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Quantifying spatio-temporal consistency in the trophic ecology of two sympatric flatfishes

Georgina L. Hunt[1,2] | Matthew R. D. Cobain[3] | Rona A. R. McGill[4] | John K. Pinnegar[5] | Georg H. Engelhard[5] | Benjamin D. Wigham[1] | Nicholas V. C. Polunin[1]

[1]School of Natural Environmental Sciences, Newcastle University, Newcastle upon Tyne, UK

[2]School of Biological Sciences, Zoology Building, University of Aberdeen, Aberdeen, UK

[3]Department of Zoology, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland

[4]National Environmental Isotope Facility, Scottish Universities Environmental Research Centre, Glasgow, UK

[5]Centre for Environment, Fisheries and Aquaculture Science (Cefas), Lowestoft, UK

Correspondence
Georgina L. Hunt, School of Biological Sciences, Zoology Building, University of Aberdeen, Aberdeen AB24 2TZ, UK.
Email: georgina.hunt@abdn.ac.uk

Abstract

Sympatric flatfish predators may partition their resources in coastal environments to reduce competition and maximise foraging efficiency. However, the degree of spatial and temporal consistency in their trophic ecology is not well understood because dietary studies tend to overlook the heterogeneity of consumed prey. Increasing the spatial and temporal scale of dietary analyses can thus help to resolve predator resource use. We applied a stomach content and multi-tissue (liver and muscle) stable isotope (δ^{13}C, δ^{15}N and δ^{34}S) approach to investigate the feeding habits of two co-occurring flatfish predators, common dab (*Limanda limanda*) and European plaice (*Pleuronectes platessa*), across four bays on the Northumberland coast (UK) over short (hours), medium (days) and long (months) temporal scales. Stomach content analyses showed spatial consistencies in predator resource use, whereas stable isotope mixing models revealed considerable inter-bay diet variability. Stomach contents also indicated high dietary overlap between *L. limanda* and *P. platessa*, while the stable isotope data yielded low to moderate levels of overlap, with cases of complete niche separation. Furthermore, individual specialisation metrics indicated consistently low levels of specialisation among conspecifics over time. We document changes in resource partitioning in space and time, reflecting diet switching in response to local and temporal fluctuations of patchily distributed prey. This study highlights how trophic tracers integrated at multiple temporal and spatial scales (within tens of kilometres) provide a more integrative approach for assessing the trophic ecology of sympatric predators in dynamic environments.

KEYWORDS
coastal, flatfishes, stable isotopes, stomach contents, sympatric, trophic ecology

1 | INTRODUCTION

Ecological niche theory suggests that the co-occurrence of predators may cause individuals to partition their resources in space and time to optimise food intake and reduce competition (Costa-Pereira et al., 2019).

Predator species may rank resources differently based on their energy gain per unit time, but this largely depends on resource availability (Pinnegar et al., 2003) and an individual's phenotypic ability to capture and handle prey (Araújo et al., 2011; Bolnick et al., 2003). Predators can afford to specialise on select prey types when resources are abundant

(Amundsen, 1995), but may expand their trophic niche to incorporate underutilised prey types if preferred resources are scarce and/or inter- and intra- competition is high (Bolnick et al., 2003). Resource partitioning can therefore vary temporally as predators readily switch their feeding strategies on a seasonal or interannual basis (Schoener, 1974), or spatially as they consume patchily distributed prey across different habitats (Linke et al., 2001).

Diet variation is often related to ontogeny or body size due to factors such as gape size (Scharf et al., 2000), but conspecifics of a given age and size can differ considerably in their resource use (Araújo et al., 2011; Ingram et al., 2018). A population of mobile "generalist" predators may comprise individuals that consume a diverse spectrum of similar prey types or specialised individuals with little or no overlap in diet composition, each consuming a sub-set of the population's overall resource base (Amundsen, 1995; Bolnick et al., 2003). Consequently, the degree of specialisation can influence the stability of populations, with subsequent effects on community dynamics and trophic interactions among predators (Bolnick et al., 2011).

Stomach content data have traditionally been used to elucidate trophic interactions in fish predators (e.g., Amara et al., 2001; Carter et al., 1991; Vinagre et al., 2011); they offer dietary taxonomic accuracy, but temporally limited snapshots of prey consumed within the last 24 h (Hyslop, 1980), and may incorporate bias if prey abundances vary in time or are patchily distributed relative to individual predator movements (Araújo et al., 2007). Stable isotope ratios of soft tissues can offer greater temporal consistency in assimilated diet due to their slower turnover (Post, 2002), albeit at the cost of reduced dietary resolution (Araújo et al., 2011). Carbon ($\delta^{13}C$) isotope ratios are widely used to identify sources of primary production that fuel marine food webs (DeNiro & Epstein, 1978), and nitrogen ($\delta^{15}N$) isotopes can determine the trophic position at which an animal is foraging (Pinnegar & Polunin, 1999). Additional tracers such as sulphur ($\delta^{34}S$) isotopes can help discriminate between production sources (e.g., benthic vs. pelagic production; Duffill Telsnig et al., 2019), which may otherwise be undetected by $\delta^{13}C$ and $\delta^{15}N$ alone (Connolly et al., 2004).

Because animal tissues vary in isotopic turnover rates, their stable isotope ratios may reflect assimilated diet over periods from days to several months (Buchheister & Latour, 2010; MacNeil et al., 2005). Fast turnover tissues with high metabolic rates (e.g., plasma and liver) represent medium-term diets as they reflect dietary changes more quickly than slower turnover tissues (e.g., muscle), which are less metabolically active and representative of longer-term diets (Carter et al., 2019; Tieszen et al., 1983). Despite the stochastic nature of feeding events, individuals consistently foraging on the same resource over time will exhibit similar isotope values between fast and slow tissues (Martínez del Rio et al., 2009), whereas individuals that shift their diet over time (e.g., seasonally) will show disparity in different tissues (Araújo et al., 2011). Consequently, interpretations of long-term diet provided by muscle tissue may be compounded by regional movements and seasonal dietary changes, which tend to exacerbate the heterogeneity of consumed isotope compositions (Buchheister & Latour, 2010). Stable isotope analysis of liver tissue can help resolve such discrepancies in resource use because it equilibrates over much shorter periods than muscle (Carter et al., 2019).

Shallow coastal waters support high densities of ecologically similar juvenile and adult fish predators, particularly flatfishes (Amara et al., 2001; Vinagre et al., 2011). Resource partitioning is expected to be common here as predators compete for similar food sources (Darnaude et al., 2001; Schückel et al., 2011), while increasing the potential for dietary specialisation among conspecifics (Araújo et al., 2011). Alternatively, predators may overlap their diets if resources are abundant enough to sustain the variety of species occupying the same coastal habitat (Darnaude et al., 2001; Vinagre et al., 2005). If resources are distributed more evenly in space, then competitive interactions are less likely than when they are aggregated, but the likelihood of inter- and intra-species competition increases as resource distributions become more heterogeneous (Ward et al., 2006), as is typical in coastal environments (Le Pape & Bonhommeau, 2015). Diet studies conducted in coastal and estuarine areas are generally focused on single species (e.g., Cobain et al., 2019) or on several species but in a single location (e.g., Cabral et al., 2002; Carter et al., 1991). Although such studies provide useful insights into resource partitioning, they do not fully capture the spatial and temporal heterogeneity of consumed prey in these often densely populated and dynamic regions (Buchheister & Latour, 2010; Mariani et al., 2011), and therefore the degree of consistency in observed dietary behaviours is poorly understood. Comparative studies of diet variation and individual specialisation in multiple dimensions can thus help to disentangle complex trophic interactions in sympatric predators.

Using a stomach content and multi-tissue stable isotope approach, we examined the trophic ecology of two ecologically similar flatfish predators, common dab Limanda limanda (L. 1758) and European plaice Pleuronectes platessa L. 1758, across multiple locations on the Northumberland coast (UK) over short (hours), medium (days) and long (months) temporal scales. We expect the potential for competition and variable prey types to result in heterogeneous resource partitioning in space and time, reflecting both population-level differences in diet and/or increased levels of specialisation. The segregating effect of inter- and intra-species competition is likely more observable when there is a greater diversity of available resources, or when resources vary more in space and time as there is more scope for resource partitioning (Costa-Pereira et al., 2019). Specfically, we hypothesised that (a) average diet compositions of L. limanda and P. platessa vary spatially over the three time scales due to spatio-temporally fluctuating prey bases, (b) dietary overlap between the two predators varies over time with seasonal shifts in prey availability that will alter levels of interspecific competition, and (c) individuals will exhibit significant levels of specialisation in resource use due to high intra-specific competition.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling

This study was conducted in four shallow bays on the Northumberland coast, north-east of England: Alnmouth Bay (55° 38′ N, 01° 60′ W), Druridge Bay (55° 27′ N, 01° 55′ W), Cambois Bay (55° 16′ N, 01° 51′ W) and Blyth Bay (55° 10′ N, 01° 48′ W) (Figure 1). These bays comprise soft, sandy sediments that are fringed by adjacent rocky habitats at depths of <20 m (Frid et al., 1991), with relatively
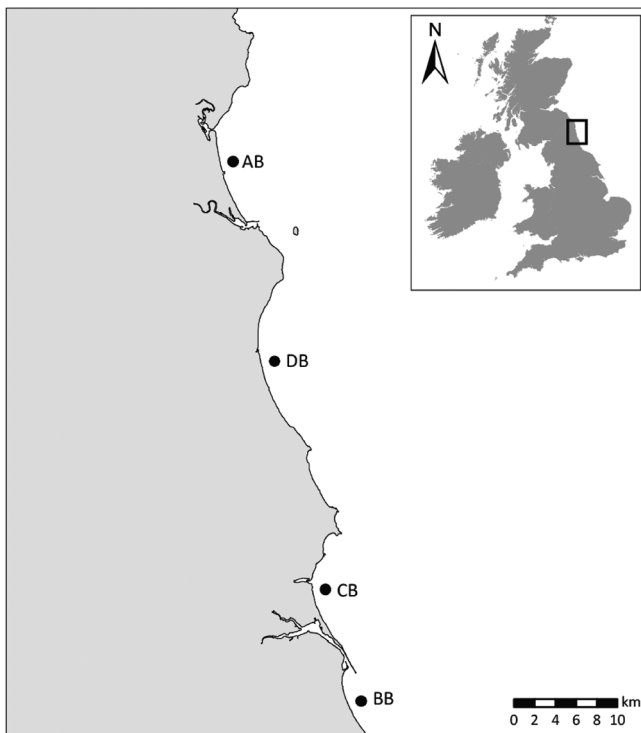
FIGURE 1 Map of the Northumberland coast (UK) with locations of sampling areas (AB, Alnmouth Bay; DB, Druridge Bay; CB, Cambois Bay; BB, Blyth Bay)

limited freshwater input and estuarine influence (Bennett & Foster-Smith, 1998). The study area has long been considered an essential habitat for predator species, including *P. platessa*, *L. limanda* and flounder *Platichthys flesus* (L. 1758) (Davis & Dunn, 1982; Walker, 1984).

Biological sampling was conducted during daylight hours between May and September 2019 using an otter trawl with an 80 mm (tight) meshed cod-end during 1-h tows at 2.5 knots (47 trawls in total). Catches were sorted, identified, counted, and total length (nearest millimetre) measured, and all *L. limanda* and *P. platessa* specimens were retained and immediately frozen on board at −20°C. All fish were humanely killed, and only specimens with no chance of survival were kept. Sampling was approved by Newcastle University's Animal Welfare and Ethical Review Board (project no.: 564) and carried out in accordance with the UK Home Office Scientific Procedures (Animals) Act requirements. To supplement intact prey items excised from stomachs for stable isotope analysis, additional samples of benthic species were collected in each sampling period using a Van Veen grab; key prey groups were identified, sorted and immediately frozen until further analysis.

2.2 | Stomach content analysis

2.2.1 | Sample preparation

Stomach contents of *L. limanda* ($n = 434$) and *P. platessa* ($n = 236$) > 15 cm were processed for dietary analyses (see Supporting

Information Table S1 in Appendix S1). A higher number of full stomachs were recorded from specimens collected during the earlier part of the season between May and July ($n = 573$) compared to August–September ($n = 97$). In the laboratory, specimens were defrosted, and stomachs were excised and weighed before and after prey items were removed. Prey items were identified to species level where possible and sorted into relatively broad categories under a binocular microscope. For each dietary group, items were counted and volume estimated (mm^3) using methods described by Hellawell and Abel (1971). Intact and non-digested prey were rinsed thoroughly with Milli-Q water and subsequently refrozen for stable isotope analysis.

2.2.2 | Dietary analyses

To account for possible diet variation due to differences in body size, we first assessed size-based differences by location based on two broadly determined size cohorts (15–24 and 25–41 cm). One-way analyses of similarities (ANOSIMs) revealed no statistically significant differences in diet between size classes in each bay ($P > 0.05$) for either predator. All stomachs were subsequently pooled and analysed across their entre size range by bay.

To quantify spatial consistency in the average diet composition of *L. limanda* and *P. platessa* by bay, we applied the index of relative importance (IRI) for each prey category (Pineas *et al.*, 1971), which balances the proportional frequency of occurrence p_F, proportional numerical abundance p_N and proportional volume p_V:

$$IRI = p_F \times (p_N + p_V)$$

For each prey group, IRI values were normalised to their total sum and expressed as a percentage (% IRI) to allow for comparisons between different bays. One-way ANOSIMs based on normalised IRI values were used to test for spatial differences in diet composition for each predator separately in the "vegan" package in R (v2.6.2; Oksanen *et al.*, 2022).

To examine dietary overlap between *L. limanda* and *P. platessa* in each bay, we applied the proportional similarity index, *PS* (Schoener, 1968):

$$PS_{ij} = 1 - \frac{1}{2} \sum_k |p_{ik} - p_{jk}|$$

where p_{ik} and p_{jk} represent the proportion of prey category k (by numerical abundance) consumed by predators i and j, respectively. PS_{ij} ranges from 0, when no prey is shared, to 1, where diets completely overlap. Dietary overlap is typically considered biologically significant when values are greater than 0.6 (Wallace & Ramsey, 1983). Differences in diet between the two predators were also tested separately for each bay using one-way ANOSIMs (based on normalised IRI values).

2.2.3 | Statistical analyses of individual specialisation

To estimate levels of individual specialisation, taken as the average pair-wise dietary overlap among individuals of the same species in each bay, we calculated the E index based on frequency data following Araújo et al. (2008):

$$E = 1 - \frac{2 \times \sum\limits_{pairs} PS_{ij}}{n(n-1)}$$

where the diets between two individuals, i and j, are those from a group of size n, and where E ranges from 0 (when all individuals consume the same resources) to 1 (when all individuals specialise on different resources). A smaller number of prey items per individual may artificially inflate estimates of individual specialisation, but Monte Carlo resampling allowed testing of whether the observed diet variation exceeded the mean null value based on stochastic sampling of the population mean diet (Araújo et al., 2008; Bolnick et al., 2002). The observed E index was therefore adjusted to account for this bias (Zaccarelli et al., 2013):

$$E_{adj} = \frac{\sum E_{obs} E_{null}}{1 - E_{null}}$$

Individual specialisation metrics were performed using the package "RInSp" (v1.2.5; Zaccarelli et al., 2013).

2.3 | Stable isotope analysis

2.3.1 | Sample preparation

For stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$), L. limanda ($n = 84$) and P. platessa ($n = 55$) representative of their size distribution (19–30 and 19–41 cm, respectively) were pseudo-randomly chosen from the total catch in July (Table 1). Analyses were conducted in this period only based on sufficient availability of specimens for both flatfishes and to enable isotopic comparisons between bays. Small plugs of dorsal muscle and liver tissue (c. 1 cm³) were excised from each fish, rinsed in Milli-Q water to remove excess skin and blood, stored in Eppendorf tubes and immediately refrozen. For intact prey items (from predator stomachs or sediment grabs), plugs of muscle tissue were taken from the abdomen of squid and shrimps, claw and thorax samples from crabs, adductor and foot samples from bivalves, fillets of white musculature from sandeel and whole polychaetes. All prey specimens were rinsed thoroughly with Milli-Q water to remove excess digestive material and to prevent contamination by sediment carbonates (Kharlamenko et al., 2001). Samples were then freeze-dried for 48 h and ground to a homogenous powder using a pestle and mortar. For smaller prey (e.g., bivalves and ophiuroids), individuals collected from the same location were pooled and homogenised together to

TABLE 1 Summary information of mean $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ stable isotope (‰) values (± S.E.) of *Limanda limanda* and *Pleuronectes platessa* liver and muscle tissue sampled in July 2019

Species	Site	Size range (cm)	Liver n	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$	Muscle n	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$
Limanda limanda	Alnmouth Bay	19–28	21	−17.54 ± 0.19	12.34 ± 0.10	19.06 ± 0.09	25	−17.78 ± 0.30	13.63 ± 0.04	19.93 ± 0.30
	Druridge Bay	20–30	17	−16.86 ± 0.27	12.51 ± 0.12	19.15 ± 0.08	26	−18.27 ± 0.04	13.14 ± 0.07	19.49 ± 0.14
	Cambois Bay	19–30	26	−16.87 ± 0.22	12.28 ± 0.06	17.87 ± 0.32	25	−18.12 ± 0.04	13.28 ± 0.08	19.11 ± 0.17
	Blyth Bay	19–30	20	−15.95 ± 0.09	12.56 ± 0.30	18.63 ± 0.12	26	−18.08 ± 0.19	13.45 ± 0.07	17.98 ± 0.19
Pleuronectes platessa	Alnmouth Bay	–	–	–	–	–	–	–	–	–
	Druridge Bay	19–41	9	−18.35 ± 0.12	12.04 ± 0.08	19.47 ± 0.10	10	−18.13 ± 0.10	13.24 ± 0.10	19.97 ± 0.14
	Cambois Bay	19–33	27	−18.10 ± 0.17	11.68 ± 0.08	17.89 ± 0.19	28	−17.96 ± 0.08	12.95 ± 0.09	18.56 ± 0.22
	Blyth Bay	19–33	19	−18.18 ± 0.17	11.63 ± 0.09	19.09 ± 0.17	25	−17.94 ± 0.07	13.05 ± 0.07	17.29 ± 0.28

obtain enough material for analysis. Ophiuroids were treated with 1 M hydrochloric acid to remove any traces of inorganic carbonates, rinsed with distilled water and freeze-dried for another 24 h. Sub-samples of 2.5 mg of homogenised tissue were weighed into 3×5 mm tin capsules and analysed using a PyroCube elemental analyser (Elementar, Hanau, Germany) coupled within an Elementar VisION isotope ratio mass spectrometer at the National Environmental Isotope Facility in East Kilbride (UK). All stable isotope values are reported relative to international standards: Vienna Pee Dee Belemnite for carbon, atmospheric air for nitrogen and Vienna Cañon Diablo Troilite for sulphur, using the delta (δ) notation and expressed in per mil (‰):

$$\delta = \left[\frac{R_{sample}}{R_{standard}} - 1 \right] \times 1000$$

where R is the ratio of heavy to light isotope (e.g., $^{15}N{:}^{14}N$).

International reference materials were run at the start and end of each C/N/S run for calibration and to correct for instrumental linearity and drift over time. For analytical precision, materials used were USGS40 (glutamic acid) for $\delta^{13}C$ and $\delta^{15}N$ (0.04 and 0.12‰ S.D., respectively) and IAEA-S-1, S-2 and S-3 silver sulphides for $\delta^{34}S$ (0.33, 0.38 and 0.82‰ S.D., respectively). Internal standards were also sequentially run between every 10 samples. Materials used for analytical precision were MSAG2 (methanesulfonamide, gelatin and water solution), M2 (methionine, glycine, gelatin, ^{15}N-alanine and water) and ANR [dorsal muscle of blue antimora *Antimora rostrata* (Günther, 1878)]. Analytical measurement standard deviations for internal materials were up to 0.1, 0.1 and 1.1‰ for $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$, respectively.

Lipid-rich tissues of fish may deplete ^{13}C relative to their isotopic composition and subsequently bias carbon data interpretations (Pinnegar & Polunin, 1999; Sweeting et al., 2006). C:N ratios for liver tissue were greater than the recommended value of 3.5 (Post et al., 2007); therefore, all $\delta^{13}C$ liver values were mathematically corrected for lipid content using the Kiljunen-Post model from Skinner et al. (2016). All $\delta^{13}C$ muscle values were not lipid corrected as C:N ratios were consistently low (<3.5; Post et al., 2007).

2.3.2 | Statistical analyses of average diet composition

To quantify spatial consistency in average diet of *L. limanda* and *P. platessa* by tissue type, Bayesian stable isotope mixing models were run using the MixSIAR package in R (v3.1.12; Stock & Semmens, 2016a). Mixing models using $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ data were run separately for each predator and tissue type with site and individuals nested within site as random effects. Models were run with two error terms (residual * process), where the residual error accounts for potential unexplained variation among the two predators (e.g., metabolic rate, digestibility) and the process error refers to variation from sampling predator isotope distributions (see Stock & Semmens, 2016b). Model convergence was evaluated using the

Gelman-Rubin diagnostic tests. The initial model using the three isotopes for *L. limanda* liver did not converge because consumer $\delta^{13}C$ values were outside the source mixing polygon. A second model using $\delta^{15}N$ and $\delta^{34}S$ was then run on *L. limanda* liver, and when plotted, consumer data were inside the source mixing polygon.

Benthic prey extracted from predator stomachs and grabs between May and July were only used in the mixing models to ensure temporal consistency with predator isotope data collected in July. Mixing models can yield biased results if there are too many source contribution estimates (Ward et al., 2011). A standard method of reducing the number of sources is to (a) logically combine a priori if source values are isotopically and biologically similar (e.g., trophic guild) or (b) if source isotope values are isotopically distinct and proportional contributions are aggregated a posteriori (Phillips et al., 2005). However, source isotope values may be statistically distinct but still exhibit similar isotope compositions. Mean isotope values and standard deviations were calculated for each prey type by bay to represent different source contributions in the mixing models (see Supporting Information Table S2 in Appendix S1). Stable isotope values of crabs, shrimps and polychaetes for all bays were compared using one-way ANOVA and Kruskal-Wallis tests, which revealed no significant differences for $\delta^{13}C$ (ANOVA, $F = 1.7$, $P > 0.05$), but significant differences were detected for $\delta^{15}N$ (Kruskal-Wallis, $\chi^2 = 28.8$, $P < 0.001$) and $\delta^{34}S$ (ANOVA, $F = 14.5$, $P < 0.001$). Despite these differences, crabs, shrimps and polychaetes were pooled into one source group ("benthic omnivores") because differences in their means values were small (c.1‰). Other prey taxa (bivalves, sandeel, squid and ophiuroids) were treated as separate source groups in mixing models.

To account for variability in trophic discrimination factors (TDF, Δ) for $\delta^{13}C$ and $\delta^{15}N$, we used significant regression equations between TDFs and their corresponding isotope ratios for muscle from Caut et al. (2009): $\Delta\delta^{13}C = -0.248 \times \delta^{13}C - 3.477$ and $\Delta\delta^{15}N = -0.281 \times \delta^{15}N + 5.879$. For liver tissue, mean values were applied as regression equations were not significant $\Delta\delta^{13}C = +0.77$ (S.E. $= 0.3$) and $\Delta\delta^{15}N = +1.61$ (S.E. $= 0.34$). The $\Delta\delta^{34}S$ for consumers is thought to be negligible (c. 0–1‰) despite the lack of published data (Hobson, 2008; Peterson & Fry, 1987). Barnes and Jennings (2007) revealed that $\Delta\delta^{34}S$ of European sea bass *Dicentrarchus labrax* (L. 1758), relative to its diet, was $-0.53‰$. However, other laboratory feeding studies have documented a $\Delta\delta^{34}S$ of 1.4‰ in brook trout *Salvelinus fontinalis* (Mitchill 1814) (Peterson et al., 1985) and 1.5‰ in broad whitefish *Coregonus nasus* (Pallas 1776) (Hesslein et al., 1993). We therefore applied a $\Delta\delta^{34}S$ of 0‰. For all TDFs, a standard deviation of 1 was applied to conservatively account for uncertainty and natural variability in individual TDFs. Mixing models were run with three chains for 1,000,000 iterations, with a burn in of 500,000, and a thinning factor of 500.

2.3.3 | Statistical analyses of dietary overlap

The "SIBER" package in R (Jackson et al., 2011) has been widely used to analyse bivariate stable isotope data. Following extensions

described by Skinner et al. (2019), we used a three-dimensional case to apply ellipsoids to trivariate data and estimate their dietary overlap. Firstly, Bayesian estimates were calculated based on sample means and covariance matrices assuming a three-dimensional multivariate normal distribution (three chains of 15,000 iterations with a burn in of 1000 and thinned by a factor of 25) using the R package "RJAGS" (Plummer, 2018). Secondly, ellipsoid volumes were calculated from each posterior draw, fitted to 75% of the data, providing a posterior distribution of ellipsoid volumes (EV_B). EV_B estimates were determined for each predator and tissue type by bay and expressed as the median volume with interquartile range of the posterior (25%–75%).

To calculate the degree of niche overlap between two ellipsoids, we applied a Bayesian approach based on functions described by Skinner et al. (2019) using R packages "rgl" (Murdoch & Adler, 2022) and "geometry" (Habel et al., 2022). These numerically estimate overlap as the volume of the intersection between three-dimensional meshes that approximate predator niches. Posterior overlaps between the two predators in each bay were calculated from 7500 iterations with a burn in of 5000 and a mesh subdivision value of 4. Overlap was given as a median percentage with 95% credible intervals, where 0% between two ellipsoids indicates completely separate niches and 100% indicates completely overlapping ellipsoids. We considered a median overlap to be significant when two overlapping niches were ≥ 60%, the same criteria applied in Schoener's PS index (Schoener, 1968).

2.3.4 | Statistical analyses of individual specialisation

To allow for direct comparison of levels of individual specialisation between different time frames (liver and muscle), we calculated the E metric for each posterior draw of mixing model outputs using the package "RInSp" (v1.2.5; Zaccarelli et al., 2013). The E_{null} was estimated for each draw by randomly sampling diets from the estimated population mean diet for each prey item. Under the assumption that one feeding event occurs per day and following incorporation rates by Thomas and Crowther (2015), liver and muscle tissues were represented by 40 and 100 feeding events, respectively. A single E_{null} value was calculated per posterior draw, and subtracted from the corresponding E, providing a posterior of E_{adj}. This approach maintains the same uncertainties within each E − E_{null} pairing. All statistical analyses were conducted in R Statistical Software (v4.2.0, R Core Team, 2022, RStudio).

3 | RESULTS

3.1 | Spatial consistency in average diet composition

The stomach content data broadly indicated high spatial consistency in the diets of L. limanda and P. platessa, as revealed by IRI values (Figure 2; Supporting Information Table S3 in Appendix S1). Sandeel (mainly Ammodytes tobianus L. 1758) appeared to be a major food resource for L. limanda across all four bays, particularly in Cambois (86.5% IRI) and Blyth Bays (88.6% IRI) (Figure 2a). Epibenthic invertebrates (crabs, shrimps and ophiuroids) were important to L. limanda in Alnmouth and Druridge Bays, comprising 43.5% and 21.1% IRI of the total diet, respectively. Crabs (mainly Corystes cassivelaunus) and ophiuroids (Ophiura ophiura and Ophiura affinis) were consumed in equal proportions in Alnmouth Bay (17% IRI). Significant differences were detected in the average diet of L. limanda stomachs between the four bays (ANOSIM R = 0.04, P = 0.001). For P. platessa, stomachs were also dominated by sandeel, with their importance varying from 97.7% IRI in Alnmouth Bay to 65% IRI in Druridge Bay (Figure 2b). Here, bivalves (mainly Abra sp. and Ensis ensis) were also of secondary importance to P. platessa diet (27.1% IRI). There were no significant
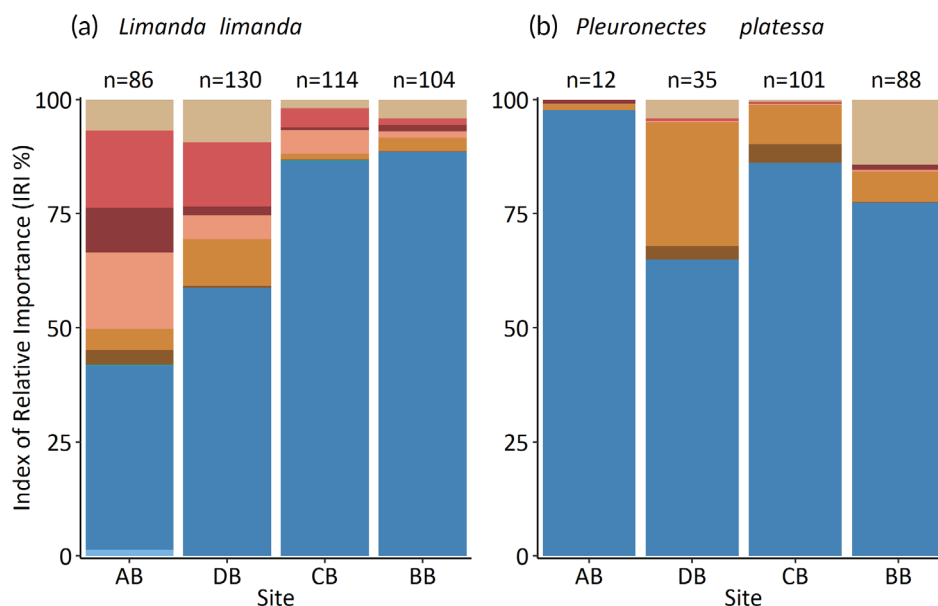
FIGURE 2 Index of relative importance (IRI %) of prey taxa in the diets of (a) Limanda limanda and (b) Pleuronectes platessa based on stomach contents sampled between May and September 2019 (AB, Alnmouth Bay; DB, Druridge Bay; CB, Cambois Bay; BB, Blyth Bay). n refers to the number of full stomachs sampled in each bay. Prey group: ■, Algae; ■, Other invertebrates; ■, Crabs; ■, Shrimps; ■, Ophiuroids; ■, Bivalves; ■, Polychaetes; ■, Squid; ■, Sandeel; ■, Other fish

differences in the average diet of *P. platessa* between the four bays (ANOSIM $R = 0.014$, $P = 0.233$). Other prey groups including polychaetes and squid made only minor contributions to the diet of *L. limanda* and *P. platessa* (Figure 2; Supporting Information Table S3 in Appendix S1).

Compared to the stomach data, there was less spatial consistency in the average diets of *L. limanda* and *P. platessa* based on mean liver isotope values (Table 1). Although *L. limanda* had similar mean $\delta^{15}N$ values across the four bays, $\delta^{13}C$ values were more depleted in ^{13}C in Alnmouth ($-17.54 \pm 0.19‰$) than in Blyth Bay ($-15.95 \pm 0.09‰$). Meanwhile, mean liver $\delta^{13}C$ and $\delta^{15}N$ values of *P. platessa* were relatively consistent between bays, but individuals exhibited higher between-bay variation in $\delta^{34}S$ (Table 1). In Cambois Bay, mean $\delta^{34}S$ liver values for *L. limanda* and *P. platessa* were more depleted in ^{34}S ($17.87 \pm 0.32‰$ and $17.89 \pm 0.19‰$, respectively) compared to the other bays.

Mixing models for *L. limanda* liver indicated that benthic omnivores and bivalves were consistently consumed by individuals across the bays; however, there was substantial inter-bay variability among the other prey groups (Figure 3a). *L. limanda* were highly reliant on ophiuroids in Cambois Bay (32.6%), but they were considerably less important to their diet in the other bays. By comparison, sandeel were predominantly consumed by *L. limanda* in Alnmouth (36.8%), Druridge (38.8%) and Blyth Bays (35.5%) (Figure 3a). Compared to *L. limanda*, *P. platessa* exhibited higher inter-bay variability in diet across all prey groups except for benthic omnivores, which were consistently consumed in small proportions (Figure 3b). Bivalves represented the most important food resource for *P. platessa* in Cambois (42.9%) and Blyth Bays (37.7%), whereas sandeel were primary contributors to their diet in Druridge Bay (34.3%). Like *L. limanda*, *P. platessa* were substantially more reliant on ophiuroids in Cambois Bay (22.2%) compared to the
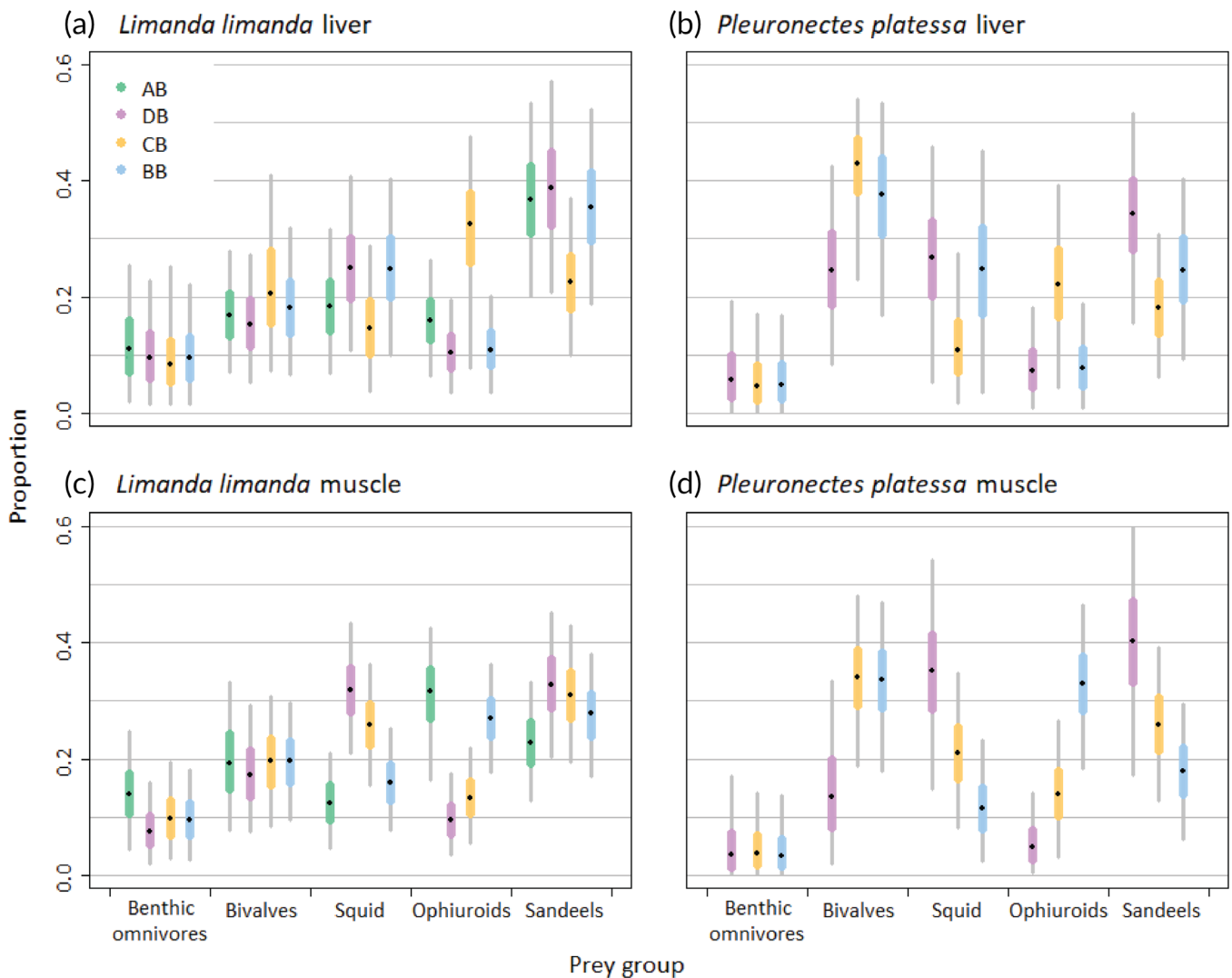
FIGURE 3 Proportional contribution of five prey groups to the diets of *Limanda limanda* and *Pleuronectes platessa* based on liver (a, b) and muscle (c, d) Bayesian mixing model estimates by bay (AB, Alnmouth Bay; DB, Druridge Bay; CB, Cambois Bay; BB, Blyth Bay). Thin grey bars represent 2.5%–97.5% credible intervals, and thick bars represent 25%–75% around the modal contribution of each prey resource. Black dots represent the median (50%). ●, AB; ●, DB; ●, CB; ●, BB

other two bays, where they contributed only 7% to their diet. By comparison, squid were of secondary importance to *P. platessa* diet in Druridge (26.8%) and Blyth Bays (24.7%). Mixing model isospace plots for each predator and tissue type with sources are provided in Supporting Information (Figures S1–S4 in Appendix S1).

Compared to liver tissue, *L. limanda* and *P. platessa* exhibited higher inter-bay consistencies based on mean muscle isotope values (Table 1). However, mean muscle $\delta^{34}S$ values for *L. limanda* and *P. platessa* were more depleted in ^{34}S in Blyth Bay (17.98 ± 0.19‰ and 17.29 ± 0.28‰, respectively) compared to the other bays. Like liver, *L. limanda* muscle mixing models also revealed similar dietary patterns towards benthic omnivores and bivalves (Figure 3c). *L. limanda* exhibited a primary reliance on ophiuroids in Alnmouth Bay (31.6%), whereas sandeel were primary contributors to their diet in Druridge (32.8%), Cambois (31.1%) and Blyth Bays (27.8%). Meanwhile, *P. platessa* muscle mixing model estimates were broadly similar to their liver counterparts (Figure 3d). *P. platessa* continued to exhibit a primary reliance on bivalves in Cambois (34.2%) and Blyth Bays (33.7%), whereas sandeel also dominated their diet in Druridge Bay (40.4%). However, ophiuroids were consumed in almost equal proportions by *P. platessa* in Blyth Bay (33%). Squid were also major prey to *P. platessa* in Druridge Bay (35.3%), but individuals were less reliant on them in Blyth Bay (11.4%).

3.1.1 | Evidence of dietary overlap

Stomach data revealed a generally high degree of dietary overlap between *L. limanda* and *P. platessa* across the bays (PS > 60%) except in Alnmouth Bay, where the two predators exhibited moderate similarity in their resource use (43%) (Table 2). There were no significant differences in diet composition between *L. limanda* and *P. platessa* in Alnmouth (ANOSIM, $R = -0.085$, $P = 0.978$), Druridge (ANOSIM, $R = -0.045$, $P = 0.943$) and Blyth Bays (ANOSIM $R = 0.007$, $P = 0.133$), but there were small yet significant differences in Cambois Bay (ANOSIM $R = 0.02$, $P < 0.05$).

L. limanda liver exhibited greater variance in isotopic space with considerably larger trophic niches than *P. platessa* (see Supporting Information Figure S5 in Appendix S1). There were cases of complete niche separation between the two predators based across all bays, but most notably in Druridge Bay (Supporting Information Figure S5a in Appendix S1). The median niche volumes of *L. limanda* liver were almost three and two times larger than those of *P. platessa* in Druridge (8.2 and 2.8‰^{3}, respectively) and Cambois Bays (20.6 and 12.5‰^{3}, respectively), whereas conspecifics in Blyth Bay had a smaller niche volume compared to that of *P. platessa* (Figure 4a). Unlike the stomach data, there were no cases of significant niche overlap between the two predators based on median volumes of the liver isotopes (Table 3). *L. limanda* liver had a relatively small niche that overlapped with *P. platessa* at Druridge (13%) and Cambois Bays (22%), while *P. platessa* overlapped more with *L. limanda* in these bays.

L. limanda muscle had consistently smaller niches across the bays, whereas *P. platessa* exhibited larger variation in isotopic space (see Supporting Information Figure S6 in Appendix S1). Similarly, the median niche volumes of *P. platessa* muscle were twice as large as the niches of *L. limanda* in Cambois (7.6 and 3.6‰^{3}, respectively) and Blyth Bays (7.3 and 3.8‰^{3}, respectively), but only marginally higher in Druridge Bay (Figure 4b). Unlike liver, *L. limanda* muscle revealed a consistently higher degree of niche overlap with *P. platessa* across the bays, with niches that significantly overlapped in Cambois (76%) and Blyth Bays (61%) (Table 3).

3.1.2 | Evidence of individual specialisation

L. limanda and *P. platessa* exhibited consistently low levels of individual specialisation across the bays based on the stomach content data, as expressed by low E_{adj} values (Table 2). However, these low E_{adj} values of individual specialisation were generally significant, particularly when a higher proportion of stomachs contained only one prey item (Table 2). Similar to the stomach data, consistently low levels of specialisation were also detected from liver isotope mixing model outputs for *L. limanda* and *P. platessa*, as provided by the posterior of E_{adj} (Table 4). However, liver E_{adj} posterior values indicated that *L. limanda* expressed slightly more individual specialisation compared to *P. platessa* across the bays. This was mirrored in the liver mixing model

TABLE 2 Dietary overlap (PS) and individual specialisation (E_{adj}) metrics based on *Limanda limanda* and *Pleuronectes platessa* stomach contents data collected between May and September 2019

	Limanda limanda			Pleuronectes platessa			
Location	Non-empty stomachs	E_{adj}	Stomachs with only one prey item	Non-empty stomachs	E_{adj}	Stomachs with only one prey item	PS
Alnmouth Bay	86	0.154*	56	12	0.022	9	0.43
Druridge Bay	130	0.283***	75	35	0.3***	18	0.74
Cambois Bay	114	0.249***	70	101	0.218***	58	0.89
Blyth Bay	104	0.196***	74	88	0.29***	62	0.86

Note: E_{adj} is the pair-wise individual dietary overlap adjusted based on the mean null value of Monte-Carlo resampling methods. PS represents Schoener's Index of similarity between the two predator species in each bay.
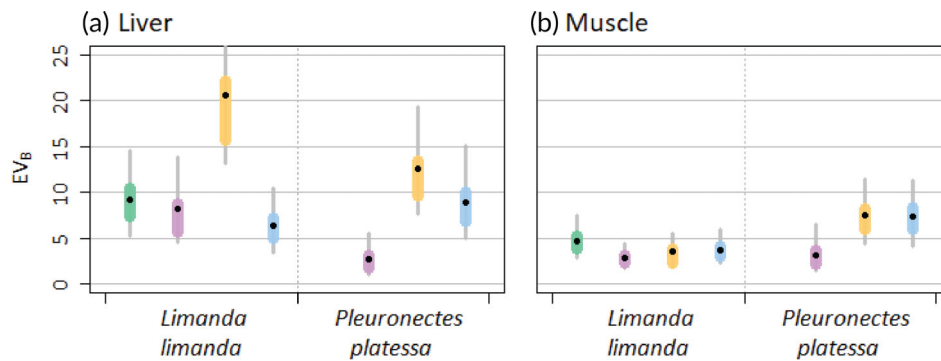
*$P < 0.05$; ***$P < 0.001$.

FIGURE 4 Bayesian 75% ellipsoid volume (EV_b) estimates based on (a) liver and (b) muscle isotope data for *Limanda limanda* and *Pleuronectes platessa* in each bay (AB, Alnmouth Bay; DB, Druridge Bay; CB, Cambois Bay; BB, Blyth Bay), presented as the median with interquartile range (IQR, 25th and 75th percentiles). Thin grey bars represent 95% C.I. ●, AB; ●, DB; ●, CB; ●, BB

TABLE 3 Median percentage dietary overlap between *Limanda limanda* and *Pleuronectes platessa* based on Bayesian 75% ellipsoid volumes (δ^{13}C, δ^{15}N and δ^{34}S values) with 95% credible intervals (showing the uncertainty in dietary overlap for each bay)

	Liver		Muscle	
Location	*Limanda limanda*	*Pleuronectes platessa*	*Limanda limanda*	*Pleuronectes platessa*
Druridge Bay	13 (0–27)	39 (1–77)	51 (26–78)	46 (15–66)
Cambois Bay	22 (1–40)	36 (17–59)	**76 (54–100)**	36 (21–55)
Blyth Bay	38 (18–66)	28 (11–50)	**61 (36–88)**	32 (16–51)

Note: Significant overlap (≥60%) is highlighted in bold. The table should be read as, for example, in Blyth Bay, 61% of the *L. limanda* muscle ellipsoid overlapped with the *P. platessa* muscle ellipsoid, and 32% of the *P. platessa* ellipsoid overlapped with *L. limanda* ellipsoid.

	Limanda limanda		*Pleuronectes platessa*	
Location	Liver	Muscle	Liver	Muscle
Alnmouth Bay	0.11 (<0.01–0.19)	0.03 (<0.01–0.08)	–	–
Druridge Bay	0.11 (<0.01–0.18)	0.03 (<0.01–0.08)	0.04 (<0.01–0.12)	0.06 (<0.01–0.15)
Cambois Bay	0.12 (<0.01–0.20)	0.03 (<0.01–0.08)	0.04 (<0.01–0.13)	0.06 (<0.01–0.16)
Blyth Bay	0.11 (<0.01–0.19)	0.03 (<0.01–0.08)	0.04 (<0.01–0.12)	0.06 (<0.01–0.16)

TABLE 4 Median and 95% credible intervals in parentheses of the posterior of E_{adj} calculated from liver and muscle stable isotope mixing model outputs for *Limanda limanda* and *Pleuronectes platessa*

TABLE 5 Temporal overview for each trophic index for *Limanda limanda* and *Pleuronectes platessa*

Trophic index	Predator	Short-term diet (stomach contents)	Medium-term diet (liver stable isotopes)	Longer-term diet (muscle stable isotopes)
Average diet composition (index of relative importance, IRI, and isotope mixing models)	*Limanda limanda*	Diet dominated by sandeel, with a reliance on epibenthic invertebrates	Reliance on sandeel and ophiuroids	Reliance on sandeel and ophiuroids
	Pleuronectes platessa	Diet dominated by sandeel, with a reliance on bivalves	Reliance on bivalves and sandeel	Reliance on bivalves, sandeel and ophiuroids
Individual specialisation (E_{adj})	*Limanda limanda*	Low	Low	Low
	Pleuronectes platessa	Low	Low	Low
Diet overlap (*PS* and Bayesian 75% ellipsoid volumes)		High	Low	Moderate

Note: *Lightest shading*, high spatial consistencies in diet; *mid-grey shading*, moderate inter-bay diet variation; *darkest shading*, high inter-bay diet variation. Prey groups represent at least one primary resource in any one bay.

average standard deviation of individual random effects, which was larger for *L. limanda* (0.24 S.D.) than *P. platessa* (0.11 S.D.). For muscle tissue, *L. limanda* and *P. platessa* E_{adj} posterior values were also low (Table 4), as reflected by minimal amounts of variation in interindividual random effects of diet (0.07 S.D. for *L. limanda* and 0.15 S.D. for *P. platessa*). This contrasts with the inter-bay diet variability observed

for conspecifics of *L. limanda* and *P. platessa* from both liver and muscle mixing model outputs (Figure 3), where the smallest average standard deviation was 0.55 (S.D.) for *L. limanda* liver and largest was 0.99 (S.D.) for *P. platessa* muscle.

4 | DISCUSSION

To the best of our knowledge, this is the first study to quantify dietary consistencies in two sympatric flatfish predators using a multi-tracer approach integrated over three dietary timeframes (*i.e.*, hours, days, months) across multiple coastal bays (tens of kilometres). Results from stomach contents and stable isotope analyses verified our hypotheses that *L. limanda* and *P. platessa* varied their average diet spatially over the three time frames, while they exhibited varying degrees of niche overlap (see Table 5). We can reject the third hypothesis because conspecifics of both predators exhibited consistently low levels of individual specialisation in time and space.

4.1 | Spatio-temporal consistency in average diet

Stomach content data revealed consistent foraging on sandeel by *L. limanda* and *P. platessa* in the short term, which were consumed in generally high proportions across the four bays. However, *L. limanda* exhibited significant spatial differences in diet as more epibenthic invertebrates (notably crabs and ophiuroids) were consumed in the most northerly bays, Alnmouth and Druridge Bays. By comparison, *P. platessa* had a less diverse diet and consistently selected more infaunal prey items (mainly bivalves) across the bays. These findings likely reflect a dietary response to changes in local prey availability, as previously observed in *L. limanda* and *P. platessa* (*e.g.*, Duineveld & Van Noort, 1986; Hinz *et al.*, 2005). Liver isotope mixing models broadly agree with the stomach data as *L. limanda* continued to exhibit a strong reliance on sandeel, and *P. platessa* to a lesser extent, across the bays in the medium term, which was expected because liver isotopes tend to represent flatfish diet over 1–3 weeks (Buchheister & Latour, 2010; Gaston & Suthers, 2004). These results coincide with peak abundances of sandeel in the summer when individuals tend to aggregate in dense schools at benthic resting sites (Engelhard *et al.*, 2008; Reay, 1970). Sandeel are lipid-rich and provide sufficient metabolised energy for maintenance (Pinnegar *et al.*, 2003), which suggest that both predators may take advantage of the high nutritional value of sandeel to satisfy their energy requirements.

Liver mixing models point to both predators exhibiting between-bay variation in their resource use, providing evidence for resource partitioning as individuals consumed patchily distributed prey. *P. platessa* exhibited an increased reliance on bivalves, particularly in Cambois and Blyth Bays, which corresponds with when they become abundant in high densities during the summer (Basimi & Grove, 1985; Rijnsdorp & Vingerhoed, 2001; Tulp *et al.*, 2010). *P. platessa* is better known as a benthivorous species that predominantly targets infaunal prey, including polychaetes and bivalves (*e.g.*, Rijnsdorp &

Vingerhoed, 2001) rather than as a sandeel predator (Engelhard *et al.*, 2013). On the Dogger Bank, Pinnegar *et al.*, (2006) showed that adult *P. platessa* consume more sandeel when this resource becomes readily available in spring, but preferentially select bivalves when sandeel are less abundant in another areas (separated by less than 28 km) during the same period (Pinnegar *et al.*, 2006). *L. limanda* and *P. platessa* are therefore likely to benefit from more lucrative prey when and where they become locally available without being wholly reliant on them (Engelhard *et al.*, 2013; Reay, 1970).

Sandeel tend to bury themselves in the sediment between September and March (Holland *et al.*, 2005; Winslade, 1974), when they are less accessible to predators. Given that muscle isotope values in this study likely reflect diets as far back as late winter and/or early spring, it is perhaps surprising that *L. limanda* and *P. platessa* continued to be consistently reliant on sandeel. Meanwhile, ophiuroids were of major importance to *L. limanda* in Alnmouth and Blyth Bays but were far less important in the other bays. Ophiuroids have been commonly observed in *L. limanda* stomachs on the Dogger Bank (Knust, 1996) and central North Sea (Duineveld & Van Noort, 1986). Off the Dutch coast, Hinz *et al.* (2005) showed that *O. albida* form a prominent part of *L. limanda* diet in winter while other prey taxa are less important. In this study, it is likely that *L. limanda* consumed more ophiuroids to derive a higher rate of food intake with minimal effort despite their low nutritional value (Hinz *et al.*, 2005).

The high degree of between-bay diet variation exhibited by *P. platessa*, as revealed by muscle isotope mixing models, may be explained by the magnitude of their annual migration patterns. Although juvenile flatfishes tend to exhibit strong site fidelity (Burrows *et al.*, 2004), sub-adult and adult populations often have lower habitat specificity as they forage over much broader areas (Gibson *et al.*, 2005). *P. platessa* migrate over large distances between summer feeding and winter spawning grounds in the North Sea (Hunter *et al.*, 2003; Hunter *et al.*, 2004a; Van Keeken *et al.*, 2007), and we may expect their "average" diet to be broadly similar across their range as individuals are not constrained by local prey resources. Given their known dispersive activities and large-scale migration patterns, it is perhaps surprising that localised differences were detected in the longer-term diet of *P. platessa* at small-spatial scales. However, some individuals have been found to exclusively forage and spawn in the same region (*e.g.*, German Bight; Hunter, Metcalfe, O'Brien, *et al.*, 2004), and hence high between-bay variability in *P. platessa* diet likely reflects local patterns of prey availability. Although limited tagging studies also suggest that *L. limanda* move over considerable distances (DeClerck, 1984; Rijnsdorp *et al.*, 1992), individuals are thought to remain in localised areas for longer periods (Saborowski & Buchholz, 1997).

Prey isotope data incorporated into mixing models were mostly derived from intact stomach contents (complemented by grab samples). This may not necessarily reflect bay-specific signatures if predator mobility is high within and among populations. However, spatial differences in resource use observed here will reflect patchily distributed prey as the two predators move across different habitats, but also over time as individuals switch feeding strategies on a seasonal basis (Schoener, 1974). Interestingly, liver and muscle mixing models

showed no mismatch in the proportion of bivalves consumed by *P. platessa* across the bays, which suggests that individuals consistently foraged on this prey type over time. This contrasts with other studies that document seasonal diet shifts in large *P. platessa* in coastal areas, where polychaetes dominate their diet in winter and bivalves in the summer (Basimi & Grove, 1985; Pinnegar *et al.*, 2006; Todd, 1915). Polychaetes comprised a minor component of *P. platessa* diet in this study, but their isotope values were indistinct from those of other prey groups (*i.e.*, crabs and shrimps), which may have limited the ability of the mixing models to differentiate between certain prey types. Further, both liver and dorsal muscle mixing models indicated that squid were major contributors to predator diet across bays, despite their rare occurrence in stomachs and low sample sizes used in isotope analyses. Although the use of three isotopes ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) rather than two ($\delta^{13}C$ and $\delta^{15}N$) allows for much better "triangulation" of diet composition proportions (Phillips *et al.*, 2005), it is possible that undefined prey types with similar signatures to squid influenced predator isotope values in the mixing models. Alternatively, these data could be a genuine reflection of their importance as a key prey resource. Squid (especially *Loligo* sp.) have increased significantly in the North Sea in recent years (van der Kooij *et al.*, 2016), yet they tend to be more readily available in summer and autumn (Bellido-Millan *et al.*, 2001; Pierce & Boyle, 2003). Moreover, prey items with larger body masses such as squid may also reflect their importance as a dominant resource in terms of biomass in contrast to smaller but more numerous prey groups (Jennings *et al.*, 2002).

The initial liver mixing model for *L. limanda* did not converge using all three isotopes due to the large spread in $\delta^{13}C$ values relative to their prey. Faster turnover tissues with high lipid content such as liver can be inherently more variable than muscle following mathematical correction (Pinnegar & Polunin, 1999), and tend to be more reactive to differences in isotopic enrichment through several physiological and metabolic processes (Skinner *et al.*, 2016; Sweeting *et al.*, 2005). The large variability in *L. limanda* $\delta^{13}C$ liver values may therefore reflect the mobilisation of liver lipids synthesised during bouts of spawning (Gallagher *et al.*, 1991; Saborowski & Buchholz, 1997).

Isotope mixing models are sensitive to variation in trophic discrimination factors, which can impact model outputs and estimates of prey contributions (Bond & Diamond, 2011; Wilson *et al.*, 2009). In fish, the lack of difference in $\delta^{34}S$ between prey and consumer (0–1‰, Barnes & Jennings, 2007; Peterson & Fry, 1987) can greatly reduce the variance of estimated contributions of prey sources in mixing models (*e.g.*, Parnell *et al.*, 2010). There are few published studies on $\Delta\delta^{34}S$ compared to $\delta^{13}C$ and $\delta^{15}N$ (Barnes & Jennings, 2007; Connolly *et al.*, 2004), despite its value as a third tracer in discriminating between primary production in coupled benthic-pelagic systems where rates of sulphate reduction greatly differ (Duffill Telsnig *et al.*, 2019), as is the case for seawater and benthic sediments (Michener & Lajtha, 2007). Interestingly, high pelagic $\delta^{34}S$ values (>21.5‰) predicted for the western North Sea (Glew *et al.*, 2019) could help explain the relatively high $\delta^{34}S$ predator and prey values in this study compared with areas of higher freshwater influence or sedimentary mixing (*e.g.*, lower $\delta^{34}S$ in coastal and estuarine fishes in the

Thames estuary and adjacent areas; Leakey *et al.*, 2008). Additionally, the substantially larger muscle $\delta^{34}S$ ranges (3.01–6.09‰) compared to those of $\delta^{13}C$ and $\delta^{15}N$ in both predators could have facilitated better discrimination in the mixing models (Barnes & Jennings, 2007).

4.2 | Dietary overlap

Stomach content data revealed significant niche overlap between *L. limanda* and *P. platessa* except in Alnmouth Bay, which can be attributed to the consumption of the same dominant prey type (sandeel). Because both predators exhibit foraging plasticity at the population level (Hinz *et al.*, 2005; Pinnegar *et al.*, 2006), they can readily overlap their diet with relatively limited competitive hindrance, particularly when food sources like sandeel tend to be periodically overabundant (Engelhard *et al.*, 2008). Although this may have reduced the potential for interspecific competition, overlapping niches do not necessarily increase competition for resources (Cabral *et al.*, 2002; Layman *et al.*, 2012). By comparison, the degree of niche overlap was low to moderate based on liver and muscle isotope data; significant overlap occurred only in Cambois and Blyth Bays. This implies that the level of competition between the two predators is low as individuals consume a diverse prey spectrum across space and over time (Papastamatiou *et al.*, 2006; Russo *et al.*, 2008). However, the potential for interspecific competition between the two predators will increase if resource distributions are heterogeneous in space and time (Ward *et al.*, 2006). Alternatively, individuals that forage on ecologically different prey may also display similar isotope values due to their incorporation into tissue over time (Skinner *et al.*, 2019), potentially blurring the degree of competition that exists between the two predators.

The degree of dietary overlap between the two predators based on liver isotope values was generally low across the bays, with cases of complete niche separation in Druridge and Cambois Bays. The larger isotopic niches and median ellipsoid volumes suggest that *L. limanda* may have diversified their diet to incorporate underutilised prey types to reduce inter-competition (Bolnick *et al.*, 2003). This is also supported by the stomach data as *L. limanda* consumed a more diverse suite of prey taxa than *P. platessa*. However, larger isotopic niches observed in *L. limanda* liver could also be attributed to overdispersed $\delta^{13}C$ liver values, which are likely driven by metabolic processes relative to periods of spawning. Conversely, the smaller, longer-term median niche volumes and niches of *L. limanda* muscle tissue suggest that individuals were consistently consuming a similar but narrower group of resources across the bays.

4.3 | Individual specialisation

Low but significant levels of individual specialisation were detected for both *L. limanda* and *P. platessa* across the bays based on their stomach contents. Significance levels of this were likely inflated by the large proportion of stomachs containing a single prey item (see

Table 2), and likely overestimated due to the stochastic effects of patchily distributed prey (Araújo et al., 2008). Similarly low but non-significant levels of specialisation were found in estuarine D. labrax, using the E_{adj} metric, whereas only higher levels during the autumn and winter were matched with statistical significance (e.g., values approaching 0.6; Cobain et al., 2019). If a population's localised environment contains abundant easy-capture prey taxa (e.g., sandeel), then conspecifics can readily consume a large proportion of this resource if handling times are short and attack success rates are high (Rosenblatt et al., 2015). Such behaviour would cause each individual to display consistent feeding patterns to conspecifics, resulting in low individual specialisation.

E_{adj} posterior values based on liver and muscle isotope mixing models also yielded consistently low levels of local-scale individual specialisation at medium and long-term time scales. These findings were perhaps surprising as conspecifics of both predators exhibited some degree of inter-bay diet variability. Possible reductions in average prey diversity over time may have caused individuals to forage on a few, energetically favourable prey types in these dietary timeframes within individual bays (Bearhop et al., 2004). As such, there is less scope for either chance (e.g., patchily distributed prey) or specialisation (Bolnick et al., 2003) within populations that target different subsets of available prey taxa, thereby reducing the level of intraspecific diet variation.

5 | CONCLUSIONS

Flatfish predators are often considered to be dietary generalists, but we provide evidence of resource partitioning with varying levels of niche overlap over time at a small spatial scale. Stomach content data showed spatial consistencies in the average resource use of L. limanda and P. platessa and high dietary overlap, largely reflected by their short-term reliance on sandeel. However, liver and muscle stable isotope analyses revealed considerable inter-bay variability in their diet, demonstrating how both predators can readily switch feeding strategies in response to changes in local prey availability, whether this be on a seasonal, spatial and/or inter-annual basis. This study provides new data on the feeding strategies of ecologically similar flatfishes, emphasising the need for a more integrative approach for assessing spatial and temporal heterogeneity of consumed prey in coastal environments. Detailed information at this level is required to fully disentangle complex trophic interactions in these highly dynamic regions.

AUTHOR CONTRIBUTIONS

G.L.H., M.R.D.C., J.K.P., G.H.E., B.D.W. and N.V.C.P. conceptualised the study, G.L.H. collected the data, G.L.H. and R.A.R.M. processed the samples, G.H. and M.R.D.C. analysed the data, G.H. led the writing of the manuscript and all co-authors contributed to revisions.

ORCID

Georgina L. Hunt https://orcid.org/0000-0002-0127-0817
Matthew R. D. Cobain https://orcid.org/0000-0003-1701-3986
Rona A. R. McGill https://orcid.org/0000-0003-0400-7288
John K. Pinnegar https://orcid.org/0000-0001-5061-9520
Georg H. Engelhard https://orcid.org/0000-0002-7821-7029
Benjamin D. Wigham https://orcid.org/0000-0001-8408-5600
Nicholas V. C. Polunin https://orcid.org/0000-0002-1480-8794

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