Oceanological and Hydrobiological Studies

International Journal of Oceanography and Hydrobiology

Volume 48, No. 4, December 2019
pages (328-336)

ISSN 1730-413X
eISSN 1897-3191

Changes in the composition and abundance of ichthyoplankton along environmental gradients of the southern Baltic Sea

by

Małgorzata Dembek[1,*],
Luiza Bielecka[2],
Piotr Margoński[1],
Tycjan Wodzinowski[1]

DOI: **10.2478/ohs-2019-0030**
Category: **Original research paper**
Received: **February 15, 2019**
Accepted: **April 23, 2019**

[1]*National Marine Fisheries Research Institute, Department of Fisheries Oceanography and Marine Ecology, ul. Kołłątaja 1, 81-332 Gdynia, Poland*

[2]*University of Gdańsk, Faculty of Oceanography and Geography, Institute of Oceanography, Department of Marine Ecosystems Functioning, Al. M. Piłsudskiego 46, 81-378 Gdynia, Poland*

* Corresponding author: *mdembek@mir.gdynia.pl*

Abstract

The research focuses mainly on the ichthyoplankton of the Baltic deeps – the inflow route from the North Sea. The ichthyoplankton was represented by eggs and larvae of nine fish species: sprat, cod, herring, European flounder, fourbeard rockling, longspined bullhead, straightnose pipefish, sand goby and great sandeel. The species composition of ichthyoplankton varied depending on the location of a given site – the number of taxa ranged from one to five. The Slupsk Furrow was the most diversified area in terms of the number of taxa, while the highest abundance of ichthyoplankton occurred in the Bornholm Basin. The sprat clearly dominated and inhabited all the surveyed depths. Of the remaining species, only cod eggs as well as eggs and larvae of the fourbeard rockling significantly contributed to this formation. They occurred within their main spawning grounds (Bornholm Deep in the near-bottom layers) and secondary spawning grounds (Slupsk Furrow and Gdansk Deep) where salinity and oxygenation of water favored their development. Biometric research has shown that the diameter of eggs was within the size range typical of the Baltic Sea.

Key words: ichthyoplankton, deeps, Baltic Sea, fish eggs

DE GRUYTER

The *Oceanological and Hydrobiological Studies* is online at www.oandhs.pl

Introduction

The location of the Baltic Sea, the largest inland brackish water body in the world, and its hydrological conditions have a significant impact on the organisms occurring there. Factors such as salinity, temperature, oxygen concentration or the availability of light directly affect the species structure, distribution, and size of organisms. The greatest differences in the occurrence of individual fish species in the Baltic Sea result from salinity (Snoeijs-Leijonmalm & Andrén 2017). The inflows from the North Sea change the hydrological conditions, which means an increase in salinity and oxygen concentration (especially in the western part of the sea; Kullenberg 1981), thus more favorable conditions for the reproduction of some species of the southern Baltic ichthyofauna, such as cod, fourbeard rockling or European flounder (Russel 1976), but also for the survival of their early stages of development (Baumann et al. 2006).

Fish are an important part of the marine ecosystem. Fisheries should be carefully managed to maintain sustainable fish stocks as well as sustainable ecosystems (Bagge & Thurow 1994). It is therefore important that these resources are continuously monitored. A very important indicator of the state of fish stocks is the assessment of the ichthyoplankton distribution (Sparholt 1994). Species of fish that live in the deeper layers of water can be transported from the Kattegat to the Baltic Sea with the supply of salt water from the North Sea (Svedäng & Bardon 2003). Examples include *Merlangius merlangus* and *Melanogrammus aeglefinus*. Their dispersion is strictly controlled by barocline inflows and by the topography of the seabed. If environmental conditions are favorable for reproduction and growth, these species can form stable populations (Snoeijs-Leijonmalm & Andrén 2017). Thus, the presence of species characteristic of the North Sea in the Baltic Sea may be one of the indicators of the inflow event.

The dominant species in the Baltic Sea – cod, sprat and herring (Sparholt 1994) – deserve special attention. Each of these species requires specific conditions for spawning and the development of eggs and larvae. However, sprat is the most tolerant of salinity gradients, which makes this species very widespread in the Baltic Sea (ICES 2002). Sprat plays an important role in the ecosystem, both as food for piscivorous organisms and as the main consumer of zooplankton (Kornilovs et al. 2001). It should be noted that the populations of sprat and cod are interrelated (Sparholt 1996). Cod feeds on sprat, while sprat, under specific hydrological conditions, can largely prey on cod eggs (Neumann et al. 2016). The dominance of one of these two species depends on a combination of the main driving factors as hydrological conditions or actual fishing pressure (Sparholt 1994). While most of the research focuses on these three species, the majority of samples have recently been collected in the Bornholm Basin, which is the spawning ground for species such as sprat, cod and fourbeard rockling (Kraus & Koester 2004; Horbowa & Fey 2013).

Due to the wide and varied spectrum of tolerance for the environmental conditions of individual fish species, the early stages of development can be used to monitor changes in marine ecosystems. An important feature is their sensitivity to changes taking place in the environment. The response to these changes is their distribution and abundance (Sparholt 1994). Knowledge of the number, distribution and survival of the early stages of fish development is particularly important for assessing their potential contribution to the recruitment process.

The objective of the study is to determine the diversity of species, quantity and size distribution of the early stages of fish development in the southern Baltic Sea, with particular regard to changes in depth and salinity gradients that significantly affect the spawning conditions of some fish species. The hydrological conditions in the southern Baltic Sea are very dynamic and therefore affect changes observed in the diversity of ichthyoplankton when moving eastward along the sampling profile.

Materials and methods

Sample collections

The research material was collected in June 2015 during an international cruise on the scientific ship r/v "Akademik Ioffe" as part of the project "Program of comprehensive research of the Baltic Sea" (Federal program "World Ocean"). Samples were collected at seven sites located in the southern Baltic Sea: two in the Arkona Basin (GA1 and GA2), one in the Bornholm Basin (GB), the Slupsk Furrow (RS), the Gotland Basin (GG), the Gdansk Deep (GGd), and in a shallower area near Krynica Morska (Krynica; Fig. 1). An additional zooplankton sample was collected in the Bornholm Basin in May 2015 on board s/y "Oceania" (site IBY5 May). The vertical distribution was discussed based on data collected in June 2015 during the r/v "Baltica" cruise (site BB23 in the Bornholm Basin).

Two to three hauls were made at each site: (i) from the whole water column (bottom to surface), (ii) from the pycnocline to the surface, and (iii) in the near-surface layer (2–0 m; Table 1). For this purpose,

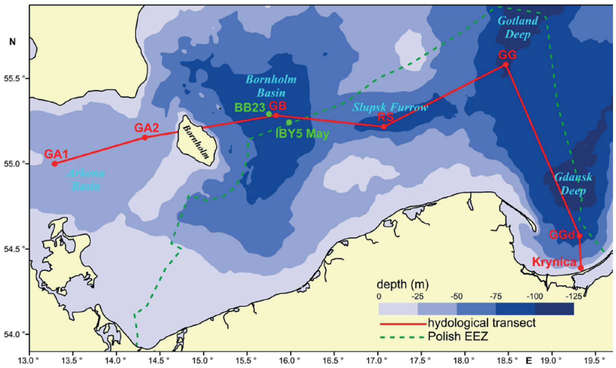

Figure 1

Map presenting the sampling sites in the southern Baltic Sea (Arkona Basin: GA1 and GA2, GB, BB23 and IBY5 in the Bornholm Basin, RS – Slupsk Furrow, GG – Gotland Deep, GGd and Krynica in the Gdansk Basin)

an open plankton net with a mesh size of 100 μm and the opening area of 0.44 m^2 was used. "Oceania" samples were collected by a WP-2 net with a closing mechanism (100 μm mesh size with a net opening of 0.25 m^2). "Baltica" samples were collected using the MultiNet system with a mesh size of 300 μm in 5 m strata from the surface to near-bottom layers. All samples were preserved in a 10% formalin solution.

Vertical profiles of hydrological parameters, including salinity and temperature using the CTD-system, were recorded at each site (except for GA1).

Ichthyoplankton data

All fish eggs and larvae were selected from the zooplankton samples. Laboratory examinations were performed using a Nikon SMZ 1500 stereoscopic microscope. The identification of eggs and larvae was performed in accordance with Russel (1976), Munk and Nielsen (2005) and Horbowa and Fey (2013). Stages IA and IB were combined into one category due to the difficulties associated with distinguishing between the early and late blasts.

The total number of eggs and larvae was counted in each sample and their abundance was calculated as the number of individuals in the cubic meter at each site (n m^{-3}). The development stages of fish eggs were determined according to Munk and Nielsen (2005).

For the purpose of the presented analysis, data from samples covering the entire water column

Table 1

Characteristics of the sampling sites in the southern Baltic Sea in 2015

Site	Coordinates	Date	Depth layer [m]	Bottom depth [m]
Arkona Deep 1	55°0'0.36''N 13°10'29.279''E	07.06.2015	2–0 25–0 46–0	46.10
Arkona Deep 2	55°9'15.48''N 14°19'36.48''E	08.06.2015	2–0 25–0 46–0	46.90
Bornholm Deep	55°10'13.08''N 15°30'0.719''E	09.06.2015	2–0 27–0 94–0	96.10
BB23	55°17'31.2''N 15°45'0''E	22.06.2015	2.5–87.5*	94.00
IBY5	55°14'509''N 15°59'037''E	29.05.2015	55–0 82–55	86.00
Slupsk Furrow	55°7'49.08''N 17°2'30.839''E	09.06.2015	2–0 65–0 94–0	93.00
Gotland Deep	55°28'41.88''N 18°20'0.6''E	10.06.2015	2–0 60–0 103–0	109.00
Gdansk Deep	54°30'24.48''N 19°10'28.92''E	10.06.2015	2–0 53–0 110–0	108.58
Krynica	54°14'0.6''N 19°11'51.36''E	10.06.2015	2–0 20–0	22.20

*stratified samples collected every 5 meters were used. In addition, data from stratified samples were also taken into account to analyze the vertical distribution of sprat egg size as they provided more information on the location of eggs in the water column.

Results

Environmental conditions

In June 2015, hydrographic conditions in the study area were characterized by vertical gradients of salinity and temperature (Fig. 2). The waters closer to the Danish Straits were still affected by the series of the North Sea inflows taking place in winter 2014. The one recorded in December 2014 was classified as the third strongest event since 1913 (Mohrholz et al. 2015). The inflows caused an increase in salinity in the deep-water layers of the Baltic Sea. Temperature above the halocline ranged between 9 and 14°C with salinity around 7 PSU. Along with increasing distance from the Danish Straits, this value of salinity occurred at greater depths (from 25 m in the Bornholm Basin to 70 m in the Gdansk Deep). Temperature dropped significantly, while at the bottom its value was slightly higher. A strong salinity gradient (halocline) was observed at a depth of approximately 45 m in the Bornholm Basin and gradually at greater depths as it moved eastward up to a depth of 70 m in the Gdansk Basin. In the Bornholm Basin, salinity increased to a maximum of 19.47 PSU in the near-bottom layers, which was the highest value observed along the sampling profile.

Ichthyoplankton composition, distribution and abundance

The species composition of ichthyoplankton in the southern Baltic Sea, collected for the purpose of this paper, included eggs of five species: sprat (*Sprattus sprattus*), fourbeard rockling (*Enchelyopus cimbrius*), cod (*Gadus morhua*) and European flounder *(Platichthys flesus)* and larvae of seven species: sprat, herring (*Clupea harengus*), fourbeard rockling, European flounder, sand goby (*Pomatoschistus minutus*), great sand eel (*Hyperoplus lanceolatus*), longspined bullhead (*Taurulus bubalis*) and straightnose pipefish (*Nerophis ophidion*). A total of nine species of ichthyofauna were identified (Table 2).

The occurrence of the early developmental stages of fish in the study area indicates that eggs and larvae of sprat as well as larvae of herring were most common. They were observed at all sites except for Krynica, located in the coastal waters of the Gulf of Gdansk. The maximum number of sprat eggs (15.51 n m^{-3}) occurred in the Bornholm Basin (IBY5)

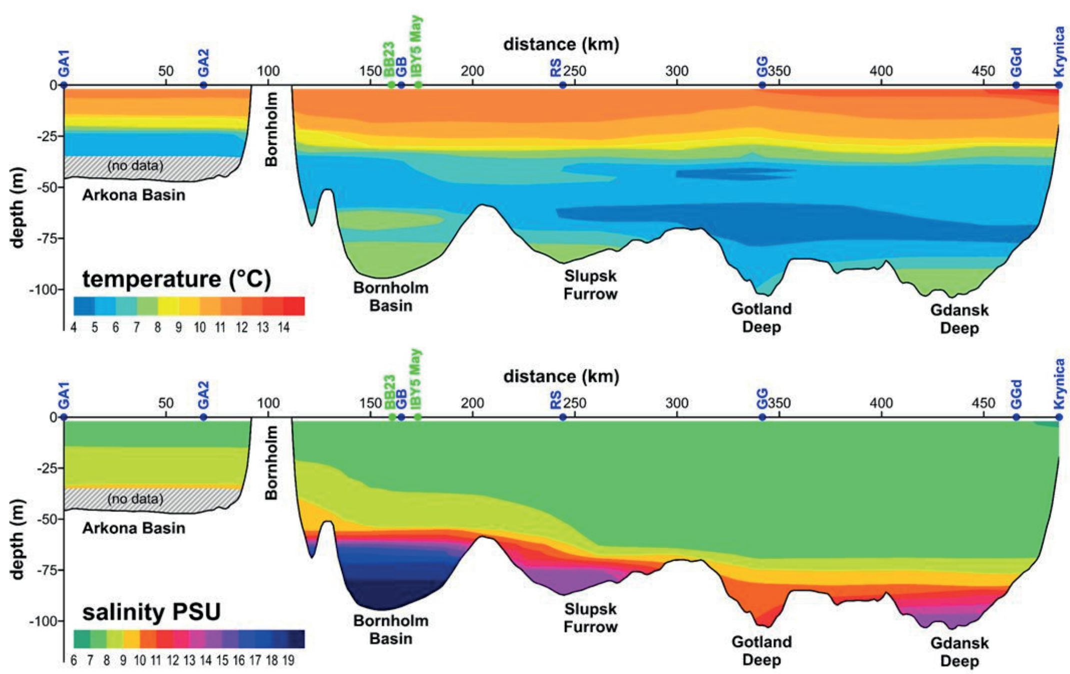

Figure 2

Water temperature and salinity in the southern Baltic Sea in June 2015

Table 2

Abundance of fish species (n m^{-3}) recorded in the southern Baltic Sea in May and June 2015

species	life stages of fish	sites							
		GA1	GA2	GB	IBY5 May	RS	GG	GGd	Krynica
Sprattus sprattus	eggs	5.45	4.28	7.58	15.51	3.62	1.13	7.17	0.00
	larvae	1.26	2.24	0.52	0.68	1.45	0.39	1.50	0.00
Clupea harengus	larvae	0.19	0.19	0.09	0.00	0.24	0.04	0.20	0.00
Gadus morhua	eggs	0.00	0.00	2.57	1.18	1.95	0.00	0.00	0.00
Enchelyopus cimbrius	eggs	0.00	0.00	0.00	0.00	2.15	0.00	0.04	0.00
	larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00
Platichthys flesus	eggs	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00
	larvae	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00
Pomatoschistus minutus	larvae	0.00	0.19	0.00	0.00	0.00	0.00	0.00	1.56
Hyperoplus lanceolatus	larvae	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Taurulus bubalis	larvae	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nerophis ophidion	larvae	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00

in May, while the largest number of sprat larvae (2.24 n m^{-3}) was recorded in the eastern part of the Arkona Deep. Ichthyoplankton, represented by four species: cod (eggs), fourbeard rockling (larvae), European flounder (larvae) and sand goby (larvae), was observed at two of the seven sites in the amount ranging from 0.04 n m^{-3} to 2.15 n m^{-3}. Other species, represented by larvae of great sand eel (0.09 n m^{-3}), straightnose pipefish (0.07 n m^{-3}) and longspined bullhead (0.09 n m^{-3}), occurred at only one sampling location. The most diversified area in terms of the number of species was the Slupsk Furrow, where five species of fish were recorded. In other regions, the number of species varied from one (Krynica) to four (GA1, GGd).

Developmental stages of *Sprattus sprattus*

Generally, the ichthyoplankton in the spring of 2015 was dominated by sprat eggs, which occurred at all sites presented in Table 3. The largest variability in sprat developmental stages was observed in the Slupsk Furrow, where five stages for eggs and four stages for larvae were recorded. The most frequent stage at all sites was stage I, with the largest number observed in the Bornholm Basin in May (11.41 n m^{-3}). Stages IV and V occurred less frequently, while stage V was recorded only at the RS site.

The occurrence of larval stages was very irregular. The most frequently recorded larval stage was the earliest one – the yolk-sac stage, occurring most frequently in the Gdansk Deep (1.34 n m^{-3}) and, as the only larval stage along the entire sampling profile, their abundance was higher than 0.5 n m^{-3}. At all sites, except for the RS, older larval stages of sprat were rare or they did not occur at all (Table 3).

Sprat egg size measurements

The size of sprat eggs in stage I ranged from 1.2 mm (GA1 and GGd) to 1.6 mm (GA2), with the largest ones occurring sporadically (Table 4). A difference in the minimum egg diameter was observed in different hauls, as smaller eggs occurred in deeper layers. The minimum size of eggs in surface hauls ranged from 1.3 mm to 1.4 mm, while the diameter of eggs in deeper hauls reached 1.2 mm at GGd and GA1 sites.

All eggs collected at the GB site in two layers (0–2 m and 0–27 m) could not be measured due to membrane deformation.

Table 3

The number of sprat early developmental stages (n m^{-3}) at four of the examined sites where the largest number of the early stages of development occurred

site	development stage								
	I	II	III	IV	V	yolk-sac stage	pre-flexion	flexion	post-flexion
GB	4.29	2.15	0.81	0.33	0.00	0.52	0.00	0.00	0.00
IBY5 May	11.41	2.73	1.37	0.00	0.00	0.68	0.00	0.00	0.00
RS	2.60	0.44	0.48	0.05	0.05	0.98	0.10	0.24	0.13
GGd	4.40	0.53	1.91	0.29	0.04	1.34	0.16	0.00	0.00

Table 4

The size of sprat eggs in stage I at different sites and depth layers

site	haul	number of eggs	mean [mm]	min. [mm]	max [mm]
GA1	0–2	2	1.48	1.4	1.55
	0–25	12	1.39	1.3	1.55
	0–46	14	1.4	1.2	1.55
GA2	0–2	10	1.45	1.3	1.55
	0–25	11	1.45	1.25	1.6
	0–46	6	1.31	1.25	1.35
GB	0–2			no data	
	0–27			no data	
	0–94	20	1.36	1.25	1.45
RS	0–65	17	1.36	1.3	1.5
	0–91.5	20	1.45	1.3	1.55
GG	0–60	8	1.44	1.4	1.5
	0–103	15	1.39	1.3	1.5
GGd	0–2			no data	
	0–53	14	1.38	1.2	1.45
	0–110	7	1.33	1.2	1.45

At the BB23 site in June 2015, a correlation between the sampling depth and the diameter of sprat eggs was also observed due to the vertical salinity gradient (Fig. 3). The minimum diameter of eggs was mainly 1.3 mm up to a depth of 47.5 m, except for a depth of 7.5 m where an egg with a diameter of 1.2 mm was also found. The largest egg size (1.65 mm) was observed at a depth of 17.5 m. The average diameter of eggs ranged from 1.38 mm to 1.45 mm up to a depth of 57.5 m. In deeper layers, the size of eggs varied considerably, with a significantly more frequent occurrence of the smallest eggs whose diameter was slightly larger than 1 mm and the largest ones reaching 1.6 mm (Fig. 3).

Discussion

The Baltic Sea is characterized by large differences in horizontal and vertical temperature, salinity, and oxygen concentration gradients. This results in large discrepancies in the species composition along these gradients. The presented analysis shows that in spring 2015 there was no large difference in the number of species occurring at the sampling sites, but their composition was often different. In total, the presence of nine fish species was recorded: sprat, herring, cod, fourbeard rockling, sand goby, great sandeel, longspined bullhead, straightnose pipefish and European flounder. Karaseva et al. (2012) found only five of the aforementioned species: sprat, cod, fourbeard rockling, sand goby and European flounder, and, additionally, plaice in the Baltic open waters in the spring of 2006. Almost all of the species observed

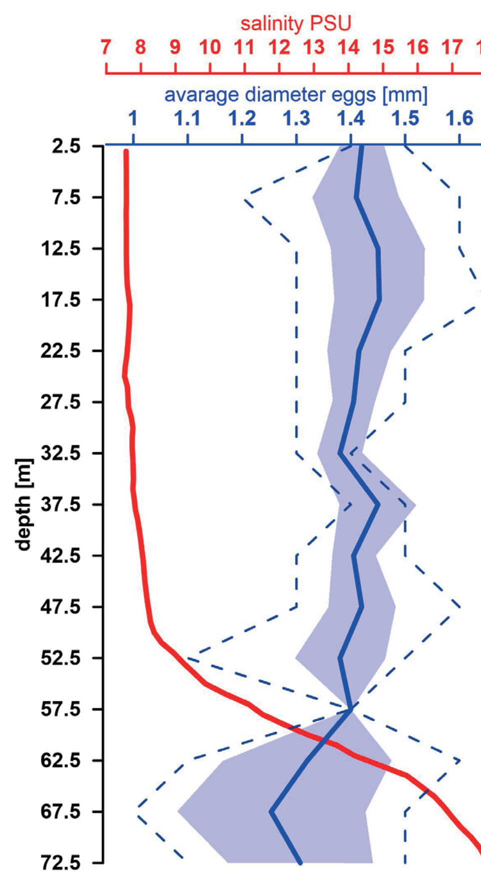

Figure 3

Average diameter of sprat eggs in stage I (solid line), standard deviation range (blue field), minimum and maximum size of eggs (dotted lines) and salinity (red line) in different depth strata at the BB23 site in spring 2015 regularly spawn in the southern Baltic Sea. Several of them, such as spring spawning herring as well as sand goby, great sandeel, straightnose pipefish and longspined bullhead, spawn in shallow waters. They use various demersal substrates such as stones, sand, submerged vegetation or (in the case of straightnose pipefish) attach their eggs to the male's abdomen (Russell 1976; Ojaveer & Kalejs 2005 after Mikelsaar 1984; Horbowa & Fey 2013). The most frequently observed species, sprat and cod, are also typical representatives of the southern Baltic Sea. There are no data suggesting that longspined bullhead breeds in the southern Baltic Sea. The species certainly spawns from March to May in the Gulf of Finland (Ojaveer & Kalejs 2005 after Mikelsaar 1984). In the open waters of the Baltic Sea, several species produce pelagic eggs: sprat, cod, fourbeard rockling and European flounder (Matthäus & Lass 1995). They spawn in areas with high salinity and oxygenation and relatively low temperatures (Horbowa & Fey 2013), with the exception of sprat whose eggs reach neutral buoyancy in the mid-water column, as low temperatures may adversely affect the development and survival of eggs (Grauman et al. 1987).

Out of the eight surveyed sites, the one located in the Slupsk Furrow was characterized by the largest number of observed species, as five out of nine (sprat, herring, cod, European flounder and fourbeard rockling) were recorded there. The highest abundance was observed in the Bornholm Basin in May. This is largely in line with the description given by Horbowa and Fey (2013) on the occurrence of early stages of fish development in the southern Baltic Sea.

According to Voss et al. (2011b), the Bornholm Basin is the only area where suitable conditions for cod reproduction exist, with salinity of 10–18 in the near-bottom layers (Voss et al. 2011b after Moller and Hansen 1994). In spring 2015, the largest number of cod eggs in this region was observed along the sampling profile. Voss et al. (2011b) described a significantly higher survival rate of cod eggs after the 2003 major inflow of saline waters from the North Sea compared to 2002 conditions due to increased salinity and oxygen concentration. It may be assumed that, for the same reason, such a large number of cod was recorded in the spring of 2015 following one of the largest inflows recorded in December 2014 (Mohrholz et al. 2015).

The largest and most widely spread species in the southern Baltic Sea in spring 2015 was sprat, accounting for at least 53% of the total ichthyoplankton, which confirms the dominance of this species in the study area in the previous research (Nissling et al. 2003). The species was reported in all sampled strata with the largest number recorded in the Bornholm Basin in May. The species is characterized by a high tolerance to salinity and the spawning takes place mostly in open waters, but sometime also closer to the coast, albeit with lower intensity (Horbowa & Fey 2013). It may be assumed that, for this reason, it was not recorded at the Krynica site, which is extremely coastal. According to Voss et al. (2011a), the sampled area is one of the main spawning grounds for sprat. Voss et al. (2011a) also found that sprat spawning is less intensive in the Arkona Basin, which is confirmed by our results from this area, where the smallest number of this species was recorded.

The Baltic Sea has specific hydrological conditions that affect the distribution and structure of organisms (Arndt 1989). Animals can be carried along with currents or water waves. Depending on their adaptation and tolerance to given factors (temperature, salinity, oxygen concentration), organisms may exceed their natural limits and live in new environmental conditions (Hinrichsen et al. 2003). Therefore, it is possible that in the southern Baltic Sea we observe species that are characteristic for other regions. For example, the longspined bullhead occurs mostly in the Gulf of Finland and is typical of sandy areas and submerged vegetation (Skóra 2001). In our samples, it occurred both in the Arkona Basin and the Gotland Deep. It is also possible that larval longspined bullhead were transported from the North Sea by large water masses, especially during the major inflow event. Data from the Ocean Biogeographic Information System show that longspined bullhead tolerates a broad range of temperatures (from 5°C to 15°C) and salinity (from 6.6 PSU to 35 PSU). Hydrological conditions observed in the Arkona Basin and the Gotland Deep in spring 2015 were favorable for the occurrence of this species.

In the study area, fish eggs were observed mostly in the very early stages of development. This is mainly due to the extremely high mortality of fish eggs, as the early stages of fish development are exposed to many factors that threaten their survival (Köster et al. 2003) – they may be consumed by other species (Bailey & Houde 1989) or may not develop as a result of inappropriate environmental conditions (Voss et al. 2006). Therefore, many fish species produce several thousand eggs during spawning to increase their chance of survival. In the case of 75 cm long cod from the Baltic Sea, the average number of eggs produced is 3 660 000, which is 100% more than eggs produced in the North Sea (Schopka 1971). Botros (1962) and Schopka (1971) observed a correlation between the length and weight of females and the number of eggs. It was also shown that younger fish are more productive (Schopka 1971).

The low number of collected fish larvae can largely be explained by the sampling method, because the plankton nets used (low speed vertical net with a small opening and 100 μm mesh size) are typical sampling gear for collecting zooplankton but not for more mobile organisms. Fish larvae are usually sampled using nets with a mesh size of 300–500 μm towed at much higher speeds to reduce net avoidance.

The diameters of sprat eggs in stage I are within the ranges reported in the existing literature. Horbowa and Fey (2013) provided diameter ranges from 1.23 to 1.58 mm for sprat in the Baltic Sea, while in our surveys the range was 1.20–1.60 mm. Russel (1976) and Munk & Nielsen (2005) described the size range from 0.8 to 1.3 mm in the North Sea. This difference in egg size diameter observed between the North Sea and the Baltic Sea is mainly caused by different salinity ranges. To achieve neutral buoyancy in the Baltic Sea conditions, pelagic eggs need to be much larger in diameter.

In general, the size and species structure as well as the distribution of very early stages of fish development are affected by interrelated factors such as the survival of fish eggs and larvae, spawning season, salinity and temperature as well as currents. In the Baltic Sea, it is particularly important to observe environmental changes as well as the abundance and distribution of ichthyoplankton to be able to estimate their potential contribution to stock recruitment.

Acknowledgements

Special thanks to Sergey Shchuka from the Institute of Oceanology P. P. Szirszowa (Russian Academy of Sciences) for his technical support during the cruise and for providing hydrological data. The research was carried out as part of the cooperation within the project "Program of comprehensive research of the Baltic Sea". The authors also thank Agnieszka Zdun for collecting the planktic materials from the IBY5 site in May 2015 and Katarzyna Horbowa for her help in the identification of ichthyoplankton.

References

Arndt, E.A. (1989). Ecological, physiological and historical aspects of brackish water fauna distribution. *Reproduction, genetics and distribution of marine organisms.* Olsen & Olsen, Fredensborg 327–338.

Bagge, O. & Thurow, F. (1994). The Baltic cod stock: fluctuations and possible causes. In *ICES Marine Science Symposia* 198: 254–268.

Bailey, K.M. & Houde, E.D. (1989). Predation on eggs and larvae of marine fishes and the recruitment problem. In *Advances in Marine Biology* 25: 1–83. Academic Press.

Baumann, H., Hinrichsen, H.H., Möllmann, C., Köster, F.W., Malzahn, A.M. et al. (2006). Recruitment variability in Baltic Sea sprat (*Sprattus sprattus*) is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. *Canadian Journal of Fisheries and Aquatic Sciences* 63(10): 2191–2201. DOI:10.1139/f06-112.

Botros, A.G. (1962). Die Fruchtbarkeit des Dorsches (*Gadus morhua* L.) in der westlichen Ostsee und den westnorwegischen Gewässern. *Kieler Meeresforschungen* 18: 67–80.

Horbowa, K. & Fey, D. (2013). *Atlas wczesnych stadiów rozwojowych ryb. 34 gatunki ryb Południowego Bałtyku i jego zalewów*. Gdynia: Morski Instytut Rybacki, 152 pp.

Hinrichsen, H.H., Böttcher, U., Köster, F.W., Lehmann, A. & John, M.S. (2003). Modelling the influences of atmospheric forcing conditions on Baltic cod early life stages: distribution and drift. *Journal of Sea Research* 49(3): 187–201. DOI: 10.1016/S1385-1101(03)00006-6.

Karaseva, E.M., Zezera, A.S. & Ivanovich, V.M. (2012). Changes in the species composition and ichthyoplankton abundance along transects in the Baltic Sea. *Oceanology* 52(4): 478–487. DOI: 10.1134/S0001437012040030.

Kornilovs, G., Sidrevics, L. & Dippner, J. W. (2001). Fish and zooplankton interaction in the Central Baltic Sea. *ICES Journal of marine science* 58(3): 579–588. DOI: 10.1006/jmsc.2001.1062.

Kraus, G. & Köster, F.W. (2004). Estimating Baltic sprat population sizes from egg production. *Fisheries Research* 69(3): 313–329. DOI: 10.1016/j.fishres.2004.06.005.

Köster, F.W., Möllmann, C., Neuenfeldt, S., Vinther, M., St John, M.A. et al. (2003). Fish stock development in the central Baltic Sea (1974–1999) in relation to variability in the environment. In *ICES Marine Science Symposia* 219: 294–306.

Kullenberg, G. & Jacobsen, T.S. (1981). *The Baltic Sea: an outline of its physical oceanography.* Great Britain: Marine pollution bulletin 12(6): 183–186. DOI: 10.1016/0025-326X(81)90168-5.

Matthäus, W. & Ulrich Lass, H. (1995). The recent salt inflow into the Baltic Sea. *Journal of Physical Oceanography* 25(2): 280–286. DOI: 10.1175/1520-0485(1995)025<0280:TRSIIT>2.0.CO;2}.

Mohrholz, V., Naumann, M., Nausch, G., Krüger, S. & Gräwe, U. (2015). Fresh oxygen for the Baltic Sea – An exceptional saline inflow after a decade of stagnation. *Journal of Marine Systems* 148: 152–166. DOI: 10.1016/j.jmarsys.2015.03.005.

Munk P. & Nielsen J.G. (2005). *Eggs and Larvae of North Sea Fishes.* Biofolia, Denmark, 533 pp.

Neumann, V., Schaber, M., Eero, M., Böttcher, U. & Köster, F.W. (2016). Quantifying predation on Baltic cod early life stages. *Canadian Journal of Fisheries and Aquatic Sciences*

74(6): 833–842. DOI: 10.1139/cjfas-2016-0215.

Nissling, A., Müller, A. & Hinrichsen, H.H. (2003). Specific gravity and vertical distribution of sprat eggs in the Baltic Sea. *Journal of Fish Biology* 63(2): 280–299. DOI: 10.1046/j.1095-8649.2003.00139.x.

Ojaveer, E. & Kalejs, M. (2005). The impact of climate change on the adaptation of marine fish in the Baltic Sea. *ICES Journal of Marine Science*. 62(7): 1492–1500. DOI: 10.1016/j.icesjms.2005.08.002.

Russell F.S. (1976). *The Eggs and Planktonic Stages of British Marine Fishes*. London: Academic Press, 524 pp.

Schopka S.A. (1971). Vergleichende Untersuchungen zur Fortpflanzungsrate bei Herings-und Kabeljaupopulationen (*Clupea harengus* L. and *Gadus morhua* L.) *Trans. Ser. Fish. Res. Board Can.* 22(1): 3–79.

Skóra, K.E. (2001). *The broad-nosed pipefish*. Polish Red Data Book of Animals. Vertebrates. Warszawa: PWRiL, 316–318.

Snoeijs-Leijonmalm, P. & Andrén, E. (2017). Why is the Baltic Sea so special to live in? *Biological Oceanography of the Baltic Sea* 23–84. DOI: 10.1007/978-94-007-0668-2_2.

Sparholt, H. (1994). Fish species interactions in the Baltic Sea. *Dana* 10: 131–162.

Sparholt, H. (1996). Causal correlation between recruitment and spawning stock size of central Baltic cod? *ICES Journal of Marine Science* 53(5): 771–779. DOI: 10.1006/jmsc.1996.0098.

Svedäng, H. & Bardon, G. (2003). Spatial and temporal aspects of the decline in cod (Gadus morhua L.) abundance in the Kattegat and eastern Skagerrak. *ICES Journal of Marine Science*. 60(1): 32–37. DOI: 10.1006/jmsc.2002.1330.

Voss, R., Clemmesen, C., Baumann, H. & Hinrichsen, H.H. (2006). Baltic sprat larvae: coupling food availability, larval condition and survival. *Marine Ecology Progress Series* 308: 243–254. DOI: 10.3354/meps308243.

Voss, R., Hinrichsen, H.H., Quaas, M.F., Schmidt, J.O., & Tahvonen, O. (2011a). Temperature change and Baltic sprat: from observations to ecological–economic modelling. *ICES Journal of Marine Science* 68(6): 1244–1256. DOI: 10.1093/icesjms/fsr063.

Voss, R., Hinrichsen, H.H., Stepputtis, D., Bernreuther, M., Huwer, B. et al. (2011b). Egg mortality: predation and hydrography in the central Baltic. *ICES Journal of Marine Science* 68(7): 1379–1390. DOI: 10.1093/icesjms/fsr061.

DE G DE GRUYTER