrobial compounds in British marine algae showed *Rhodomela confervoides* to be a producer of antibiotics while *Furcellaria fastigiata, Ceramium rubrum, Ectocarpus siliculosus* and *Pilayella littoralis* showed doubtful or no activity. But, as the authors used only bacteria as test organisms, this does not rule out the possibility that other organisms are affected differently by the different kinds of compounds the algae produce. Not only antibiotics, but also for example brominated phenols, monoterpenes, polyphenolics, and other more or less toxic substances are produced (Hay and Fenical 1988). *Pilayella littoralis*, for instance, has been shown to produce toxic substances while decomposing in huge amounts entrapped in sandy beaches (Quinlan et al. 1983). The toxic substances were not known.

Although not demonstrated clearly enough in experiment 1–87, there seems to be some sort of relation between the mortality of eggs and the amounts of algae. The

chamber with high oxygen saturation and 100 g of *Pilayella/Ectocarpus* showed a higher mortality than the corresponding chamber with only 50% saturation. The experiments made in 1988 failed, too, to give a clear picture of such a relation. Experiments 1–88 and 2–88 indicate such a relationship, but the pattern is broken by experiment 3–88. The lack of replicates makes it difficult to explain these observed differences.

The seasonal mortality pattern observed *in situ* by Aneer (1985) was not clearly reflected in the 1988 experiments. There are indications of such a pattern in the final mean mortalities for chambers 5–7 (Figs. 3–5 and Tables 3–5), but the technical disturbance affecting chambers 3 and 4 during experiment 3–88 impedes the overall interpretation.

It is possible that the collection of algae in the field and the subsequent sorting of the material before starting the experiments led to an unintentional and unnatural selection of algal material favouring algae that were not representative for the conditions of the respective algal communities in the sea, *i.e.* too healthy algae could have been selected. The possible effects of such an unintentional sorting could lead to biased results. In this context it is also impossible to judge possible effects of the picking, handling, and keeping of the algae before and during the experiments.

Dead eggs, after having been dead for about 24 hours or more, frequently became fungus-infected. In some cases it was evident that the fungus spread from dead eggs to live ones but at the same time it was also evident that some eggs with live embryos could withstand fungus attacks from neighbouring eggs. The egg capsule of herring eggs is relatively thick with a solid central layer (Odense and Rosenthal 1986; Rosenthal and Odense 1986) which makes it less probable that fungal infection shall take place inside the egg capsule (Messieh and Rosenthal 1989). In my opinion, it seems that the fungus effects on the eggs studied in this study were secondary effects on eggs that were already weakened or dead by other factors.

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