Predation on Atlantic herring (*Clupea harengus*) eggs by the resident predator community in coastal transitional waters

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Abstract

Atlantic herring (*Clupea harengus*) migrates from offshore to coastal areas to spawn and their eggs and larvae may substantially increase prey resources for resident predators. We combined an in situ predator exclusion experiment using eggs naturally spawned on submerged aquatic vegetation and field observations of predator abundance to estimate the magnitude of predation mortality of herring eggs. During our predator exclusion experiment, performed in an important spawning ground in the southwest Baltic Sea, 20% of the herring eggs were consumed resulting in an extrapolated predation of 42% of all eggs between spawning and hatch. Abundance and stomach content analyses indicated that one predator (threespine stickleback, *Gasterosteus aculeatus*) was responsible for the majority of the predation impact. Predation mortality estimates from this in situ study were more than 10-fold higher than those of an empirical egg predation model for the same predator in the same region. Our findings highlight the potential of resident predators to regulate the survival of early life stages of ocean-going fishes that rely on the nursery functions of inshore transitional waters.

By postulating the "critical period hypothesis" in order to explain the variability in fish recruitment, Johan Hjort (1914, 1926) set the main direction of fishery science for decades. Essentially, Hjorts hypothesis emphasizes the importance of appropriate environmental conditions during the period of first feeding, i.e., when the fish larvae have resorbed their yolk reserves and switch to exogenous food sources. Subsequently, bottom-up processes and their implication for larval fish survival became an ultimate research issue, leading to the development of a couple of fundamental hypotheses linking recruitment of pelagic fishes with foraging conditions for the larvae, such as the "match-mismatch hypothesis" of Cushing (1974), the "stable ocean hypothesis" of Lasker (1978) or the "stable retention hypothesis" of Iles and Sinclair (1982). In contrast, top-down mechanisms have gained significantly less attention, although in the late 1970s and early 1980s, predation was already considered to be the ultimate cause of mortality of marine fish early life stages (Bailey and Houde 1989) while bottom-up factors were merely seen as modulators of predation mortality (Houde 2008). Within complex marine food webs, quantifying a single predator's contribution to the natural mortality of early life stages of fish remains difficult (Hunter 1984) and the number of corresponding publications is limited (Houde 2008). The majority of these studies have focused on pelagic eggs or larvae (e.g., Bailey 1984; Möller 1984; McGurk 1986; Purcell 1989) while, in contrast, quantitative research on the predation of marine demersal fish eggs, is rare and has mostly been conducted from in situ observations and not from controlled experiments (Kotterba et al. 2014).

Atlantic herring (*Clupea harengus*) is a commercially important target species of North Atlantic fisheries intensively exploited since medieval times (Sahrhage and Lundbeck 1992). This litho-phytophilous spawner (Balon 1975) deposits adherent eggs onto stones or submerged aquatic vegetation. The spawning season might spread over several weeks or months, increasing the probability of spatiotemporal overlaps between herring eggs and potential predators. For example, in the Western Baltic Sea, herring spawns in waves from mid-March to mid-June (Scabell 1988; Moll unpubl.) providing a continuously available prey resource to

resident predators even during periods of relatively low productivity in early spring.

Although *C. harengus* is among the most thoroughly-studied fish species world-wide (Blaxter and Holliday 1963; Whitehead 1985; Dickey-Collas et al. 2009), a surprising amount of uncertainty exists on the factors driving recruitment success (Polte et al. 2014). Similar to work on other species, research on herring recruitment has mainly focused on bottom-up processes (physics and prey) affecting larval survival while studies aiming at top-down processes (predation of the benthic eggs) remained rare. Quantitative studies have been performed on the predation of Pacific herring (*Clupea pallasii*) eggs in spawning areas of the Northeastern Pacific. In that region, studies suggested that avian predation on intertidally spawned eggs represented a major cause of spawn mortality (Bishop and Green 2001; Lok 2008; Anderson et al. 2009) but the broad variety of local egg predators also includes invertebrates and mammalian top predators (Palsson 1984; Fox et al. 2015). Diving water fowl are known to feed on the spawn of *C. harengus* in adjacent waters of the Northern Atlantic Ocean (Jamieson et al. 2001; Zydelis and Esler 2005) and piscine predation on herring eggs has also been observed (Scabell 1988; Rajasilta et al. 1993). Despite the plethora of observations, studies quantifying herring egg predation rates are rare (but *see* Richardson et al. 2011; Kotterba et al. 2014).

Similar to other herring groups, spring-spawning herring in the western Baltic Sea undergo an extensive migration between offshore feeding and inshore spawning grounds along the Baltic Sea coast (Aro 1989). Consequently, all life-stages of these fishes are at least temporarily found in transitional waters in between marine and limnic ecosystems relying on the equilibrium of influences from both. Along major environmental gradients in these waters (e.g., Baltic Sea salinity gradient), interactions of herring and the resident fauna strongly depend on the long-term stability of major ecosystem characteristics.

We examined how top-down mechanisms might impact the survival of eggs of herring in the Western Baltic Sea. Hypothesizing a significant predation effect of the resident predator community on the survival of herring eggs, we combined field observations with an in situ predator exclusion experiment to investigate the trophodynamic interactions resulting from the temporary co-occurrence of herring spawn and resident predators.
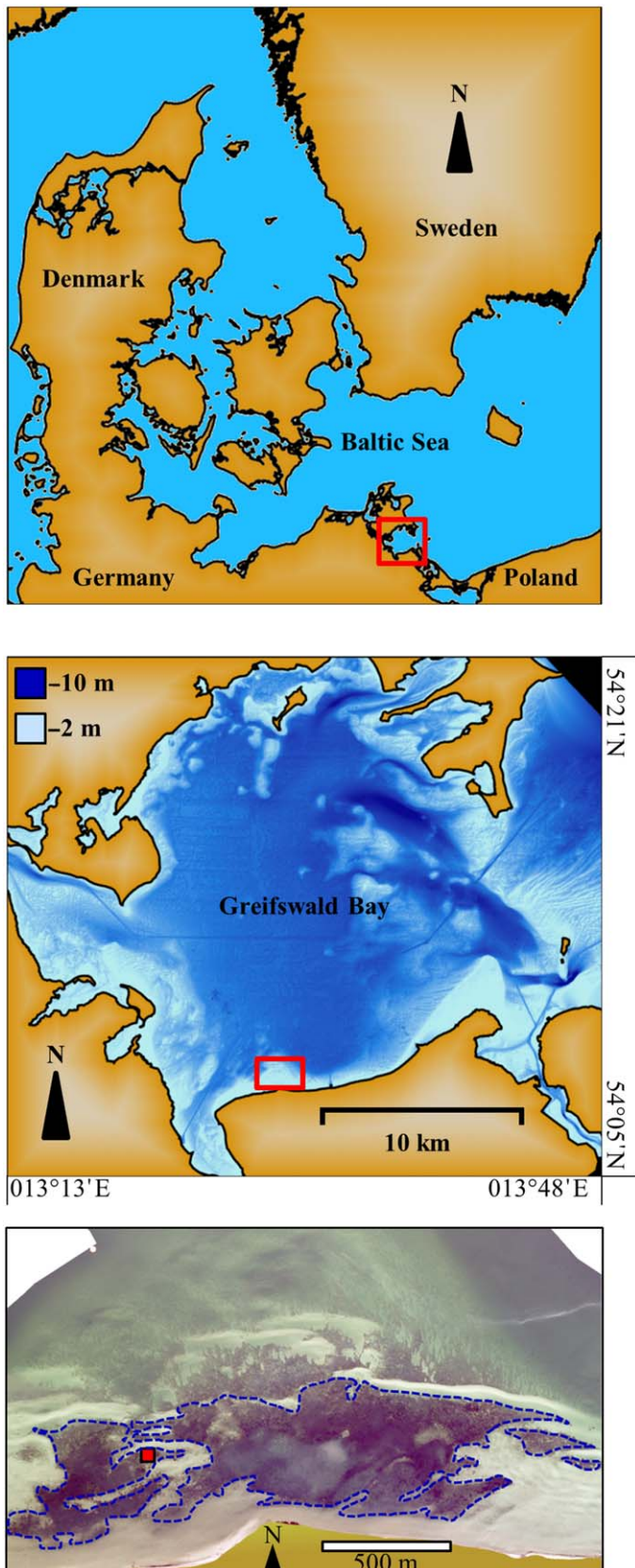
Material and methods

Study area

The study was conducted in Greifswald Bay, an important herring reproduction area on the south-western coast of the Baltic Sea (Scabell 1988; Kanstinger et al. 2016; Fig. 1). The 514 km^2 bay is fairly shallow with a mean and maximum depth of 5.8 m and 13.6 m, respectively (Reinicke 1989).

Tidal amplitudes in the semi-enclosed bay do not exceed 10 cm and water exchanges with the adjacent Pomeranian Bay are mainly wind driven (Stigge 1989). The bay is mesohaline, with an average salinity between 6 and 8. The system suffers from eutrophication (Munkes 2005) but, due to frequent wind-induced mixing of the water column, dissolved oxygen concentrations are relatively high, even close to the bottom. The shallow littoral zone of the bay is characterized by a depth-stratified community of submerged aquatic vegetation (SAV), dominated by flowering plants such as pondweeds (Potamogetonaceae) and eelgrass (*Zostera marina*), as well as a diverse community of macro algae (Geisel and Meßner 1989; Kanstinger et al. 2016). The local fish community comprises a total of 61 freshwater and marine species (Winkler 1989*a*) but is (besides herring) dominated by the threespine stickleback (*Gasterosteus aculeatus*) during the herring spawning season between March and May (Kotterba et al. 2014).

Predator exclusion experiment

In spring 2012, we conducted a predator exclusion experiment on a littoral spawning bed on the southern coast of Greifswald Bay that is regularly frequented by herring (Scabell 1988; Kanstinger et al. 2016). The experiment was conducted during a peak herring egg abundance based on weekly monitoring at this particular spawning site (Moll et al., unpubl.). Treatments were installed on 4th May in an area having a mean depth of 0.8 m (Fig. 1) and a relatively homogenous distribution of SAV (dominated by pondweeds, family Potamogetonaceae) with an average concentration of herring eggs (approximately 58,000 eggs per m^2 sea floor). Three treatments were used with six replicates each: (1) predator exclusion (Fig. 2A) where the SAV with adherent herring eggs was protected by a round cage (diameter: 65 cm, height: 40 cm) equipped with 5-mm mesh netting, (2) a control group (Fig. 2B) left completely unprotected, and (3) an artefact control (Fig. 2C) to examine the potential effects on egg mortality caused by the structure of the cages. The latter controls had a protective cage without netting on the side walls thus leaving an opening for predators to access the herring spawn inside. Small labels attached to the sea bottom marked the center of the investigation area in each replicate. At the beginning of the experiment, a Van Veen grabber (sampling area: 400 cm^2) sample was taken directly north of the label. At the end of the experiment, the area south of the label was sampled. The grab samples contained plants and adhesive herring eggs and were fixated with a buffered formalin solution (4%, in seawater) before being transferred to the laboratory. Since potential successive spawning events would have corrupted the experimental results, additional control units were installed in the immediate vicinity of the experiment to test for any subsequent spawning events. Since it is not known whether herring prefers certain substrates for egg deposition, two differing designs were used for

spawning controls according to previous observations on positive substrate selection: (1) Horizontal quadratic nets (1 m^2, mesh size: 5 mm; Fig. 2D, $n = 6$) and (2) two different types of artificial plants (plastic replica of *Monstera deliciosa* and *Encephalartos* sp.; Fig. 2E,F; $n = 6$ for each). Weather conditions and hydrological parameters (sea surface temperature, salinity, dissolved oxygen saturation) were recorded at the beginning and at the end of the experiment. Based on earlier studies on the relation between water temperature and the duration of Baltic herring egg development (Klinkhardt 1986; Peck et al. 2012), the experiment was run for 96 h (until the 8th of May) to minimize hatching effects on the experimental results.

Laboratory sample processing

The wet weight (digit (d) = 0.01 ± 0.01 g) of the entire sample and the general SAV composition was recorded prior to the retrieval of three random subsamples (*see* Supporting Information material for details). For each subsample, the wet weight was measured (total subsample and SAV only; $d = 0.01 ± 0.01$ g) and herring eggs were counted and weighed ($d = 1 ± 1$ μg) after separation from the SAV. The dry weights of the herring eggs ($d = 1 ± 1$ μg), SAV and the rest of the whole sample ($d = 0.01 ± 0.01$ g) were determined after drying for 24 h at room temperature and subsequent drying at 80°C for a minimum of another 24 h.

Predator identification

Potential predators of herring eggs were sampled prior to and after the experiment using a beach seine towed along a 100 m transect parallel to the shore line in the direct vicinity of the experimental plots at daytime. The total catch was weighed ($d = 1 ± 1$ g) and a random subsample comprising approximately 20% of the catch was immediately frozen on dry ice (–80°C) to halt the digestion of prey. The rest of the catch was released while the subsample was later analyzed in the laboratory: The species composition was determined and individual predators were measured (total length from snout tip to the end of the caudal fin) and weighed (wet weight in gram; $d = 0.01 ± 0.01$ g). From a random subsample of individuals of the dominant species, the stomach content was analyzed and prey items were determined to the lowest possible taxon for fish prey and macroinvertebrates and to the order/family level for small invertebrates (e.g., copepods).

Fig. 1. Study site location. Uppermost chart illustrates the location of Greifswald Bay (red rectangle) within the Western Baltic Sea. Map in the middle shows the general bathymetry of the bay and the location of the study site "Gahlkower Haken" at the southern coast of the bay. Lowermost panel is an aerial view of the shallow Gahlkower Haken with the area used for the experiment (red box). The area enclosed by the broken line represents a spawning bed of herring (∼1.77 km^2) characterized by a homogenous water depth (∼1 m), SAV coverage and composition. Source of elevation data: Federal Maritime and Hydrographic Agency of Germany (BSH).
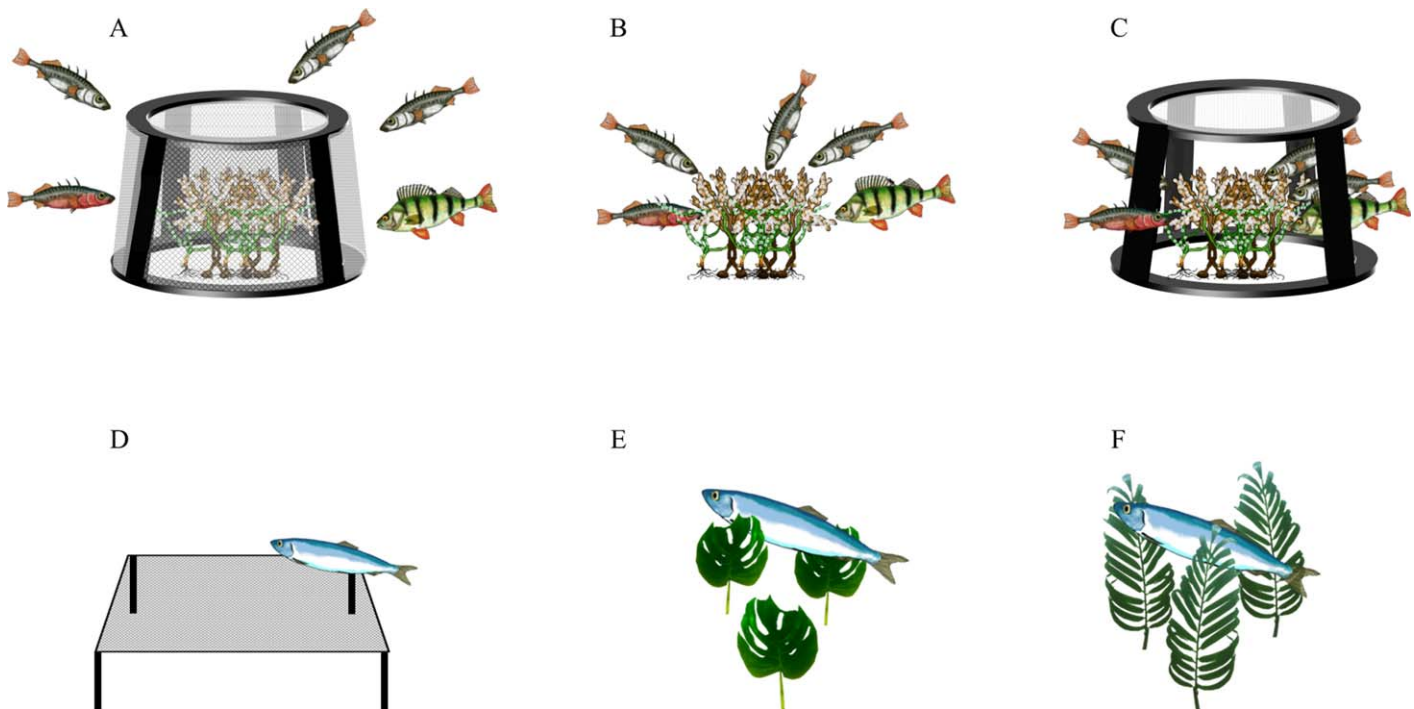
Fig. 2. Schematic design of the experimental setup. (**A**) Predator exclusion treatment, (**B**) control areas without protection, (**C**) artefact controls using cages with open side walls, (**D**–**F**) spawning controls, (**D**) horizontal net, (**E**) artificial *M. deliciosa* leafs, and (**F**) artificial *Encephalartos* sp. leafs. Each treatment was applied in six replicates. *Note*: schematics are not drawn true to scale.

We used different techniques to determine an appropriate sample size for the stomach content analyses of threespine stickleback including the method suggested by Cochran (1977) and Rasch et al. (2007) resulting in a sample size of 30 individuals (*see* Supporting Information material for details).

Spatial spawn distribution

In Spring 2014, we investigated the spatial distribution of herring eggs during spawning events at the last week of March (30th) and the first week of April (6th). A grid of 197 sampling stations with a distance of 100 m in between vicinal stations was laid on an area of 1.9 km^2 in total (Fig. 3a). The grid covered water depths from 0.3 m to approximately 4.0 m and thus included the core extension of SAV meadows at the study site (Fig. 3a). Each station was sampled with a small Van Veen Grabber (sampling area of 250 cm^2) which was deployed from a kayak. Due to harsh wind conditions on 30th March, only 139 stations were sampled resulting in increased distances between the sampled stations; nevertheless the entire study site was covered (Fig. 3a). On board the kayak, SAV composition (volume proportion of different taxa) and herring egg mortality was macroscopically estimated in percent. The amount of herring eggs in the samples was classified in one of four categories: 0 = no herring eggs, 1 = single or a few herring eggs in the sample, 2 = several herring eggs in the sample but still in a monolayer; 3 = many herring eggs, accumulated in multiple layers and clumps; 4 = many herring eggs in clumps with a total volume exceeding the volume of SAV in the sample (for more details of the kayak sampling *see* Supporting Information).

Data analyses

We used the relations between the dry weights of the subsamples and the corresponding dry weights of the entire samples to extrapolate the total number of eggs in each replicate. For each treatment, the arithmetic mean of egg concentration per treatment was estimated at the beginning and at the end of the experiment. The egg loss during the experiment was estimated by subtracting the mean total egg number at the end of the experiment from the respective egg numbers found at the beginning of the experiment. To exclude other potential causes for egg loss (e.g., by hatching) from our predation estimates, we applied the following approach: Assuming that the unprotected control plots include all potential factors of egg loss (gross egg loss), the results of the caged plots were subtracted from this gross egg loss to receive the net egg loss which can then be related to predation.

We conducted a priori tests on normal distribution (Kolmogorov–Smirnov test) and variance homogeneity (Levene test) to test for the adequacy of using analyses of variance (ANOVA) for the comparisons between different treatments
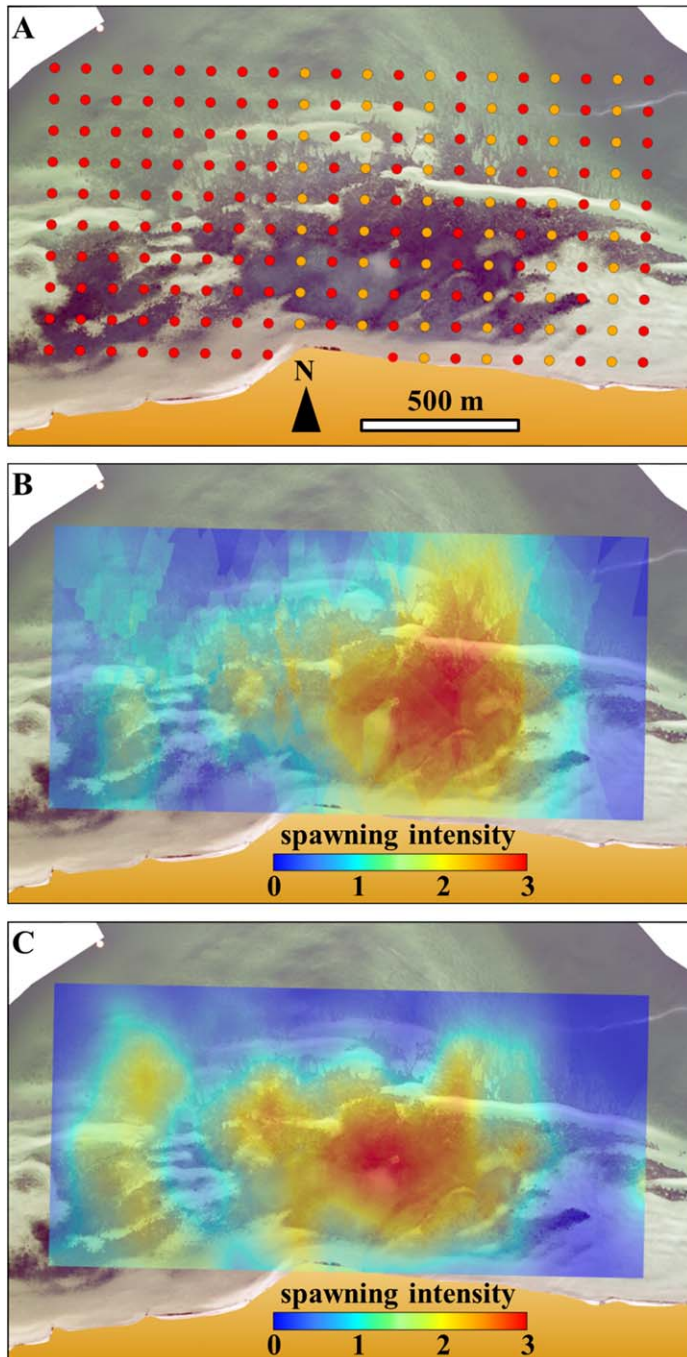
Fig. 3. Case study on the small scale spatial distribution of herring spawn within the study site "Gahlkower Haken" during the herring spawning season in spring 2014. (**A**) Aerial View on the study site including the grid of sampling stations for the semi-quantitative analysis of herring spawn. Red dots indicate stations sampled on 30th March and 6th April 2014, orange dots indicate stations sampled only on 6th April. (**B, C**) Same view with an overlay showing the interpolated spawning intensity based on ordinal scaled quantifications in the field. Scale of spawn concentration ranges from 0 (no eggs, blue) to 3 (eggs in multiple layers, red). (**B**) Results of the sampling on 30th March. (**C**) Results of the sampling on 6th April.

of the experiment. When needed, the data were square root transformed to obtain homogeneity of variances. A one-way ANOVA was performed to test for significant differences in egg concentrations among the treatments at the beginning and at the end of the experiment. If the corresponding demands were fulfilled, a two sample t-test was performed for each treatment to compare egg concentrations found prior to the exposure in the field with those observed at the end of the experiment. Alternatively, a Mann–Whitney U-test was conducted. A regression analysis was performed to examine the relation between the initial herring egg concentration and the proportion of spawn that was removed by predators from the six unprotected controls.

The data recorded with a hand-held GPS device (Garmin[®] eTrex Vista[®] HCx) were used to determine the exact area sampled with the beach seine (03 May 2012: 644 m^2; 08 May 2012: 625 m^2). Predator abundances were calculated as number of individuals per area.

The estimation of the specific contributions of the resident predators to the total predation mortality of herring eggs was based on the predators' abundances, their average total weight and the results from the stomach content analyses. Accordingly, the predator-specific predation impact (PI$_i$) was calculated with the following equation:

$$\text{PI}_i = C_{\text{HE}_i} \times \left(\sum_{i=1}^{n} C_{\text{HE}_i} \right)^{-1} \times 100\%$$

where n is the number of predator species included in the calculation and $C_{\text{HE}i}$ represents the average amount of herring spawn found in the stomachs of individuals of predator i. $C_{\text{HE}i}$ was calculated according to the following equation:

$$C_{\text{HE}_i} = \text{WW}_i \times \frac{\text{SC}_{\text{HE}_i}}{100\%} \times \frac{\text{CI}_i}{100\%} \times A_i$$

where WW_i represents the total wet weight of the predator i, $\text{SC}_{\text{HE}i}$ is the average share of herring eggs in the predator stomachs (in %); A_i is the numerical abundance of predator i during the experiment and CI_i represents the consumption index of predator i as suggested by Winkler (1989b). CI_i was calculated according to the following equation:

$$\text{CI}_i = \frac{\text{SC}_i}{\text{WW}_i} \times 100\%$$

where SC_i represents the stomach content weight and WW_i the total wet weight of the predator i.

PI$_i$ estimates were based on the assumption that our beach seine catches are representative in regard to the composition of the resident predator community. We further assumed a similar feeding ecology of $G.\ aculeatus$ and $Pungitius\ pungitius$ (Hynes 1950; Hart 2003) and used values of the former species to compensate for missing data for the latter species (i.e., $\text{CI}_{G.\ aculeatus} = \text{CI}_{P.\ pungitius}$ and $\text{SC}_{\text{HE}G.\ aculeatus} =$

$SC_{HE_{P. \ pungitius}}$). No data was available for the resident cyprinids, thus we assumed a theoretical consumption index of 3% and a herring spawn contribution of 50% to the total stomach content. We compared our findings with the results of an empirical herring egg predation model for threespine stickleback that was introduced by Kotterba et al. (2014).

We extrapolated the predation mortality of herring eggs from our experiment duration to the temperature dependent duration of the entire embryonic period (from spawning to hatch, Peck et al. 2012) assuming that including both, predator samples at the beginning and at the end of the experiment copes for potential changes in predation intensity during the experiment:

$$MP_{total} = \frac{MP_{experiment} \times HP}{96 \, h}$$

where $MP_{experiment}$ is the predation mortality observed during the experiment run for 96 h (in %) and HP is the mean time from fertilization to peak hatching at a given temperature according to Peck et al. (2012). Based on the PI_i and the MP_{total} estimates, we extrapolated the predator-specific predation impact for the total area ($1.77 \, km^2$) of the investigated spawning bed (Fig. 1). This area encompasses distinct sub-areas with homogenous water depths (0.8–1.2 m) and equal SAV compositions and coverages. Since spawning intensity is mainly driven by the availability of spawning substrate such as SAV (Kanstinger et al. 2016), we assumed our experiment to be representative for the entire spawning bed.

Data on spatial herring egg distribution in spring 2014 were used as additional information on the suitability of the chosen experimental site to represent a valid spawning ground. The Kriging method for spatial Interpolation (Spatial analyst feature implemented in the ArcGIS® 10.2 software package) was used to generate distribution maps of herring eggs.

Results

Predator exclusion experiment

At the beginning of the experiment, neither the biomass of macrophytes per square meter (ANOVA, $F_{2,15} = 0.429$, $p = 0.659$) nor the concentration of herring eggs per m^2 (ANOVA, $F_{2,15} = 0.132$, $p = 0.877$) differed significantly among the distinct treatments (caged, unprotected, and artifact control) which indicates equal preconditions for all experimental treatments. Four days later, the mean egg concentration in the unprotected control treatment was significant lower (–78%) compared to the beginning of the experiment (independent sample t-test: $t_{10} = 2.819$, $p = 0.032$). We also observed differences in egg concentrations in the caged treatment (–58%) and the artefact controls (–62%); although these differences were not statistically different (cages: independent sample t-test: $t_{10} = 1.207$, $p = 0.255$; artefact controls: Mann–Whitney
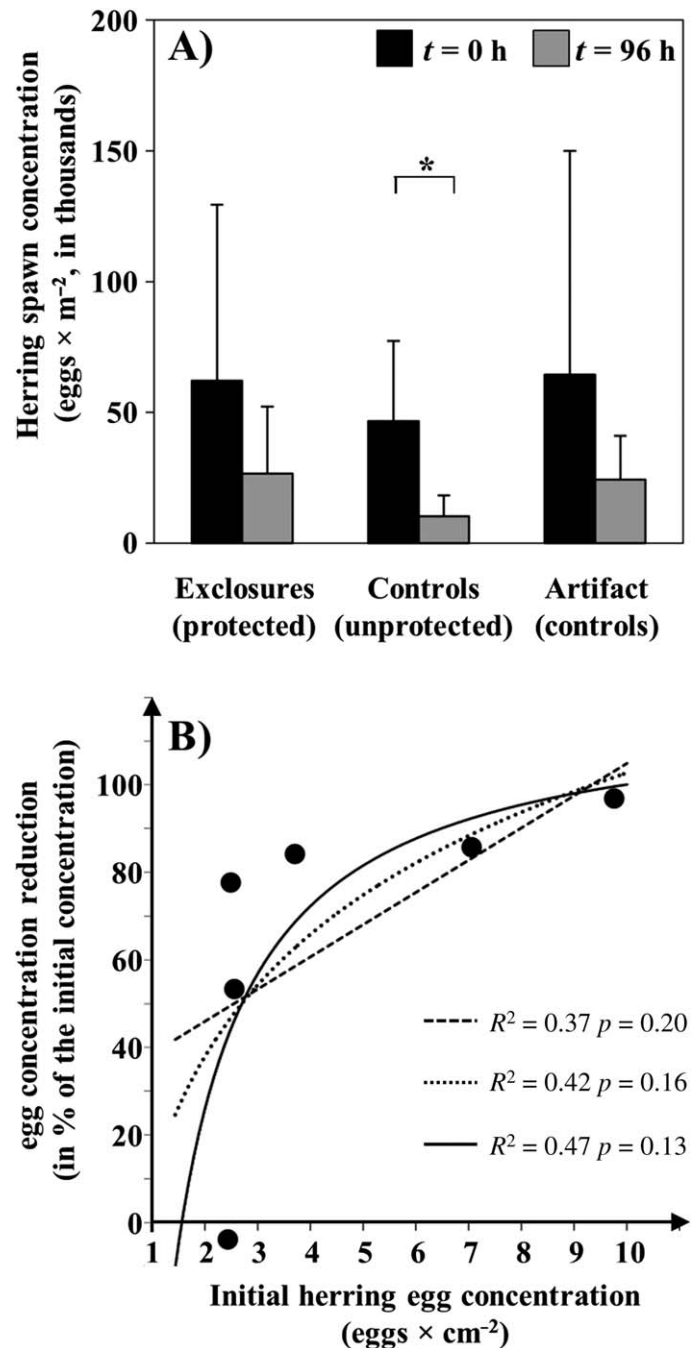

Fig. 4. Results of the predator exclusion experiment. (**A**) Mean herring spawn concentration prior to (black bars) and after (gray bars) the exposure to the in situ predator community for each of the treatments ($n = 6$; error bars indicate the standard deviation; asterisk indicates a significant difference of $p \leq 0.05$). (**B**) Reduction of egg concentration (as percent of the initial egg concentration) plotted against the initial concentration of herring spawn. Broken line represents the curve of a linear regression, dotted line indicates the curve of a logarithmic regression function and the solid line is the curve of a hyperbolic regression. The corresponding regression parameters (R^2 and p) are given in the figure legend.

Table 1. Catch composition of beach seine catches conducted prior to the beginning (03 May 2012); at the end of the predator exclusion experiment (08 May 2012) and aggregated for the whole period (total).

Date and conditions	Species	Mean TL (mm ± SD)	Mean WW (g ± SD)	Abundance (n m^{-2})	Abundance (g m^{-2})
03 May 2012	G. aculeatus	65.1 ± 5.6	3.20 ± 0.94	3.141	10.750
SST = 11.8°C	P. pungitius	48.4 ± 3.4	0.86 ± 0.19	0.072	0.062
Sal = 6.7	P. fluviatilis	76.9 ± 8.4	4.27 ± 1.45	0.012	0.053
Sat$_{DO}$ = 115%	A. alburnus	98*	6.65*	0.009	0.060
08 May 2012	G. aculeatus	62.2 ± 6.8	2.59 ± 0.89	3.113	8.453
SST = 12.7°C	P. pungitius	46.8 ± 3.0	0.81 ± 0.81	0.079	0.060
Sal = 7.3	P. fluviatilis	67.9 ± 6.8	3.13 ± 1.13	0.024	0.073
Sat$_{DO}$ = 112%	R. rutilus	79.5 ± 2.1	5.33 ± 1.34	0.008	0.034
Total	G. aculeatus	62.9 ± 6.5	2.74 ± 0.94	3.127	9.619
SST = 12.3°C	P. pungitius	47.3 ± 3.1	0.82 ± 0.17	0.075	0.061
Sal = 7.0	P. fluviatilis	70.3 ± 8.2	3.47 ± 1.31	0.018	0.063
Sat$_{DO}$ = 114%	A. alburnus	98*	6.65*	0.005	0.031
	R. rutilus	79.5 ± 2.1	5.33 ± 1.34	0.004	0.017

TL, total length; SD, standard deviation; WW, wet weight (* no SD is shown since only 1 individual was measured); SST, sea surface temperature; Sal, salinity; Sat$_{DO}$, saturation of dissolved oxygen.

Table 2. Stomach samples analyzed to evaluate the specific contribution of selected predators to the overall predation effect observed in the predation experiment in spring 2012. Data is shown for both hauls and in an aggregated form (all individuals treated as one group; "total"). $\overline{m}_{HS}$ represents the mean herring spawn concentration in the control treatment (± standard deviation, SD) n stomachs is the number of stomachs analyzed for the presence of herring spawn, $\overline{n}_{HE}$ is the mean number of herring eggs found in the predator stomachs (±SD) and $\overline{SCW}_{HE}$ is the mean weight of herring spawn within the predator stomachs (±SD).

Date	$\overline{m}_{HS}$ (g×m^{-2}) ± SD	Species	n stomachs	$\overline{n}_{HE}$ ± SD	$\overline{SCW}_{HE}$ (g) ± SD
03 May	94.13 ± 47.43	G. aculeatus	20	88 ± 103	0.082 ± 0.090
		P. fluviatilis	7	75 ± 90	0.083 ± 0.091
08 May	29.91 ± 13.29	G. aculeatus	10	40 ± 61	0.053 ± 0.043
		P. fluviatilis	8	0.5 ± 1.4	0.003 ± 0.009
Total	62.02 ± 47.20	G. aculeatus	30	72 ± 93	0.072 ± 0.078
		P. fluviatilis	15	35 ± 70	0.041 ± 0.072

U-test, U_{10} = 15.000; p = 0.589; Fig. 4A). There was a tendency for the proportion of eggs consumed by predators to increase with increasing initial herring egg concentration but no significant function could be fit to these data (Fig. 4B). The difference in egg loss between the caged and the unprotected treatment indicates a net predation effect of 20% during the 96 h the experiment was run. Considering the temperature-dependent development time required until peak hatching (HP = 203 h at 12.3°C according to Peck et al. 2012), this net predation extrapolates to 42% for the entire herring embryonic phase (from spawning to hatching). Extrapolated to the total area of the investigated spawning bed (approximately 1.77 km^2 according to Moll, unpubl.) this equals a total loss of approximately 21.2 billion eggs (46 metric tons). Assuming a balanced gender ratio (1 : 1) and that an average western Baltic herring female carries 45,000 eggs (Anwand 1962), a total of 942,000 spawners would be required to produce this number of fertilized eggs.

We found no attached herring eggs on any of the distinct spawning controls (Fig. 2D–F) indicating that no further spawning had occurred during the experiment. Effects of subsequent spawning events during the experiment were therefore excluded.

Predator quantification

Five different species of fish were caught in the beach seine hauls conducted in the vicinity of the predator exclusion cages prior to and after the experiment. *G. aculeatus* was by far the most dominant species, followed by *P. pungitius*, *Perca fluviatilis*, *Alburnus alburnus*, and *Rutilus rutilus* (Table 1). Both before and after the experiment, the stomach content of *G. aculeatus* was dominated by herring eggs (~70% of the wet weight of stomach contents) although the proportion and total amount of herring eggs slightly decreased from the first to the second sampling (Table 2; Fig. 5). Invertebrates represented a minor proportion
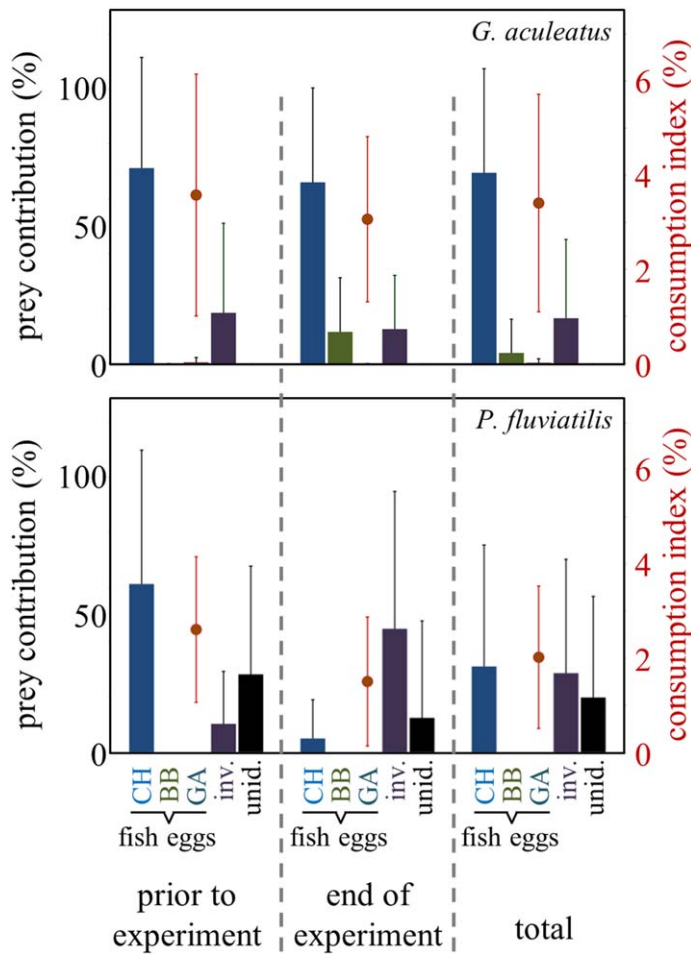
Fig. 5. Relative prey contributions to the stomach contents of selected predators (upper panel: *G. aculeatus*; lower panel: *P. fluviatilis*) estimated from samples prior to the predator exclusion experiment (03 May 2012) and at the end of experiment (08 May 2012). Bar represent mean percentages of distinct prey types (CH, herring eggs; BB, garfish (*Belone belone*) eggs; GA, stickleback eggs; inv, invertebrates; unind., unidentifiable prey items) in predator stomachs (primary vertical axis on the left side) sampled prior (3rd May) and at the end (8th May) of the experiment. "Total" represents aggregated data from both dates. The consumption index is given as points (secondary vertical axis on the right side). Error bars represent standard deviations for each data set.

(<20%) of the stomach content and were, in most cases, copepods and small isopods (*Idotea* sp.). The stomach content of river perch was dominated by herring eggs at the beginning of the experiment but the proportion of invertebrates increased in fish captured during the second sampling (mainly *Idotea* sp., Table 2; Fig. 5). The contribution of herring eggs to the stomach contents of river perch and threespine stickleback was similar (Table 2). However, the abundance of threespine stickleback was more than 170 times higher than that of river perch (Table 2) resulting in an estimated stickleback predation impact (PI) of approximately 99% (Table 3).

Table 3. Contribution of different predators to the total predation mortality of herring eggs based on the extrapolated egg loss and the results of the beach seine catches. A) Estimates excluding the cyprinids caught in the beach seine B) Estimates including the cyprinids. Asterisks indicate assumed values (e.g., values for *P. pungitius* are based on measured values of *G. aculeatus*) filling gaps of non-measured parameters.

	CI (%)	SC_{HE} (%)	PI_{HE} (%)	$C_{HEtotal}$	RE
A) Excluding cyprinids					
G. aculeatus	3.41	69.45	99.1	2.10×10^{10}	9.33×10^{5}
P. pungitius	3.41*	69.45*	0.7	1.51×10^{8}	6.70×10^{3}
P. fluviatilis	2.02	31.26	0.2	4.08×10^{7}	1.81×10^{3}
Total	–	–	100%	2.12×10^{10}	9.42×10^{5}
B) Including cyprinids					
G. aculeatus	3.41	69.45	98.7	2.09×10^{10}	9.30×10^{5}
P. pungitius	3.41*	69.45*	0.7	1.50×10^{8}	6.67×10^{3}
P. fluviatilis	2.02	31.26	0.2	4.06×10^{7}	1.81×10^{3}
A. alburnus	3.00*	50.00*	0.2	5.14×10^{7}	2.29×10^{3}
R. rutilus	3.00*	50.00*	0.2	3.30×10^{7}	1.47×10^{3}
Total	–	–	100%	2.12×10^{10}	9.42×10^{5}

CI, consumption index of the predator based on all samples (03 May 2012 and 08 May 2012); SC_{HE}, share of herring eggs in predator stomach contents (in %); PI_{HE}, predation impact of predator, i.e., the proportion of the observed predation mortality that can be assigned to the specific predator; $C_{HEtotal}$, the total number of eggs consumed by the predator in the spawning bed; RE, the corresponding reproductive equivalent (number of spawners).

Spatial spawn distribution

The semi-quantitative investigations on spatial spawn distribution in spring 2014 showed a clear SAV-dependent distribution of herring eggs on the studied spawning ground in Greifswald Bay. Herring eggs were found exclusively at stations where macrophytes were in the sample while no eggs were found at stations located on sand bars or in sublittoral areas below 3.5 m (depth limit of SAV coverage). The majority of the spawn appears to concentrate in the core of the shallow pondweed zone in water depths of approximately 1 m (Fig. 3). The experimental site was not located in the center of spawn concentration as defined 2 yr later. However, it was located in an area with interpolated spawning intensities of the categories 1 and 2 (Figs. 1, 3).

Discussion

Exclusion cage experiments are an established tool to analyze the effect of resident predators on benthic food webs (Reise 1979; Schubert and Reise 1986; Moksnes et al. 2008; Hammerschlag-Peyer et al. 2013); however, their application for investigating predation impacts on demersal eggs of marine fish is rare and mainly focused on bird predation on intertidally spawned herring eggs in coastal areas of the northeastern Pacific Ocean (Steinfeld 1972; Palsson 1984;

Bailey and Houde 1989). We established a standardized modification of this technique to study in situ predation on permanently submerged spawning beds of herring and documented a considerable predation with an estimated egg loss of 42% over the entire embryonic phase.

The discrepancy between the egg losses observed for the unprotected control and the artefact controls (Fig. 4A) can be explained by the breeding behavior of male threespine stickleback. At the beginning of May, *G. aculeatus* had already started to spawn in the study area. Male sticklebacks preferably build their nests inside of complex structures and concealments (Kynard 1979; Sargent and Gebler 1980) and aggressively protect their nests and the adjacent district against potential rivals and spawn predators (Huntingford 1976). As a consequence, artefact controls (open side walls) were used as spawning sites by male stickleback which, in turn, attacked any potential predators of herring spawn (and scientists) approaching the cages. More generally, the design of the artefact controls might also keep certain predators from preying on the eggs. For example, it is rather unlikely, that diving ducks would enter those cages for feeding.

Despite the restricted experiment duration, we consider the reduction in egg number at the caged treatment to be primarily caused by hatching of herring larvae since we cannot exclude that at least a part of the naturally spawned eggs had reached the peak hatching period (Peck et al. 2012) during the experiment. We therefore assumed that the difference between the caged and the unprotected treatment represents the net predation impact.

Population-level predation effects

Predation on demersal eggs of marine fish can be intense and may influence recruitment success. For example, in some reef fish, predator aggregations can cause 100% mortality of demersal eggs (Emslie and Jones 2001). In temperate waters, demersal egg predation has also been considered to potentially affect the recruitment success of fish species (e.g., Nilsson et al. 2004; Nilsson 2006). Our results for Atlantic herring (approximately 42% loss) are within the wide range of the predation mortality (30–100%) previously reported for Pacific herring eggs in coastal areas of the northeast Pacific (Steinfeld 1972; Palsson 1984; Bishop and Green 2001). By the means of model approaches, Richardson et al. (2011) suggested that egg predation had a significant effect on the year-class strength of northwest Atlantic herring stocks. Our study also highlights the importance of including egg predation by resident predator communities into future population models and management plans since this source of mortality may explain a significant proportion of intra- and inter-annual recruitment variability (Kotterba et al. 2014). Nevertheless, estimates will be context- and undoubtedly site-specific.

Kotterba et al. (2014) demonstrated that the intensity of predation is modulated by the magnitude of spawning activity of herring. A similar, albeit not significant trend was found in the present study. Assuming that the spatial herring egg distribution on the investigated spawning bed follows comparable patterns throughout different years (based on personal multi-annual observations in the study site), our investigations on the spawn distribution indicate that the experiment was not located in the center of highest spawn concentration (Figs. 1, 3). Furthermore, our extrapolations were focused on these parts of the spawning ground which were characterized by the same SAV coverage and composition as the experiment site (Fig. 1) excluding seagrass meadows in deeper areas which are known to be used as spawning beds as well (Scabell 1988; Kanstinger et al. 2016). Consequently, the average predation mortality of the entire spawning ground might have been underestimated.

The predation on herring eggs is probably lower during earlier periods of the spawning season, where spawn concentrations are usually higher, the abundance of predators is relatively low (Kotterba et al. 2014) and predator appetites are lower due to relatively cold water temperatures (e.g., *see* Akimova et al. 2016). Our experiment was run during the second half of the herring spawning season when predators were likely more active. During this latter period, a strong relation exists between the abundance of newly hatched larvae and later life-stages suggesting that egg survival during the second half of the spring spawning season might be of extraordinary importance for the cohort survival (Polte et al. 2014).

Specific predator importance

On the northeastern Pacific coast, many different predators such as invertebrates (Palsson 1984; Fox et al. 2014), birds (Bishop and Green 2001; Lok et al. 2008) and even mammalian apex predators (Fox et al. 2015) can strongly benefit from consuming easily accessible, intertidally spawned herring eggs during low tide. In permanently submerged spawning beds, however, mortality due to terrestrial predators and non-diving water fowl is expected to be negligible. In these habitats such as coastal areas of the Baltic Sea, avian predation is restricted to that by diving ducks such as the long-tailed duck (*Clangula hyemalis*) (Leipe 1985; Stempniewicz 1995) or Steller's Eider (*Polysticta stelleri*) (Zydelis and Esler 2005) and aquatic invertebrates and piscine predators (Kotterba et al. 2014). We observed no diving ducks at the study site during the experiment which is in accordance with Skov et al. (2011) who described a dramatic decrease of these water fowl populations in the Baltic Sea in recent years. During spring-time, the invasive estuarine mud crab (*Rhithropanopeus harrisii*) represents the main potential invertebrate predator of herring eggs in the study area. However, Möller (2006) investigated the feeding ecology of *R. harrisii* in Greifswald Bay and found only a marginal predation on herring eggs by this decapod. We therefore assumed the predation effects of water birds and this invertebrate to be of minor importance for our experimental results.

Based on our findings, one fish species, the threespine stickleback, was responsible for the majority of the predation losses even when we assumed some predation by resident cyprinids (Table 3). Threespine stickleback has been previously documented to prey on herring eggs (Scabell 1988; Rajasilta et al. 1993; Kotterba et al. 2014). Our estimate of the large (99%) contribution of stickleback to predation losses of herring eggs is much higher than that (9%) predicted by a predation model of Kotterba et al. (2014) which was applied to our empirical data set. While our results are based on the relative abundance of sticklebacks according to the beach seine catches, the empirical model relies on the absolute abundance of sticklebacks in the field (*see* Kotterba et al. 2014 for details). Thus, the difference may primarily stem from an underestimation of the absolute stickleback abundance and might represent the range wherein the actual herring egg predation by *G. aculeatus* can be expected. This is supported by observations with a time-lapse camera during another predator exclusion experiment in the study area (Kotterba et al. 2014) which indicated a similar composition of the predator community as found in the beach seine catches. Although we cannot completely exclude that other potential predators such as the nocturnal flounder (*Platichthys flesus*) or invertebrates (Palsson 1984; Torniainen and Lehtiniemi 2008) might act as additional consumers of herring eggs, none of these reach such a dominant abundance as *G. aculeatus* on the spawning beds in spring. We therefore consider the threespine stickleback to be by far the most important resident predator with a PI probably closer to the upper limit of the margin given above. Regardless of the discrepancy in predation estimates, the results of the present study suggest that the recent increase in the size of the stickleback population in the Baltic Sea (Bergström et al. 2015) will likely increase the predation impact on herring eggs in future.

Benefits for the resident predator community

Southwest Baltic herring begin to spawn in early spring when the abundance of zooplankton is relatively low (Brenning 1989; Paulsen et al. 2014). The pulse of spawning activity may, therefore, be particularly important as prey during this season (Willson and Womble 2006). There are many examples of the importance of ephemeral yet abundant prey such as spawning runs of Pacific salmon (*Oncorhynchus* spp.) and bears (*Ursus* spp.) in North America (Willson et al. 1998), the "sardine (*Sarginops sagax*) run" and a broad variety of piscine, avian, and mammalian predators in South Africa (O'Donoghue et al. 2010) as well as Pacific herring and terrestrial predators in the Northeastern Pacific (Willson and Womble 2006; Fox et al. 2014, 2015). Considering the stomach contents of the piscine predators analyzed in this study, predators appear to target herring eggs during the spawning season (Fig. 5). While the import of carbon and energy from herring spawning appears negligible in relation to the total annual primary production, it might nevertheless play an important role in supporting resident, secondary consumers in early spring (Hay and Fulton 1983).

Our study underscores the importance of interactions between offshore and inshore communities. A broad variety of marine fishes perform spawning migrations into coastal areas, transitional inshore waters or even into freshwater systems. Well-known examples include striped bass *Morone saxatilis* (Walbaum 1792) (Carmichael et al. 1998), shad and river herring *Alosa* spp. (Limburg and Waldman 2009), capelin *Mallotus villosus* (Müller 1776) (Nakashima and Wheeler 2002), and smelts *Osmerus* spp. (Limburg and Waldman 2009). The prevalence of anadromy as a life history strategy of marine fish highlights how the food webs of oceanic ecosystems will depend on the proper functioning of nearshore and transitional waters as nursery habitats. Evaluating how anthropogenic coastal habitat alteration (including eutrophication, habitat fractioning, climate change driven regime shifts, and the introduction of non-native species) may have impacts to marine food webs will require a better understanding of the interactions between the resident community and its temporary cohabiters.

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Acknowledgments

Conflict of Interest

None declared.