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Lethal effect of filamentous algal blooms on Atlantic herring (*Clupea harengus*) eggs in the Baltic Sea

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Abstract

1. During this study, the effects of epiphytic filamentous algae on the survival of demersal spawned fish eggs were investigated in one of the most important spawning grounds of herring in the western Baltic Sea, which is subject to intense and ongoing eutrophication.
2. In coastal marine ecosystems all over the world, eutrophication is a primary water quality issue, often resulting in mass developments of bloom-forming algae. Macro-algal blooms have immense ecological effects, as they alter the structure and the function of an ecosystem. Numerous fish species are affected, as they depend on those coastal areas for spawning and as juvenile habitats.
3. A comparison of the survival of herring eggs on two natural spawning beds revealed an immense impact of a filamentous algal bloom. The mortality rate reached nearly 100% in the area with massive occurrence of filamentous brown algae.
4. Hypothesizing that the presence of filamentous algae facilitates herring egg mortality, field and laboratory experiments were conducted and revealed particular effects of distinct algal species. The survival rate of artificially spawned eggs on algal substrates and control substrates was compared. Whereas filamentous forms of the green alga *Ulva intestinalis* induced no immediate effect, significantly higher egg mortality was documented in experiments with the filamentous brown alga *Pylaiella littoralis*.
5. Considering the ecological and economical importance of herring and other coastal spawners on the one hand and the persisting and increasing effects of eutrophication and climate change on the other hand, the results of our study clearly underpin the necessity to increase global efforts to reduce nutrient loads in coastal waters.

KEYWORDS

algae mats, coastal eutrophication, demersal spawn, epiphytes, fish egg mortality, *Pylaiella littoralis*, *Ulva intestinalis*

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1 | INTRODUCTION

Coastal waters, lagoons, and estuaries are ecosystems that are highly influenced by human activities around the world. At the same time, the littoral zone is a habitat inhabited by several life stages of diverse aquatic flora and fauna. Many fish species, for example, depend on those areas for spawning and as juvenile habitats. However, factors like coastal modification, cultivation, and eutrophication are ubiquitous and can lead to severe habitat degradation.

Smith and Schindler (2009) postulated that eutrophication has become the primary water quality issue for most of the freshwater and coastal marine ecosystems in the world, and their position was supported by a number of other studies (e.g. European Environment Agency, 2015; Howarth, 2008; Nixon, 1995; Selman, Greenhalgh, Diaz, & Sugg, 2008). A major consequence of eutrophication is an increasing abundance but decreasing diversity of aquatic vegetation (Rabalais, 2002; Worm, Lotze, Hillebrand, & Sommer, 2002). Nitrogen enrichment stimulates an accelerated nutrient uptake, faster growth, and more frequent blooms (Bricker et al., 2008; Gorgula & Connell, 2004; Teichberg et al., 2010; Teichberg, Martinetto, & Fox, 2012), resulting in a limited depth distribution of benthic vegetation because of reduced light penetration, overgrowth, and shading of perennial macrophytes by epiphytes (Burkholder, Tomasko, & Touchette, 2007; Duarte, 1995; Kautsky, 1991; Orth et al., 2006; Taylor, Nixon, Granger, & Buckley, 1995; Valiela et al., 1997; Vogt & Schramm, 1991). Reports on 'harmful algal blooms' related to microalgae species and their effects on aquatic organisms, especially fish, are numerous (reviewed by Anderson, Cembella, & Hallegraeff, 2012; Landsberg, 2002), but they are scarce with regard to macroalgae.

The focus of this study is the effect of macroalgal blooms on fish eggs, and thus considers a previously rather neglected aspect of eutrophication. Valiela et al. (1997) summarized that harmful effects of macroalgal blooms differ from microalgal blooms as they usually do not release toxic substances. However, those blooms last longer and have major ecological effects, as they alter the structure and the function of affected ecosystems. For example, early life stages of fish are severely influenced by such habitat changes (Caddy, 2007). Green-tide-affected sites are reported to be less favourable nursery grounds because of high macroalgal density (Le Luherne et al., 2017). The effects on juvenile fish were investigated in the Baltic Sea (Jokinen, Wennhage, Ollus, Aro, & Norkko, 2016) and Skagerrak (Pihl, Modin, & Wennhage, 2005) and revealed a negative effect of increasing vegetation cover and macroalgal blooms respectively on different flatfish species developing in coastal areas. However, the effect on fish species spawning their benthic eggs directly on aquatic vegetation in shallow coastal areas has not yet been comprehensively investigated, even though those 'stationary' eggs are especially highly vulnerable to changes in their immediate environment. This study focuses on herring (*Clupea harengus*), an important component of oceanic food webs and an important fishery resource, and thereby an ideal model organism for evaluating wide-ranging eutrophication-linked effect chains. Exudates of the filamentous brown algae *Pylaiella littoralis* were assumed to have a toxic impact on herring eggs (Aneer, 1987).

However, during that laboratory study, the algal effect was not found to be particularly pronounced, and the transferability of results to natural spawning grounds has not been tested. This reveals the lack of specific knowledge regarding the effect of filamentous algae on the survival of fish eggs. During recent years, the local climate in the western Baltic Sea has changed from several weeks of ice cover to long periods of mild water temperatures in winter, which is promoting early and massive occurrence of *P. littoralis* (Kiirikki & Lehvo, 1997), thereby expanding the period of herring egg and algae overlap (L. von Nordheim, personal observation). Such synergistic effects of changing climate and eutrophication might have severe impacts on future ecosystem functioning and underlines the need for reliable information on the full set of consequences of eutrophication-linked macroalgal blooms.

This study focuses on two algal species (*P. littoralis* and *Ulva intestinalis*) that are known to form massive spring blooms (Raffaelli, Raven, & Poole, 1998; Salovius & Bonsdorff, 2004) and which are used as spawning substrate by herring (Aneer & Nellbring, 1982; Kääriä, Rajasilta, Kurkilahti, & Soikkeli, 1997). Hypothesizing that the presence of filamentous algae increases herring egg mortality, we compared the survival of eggs on natural spawning grounds affected and unaffected by a filamentous brown algal bloom. Additionally, we conducted field and laboratory experiments, testing the effect of the filamentous brown alga *P. littoralis* and a filamentous form of the green alga *U. intestinalis* on herring egg survival.

2 | MATERIAL AND METHODS

The study was conducted in the 'Greifswalder Bodden' lagoon, a major spawning and nursery area of western Baltic spring-spawning herring (Biester, 1989; Polte, Kotterba, Moll, & von Nordheim, 2017). This shallow brackish lagoon in the western Baltic Sea (Figure 1) covers an area of 514 km², has an average depth of 5.8 m (maximum 13.5 m), salinity ranges between 7 and 8 (Schiewer, 2001), and pH values vary between 8.0 and 8.5 during the spring herring spawning season. The lagoon is regularly covered by ice shields in winter, and in summer the water temperatures regularly rise above 20 °C. In spring, the water column is mostly well mixed, with oxygen levels remaining close to saturation (100%); and the almost exclusively wind-driven fluctuations in sea level vary from zero up to 1.5 m (Stigge, 1989).

The Greifswalder Bodden is affected by high nutrient levels (mean values 2007–2012: total nitrogen (N) 48.65 µmol L⁻¹ and total phosphorus (P) 1.61 µmol L⁻¹) above thresholds (total N 17.7 µmol L⁻¹ and total P 0.59 µmol L⁻¹) to achieve a 'good ecological status' (Bund/Länder-Ausschuss Nord und Ostsee, 2014; Federal Ministry for the Environment, Nature Conservation and Nuclear Safety, 2018). After a vegetation shift from a macrophyte-dominated to a phytoplankton-dominated system during the second half of the last century, the present vegetation is a mixture of marine, brackish, and freshwater species with perennial macrophytes limited to shallow areas of less than 3.5 m water depth (Kanstinger et al., 2018; Munkes, 2005).

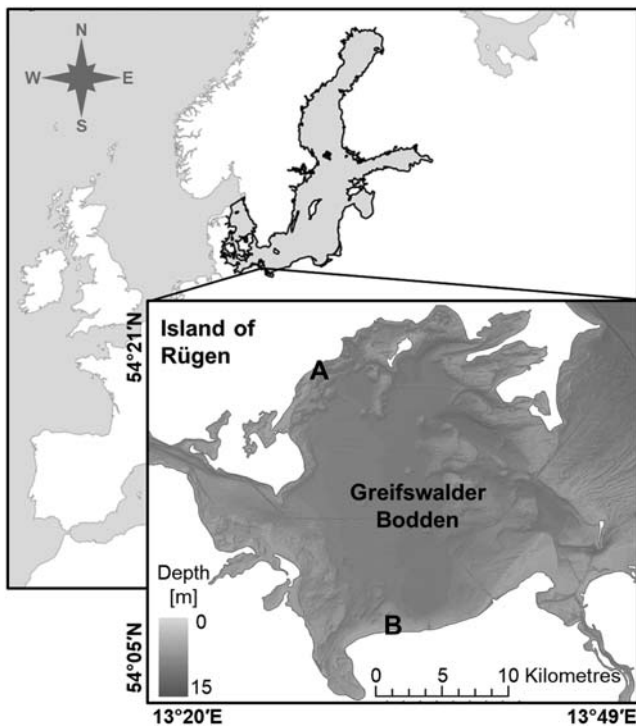


FIGURE 1 Investigation area 'Greifswalder Bodden' and its location in the Baltic Sea (framed in black) with relevant locations for the experiments (A and B). Bathymetry data: received by courtesy of Federal Maritime and Hydrographic Agency of Germany

2.1 | Experiments

Three different experimental set-ups were used to investigate potential lethal effects of filamentous algae. In all experiments, the survival rates of artificially spawned herring eggs (see Section 2.3) were determined as standardized values. Filamentous algae effects on selected spawning grounds were investigated by incubating eggs spawned onto different macrophytes (no epiphyte species) at two different natural spawning grounds, of which one was affected by a filamentous algal bloom. The following experiments were then carried out to examine whether direct egg–algae contact plays a role or whether the mere presence of the filamentous algae has an indirect influence. In field experiments on filamentous algal effects, herring eggs were

spawned directly on filamentous algae (*P. littoralis* and *U. intestinalis*) and control substrates and the survival rates were compared (direct effect). In laboratory experiments on filamentous algal effects, direct effects of the same filamentous algae were tested similar to the field experiments and an additional 'indirect' treatment was included with eggs spawned on the control substrate and filamentous algae added to the aquarium water (direct and indirect effects) (Figure 2).

2.2 | Collection of spawning substrates

Macrophytes and algae, used as spawning substrates in the experiments, were collected by snorkelling in 1–1.5 m deep water in Greifswalder Bodden (Figure 1, locations A and B). In all set-ups, pieces of nylon netting ($3 \times 11 \text{ cm}^2$, mesh size 4 mm) were used as a physiologically non-active control, hereinafter referred to as 'neutral substrate', allowing comparison between different experiments. Experiments on the effects of dominant filamentous algae on herring egg mortality were conducted in two consecutive years. In spring 2016, the filamentous brown alga *P. littoralis* was collected at location B, and in 2017 the filamentous green alga *U. intestinalis* was collected at location A. In both years, the algae were separated from other plant material, rinsed in habitat water, and stored in aerated barrels until they were deployed in the experiments on the next day.

2.3 | Artificial spawning

During the spring spawning season, ripe herring were caught in Greifswalder Bodden with gill nets on board a research vessel. Mature fish were used to artificially spawn eggs onto different substrates. The different substrates were subsequently placed into a dish filled with habitat water, and female herring were strip spawned onto their surface. When substrates were consistently covered with single egg layers, they were fertilized in buckets containing a seawater–sperm mixture of the mixed milt of 10 males. Potential parental effects that might influence the fitness of embryos (Geffen & Nash, 2012) were reduced by using eggs of one female for only one replicate of each treatment, whereas the sperm mixtures (each derived from multiple males) were used for a maximum of three replicates. After 10 min

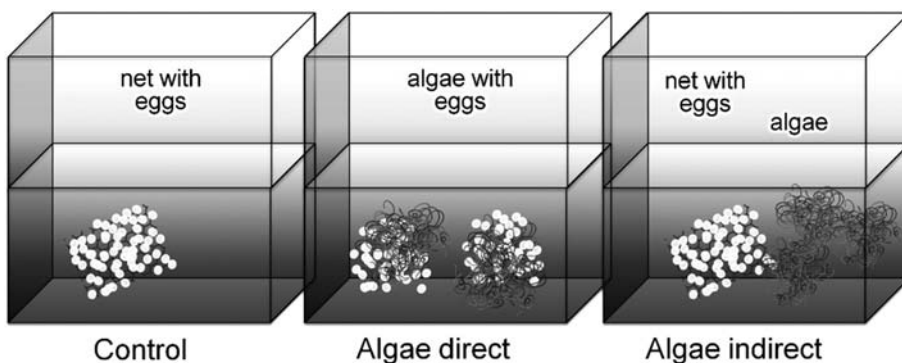


FIGURE 2 Experimental treatments: substrates that were added into the aquaria/cages to analyse the direct and indirect effects of algae on herring eggs ('net' was used as neutral substrate)

fertilization time the substrates with attached eggs were rinsed with seawater and transported to the respective experimental sites (field and laboratory) on the same day.

2.4 | Experimental periods

For all experiments, degree-days ($^{\circ}\text{d}$) were used as a unit to standardize the egg development stages among experiments run under slightly different temperature conditions and were calculated by multiplying temperature ($^{\circ}\text{C}$) with egg developmental time (days) (Apstein, 1909; Klinkhardt, 1996; Peck, Kanstinger, Holste, & Martin, 2012). The duration of the experiments was adjusted to weather conditions and water temperatures, as most herring larvae hatch between $^{\circ}\text{d}$ 90 and $^{\circ}\text{d}$ 120 (Peck et al., 2012), and samples of each replicate were regularly taken (see Section 2.8) at the beginning (until $^{\circ}\text{d}$ 30), after half of the developmental time ($^{\circ}\text{d}$ 45– $^{\circ}\text{d}$ 56) and at the end ($^{\circ}\text{d}$ 85– $^{\circ}\text{d}$ 92, before larvae hatch) of the experiments.

2.5 | Filamentous algae effects on selected spawning grounds

In 2016, field experiments on the survival of herring eggs were conducted on two different locations in Greifswalder Bodden (Figure 1, locations A and B). On the southern coast of the bay (location B: Gahlkow), filamentous algae were abundant (in particular, the brown alga *P. littoralis*) and on the northern shore (location A: close to Altkamp), filamentous algae were scarce. Both locations were compared regarding the percentages of dead herring eggs (21 replicates: seven units of four plant species). To reproduce natural conditions as much as possible, different macrophyte species that are naturally frequented by spawning herring (*Fucus vesiculosus*, *Furcellaria lumbricalis*, *Zostera marina*, *Stuckenia pectinata*) were used as substrates. The macrophytes were artificially covered with eggs (see Section 2.3), installed in the field at locations A (start: 27 April 2016; duration: 8 days; water: temperature 7–13 $^{\circ}\text{C}$, salinity around 7.9, and pH around 8.3) and B (start: 14 April 2016; duration: 8 days; water: temperature 9–10 $^{\circ}\text{C}$, salinity around 7.5, and pH around 8.3), and sampled three times: 1 day after fertilization, at $^{\circ}\text{d}$ 45, and at $^{\circ}\text{d}$ 80.

During the experiment, dissolved oxygen was continuously measured in the water column at both locations. To analyse diurnal fluctuations of oxygen due to photosynthesis or respiration, data were separated into daytime values (4:00 a.m.–6:00 p.m. UTC) and nighttime values (6:00 p.m.–4:00 a.m. UTC) respectively.

2.6 | Field experiments on algal effects on egg survival

Herring eggs were attached directly to specific filamentous algae or to a neutral substrate as control and incubated in gauze cages (cubical

metal frames, edge length 10 cm, covered with 500 μm gauze) in the field. Each replicate was stored in a separate cage, protecting the eggs from predation and at the same time keeping the experiment positioned close to natural spawning beds (Greifswalder Bodden, location A) on the seafloor at 1 m water depth. A data logger (PME miniDO₂T Logger) was mounted beside the set-up for continuous monitoring of dissolved oxygen and water temperature.

The *P. littoralis* approach was installed in the field ($n = 9$) on 27 April 2016 for a duration of 8 days, with water temperatures from 9 to 13 $^{\circ}\text{C}$, a salinity of 7.9, and pH 8.3. Samples were taken 1 day after spawning, at $^{\circ}\text{d}$ 55, and shortly before hatch at $^{\circ}\text{d}$ 92.

The *U. intestinalis* approach was started on 13 April 2017 and ran 10 days at water temperatures between 8 and 9 $^{\circ}\text{C}$, a salinity of 7.8, and pH 8.4. Samples were taken 1 day after spawning, at $^{\circ}\text{d}$ 43, and shortly before hatch at $^{\circ}\text{d}$ 85. Unfortunately, some of the cages were washed away by heavy wave action during a storm event; accordingly, the number of replicates was reduced to $n = 4$.

2.7 | Laboratory experiments on algal effects on egg survival

Substrates with artificially attached herring eggs were incubated in aerated aquaria with 2 L of habitat water and a natural day–night rhythm of sunlight. Each replicate of a substrate type was incubated in a separate aquarium, and abiotic parameters were monitored every 1–3 days; aquaria were kept under standardized conditions across replicates. Similar to the field experiments, the direct effect of algal substrates on egg survival was tested against a control (neutral substrate) and additionally the indirect effect of algae was analysed in a third treatment with eggs spawned on the neutral substrate and algae added to the surrounding water (Figure 2).

Laboratory experiments were started on the 27 and 28 April 2016 investigating the direct and the indirect effects of *P. littoralis* ($n = 6$). Experiments were run for 9 days at water temperatures from 6 to 13 $^{\circ}\text{C}$, a salinity of 8, and pH 8. Samples were taken 1 day after spawning for determination of the fertilization success, at $^{\circ}\text{d}$ 56, and shortly before hatch at $^{\circ}\text{d}$ 89.

The laboratory experiment investigating the direct and indirect effects of *U. intestinalis* was started on the 26 April 2017 and ran 11 days under water temperatures between 6 and 10 $^{\circ}\text{C}$, a salinity of 8.4, and pH 8.4 ($n = 6$). Samples were taken 2 days after spawning for determination of the fertilization success, at $^{\circ}\text{d}$ 45, and shortly before hatch at $^{\circ}\text{d}$ 80.

2.8 | Sample processing and data analyses

In all experiments, sampling was conducted by removing a subunit of each replicate and preserving it in 4% borax-buffered formalin. Fixed samples can be stored for a long time and further analyses can be done in the laboratory, because originally vital eggs remain transparent and dead eggs opaque white. The fertilization success was

determined by counting fertilized eggs in each replicate and relating them to the total number of counted eggs (total $n \geq 100$).

The egg survival was determined for all samples taken during half-time egg development and shortly before hatch. Random subsamples (of each sample) of at least 400 eggs (except for the first experiment, where subsamples contained at least 100 eggs) were processed and the percentage of living eggs was calculated. Samples of algal substrates were processed by carefully separating the eggs from each other and counting living and dead eggs under the microscope. Digital images were taken of the neutral substrates (pieces of netting: good visibility of eggs, since eggs were distributed homogeneously) and analysed with imaging software (Image J 1.47v, Wayne Rasband, National Institutes of Health, USA) by determining the percentages for each replicate in three randomly placed rectangles (total ≥ 400).

Statistical analyses were conducted using SPSS 21 (IBM Statistics), R (version 3.2.3, R Foundation for Statistical Computing), and Microsoft Office 2007. Differences between egg survival rates in algae and control treatments were tested according to the given requirements of each data set. For most data the *t*-test was applicable. However, if homoscedasticity of variances was not initially fulfilled or could not be achieved by angular transformation, Welch's *t*-test was used as it is considered robust against deviation from such requirements. Cohen's *d* was used for interpretation of effect size and evaluated after Cohen (1988), where $d = |0.2|$ is considered as small, $d = |0.5|$ as medium, and $d = |0.8|$ as large effect size. Results of the laboratory experiment with *U. intestinalis* (three different treatments) were compared with a one-way analysis of variance (ANOVA). The significance level for all statistical analyses within the study was set to $P \leq 0.05$.

3 | RESULTS

The fertilization rate was above 98% in all treatments. Accordingly, impacts from limited fertilization success were considered negligible for further analyses. Oxygen saturation during field experiments and in all aquaria continuously stayed above 80%.

3.1 | Filamentous algae effects on selected spawning grounds

The comparison of herring egg survival rates in an area affected by the mass occurrence of *P. littoralis* (location B) and an area that was almost unaffected by filamentous brown algae (location A) revealed a clear trend (Figure 3). After half of the egg development, the mean egg mortality was significantly higher at location B with *P. littoralis* ($95.67 \pm 13.04\%$) than at location A ($21.58 \pm 10.87\%$, $t = 7.716$, $df = 54$, $P = 0.008$). Shortly before the larvae would have hatched, almost no eggs had survived at the *P. littoralis* location B (mean mortality $99.95 \pm 0.21\%$) whereas a significantly lower mean mortality was observed at location A ($33.04 \pm 27.46\%$, $t = 42.837$, $df = 54$, $P < 0.001$).

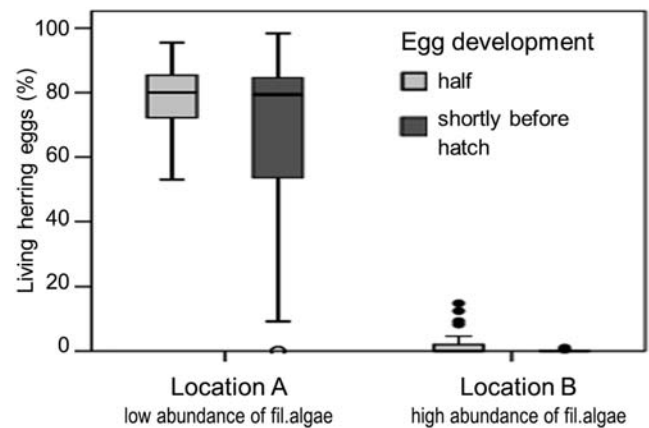


FIGURE 3 Boxplots showing the median survival rate of herring eggs in two different areas (location A: scarce filamentous algae; location B: high abundance of filamentous algae). On each box, the central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles; whiskers show the 1.5 interpercentile range, and dots represent outliers

The oxygen saturation during the experimental period was constantly around 100% in both areas. Some higher diurnal fluctuations were observed at location B with filamentous algae, but the values did not fall below 80% at any time (minimum values: location A, night 91%, day 93%; location B, night 82%, day 82%).

3.2 | Effects of *Pylaiella littoralis* on herring egg survival

Generally, the survival in all herring egg treatments containing *P. littoralis* was significantly lower than those without filamentous brown algae (Figure 4, Table 1). In the field experiment, after half of the egg development, survival in the control was significantly higher than on *P. littoralis* ($t = 2.191$, $df = 16$, $P = 0.044$) but with a strong effect size ($d = 0.8$). In the laboratory experiments, a strong negative effect of *P. littoralis* already appeared after half of the egg development. The direct effect of *P. littoralis* led to a significantly lower egg survival than observed in the control ($t = 21.033$, $df = 10$, $P < 0.001$, very strong effect size of $d = 10.3$). The laboratory experiment on the indirect effect also revealed a significantly better egg survival in the control than in *P. littoralis* water (Welch-test [5.186] = 4.206 , $P = 0.008$, strong effect size $d = 2.4$). Shortly before hatch, similar patterns became visible but revealed even higher significance levels. In the field experiment, survival in the control was significantly higher than on *P. littoralis* ($t = 21.028$, $df = 16$, $P < 0.001$, with a very strong effect size, $d = 9.8$). Similar tendencies were observed in the laboratory between the control and *P. littoralis* ($t = 9.975$, $df = 10$, $P < 0.001$), with a strong effect size of $d = 6.8$. The second laboratory experiment revealed a significantly higher survival of herring eggs in the control than on the neutral substrate indirectly influenced by *P. littoralis* ($t = 10.822$, $df = 10$, $P < 0.001$, very strong effect size of $d = 8.2$).

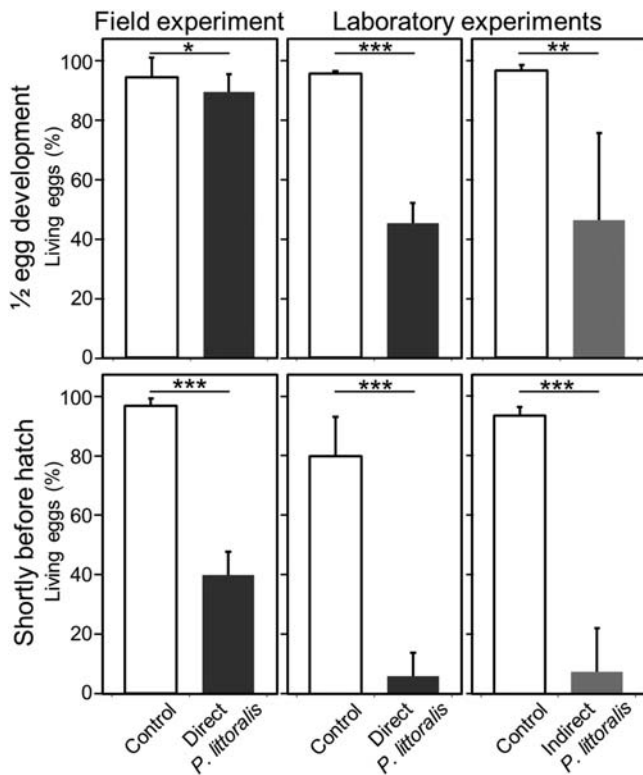


FIGURE 4 Percentage of living herring eggs (mean values with SDs indicated by error bars) after half of the egg development (top) and shortly before hatch (bottom) under different experimental treatments with *Pylaiella littoralis*: field experiment with herring eggs spawned on neutral substrate (control) and on *P. littoralis* ($n = 9$); laboratory experiments on direct effects with similar substrates ($n = 6$) and on indirect effects with herring eggs spawned on neutral substrates and then incubated in water with *P. littoralis* ($n = 6$); *** $P \leq 0.001$; * $P \leq 0.01$ or $P \leq 0.1$, t -test or Welch test respectively

3.3 | Effects of *Ulva intestinalis* on herring egg survival

Experiments on the effect of *U. intestinalis* as spawning substrate for herring eggs did not result in any significant differences between the control and the direct or indirect *U. intestinalis* treatments (field experiment: t -test, $P > 0.1$; laboratory experiment: ANOVA, $P > 0.1$) (Figure 5, Table 1). In the field experiment, the egg survival rate in the control was lower than on *U. intestinalis* after half of the development, but slightly higher shortly before hatch. In the laboratory experiment, the percentage of living eggs after half of the development was similar in the control and on the *U. intestinalis* treatments. And shortly before hatch, a slightly lower egg survival was observed in the control than in the *U. intestinalis* treatments.

4 | DISCUSSION

This study demonstrates that particular filamentous algae can drastically affect herring egg survival even without direct physical contact.

TABLE 1 Herring egg survival under the influence of filamentous brown and green algae in field and laboratory experiments (mean percentages \pm SD of living eggs)

Time and treatment	Field values (%)	Laboratory values (%)
<i>Pylaiella littoralis</i>		
Half-time egg development		
Control	94.23 \pm 6.67 ($n = 9$)	95.38 \pm 0.86 ($n = 6$)
Algae direct	89.20 \pm 6.00 ($n = 9$)	45.04 \pm 6.85 ($n = 6$)
Control		96.46 \pm 1.89 ($n = 6$)
Algae indirect		46.09 \pm 29.34 ($n = 6$)
Shortly before hatch		
Control	96.61 \pm 2.51 ($n = 9$)	79.88 \pm 13.16 ($n = 6$)
Algae direct	39.66 \pm 7.84 ($n = 9$)	5.93 \pm 7.82 ($n = 6$)
Control		93.35 \pm 3.04 ($n = 6$)
Algae indirect		7.40 \pm 14.53 ($n = 6$)
<i>Ulva intestinalis</i>		
Half-time egg development		
Control	58.94 \pm 14.99 ($n = 4$)	88.40 \pm 7.26 ($n = 6$)
Algae direct	75.43 \pm 13.42 ($n = 4$)	81.46 \pm 7.26 ($n = 6$)
Algae indirect		81.46 \pm 27.68 ($n = 6$)
Shortly before hatch		
Control	37.72 \pm 12.55 ($n = 4$)	56.00 \pm 28.28 ($n = 6$)
Algae direct	34.95 \pm 21.78 ($n = 4$)	70.76 \pm 19.52 ($n = 6$)
Algae indirect		74.20 \pm 28.81 ($n = 6$)

Results of the experiments clearly support the hypothesis that the filamentous brown alga *P. littoralis* has a significantly negative effect on herring eggs in the Baltic Sea.

Complete mortality of eggs was observed in combination with massive filamentous algae mats in the field. A mean herring egg mortality of almost 100% shortly before the larvae would hatch, in contrast to 33% ($\pm 27\%$) at a location with low filamentous algal abundance, shows the scale of the possible impact of those algae. The commonly assumed mechanism would be oxygen depletion in the water body because of either excessive night-time respiration of high plant biomasses or algal decay (Anderson, 2009; Aneer & Nellbring, 1982; Burkholder et al., 2007; Valiela et al., 1997). In shallow waters, hypoxia, induced by drifting algal mats, often causes major risks for the local fauna, especially for non-mobile species (Arroyo, Aarnio, Mäensivu, & Bonsdorff, 2012; Berezina, 2008; Lyons et al., 2014). Field observations in the Askö area (Baltic Sea, Sweden) revealed a significantly higher egg mortality on filamentous algae than on coarse algae in one of three study periods, and mortality was attributed to low oxygen levels during the night (Aneer, 1985). However, Atlantic herring eggs are reported to be tolerant to oxygen fluctuations above 50% saturation (Braun, 1973). Since diurnal oxygen levels never fell below 80% during our experiments, the observed egg mortalities are probably

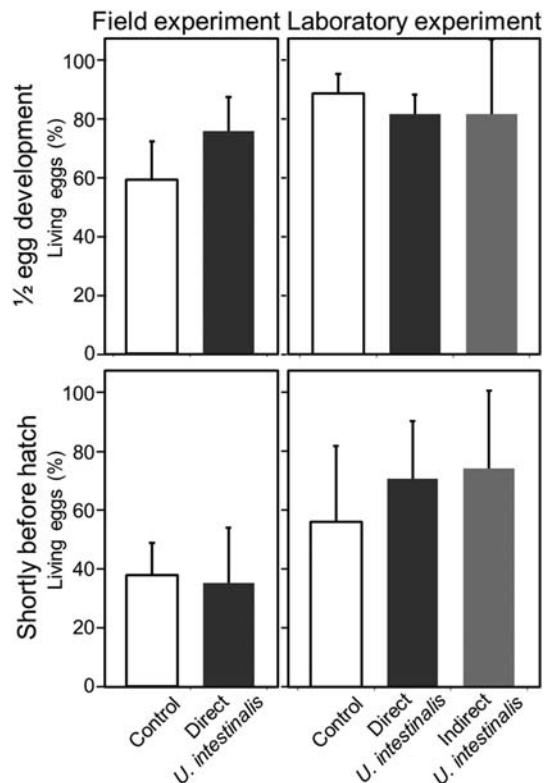


FIGURE 5 Percentage of living herring eggs (mean values with SDs indicated by error bars) after half of the developmental time (top) and shortly before hatch (bottom) under different experimental treatments with *Ulva intestinalis*: field experiment with herring eggs spawned on neutral substrate (control) and on *U. intestinalis* ($n = 4$); laboratory experiment with similar substrates for direct effect analysis and with herring eggs spawned on neutral substrates, incubated in water with *U. intestinalis* for analyses of indirect effects ($n = 6$)

caused by other stressors. However, future studies should examine the oxygen regime on spatial microscales (i.e. within egg clumps).

Experiments with filamentous algae, known for their eutrophication-associated blooms in coastal waters, revealed specific effects on the survival of Atlantic herring eggs. Although filamentous forms of the green algae *U. intestinalis* induced no immediate impact, significantly higher egg mortalities were documented in experiments with *P. littoralis*. Both the direct and indirect influences (algae as immediate spawning substrate or as free-floating fragments in the incubation tank) have been shown to significantly increase egg mortality rates compared with treatments without *P. littoralis*. Field experiments are a valuable tool to transfer the results of the laboratory experiments to *in situ* conditions, which are not influenced by limited water exchange and a corresponding lower dilution potential. With high water exchange *in situ*, the large negative influence of those algae became visible only after a longer incubation period, emphasizing the importance of conducting experiments under both laboratory and field conditions to gather comprehensive knowledge about biological processes.

The results of this study agree in part with the study of Aneer (1987), who detected negative effects of a '*Pylaiella littoralis*-*Ectocarpus siliculosus*-mixture' on herring egg survival in a laboratory experiment. The indirect effect was tested by introducing water into egg chambers after it passed through a cylinder with algae. A fresh algae mix resulted in 30% mortality of eggs (no algae treatment: 14%), whereas the same algae mix in a decomposed stage had no significant effect (15% of dead eggs compared with 13% without algae). Aneer (1987) speculated that toxic exudates, released during a short time after detachment, were the cause. However, this has never been experimentally verified. In contrast to Aneer (1987), this study systematically tested the influence of *P. littoralis* on herring eggs in field and laboratory experiments. Our results indicate that the lethal effect is not limited to fresh algae, because experiments were conducted with already detached algae that were washed into the littoral zone. Furthermore, the percentage of dead eggs was much higher in all brown algae treatments of this study, with at least 60% shortly before hatch compared with not more than 20% in the respective control.

Generally, blooms of filamentous macroalgae often have multiple negative consequences for affected ecosystems; for example, light-dependent depth limitation of benthic macrophyte distribution due to shading or extreme oxygen consumption during decay of algae mats formed by detached filaments (Anderson, 2009; Kautsky, 1991; Orth et al., 2006; Valiela et al., 1997). Furthermore, fish eggs attached to filamentous algae covering the benthic vegetation can particularly be drastically affected, if those filaments are detached by hydrodynamic forces (storm events) and washed to shore or the open sea, where eggs hardly survive (Moll, Kotterba, von Nordheim, & Polte, 2018). Although those effects are rather nonspecific or act as part of ecological cascades, this study proves an explicit lethal effect of the filamentous brown alga *P. littoralis* on herring eggs. A filamentous form of the green alga *U. intestinalis* was investigated as a second eutrophication-promoted species. During the experiments, this species had a rather positive effect on the egg survival. However, regarding the negative effects of filamentous algae outlined herein, they would most likely not be compensated by positive aspects under natural conditions on spawning grounds. Furthermore, egg survival was generally rather low at the end of the green algae field experiment, with mean values around 35% on both substrates (algae and control). This might be due to unfavourable weather conditions during the experimental period, as heavy storms resulted in increased wave action and silting. But as those factors were influencing both treatments to the same extent, the experimental result is still reliable.

It is common scientific sense that eutrophication-linked mass blooms of filamentous, mat-forming algae have negative, often drastic effects on the resident community of the affected ecosystems. In contrast, some studies discuss the potential of algal mats formed by particular species to serve as temporal, nutrient-rich habitat for macrobenthos (Salovius, Nyqvist, & Bonsdorff, 2005) or as a refuge from hypoxia for some invertebrates (Coffin et al., 2017). This can probably be the case in heavily altered ecosystems with no or little remains of perennial benthic macrophytes. In those systems, the algae might, owing to the lack of alternatives, serve as habitat or as

spawning substrate for demersal spawning fishes such as Atlantic herring. However, considering all disadvantages of these algae, including the direct negative effects on herring eggs demonstrated in this study, a spawning area merely offering filamentous algae cannot keep up with a pristine ecosystem that is dominated by perennial benthic macrophytes.

We can only speculate on the actual mechanisms causing high egg mortality related to the presence of *P. littoralis*. An explanation could be the immediate effects of exudates released by the algae (speculated by Aneer, 1987). Phenols (phlorotannins), for example, are produced by brown algae as secondary metabolites, functioning as protection against herbivores and as antibacterial agents (reviewed by Creis, Gall, & Potin, 2018; Targett & Arnold, 1998). However, not all brown algae seem to have a negative effect; for example, *F. vesiculosus* has a very effective antifouling mechanism (Wahl et al., 2010) but also turned out to be a favourable spawning substrate for *C. harengus* (Polte & Asmus, 2006); L. von Nordheim personal observation in the Baltic Sea). Furthermore, exudates are probably diluted quickly in the field, and their physiological effect is presumably restricted to the spatial microscale. Possibly, high egg mortality rates are induced by reactive oxygen species released by algae as a component of stress responses during, for example, thermal stress, exposure to high radiation, pollutants, or as pathogen defence (Bischof & Rautenberger, 2012; Lesser, 2006; Mallick & Mohn, 2000; Potin, 2008). To the best of our knowledge, no information exists on the potential vulnerability of fish eggs against oxygen radicals released by algae, but this should be subject to future studies. Other aspects might be the documented association of brown algal exudates with hydrophobic polychlorinated biphenyls or the metal sorption capacity of *P. littoralis* as such pollutant enrichments might induce toxicity (Carrilho & Gilbert, 2000; Lara, Wiencke, & Ernst, 1989).

High structural complexity of spawning substrates evidently benefits herring egg development (von Nordheim, Kotterba, Moll, & Polte, 2018), but the mucilaginous and filamentous structure could cause the opposite effect. Potentially, eggs might be suffocated by dense algal accumulations, resulting in a lack of oxygen-rich surrounding seawater. However, this cannot explain the results in our experiment, because egg mortality was high in all *P. littoralis* treatments, even if those algae were not the direct spawning substrate, and the filamentous green algae tested had no negative effects. Potentially, the lethal impact might also be induced by protists (e.g. dinoflagellates or diatoms) associated with the algae. Both taxa are well known to include toxic species. A closer look at the diatom community on *P. littoralis* in the Baltic Sea reveals that filamentous algae host numerous diatom species (Snoeijs, 1995). However, to our knowledge, a negative impact on vertebrates has not been documented yet. Furthermore, the dinoflagellate *Prorocentrum lima* is described as to be attached to *P. littoralis* and to induce diarrhoeal shellfish poisoning in the northern USA (Maranda, Corwin, Dover, & Morton, 2007). But such incidents have not been described for the Baltic Sea so far.

Although the mechanism is as yet unclear, this study proved the extreme negative impact of filamentous algae on herring egg survival

and can therefore be regarded as a strong motivation to increase research efforts on the particular mechanisms. Preliminary findings indicate that *P. littoralis* benefits from mild and ice-free winters, as Kiirikki and Lehvo (1997) documented maximum abundances after ice-free winters. Recently, we observed mass occurrences very early in years with warm winter–spring temperatures; for example, 2016 in mid-April and 2017 in mid-March. The main reproduction period of *P. littoralis* is in winter. Accordingly, it grows rapidly in spring when the water temperatures rise and the light regime changes; during late spring and early summer the filaments degenerate and detach, and during summer only the basal parts remain (Kiirikki & Lehvo, 1997). Hence, first, this alga benefits from high levels of nutrients, which are constantly available in the eutrophic study system Greifswalder Bodden (and in most other coastal areas all over the world as well), and second, is promoted by mild winters and rising water temperatures early in the year, as documented with increasing frequency for the temperate climatic zone (Haapala, Ronkainen, Schmelzer, & Sztobryn, 2015; Schwartz, Ahas, & Aasa, 2006). Spring blooms of these algae frequently appear on the Baltic coast (Lotze, Schramm, Schories, & Worm, 1999), and recent mild winter conditions seem to increase the overlap of *P. littoralis* vegetation periods and the herring spawning season.

Macroalgal blooms are promoted by eutrophication and their impacts on marine and estuarine ecosystem functioning and services are a global issue (Caddy, 2007; Lyons et al., 2014; Teichberg et al., 2012). Anderson et al. (2012) defined harmful algal blooms specifically as events causing injuries to humans, socio-economics, or ecosystems. Since the latter two criteria are observed as a consequence of the massive occurrence of *P. littoralis*, we would denote this species as a harmful alga. Immense herring egg mortality, for instance, linked to *P. littoralis* blooms emphasizes the problematic current situation in coastal Baltic Sea habitats (Aneer, 1985; this study). However, this is not only a local problem, as eutrophication has become an issue in most of the freshwater and coastal marine ecosystems in the world (Smith & Schindler, 2009).

Accordingly, areas of high ecological importance, determined according to their function as key marine habitats for important ecosystem components, should be identified and become a basis for the establishment of specially designed protected areas and the implementation of measures supporting natural regeneration. In the light of cumulative effects with rising temperatures, the habitat conditions in eutrophic ecosystems must be improved by further reduction of nutrient inputs to maintain or even restore the ecological function of coastal ecosystems as herring nursery areas in particular, and as habitat for numerous other species in general.

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