Seasonal depth distribution and thermal experience of the non-indigenous round goby *Neogobius melanostomus* in the Baltic Sea: implications to key trophic relations

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Abstract Native to the Ponto-Caspian region, the benthic round goby (*Neogobius melanostomus*) has invaded several European inland waterbodies as well as the North American Great Lakes and the Baltic Sea. The species is capable of reaching very high densities in the invaded ecosystems, with not only evidence for significant food-web effects on the native biota and habitats, but also negative implications to coastal fishers. Although generally considered a coastal species, it has been shown that round goby migrate to deeper areas of the Great Lakes and other inland lakes during the cold season. Such seasonal movements may create new spatio-temporal ecosystem consequences in invaded systems. To seek evidence for seasonal depth distribution in coastal marine habitats, we compiled all available catch data for round goby in the Baltic Sea since its invasion and until 2017. We furthermore related the depths at capture for each season with the ambient thermal environment. The round goby spend autumn and winter at significantly deeper and offshore areas

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compared to spring and summer months; few fish were captured at depths < 25 m in these colder months. Similarly, in spring and summer, round goby were not captured at depths > 25 m. The thermal conditions at which round goby were caught varied significantly between seasons, being on average 18.3 °C during summer, and dropping to a low 3.8 °C during winter months. Overall, the fish sought the depths within each season with the highest possible temperatures. The spatial distribution of the round goby substantially overlaps with that of its main and preferred prey (mussels) and with that of its competitor for food (flatfish), but only moderately with the coastal predatory fish (perch), indicating thereby very complex trophic interactions associated with this invasion. Further investigations should aim at quantifying the food web consequences and coupling effects between different habitats related to seasonal migrations of the round goby, both in terms of the species as a competitor, predator and prey.

Introduction

Migration is a common phenomenon within many taxa of animals, terrestrial as well as aquatic. One way to define migration is as a synchronized, large-distance movement of a population between separate habitats, which usually occurs with a regular periodicity (Leggett 1977; Dingle and Drake 2007; Lucas and Baras 2001). Such spatial displacement, often of substantial biomasses may exert significant impact on community structure and function, flux of energy and nutrients between different areas and habitats, and on species interactions (Deegan 1993; Varpe et al 2005; Marczak et al 2007; Bauer and Hoye 2014; van Deurs et al 2016). Not surprisingly, migration has received substantial attention by scientist for decades. This includes not only describing and characterizing the observed patterns and their implications for trophic interactions, but also relating the spatial displacement to causal drivers, e.g. seasonal changes in habitat-specific trade-offs between predation risk and growth rate, spawning, or avoidance of unfavorable or seeking of preferred environmental conditions (Brodersen et al

2008; Kanciruk and Hernkinn 1978; Quinn and Dittman 1990, O'Driscoll 2004, Sigler and Csepp 2007).

In some cases, actively migrating mobile non-native taxa are of concern due to their ability to colonize new areas and pose threat to native species. Examples of these are the Chinese mitten crab *Eriocheir sinensis*, the snow crab *Chionoecetes opilio*, the lionfish *Pterois* spp. and the round goby *Neogobius melanostomus* (Herborg et al 2003; Nichol & Somerton 2015; Tamburello & Côté 2015; Kornis et al 2012). Round goby is invasive on both sides of the Atlantic Ocean by occurring in high numbers in the North American Great Lakes, the Baltic Sea and several European inland waterbodies (Kornis et al. 2012). Because of large areas colonized and high population sizes achieved, major effects on the native species and communities have been documented in the wake of its invasion (Crane and Einhouse 2015; Karlson et al. 2007; Bergstrom and Mesinger 2009; Poos et al. 2010; French and Jude 2001). Recent investigations in the Great Lakes and other inland lakes of North America show that in these environments, this species engages in annual nearshore/offshore migrations, typically of the entire populations, and that this seasonal migration of the round goby displaces a large biomass, with substantial ecological impacts (Andres et al. 2020, Pennuto et al. 2021). In general, the round goby has a generalist feeding strategy and preys upon a wide range of different pelagic and benthic invertebrates (Skabeikis and Lesutiene 2015; Nurkse et al. 2016) and also fish eggs and small fish (Schrandt et al. 2016; Wiegleb et al. 2019). Through direct predation the round goby has likely caused a major decline of dominant benthic macroinvertebrates (and mussels in particular) in shallow areas in the Baltic Sea (Skabeikis et al. 2019). The round goby has also become an important competitor with native benthic feeding fish (e.g. flounder *Platichthys flesus*) over macroinvertebrate prey (Karlson et al. 2007; Lederer et al. 2008; Skabeikis et al. 2019). To be able to evaluate the impact a non-native invasive species has on the invaded system, it is thus imperative to understand the species ecology, including migration patterns, for planning of any mitigation measures (Ojaveer et al., 2015).

With a temperate climate, the Baltic Sea provides a seasonally strongly variable habitat for the round

goby, with water temperatures on average varying between 17 and 18 °C in summer, dropping to around zero in winter. The seasonal changes in temperature are superimposed by the typically two-layer salinity stratification. Cold water bodies, formed during winter, persist long into the summer season below the halocline, whereas a summer seasonal thermocline develops above the halocline in the surface waters at depths of about 15–20 m. Therefore, the range of the surface temperature variation may be as large as 25 °C, while within the deeper water layers, e.g. of the Gotland Deep, is on average only 5 °C (range 3–8 °C) (BACC 2015).

In this study, we used catch data from 1994 to 2017 to investigate pan-Baltic seasonal depth distributions of the round goby, and correlated this with the thermal environment at the place of capture. We hypothesize that (1) there is a seasonal pattern in depth distribution of round goby, and (2) the seasonal pattern in depth distributions of round goby relates to avoidance of cold-water temperatures in shallow waters during the cold period of the year. In addition, we compared how round goby depth distribution overlaps with the preferred major macrozoobenthic prey (the blue mussel *Mytilus edulis*), a major competitor for food (flounder *Platichthys* spp.) and an important piscivorous predator in coastal areas (perch *Perca fluviatilis*).

Materials and methods

Data

Data represents a compilation of altogether 1084 pan-Baltic catches of round goby from 1994 to 2017. All available data were used, although data were not available for all years in all areas (Table 1 and Fig. 1). Individual catches of round goby were allocated to one of four quarters (Q); Q1 (January-March), Q2 (April-June); Q3 (July–September) or Q4 (October-December). Information on depth and gear type was available for each catch, except for 12 catches (1.1%), where information on bottom depth was extracted from the ETOPO1 Global Relief Model that includes Baltic Sea Bathymetry by using the function "getNOAA.bathy" at resolution of 1 min from the R package marmap (Amante and Eakins 2003; R Core Team 2016; Pante et al. 2017). Information about the bottom water temperature at the catch locations (i.e. temperatures

experienced by the caught goby) was obtained for 801 of the 1084 catches (74%). To evaluate depth-specific thermal experience of round goby at the remaining locations, we extracted all available bottom water temperature measurements from 1994 to 2017, for the area between 53 and 60°N and 08–30°E, from the ICES hydrographic database (ICES Dataset on Ocean Hydrography, The International Council for the Exploration of the Sea, Copenhagen 2017) and calculated the average bottom temperature for each quarter and 5 m depth intervals. These data were only used for visual interpretation of the relationship between bottom temperature and total number of fish summed at 5 m depth interval. Comparison of the bottom temperature profiles of the western and eastern part, as well as the southern and northern part of the region revealed a highly comparable pattern, thus a single depth profile for the whole region was used. The total number of round gobies from one catch divided by mean of observations from each gear type is here defined as standardized Catch Per Unit Effort (stand CPUE).

Statistical analysis

We tested the following two hypotheses (1) there is a seasonal pattern in depth distribution of round goby, and (2) the seasonal pattern in depth distributions of round goby relates to avoidance of cold-water temperatures in shallow waters during the cold period of the year. A post hoc analysis (Kruskal–Wallis and Dunn's Multiple Comparison test) was performed to statistically test hypothesis 1 (i.e. to examine whether depth of catches changed significantly between quarters) (R Core Team 2016). A linear mixed intercept model was used to statistically test the second hypothesis. The linear mixed-effects model (LME) from the NLME package in R was used for modelling (Pinheiro et al. 2016; R Core Team 2016). For reduction of the fixed structure, we used maximum likelihood (ML) estimation procedure and a backward selection routine based on manual calculations of Log Lik values for each of the variables in the model. The Akaike´s Information Criterion (AIC; Burnham and Anderson 1998) was used in model comparison. Restricted maximum likelihood (REML) estimation procedure of the final model was used for better estimation of the random variance comparing to ML estimation (Zuur et al. 2009). Model validation was

Table 1 Overview of the compiled data (1994–2017) used in the present study, including fishing gear types (N = 21), number of catches (number in front of bracket) and total number of fished round gobies for all corresponding catches (number in bracket). The in total 1084 catches containing round goby comprised a total number of 43,745 individual round gobies

Geartype	Quarter 1			Quarter 2			Quarter 3			Quarter 4		
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
TV3[a]			2(3)								2(7)	
TV3-520	13(712)	10(10)	11(38)		15(524)	25(83)	7(69)	35(6979)	50(2744)	37(5793)	49(1010)	4(5)
TV3-930		35(1322)	9(521)	1(273)							11(21)	1(4)
Beamtrawl											2(47)	
GOV											1(1)	
Aalzeese									2(12)	23(133)		
Bott Trawl[b]						2(9)	10(97)	9(222)	1(69)	2(106)	4(111)	
5 trap set					11(142)	2(3)	11(89)	6(12)	15(50)	8(86)		
Fyke net				1(44)	3(255)	6(548)	7(442)	7(315)	6(322)	6(398)	1(18)	
Gill net			1(50)	1(40)	2(130)		1(7)	2(51)	2(63)	2(38)	1(7)	
Pel Trawl[c]		1(32)										
OTB	2(5)		1(1)									3(9)
3MK								1(9)			1(7)	
JFT		2(3)	1(2)						6(35)			
Ext N Gil[d]			24(52)	103(1950)	103(1268)	6(125)				31(44)	25(31)	
Net type 1							22(437)	25(172)	3(71)			
Net type 2							52(2893)	78(11,074)	2(359)			
Net type 3										10(103)	5(25)	
Beachseine								25(377)				
Netlænke										46(297)		
Nor c net[e]							30(163)	1(1)				
Total	15(717)	48(1367)	49(667)	106(2307)	134(2319)	41(768)	140(4197)	189(19,212)	87(3725)	165(6998)	102(1285)	8(18)

[a] No information on size of TV3

[b] Bottom trawl

[c] Pelagic trawl

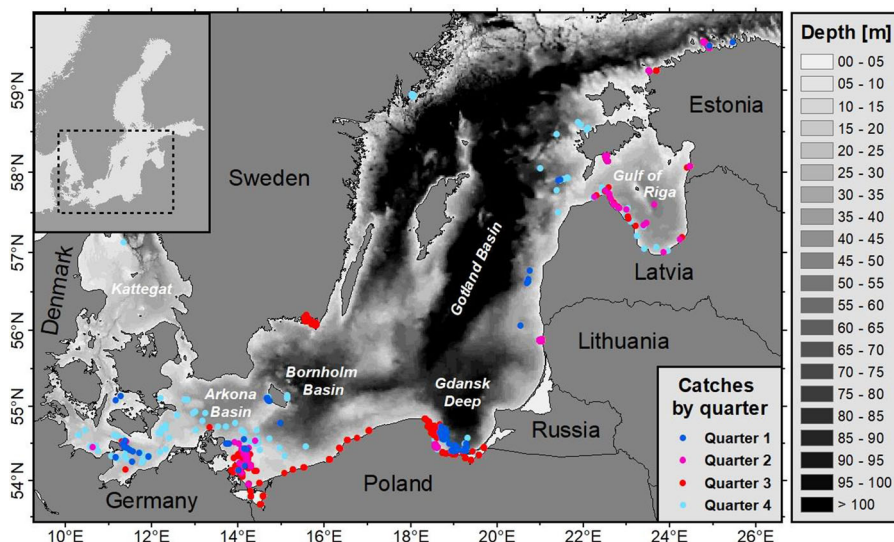[d] Extended Nordic Gillnet

[e] Nordic coast net

Fig. 1 Positions of catches containing round goby in the period 1994–2017 by quarter. Quarter 1 (dark blue) is January-March, quarter 2 (pink) is April-June, quarter 3 (red) is July–September and quarter 4 (light blue) is October-December. In total, 1084 catches contained round goby, comprising a total number of 43,745 individual round gobies

done by checking the assumptions of normality and independence of residuals.

The linear mixed intercept model included a log transformation of the response variable, stand CPUE. Due to high variance in observations of round goby between gear types (Fig. S1 A and B), we allowed the within-gear type errors (residuals) to vary between gear types by using varIdent variance structure in the model. Because observations from 8 of the 21 gear types had incomplete information on temperature, the linear mixed model only contained 13 types of gear. The full model for examination of whether water temperature drives the depth distribution of round goby included a fixed effect of the observed temperature for each catch and a factor named quarter with 4 levels (i.e. Q1-Q4) to account for differences in standardized CPUE over the year and gear type (13 levels) as random effect to capture systematic deviations in the standardized CPUE for different gear types:

(**Temperature) model**) $Log(standCPUE)_i = \mu + \alpha(quarter_i) + \beta * temperature_i + \gamma(geartype_i) + \varepsilon_i i = 801$

(**Model assumptions**) $\varepsilon_i \sim \text{i.i.d.N}\left(0, \sigma^2_{geartype_i}\right)$, $\gamma(geartype_i) \sim \text{i.i.d. N}\left(0, \sigma^2_\gamma\right)$

To test the robustness of the post hoc analysis as stated above we performed the same test on a subset of data (i.e. gear type = TV3-520, N catches = 236). Only data from the same gear type and with data from all four quarters were used in the analysis. Missing information of temperature on all catches from gear type TV3-520 made it impossible to test the second hypothesis.

Calculation of spatial overlap between the round goby and trophically associated species

Overlap of the distribution area of the round goby and trophically-associated species was measured as a percentage of the distribution area of blue mussel, perch and flounder where the round goby was present. The overlap was calculated for three quarters (Q2-Q4; i.e. spring, summer and autumn), when trophic interactions with involvement of fish generally occur in the Baltic Sea. Map analysis was carried out with ArcMap (ArcGIS 10.6) tool Raster Calculation, under Spatial Analyst Tools—Map Algebra (https://desktop.arcgis.com/en/arcmap/10.3/tools/spatial-analyst-toolbox/raster-calculator.htm).

First, new raster layers were made for the round goby and the three trophically associated species, blue mussel, flounder and perch by applying conditional tool "Con" with binominal values (0 and 1): 0—where a given taxon was not present, 1—a given taxon was present. Potential round goby habitats were divided

into quarters (Q2–Q4), which all correspond to the depth ranges describing the interquartile areas in Fig. 2a.

Secondly, raster calculation subtraction between rasters was used (e.g. raster "*M. edulis*" – raster "round goby Q2"). New output rasters had two values 0 and 1, where 0 presented overlap between layers of a trophically associated species and the round goby, and 1 presented the area, where a trophically associated species was present but round goby was not. To calculate the overlap percentage between a trophically associated species and round goby, pixel values were used.

Spatial overlap was calculated based on the formula:

$$\text{Overlap percentage} = P0 * 100\%/(P0 + P1),$$

where:

P0 = Pixel values for the overlap area,

P1 = Pixel values for the habitat area of trophically associated species (Fig. 4E-G), where there was no overlap with potential round goby habitat.

Results

Observations and post hoc analysis

The depth at which round goby were caught varied significantly between quarters ($p < 0.001$), except for Q2 and Q3, where fish were caught in shallow water of average depths of 9.4 and 8.2 m, respectively (Fig. 2a). Catches during autumn- and wintertime (Q4 and Q1) revealed that fish spend this period of the year at much deeper waters, especially in Q1 (January to March) where the fish on average were caught at 35.6 m (Fig. 2a). The maximum depth that a round goby was caught at was 90 m in Q4, at the northwest coast of the Estonian island Saaremaa.

The water temperature at which round goby were caught varied significantly between quarters ($p < 0.001$) except for Q2 and Q4 (Fig. 2b). Fish experienced the highest temperatures during summer (Q3) with an average of 18.3 °C, which dropped to a low 3.8 °C during January-March (Q1). In contrast, the temperatures experienced by the fish in spring/early summer (Q2) and autumn/early winter (Q4) was highly comparable, 11.3 and 10.4 °C, respectively. Thus, overall the fish experienced a span in average
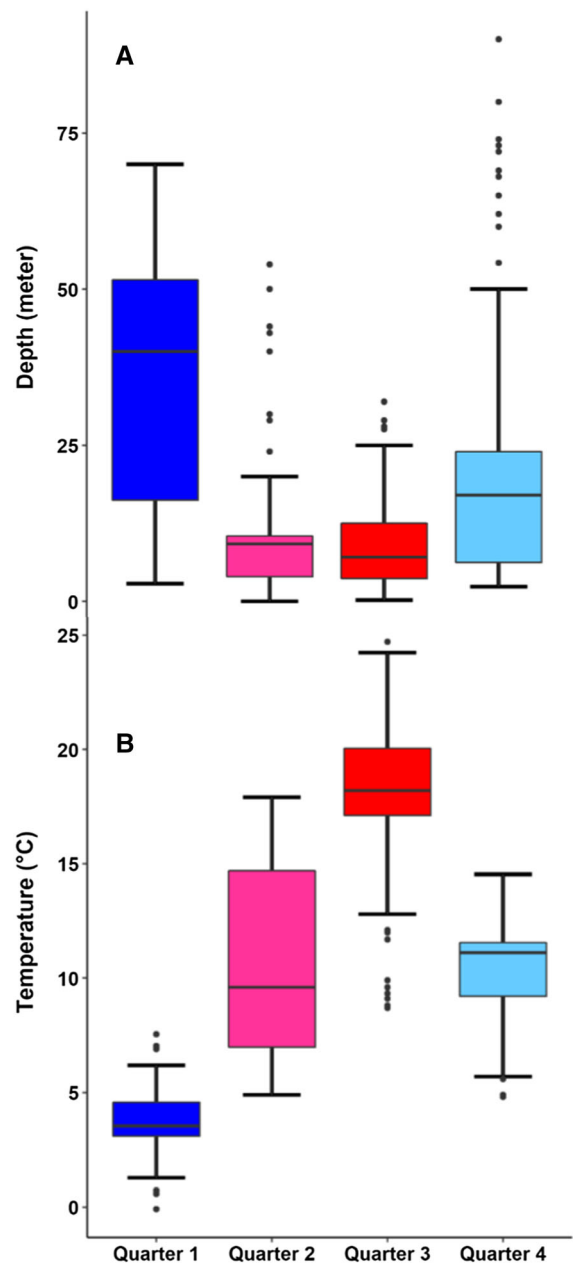

Fig. 2 Seasonal depth (a) and thermal experience (b) in relation to quarter for goby caught between 1994 and 2017. Quarter 1 is January-March, quarter 2 is April–June, quarter 3 is July–September and quarter 4 is October-December. Solid line is the median, box is the interquartile area (bottom and top are 25th and 75th percentiles, respectively). Whiskers show either the max/min observation if within 1.5 of the interquartile range or 1.5 times the interquartile range. For details of used gear types and number of catches see Table 1

temperature of 14.5 °C during the annual cycle. The lowest temperature where round goby was fished was

0.1 °C at 14 m depth in Q1, whereas the highest was 24.7 °C at 4 m depth in Q3 (Fig. 2b).

Comparison of total number of round goby caught at each 5 m depth interval in each quarter (Fig. 3a) and bottom water temperature profiles extracted from the ICES database (Fig. 3b), revealed that in three out of four quarters, the depth at which the highest catch was obtained, was linked with the highest bottom water temperature. The exception was Q1, where the fish would have experienced a few degrees higher
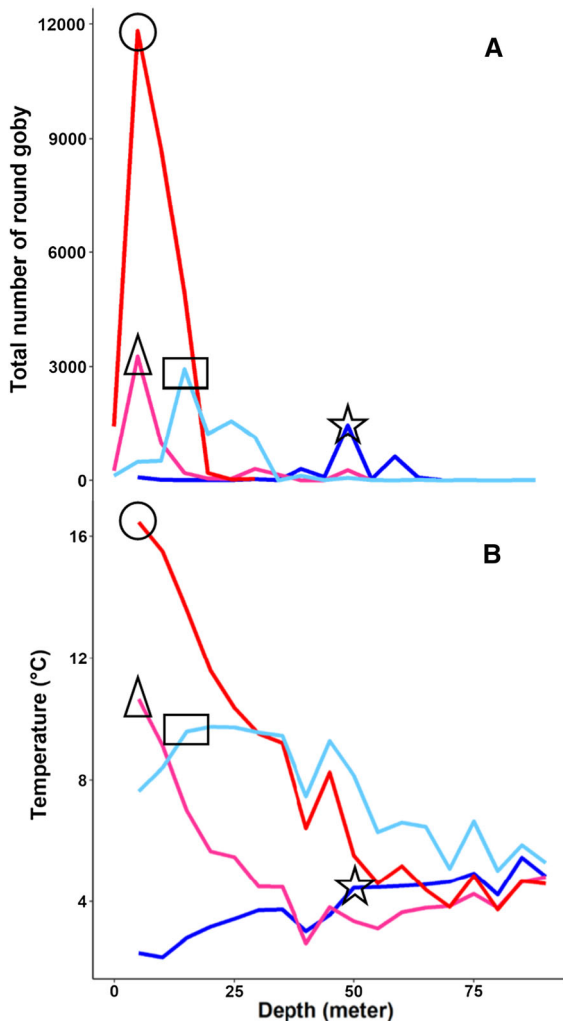

Fig. 3 a The total number of round goby caught at each 5 m depth interval for each quarter (dark blue: Q1; pink: Q2; red: Q3 and light blue: Q4). The four symbols indicate the peak of number of fish for each quarter (star for Q1, triangle for Q2, circle for Q3 and square for Q4). **b** Bottom temperatures (ICES database) in relation to depth for Q1-4. The four different symbols (see A) illustrate at what temperature number of caught round goby at a given depth was highest

temperatures had they migrated 35-40 m deeper (i.e. to 85–90 m or deeper) (Fig. 3a and b).

Statistical modelling

The linear mixed intercept model confirmed our second hypothesis that seasonal depth distribution of the fish is linked to the thermal conditions: the round goby avoids cold temperatures during winter at shallow depths. The full model was not reduced as both temperature and quarter turned out to be significant (Table 2) and model reduction only increased AIC (i.e. insufficient model reduction). The effect of temperature supported our observations that round goby seem to seek areas (depths) with highest possible temperatures as the overall temperature effect turned out to be positive for stand CPUE of round goby throughout a whole year ($\alpha = 0.049$, $p = 0.002$) (Table 2). The significance of the factor quarter revealed that mean stand CPUE differed over the year resulting in 4 different intercepts of the final model (Table 2).

Test of robustness

Depth from catches using the TV3-520 gear differed significantly in depth over the year ($p < 0.001$). Fish were caught in significantly deeper water in Q1 (27.7 m) and Q4 (23.4 m) compared to Q2 (16.0 m) and Q3 (14.3 m). The water temperature at which round goby were caught with TV3-520 varied significantly between quarters ($p < 0.001$). The highest temperature fish experienced was in summer (Q3) with an average on 17.0 °C. In contrast, the coldest temperature experienced by the fish was found in winter (Q1) with an average of 2.5 °C. In Q2 and Q4, fish experienced more comparable temperatures, however still significant from each other (13.0 °C and 10.5 °C, respectively, $p = 0.001$).

Spatial overlap with trophically associated species

The highest overlap between the distribution of the round goby and the three investigated trophically associated species (Fig. 4) was observed for flounder (competitor) and blue mussel (preferred prey) in autumn (70.0 and 50.1%, respectively), while the lowest overlap was always observed for perch ($\leq 20\%$; Table 3), predator on round goby.

Table 2 Summary of fixed and random effects and their associated parameters retained in the final temperature model for log(stand CPUE). Parameter estimates by REML, their standard errors (SE), degrees of freedom (DF) and significance values (P) are shown

Parameter	Estimate	SE	DF	P
Fixed effects				
Quarter:			784	< 0.001
Quarter 1	− 1.897	0.355		
Quarter 2	− 1.040	0.372		
Quarter 3	− 1.453	0.412		
Quarter 4	− 2.207	0.358		
Temperature	0.049	0.016	784	0.002
Random effects (SD units)				
Among-geartype (σ_γ^2)				0.947
Within-geartype (residuals) ($\sigma_{geartype_i}^2$)				1.219
N = 801				

Discussion

The present study has resolved one of the major gaps in our knowledge related to the seasonal distribution pattern of the round goby in one of its invasion hotspots—the Baltic Sea. Using all available round goby catch data in the Baltic Sea since its introduction in the early 1990s, we were able to show that the round goby stay in deeper water layers during the cold season as compared to spring and summer. This ultimately reveals a pronounced seasonal migration between shallow coastal waters and offshore areas, which can be related directly to different thermal conditions between the seasons. This finding mirrors the annual inshore/offshore seasonal migration of round goby documented in some North American lakes (Andres et al. 2020, Pennuto et al. 2021) and previously suggested in Europe (Sapota and Skora 2005; Christoffersen et al. 2019). These migration events have been shown to translocate significant amounts of energy, prey, and nutrients in a range of lake sizes (Johnson et al. 2005, Andres et al. 2020, Pennuto et al. 2021). ECThe deepest location previously recorded was 130 m in the North American Great Lakes (Walsh et al. 2007) (although based on much less extensive spatial data), as opposed to 90 m in the Baltic Sea in this study.

Potential drivers of the described migration

Migration in fish can be triggered by various drivers, like the nutritional state of the individual, food-web interactions (incl. cannibalism, predator avoidance), or environmental factors such as temperature, salinity and oxygen conditions (Kanciruk and Hernkind 1978; Brönmark et al. 2008; Bazazi et al. 2011). Many species living at temperate latitudes retreat to avoid cold exposure (Sunday et al. 2014), and maybe not surprisingly, our results reveal the same for round goby which avoids the shallow coastal waters during the coldest period where water temperatures can decrease below 0 °C. Notably, our data show that round goby not only avoid the very cold shallow water during winter, but that the fish actively seeks the highest available temperature within the depth range in the different seasons. In other words, round goby selects depths that offer the highest possible temperatures for the season.

Mobile ectotherms possess the advantage of being able to actively choose a thermal environment that enables them to maintain a sufficient or even high physiological performance (Reynolds and Casterlin 1979; Sunday et al. 2014), and the observed 'thermophilic behavior' may be a relic from the species place of origin, to which their physiology is adapted. In this context, it is important to note that water temperatures are higher in their native Ponto-Caspian region (average summer temperatures of aprox. 22–28 °C) compared to the invaded Baltic Sea (Dumont 1998; Olenin 2002; Schiewer 2008). In a recent laboratory study, Christensen et al. (2021) offered Baltic round goby a thermal range from 5 to 25 °C, and found that the fish preferred on average 21 °C. Furthermore, most fish stayed within a thermal range of 18 and 24 °C, and had the highest aerobic performance between 15 and 28 °C. A dislike for
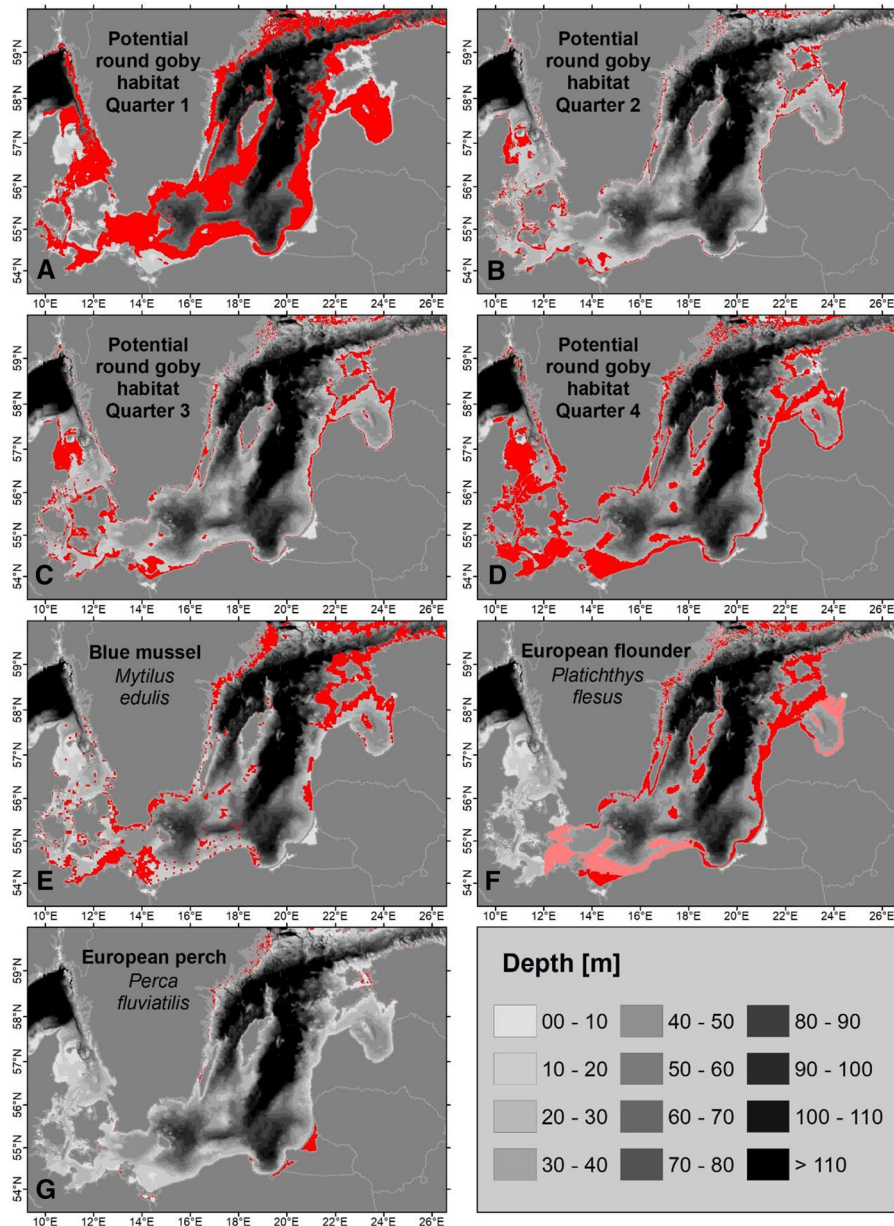
Fig. 4 Potential overlap of round goby with three Baltic key species that interact with round goby as either prey (Blue mussel), competitor for food (Baltic flounder), or predator (European perch). **a–d** Potential habitat of round goby in Q1, Q2, Q3 and Q4, respectively, based on the catch data in the present study. Red areas correspond to the depth ranges describing the interquartile areas in Fig. 2. **e** Occurrence of Blue mussel (*Mytilus edulis*) (red areas; data from HELCOM Map & Data Service https://helcom.fi/baltic-sea-trends/data-maps/), **f** Spawning areas of Baltic flounder (*Platichthys solemdali*) (red areas; data obtained from HELCOM Map & Data Service https://helcom.fi/baltic-sea-trends/data-maps/), **g** Recruitment areas of European perch (*Perca fluviatilis*) (red areas; data from HELCOM Map and Data Service https://helcom.fi/baltic-sea-trends/data-maps/)

cold waters may also explain why round goby, despite a pan-Baltic distribution, have only been observed in very few numbers in the northernmost (and coldest) areas of the Baltic Sea, more specifically in Raahe in the southern part of the Bothnian Bay, but not in any adjacent or more northerly areas (Puntila et al. 2018).

Table 3 Overlap of the distribution area of the round goby and trophically-associated species in the Baltic Sea, measured as a percentage of the distribution area of blue mussel (*Mytilus edulis*), perch (*Perca fluviatilis*) and flounder (*Platichthys flesus*) where the round goby was present

Species	Quarter of the year	% overlap
Blue mussel	2	22.4
Blue mussel	3	31.8
Blue mussel	4	50.1
Perch	2	16.8
Perch	3	20.0
Perch	4	16.2
Flounder	2	21.4
Flounder	3	33.1
Flounder	4	70.0

In addition, being in shallow (warmer) waters during spring and summer offers good living conditions related to the high availability of preferred prey (e.g. bivalves and arthropods), spawning opportunities, and favoured hard-bottom substrates (Sapota, 2004).

The ecological implications of biomass movement: round goby as a predator

Our depth distribution maps show that annually, blue mussels and round goby co-occur in over 70% of the of the habit available to both species (Fig. 4), and further calculations (based on the presence of the round goby in the distribution area of blue mussels) suggest the highest impact risk of round goby in autumn (Q4). Irrespectively of their size, round goby prefers the smaller blue mussels (Schwartzbach et al. 2019), and there is evidence that they feed efficiently on newly

settled mollusks, causing a severe constraint for blue mussel recovery (Skabeikis et al. 2018). Mussels are important ecosystem engineers, that provide habitat for a diverse fauna and flora, and they furthermore mitigate eutrophication effects thorough filtration (Donadi et al. 2015; Chowdhury et al. 2016; Petersen et al. 2016). A substantial removal of mussels will likely affect the whole ecosystem functioning in the affected (mostly near-coastal shallow) areas.

Round goby caught in winter in the NE Baltic Sea with stomachs containing the soft-shelled clam *Limecola balthica* (Linnaeus, 1758) (K. Nõomaa, unpubl. data), suggest that they also feed during the winter. Considering that the fish does spend an extended period in deeper waters, some impact may be expected, and the nature of the impact and its' magnitude should be further investigated.

The ecological implications of biomass movement: round goby as a competitor

Resource competition (such as for prey, habitat and space) is an important factor for shaping biotic communities in aquatic ecosystems. There are several examples of competitive superiority of the round goby leading to outcompeting of native fish in invaded freshwater habitats (e.g. Balshine et al. 2005; Bergstrom and Mensinger 2009). Food competition with native fishes also occurs in the Baltic Sea: after the round goby invasion, flounder and turbot (*Psetta maxima*) juveniles were found to shift diets, resulting in an increased diet overlap with other species, and a lower feeding success, which together may have affected recruitment success of the fish (Ustups et al. 2015). Our analysis revealed potentially major overlap (up to 70%) between the major competitor for food, the flounder, and the round goby distribution, which supports the above. Also, depth distribution of the round goby overlaps with small native gobies *Pomatoschistus* spp., which predominantly inhabit shallow coastal areas, and the available evidence suggests that these small native gobies are negatively affected by round goby (Hempel et al. 2016). This effect may further cascade in the foodweb and affect recruitment abundance of a very valuable coastal commercial species—pikeperch (*Zander lucioperca*), for which larvae and early juveniles of *Pomatoschistus* spp. serve as the primary prey for early juveniles (Müller-Karulis et al. 2013). Although there is evidence that

juvenile pikeperch can prey on the round goby (Hempel et al. 2016), the net effect of the round goby on the early juvenile stages of pikeperch is likely reduction of its primary food resource.

In addition to fish, round goby competes for the same prey with fish-eating birds. Dramatic decline in blue mussel availability and a changed size structure at depths < 20 m, associated with round goby distribution during the warm season (present study) and directly caused by round goby predation, induced a dietary shift in wintering long-tailed duck (*Clangula hyemalis*) towards fish prey in a coastal rocky habitat in the southern Baltic Sea. Such a shift has led to a reduction in carrying capacity of the bird in the study area, and shows that coastal habitats with low blue mussel biomass become less attractive wintering sites for seabirds (Skabeikis et al. 2019).

The ecological implications of biomass movement: round goby as prey

Introduction of non-native species can also be beneficial for some species in the invaded ecosystems. Although the individual/population level beneficial effects of the introduction of round goby on predatory fish still needs to be resolved within the Baltic Sea, round goby now serve as an important prey for both piscivorous fish and fish-eating birds (Stapanian et al. 2011; Crane et al. 2015; Hempel et al. 2016). Some fish-eating birds can switch to the round goby (Bzoma and Meissner, 2005), displaying increased consumption rates (Johnson et al. 2005) and indirect evidence of increases in population size; e.g. that grey heron (*Ardea cinerea*) population has increased in the southern Baltic Sea because of the rapid expansion of the round goby (Jakubas 2004). Our study evidenced that the distribution area of the round goby only moderately overlaps with that of one of the most abundant coastal predatory fishes perch), but this overlap undoubtedly offers a new (potentially) nutritionally profitable prey resource for the coastal piscivorous species (Brauer et al. 2020). This also adds to Liversage et al. (2017), who found that round goby densities do not significantly affect perch feeding, which is most likely affected by other environmental factors. The predominantly shallow-water occurrence of round goby, as evidenced in our study, may result in predation release of juveniles of commercial fish species from fish-eating birds

(Johnson et al. 2005). The main top predatory fish in the Baltic, cod (*Gadus morhua*) traditionally preys mainly on clupeids, but may shift to include substantial shares of round goby where these are abundant in coastal areas (Almqvist et al. 2010; Funk et al. 2020). In addition, from 2007 onwards, round goby has occurred in cod stomachs (Huwer et al. 2014), suggesting that they act as prey also for cod foraging on deeper waters.

Grey seal (*Halichoerus grypus*), and also to some extent harbour seal (*Phoca vitulina*), likewise consume round goby in the southern and southwestern Baltic Sea. While the share of round goby in harbour seal diet in 2001–2005 and 2013 was negligible (1%), round goby constituted 17% of the grey seal diet in 2012–2013 (Scharff-Olsen et al. 2019). More recently (2017), round goby was the fish species with the highest occurrence in scats from a haul-out site by Rødsand (where round goby were first observed in 2011; Azour et al. 2015), occurring in 45 to 62% of the scats sampled in spring, summer and autumn in 2017 (no samplings in winter) (Kroner unpubl. data). Thus, locally, round goby can be an essential component of grey seal diets. As seals require food during the whole year, the seal—round goby interaction likely takes place both in shallower coastal areas as well as offshore and our round goby seasonal occurrence data is of high value for seal ecologists to interpret seal feeding ecology.

Limitations of the research

All available data on the round goby catches were compiled to provide a pan-Baltic perspective. Therefore, sampling techniques and applied fishing gears differ between seasons, years, and areas. It should be acknowledged that data obtained from some gear types may not be fully representative of the round goby distribution. For example, shallow-water and hard-bottom habitats can be underrepresented in the data from active gears, e.g. bottom trawls (Smoliński and Radtke 2017). On the contrary, some of the passive gears (e.g. gillnets) are not used in the deeper areas. However, applied standardization of Catch Per Unit Effort and mixed-effects modeling allowed for the partial control of these confounding effects of varying sampling techniques in the estimation of depth distribution and thermal preference of round goby.

Lack of balance in the spatial and temporal coverage of the data should be considered when interpreting the results. We utilized only data from scientific surveys, but possible integration of the data from the commercial and recreational catches could be helpful to potentially improve the spatial and temporal resolution of future analyses (Støttrup et al. 2018).

Implications on future research, monitoring and assessment

As round goby occurrence and abundance data will continue to originate from various sources (there is no commonly agreed round goby monitoring protocols in the Baltic Sea), results of the current study provide the general background for interpretation of the locally collected seasonal data (e.g. those following the HELCOM coastal fish sampling guidelines). One of the immediate tasks should be estimation of the round goby abundance and density in different areas of the Baltic Sea by depth strata, to be further used not only for impact assessment and reporting purposes for the Descriptor 2 (non-indigenous species) of the European Union's Marine Strategy Framework Directive, but also future predictions, and to support developing mitigation measures.

Our results show pronounced seasonal migration of the round goby from the very shallow coastal areas to the deep offshore regions and vice versa, similar to findings in North American freshwater environments (Andres et al. 2020, Pennuto et al. 2021). Both the spatial distribution (Kotta et al. 2016) as well as biomass of the round goby has increased over time in the Baltic Sea (up to 350 individuals/100m^2; Sapota and Skora 2004; Puntila et al. 2018), which has resulted in increased translocation of organic matter and energy to deeper offshore regions over time. Further investigations should be aimed at quantifying the food web consequences and coupling effects between different habitats associated with seasonal migrations of the round goby, both in terms of the species as a competitor, predator and prey.

Declarations

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