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Juvenile and Adult Three-Spined Sticklebacks Exhibit Different Habitat Use in Shallow Baltic Sea Bays

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ABSTRACT

Three-spined sticklebacks (*Gasterosteus aculeatus*) have become dominant in many Baltic Sea coastal fish assemblages, yet life-stage-specific habitat use remains poorly understood. We surveyed shallow water habitats along the coast of Gotland, Sweden, to examine how juvenile and adult stickleback abundances relate to variables such as submersed aquatic vegetation (SAV) biomass and vertical structure, macrophyte species richness, biomass of drift filamentous algae and potential invertebrate prey abundance. Juvenile stickleback abundance increased with SAV variables, macrophyte species richness, and drift filamentous algae, whereas, in contrast, adult abundance was only significantly associated with potential prey (invertebrate abundance). Our findings reveal life-stage-specific habitat associations of three-spined sticklebacks and highlights the importance of both long-living vegetation and ephemeral drift algae in supporting juvenile sticklebacks. This study contributes to a better understanding of sticklebacks' coastal ecology in the central Baltic Sea.

1 | Introduction

The three-spined stickleback (*Gasterosteus aculeatus*, hereafter 'stickleback') is a mesopredatory teleost fish with a broad distribution across the Northern hemisphere (Fang et al. 2018). This species displays high evolutionary plasticity and has adapted to a wide range of environmental conditions, with populations occurring in freshwater, brackish and marine environments (Bell 1976; Kaeuffer et al. 2012).

In the brackish Baltic Sea, sticklebacks have dramatically increased in offshore and coastal environments over the past few decades (Bergström et al. 2015; Olsson et al. 2019). Particularly in the central Baltic Sea, stickleback biomass rose from 4% to nearly 10% of the pelagic fish biomass during the 2010s (Olsson et al. 2019), causing a gradual shift in species dynamics in this

region (Eklöf et al. 2020). The presence of sticklebacks in the coastal zone is primarily concentrated between spring and early autumn. Sticklebacks in this system typically mature at about 2 years (Bergström et al. 2015; DeFaveri and Merilä 2013). As adults, they migrate from deeper offshore waters to very shallow (< 3 m) coastal areas to spawn in early spring (Bergström et al. 2015). Juveniles remain in coastal habitats until the end of summer to early autumn, after which they migrate offshore along with most of the remaining adults (Bergström et al. 2015).

The growing presence of sticklebacks in coastal Baltic Sea communities has been linked to important ecological impacts, such as the weakening of recruitment of the larger predatory fish northern pike (*Esox lucius*) and European perch (*Perca fluviatilis*; Byström et al. 2015; Nilsson et al. 2019). Indeed, in some shallow bays along the Swedish Baltic Sea, sticklebacks

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have now been found to be the dominant species (Staveley et al. 2020; Eklöf et al. 2020; Schmidt and Staveley 2025). By feeding on grazing invertebrates, sticklebacks also facilitate filamentous algae, which reinforces the effects of eutrophication (Donadi et al. 2017; Eriksson et al. 2009; see also Olin et al. 2022, for a review of the causes and consequences of the increased presence of sticklebacks in the Baltic Sea). Due to their increasing presence in coastal habitats, understanding how sticklebacks use these environments across life stages is critical.

While migration and habitat use of sticklebacks in the Baltic Sea are well studied (e.g., Bergström et al. 2015; Candolin 2004; Candolin and Salesto 2006; Yanos et al. 2021), ontogenetic variation in habitat use remains poorly understood, despite the seasonal overlap of juveniles and adults in coastal waters. In a study in the Northern Baltic Sea, Gagnon et al. (2017) provided important insights into these differences, showing that juvenile abundance correlated positively with submersed aquatic vegetation (SAV) cover, while adult abundance correlated negatively. The study also examined potential associations of juvenile sticklebacks with drift filamentous algae, favoured by eutrophication, but found inconclusive evidence for their importance, which highlights the need for further research to clarify their role as nursery habitats.

To address these knowledge gaps, this study investigates how the abundances of juvenile and adult sticklebacks in shallow habitats along the north-east coast of Gotland, Sweden (central Baltic Sea), are influenced by key habitat and prey variables. Specifically, we examine the following variables: (i) SAV biomass and vertical structure; (ii) macrophyte species richness (including SAV and non-filamentous macroalgae); (iii) drift filamentous algae mats' biomass; and (iv) abundance of potential invertebrate prey.

2 | Methods

2.1 | Site Description

The study was conducted in two bays located along the north-east coast of the island of Gotland, Sweden: Valleviken (57.7807 N, 18.9558 E) and Lergrav (57.7934 N, 18.9912 E; Figure 1A). The bays are moderately sheltered from the south-westerly winds prevailing in this region. The substrate in both bays is largely composed of sand and clay, with coarser sediments and boulders present more sporadically (Ljunggren 2025). Boat traffic is generally very low, with only few recreational boats travelling to the bayheads observed during the study period.

In these shallow bays, macrophyte communities consist primarily of freshwater SAV species including sago pondweed *Stuckenia pectinata* (hereafter '*Stuckenia*') and marine macroalgae such as bladderwrack *Fucus vesiculosus* (hereafter '*Fucus*'). Alongside these long-lived macrophytes, drifting mats of ephemeral filamentous algae and cyanobacteria are common. The invertebrate communities are dominated by molluscs, particularly Hydrobiidae snails, with amphipods in the genus *Gammarus* and chironomid larvae also abundant (D'Agata et al. 2025).

2.2 | Biological Surveys

Biological surveys were conducted over 4 weeks between July and August 2021. Fish, vegetation, π and invertebrate communities were surveyed at 22 sampling stations, 11 in Valleviken and 11 in Lergrav (Table A1). One station in Lergrav was later removed from further analyses due to high turbidity, which impacted the reliability of the fish survey (i.e., visibility < 2.5 m). The stations were haphazardly placed within areas with water depths between 0.5 and 3.0 m, providing that there was a minimum distance of at least 30 m between stations and at least 5% vegetation cover. Each station was a circular area of 10 m diameter delineated by a measuring tape attached to a central weighted buoy (station area: 78.54 m²).

2.2.1 | Underwater Visual Census

To assess the relative abundance of juvenile and adult sticklebacks, underwater visual censuses (UVCs) were conducted by snorkelling during daylight hours (10:00–17:00). While UVCs have known limitations in accurately describing overall fish communities due to, for instance, observer disturbance causing fish to hide or flee (Emslie et al. 2018), this method has been successfully used to investigate habitat-fish relationships (e.g., Eggertsen et al. 2022). All fishes were identified to the lowest taxonomic level possible, and their standard length (SL) was estimated in intervals of 1 cm. SL was preferred to total length (TL) as the pale caudal fin of sticklebacks may be difficult to clearly discern underwater, potentially leading to less reliable measures of TL estimates. In the months prior the UVCs, the observer was trained through the following protocol: first, estimating underwater object sizes using various objects of known dimensions; second, calibrating estimates on objects of unknown size, verified by measuring with a ruler until accuracy was achieved; third, observing fish behaviour and estimating school sizes by counting sub-sets, with photographs for verification when possible. The UVC consisted of two steps: a stationary point visual census to record pelagic species followed by systematic swimming close to the sea floor to record benthic and concealed species, based on Berkström et al. (2013) and Bohnsack and Bannerot (1986). Fish were recorded within a cylindrical volume of water extending from the surface to the seabed, with a radius of 2.5 m (area at the bottom: 19.6 m²). A smaller radius than that used by Berkström et al. (2013) and Bohnsack and Bannerot (1986) was chosen to account for the high turbidity often characteristic of Baltic Sea waters, especially during the highly productive summer months (Kyryliuk and Kratzer 2019). At each station, the stationary point visual census was performed for 3 min. The choice of a 3-min survey was based on preliminary trials, which initially tested 5 min and then 3 min surveys. These tests indicated that 3 min were sufficient to survey the cylindrical volume of water under our study conditions, as extending the survey to 5 min did not substantially increase the number of individuals recorded. A similar 3-min approach for stationary point surveys has also been previously successfully applied in Baltic Sea coastal habitats (Mattsson 2019). While at the surface, the snorkeler slowly rotated in one direction, scanning the volume of water. During this period, all fishes swimming in the water column were recorded. To avoid double-counting, previously identified individuals that re-entered the field of view,

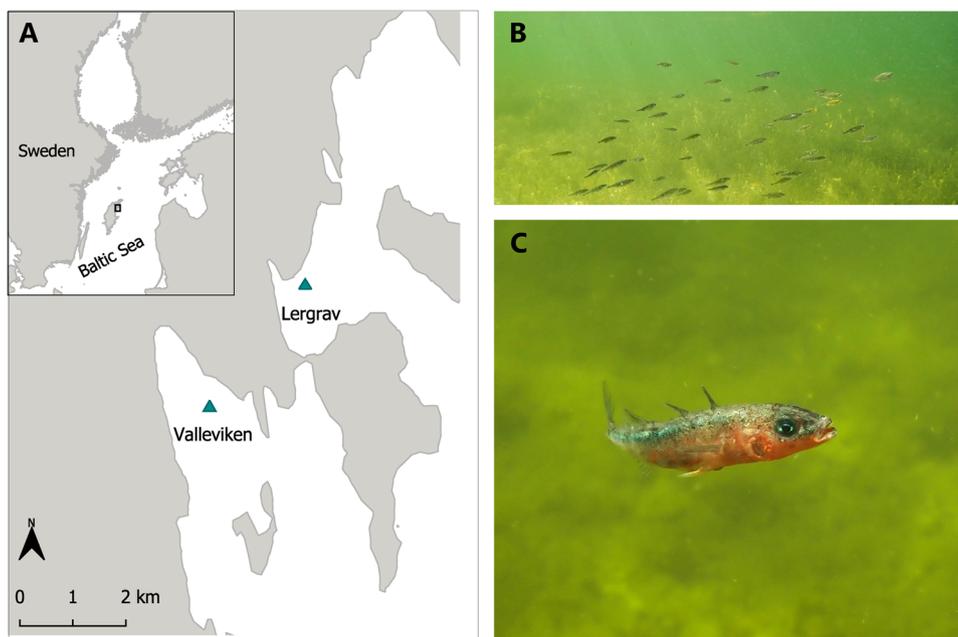


FIGURE 1 | (A) Map of the study bays on the north-eastern coast of the island of Gotland, Sweden; (B) A shoal of juvenile sticklebacks over vegetation in Valleviken; (C) An adult male stickleback in nuptial colouration, east-coast of Gotland. Photos by C. D'Agata.

for example, males in nuptial colours or bold individuals, were not noted again. For fish schools, abundances were estimated by counting the number of individuals in a sub-set and then multiplying it by the number of similar sub-sets observed in the school. Following the stationary point visual census, the observer conducted a benthic survey by swimming close to the sea floor. Starting from the centre of the UVC station, the observer swam outward and then back in a systematic, radial pattern, gradually covering the area of the UVC station. During this survey, concealed and benthic fish species were recorded, with vegetation gently parted as needed to detect hidden individuals. All surveys were conducted by the same snorkeler (C. D'Agata) to ensure consistency in observation and identification. The present study was conducted in parallel with another project investigating vegetation–coastal fauna associations. For that project, a baited remote underwater video (BRUV) system, using a small piece of herring as bait, was deployed approximately 1 h before the start of each UVC. While the BRUV was not part of the present study, we note that the bait plume may have influenced stickleback distribution during the UVC. However, since the procedure was applied consistently across all 21 stations, any potential bias is expected to be systematic, allowing meaningful comparisons of relative abundance patterns.

2.2.2 | Vegetation and Invertebrates

From recent investigations by D'Agata et al. (2025), vegetation vertical structure was assessed using three 0.5×0.5 m (0.25 m^2) haphazardly placed square plastic frame per station. Within each frame, the percentage cover (LC) of vegetation was estimated across five height layers: < 10 cm, 10–30 cm, 30–50 cm, 50–70 cm and > 70 cm (adapted from Schulz 2009; maximum cover = 100%). Each height layer was assigned a weight (LV) from 1 to 5, with

higher values corresponding to taller vegetation, allowing taller vegetation to contribute more to the index.

A standardised vertical structure index (VI) was then calculated using the formula:

$$VI = \frac{\sum_{i=1}^5 LC_i \times LV_i}{500}$$

where, for each station, LC_i is the percentage vegetation cover in the i th height layer and LV_i is its assigned weight. The denominator (500) represents the maximum possible value (i.e., 100% cover in the tallest layer, with a weighted value = 5). The resulting index provides a standardised measure of vertical vegetation complexity at each station.

Vegetation species richness at each station was calculated by combining all submerged aquatic vegetation (SAV) and non-filamentous macroalgae species recorded through three sources: (1) frames used in the estimation of vertical structure, (2) quantitative sampling (described below) and (3) visual inspection of the entire station area to detect less common species. Filamentous algae were excluded from the species richness calculation.

Finally, at each station, a quantitative sample of macrophytes, filamentous mats and associated invertebrates (≥ 1 mm) was collected using a mesh bag (radius 0.18 m, area $\sim 0.1 \text{ m}^2$, mesh < 0.5 mm). The bag was gently lowered over the vegetation, which was then cut just above the substrate and brought to the surface. Samples were stored on ice and later frozen at -20°C .

In the laboratory, macrophytes were sorted and identified to species or genus level. Epiphytic algae were rare and scraped, if present. Drift filamentous algae and cyanobacteria were grouped under 'filamentous mat'. Invertebrates were sorted, identified

to the lower taxonomic level possible and counted. Finally, dry weights (g) of all macrophytes, filamentous mats and macroinvertebrates (i.e., ≥ 1 mm in size) were measured after drying at 60°C for 14 days. See D'Agata et al. (2025) for further detailed descriptions of the vegetation and invertebrate surveys.

2.3 | Statistical Analysis

Generalised linear models (GLMs) were fitted for juvenile and adult stickleback abundances to explore life-stage-specific relationships with vegetation and potential prey. GLMs were chosen because they allow the direct modelling of untransformed count data, allowing for increased interpretability (O'Hara and Kotze 2010). Sticklebacks with a SL of less than 4 cm were pooled as 'Juveniles', the remaining as 'Adults'. The threshold of 4 cm was selected based on the mean length of stickleback young-of-the-year recorded in the central Baltic Sea (Bergström et al. 2015).

Four vegetation measures of habitat quantity and complexity were applied as predictor variables: SAV vertical index (dimensionless), SAV dry biomass (g), dry biomass of filamentous algae mats (g) and macrophyte species richness (cumulative number of non-filamentous macroalgae and SAV species).

Prey availability was quantified using abundance and taxonomic data from our quantitative sampling of invertebrates. To focus on prey items relevant to sticklebacks, we selected taxonomic groups that have been identified in previous stomach content analyses as important components of stickleback diets (Gagnon et al. 2019; Genelt-Yanovskaya et al. 2023; Pawelec et al. 2016). These studies highlighted the importance of Insecta and Crustacea as key prey items, but also soft bodied organisms such as Nematoda and Annelida. The abundances of these taxa (Table A4) were then pooled under the variable 'Potential prey', representing the overall availability of invertebrate prey accessible to sticklebacks. To account for factors not explicitly represented by the models' predictors, 'Bay' was added as a fixed factor with two levels.

Multicollinearity among the predictors was checked by calculating the variance inflation factor (VIF) using the *usdm* package v.2.1-7 (Naimi et al. 2014). All variables had VIF values < 3 , which is well below the commonly accepted threshold value of 5 (Zuur et al. 2010), indicating that collinearity is unlikely to bias model estimates; we therefore retained all variables for the analysis.

The models were fitted using the package *glmmTMB* v. 1.1.10 (Brooks et al. 2017). The *DHARMA* package v. 0.4.7 (Hartig 2022) was used to produce diagnostic QQ-plots to evaluate residual distributions and test for zero inflation and overdispersion. For juvenile sticklebacks, abundance was modelled using a negative binomial distribution with a log-link, including a zero-inflation component to account for excess zeros in the data:

$$\begin{aligned} \log(\mu) = & \beta_{0+}\beta_1 \text{ potential prey abundance} \\ & + \beta_2 \text{ filamentous algae biomass} + \beta_3 \text{ vertical index} \\ & + \beta_4 \text{ SAV biomass} + \beta_5 \text{ vegetation richness} + \beta_6 \text{ bay} \end{aligned}$$

With a zero-inflation component modelled as:

$$\log \text{it}(\pi) = Y_0$$

where π is the probability that a zero count represents a station with no juveniles, and Y_0 is the intercept.

For adults, abundance was modelled using a negative binomial distribution with a log-link using the same predictors, but without a zero-inflation component:

$$\begin{aligned} \log(\mu) = & \beta_{0+}\beta_1 \text{ potential prey abundance} \\ & + \beta_2 \text{ filamentous algae biomass} + \beta_3 \text{ vertical index} \\ & + \beta_4 \text{ SAV biomass} + \beta_5 \text{ vegetation richness} + \beta_6 \text{ bay.} \end{aligned}$$

To assess and visualise the relative contribution of predictors with different units, such as biomass, vertical index, species richness and potential prey abundance, standardised effect sizes were calculated using the package *parameters* v.0.23.0 (Lüdecke et al. 2020), and plotted using *ggplot2* v.3.5.1 (Wickham 2016).

To visualise patterns of co-occurrence of potential prey taxa and juvenile and adult sticklebacks, a Non-metric MultiDimensional Scaling (NMDS) with two dimensions was performed using the function *metaDMS()* in the *vegan* package v. 2.6-8 (Oksanen et al. 2024). The function applied a square root and a Wisconsin double standardisation. Potential prey taxa recorded in less than three stations were removed from the analysis to limit the influence of single occurrences.

All statistical analyses and plotting were conducted in R environment v. 4.3.1 (R Core Team 2021).

3 | Results

3.1 | Summary From the Biological Surveys

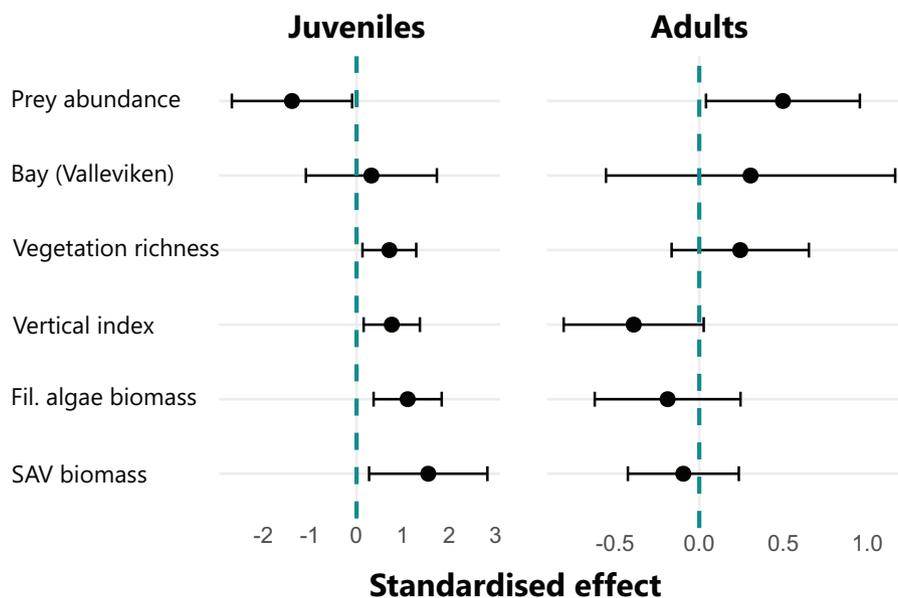
A total of 796 fishes were identified to either species or genus level across both bays. Sticklebacks dominated the assemblages, with 508 individuals (64% of all identified fishes, Table A2). Of these, 83% were juveniles (421 individuals, Table A2), which indicates a clear predominance of younger age classes, though not unsurprising given the time of year the survey was conducted. The remainder of the fishes were Gobiids from the genus *Pomatoschistus* (likely the sand goby *P. minutus* and/or common goby *P. microps*, which could not be distinguished in the field) and the nine-spined stickleback (*Pungitius pungitius*), which comprised 36% (285 individuals) and $< 1\%$ (three individuals) of the total assemblage, respectively (Table A2).

Macrophyte species richness was generally low at both bays, with a maximum of four species and mean of 2.62 ± 0.95 (SD) species per station. The dominant species were *Stuckenia* and Eurasian milfoil (*Myriophyllum spicatum*), which were present in 19 and 14 stations, respectively (Table A3). *Fucus*, primarily encountered in its free-living form, was the dominating macroalgae. Drifting filamentous algae were present in all but one sampling station.

TABLE 1 | Summary of the GLMs for the abundance of stickleback juveniles (left) and adults (right)

Predictors	Juveniles			Adults		
	Beta	95% CI	p value	Beta	95% CI	p value
Prey abundance	-0.01	-0.03, 0.00	0.035	0.01	0.00, 0.01	0.032
Filamentous mat biomass	0.96	0.32, 1.6	0.003	-0.16	-0.54, 0.21	0.4
Vertical index	0.08	0.02, 0.14	0.014	-0.04	-0.08, 0.00	0.066
SAV biomass	0.74	0.13, 1.4	0.018	-0.05	-0.20, 0.11	0.6
Vegetation richness	0.72	0.13, 1.3	0.017	0.25	-0.17, 0.67	0.2
Location (Bay: Valleviken)	0.32	-1.1, 1.7	0.7	0.31	-0.55, 1.2	0.5

All biomasses are expressed as dry weights (g). Values in bold are significant.
Abbreviation: CI, confidence interval.

**FIGURE 2** | Forest plot of standardised effect sizes (as standard deviation of the mean) and 95% confidence intervals of predictors in the models of juvenile and adult stickleback abundances. Predictors with confidence intervals crossing zero are not statistically significant.

Eelgrass (*Zostera marina*) was present in one station in Valleviken (Table A3).

A total of 1844 potential preys were recorded. Overall, the community was heavily dominated by four taxa: chironomid larvae, amphipods in the genus *Gammarus*, the small tanaid *Heterotanais oerstedii* and the isopod *Lekanesphaera rugicauda*, which together accounted for 88% of the potential prey community (Table A4).

3.2 | Importance of Vegetation and Invertebrates on Juvenile and Adult Sticklebacks

The GLM model for stickleback juveniles revealed a significant positive relationship with all the vegetation variables tested (Table 1 and Figure 2), thus showing that habitat complexity and vegetation species richness are important for this younger life stage. Among these, SAV biomass had the strongest standardised effect, followed by filamentous mat biomass, vertical index and

finally macrophyte richness (Figure 2). Abundance of potential prey was also significant, but with a negative relationship to stickleback juveniles (Table 1 and Figure 2). Location, that is, Bay, had no significant effect on juveniles.

In contrast to juveniles, only invertebrate abundance significantly influenced adult sticklebacks, in a positive relationship (Table 1 and Figure 2). Most of the vegetation variables were negatively associated with adult sticklebacks, but the relationships were, together with location, non-significant (Table 1 and Figure 2).

The NMDS ordination revealed that potential prey taxa associated with both juvenile and adult sticklebacks were largely similar (Figure 3). *H. oerstedii* and *Gammarus* spp. clustered closely with both life stages, while Annelida (predominantly *Hediste diversicolor*) were more strongly associated with juveniles, and *L. rugicauda*, chironomid larvae and naiads of *Trichoptera* with adults. These patterns suggest some degree of overlap between the two life stages and potential preys, in particular two of the most abundant taxa (*H. oerstedii* and *Gammarus* spp.).

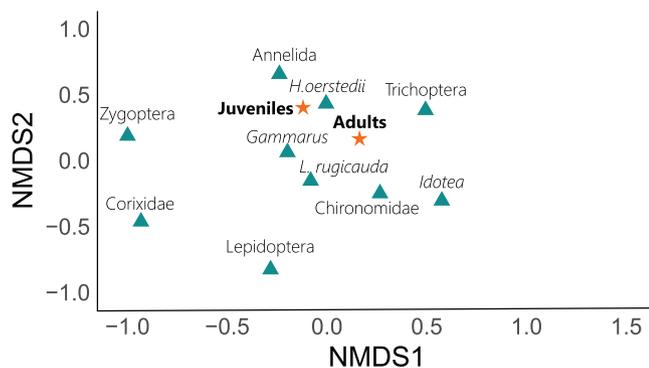


FIGURE 3 | Non-metric MultiDimensional Scaling (NMDS) ordination of juvenile and adult stickleback abundance (in bold) together with the main taxonomic groups representing their potential prey. The triangles represent species position in the reduced two-dimensional ordination space. Stress = 0.18.

4 | Discussion

This study provides novel evidence on differences in habitat use between juvenile and adult sticklebacks in shallow bays in the central Baltic Sea, with vegetation characteristics and prey availability influencing their abundances in distinct ways.

SAV was an important habitat for juvenile sticklebacks. This is consistent with previous findings from freshwater (Sillett and Foster 2000), brackish (Bučas et al. 2022) and marine systems (Genelt-Yanovskaya et al. 2023), where juvenile sticklebacks were found in association with a range of SAV species. In particular, vegetation biomass and canopy height, commonly used as measures of habitat complexity, have been shown to influence the distribution of both fish and invertebrates (e.g., Heck and Wetstone 1977; Jinks et al. 2019). Juvenile sticklebacks are exposed to predation pressure from various predators in the water column, including perch, pike and cannibalistic adults (Foster et al. 1988; Jacobson et al. 2019). Since increasing structural complexity decreases the efficiency of mobile visual predators (Farina et al. 2014; Persson and Eklov 1995), high SAV biomass likely increases the probability of juvenile stickleback survival. Taller SAV may also shelter stickleback juveniles from avian predators (Sohel and Lindström 2015), an interaction that remains poorly understood but could further influence predator/prey dynamics (Heck Jr. and Orth 2006) and, consequently, juvenile habitat use.

Macrophyte species richness also emerged as a positive predictor of stickleback juvenile abundance. Although the low number of species in the assemblages makes it difficult to rule out a potential sampling effect (Stachowicz et al. 2007), complementarity is a plausible explanation. The morphological differences among macrophyte species likely increase habitat structural heterogeneity in species-rich stations, providing additional refuge opportunities for juvenile sticklebacks and therefore supporting higher abundances. Together, these results provide strong evidence for the importance of vegetated habitats for juvenile sticklebacks, highlighting structural complexity as a key factor shaping their distribution.

Other than macrophytes, drifting filamentous algae were also important for juvenile sticklebacks. These algae provide fine-scale structural complexity characterised by small interstitial spaces. The size of these spaces can influence predator-prey interactions by sheltering smaller prey while excluding larger predators (Bartholomew et al. 2000; Warfe et al. 2008). In the northern Baltic Sea, Gagnon et al. (2017) found that the association of drift filamentous algae with juvenile sticklebacks varied across the summer, which was also due to their drifting away from the study area over time. The authors suggested that the ephemeral nature of these algae may limit their potential as reliable nursery habitats. In the present study, the drift filamentous mats persisted throughout the survey period, which may help explain the positive relationship we detected; however, whether this relationship would hold later in the season, requires further investigation.

Potential prey abundance was negatively associated with juvenile stickleback abundance, indicating that juvenile sticklebacks may prioritise shelter over foraging. This interpretation, however, requires caution. While the sampling method used in this study was effective in capturing organisms ≥ 1 mm, it did not seize smaller prey items, such as small eggs or zooplankton, introducing a potential bias in the characterisation of the prey community available to juveniles. Stomach content analyses from the southern Baltic Sea showed, for instance, that planktonic crustaceans and fish eggs are frequent components of the diet of juvenile sticklebacks (Pawelec et al. 2016; Hangelin and Vuorinen 1988). Similarly, a study in shallow water environments in the White Sea revealed a dominance of copepods in the diet of juvenile sticklebacks (Demchuk et al. 2015), providing further evidence of the importance of planktonic organisms during the juvenile stage. Diet composition, however, also depended on seasonal and site-specific conditions (Pawelec et al. 2016; Genelt-Yanovskaya et al. 2023), which further highlights the importance of temporal and local factors influencing stickleback habitat use.

In contrast to juveniles, adult stickleback abundance was driven by the abundance of potential prey, rather than vegetation. This result indicates an ontogenetic shift in habitat use, consistent with findings from freshwater systems where the strong association of juveniles with vegetation declined as sticklebacks grew larger (Foster et al. 1988). However, sticklebacks are known to increase their use of structurally complex habitats under high predation pressure (Ajemian et al. 2015); therefore, the patterns observed in this study may also reflect a generally low predation risk in the area, which allows adults to prioritise foraging in prey-abundant habitats regardless of vegetation structure (Gagnon et al. 2019).

The NDMS analysis revealed that both juvenile and adult sticklebacks co-occurred with amphipods in the genus *Gammarus*. These organisms are known to be highly palatable to sticklebacks (Gagnon et al. 2019; Sieben et al. 2011) and were also among the dominant potential prey taxa in our samples. In the Baltic Sea, common *Gammarus* species such as *G. locusta*, *G. salinus* and *G. zaddachi* have several generations per year, with juveniles present in the late summer and autumn months (Kolding 1981). Numerous juveniles of *Gammarus* were also noted in our quantitative invertebrate samples, which indicates the presence of suitable size ranges of this potential prey for both juvenile

and adult sticklebacks (Gagnon et al. 2019). The NMDS further indicated that juveniles co-occurred spatially with Annelida, whereas adults were positioned closer to chironomid larvae and the isopod *L. rugicauda*, both among the dominant taxa in our samples. Jakubavičiūtė et al. (2017) documented annelids as important food items for smaller sticklebacks, and chironomids as a key component in the diet of both juveniles and adults, supporting the plausibility of these associations.

Together with the contrasting responses to overall potential prey abundance observed in the GLMs, these patterns are consistent with life-stage dietary niche differentiation (Genelt-Yanovskaya et al. 2023). Adults appear to occur in areas of high benthic prey density, while juveniles occupy habitats where they likely prioritise shelter or feed on smaller prey (e.g., zooplankton, consistent with stomach content evidence discussed above; Pawelec et al. 2016; Demchuk et al. 2015; Hangelin and Vuorinen 1988) that our sampling method did not capture. This interpretation is supported by the analysis of Jakubavičiūtė et al. (2017), which found evidence that larger sticklebacks (i.e., TL > 6.5 cm) appear to feed on benthic organisms such as amphipods and isopods to a larger extent than juveniles.

It is important to acknowledge some caveats of the present study. First, UVCs have known limitations in providing accurate descriptions of fish communities, primarily due to the observer effect and the challenges of detecting fish in complex vegetation. The observer effect refers to the disturbance caused by the presence of an observer, which can alter natural fish behaviour by inducing hiding or fleeing responses (Emslie et al. 2018). Detection difficulties are particularly relevant in dense vegetation, where the canopy can limit the observer's ability to see fish from above (Castro-Fernández et al. 2025). Although these factors may have affected absolute counts, UVCs remain widely used for investigating fish–habitat associations (e.g., Eggertsen et al. 2022), and can be a valuable method to investigate commonly occurring and visually conspicuous species such as sticklebacks.

An additional caveat concerns the deployment of the BRUV about an hour before each UVC. The bait may have attracted sticklebacks, potentially altering their natural distribution during the subsequent UVC. Juveniles and adults may respond differently to the bait, so differential effects on age classes cannot be ruled out. However, because the same procedure was applied consistently across all 21 survey stations, relative comparisons remain meaningful. The observer presence during UVCs may have counteracted, at least partially, the eventual localised attractive influence of the bait. While the combined effects of these two factors cannot be disentangled, the relative patterns observed across vegetation types still provide useful insights into stickleback habitat associations. Future UVC surveys should be conducted in undisturbed sites or use unbaited stereo-video systems, which remove observer disturbance while allowing fish size measurement (e.g., Harvey et al. 2001; Perry et al. 2018). Although such systems face similar challenges to UVCs in detecting fish within dense vegetation, they provide a valuable approach for studying fish–habitat associations.

In conclusion, our study advances understanding of ontogenetic shifts in stickleback habitat use by highlighting that co-occurring juveniles and adults respond differently to key ecological factors.

By showing life-stage-specific associations with vegetation and prey availability, these findings provide novel insights into habitat use of this rapidly expanding species in the central Baltic Sea.

Author Contributions

Chiara D'Agata: conceptualisation (equal) data curation (lead), formal analysis (lead), investigation (lead), methodology (lead), visualisation (lead), writing – original draft (lead), writing – review and editing (equal). **Thomas A. B. Staveley:** conceptualisation (equal), formal analysis (supporting), methodology (supporting), supervision (lead), writing – original draft (supporting), writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code used for this study are available on Figshare: <https://doi.org/10.6084/m9.figshare.30084682>

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

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