Parasite diversity in plaice (*Pleuronectes platessa*): potential tool for stock identification in Icelandic waters?

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Abstract

Understanding the stock structure of a commercial species is essential for sustainable management. Failure to do so can lead to the depletion of regional sub-populations, erosion of genetic diversity, and ecosystem services loss. Plaice, *Pleuronectes platessa*, is a commercially exploited species inhabiting the continental shelf around Iceland. Despite a tagging study providing support for strong spawning site and feeding ground fidelity, and otolith microstructure analysis revealing local population structure, plaice is managed as a single stock in Icelandic waters. Here, we describe and quantify the parasite fauna of plaice, and assess the potential of parasites as biological tags for stock identification of plaice in Icelandic waters. A total of 82 plaice were sampled from different geographical locations (North and South) and seasons (summer and winter) in Iceland. Our sampling identified 11 parasites, five of which are new parasite records for plaice in Icelandic waters: the trematodes *Zoogonoides viviparus* (adults) and *Rhipidocotyle* sp. (metacercariae), and the nematodes *Contracaecum osculatum* (larvae), *Dichelyne* sp. (adults), and *Hysterothylacium aduncum* (larvae and adults). Additionally, we recovered metacercariae of the trematode genus *Apatemon*, which has not been recorded previously from plaice. Two parasites were identified as potential biological tags for stock identification, namely the nematode *A. simplex* and the trematode *Z. viviparus.* Our findings support a complex stock structure for plaice in Icelandic waters and the need for an integrative strategy to stock identification to provide fine spatial scale data required to inform fisheries managers.

Key words: *Anisakis*, fisheries management, integrative strategy, Pleuronectiformes, stock discrimination, *Zoogonoides*

Introduction

Overfishing poses a significant global threat to the oceans, along with other human impacts such as pollution, deteriorating water quality, invasive species, and human-induced climate change (Arthington et al., 2016), particularly in coastal areas worldwide (Halpern et al., 2008). These activities harm target species and profoundly altering the structure and functioning of marine food webs risk triggering trophic cascades, thus weakening ecosystem resilience (Bascompte et al., 2005; Casini et al., 2008; Jackson et al., 2001). One of the foundations of sustainable fisheries management is stock identification, essential for understanding stock structure (Cowen et al., 2007; Cope & Punt, 2011; Zemeckis et al., 2014; Cadrin, 2020; Hansell et al., 2020). This knowledge is invaluable for effective management strategies to rebuild fish stocks and promote sustainable fishing practices (Punt, 2023). A good stock assessment will enable efficient biological identification of the fish, which is important for understanding genetic diversity, population structure, and potential gene flow between neighboring populations of the same species (Begg et al., 1999; Cadrin et al., 2023). This information is important for conservation efforts, sustainable management practices, and the prediction of population resistance to environmental change (Kerr et al., 2010).

Conducting stock assessments is complex, even after correct stock identification (Punt, 2023). Fish are highly mobile, constantly moving to feed, migrate, and spawn, and direct counting is not feasible (Cadrin et al., 2023). These factors can contribute to poor stock assessment and, consequently, to inefficient stock management practices, which can lead to the overexploitation of specific stocks (Ying et al., 2011). To deal with these complexities, scientists use various data collection methods such as relying on fishing reports and deploying research vessels to monitor catch rates, studying fish biology, and estimating abundance.

A variety of different methods and techniques have been developed to assess stock identification. These include methods based on morphology, meristics, otolith-based, parasites as biological tags, and genetics (among others). These have been summarised in Cadrin et al., (2014). The use of parasites as biological tags for stock identification is well-established (Timi & Mackenzie, 2015) and shown to be efective (Poulin & Kamiya, 2015). The theory behind the use of parasites as biological tags rests on the theory of decay of similarity where the similarity in parasite communities increases as the geographic distance between host populations decreases (Poulin, 2003). It further relies on the geographic range of a host species overlapping with the endemic areas of some of its parasites (MacKenzie & Abaunza, 1998). Nevertheless, for a parasite to be considered a tag, it must meet several

criteria. The parasite must vary significantly in infection according to the regions studied; live for a long time in the host, the duration depending on the study; be easy to detect and identify to avoid wasting time; be easily detected, site-specific parasites being ideal; not alter host behavior through pathological effects (MacKenzie & Abaunza, 1998).

Knowing which parameters influence the study area is essential to interpret suitable biological tags. Several factors can affect the distribution or diversity of parasites, including biotic parameters such as temperature, currents, and salinity (Bommarito et al., 2022). Changes in these parameters can influence the presence and prevalence of parasites. Iceland sits on the Greenland-Scotland Ridge, which forms a boundary between the southern/western and northern/eastern parts of the Iceland Shelf (Pampoulie et al., 2024). It is influenced by two major currents, forming distinct oceanographic regions along the Northwest-Southeast axis (Astthorsson et al., 2007). Waters to the South of Iceland are influenced by the North-Atlantic Current and are characterised as warmer and more saline than waters to the North of Iceland, which are more variable and shaped by the East Greenland Current (Astthorsson et al., 2007). Given the dynamic environmental gradients and distinct oceanographic features characterising the waters to the North and South of Iceland, it is hypothesised that fish collected from these distinct areas are exposed to different environmental conditions, currents, and thus likely feeding on different prey (or at least in different proportions); factors potentially contributing to them harbouring different parasite faunas.

The European plaice (*Pleuronectes platessa* L.), a flatfish belonging to the family Pleuronectidae, is found in Icelandic waters. It is most abundant in the southwest and west of Iceland, mainly at depths of 200 m on sandy or muddy substrates (Jónsson & Pálsson, 2013). The species exhibits sexual dimorphism with females (~55 cm) reaching larger overall sizes than males (~45 cm), and length at maturity at 38 cm for females and 33 cm for males (MFRI, 2024). Sexual maturity is defined by size, not age. Plaice migrate between feeding and spawning grounds between January and March, with spawning occurring at depths of 50-100 m, close to the coasts in areas of strong water movement between March and June (Dipper, 2022). Plaice initially feed on various small benthic organisms, particularly annelids, harpacticoid copepods, amphipods, and small decapods; transitioning to bivalves (molluscs) as they grow (De Raedemaecker et al., 2011).

In Iceland, the plaice is managed as a single stock (MFRI, 2024) and those from the Icelandic and Faroese shelves are considered genetically distinct from those inhabiting other waters in the Northeast Atlantic (Hoarau et al., 2004; Le Moan et al., 2021). The Faroese

shelf, which is located around the Faroe Islands, is situated in the North Atlantic Ocean, between Iceland and Norway (Figure 1).

In December 2019, ICES (International Council for the Exploration of the Sea) agreed with Iceland to include plaice in its assessment process, and in 2022 decided to use a SAM (Stock Assessment Model in State Space). This new SAM model is a statistical catch-at-age model based on commercial data (since 1979), the Icelandic spring groundfish survey (from 1985), and estimated annual recruitment at three years old (MFRI, 2024). Plaice fishing is concentrated mainly in the West, Southwest, and Northwest, using bottom and pelagic trawls, with few catches using gillnets and longlines (MFRI, 2024). Catches of plaice have been relatively stable in the last 25 years, ranging between 4,926 mt (2001) and 8,678 mt (2021) (MFRI, 2024). Nevertheless, spatial and temporal regulations have been put in place to protect its spawning areas, i.e., specific spawning grounds in the West and South-West of Iceland are closed to fishing during the spawning period in April.

Eight parasite species have been reported previously in Icelandic waters from the plaice: (1) the copepod *Acanthochondria cornuta* (Müller, 1776) in the gills (Kabata, 1959); (2) the copepod *Lepeophtheirus pectoralis* (Müller, 1776) on the skin and fins (Stephensen, 1940); (3) the myxosporean *Myxobolus platessae* (Woodcock, 1904) found in the cartilage (from the Southwest of Iceland) (Karlsbakk et al., 2017); (4) the larval nematodes *Anisakis* sp., (5) *Contracaecum* sp., (6) *Hysterothylacium* sp., and (7) *Phocanema decipiens* (Krabbe, 1878) in the muscles and the viscera (Hauksson, 1992); and (8) the adult trematode *Podocotyle atomon* (Rudolphi, 1802) (Brinkmann, 1956). Although there has been no specific use of parasites as biological tag for assessing plaice stock dentification in Iceland, Hauksson & Ólafsdóttir (1996) did report a greater parasite abundance in plaice collected in the West relative to those collected from the East (supporting the Greenland-Scotland Ridge boundary). The nematode *Cucullanus heterochrous* Rudolphi, 1802, anisakid nematode larvae, and the myxosporean *Myxobolus æglefini* Auerback, 1906 (possibly *M. platessae*), have been suggested as potential biological tags for plaice from three different spawning grounds in the North Sea (Wickins & MacFarlane, 1973), a different region from the current study area.

This study aims to describe and quantify the parasite fauna of plaice, and assess the potential of parasites as biological tags for stock identification of plaice in Icelandic waters, considering seasonal variations (Winter, Summer) and localities (North, South). The anticipated outcome is that abundance of certain parasites will vary across different seasons

and localities, making some of these suitable biological tags and therefore providing insights into the stock structure of plaice in Icelandic waters.

Material and methods

Samples collection

A total of 82 plaice were sampled from fishermen in 2023 from seven sites in Northern Iceland and along the Reykjanes Peninsula in the south, at depths ranging between 18 and 125 m (fig. 1; Table 1). Three northern sites were sampled twice times in winter (February) and once in summer (August), while three southern sites were sampled twice in winter (March) and once in summer (October). The fish were grouped by location and season into four groups: North Winter (NW; N=27), South Winter (SW; N=14), North Summer (NS; N=20), and South Summer (SS; N=21). We had no control over the provenance and timing of our samples as we relied solely on the generosity of local fishermen. During the necropsy, each fish was measured (Total Length [TL]; cm) and sexed (Males, Female, Immature). The following organs/sites were examined for macroparasites: skin, fins, mouth, nares, gills, eyes, brain, body cavity, gonads, heart, liver, mesenteries, spleen, and digestive tract. All were examined fresh except for the gonads, liver, mesenteries, and digestive tract, which were placed individually in labelled bags and frozen at -30ºC for later examination. All parasites found were collected and preserved in 96% ethanol for molecular analyses. For the digestive tract (stomach and intestine), parasites were separated into those collected from the external surface and from the mucosa. Additionally, otoliths were extracted and stored dry in envelopes, and genetic samples (gill filaments) were retained and stored in 96% ethanol (for future studies). Otolith contour reconstructions, based on the mean elliptical Fourier harmonics from the four sampled regions, revealed shape differences in the otoliths of the north winter group compared to the three other groups. However, the linear discriminant analysis (LDA) model yielded a relatively high classification error of 59.76%, indicating limited effectiveness in distinguishing among the four plaice populations. These results suggest that the current LDA model does not adequately classify the data and may require refinement; that's why we have chosen not to include it.

Molecular analysis

Genomic DNA was extracted from each parasite morphotype from the different organs, aiming for three extractions per morphotype per organ when feasible. Morphotypes were defined based on body shape, size, colour, and encystment shape. These were identified and

recorded consistently between organs and between different individual fish. Individual samples of smaller parasites, like trematode metacercariae, were placed in distinct tubes for DNA extraction. In the case of nematodes, a small section (disc, approximately 1 mm thick) from the parasite's central part was extracted (Devlin et al., 2004). A total of 36 distinct parasite forms were processed; the parasites were labeled based on the morphological identification conducted earlier (for instance, "nematode type 1"), indicating the specific organ in which they were not discovered and whether they were located on the inside or outside of each respective organ. While copepods were counted and identified, they were not included in the molecular work. Small parasites, such as metacercariae, were placed individually in separate tubes, while a central section of larger parasites, such as nematodes, was used for extraction, with the remaining tissue preserved in ethanol as a hologenophores/paragenophores (Pleijel et al., 2008). Different gene regions were amplifed via PCR for specific taxa. The ITS region was amplified using primers 93 and 94 (Nadler et al., 2005) for nematodes, the 28S rDNA region using primers T01N and T13N (Harper & Saunders, 2001) for unknowns (Cysts of Unknown Etiology; CUE), the 28S rDNA region using primers BD3 (Hernández-Mena et al., 2014) and 536 (Stock et al., 2001) for trematodes, and the mitochondrial COI region using primers LCO1490a (García-Varela & Pérez-Ponce de León, 2008) and HCO2198 (Folmer et al., 1994.) for acanthocephalans, using protocols described in Nadler et al. (2005; nematodes), García-Varela & Nadler (2005; trematodes), and García-Varela & Pérez-Ponce de León (2008; acanthocephalans). PCR reactions (25 µL) contained 12.50 µL of MyTaq 2x Master Mix (New England Biolabs), 0.35 µL of both forward and reverse primers (50 nM), 0.5 µL of DNA template, and 11.30 µL of ddH_2O. PCR products were visualised under UV light (1.5% agarose gel and Ethidium Bromide). Ten µL of each successful PCR products were purified using 2 µL of ExoSAP-IT (Applied Biosystems). Purified PCR were bi-directionally sequenced (Sanger sequencing) at Microsynth (Germany) using PCR primers (20 nM) and internal primers BD2 (Luton et al., 1992) and 504 (García-Varela & Nadler, 2005) for trematodes. Sequences were manually edited with Sequencher 5.4.6 (Gene Codes Corporation) and screened for orthology using BlastN (McGinnis & Madden, 2004).

Statistical analyses

Parasite abundance, mean intensity of infection, and prevalence were calculated according to Bush et al. (1997) for each parasite taxon for each organ. Statistical analyses were performed

in R Software, version 4.0.5 (R Core Team 2021). Although we grouped August and October samples together under "Summer", i.e. both these months are not consecutive but are considered within the feeding season for plaice in Icelandic waters (Hjorleifsson & Pálsson, 2001), we performed a Mann-Whitney test to examine whether parasite abundance and the number of fish of the same sex differed between the two months. A three-factor ANOVA was used to examine the effects of sex, locality, and season (and their interactions) on fish size. Assumptions for normality (Shapiro-Wilk test) and variance homogeneity (Levene's test) were validated, followed by post hoc Tukey tests for significant differences. A GLMM using the packages *lme4*, *MASS*, and *caret* on R to examine the effects of fish length, season, and locality on parasite abundance, with fish ID as a random effect to account for individual variation. Interaction terms were tested for ecological relevance, and variance inflation factors (VIFs) identified collinearity, leading to the exclusion of the gender variable. The best model, determined by the lowest Akaike Information Criterion corrected for small sample size (AICc), included fixed effects for length, season, and region. Diagnostic checks confirmed model assumptions. Linear Discriminant Analysis (LDA) was performed using *klaR*, *psych,* and *MASS*, to identify the best combinations of individual parasite species abundance per organ to distinguish fish groups by season and region. For the LDA, only parasite present in at least 5% of sampled fish were considered (Osuna-Cabanillas et al., 2024).

Results

Sex was assigned for 81 plaice and grouped by region and season; the sex of one of the individuals could not be identified. Total length and parasite abundance data for plaice sampled in the North and South during the Winter and Summer seasons are summarized in Table 2.

In summer, after a Mann-Whitney test with a p-value > 0.05 to see if there was a difference between the sexes in these two months (no difference here), we considered these two groups to form the summer group. However, there was a difference in parasite abundance with a Mann-Whitney test with a p-value < 0.001. Despite the differences in parasite abundance, we had to group the August and October samples to form the summer group because the number of samples was too small if they were split into their respective groups.

An ANOVA showed a significant difference in fish size across the four study groups: north summer (NS), north winter (NW), south summer (SS), and south winter (SW) ($p <$

0.001). Residuals deviated significantly from normality (Shapiro-Wilk, $p < 0.001$) but only due to extreme values (Q-Q plot not shown). Variances were homogeneous between groups (Levene's test, $p = 0.344$). Tukey's post hoc tests identified significant size differences between NW and NS ($p < 0.05$) and SW and NW ($p < 0.001$). Average sizes were 35.44 cm (± 5.17 cm) for NW, 40.20 cm (± 4.46 cm) for NS, and 43.15 cm (± 4.24 cm) for SW.

An ANOVA revealed a significant difference in fish size according to sex ($p < 0.001$). Residuals did not deviate significantly from normality (Shapiro-Wilk, $p = 0.086$), and variances were homogeneous (Levene's test, $p = 0.283$). Tukey's post hoc tests showed significant size differences between immature fish and females (adjusted $p < 0.001$) and between immature fish and males (adjusted $p < 0.001$), but not between males and females (adjusted $p = 0.942$). Average sizes were 40.65 cm (± 5.95 cm) for males, 41.22 cm (± 3.86 cm) for females, and 33.57 cm (± 3.27 cm) for immature fish.

In the South region, the GLMM showed the variation of the parasite abundance as a function of the TL to not be statistically significant ($p = 0.410$), and fish size explained only 2.1% of the variance in parasite abundance ($R^2 = 0.021$). Similarly, in summer, the relationship was not statistically significant ($p = 0.399$), and fish size explained only 1.8% of the variance ($R^2 = 0.018$). In winter, the relationship was not statistically significant ($p = 0.829$), with an $R^2 = 0.001$. In the North region, on the other hand, the relationship was statistically significant ($p = 0.006$), and fish size explained 15.7% of the variance in parasite abundance ($R^2 = 0.157$). Species richness as a function of total fish size reveals a non-significant relationship ($p = 0.152$) and a low coefficient of determination ($R^2 = 0.026$), indicating that total fish size explained only 2.6% of the variance in species richness in our sample.

The identities of the following taxa were confirmed molecularly. A 1760 bp sequence was obtained from the metacercaria from the eyes (GenBank accession number PV612099) and was assignable to the genus *Apatemon* (72% sequence coverage) with 99.7-99.8% sequence similarity with *Apatemon* sp. GenBank accession numbers LC599500, LC599501 (Nakao & Sasaki, 2021), and PQ582086 (Kudlai et al., 2024). The adult trematodes from the intestine (1767 bp; GenBank accession number PV612653) was assignable to *Zoogonoides viviparus* (Olsson, 1868) (71% sequence coverage) with 100.0% sequence similarity with GenBank accession numbers AY222271 (Olson et al., 2003), and OP956064–OP956067 (Kremnev et al., 2023). The larval nematodes from the gonads, liver, mesenteries, inner intestine, and outer intestine (968-984 bp; GenBank accession numbers PV671709-PV671734) were assignable to *Anisakis simplex* (Rudolphi, 1809) *sensu lato* (99-100%

sequence coverage) with 99.0-100.0% sequence similarity with GenBank accession numbers PP189864, and PP189865 (*A. simplex*) (Kumas et al., 2024) and MT820019-MT820022 (*Anisakis pegreffii* Campana-Rouget & Biocca, 1955) (unpublished sequences). Larval nematodes from the heart, liver, mesenteries, and outer stomach, and adult nematodes from the intestine (909-1055 bp; GenBank accession numbers PV671735-PV671750) were assignable to *Hysterothylacium aduncum* (Rudolphi, 1802) (95-100% sequence coverage) with 99.9-100.0% sequence similarity with GenBank accession numbers JQ934881 and JQ934883 (Vardić Smrzlić et al., 2012). A single larval nematode from the liver (987 bp; GenBank accession number PV671708) was assignable to *Contracaecum osculatum* (Rudolphi, 1802) (97% sequence coverage) with 100.0% sequence similarity with GenBank accession numbers MT258496-MT258528 (Mohamed et al., 2020). A single larval nematode from the liver (921 bp; GenBank accession number PV671707) was assignable to *Phocanema decipiens* (Krabbe, 1878) (99% sequence coverage) with 99.9% sequence similarity with GenBank accession numbers JQ673262 and JQ673263 (Buchmann & Kania, 2012). Adult nematodes from the the stomach and intestine (1023-1097 bp; GenBank accession numbers PV671751-PV671755) were morphologically assigned to the cucullanid genus *Dichelyne* Jägerskiöld, 1902. These sequences (85-86% sequence coverage) had 91.5-91.8% sequence similarity with GenBank accession numbers KF470876, KF470877, KF470880 (Li et al., 2014).

In the SW samples, the most abundant parasite were metacercariae of the trematode *Rhipidocotyle* sp. in the gills, with a mean abundance of 20.86, a prevalence of 42.86%, and a mean intensity of 48.67 per infected host. However, the nematode *A. simplex s. l.* in the liver also has a high prevalence of 57.14% (Table 3). In the NW samples, the most abundant parasite was the adult trematode *Z. viviparus* in the intestine, with a mean abundance of 11.00, 55.56% prevalence, and a mean intensity of infection of 19.80 (Table 4). In the SS, the most abundant parasite was *Z. viviparus* (adults) in the intestine, with a mean abundance of 27.52, a prevalence of 52.38%, and a mean intensity of infection of 52.55. However, the nematode in the liver *A. simplex,* has a mean abundance of 0.33, a prevalence of 19.05%, and a mean intensity of infection of 1.75 (Table 5). In the NS, the parasite with the highest abundance was the cucullanid nematode in the intestine, with a mean abundance of 0.30, 20.00% prevalence, and a mean intensity of infection of 1.50 (Table 6).

Linear discriminant analysis (LDA) revealed clustering based on parasite community composition among our four groups. The LD1 axis explains 55.79% of the variance, and the LD2 axis 25.26%. There was noticeable overlap between the four groups, NS, NW, SS, and

SW. However, the SW shows differences in the parasite community along the LD1 axis due to *A. simplex* larvae in the liver, *Z. viviparus* adults in the intestine, and *Dichelyne* sp. in the intestine (Fig. 2). Furthermore, the NW group show differences in the parasite community along the LD2 axis due to *H. aduncum* larvae in the liver and *Dichelyne* sp. from the intestine (Fig. 2).

Discussion

In this study, we identified several parasites in plaice, some of which had never been reported before from Icelandic waters from this host, such as the trematodes *Z. viviparus* (adults) and *Rhipidocotyle* sp. (metacercariae), in addition to the nematodes *C. osculatum*, *Dichelyne* sp., and *H. aduncum*. Furthermore, to our knowledge, *Apatemon* has not been recorded from plaice (*P. platessa*) previously. Non-specific records of *Contracaecum* and *Hysterothylacium* have been reported from plaice in Icelandic waters previously (see Hauksson, 1992). In this study, we used molecular tools to confirm the specific identifications for *C. osculatum* and *H. aduncum*, thus providing these new species records from plaice in Icelandic waters.

Otolith microstructure analysis of juvenile plaice sampled from 31 beaches around Iceland echoed the conclusion of local population structure of plaice in Icelandic waters (Gunnarsson et al., 2010). The low genetic diversity of plaice in Icelandic waters (see Hoarau et al., 2004) is likely a result of some straying between spawning grounds (Sólmundsson et al., 2005). At the very least, our results provide another line of evidence suggesting that the stock structure of plaice in Icelandic waters should be revisited. On their own, in this instance, tagging (Sólmundsson et al., 2005), otolith microstructure analysis (Gunnarsson et al., 2010), and parasites might not provide sufficient information for fine-scale management of plaice in Icelandic waters. A tagging study based on 1313 plaice tagged in the spawning grounds (183 recaptures) and 857 on the feeding grounds (55 recaptures), found strong spawning-site and feeding ground fidelity (94% and > 90%, respectively), suggesting complex stock structure in Icelandic waters (Sólmundsson et al., 2005). However, a targeted integrative approach should be employed to better understand the stock structure of this species and inform management. We found two parasite species demonstrating potential as biological tags in the south and north regions of Iceland, namely the nematode *A. simplex s. l* and the trematode *Z. viviparus* due to their influence along the LD1 axis of the LDA. *Dichelyne* sp. was not considered a suitable biological tag due to variability in seasonal abundance (see below). Additionally, *H. aduncum* was not considered a suitable biological tag for stock identification due to its relatively low prevalence and abundance (Tables 3-6).

371 *Anisakis simplex* has been identified as a biological tag in several marine teleosts in
372 the Northeast Atlantic to discriminate between stocks, such as beaked red fish (*Sebastes*
373 *mentella*) (Klapper et al., 2016), herring (*Clupea harengus*) (Grabda, 1974), and horse
374 mackerel (*Trachurus trachurus*) (Mattiucci et al., 2008), to name but a few. We recovered *A.*
375 *simplex s. l.* on gonads, liver, outer intestine, and mesenteries. The ones found inside the
376 intestine were likely passing through with digested prey. *Anisakis simplex* eggs are released
377 into the water with the definitive host's (marine mammals) fæces, hatching into L2 stage
378 larvae and floating freely in the water (Nagasawa, 1990). Crustaceans, mainly euphausiids
379 (krill), ingest them and develop into L3-stage larvae in these hosts (Klimpel & Palm, 2011;
380 Lunneryd et al., 2015). Stage L3 larvae infect fish and cephalopods when they consume the
381 infected crustaceans. Fish, cephalopods (Nagasawa, 1990), and seabirds (Johnston et al.,
382 1942; Shamsi et al., 2017) can act as paratenic hosts, transmitting the larvae throughout the
383 marine food chain. *Anisakis simplex* has been recovered from plaice in the North Sea and
384 west of Scotland (Levsen et al., 2018), Skattegat (Nielsen et al., 2002), and from the Faroe
385 Islands (Køie, 1993), to name a few. In Iceland, *A. simplex* larvae have been recorded
386 previously from plaice as *Anisakis* sp. (Hauksson, 1992) and *A. simplex* (Levsen et al., 2018).
387 Additionally, several other marine teleost species (presented in alphabetical order based on
388 common names) are known to harbour *A. simplex* in Icelandic waters: (1) anglerfish (*Lophius*
389 *piscatorius*) (Eydal & Ólafsdóttir, 2002); (2) the American plaice (*Hippoglossoides*
390 *platessoides*) (Hauksson, 1992); (3) the vent of Atlantic salmon (*Salmo salar*) (Helgason et
391 al., 2008); (4) the musculature and visceral organs of beaked redfish (*S. mentella*) (Klapper et
392 al., 2015); (5) in the body cavity of the capelin (*Mallotus villosus*) (Palsson & Beverley-
393 Burton, 1984); (6) cod (*Gadus morhua*) (liver) (Klapper et al., 2018; Severin et al., 2020); (7)
394 saithe (*Pollachus virens*) filets, gills, and viscera (Hauksson, 1992; Højgaard, 1997); (8)
395 three-spined stickleback (*Gaterosteus aculeatus*) (Richter, 2003); and (9) witch flounder
396 (*Glyptocephalus cynoglossus*) (Hauksson, 1992). Marine mammals in Iceland, mainly
397 harbour (*Phoca vitulina*) and grey (*Halichoerus grypus*) seals, will prey upon fish and
398 cephalopods, allowing the development of the larvae into adult stages, completing the life
399 cycle (Hauksson & Ólafsdóttir, 1995; Ólafsdóttir & Hauksson, 1998; Zuo et al., 2018).
400 *Phocanema decipiens*, another anisakid nematode, is considered more abundant in plaice
401 collected from Hvalseyjar, in close proximity to grey seal colonies, relative to Snaefellsnes,
402 where there is no grey seal colony (Hauksson & Ólafsdóttir, 1995). However, we did not
403 explore this pattern for *A. simplex* but it could explain the potential of this species as a
404 biological tag in Iceland. As a future perspective, it might be worth considering distance to

405 the nearest seal colony as a factor in assessing the potential of anisakid nematode parasites as
406 biological tags.
407 The trematode *Z. viviparus* was recovered from plaice in Iceland for the first time in
408 our study but it has been collected previously from *H. platessoides* (Ólafsdóttir, 1999) and *L.*
409 *piscatorius* (Eydal & Ólafsdóttir, 2002) in Icelandic waters. The species is known to be
410 abundant in Northeast Atlantic flatfishes (Køie, 1976) such as flounder *Platichthys flesus*
411 (e.g., Schmidt et al., 2003), common dab *Limanda limanda* (e.g., Køie, 1983, 2000), and
412 plaice (e.g., Nicoll, 1915; Wickins & MacFarlane, 1973; Køie, 2000) and has been used
413 previously to discriminate between stocks of *Pla. flesus* in the Northeast Atlantic (Gibson,
414 1972) and in *H. platessoides* in the Northwest Atlantic (Scott, 1975) but not in plaice. Eggs of
415 *Z. viviparus* are excreted by the fish definitive host into the water, where they hatch into
416 miracidia larvae. The sporocysts are typically found in the gastropod *Buccinum undatum* L.
417 (Lebour, 1918). The cercariae leave the gastropod and infect a secondary intermediate host,
418 often polychaetes (Orrhage, 1974; Kremnev et al., 2023) or bivalves (Kremnev et al., 2023),
419 where they encyst into metacercariae. The second intermediate host is ingested by a fish,
420 where they transform into adults. As plaice feed mainly on benthic organisms (De
421 Raedemaecker et al., 2011), they likely ingest an infected benthic intermediate host and
422 become infected. The benthic bivalve and polychaete fauna comprising the stomach contents
423 of plaice from both the North and South of Iceland should be examined quantitatively to gain
424 insights into their respective diets and potential transmission routes for trophically-
425 transmitted parasites such as *Z. viviparus*.
426 The LDA result (Figs 2) shows that the Winter groups are separated from the Summer
427 groups; South along the LD1 axis and North along the LD2 axis. The Winter groups has a
428 much greater abundance of the nematode *Dichelyne* sp. in the intestine of plaice, i.e., 2.14
429 and 2.30 in the North (Table 3) and South (Table 4), respectively, relative to the Summer
430 groups, i.e. 0.00 in the South (Table 5) and 0.30 in the North (Table 6), respectively.
431 *Dichelyne heterochrus* is a nematode parasites described from plaice in the Northeast Atlantic
432 such as in the English Channel (Baylis & Jones, 1933), the West coast of Scotland
433 (MacKenzie & Gibson, 1970), the North Sea (Wickins & MacFarlane, 1973), from Faroese
434 waters (Køie, 1993), to name but a few. Furthermore, it has been identified from Icelandic
435 waters in *H. platessoides* (Ólafsdóttir, 1999). Although we cannot confirm the specific
436 identification of our specimens, they are likely to be assignable to this species. The greater
437 abundance of this species in Winter is not surprising as it has an annual life cycle; peak
438 abundance in the Fall and dying between late-winter and summer (MacKenzie & Gibson,

1970). Lower water temperatures in Iceland could affect temporally the life cycle of *D. heterochrus* by slowing its growth and delaying mortality. Patterns of differing seasonal abundance for *Z. viviparus* are unclear but might be related to differing seasonal abudance of the gastropod or secondary intermediate hosts.

Metacercariae of the trematode genus *Apatemon*, identified as *A. gracilis* (Rudolphi, 1819), have been recovered previously from the eyes of Icelandic freshwater fishes, namely *G. aculeatus* (Blair, 1973; Richter 2003; Karvonen et al., 2013), *S. salar* (Richter, 1982), sea tout (*Salmo trutta*) (Richter, 1982), and Arctic charr (*Salvelinus alpinus*) (Richter, 1982). We recovered two individuals from the eyes of plaice in fully marine environments. Plaice use shallow intertidal, subtidal, coastal, and estuarine habitats as nursery areas (e.g., Gunnarsson et al., 2010; Lauria et al., 2011; Ciotti et al., 2014). It seems likely that the metacercariae were acquired by plaice in the nursery areas and retained subsequent to their ontogenetic migration.

Rhipidocotyle metacercariae have been recovered from plaice in British waters previously (e.g. MacKenzie & Gibson, 1970; Pulsford & Matthews, 1984) but never before reported from Icelandic waters. Infections only affect age 0 and 1 plaice, and are believed to be seasonal, occuring during the summer months (MacKenzie & Gibson, 1970; Pulsford & Matthews, 1984). These metacercariae were recovered from plaice both in the North and South of Iceland, with greater abundance observed during the winter months. However, all of our plaice were > 1 year of age (based on size distribution of our samples), suggesting that the observed infections were acquired in the past and retained.

The presence and abundance of rare parasite species can vary considerably between host populations, mainly when populations are geographically distant. Parasites that do not have a high dispersal capacity, which is often linked to the movement of their hosts, can be good tags because the similarity of their community decreases rapidly due to their distance (MacKenzie & Abaunza, 1998). The rarity of some parasite species increases their discriminatory power in differentiating stocks; these species are more likely to be specific to specific regions or populations. These parasites are associated with particular host populations or environmental conditions, which can help distinguish stocks and identify fish populations' ecological niches or migratory behaviours (MacKenzie & Abaunza, 1998). However, the presence of these parasites in samples can cause variability and noise, making their results less reliable if the sample size is small (Sindermann, 1983). Herein, we excluded parasites that were rare (prevalence <5%) across our entire sample (Osuna-Cabanillas et al., 2024) as these had a disproportionate effect on our results (LDA including all parasites, result

not shown). Furthermore, it ensured that we had a greater sample size than parasite species for each group (see Tabachnick & Fidell, 2001). Common parasites are widely distributed, which allows for more robust datasets that are less prone to sampling errors than with rare parasites. Common parasites are ideal for large-scale studies with general trends over large geographic areas (MacKenzie & Abaunza, 1998). However, due to their widespread presence, these parasites can mask subtle differences between closely related populations, thus reducing their effectiveness for fine-scale ecological differentiation (Marcogliese & Jacobson, 2015).

Sampling for the summer group took place in August in the north of Iceland, with an additional sampling in October to the south of Iceland due to fishermens catch and availability. Despite the feeding season for plaice in Icelandic waters extending from June to November, including August and October samples in the summer group may distort parasite abundance data, as an ANOVA showed similar sex distributions between August and October but a significant difference in parasite abundance. Parasite abundance was 0.6 per fish in August and 33.0 in October. This difference could be explained by water temperature. Parasites are more abundant in warmer water (Klimpel & Palm, 2011). In October, sampling occurred in the south, influenced by the warm Atlantic current, while August sampling was in the north, affected by the cold East Greenland current (Astthorsson et al., 2007; Pampoulie et al., 2024). Seasonal shifts in temperature, salinity, and currents from summer to autumn impact nutrient availability, phytoplankton production, and the food web, influencing parasite abundance (Marcogliese & Jacobson, 2015). However, in the interest of keeping sample sizes consistent between groups, we made the informed decision of combining these August and October samples, while recognising that this might affect observed patterns.

ANOVA showed a significant difference in mean fish size between the North in summer and Winter ($p < 0.05$) and between the South in Winter ($p < 0.001$), and the North in Winter ($p < 0.001$). The group with the largest fish size, South Winter (43.15 cm), also has the highest parasite abundance (32.93). Environmental conditions can influence these size differences, as warmer temperatures in summer and in southern Iceland favor juvenile growth. Young fish grow best in waters between 7–15°C, optimizing their metabolism (Fonds et al., 1992; van der Sleen et al., 2018). However, this difference might be related to a greater proportion of immature fish (i.e., smaller) being sampled during the Winter. Larger fish tend to host more parasites due to increased surface area, body volume, lifespan, and exposure to varied environments and prey (Kuris et al., 1980; Poulin, 1995; Morand & Poulin, 1998; Bagge et al., 2004; Kamiya et al., 2014; Rasmussen & Randhawa, 2018).

However, species richness per total fish length (cm) (Fig 3.4) explains only 2.6% of the variance, indicating low explanatory power and no clear trend that larger fish systematically host more parasite species. Ideally, only mature fish would have been sampled but we were limited due to fishermens catch and availability. We did not repeat analyses on mature fish only due to the low number of samples per group this approach would have yielded, i.e., low statistical power.

The discriminative power of parasites was not evaluated in this instance. Despite sample size per group not impacting on the ability of parasites to discriminate between fish stocks (Poulin & Kamiya, 2015), it has been recommended that sample sizes of 50 per group be used in order to provide reliable estimates of covariance (see Tabachnick & Fidell, 2001). Therefore, a larger sample size of plaice is recommended for future studies, as this could reduce variability, enhance detection of biological signals for stock identification, and improve model robustness.

In conclusion, *A. simplex* and *Z. viviparus* show potential as biological tags for distinguishing northern and southern groups of plaice in Icelandic waters. To refine our findings, increasing sample size, standardizing samples, and expanding regional sampling to include east and west Iceland would improve the accuracy of our results. Additionally, collecting stomach contents during dissections would help identify each group's diet, providing insights into their prey and contributing to information regarding potential transmission routes of the different parasites in the different marine ecoregions of Iceland.

Results based on parasite data herein are consistent with those for tagging and otolith microstructure. However, an integrative strategy to stock identification in plaice is required in order to provide fine spatial scale data required to inform fisheries managers.

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Conflict of interest declaration

The authors declare none.

Ethical standards

Fish analysed in this study were collected from commercial capture, hence no ethics protocols were required.

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Table 1. Overview of collection information and sample sizes for plaice sampled in this study (N=82).

Date	N	Region	Season	Latitude	Longitude	Depth (m)
10.02.2023	10	North	Winter	N66°06´33	W18°33´31	80
01.03.2023	7	South	Winter	N63°57´06	W22°48´20	77
20.03.2023	7	South	Winter	N63°55’37	W22°46’49	68
31.03.2023	17	North	Winter	N65°42´44	W20°26´03	53
03.08.2023	20	North	Summer	N65°49'36	W20°30'43	124
06.10.2023	21	South	Summer	N64°05'58	W22°34'20	18

Table 2. Summary of mean Total Length (TL) and mean Parasite Abundance (with standard deviation; SD) per plaice (*Pleuronectes platessa* L.) (N = 81) sampled from the north and south of Iceland in both Summer and Winter.

Locality	Season	Sex	N	Mean TL (cm ± SD)	Parasite Abundance (± SD)
North & South	**Summer & Winter**	Female	18	41.22 (± 3.86)	20.83 (± 5.49)
		Male	40	40.65 (± 5.95)	18.42 (± 6.41)
		Immature	23	33.57 (± 3.27)	21.30 (± 4.58)
North			**47**		
		Female	8	42.00 (± 4.24)	2.75 (± 1.07)
		Male	21	39.24 (± 4.97)	2.91 (± 0.60)
		Immature	18	33.30 (± 3.27)	21.17 (± 4.29)
South			**34**		
		Female	10	40.60 (± 3.63)	35.30 (± 7.68)
		Male	19	42.21 (± 6.65)	31.68 (± 9.69)
		Immature	5	34.20 (± 3.56)	21.80 (± 6.28)
	Summer		**41**		
		Female	10	39.60 (± 3.86)	26.40 (± 7.47)
		Male	26	40.58 (± 6.13)	10.62 (± 4.95)
		Immature	5	34.20 (± 3.56)	21.80 (± 6.28)
	Winter		**40**		
		Female	8	43.25 (± 3.73)	13.00 (± 2.14)
		Male	14	40.70 (± 5.82)	27.71 (± 9.11)
		Immature	18	33.39 (± 3.27)	21.06 (± 4.29)
North	**Winter**	All	27	35.44 (± 5.17)	15.52 (± 3.39)
South	**Winter**	All	13	43.15 (± 4.24)	32.93 (± 8.82)
North	**Summer**	All	20	40.21 (± 4.46)	0.60 (± 0.18)
South	**Summer**	All	21	39.16 (± 6.57)	30.33 (± 7.75)

Table 3. Parasite community from the group South Winter of *Pleuronectes platessa* (N = 14) for each organ. Values correspond to mean Abundance (Prevalence %) [mean Intensity of infection]. The parasite(s) may be located outside (Ext) or inside (Int) of the organ. "-" correspond to 0.00 (0.00) [0.00]. Organs not listed were uninfected.

	Brain	Eyes	Flesh	Gills	Gonads	Intestine (Int)	Intestine (Ext)	Liver	Mesent.	Stomach (Int)	Stomach (Ext)
ACANTHOCEPHALA											
Unidentified (C)	-	-	-	-	-	-	-	0.07(7.14) [1.00]	-	-	-
CRUSTACEA											
Acanthochondria sp.	-	-	-	1.21(50.00) [2.43]	-	-	-	-	-	-	-
NEMATODA											
Anisakis simplex (L)	-	-	-	-	0.14(7.14) [2.00]	-	0.07(7.14) [1.00]	3.29(85.71) [3.83]	0.14(7.14) [2.00]	-	-
Contracaecum osculatum (L)	-	-	-	-	-	-	-	0.07(7.14) [1.00]	-	-	-
Dichelyne sp. (A)	-	-	-	-	-	2.14(71.43) [3.00]	-	-	-	-	-
Hysterothylacium aduncum (A)	-	-	-	-	-	-	-	-	-	-	-
Hysterothylacium aduncum (L)	-	-	-	-	-	-	-	0.14(7.14) [2.00]	-	-	0.21(14.29) [1.50]
Phocanema decipiens (L)	-	-	-	-	-	-	-	-	-	-	-
TREMATODA											
Apatemon sp.	-	0.07(7.14) [1.00]	-	-	-	-	-	-	-	-	-
Rhipidocotyle sp. (M)	-	-	-	20.86(42.86) [48.67]	-	-	-	-	-	-	-
Zoogonoides vivparus (A)	-	-	-	-	-	2.21(35.71) [6.20]	-	-	-	-	-
Unidentified (A)	0.07(7.14) [1.00]	-	-	-	-	-	-	-	-	0.21(14.29) [1.50]	-
Unidentified (M)	0.07(7.14) [1.00]	-	0.07(7.14) [1.00]	0.07(7.14) [1.00]	-	0.07(7.14) [1.00]	-	0.07(7.14) [1.00]	0.21(14.29) [1.50]	-	-
OTHER											
CUE	-	-	-	0.07(7.14) [1.00]	-	-	-	-	-	-	-

A, Adult; **C**, Cystacanth; **CUE**, Cyst of Unknown Etiology; **L**, Larvae; **M**, Metacercariae; **Mesent**, Mesenteries

Table 4. Parasite community from the group North Winter of *Pleuronectes platessa* (N = 27) for each organ. Values correspond to mean Abundance (Prevalence %) [mean Intensity of infection]. The parasite(s) may be located outside (Ext) or inside (Int) of the organ. "-" correspond to 0.00 (0.00) [0.00]. Organs not listed were uninfected.

	Body (Ext)	Brain	Eyes	Gills	Heart	Intestine (Int)	Intestine (Ext)	Liver	Mesent.	Stomach (Int)	Stomach (Ext)
ACANTHOCEPHALA											
Unidentified (C)	-	-	-	-	-	-	-	0.04(3.70) [1.00]	0.04(3.70) [1.00]	-	-
CRUSTACEA											
Acanthochondria sp.	-	-	-	0.04(3.70) [1.00]	-	-	-	-	-	-	-
NEMATODA											
Anisakis simplex (L)	-	-	-	-	-	0.15(7.41) [2.00]	-	0.56(33.33) [1.67]	0.22(14.81) [1.50]	-	-
Contracaecum osculatum (L)	-	-	-	-	-	-	-	-	-	-	-
Dichelyne sp. (A)	-	-	-	-	-	2.30(55.56) [4.13]	-	-	-	0.11(7.41) [1.50]	-
Hysterothylacium aduncum (A)	-	-	-	-	-	0.11(7.41) [1.50]	-	-	-	-	-
Hysterothylacium aduncum (L)	-	-	-	-	0.04(3.70) [1.00]	-	-	0.48(25.93) [1.86]	0.11(7.41) [1.50]	-	0.04(3.70) [1.00]
Phocanema decipiens (L)	-	-	-	-	-	-	-	0.04(3.70) [1.00]	-	-	-
TREMATODA											
Apatemon sp.	-	-	0.04(3.70) [1.00]	-	-	-	-	-	-	-	-
Rhipidocotyle sp. (M)	-	-	-	1.00(40.74) [2.45]	-	-	-	-	-	-	-
Zoogonoides vivparus (A)	-	-	-	-	-	11.00(55.56) [19.80]	-	-	-	-	-
Unidentified (A)	-	-	-	-	-	-	0.07(3.70) [1.00]	-	-	-	-
Unidentified (M)	0.04(3.70) [1.00]	-	-	0.19(3.70) [5.00]	0.04(3.70) [1.00]	0.04(3.70) [1.00]	-	-	0.04(3.70) [1.00]	-	-
OTHER											
CUE	-	0.04(3.70) [1.00]	-	-	-	-	-	-	0.04(3.70) [1.00]	-	-

A, Adult; **C**, Cystacanth; **CUE**, Cyst of Unknown Etiology; **L**, Larvae; **M**, Metacercariae; **Mesent**, Mesenteries

Table 5. Parasite community from the group South Summer of *Pleuronectes platessa* (N = 21) for each organ. Values correspond to mean Abundance (Prevalence %) [mean Intensity of infection]. The parasite(s) may be located outside (Ext) or inside (Int) of the organ. "-" correspond to 0.00 (0.00) [0.00]. Organs not listed were uninfected.

	Body (Ext)	Brain	Eyes	Flesh	Gills	Heart	Intestine (Int)	Intestine (Ext)	Liver	Mesent.	Stomach (Int)	Stomach (Ext)
ACANTHOCEPHALA												
Unidentified (C)	-	-	-	-	-	-	-	-	-	-	-	-
CRUSTACEA												
Acanthochondria sp.	-	-	-	-	0.33(14.29) [2.33]	-	-	-	-	-	-	-
NEMATODA												
Anisakis simplex (L)	-	-	-	-	-	-	-	0.10(4.76) [2.00]	0.57(33.33) [1.71]	0.14(4.76) [3.00]	-	-
Contracaecum osculatum (L)	-	-	-	-	-	-	-	-	-	-	-	-
Dichelyne sp. (A)	-	-	-	-	-	-	-	-	-	-	0.05(4.76) [1.00]	-
Hysterothylacium aduncum (A)	-	-	-	-	-	-	-	-	-	-	-	-
Hysterothylacium aduncum (L)	-	-	-	-	-	-	-	-	0.19(19.05) [1.00]	-	-	-
Phocanema decipiens (L)	-	-	-	-	-	-	-	-	-	-	-	-
TREMATODA												
Apatemon sp.	-	-	-	-	-	-	-	-	-	-	-	-
Rhipidocotyle sp. (M)	-	-	-	-	0.14(4.76) [3.00]	-	-	-	-	-	-	-
Zoogonoides vivparus (A)	-	-	-	-	-	-	27.52(52.38) [52.55]	-	-	-	-	-
Unidentified (A)	-	-	-	-	-	-	14.29(4.76) [30.00]	-	-	-	-	-
Unidentified (M)	-	-	-	-	-	-	-	-	-	-	-	-
OTHER												
CUE	-	-	-	-	-	-	-	-	-	-	-	-

A, Adult; **C**, Cystacanth; **CUE**, Cyst of Unknown Etiology; **L**, Larvae; **M**, Metacercariae; **Mesent**, Mesenteries

Table 6. Parasite community from the group North Summer of *Pleuronectes platessa* (N = 20) for each organ. Values correspond to mean Abundance (Prevalence %) [mean Intensity of infection]. The parasite(s) may be located outside (Ext) or inside (Int) of the organ. "-" correspond to 0.00 (0.00) [0.00]. Organs not listed were uninfected.

	Body (Ext)	Brain	Eyes	Flesh	Gills	Heart	Intestine (Int)	Intestine (Ext)	Liver	Mesent.	Stomach (Int)	Stomach (Ext)
ACANTHOCEPHALA												
Unidentified (C)	-	-	-	-	-	-	-	-	0.05(5.00) [1.00]	-	-	-
CRUSTACEA												
Acanthochondria sp.	-	-	-	-	0.20(10.00) [2.00]	-	-	-	-	-	-	-
NEMATODA												
Anisakis simplex (L)	-	-	-	-	-	-	-	0.05(5.00) [1.00]	-	-	-	-
Contracaecum osculatum (L)	-	-	-	-	-	-	-	-	-	-	-	-
Dichelyne sp. (A)	-	-	-	-	-	-	0.30(20.00) [1.50]	-	-	-	-	-
Hysterothylacium aduncum (A)	-	-	-	-	-	-	-	-	-	-	-	-
Hysterothylacium aduncum (L)	-	-	-	-	-	-	-	-	0.05(5.00) [1.00]	-	-	-
Phocanema decipiens (L)	-	-	-	-	-	-	-	-	-	-	-	-
TREMATODA												
Apatemon sp.	-	-	-	-	-	-	-	-	-	-	-	-
Rhipidocotyle sp. (M)	-	-	-	-	-	-	-	-	-	-	-	-
Zoogonoides vivparus (A)	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified (A)	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified (M)	-	-	-	-	-	-	-	-	-	-	-	-
OTHER												
CUE	-	-	-	-	-	-	-	-	-	-	-	-

A, Adult; **C**, Cystacanth; **CUE**, Cyst of Unknown Etiology; **L**, Larvae; **M**, Metacercariae; **Mesent**, Mesenteries

Figure captions

Figure 1. Map of Iceland, including prevailing currents, showing the six different capture sites for each study group: North Summer N = 20, North Winter N = 27, South Summer N = 21, and South Winter N = 14. Note that two of the localities are similar in South Winter (see Table 1) and their points overlap completely.

Figure 2: Bi-plot of Linear discriminant analysis scores for the parasites of the Icelandic plaice (*Pleuronectes platessa*) by sampling region of the most abundant parasites (present at least 5% in each fish). The 95% ellipses illustrate the distribution and concentration of points associated with each group. The larger the ellipse, the greater the variability within the group (NS, North-Summer; NW, North-Winter; SS, South-Summer; SW, South-Winter).