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Baltic herring (*Clupea harengus membras*) spawning grounds on the Lithuanian coast: current status and shaping factors*

KEYWORDS
Spawning bed distribution
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Abstract

During the 2009 and 2010 seasons Baltic herring (*Clupea harengus membras* L.) spawning grounds were investigated by SCUBA divers off the Lithuanian Baltic Sea coast. The most important spawning substrate was a hard bottom overgrown with red algae *Furcellaria lumbricalis*, but only 32.8% of potentially suitable spawning locations had herring eggs. Bottom geomorphological analysis using multibeam bathymetry revealed that the distribution of spawning beds is not random, but is determined rather by small-scale geomorphological features. The majority of the detected spawning locations were on local elevations characterised by 2.4 ± 1.1 m depth differences and 4.8 ± 1.8 slopes.

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1. Introduction

Baltic herring (*Clupea harengus membras* L.) is one of the dominant fish species in the Baltic Sea (Rajasilta et al. 2006). This makes it not only an important resource for commercial fishing (Cardinale & Arrhenius 2000) but also an important part of the pelagic ecosystem. Baltic herring spawn throughout the Baltic, and as a result of the strong environmental gradients different populations have unique biological and spawning characteristics (Geffen 2009).

In the period from 1991 to 2010 Baltic herring catches in the Lithuanian economic zone varied from 0.7 to 6.5 thousand tons per year, making it the most important fish resource (Fedotova 2010). However, Baltic herring stocks are constantly changing, owing to anthropogenic impact and natural hydrological regime shifts in the Baltic Sea and the North Atlantic region (ICES 2008), indicating that careful management is needed for this species.

Previous mappings of the Baltic herring spawning grounds in Lithuanian coastal waters were carried out by the Baltic Fishery Research Institute (BaltNIIRH, Riga). In 1976 using SCUBA divers they documented two spawning grounds: near the town of Palanga and the village of Karklė (BaltNIIRH 1989). However, that mapping was supported only by 7 actual finds of herring eggs (3 off Palanga and 4 off Karklė) and was therefore relatively imprecise. Repeated BaltNIIRH surveys after the 'Globe Assimi' oil-tanker disaster in the port of Klaipėda in 1981, which resulted in a massive (16 000 tons) oil spill, showed that the spawning ground off Karklė (closer to the disaster site) had been destroyed (Koroliov 1991). Since then, no mapping of the Baltic herring spawning grounds has been carried out.

Although the patterns of Baltic herring spawning have been studied intensively in other Baltic Sea regions, the factors shaping its distribution are not fully understood. Although there are a few reports stating that spawning beds are often found close to the deeper areas (Kääriä et al. 1988, 1997, Rajasilta et al. 1993), the precise relationship between bottom geomorphology and spawning beds has not been analysed. To do so, high resolution bathymetric data with modern analytical tools are needed.

The aim of this study is to evaluate the current status of the Baltic herring spawning grounds in Lithuanian coastal waters and to assess the factors determining their spatial distribution, with special emphasis on small-scale geomorphological features of the sea bed. This is important for gaining a better understanding of Baltic herring spawning patterns and for the better management of herring stocks and their restoration.

2. Material and methods

2.1. Study area

The Lithuanian coast in the south-eastern Baltic Sea is exposed to all westerly directions, with a wind fetch exceeding 200 km. The coastline is straight, with no inlets, islands or any other features providing shelter. In the southern part, along the Curonian spit, coastal bottom sediments are dominated by sand, while in the northern part they consist of a complex mosaic of moraine clay, large boulders, cobbles, pebbles, gravel and sand (Gulbinskas & Trimonis 1999). In general, Baltic herring do not spawn on soft substrates (Rajasilta et al. 1989, Kääriä et al. 1997), and no spawning events along the Curonian Spit have been registered. Therefore, only the northern part of the Lithuanian coast was investigated during this study.

The average near-bottom salinity in the area ranges from 6 to 7.5 PSU, but may occasionally drop to less than 5 PSU (Daunys et al. 2007) as a result of freshwater inflows from the Curonian Lagoon. The hyper-eutrophic waters of the lagoon propagate into the sea, reducing underwater visibility from 3–6 m to 0–2 m (typically no more than 1 m) and inducing a faster rate of organic matter deposition on the bottom.

Bottom biotopes in the study area are distributed according to depth and substrate availability (Olenin & Labanauskas 1994). From the shore to 3 m depth the moving sand biotope is predominant, with occasional large boulders overgrown by filamentous green algae. At greater depths hard substrates become more common; they are occupied by red algal communities: at 3–4 m depth by *Polysiphonia fucoides* and from 4 to 16 m by *Furcellaria lumbricalis* (Bučas 2009). The most conspicuous macrozoobenthos species on the hard substrates are blue mussels *Mytilus trossulus* and bay barnacles *Balanus improvisus* (Olenin & Daunys 2004).

2.2. Field sampling

The Baltic herring spawning grounds were mapped in 2009–2010 during the spawning period (March–May). In the 2009 season the sampling points were evenly distributed (the average distance between the sampling points was approximately 800 m) over the *F. lumbricalis* biotopes, reported to be the most important for Baltic herring spawning in Lithuanian coastal waters (BaltNIIRH 1989, Olenin & Labanauskas 1995, Maksimov et al. 1996, Fedotova 2010) (Figure 1). In the 2010 season sampling efforts were concentrated in the central part of the study area, where high resolution (1.9×1.9 m per pixel) multibeam bathymetry (KU MARSTEC, unpublished data) opportunistically became available. This data allowed

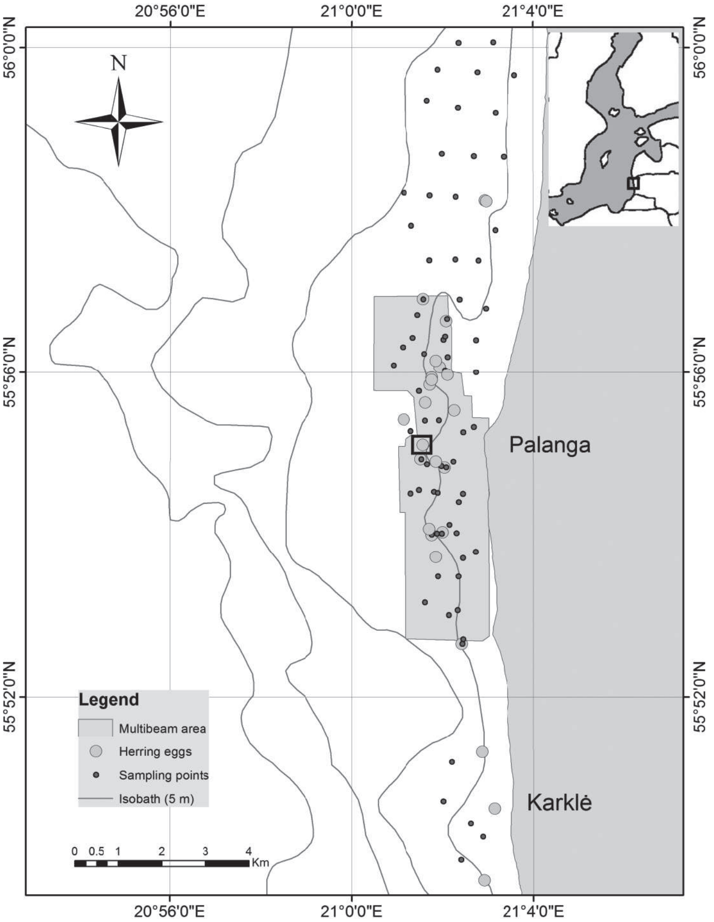

Figure 1. Sampling points and detected spawning beds. The black square at top right shows the location of the study area. The black square in the middle indicates the spawning bed where a detailed inspection was carried out in 2009

the small geomorphological bottom features to be derived for the assessment of their role in the distribution of Baltic herring spawning beds.

Baltic herring eggs are relatively small (< 2 mm) and semi-transparent, therefore hardly detectable by remote methods (e.g. underwater video), especially in low visibility conditions. Field data were collected by SCUBA divers. At each sampling point the diver recorded the presence/absence of Baltic herring eggs and spawning substrate. Additionally, a benthic sample was collected from the substrate using a 0.04 m^2 frame (Kautsky 1993). The benthic samples were analysed using a Nikon Eclipse E200 microscope to confirm the presence/absence of eggs, and developmental stages (from *a* to *q*) were distinguished according to Veersalu & Saat (2003).

Table 1. SCUBA sampling data during 2006–2010

	Start date	End date	Number of locations	Min depth [m]	Max depth [m]
2006–2008	April	May	5	6	11
2009 season	7 April	29 April	52	4	14
2010 season	19 April	7 May	41	3	10

In 2009–2010 93 points were sampled by SCUBA divers. Opportunistic data from five occasional findings of Baltic herring eggs in 2006–2008 (KU MARSTEC unpublished data) were added (Table 1, Figure 1). The total data consisted of 98 sampling points, 56 of which were in the multibeam area (Figure 1). The samples were collected at depths from 3 to 14 m, whereas most of them within the 5–10 m depth interval (Figure 2).

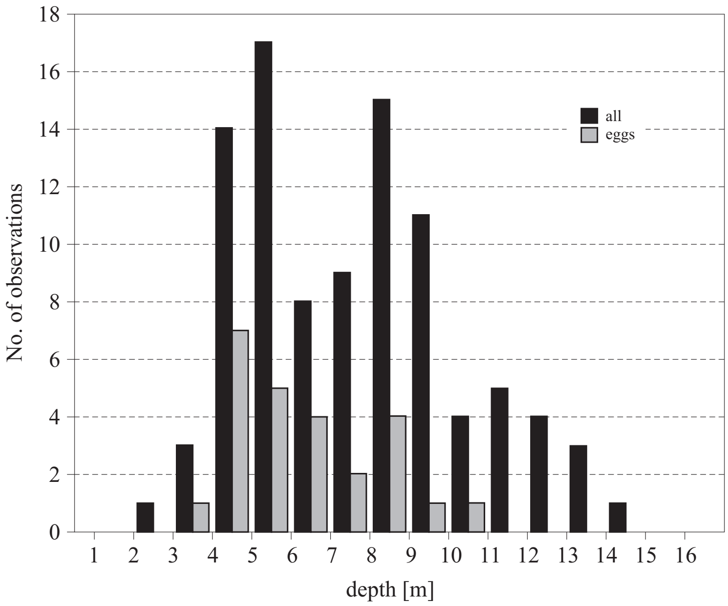

Figure 2. Depth distribution of sampling points and herring egg findings

Weather conditions were very calm during the 2009 season, allowing us to perform an additional detailed survey of a single spawning bed: five transects, the lengths of which ranged from 46 to 149 m (Figure 3). The presence/absence of Baltic herring eggs was recorded by divers who used a floating buoy to signal their findings and position to the crew on the boat. During the same season the sampling window was relatively wide (22 days) with more or less evenly distributed sampling dates, which allowed egg development to be monitored.

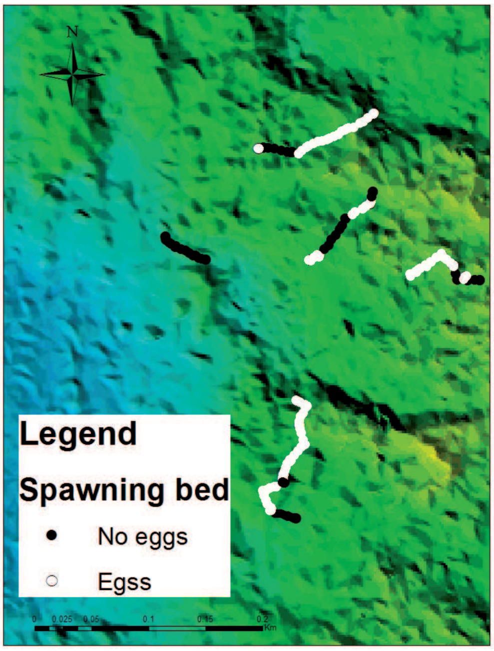

Figure 3. Spawning bed inspected in 2009. Five transects were done; the detailed bathymetry is shown. The white transect segments indicate the parts with herring eggs, and the black segments have no eggs

2.3. Bottom geomorphological analysis

The effect of bottom geomorphology on the distribution of Baltic herring spawning beds was analysed using seabed surface profiles. An east-west profile direction was chosen in accordance with western Baltic herring spawning migration patterns in Lithuanian waters (Fedotova 2010). The patchiness of the spawning beds was substantial. We therefore assumed that small-scale bottom geomorphological features were important factors shaping the distribution of spawning beds and could affect these within a 100 m radius around the detected spawning location. Therefore, for each point where spawning was recorded, 200 m long bottom surface profiles were drawn eastwards and westwards using a IVS3D Fledermaus 7 profiling tool with the spawning location in the middle. As a result we obtained two 100 m bottom surface profiles for each spawning location: towards the coast (eastwards) and towards the open sea (westwards). The bottom slope was estimated from these profiles, since it is an important geomorphological descriptor describing surface steepness and direction. The slope is calculated as the ratio of the vertical (elevation) difference to the horizontal range. In this study bottom slopes were derived in two ways: as an average along the whole 100 m profiles and as an average along 10 m segments in order to indicate more local effects. Because of the direction of the bottom profiles, negative slope values correspond to western slopes (from west to east) and positive values correspond to eastern slopes (from east to west).

3. Results and discussion

3.1. Start of the spawning season

For many fish species spawning is triggered by water temperature. Owing to the variety of spawning strategies of the Baltic herring this temperature is different for different populations (Elmer 1983, Evtjukhova & Berzinsh 1983, Aneer 1989, Kornilovs 1994, Klinkhardt 1996, Krasovskaya 2002). Baltic herring spawning usually starts in March (sometimes in February) in the south-western and southern areas of the Baltic Sea when the water temperature reaches 4°C (Klinkhardt 1996), continues till the middle of summer and finishes in the northern parts at water temperatures up to 15–16°C (Krasovskaya 2002). Generally, spawning temperatures tend to increase with latitude, resulting in later spawning seasons for the northern populations (Jørgensen et al. 2005).

Water surface temperature was measured daily by the Lithuanian Environmental Protection Agency, Marine Research Department (EPA-MRD) at the Palanga meteorological station, which is located close to the centre of the multibeam area (Figure 1). The first eggs were found when the surface water temperature was 5.9°C in 2009 and 6.4°C in 2010

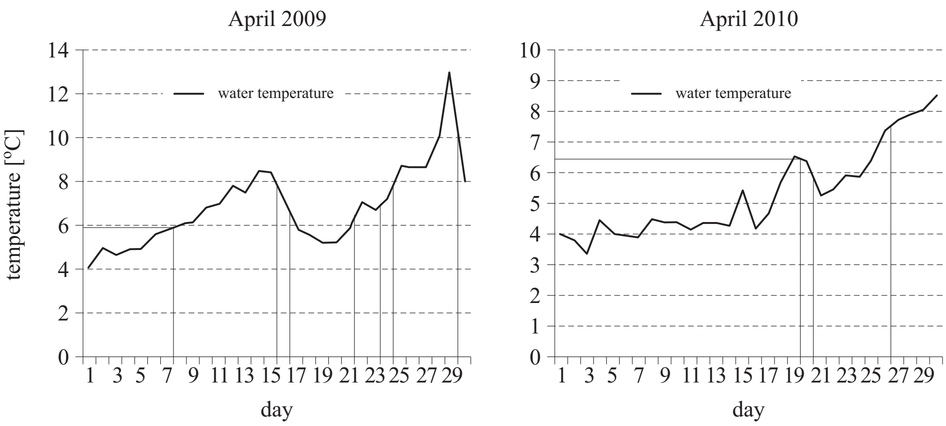

Figure 4. Water temperature at Palanga meteorological station in April 2009 and April 2010 (unpublished EPA-MRD data). First eggs finding day and temperature are indicated by vertical and horizontal lines; other sampling days in April are shown as vertical lines

(Figure 4); in our area, therefore, spawning most likely begins when the temperature reaches approximately 6°C. These values are in good agreement with the general trend of herring spawning temperatures along the Baltic Sea (Krasovskaya 2002, Jørgensen et al. 2005).

3.2. Distribution of spawning beds

Baltic herring eggs were found at 25 sites, 18 of them located within the multibeam area (Figure 1). The majority (80%) of eggs were found within a depth interval from 4 to 8 m, with a mean depth of 6.5 ± 1.8 m (Figure 3). After a detailed inspection in 2009 we found that spawning beds seemed to be extremely patchy, where continuous egg deposits extended over a distance of ca 50–70 m, and in many cases much less (Figure 2).

Herring eggs were present from Karklė to Palanga (Figure 1), meaning that the Karklė spawning ground had successfully recovered from the 'Globe Assimi' oil-spill incident in 1981. Moreover, areas with detected spawning locations were larger than during previous mapping efforts (BaltNIIRH 1989). Our data suggest that most probably there are not two separate spawning locations but rather a single continuum, and that the previously reported pattern is due to the patchiness of the spawning beds.

3.3. Spawning substrate

Generally Baltic herring does not spawn on soft bottom substrates (Rajasilta et al. 1989, Kääriä et al. 1997), but prefers hard substrates with vegetation. Most likely there are no preferences for specific algal species: for example, in the coastal waters of Finland Baltic herring spawns on at least 32 different plant species (Aneer 1989).

During this study Baltic herring eggs were found on three different substrates: perennial red algae (*F. lumbricalis* and *P. fucoides*), and boulders without vegetation but overgrown by blue mussels *Mytilus trossulus*. The majority of eggs occurred on *F. lumbricalis* (21 locations out of 25), *P. fucoides* (3 locations), and on *M. trossulus* (1 location). In earlier studies only *F. lumbricalis* meadows were regarded as a substrate important for Baltic herring reproduction (BaltNIIRH 1989, Olenin & Labanauskas 1995, Maksimov et al. 1996, Fedotova 2010). Although the significance of *F. lumbricalis* in providing spawning substrate is undeniable, other substrates were used too. Of total 98 points sampled, 64 had significant (more than 10%) *F. lumbricalis* cover, therefore eggs were present in only 32.8% (21 out of 64) of potentially suitable *F. lumbricalis* locations.

3.4. Egg development

The prolonged sampling period in 2009 allowed us to collect eggs at all developmental stages, from the very first (*a*–*e*) to the very last ones (*p*–*q*) (Table 2). Comparing eggs collected on the same day from different depths (Table 2, see 15 April and 23 April), it seems that the development of eggs laid in shallower areas was lagging behind that of eggs laid in deeper areas. It is known that Baltic herring spawns in waves (Krasovskaya 2002): this could be the result of earlier spawning in deeper areas.

Table 2. Egg developmental stages, spawning substrate and depth during the 2009 field season

Date	Spawning substrate	Depth [m]	Egg stage (Veersalu & Saat 2003)
7 April	*F. lumbricalis*	8	*a*–*e*
	M. trossulus	8.5	*a*–*e*
	F. lumbricalis	10.5	*a*–*e*
15 April	*F. lumbricalis*	6.5	*h*–*i*
	P. fucoides	4	*f*–*g*
16 April	*F. lumbricalis*	7	*m*–*n*
21 April	*F. lumbricalis*	9	*m*–*n*
23 April	*F. lumbricalis*	8.5	*m*–*n*
	F. lumbricalis	4.8	*h*–*i*
	F. lumbricalis	6	*n*–*o*
24 April	*F. lumbricalis*	9	*o*–*p*
29 April	*F. lumbricalis*	8	*p*–*q*

In this study three spawning locations were visited twice. Two of them (one with *F. lumbricalis* and one with *M. trossulus*) were visited on 7 April 2009, when eggs were found in the very early developmental stages (*a*–*e*). Three weeks later on *F. lumbricalis* we found eggs in the final developmental stages (*p*–*q*) and already empty egg shells, whereas no eggs or empty egg shells were present on *M. trossulus*. Since the two spawning locations are only 980 m apart and the respective depths are 8 and 8.5 m, indicating similar environmental conditions, the eggs on *M. trossulus* probably failed to develop and hatch.

The third spawning bed, which is dominated by *F. lumbricalis*, was visited twice within a period of three days at the end of April 2009. The sample taken on 21 April 2009 contained eggs in the embryonic developmental stages (*m*–*n*), and 3 days later the eggs had embryos already in developmental stages (*o*–*p*).

According to Rajasilta et al. (1989, 1993, 2006) red algae (including *F. lumbricalis*) have a negative effect on Baltic herring eggs, causing higher egg mortality. However, in this study, the embryos in the eggs collected from *F. lumbricalis* thalli developed normally to the very last developmental stages, resulting in successful mass hatching. One of the advantages of *F. lumbricalis* as a spawning substrate could be the extensive 3D structure of the firm *F. lumbricalis* thalli. This can accommodate a larger number of eggs while ensuring their proper aeration compared with other spawning surfaces, on which eggs may be laid in multilayers. It is known that embryonic oxygen uptake increases in the later development stages (Silva & Tytlerb 1973); in multilayer mats only the eggs in the upper layers develop successfully to the last stages, whereas the eggs in the deeper layers abort (the abortion stage is layer-dependent: the deeper the egg, the earlier the abortion stage) and/or show severe embryonic abnormalities (Messieh & Rosenthal 1989), most likely due to the lack of oxygen. This is less likely to happen when *F. lumbricalis* is used as a spawning substrate.

3.5. Particulars of seabed relief in the spawning locations

The locations of Baltic herring spawning beds are usually very specific (Geffen 2009), and there are reports that Baltic herrings return to the same spawning beds year after year (Oulasvirta & Lehtonen 1988, Bergstrm et al. 2007). This occurs even if there is a strong anthropogenic impact in the area (Rajasilta et al. 2006).

During this study the hydrological conditions between two spawning seasons were very different: in 2009 there was strong upwelling resulting in colder water and higher salinity. In 2010 the upwelling was not significant and the water in the coastal area was mixed with hyper-eutrophic Curonian Lagoon waters, resulting in greater turbidity and lower salinity. Moreover, the winter in 2010 was much colder and longer compared with 2009, resulting in later spawning (Figure 4). Despite these differences, the spatial pattern of the spawning persisted, indicating that there are more stable factors determining the distribution of the spawning beds than just the hydrological conditions. One such factor could be the bottom geomorphology, which was tested in this study in terms of the bottom slope.

Table 3 shows the average 100 m profile slopes to the east and west of the sampling points, the average profile depth gradients as well as the average maximum westward and eastward slopes values for 10 m segments with corresponding standard deviations. Graphical representations of the bottom profiles are shown in Figure 5.

The general bottom slope pattern, i.e. the continuous seaward increase in depth, was confirmed in only 5 profiles (12, 13, 14, 15 and 16). The relief

Table 3. Geomorphological characteristics of bottom profiles at the spawning locations. Positive values indicate eastward slopes and negative ones westward slopes

Direction from spawning point	Average slope (100 m)	Max westward slope (10 m)	Max eastward slope (10 m)	Depth gradient (within 100 m)
eastwards	0.6 ± 0.9	-2.1 ± 1.7	4.1 ± 2.4	1.9 ± 1.0
westwards	-0.7 ± 0.9	-4.8 ± 1.8	3.4 ± 2.3	2.4 ± 1.1

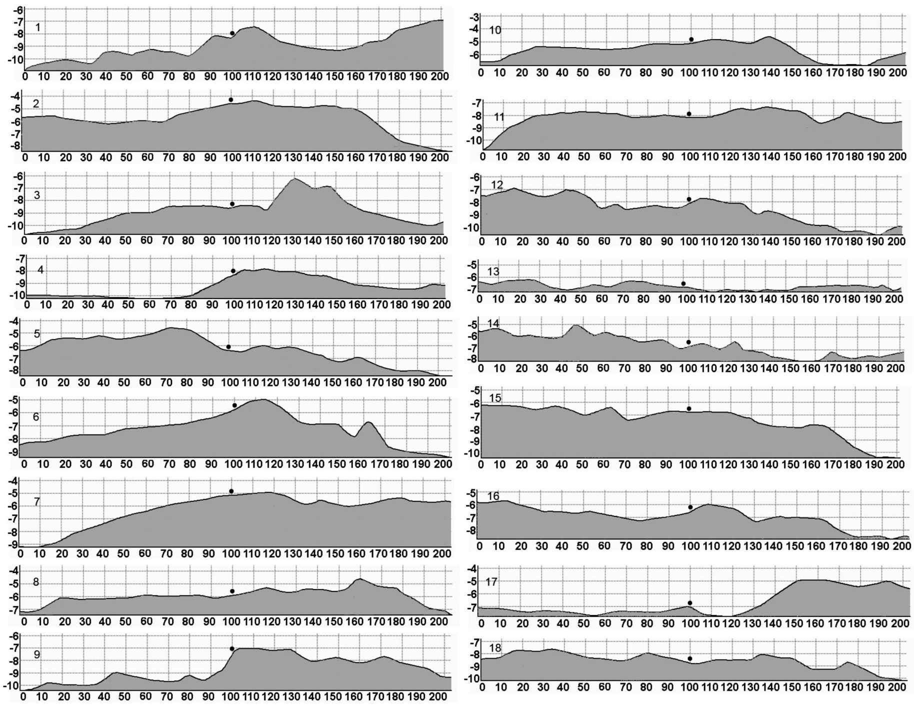

Figure 5. Seabed profiles (200 m (x-axis) east-west direction) at the spawning locations. The coastal side is on the left, and detected spawning locations are indicated in the centre by black dots. On the y-axis the depth is given in metres

in the majority of profiles was more complex: the average slopes for 100 m profiles (Table 3) indicate that towards the shore eastward slopes prevailed over westward ones, contradicting the natural tendency for depth to decrease close to the shore. In the seaward direction (west) over a distance of 100 m the majority of detected spawning locations shared a significant depth gradient (mean value 2.4 ± 1.1 m), and there was at least one 10 m segment with a relatively steep westward slope (mean value -4.8 ± 1.8) (Table 3, Figure 5).

The spawning locations plotted on the multibeam bathymetry map seems to correspond to local bottom elevations (Figure 6), and three relatively large spawning beds, extending for several hundred metres, can be distinguished (Table 4). Although these areas are geomorphologically similar, they differ biologically: two of them are dominated by the red alga *F. lumbricalis*, whereas the third is dominated by red alga *P. fucoides*, suggesting that for Baltic herring choosing spawning beds, bottom geomorphology plays a more important role than biology (e.g. spawning substrate). Besides those bigger spawning beds, eggs were found on several smaller-scale local elevations (Figure 6).

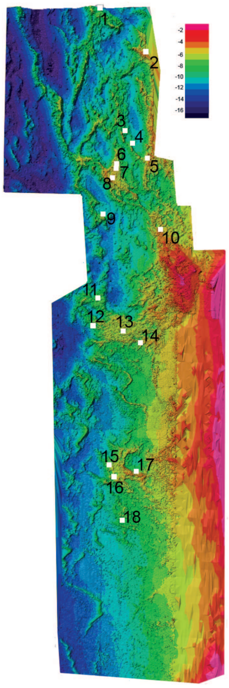

Figure 6. Location of detected spawning beds on the multibeam bathymetry map (only presences are shown)

Table 4. General characteristics of large spawning beds

	Length	Width	Depth interval	Min depth	Max depth
Area 1 (points 6–8)	540	350	2	5.5	7.5
Area 2 (points 12–14)	330	650	2.5	5.5	8
Area 3 (points 15–17)	390	330	2.5	5	7.5

The Lithuanian coast does not have any sheltered areas, preferred by other populations of the Baltic herring during spawning (e.g. Aneer et al.

1983, Kääriä et al. 1997, Krasovskaya 2002, Rajasilta et al. 2006), which probably explains why in our area Baltic herrings spawn at greater depths (4–8 m) than the 0.5–4 m typical of sheltered areas (Aneer et al. 1983). Despite the different average spawning depth, the spawning onset temperature (ca 6°C) remains in agreement with the overall trend in the Baltic (Klinkhardt 1996, Krasovskaya 2002). With increasing spawning depth, Baltic herring have limited access to algal beds, because only two red algae species (*F. lumbricalis* and *P. fucoides*) form sufficiently dense cover suitable for successful egg development. Although in this study eggs were also found on unvegetated substrates, this was recorded at only one location (of 31 unvegetated locations sampled) and during a repeat survey, no eggs were not found on such a substrate, signifying the importance of vegetation cover.

The spawning locations remained constant from season to season: we believe that the most probable reason for such consistency is the local geomorphology – a combination of slopes and depth gradients. The latter are relatively stable over time compared to the hydrological conditions. Other authors reported that the spawning locations were often close to deeper areas (Kääriä et al. 1988, 1997, Rajasilta et al. 1993), which is in good agreement with our findings. It suggests that the observed phenomenon is not specific to the Lithuanian coast, but is indicative rather of a more general pattern, typical of other Baltic herring populations.

4. Conclusions

Baltic herring spawning beds remain constant from year to year even at a small spatial scale, and their distribution does not depend on seasonal hydrological conditions. The spawning beds are very patchy and only one third of the potentially suitable area (a vegetated hard bottom in the 4–8 m depth interval) is actually used for spawning in our area.

Although the Baltic herring is not substrate-specific during spawning (it seems that bottom geomorphology plays a more important role), the substrate is important for egg development: eggs spawned on *M. trossulus* were not found during a repeat survey and most probably failed to develop and hatch. Our data confirm the findings of other authors that in Lithuanian coastal waters a seabed dominated by *F. lumbricalis* is the most important one for herring reproduction (BaltNIIRH 1989, Olenin & Labanauskas 1995, Maksimov et al. 1996, Fedotova 2010), even if only one third of it is actually used for spawning. The red algae *P. fucoides* also acts as a suitable spawning substrate.

Slope proved to be good geomorphic descriptor for Baltic herring spawning beds. The majority of detected spawning locations are characterised by relatively steep seaward slopes, significant changes in depth and are on local seabed elevations.

The significance of relatively small geomorphological features suggests that any estimates or models of spatial spawning grounds using rough bathymetric data are going to significantly overestimate actual spawning areas; the availability of high resolution bathymetry is essential. Owing to the substantial patchiness of the spawning beds it is easy to falsely detect their absence, therefore presence-only approaches (e.g. maximum entropy modelling) are preferable to presence-absence methods (e.g. logistic regression).

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