Aquatic Invasions (2020) Volume 15, Issue 4: 671–682

Research Article

First record of niche overlap of native European plaice (*Pleuronectes platessa*) and non-indigenous European flounder (*Platichthys flesus*) on nursery grounds in Iceland

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Citation: Henke T, Patterson WP, Ólafsdóttir GÁ (2020) First record of niche overlap of native European plaice (*Pleuronectes platessa*) and non-indigenous European flounder (*Platichthys flesus*) on nursery grounds in Iceland. *Aquatic Invasions* 15(4): 671–682, https://doi.org/10.3391/ai.2020.15.4.08

Received: 24 January 2020
Accepted: 19 June 2020
Published: 1 October 2020

Thematic editor: Charles Martin

Abstract

Fifteen non-indigenous species have been recorded in Icelandic waters over the past decades, of which six have been classified as invasive or potentially invasive. One of these potentially invasive species is the European flounder (*Platichthys flesus*). *Platichthys flesus* is a recent arrival that was firstly identified in 1999 and has, since then, established a population around the whole country. In this study we evaluated if there is niche overlap between juvenile *P. flesus* and native juvenile European plaice (*Pleuronectes platessa)* on nursery grounds at three sites in west Iceland. Considering the presumed clockwise spread of *P. flesus*' population around the country, the southernmost site, Borgarfjörður, was treated as the site of earlier settlement of *P. flesus*. Similarly, the northernmost site, Önundarfjörður, was treated as the site of later settlement. We used stomach content and stable isotope analyses to examine if there was a significant niche overlap between *P. flesus* and *P. platessa* and to examine if the extent of niche overlap varied between sites. Multiple cohorts of *P. flesus* and native *P. platessa* were present at all sites and there was high niche overlap between species with no indication of trophic niche segregation nor change with time from establishment of *P. flesus*. The current study has shown the co-occurrence and niche overlap of non-indigenous *P. flesus* and native *P. platessa* on nursery grounds in Iceland and highlighted the establishment of *P. flesus* in Iceland as a rare case study to investigate colonisation processes of non-indigenous fish species in sub-arctic marine environments.

Key words: global change, invasive species, juveniles, trophic competition, stable isotopes

Introduction

Invasive species are defined as introduced, non-indigenous species that negatively impact native fauna or flora (Bax et al. 2003; Ricciardi 2003; Rahel and Olden 2008). Fifteen non-indigenous species of various taxa have been reported in Icelandic marine environments in recent years (Gunnarsson et al. 2015), of those, six have been classified as potentially invasive, including the European flounder *Platichthys flesus* (Linnaeus, 1758) (Astthorsson and Palsson 2007; Thorarinsdóttir et al. 2014; Micael et al. 2020). Although the introduction pathway of *P. flesus* is not documented, it

is thought to have been introduced with ballast water (Astthorsson and Palsson 2007; Gunnarsson et al. 2015). Since its first sighting in the southwest of Iceland in 1999, a clockwise spread of the population has been documented (Jónsson et al. 2001; Kristinsson 2013). The population reached a nationwide distribution in 2017 with an observation of *P. flesus* in the East (NA 2017). Despite its classification as potentially invasive, there is currently little known about *P. flesus* ecology and potential impacts. Previous research has highlighted potential trophic competition and direct predation on native salmonids in the fjords Borgarfjörður and Önundarfjörður (O'Farrell 2012; Hlinason 2013). The only other invasion of *P. flesus* has been documented for the Great Lakes in North America where it arrived via ballast water from Europe but failed to establish a population (Cudmore-Vokey and Crossman 2000; Fuller 2015).

Invasive marine species are predicted to increase rapidly in sub-arctic and arctic environments in the next decades, and this may be facilitated by an increasing sea water temperature (Ruiz et al. 1997; Dukes and Mooney 1999; McNeely 2001). Irrespective of the introduction pathway of *P. flesus*, it is important to monitor how its presence affects native fauna. Moreover, the recent establishment of *P. flesus* in Iceland offers an opportunity to empirically document establishment of a coastal fish species in a relatively species poor ecosystem. This in turn may allow general conclusions to be drawn on the patterns of invasive species biology in sub-arctic seas.

Trophic effects of invasive species on native communities are among the most common negative ecological impacts (Thomsen et al. 2014; Gallardo et al. 2016), often involving direct interactions between native and invasive species, such as resource competition or predation (Crooks 2002). It's common for several species of juvenile flatfish to coexist on nursery grounds in shallow coastal or estuary waters, but small-scale niche divergence is often present and may facilitate coexistence (Amara et al. 2001; Rooper et al. 2006; Cabral et al. 2007; De Raedemaecker et al. 2012). In Iceland 0-group European plaice (*Pleuronectes platessa* Linnaeus, 1758) uses nursery grounds in very shallow coastal waters (Gunnarsson et al. 2010). Given the relatively low invertebrate species diversity at these sites (Ingólfsson 2006), niche overlap of juvenile *P. platessa* and the non-indigenous *P. flesus* could be substantial if they co-occur which in turn would have significant management implications.

In the current study we evaluated if juvenile *P. flesus* coexisted with juveniles of the commercially harvested *P. platessa* on nursery grounds across western Iceland and if there was a significant trophic niche overlap between juveniles of the two species. Juveniles of other flatfish species were not expected to be present on the nursery grounds. Finally, we investigated if niche overlap was similar at a nursery site where *P. flesus* has been established for close to twenty years compared to sites where it was more recently established. The last question has important management implications as it could be expected that niche segregation may develop over time from establishment.

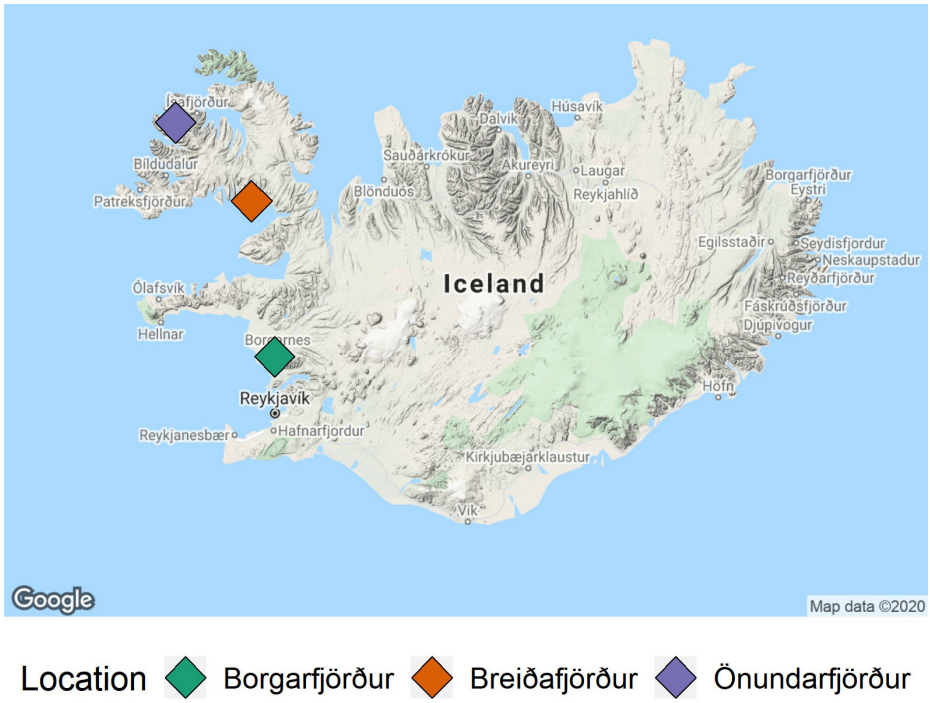

Figure 1. Iceland with the sampling sites indicated.

Materials and methods

Sampling

Sampling was carried out in the summer of 2017, in weeks 27, 28 and 33 in Borgarfjörður (64°31′17.7″N; 21°53′41.0″W), in weeks 28, 31, 34 and 37 in Önundarfjörður (66°00′41.0″N; 23°25′22.2″W) and in week 34 in Breiðafjörður (65°35′00.6″N; 22°07′59.0″W and 65°28′42.2″N; 22°08′15.8″W) (Figure 1). Based on the documented clockwise spread around the country, the southernmost site Borgarfjördur and the northernmost site Önundarfjördur were considered as the locations of earlier establishment and later establishment, respectively. Located geographically between the two main sampling sites, the settlement of *P. flesus* in Breiðarfjörður cannot be confidently determined in relation to the settlement of the other two sites. Juveniles were caught during incoming tide with a beach seine (10 m × 1.5 m, mesh size of 6 mm). In order to exclude adults, individuals, only *P. flesus* and *P. platessa* smaller than an arbitrary set size limit of 20 cm were removed from the net and euthanized at site with an overdose of phenoxyethanol. All larger flatfish and other bycatch were released. Bycatch included brown shrimp (*Crangon crangon* Linnaeus, 1758), three-spined stickleback (*Gasterosteus aculeatus* Linnaeus, 1758), and juvenile lumpfish (*Cyclopterus lumpus* Linnaeus, 1758). Juveniles of both species and mixed cohorts were caught in most tows.

Analysis of stomach content

In the laboratory, the species was determined for each fish based on fin ray counts and characteristic morphological features. Furthermore, for each

P. flesus it was documented whether it was a dextral ("right-sided") or sinistral ("reversed sided") morph. The standard length (SL) and wet weight were measured for every fish before they were gutted. Additionally, dorsal muscle samples were collected for stable isotope analysis. The stomachs and guts were fixed in 5% formaldehyde and placed in 70% ethanol after one week. Diet items were identified to the lowest taxonomic level possible and counted under a stereomicroscope (Olympus Szx2-ILLT), only considering the heads of individuals. For each sampling event, a maximum of 30 haphazardly chosen stomachs were identified per species.

Analysis of stable isotope values

Dorsal muscle samples were dried at 55 °C for ~ 24 hours, lipids were removed from the tissue samples using a traditional chloroform/methanol extraction following the methodology of Folch et al. (1957). Stable isotope values were obtained at the Saskatchewan stable isotope laboratory. A Thermo Finnigan Flash 1112 EA was used, coupled to a Thermo Finnigan Delta Plus XL through a Conflo III. Carbon isotope ratios were corrected for ^{17}O contribution using the Craig correction, and reported in per mil notation relative to the VPDB scale. Nitrogen isotope ratios were reported in per mil notation relative to AIR. Carbon data was calibrated against the international standards L-SVEC ($\delta^{13}C$ = −46.6‰ VPDB) and IAEA-CH6 ($\delta^{13}C$ = −10.45‰ VPDB). IAEA-CH7, an intermediate international standard, gave the following result during calibration of the in-house standards: $\delta^{13}C$ = −32.15 ± 0.04‰ VPDB (n = 11), which is in line with the accepted value of $\delta^{13}C$ = −32.15 ± 0.10‰ VPDB. Nitrogen data was calibrated against the international standards USGS-25 ($\delta^{15}N$ = −30.4‰ AIR) and IAEA-305A ($\delta^{15}N$ = 39.8‰ AIR). IAEA-NO3, an intermediate international standard, gave the following result during calibration of the in-house standards: $\delta^{15}N$ = 3.96 ± 0.08‰ AIR (n = 8). The result is in accordance with the accepted value of $\delta^{15}N$ = 4.7 ± 0.2‰ AIR. Precision of data were monitored through routine analyses of in-house standards which were stringently calibrated against the IAEA standards mentioned above. Precision of $\delta^{13}C$ and $\delta^{15}N$ measurements were 0.12‰ and 0.22‰, respectively (n = 18 and 20). %C and %N measurements had a precision of ± 10% of the reported percentage.

Statistical analysis

Shannon-Wiener and Morisita indices were calculated for each species at each site using the diet item count data to evaluate niche width and niche overlap, respectively (Krebs 2014). These diet-based values will indicate short term variation in the prey of both species. To assess potential long-term variation in baseline values such as the carbon source and the rate of primary production, niche calculations based on stable isotopes were carried out. A correlation between these analyses was not expected. Variation in $\delta^{13}C$ and $\delta^{15}N$ values between the two species was examined

with a generalised linear mixed model of log transformed SI values. The main aim is to test if the stable isotope values of *P. platessa* and *P. flesus* differ suggesting species variation in niche. However, we expect both carbon and nitrogen values to vary between sites, specifically along a south-north gradient (Hansen et al. 2012). Furthermore, we expect to observe a variation of these values with juvenile size, importantly higher nitrogen values in larger fish (Fry 1983). Therefore, both juvenile length and site were included in the model. Each value, $\delta^{13}C$ or $\delta^{15}N$, formed the dependant variable and species, site and fish length were set as fixed effects. To examine if stable isotope values varied differently with size or with site for each species, we included an interaction effect between species and site and species and length. Sample week was included as a random effect in the model. The Satterthwaite approximation, as implemented in the R package lmerTest, was used to approximate p-values. Stable isotope niche width was calculated for each species at each site with the Bayesian estimator of SEA_B (Bayesian standard ellipse area) in the R package SIBER (Jackson et al. 2011) using default settings for priors and iteration length. The niche overlap between species at each site was calculated as probability of finding species A in the niche region of species B, using the R package nicheROVER (Swanson et al. 2015).

Results

The 305 measured fish consisted of 121 juvenile *P. platessa* with recorded sizes between 1.7 and 10.6 cm and 184 *P. flesus* between 1.8 and 17.6 cm. Sizes differed between sites and months, however, the presence of multiple cohorts of juveniles from both species at the nursery grounds was confirmed with analysis of otoliths (Henke 2018). 15 out of the 184 (8.15%) juvenile *P. flesus* were documented as sinistral. The sinistral morph was present in every obtained sample except for week 28 in Önundarfjörður. The samples included 1 or 2 individuals of the sinistral morph except for the Borgarfjörður sample of week 33 and the Breiðarfjörur sample of week 34 where 6 and 4 individuals were counted, respectively. Of the 23 different stomach content categories identified in the stomachs, Chironomidae larvae and Polychaeta were most common for *P. flesus* and Polychaeta and Harpacticoida for *P. platessa* (Figure 2). Other frequently found items included Nematoda, Gammaridae, Harpacticoida, Turbellaria and Gastropoda (Figure 2).

Platichthys flesus had greater niche widths at all sites both measured by the Shannon-Wiener index and SEA_B estimates (Table 1). Despite the variation in size a strong overlap was detected between *P. flesus* and *P. platessa.* The Morisita index was 0.24 in Borgarfjörður, 0.98 in Breiðafjörður and 0.51 in Önundarfjörður (Table 1). The probabilistic niche overlap calculated with nicheROVER revealed for all sites a higher probability of juvenile *P. platessa* occurring within the niche range of *P. flesus* than vice versa

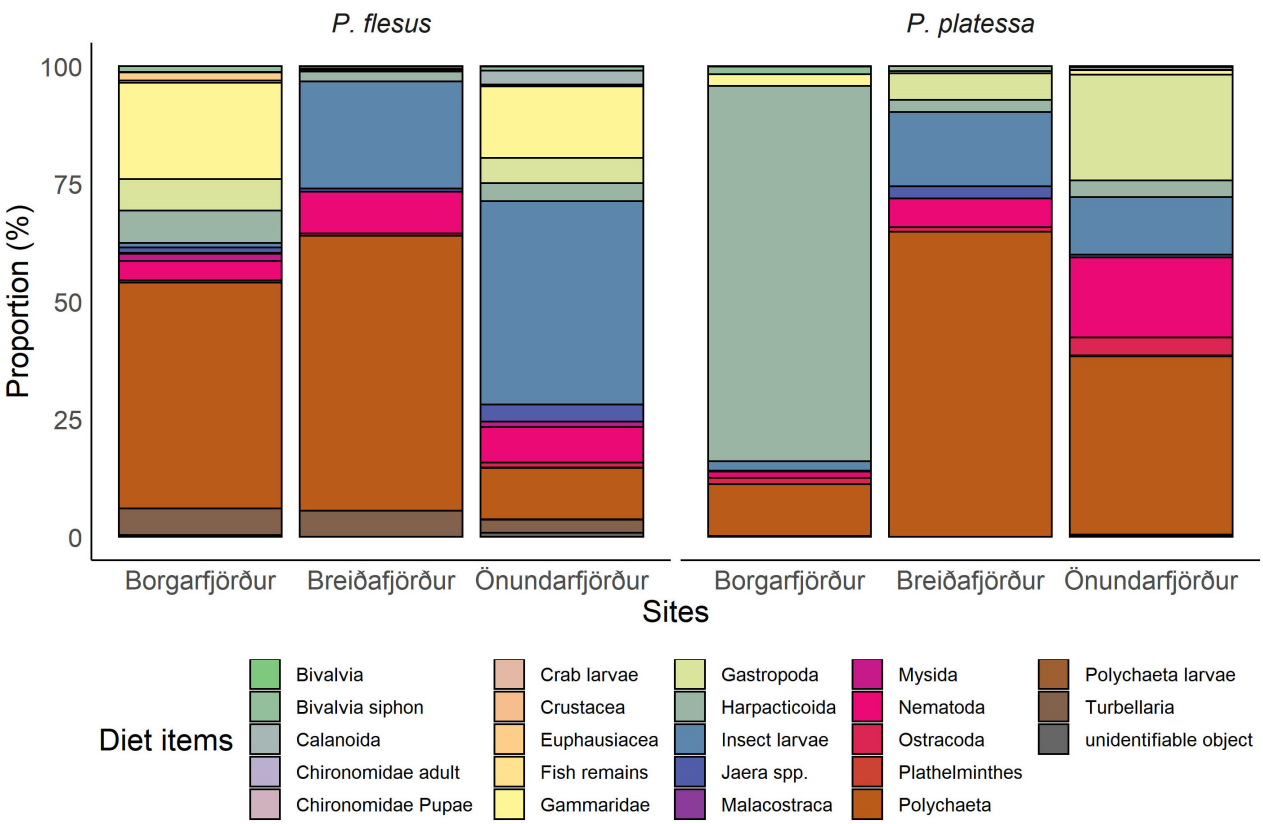

Figure 2. The average proportion of diet items per species and per site.

Table 1. Summary of samples, juvenile sizes, stable isotope values and niche measures at all sites. A total of 305 fish (121 *P. platessa* and 184 *P. flesus*) were considered for this study. Out of these 305 fish, 297 (121 *P. platessa* and 176 *P. flesus*) were included in the stomach content analysis (SC analysis). Furthermore, 113 fish (47 *P. platessa* and 66 *P. flesus*) were analysed for stable isotopes (SI analysis). These fish included 8 *P. flesus* that were not previously analysed for their stomach content and were included because their size allowed the collection of the necessary amount of tissue.

		Borgarfjörður		Breiðafjörður		Önundarfjörður	
		P. flesus	*P. platessa*	*P. flesus*	*P. platessa*	*P. flesus*	*P. platessa*
Fish in SC analysis	n	60	63	41	6	75	52
	Length, mean ± SD	9.71 ± 2.45	3.65 ± 2.21	4.89 ± 3.19	5.33 ± 0.35	5.02 ± 2.61	4.42 ±1.02
	Shannon-Wiener index	1.71	0.81	1.24	1.21	1.92	1.66
	Morisita index	0.24		0.98		0.51	
Fish in SI analysis	n	20	21	16	6	30	20
	Length, mean ± SD	10.02 ± 1.64	5.70 ± 2.20	6.21 ± 3.14	5.33 ± 0.35	6.77 ± 2.55	5.17 ± 0.52
	$d^{13}C$, mean ± SD	−16.10 ± 0.93	−15.47 ± 0.60	−12.64 ± 0.74	−12.65 ± 0.38	−14.00 ± 0.70	−13.67 ± 0.63
	$d^{15}N$, mean ± SD	11.75 ± 0.83	11.78 ± 0.67	12.64 ± 0.55	12.77 ± 0.27	11.38 ± 0.67	11.80 ± 0.37
	SEA_B (95% CI)	1.58 (1.03−2.53)	1.01 (0.63−1.56)	1.15 (0.66−1.92)	0.27 (0.11−0.68)	1.35 (0.94−1.96)	0.70 (0.44−1.12)

(Figure 3). The lowest probability was documented for Borgarfjörður (86.48%) and the highest for Breiðarfjörður (98.92%) (Table 3). Conversely, the probabilities of finding *P. flesus* within the niche range of *P. platessa* ranged from 41.99% in Breiðarfjörður to 65.66% in Borgarfjörður (Table 3).

There was significant variation in $\delta^{13}C$ values between sites. Larger juveniles had lower $\delta^{13}C$ values and *P. platessa* had slightly lower $\delta^{13}C$ values

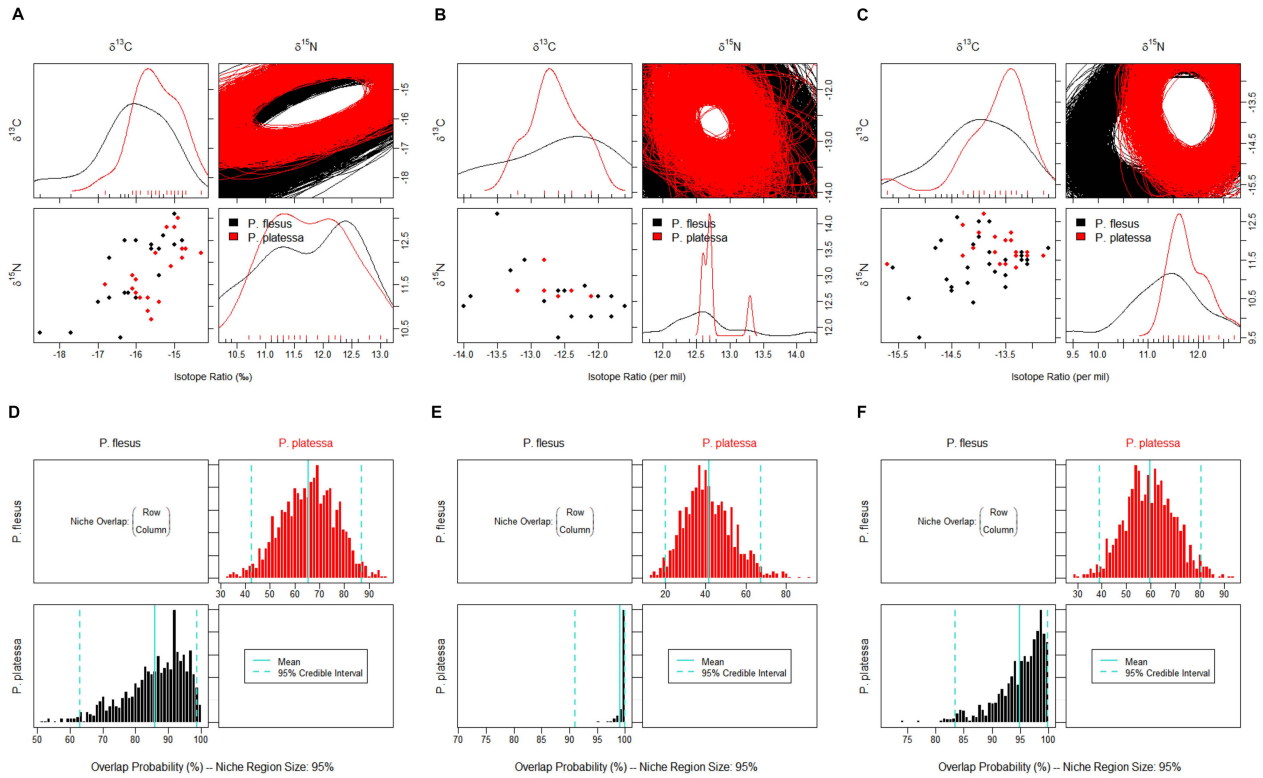

Figure 3. Projection of niche regions and niche overlap per site (A, D = Borgarfjörður, B, E = Breiðafjörður, C, F = Önundarfjörður). The projections for niche regions show the niche regions of both species (upper right), the density distributions for $\delta^{13}C$ (upper left) and $\delta^{15}N$ (bottom right) and a scatterplot representing raw data (bottom left). The overlap is displayed as the distribution of percentage overlap of 95% niche regions between *P. flesus* and *P. platessa*. The values are read as the probability of species A (represented by row) being found in the niche region of species B (represented by column).

Table 2. Results from the generalized linear mixed model (GLMM) that was used to examine variation in carbon and nitrogen stable isotope values between species as well as with size and between sites. The results highlight that a combination of factors structure the variation. Importantly there are significant differences between sites as well as significant interaction terms for fish length and SI variation.

		Estimate	SE	t-value	p-value
$\delta^{13}C$	Intercept	−14.52	0.35	−41.65	0.00
	Fish length	−0.15	0.03	−4.92	0.00
	P platessa	−1.79	0.48	−3.70	0.03
	Site Önundarfjörður	1.50	0.21	7.14	0.00
	Site Breiðafjörður	2.92	0.24	11.93	0.00
	Fish length: *P. platessa*	0.31	0.07	4.74	0.00
$\delta^{15}N$	Intercept	11.36	0.32	35.44	0.00
	Site Breiðafjörður	1.17	0.23	5.17	0.00
	Fish length: *P platessa*	0.17	0.06	2.72	0.01

Table 3. Probabilistic niche overlap (95% niche regions) values calculated with nicheROVER (Swanson et al. 2015). The values represent the probability of species A (represented by row) being found in the niche region of species B (represented by column).

	Borgarfjörður		Breiðafjörður		Önundarfjörður	
	P. flesus	*P. platessa*	*P. flesus*	*P. platessa*	*P. flesus*	*P. platessa*
P. flesus	NA	65.66	NA	41.99	NA	60
P. platessa	86.48	NA	98.92	NA	94.56	NA

than *P. flesus*. $\delta^{15}N$ values in Breiðafjörður were higher than at the other sites (Table 2). The interaction term of species and size was significant for both $\delta^{13}C$ and $\delta^{15}N$ values. Post-hoc examination of these effects showed

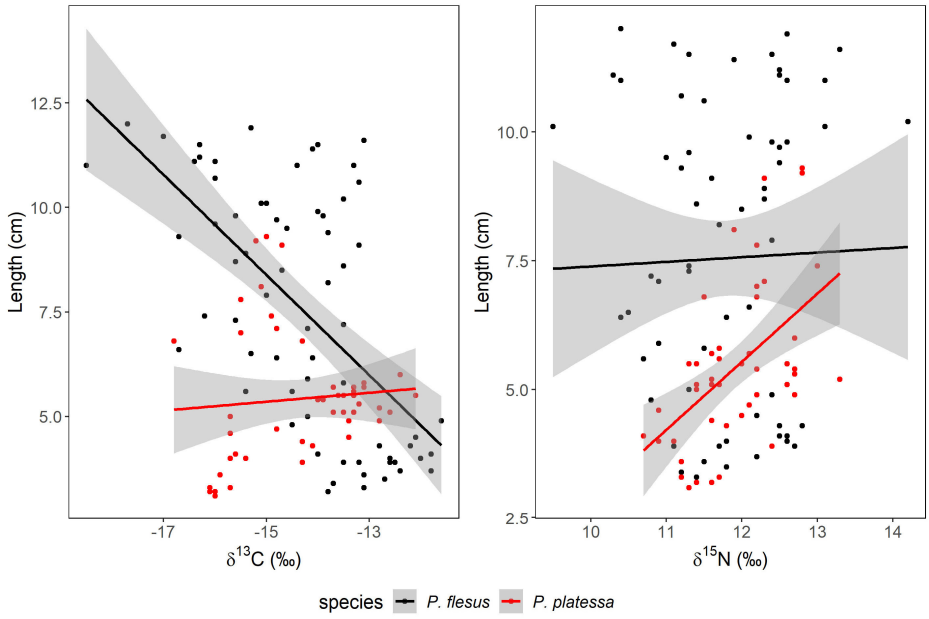

Figure 4. The figure depicts how $\delta^{13}C$ (A) and $\delta^{15}N$ (B) varies with fish length for each of *P. platessa* and *P. flesus*. The interaction effect of length and species was significant in a GLMM (see main text for details) highlighting the different pattern of the two species.

that carbon decreased more markedly with size in P. *flesus* whereas nitrogen increased with size only for *P. platessa* (Figure 4).

Discussion

The current study is the first to confirm the coexistence of the non-indigenous, and potentially invasive, *P. flesus* and native juvenile flatfish on nursery grounds in Iceland. Although this study did not examine large scale distribution or temporal variation, it shows that *P. flesus* and *P. platessa* juveniles overlap on nursery grounds across western Iceland and that more than one cohort of both species were simultaneously present at sites. Furthermore, both the dextral and sinistral morphs of *P. flesus* were present in the samples. Fifteen out of 184 individuals were sinistral, constituting to 8.15%. This percentage is in accordance with the 5.6% documented by Russo et al. (2012) for *P. flesus* in Dublin bay, Ireland as well as the results of Magnúsdóttir (2014) that indicate 7% for sampling areas in western Iceland.

Previous research studies have shown small scale habitat partitioning between juvenile flatfish species (Rooper et al. 2006; Cabral et al. 2007). Contrary to the expectation of species coexistence on nursery grounds with finite resources, the current study found little evidence for such resource partitioning between *P. flesus* and *P. platessa* juveniles. However, it is likely that habitat partitioning does occur between these species. This is evidenced by the fact that juvenile *P. flesus* are rarely caught in annual flatfish surveys conducted by the Marine Research Institute of Iceland at depths of 10–50 metres (Sigurðsson and Pálsson 2018). Conversely, variable cohorts of *P. flesus* juveniles are frequently caught in shallow waters

around Iceland where they may co-occur mainly with 0-group *P. platessa* as presented in this study. 0-group *P. platessa* are flexible in habitat use and a recent shift to greater depths has, for example, been observed in the Wadden Sea without detrimental effects on juvenile growth (Freitas et al. 2016). Currently, juvenile *P. flesus* and juvenile *P. platessa* can be observed co-occurring in very shallow coastal waters in Iceland. However, a continuous presence of the recently non-indigenous *P. flesus* could eventually lead to an increased segregation between juveniles of both species.

In addition to site co-occurrence the current study reports high trophic niche overlap between the species, indicated by both stable isotope values (nicheROVER; Swanson et al. 2015) and stomach contents (Morisita index; Krebs 2014). Moreover, the variation in stable isotope values between species, e.g. significantly lower $\delta^{13}C$ values in *P. platessa*, seems minimal compared to variation between sites. This in turn highlights that geographical variation in stable isotope baseline values, for example, caused by site-specific primary producers, is an important source of the observed variation but that species specialisation is not. There was a mixture of juvenile size classes present at all sites, but the size distribution varied between sampling times that made comparison of cohorts difficult without a much larger data set. The high similarity of the trophic niche, despite the size variation, may highlight uniform trophic resources that allow limited trophic segregation. Trophic variation is generally expected to increase with size and the trophic niche of juveniles often includes ontogenetic niche shifts (Mittelbach et al. 1988). In the current study $\delta^{13}C$ values decreased with juvenile size, perhaps reflecting a higher dependence of the smallest juveniles on primary production in very shallow waters. Examination of the interaction term of juvenile size and species further suggests that the pattern is primarily driven by lower carbon values of larger *P. flesus* juveniles (Table 2, Figure 4). Meanwhile $\delta^{15}N$ values, a proxy for trophic level, did not vary consistently with juvenile size or between species (Table 2). However, there is a clear increase in nitrogen values with size noted for *P. platessa* (Figure 4).

The presence of both morphs of *P. flesus* on the sampled nursery grounds could result in differences in niche overlap between the morphs and *P. platessa.* Russo et al. (2012) recorded an apparent difference in feeding strategies between the two morphs of *P. flesus.* Due to the low number of sinistral *P. flesus* available for each sampling, the difference between the morphs could not be tested for significant results in regard to stomach content and stable isotopes.

Finally, there was not much support for change in niche overlap with time from establishment. The earliest site of establishment, Borgarfjörður, does display considerably lower trophic overlap than at the other sites but only based on stomach content (0.24, Table 1). This was not further supported by the probabilistic niche overlaps calculated with nicheROVER

(Table 3). These values suggest that the probability of finding *P. platessa* within in the niche range of *P. flesus* is with 86.48% in Borgarfjörður only slightly smaller compared to the 94.56% in Önundarfjörður (Table 3). Moreover, species niche variation within sample sites should be interpreted in context with the considerable between-site variation that is present in the data.

Concluding remarks

This study is the first to show a niche overlap of juveniles of the non-indigenous *P. flesus* and the native *P. platessa* on nursery grounds in Iceland. Three cohorts of both species were found on the nursery grounds. High trophic overlap was observed despite size variation both with metrics reflecting short term diet, e.g. stomach content, and longer-term diet, e.g. stable isotope values. Juveniles of the two species commonly co-exist in temperate marine waters but often with small scale niche specialisation that may facilitate co-existence (Russo et al. 2008; Mariani et al. 2010). Therefore, the recent establishment of *P. flesus* in Iceland offers a framework to investigate the colonisation of a non-indigenous fish species in the sub-arctic marine environment. In these environments, niche use and niche segregation may differ from established systems. Moreover, the study has current management implications because of the high niche overlap of the non-indigenous *P. flesus* and the native *P. platessa,* potentially resulting in competitive effects on the native *P. platessa* juveniles.

Acknowledgements

We would like to acknowledge SM Einarsson for recommending the sample site in Borgarfjörður, O Simmons, A Nickel and R Edvardsson for assistance with sampling. We sincerely thank the three anonymous reviewers whose comments have helped to improve this manuscript.

Ethics and Permits

The sampling was licenced by landowners. Ecological sampling of fish with an immediate lethal endpoint does not require a specific licence from the Committee of Animal Welfare in Iceland (Ministry for the Environment and Natural Resources, regulation 460/2017).

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