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SHORT COMMUNICATION

Trophic ecology and seasonal occurrence of two Red List fish species in the Western Baltic Sea—two of a kind?

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Abstract

Improving the conservation status and the management of Red List species requires knowledge on the biology and distribution of the organisms as well as an evaluation of the appropriateness of management measures. This study provides information on the trophic ecology and seasonal abundances of two Red List fish species from the Western Baltic Sea, snake blenny *Lumpenus lampretaeformis* (Walbaum, 1792), classified as "critically endangered" according to the German Red List, and eelpout, *Zoarces viviparus* (Linnaeus, 1758), classified as "near threatened" based on the HELCOM Red List. Beam trawl surveys were conducted to document abundances of both species in summer and winter in a marine protected area (MPA), where mobile bottom-contacting fishing gears will be excluded in the near future. The MPA is located in the German EEZ (exclusive economic zone) and aims to protect sandbank and reef habitats. Stomach content and stable isotope analyses (nitrogen and carbon) were performed to examine the diet of eelpout and snake blenny. To be able to position the two fish species in the food web, stable isotopes of macrozoobenthos, POM (particulate organic matter) and sand goby (*Pomatoschistus minutus*) were analysed as well. Eelpout and snake blenny were present in the study area in summer and winter, but reached higher abundances in summer. Diet composition overlapped strongly reflected by a similar trophic level, indicating potential food competition of the two species. Prey items were dominated by macrozoobenthos (Mollusca, Annelida, Arthropoda). Our study provides new information on the trophic position and seasonal abundance of the two fish species within an area soon to be placed under protection from mobile bottom-contact fishing. It therefore also provides a baseline to evaluate potential positive repercussions following the exclusion of mobile bottom-contacting fishing gears and might thus help to increase the understanding of fishing impacts on benthic ecosystems contributing to more effective conservation and management measures.

Keywords Marine protected area · *Lumpenus lampretaeformis* · *Zoarces viviparus* · Diet composition · Stable isotopes

Introduction

Marine ecosystems are exposed to various pressures and drivers of change (Franco et al. 2020; Gruber 2011). The Baltic Sea, a semi-enclosed brackish water body in Northern Europe, is strongly affected by climate change and other anthropogenic

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stressors (e.g. Reusch et al. 2018). It is naturally poor in species as well as in genetic and functional diversity due to its young age and brackish water (Elmgren and Hill 1997). Thus, the protection of biodiversity is of key importance to ensure the resilience of the ecosystem (HELCOM 2009). Significant threats to biodiversity in the Baltic Sea include maritime activities (e.g. fishing), physical damage and disturbance, recreational activities, eutrophication, hazardous substances, alien species, noise pollution, hunting and climate change (e.g. Ojaveer et al. 2010; HELCOM 2009). To counteract these stressors, different management measures have been implemented, such as the establishment of Marine Protected Areas (MPAs) (Kriegl et al. 2021).

Eelpout, *Zoarces viviparus* (Linnaeus, 1758), and snake blenny, *Lumpenus lampretaeformis* (Walbaum, 1792), represent examples of internationally defined near threatened and nationally recognised critically endangered Red List species in the Baltic Sea, respectively (HELCOM 2013b, c, Thiel et al. 2013), but the underlying reason(s) for their insufficient status are unknown and knowledge gaps in their ecology exist. Within the Baltic Sea, *Z. viviparus* is widely distributed from the western entrance up to the northern basins and from shallow coastal waters to a depth of 40 m (Andriashev 1986; Carl and Møller 2019; HELCOM 2013b; Wheeler 1969). Due to its stationary behaviour, it has become an important indicator species for monitoring the environmental state of benthic ecosystems (e.g. contaminants) (Bergek et al. 2012). However, during the last three eelpout generations, a substantial decline in population size of around 30% is assumed in the Baltic Sea (HELCOM 2013a). Although the causes for the decreasing trend are largely unknown, besides others, by-catch in fisheries has likely contributed to the decline (HELCOM 2013c). The distribution of *L. lampretaeformis* in the Baltic Sea is uncertain and reliable data on population size and trends are missing (HELCOM 2013c). In general, the species occurs from shallow coastal waters down to a depth of 373 m (Coad and Reist 2004; Fahay 2007). Due to irrigation and burrowing activities with mean sediment depths of 7.2 cm (Atkinson et al. 1987), the species is suggested to affect biochemical cycling. The diet of eelpout and snake blenny consists of different macrozoobenthic organisms, such as bivalves, crustaceans, gastropods and polychaetes, but they can also feed on small fish and algae (Carl 2019; Carl and Møller 2019; Gordon and Duncan 1979; Makushok 1986; Więcaszek et al. 2018). Since fishing is supposed to be one of the reasons for the decreasing population size of *Z. viviparus* (HELCOM 2013c), it is very likely that fishing with mobile bottom-contacting gears (MBCG) has an impact on the status of both species due to their strong association with the benthic habitat. In our study, we provide new information on the basic ecology of *L. lampretaeformis* and *Z. viviparus* by describing their seasonal abundance and feeding ecology, based on stomach content and stable isotope analyses of carbon and nitrogen. We focus on an area in the western Baltic Sea, where MBCG will partly be excluded most likely by the end of 2023. The commonly used stomach content analysis allows an accurate determination of the prey species and recalculation of the prey size. However, it only provides a snapshot in time of the ingested food, and rapidly digestible soft tissues may be underrepresented in the stomachs. In contrast, carbon stable isotopes provide an insight into the diet over a longer period of time, while the analysis of nitrogen stable isotopes allows assessing the trophic level of an organism (e.g. Pitt et al. 2009; de la Vega et al. 2023). Our study (i) will help to improve the understanding of the biology of eelpout and snake blenny and (ii) might serve as a baseline to investigate potential changes in abundance and trophic ecology of the two species after the exclusion of MBCG in the MPA and thus increase the understanding of fishing impacts on benthic ecosystems.

Materials and methods

Sampling area

The sampling area is located in the western Baltic Sea close to the island of Fehman (Fig. 1). Salinity near the bottom usually ranges between 17 and 23, and depth between 17 and 23 m. The eastern part of our study area belongs to the German MPA "Fehmarnbelt" (total size of the MPA: 27.992 ha), where mobile bottom-contacting gears (MBCG) will be excluded most likely by the end of 2023, while the western part serves as a future reference area, i.e. no exclusion of MBCG. Current investigations illustrate no differences in fishing effort, oceanographic conditions and biodiversity, comprising species abundances and biomasses from bacteria to fish, between the two sub-areas (pers. observation). Therefore, we combined the sub-areas for our analyses, which represent the current state of fishing pressure.

Fish sampling

To analyse the seasonal abundance and to collect fish samples for stomach content and stable isotope analyses of *Z. viviparus* and *L. lampretaeformis*, fishing hauls were conducted with a 2 m and 3 m beam trawl with a towing time of 2.5 and 5 min, respectively, in the study area in summer (May and July 2020 & June 2021) and winter (January/February 2021) (Fig. 1 and Table 1). To compare fish abundances amongst seasons, numbers of fish caught were calculated per hour of trawling.
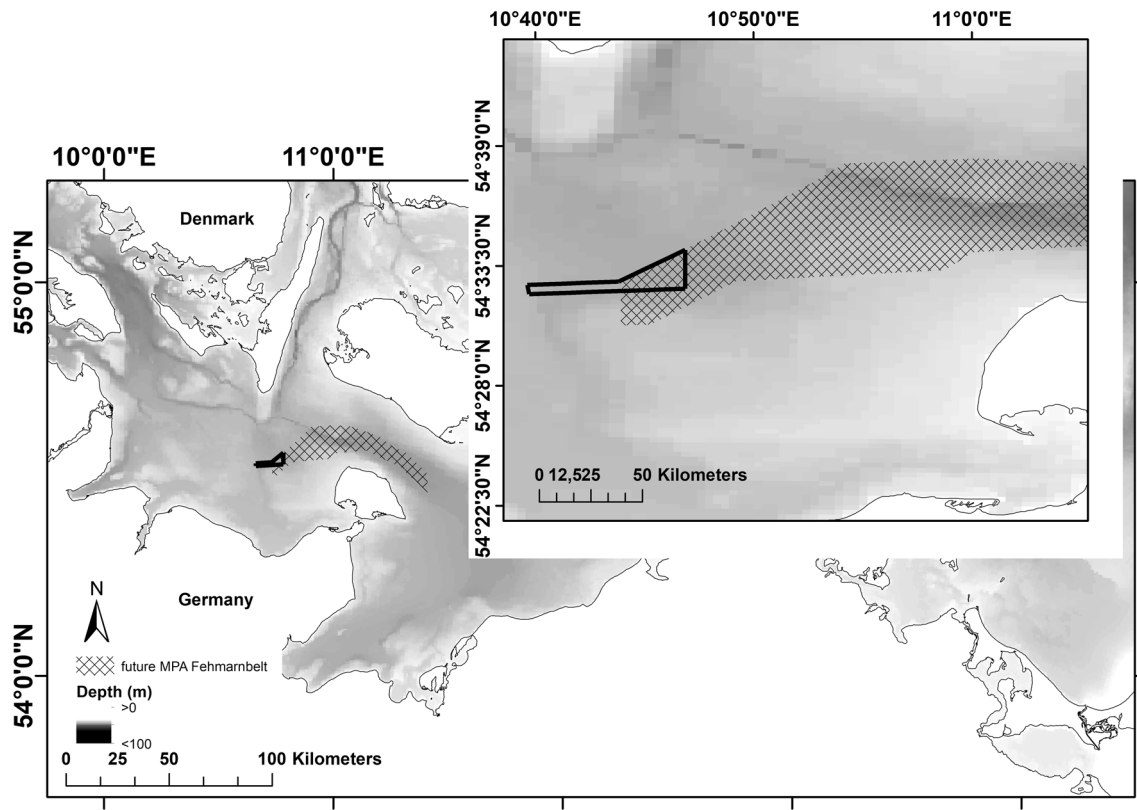
Fig. 1 Map of the western Baltic Sea showing the sampling area (black outlined) and the MPA "Fehmarnbelt" (cross-hatched area)

Table 1 Number of hauls per season, gear and depth

Date	Gear	Mesh size codend	Number of hauls	Depth (m)
23.05-26.05.2020	2-m beam trawl	10 mm	6	20–23
	3-m beam trawl	20 mm	8	
	TV520	20 mm	1	
09.07-14.07.2020	2-m beam trawl	10 mm	9	17–22
	3-m beam trawl	20 mm	9	
	TV520	20 mm	1	
20.01-26.01.2021	2-m beam trawl	10 mm	8	19–23
	3-m beam trawl	20 mm	12	
16.06.-17.06.2021	2-m beam trawl	10 mm	8	22–23
	3-m beam trawl	20 mm	8	

Additional hauls were conducted with a larger bottom trawl (TV520) to increase the number of individuals and to fish larger individuals exclusively for the diet analyses. Individuals were frozen immediately after fishing.

Stable isotope (SI) analyses were performed for 20 and 18 individuals of *L. lampretaeformis* and *Z. viviparus*, respectively, fished in summer 2020 (May and July). These samples represented a subset of the specimen considered in the stomach content analyses. To compare the SI signatures of eelpout and snake blenny to another commonly occurring benthic fish, SI of 13 sand goby *Pomatoschistus minutus* individuals, sampled with the same hauls, were analysed additionally. To do so, a piece of dorsal muscle of each individual fish was freeze-dried and grounded in the lab (for further handling see SI section).

Stomach content analysis

Stomach content analyses were conducted for all fished individuals from summer 2020 and winter 2021. A total of

64 and 51 gastrointestinal tracts (stomach + intestine) were analysed of *L. lampretaeformis* and *Z. viviparus*, respectively. Prey items were identified to the lowest possible taxon using a binocular microscope, and presence of prey taxa was documented. The frequency of occurrence of identified prey items was calculated as the percentage of stomachs, in which the prey item occurred.

Particulate organic matter (zooplankton/phytoplankton) sampling

Water sampling for SI analysis was performed using a stainless-steel rosette equipped with six 4L Niskin bottles at three stations in the sampling area in May and June 2020. For each station, water was sampled at 2-, 5- and 10-m depth, pooled and filtered on 500-μm gauze to remove larger particles. Afterwards, samples were filtered through two additional mesh size gauzes, 200 μm and 55 μm, and residues from 55 to 200 μm particulate organic matter (POM) size fractions were washed from the gauze with pre-filtered seawater, and gently vacuum filtered on combusted Whatman GF/F filters (450 °C, 4 h, 25 mm, nominal pore size 0.7 μm) for SI analyses. The composition of the 55–200-μm POM fractions (zooplankton) was verified using a stereomicroscope and was mainly composed of zooplankton with relative low amounts of detrital material. The remaining filtrate (1 L) was gently vacuum filtered on combusted Whatman GF/F filters (450 °C, 4 h, 25 mm, nominal pore size 0.7 μm) for SI analyses of the < 55-μm fraction of POM (phytoplankton). A total of 12 phytoplankton and 11 zooplankton samples were prepared and analysed.

Macrozoobenthos sampling

To examine macrozoobenthos occurrence in the study area, samples were taken with a 0.1 m^2 van Veen grab in May/June 2020 (10 stations) and January 2021 (2 stations). At each station, three grab samples were taken and washed through a 1-mm sieve. Organisms were preserved on board in a 4% buffered formaldehyde–sea water solution. The retained material was sorted in the laboratory with a stereomicroscope, identified to the lowest possible taxonomic (mainly species) level, counted and weighted to obtain abundance and biomass. Ash-free dry weight biomass (AFDW) was derived from wet weight using conversion factors (Gogina et al. 2022). Abundance and biomass were averaged per three replicates and recalculated to ind/m^2 and mg/m^2 units.

To assess the position of *L. lampretaeformis* and *Z. viviparus* within the trophic structure at the study site, additional SI analyses were conducted for the macrozoobenthos species *Arctica islandica* ($n = 13$), *Ophiura albida* ($n = 10$)

and *Pagurus bernhardus* ($n = 6$). Those samples were sampled together with the fish samples in the 2-m and 3-m beam trawls performed in May and July 2020 (Table 1). Bivalves were dissected, shells removed and gutted before SI analysis.

Stable isotope analysis

Stable isotope analysis was performed only for summer 2020 samples. For analyses of phyto- and zooplankton stable isotopes, carbonates were removed from POM filters for δ^{13}C analyses with hydrochloric acid fumes in a vacuum-enclosed system. δ^{15}N values were determined on untreated filters to avoid any potential bias due to acidification. All Whatman GF/F filters were freeze-dried and sealed in a tin capsule.

For δ^{13}C stable isotope analyses of fish samples, lipids and calcified structures were removed from muscle samples. To do so, samples were acidified in glass vials with 1 mol L^{-1} hydrochloric acid, dried at 50 °C and homogenised again (Bunn et al. 1995; Pinnegar and Polunin 1999). Lipids were extracted from fish samples using repeated rinses with 2 ml cyclohexane to avoid bias due to the depletion in ^{13}C in lipids relative to the diet (Tieszen et al. 1983) before δ^{13}C analyses. Afterwards, samples were dried at 50 °C to constant weight and ground again. Muscle samples for δ^{15}N stable isotope analyses were not treated because lipid removal may affect isotopic composition of nitrogen. Muscle samples for the analyses of both isotopes were weighed in tin capsules and were analysed using an elemental analyser coupled with an isotope ratio mass spectrometer at the LIENSs stable isotope facility of the University of La Rochelle, France. Isotope values are expressed using the δ notation as deviations from the international standards (Vienna Pee Dee Belemnite for δ^{13}C and atmospheric N$_2$ for δ^{15}N) and based on the equation:

$$\delta^{13}C \text{ or } \delta^{15}N = \left[\left(\frac{R_{sample}}{R_{standard}} \right) - 1 \right] \times 10^3 \tag{1}$$

where R is ^{13}C/^{12}C for δ^{13}C or ^{15}N/^{14}N for δ^{15}N (Graeve et al. 2019).

Carbon and nitrogen concentrations and δ stable isotope values were calibrated (accuracy < 0.15‰ for both isotopes) with reference material (USGS-24, IAEA-CH6, − 600 for carbon; IAEA-N2, -NO-3, − 600 for nitrogen). The trophic positions (TP) of *L. lampretaeformis* and *Z. viviparus* were calculated using the following formula:

$$TP = \lambda + \frac{\left(\delta^{15}N_{secondary\ consumer} - \delta^{15}N_{base} \right)}{\Delta n} \tag{2}$$

where λ represents the estimated trophic position of the baseline organism, the bivalve *Arctica islandica* and $\delta^{15}N_{base}$ denotes its average δ^{15}N value (average $\delta^{15}N_{base} = 8.6 \pm 0.27$). *Arctica islandica* is a filter feeder inhabiting the Baltic

Sea (Gogina and Zettler 2010) and was therefore assigned to the second trophic position. For the baseline estimation, the three smallest bivalve specimens present in the samples were used, as it is assumed that smaller individuals have a lower isotope turnover rate similar to the one of fish (Pinnegar and Polunin 1999; Tieszen et al. 1983). The respective $\delta^{15}N$ value of a fish sample was used for $\delta^{15}N_{\text{secondary consumer}}$. Δn represents the fractionation factor of $\delta 15N$ in parts per thousand between a source and a consumer. The trophic fractionation factor between the fish and their macrozoobenthic diet was assumed to be 3.2 ± 1.3 (Sweeting et al. 2007).

Data and statistical analysis

To compare abundances of eelpout and snake blenny between seasons, a one-way ANOVA with the Holm-Sidak method was performed in SigmaStat (version 13.0). All other analyses were performed in R (R Core Team 2021 version 4.1.1). A permutational multivariate ANOVA (PERMANOVA) with 9999 permutations using the Bray-Curtis dissimilarity was performed (*vegan*-package, Oksanen et al. 2020) to test for differences between the trophic niches of *L. lampretaeformis* and *Z. viviparus*. Prior to this, a permutational test of multivariate dispersion (PERMDISP) was carried out (package *vegan*, Oksanen et al. 2020) to check that multivariate dispersions were equal between the fish species. A Wilcoxon test with 0.05 significance level was used to test whether macrozoobenthos abundances differed between seasons (package *ggplot2*, Wickham 2016). The quantification of trophic niche overlap between the two fish species was estimated as the probability of a randomly selected individual of one species occupying the trophic niche of the other species using a probabilistic method (Swanson et al. 2015; Suppl. Fig. S1).

Results

Seasonal abundance

Both, *L. lampretaeformis* and *Z. viviparus* occur in winter and summer in our study area, and seasonal abundance trends are similar for both species and gear types with relatively higher abundances in summer compared to winter. However, differences in abundances were only significant for some months (Fig. 2), while the 2-m beam trawl seemed to have a better catchability of the two species than the 3-m beam trawl (not tested).

Macrozoobenthos data

Macrozoobenthos data showed lower taxon richness in winter, with 51 taxa collected in June 2020 compared to only 30 in January 2021 (Table 2). Both abundance (Wilcoxon test: $p = 0.020$) and biomass (Wilcoxon test: $p < 0.001$) of macrozoobenthic organisms, pooled across taxonomic groups, were significantly higher in summer than in winter. However, resolved to specific taxonomic groups, abundances were significantly higher in summer only for bivalves, polychaetes, cumaceans and echinoderms (Wilcoxon tests: $p = 0.028$, $p = 0.022$, $p < 0.001$ and $p = 0.002$, respectively), while gastropod abundance was higher in winter, though this difference was marginally insignificant ($p = 0.058$, Fig. 3). Seasonal differences in other groups were below significance level. At the species level, the bivalves *Varicorbula gibba* and *Abra alba*, the brittle star *Ophiura albida*, and the cumacean *Diastylis rathkei* accounted for over 50% of cumulative abundance in summer. In winter, dominance of benthic macrofauna abundances shifted towards polychaetes such as *Levinsenia gracilis*, *Aricidea suecica* (both known as non-selective surface or burrowing deposit feeders, and
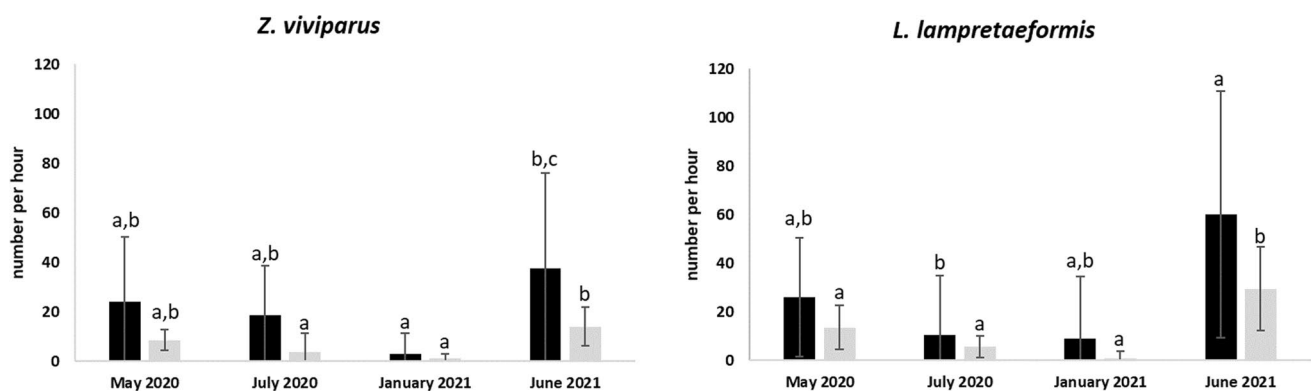

Fig. 2 Abundance of *L. lampretaeformis* and *Z. viviparus* (mean number and standard deviation per fishing hour) in each month separated into 2 m (black) and 3 m (grey) beam trawl catches. Significant differences between abundances are indicated with different letters for each trawl type, respectively

Table 2 Overview of macrozoobenthos variables sampled in June 2020 (summer) and January 2021 (winter). *AFDW biomass* Ash-free dry weight biomass

Group	Number of taxa		Abundance, ind/m^2		AFDW biomass, mg/m^2	
	Jun-20	Jan-21	Jun-20	Jan-21	Jun-20	Jan-21
Polychaeta	17	11	381	234	2034	816
Bivalvia	7	7	572	116	95772	35661
Bryozoa	5	3	na	na	na	na
Echinodermata	3	1	319	39	1094	209
Gastropoda	3	2	15	49	74	8
Nemertea	3	2	9	10	153	46
Cumacea	2	1	155	3	70	5
Porifera	2	0	0	0	0	0
Anthozoa	1	1	19	5	8.64	0.77
Ascidiacea	1	0	na	na	na	na
Cirripedia	1	0	0	0	0	0
Decapoda	1	0	0	0	0	0
Hydrozoa	1	0	0	0	0	0
Mysida	1	0	5	0	1.93	0
Oligochaeta	1	1	12	7	0.79	0.23
Phoronida	1	1	7	29	1.11	3.96
Pycnogonida	1	0	2	0	0.004	0
Total	51	30	1495	491	99209	36751

Fig. 3 Abundance (ind./m^2) of macrozoobenthic organisms in June 2020 (summer) and January 2021 (winter) at the study site
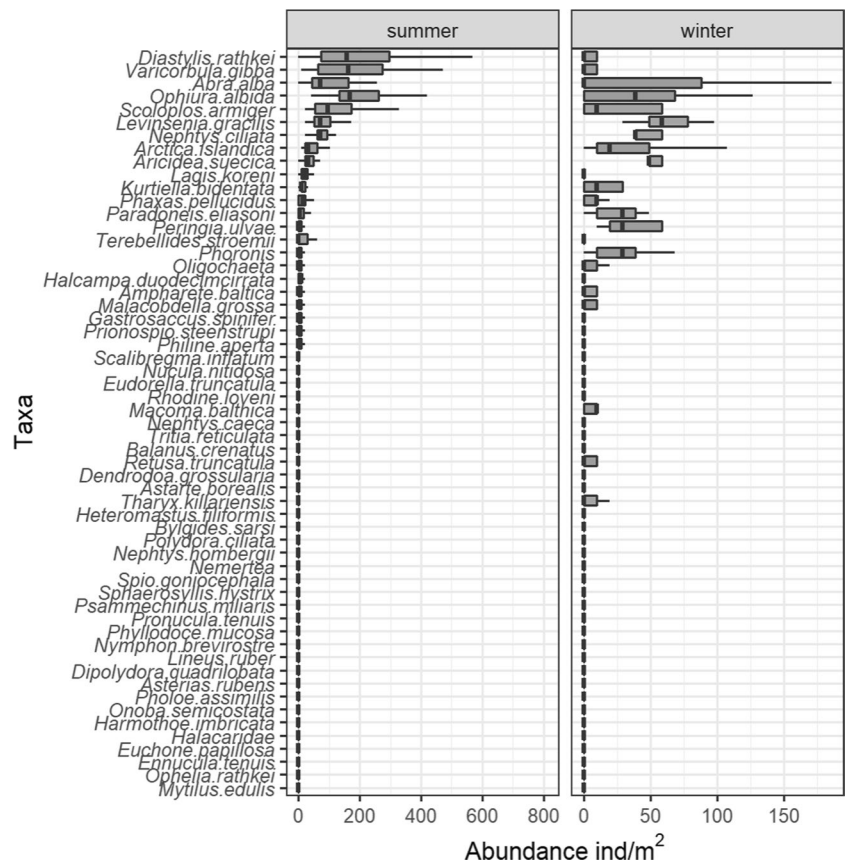
together accounting for over 20% of total abundance), and to the detritus-feeding gastropod *Peringia ulvae*. Both *A. alba* and *O. albida* retained high dominance, but their average abundance was reduced by the factors of 2.5 and 4.2, respectively (Fig. 3).

Stomach content analysis

Six out of 64 analysed stomachs of *L. lampretaeformis* were empty. Prey composition of the remaining samples consisted of a total of 22 macrozoobenthos taxa. The most frequently found taxa included unidentified bivalves, followed by crustaceans of the order Cumacea, polychaetes and gastropods. Prey composition of individuals caught in summer was more diverse than prey composition in winter (Table 3). In winter, smaller individuals of *L.*

lampretaeformis fed more on ostracods and oligochaetes, while larger individuals consumed more individuals of the gastropod *Retusa obtusa* compared to summer (Suppl. Tab. S1). However, due to the smaller samples size in winter, the results should be interpreted with caution, which also applies to *Z. viviparus*.

A total of 51 stomachs of *Z. viviparus* were analysed (of which one stomach was empty), and 21 prey taxa were identified. The majority of benthic prey organisms were identified as bivalves, amongst which *Macoma balthica* was most frequent, followed by Cumacea and polychaetes (Table 3). Similar as for *L. lampretaeformis*, prey composition was more diverse in summer compared to winter.

Individuals of *Z. viviparus* in the length class 8–16 cm mostly fed on polychaetes in winter, but consumed more bivalves in summer (Suppl. Tab. S1).

Table 3 Overview of prey items [%] based on presence/absence data, of *Zoarces viviparus* and *Lumpenus lampretaeformis* in different seasons

	Lumpenus lampretaeformis		*Zoarces viviparus*	
	Summer	Winter	Summer	Winter
Mean total length in cm (± SD)	21.6 (± 4.7)	16.5 (± 5.8)	14.4 (± 4.4)	12.9 (± 1.8)
Investigated full stomachs	53	5	44	6
Empty stomachs	6	0	1	0
Prey presence (%)				
Bivalvia unidentified	89	60	95	50
Macoma balthica	58	0	57	33
Musculus subpictus	2	0	0	0
Mya arenaria	13	0	20	0
Phaxas pellucidus	2	0	9	0
Thracia phaseolina	0	0	7	0
Varicorbula gibba	2	0	14	0
Gastropoda unidentified	11	20	7	0
Brachystomia scalaris	0	0	7	0
Hydrobia spp.	2	0	0	0
Philine aperta	25	0	5	0
Retusa obtusa	23	60	2	0
Amphipoda unidentified	9	0	2	0
Caprellidae	0	0	2	0
Copepoda	6	0	0	0
Calanoida	2	0	0	0
Cumacea	75	20	84	33
Cyathura carinata	2	0	0	0
Mysida	2	0	0	0
Ostracoda	47	40	25	0
Oligochaeta	28	60	5	17
Polychaeta	64	20	30	67
Lagis koreni	0	0	2	0
Nereididae	2	0	0	0
Ophiuroidea	0	0	7	0
Hydrozoa	0	0	2	0
Nematoda	19	40	9	33
Rhodophyta	42	20	20	0

Stable isotope analyses

At the study site, planktonic organisms occupied the lowest trophic level (Fig. 4), while macrozoobenthic organisms like *A. islandica*, *O. albida* and *P. bernhardus* occupied an intermediate level (for detailed isotope values, see Suppl. Tab. S2) in summer. In the same season, fish made up the third trophic group displaying a rather similar isotope signature of the three species *L. lampretaeformis*, *Z. viviparus* and *P. minutus*. Both, *L. lampretaeformis* and *Z. viviparus*, possessed an estimated average trophic level of 3.4. The trophic niches of the two species overlapped to a large degree (Fig. 4) and their trophic signature assessed by means of a PERMANOVA did not differ significantly ($p > 0.05$). The probability of an individual of *L. lampretaeformis* occurring in the trophic niche of *Z. viviparus* was 68.75%, while the opposite scenario was quantified with 86.35% (See Suppl. Fig.S1).

Discussion

Our study provides important insights into the feeding ecology of *L. lampretaeformis* and *Z. viviparus* and serves as a basis for identifying potential changes in abundance and diet after the exclusion of MBCG in the studied area. Although *L. lampretaeformis* and *Z. viviparus* occupied the studied area both in summer and winter, abundances differed between seasons. The higher numbers of *L. lampretaeformis* caught in summer might be linked to differences in their seasonal behaviour, as the species predominantly occupies

its caves in winter, which may result in lower catches during that time (Gordon and Duncan 1979, Fulton 1890, Atkinson et al. 1987, Nash 1982). However, seasonal vertical migrations, which are most likely causing the lower abundance of *Z. viviparus* in winter (Hedman et al. 2011; Mattsson et al. 2001) might also be responsible for variations in *L. lampretaeformis* abundances, but have not been described for this species in the Baltic Sea, so far.

Based on stomach contents, both fish species mainly feed on benthic organisms, which is in accordance with previous literature (e.g. Andriashev 1986; Carl 2019; Carl and Møller 2019; Gordon and Duncan 1979; Herrmann 2004; Muus and Nielsen 2013; Więcaszek et al. 2018). The diet of *L. lampretaeformis* mostly contains bivalves and Cumacea, as well as polychaetes and oligochaetes, which is similar to the diet of *Z. viviparus* mostly consuming bivalves, such as *M. balthica*, and crustaceans of the order Cumacea. Due to the similar food spectrum and the same trophic level (TL 3.4), the high probability of one species occupying the trophic niche of the other is not surprising and indicates a potential food competition between the two species. However, we did not analyse numbers of prey species in the stomachs, but focused on mere presence in the stomachs. It might therefore be possible that abundances of specific prey species found in the stomachs differ between the two fish species, which would indicate a preference for different macrozoobenthic organisms. Furthermore, competition might be reduced due to differences in diel activity since *L. lampretaeformis* is mainly active at dawn and dusk (Carl 2019; Nash 1980), while *Z. viviparus* hunts at nighttime (Carl and Møller 2019). The results of the
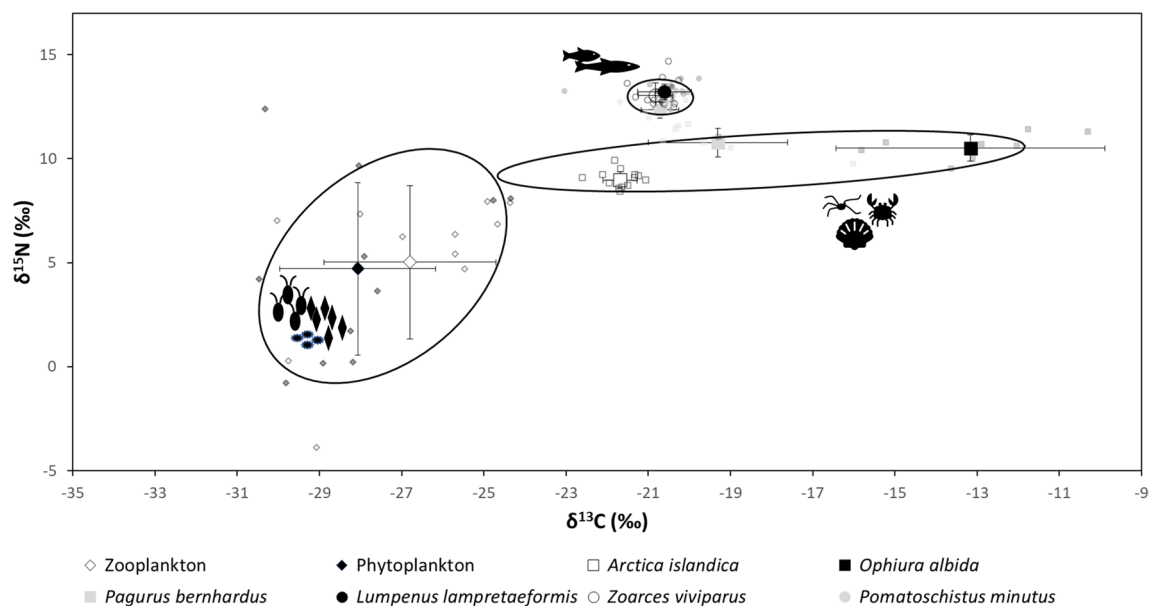

Fig. 4 Trophic structure at the study site in summer with mean values of $\delta^{13}C$ and $\delta^{15}N$ from different organisms including fish, macrozoobenthos and phyto-/zooplankton. Confidence ellipse: 95% and standard deviation

SI analyses illustrate the higher trophic position of both fish species in comparison with the investigated macrozoobenthic species. Stable isotope data suggest that both fish species feed on bivalves in summer, which rely on pelagic food resources. As observed for other ecosystems, production from the water columns is thus channeled through the macrozoobenthos to higher trophic levels such as fish and might explain the δ^{13}C values (Le Loc'h et al. 2008).

Abundances of macrozoobenthic organisms differed between summer and winter at the study site, with most prey organisms displaying lower abundances and biomass in winter, suggesting that the availability of prey does indeed vary between seasons. Furthermore, we observed a lower biodiversity of the macrozoobenthic community in winter, which might explain a less diverse prey composition in the stomachs of both fish species in winter. This might indicate that the diet composition of *L. lampretaeformis* and *Z. viviparus* is adapted to the seasonal availability of food sources as it has been described for other fish species (Herlevi et al. 2018). However, differences in sampling effort regarding the macrozoobenthos data between summer and winter (10 versus 2 sampled stations) should be kept in mind, as well as the lower number of stomachs analysed in winter compared to summer, which is why results should be interpreted with care.

This study contributes to a more detailed understanding of the ecological characteristics of *L. lampretaeformis* and *Z. viviparus*. Stable isotope and stomach content analyses suggest a strong overlap of diet composition and a similar trophic level in summer. Furthermore, the study provides a baseline to investigate the potential physical disturbance of MBCG on abundance and species composition of macrozoobenthos and the two fish species, as well as the consequences for the food web when MBCG will be excluded in the area in the near future. Therefore, it can be used to understand possible changes in the conservation status of the investigated species in connection to the exclusion of MBCG within the MPA.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval All applicable international, national and/or institutional guidelines for animal testing, animal care and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities.

Data availability The datasets used for the case study are available from the corresponding author on reasonable request.

Author contribution D. O.: conceptualization, design, funding acquisition, supervision, field work, writing first draft, review, analysis, writing revision. L. K.: conceptualization, design, field work, lab work, analyses, writing first draft, review. M. P.: field work, lab work, analysis, review. C. H.: statistics, review. M. K.: field work, lab work, review. M. G.: field work, analysis, review. HS: funding acquisition, supervision lab work, review. P. M. A.: conceptualization, design, supervision, review.

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