# Low trophic redundancy among temperate wrasse species implies ecosystem risks associated with a multi-species inshore fishery

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Abstract

Understanding levels of resource-use overlap or trophic redundancy both within and between species can help predict ecosystem-level impacts of fishery removals, and ultimately help define management priorities to preserve ecosystem function. Here, we use stable isotope analysis to investigate inter- and intra-specific variation and overlap in resource use among co-occurring temperate wrasse (Labridae) species. We use the results as a first step to predicting the potential for ecosystem-level impacts of the recently developed multi-species inshore fisheries for live wrasse on the south coast of England and west coast of Scotland. We highlight the likely importance of the primary target species (ballan wrasse), particularly individuals of a landable size, to maintaining the overall function of inshore reef ecosystems, evidenced by the unreciprocated resource use overlap that this species provides for other wrasse species. We also highlight that trophic redundancy is typically low both between and within wrasse species, suggesting the maintenance of both species diversity and demographic structure of wrasse populations should be a priority when developing fishery management measures. Live wrasse fisheries operate within various Marine Protected Areas (MPAs) across the south coast of England and in Scotland. An overarching aim of ecosystem-based fisheries management, particularly within MPAs, is to support diversity and redundancy within an ecosystem to help maintain resilience to future perturbations. Our study provides some of the first quantitative evidence to support the classification of wrasses (particularly ballan and corkwing) as influential species, defined as having a key role affecting the structure and function of the habitat, within MPAs designated for reef habitats.

**Keywords:** stable isotopes, trophic redundancy, live wrasse fisheries, niche overlap

## Introduction

In the marine environment, ecosystem-wide ecological impacts of anthropogenic disturbances such as fisheries are difficult to quantify as, often, relationships between fishing and impacts cannot be formally established. Furthermore, many inshore fisheries target multiple species simultaneously, which can exacerbate the complexity of predicting impacts. Nevertheless, predicting community-level consequences of anthropogenic perturbations such as fishing has never been more important. This is particularly the case given the recent shift towards an ecosystem-based approach to the management of fisheries and protected areas (Pikitch et al. 2004, Defra 2018, 2023, Fisheries Act 2020), which is being undertaken against a background of improving efficiency of fishing gears, rapid developments in technology, and intensification of other exogenous pressures on marine ecosystems such as climate change.

Predicting ecosystem-level responses to anthropogenic disturbance requires an understanding of factors that contribute to population regulation, such as competition, predation, recruitment and environmental variation. Trophic interactions between co-occurring species are particularly important to consider as the stability of ecosystems can often depend on the preservation of food-web structure (de Ruiter et al. 1995, Thompson et al. 2012). Trophic redundancy, whereby species have similar trophic interactions, occupy comparable trophic niches, and perform similar functional roles, is one means by which food-web structure, and hence ecosystem function, can be maintained (Walker 1992). Ecosystems with higher redundancy are less likely to undergo significant changes to overall functionality in the event of species declines resulting from anthropogenic disturbance, as connectivity within and across trophic levels will be maintained (Walker 1992, Naeem 1998, Thompson et al. 2012).

Trophic interactions and resource use can be investigated using stable isotope analysis of animal tissues (Bearhop et al. 2004, Layman et al. 2012, McCue et al. 2020). Ratios of carbon isotopes (expressed as δ13C values) and sulfur isotopes (expressed as δ34S values) vary considerably among primary producers due to differences in photosynthetic carbon fixation and sulfate sources between producers, but change relatively little with progression through a food web, so can be used to determine original sources of dietary carbon (DeNiro & Epstein 1978, Post 2002, Inger & Bearhop 2008), identify benthic versus pelagic source pools (Peterson & Howarth 1987, Currin et al. 1995), distinguish nearshore versus offshore environments (Barros et al. 2010), or differentiate marine and fresh water (or terrestrial) sources (Jones et al. 2010). Meanwhile, the ratio of nitrogen isotopes (expressed as δ15N values) exhibits stepwise enrichment with trophic transfers, so is a powerful tool for estimating relative trophic position of organisms (DeNiro & Epstein 1981, Minagawa & Wada 1984, Post 2002). The combination of the three isotope values can be used to describe fields in geometric isotopic space, often referred to as its isotopic niche, which can be used as a proxy for a subset of a species’ or group’s ecological niche (Newsome et al. 2007). The degree of overlap of the isotopic niches of co-occurring species can then be used to infer the potential for trophic overlap and functional redundancy in food webs (e.g. Matich et al. 2017).

In recent years, interest has escalated in using temperate wrasse species as part of parasitic louse control strategies in salmonid aquaculture (Bjordal 1991, Gonzalez & de Boer 2017). The continued rapid expansion of the salmon aquaculture industry, and resultant high demand for cleaner fish, has led to large numbers of wrasse being removed from the coastlines of the United Kingdom, Norway, and Ireland. Each year, several million wrasse are used for this purpose in Norway alone (Skiftesvik et al. 2014a) and tens of thousands of wrasse are caught from small geographic ranges on the south coast of England for live transfer to Scottish salmon farms (Henly et al. 2021), with no such estimate for the scale of the Scottish fishery (Riley et al., 2017). Despite the benefits of using wrasse for parasite treatment in the aquaculture sector (relative to e.g. chemical or pharmaceutical control) (Bjordal 1988, Skiftesvik et al. 2013), the ongoing removal of large numbers of fish from wild populations poses questions concerning the sustainability and potential impacts of such exploitation on wild stocks and the functioning of the inshore reef ecosystems they inhabit (Henly et al. 2021). Understanding the relative ecological roles and resulting potential for direct and indirect impacts of wrasse removal has been identified as a research priority to allow for the development of effective management of these fisheries (Henly et al. 2021). Of particular relevance, the Fisheries Act 2020 requires development of a Wrasses Complex Fisheries Management Plan (FMP), due to be prepared by UK Department for Environment Food and Rural Affairs (Defra) over 2023–2025.

Previous studies have highlighted typical prey groups for temperate wrasse species, but at relatively low taxonomic resolution (Dipper et al. 1977, Sayer et al. 1995, Deady & Fives 1995b a, Figueiredo et al. 2005, Matić-Skoko et al. 2013). In many cases, the apparent mesopredatory status of wrasse has led to predictions that the overexploitation of one or more of the target species could have indirect effects on other groups within the ecosystem, which ultimately could lead to trophic cascades and a shift in ecosystem function (Figueiredo et al., 2005; Norderhaug et al., 2005). Wrasse are also facultative cleaners in the wild: their nutrition is partially made up by interactions that remove ectoparasites from other species (Potts 1973, Hilldén 1983, Henriques & Almada 1997). A substantial removal of these cleaners could therefore have considerable implications for the parasite load and resultant health of client species and hence lead to knock on impacts for inshore reef ecosystems (Vaughan et al. 2017). However, the level of interspecific trophic redundancy of wrasse has not been studied, so the overall risk level of ecosystem‑wide impacts of wrasse removal is unclear.

In practice, live wrasse fisheries are highly size selective, often with minimum and maximum conservation reference sizes in place for each species set by relevant management authorities (for example, Marine Scotland in Scotland, or the Inshore Fisheries and Conservation Authorities (IFCAs) in England). Intraspecific, ontogenetic trophic niche shifts could therefore increase the risk of ecosystem-level impacts if the retainable portion of the catch represent a distinct trophic niche and were to be overexploited. Identifying levels of functional/trophic redundancy, both between and within wrasse species, will assist the prediction of potential ecosystem impacts of wrasse fisheries, focus conservation efforts and management measures, and determine species conservation priorities.

Here, we define three-dimensional isotopic niches of wrasse species from two key fishery locations in the UK and use these to (i) characterise the relative isotopic niche area and core isotopic niche overlap of six temperate wrasse species, (ii) determine whether these vary between and within species across different locations, (iii) examine relative changes in wrasse isotopic composition by size (as a proxy for ontogenetic changes in diet), and (iv) use these results as a first step to predicting the potential for ecosystem-level impacts of the live wrasse fishery.

## Methods

### Study site and sample collection

Sample collection was conducted in mid-September and mid-October 2019 in two locations. The first on the fishing grounds between Portland and Ringstead in Dorset, England (hereafter “Dorset”) and the second on the fishing grounds between Elgol and Soay on the Isle of Skye, Scotland (hereafter “Isle of Skye”) (Figure S1). Samples of six wrasse species, namely ballan (*Labrus bergylta*), corkwing (*Symphodus melops*), cuckoo (*Labrus mixtus*), goldsinny (*Ctenolabrus rupestris*), rock cook (*Centrolabrus exoletus*) and Baillon’s (*Symphodus bailloni)*, were collected from Dorset, and five species (all except Baillon’s, which is not commonly found in such northerly latitudes) collected from the Isle of Skye (Table 1). These sampling locations were chosen so that the samples could be collected opportunistically on board commercial fishing vessels in locations frequently targeted by wrasse fishermen. Wrasse were caught using either rod-and-line or in pots over the course of one day (Isle of Skye) or three days (Dorset). Permission from the relevant management authorities was obtained to collect samples above and below the voluntary minimum and maximum conservation reference sizes (CRS). For each individual the total length (cm) was recorded and the fish killed using an approved Schedule 1 method in compliance with UK Home Office Scientific Procedures (Animals) Act Requirements and the University of Exeter’s Ethics Policy.

Whole fish were placed onto ice as soon as possible following termination and transferred to a -20°C freezer at the earliest opportunity. A sample of dorsal white muscle tissue (~1 cm3) was removed and freeze dried at -57°C overnight, and then ground to a fine homogenous powder using a pestle and mortar. Subsamples of 0.8–1.2 mg of tissue were weighed into 6 x 4 mm tin capsules and successively analysed for δ15N, δ13C, and δ34S using a Thermo Fisher Scientific Isolink elemental analyser interfaced with a Delta V Plus isotope ratio mass spectrometer, at the Natural Environmental Isotope Facility (NEIF) Stable Isotope Ecology Laboratory (SIEL) at the Scottish Universities Environmental Research Centre (SUERC) between October 2022 and January 2023. This system has been optimised by the SIEL for sulphur isotope analysis, since most samples have low sulphur concentrations. Stable isotope ratios are reported using the delta (δ) notation (McKinney et al. 1950).

International and internal reference materials were placed at the start of each N/C/S run (~90–100 samples per run). International reference materials were USGS88, USGS43, USGS91, and USGS42 (RSIL 2019, 2020b a). In addition, two internal standards: WMK (powdered wild mandrill keratin from Lope National Park, Gabon) and ALAGEL (alanine spiked with 13C and mixed with gelatin). All of these reference materials were used to anchor all data to the atmospheric nitrogen (AIR), Vienna Pee Dee Belemnite (V-PDB) and Vienna Canyon Diablo Troilite (V-CDT) scales. Further, Internal reference materials CNS1.1, CNS 2.1 and CNS3.1 were placed every 8–10 samples to correct for instrumental drift, and differently sized aliquots of CNS1.1 used to characterise and correct any linearity effects (Werner & Brand 2001) (Table S1).

High lipid content in fish muscle tissue can skew carbon isotope data interpretations as lipids are depleted in 13C relative to proteins (Focken & Becker, 1998). Carbon stable isotope data were therefore lipid corrected arithmetically using the lipid normalising model reported in Kiljunen *et al*. (2006).

### Data analysis

All analyses were carried out in R statistical software version 4.2. or later (R Core Team 2022).

Multivariate normality of the stable isotope data was checked using a combination of Henze-Zirkler’s test (Henze & Zirkler 1990) and visual assessments of multivariate QQ plots in the ‘MVN’ R package (Korkmaz et al. 2014). All species in each area conformed to multivariate normality except goldsinny and rock cook in the Isle of Sky and ballan and corkwing in Dorset. For rock cook and goldsinny in the Isle of Skye and corkwing in Dorset, these non-normal results were each driven by one individual, with a higher δ15N values, lower δ34S values, and higher δ34S value, respectively. For ballan wrasse in Dorset, univariate normality tests showed that both δ15N and δ34S data were normally distributed, but δ13C data were left-skewed (a tail towards more negative values). As the multivariate Chi-Square QQ-plot for this species had no major deviations from normality and the individuals driving the non-normality for other species represent individuals with differing resource uses (Jackson et al. 2011), data were considered well-described by the multivariate normal distribution for all further analysis.

Summary information for the isotope data (mean, standard error and range of δ13C, δ15N, and δ34S values) were calculated for each species in each location, and for subsets within each group that reflect individuals within and outside of minimum and maximum size limits (i.e. those that would have been ‘landed’ and ‘returned’ during routine fishing, respectively) currently imposed by the respective management authorities in Dorset and the Isle of Skye. In Dorset, the size limits are set out in Southern IFCA’s Minimum Conservation Reference Size Byelaw (SIFCA 2021a) and Wrasse Code of Practice (for maximum sizes; SIFCA 2021b): ballan, 18–28 cm; corkwing, 14–22 cm; goldsinny and rock cook, 12–18 cm; cuckoo, prohibited to land; and Baillon’s is not mentioned so assumed to be returned. In the Isle of Skye, the size limits are set out in Marine Scotland’s Licence Conditions for the Harvesting of Wild Wrasse (Marine Scotland 2022): ballan and cuckoo, 12–24 cm; goldsinny, corkwing, and rock cook, 12–17 cm.

Following the methods laid out in Skinner *et al.* (2019), for each species in each location, Bayesian estimates of the covariance and means of the data were calculated (15,000 iterations with a burn‐in of 10,000 and a thinning factor of 25). Bayesian tri-variate ellipsoids (EVB), were fitted to 75% of the data and used as a proxy for niche volume, and their median volume and interquartile range (25%–75%) were determined. The degree of ellipsoid overlap between species within each area was calculated by approximating each ellipsoid as a three-dimensional mesh using the R package ‘rgl’ (Murdoch *et al.* 2023), and defining the intersection of these meshes as a convex hull using the R package ‘geometry’ (Roussel *et al.* 2023). Overlap was calculated based on EVB where Bayesian posteriors were determined from 7,500 iterations with a burn‐in of 5,000 and a subdivision value of 4. Overlap was expressed as a median percentage with 95% credible intervals where 100% overlap indicates completely overlapping ellipsoids and 0% indicates entirely distinct ellipsoids. When the overlap between two species was ≥60%, niche overlap was considered significant (Schoener 1968, Matley et al. 2017, Skinner et al. 2019, Cybulski et al. 2022). Bayesian ellipsoids were also generated for the data subsets described above (landed/returned) and their volume and overlap calculated.

We tested for any effects of body size on trophic interactions using linear models (LMs). The δ13C, δ15N, or δ34S values were the response variables, with location (Dorset/Isle of Skye) and total length (cm) (and their interaction) as putative predictors. As Baillon’s wrasse were only present in Dorset only length was included as a putative predictor. Model diagnostics were checked based on simulated residuals using the R package ‘DHARMa’ (Hartig 2020). Details of model selection are outlined in Supplement 1).

## Results

### Interspecific variation

There were differences in the isotope values among the wrasse species sampled in both areas (Table 1, Figure 1). In Dorset, individual δ13C values ranged from −21.6‰ (ballan) to −15.8‰ (corkwing), δ15N values ranged from 12.08‰ (rock cook) to 16.30 (ballan), and δ34S values ranged from 15.40‰ (corkwing) to 20.65‰ (corkwing). In the Isle of Skye, δ13C values ranged from −19.2‰ (ballan) to −14.9‰ (ballan), δ15N values ranged from 12.22‰ (rock cook) to 15.93‰ (cuckoo), and δ34S values ranged from 14.21‰ (cuckoo) to 20.72‰ (ballan).

In Dorset the isotopic niche volume of corkwing wrasse was the largest (14.46 ‰3) – over twice the volume of all other species except ballan wrasse (9.27 ‰3), which had the second largest niche volume – whereas in the Isle of Skye, the isotopic niche volume of ballan wrasse was the largest (15.51 ‰3) and over three times the size of all other wrasse species (Table 2). All other species had median niche volumes that were of a similar size; between 2.74 – 4.07 ‰3 in the Isle of Skye, and 2.88–5.88 ‰3 in Dorset (Table 2).

There was limited evidence of significant niche overlap among wrasse species in either Dorset or the Isle of Skye (Figure 2–3). In Dorset, Baillon’s, ballan and corkwing wrasse each had a niche that significantly overlapped that of some other wrasse species, but generally not each other: except corkwing, which overlapped Baillon’s (median overlap: 73%) (Figure 3a). Each of these species’ niches significantly overlapped the niche of goldsinny (61%, 76% and 76%, respectively), whereas only ballan and corkwing significantly overlapped rock cook (ballan: 60%, corkwing: 74%) and only ballan significantly overlapped cuckoo wrasse (73%). Neither cuckoo, goldsinny or rock cook in Dorset overlapped the niches of any other wrasse species significantly. For both ballan and corkwing wrasse, the degree of significant niche overlap of other species was highest for landed individuals (Figure 3b–c).

In the Isle of Skye, the number of instances of significant niche overlap were fewer, with only ballan wrasse having a niche that significantly overlapped some other species (Figure 4a). The niches of corkwing and goldsinny were almost fully encompassed by ballan wrasse (92% and 98%, respectively). The occurrences of significant niche overlap were highest for landed individuals of ballan wrasse (Figure 4b). There were no further instances of significant niche overlap in the Isle of Skye, and the niches of cuckoo and rock cook were completely separate (Figure 4a).

### Intraspecific variation

δ15N values increased with body size for all species except corkwing and Baillon’s wrasse, and this relationship varied between locations for ballan wrasse and rock cook (Figure 5a–d, Table 3a), although the ranges of body sizes sampled varied between these locations. There was also an effect of body size on δ13C values for ballan and goldsinny, which varied between sites (Figure 5e–f, Table 3b) and on δ34S values for cuckoo wrasse (Figure 5g, Table 3c). Raw data for all species-isotope combinations plotted against total length (cm) and model summaries for all remaining models that passed model diagnostic checks are presented in Figures S2-S4 and Table S3.

In Dorset, the isotopic niche volume of the retainable individuals of ballan, corkwing and goldsinny were larger than their returned conspecifics, whereas in the Isle of Skye this was only the case for ballan wrasse; returned individuals of corkwing, cuckoo and rock cook each had niche volumes larger than those of their retainable conspecifics (Table 2).

There were limited occurrences of significant niche overlap between landed and returned individuals of the same species within each location (Table S4). In Dorset and the Isle of Skye, landed ballan significantly overlapped their conspecifics that were over the maximum CRS (median overlap: 65% and 84%, respectively; Figure 3 & 4). Landed corkwing in Dorset also overlapped their smaller returned conspecifics by 92% (Figure 3), whereas in the Isle of Skye it was the smaller corkwing that significantly overlapped the landed individuals (77%; Table S4). There were no other occurrences of significant intraspecific niche overlap (Table S4).

## Discussion

Understanding variation in ecological roles within and among co-occurring species is key to predicting the potential for ecosystem-wide impacts of fisheries and implementing management measures to preserve ecosystem function. In this study, we used stable isotope data as a means to infer the inter- and intra-specific variation in resource use of co-occurring temperate wrasse species from two locations where intense exploitation of these species occurs. We demonstrate that there is likely to be limited trophic redundancy both between and within wrasse species, and that this may have implications for the overall health of rocky reef ecosystems if the live wrasse fishery is not managed sustainably.

### Methodological considerations for trophic inference from stable isotope data

Despite their utility, there are a number of complications associated with the use of stable isotopes in trophic inference, many of which are reduced in this study. Firstly, analysis of raw δ values, as presented here, can be sensitive to the relative δ values of source pools, so variation in consumer δ values may in fact be a result of high variance in the isotope values of source materials as opposed to diverse resource use among individuals (Layman et al. 2012). Isotope values are therefore often transformed relative to baseline isotope values of source material to make their inference more ecologically meaningful. For example, δ15N values can be converted into trophic positions, which reflect a tangible characteristic of the organism. However, such transformations require extensive additional information, including adequate temporal and spatial characterisation of isotopic baselines, as well as assumptions or knowledge of trophic discrimination factors (Post 2002).

The collection of extensive *a priori* information including sampling of source pools to characterise isotopic baselines was not within the scope of this study, so some care should be taken when making inferences from the raw isotopic data. However, the samples obtained in both locations were all collected from areas of rocky reef ecosystem, each over the course of 1–3 days, within narrow geographic ranges. Additionally, evidence suggests that wrasse have limited home range sizes and long periods of site residency (Sjolander et al. 1972, Potts 1984, 1985, Sayer 1999, Villegas-Ríos et al. 2013, Skiftesvik et al. 2014b). Therefore, the possibility that either spatial or temporal variability in baseline isotope values is driving variation in wrasse isotope values is considerably reduced, as the wrasse caught are likely to have co-occurred within their respective sampling areas over the period of tissue turnover.

Secondly, variation in stable isotope values can be driven by many underlying biological and chemical processes, which often vary with body size (Martínez del Rio et al. 2009). Therefore any differences in the size ranges sampled for each species could impact apparent isotopic niches. In this study, there are inconsistencies in the ranges of body sizes sampled between locations (generally a greater range of body sizes were sampled in Dorset compared to the Isle of Skye). We therefore avoid making direct comparisons of isotope values and niche metrics between locations where possible.

Finally, it is necessary to highlight that isotopic niche values are not a direct representation of trophic niche, but instead can be used as a proxy for a subset of the fundamental niche (the Hutchinsonian n-dimensional hypervolume; Hutchinson 1957, Newsome et al. 2007, Hette-Tronquart 2019). For instance, distinct diets may have common isotopic niche dimensions, however, distinct isotopic niches generally imply differentiation in diet. We therefore emphasise that the isotope data presented here are used as a tool to compare patterns of functional/trophic characteristics between different species of wrasse, rather than as direct proxies of diet intake. Nonetheless the isotope-based trophic inferences provide a valuable first step in identifying potential ecological impacts of wrasse removal.

### Interspecific variation and overlap

We found limited isotopic niche overlap among species and some interspecific variation in isotopic niche volume within each sampling location. We therefore infer systematic and sustained differences in resource use between sympatric species. This is perhaps surprising given that the different wrasse species are broadly recognised for their omnivorous, mesopredatory status and feed on similar food groups; each species’ diet consists of mainly hard-bodied molluscs and crustaceans, alongside less important accessory food groups including polychaetes, ascidians, echinoderms, fish and algae, and ectoparasites from cleaning interactions (Dipper et al. 1977, Hilldén 1983, Sayer et al. 1995, 1996, Deady & Fives 1995b a, Henriques & Almada 1997, Figueiredo et al. 2005, Norderhaug et al. 2005, Matić-Skoko et al. 2013).

It is predictable that the larger wrasse species (ballan and corkwing, which grow to ~60 cm and ~28 cm, respectively), occupy a larger isotopic niche and show some of the highest occurrences of niche overlap with the smaller species (goldsinny and rock cook, which rarely reach 18 cm). While maximum prey size is generally limited by the mouth gape of the predator, minimum size is not (Hickley et al. 1994), meaning larger-growing wrasse species are likely able to choose from a wider variety of prey categories, as observed by Norderhaug *et al.* (2005). Broadening the range of potential food items with growth for these species is also likely enabled by jaws and teeth becoming stronger as they grow (Dipper et al. 1977, Deady & Fives 1995a b, Figueiredo et al. 2005). Conversely, cuckoo wrasse, which also attain large sizes (up to 40 cm), showed relatively small niche volumes and some of the lowest occurrences of significant overlap with co-occurring wrasse in both locations, suggesting they may exhibit both greater dietary specialisation and differing resource utilisation to the other wrasse species in these locations.

The interspecific variation in niche size and overlap seen here could be brought about by various mechanisms. Firstly, fine-scale interspecific habitat preferences (for which there is ample evidence; Skiftesvik et al. 2014b, Halvorsen et al. 2020, Henly et al. 2021, Henly 2023) could be driving differences in relative prey availability, which in turn drives isotopic niche variation. Halvorsen *et al.* (2020) and Henly *et al.* (2021) showed evidence of interspecific variation in preferred depth for different wrasse species (supported here by interspecific variation in mean δ13C and δ34S values), while Skiftesvik *et al.* (2014) and Henly *et al.* (2021) highlighted varying abundances of wrasse across exposure gradients. New evidence also suggests that wrasse exhibit interspecific thermal habitat separation (Henly 2023). As the relative abundances of prey are also likely to vary across these environmental gradients, this could be one factor driving the observed interspecific differences in resource use.

Secondly, interspecific competition for prey could lead to resource partitioning - the division of resources within a system allowing species to coexist (Pianka 1974, Schoener 1974). The niche overlap hypothesis suggests that as the intensity of diffuse competition (the total competitive effects of a number of interspecific competitors) increases, there are likely to be lower levels of niche overlap between species (Pianka 1974). Given that the wrasse species studied here are reported to feed on similar prey items (hard bodied prey, dominated by molluscs and crustaceans), it is possible that there is some degree of resource partitioning among these species. However competition, and hence resource partitioning, are only likely if high quality resources are limiting (Colwell & Futuyma 1971, Pianka 1976, Hurlbert 1978). It is difficult to determine whether the prey items available to wrasse are limiting in the locations used for this study, but the sampling procedure and limited movement patterns of wrasse described in Section 4.1, alongside the reasonably high densities of wrasse found in these locations (L. Henly, unpublished data; Jackson-Bué et al. 2023) suggest there is a high likelihood that prey are derived from the same general locality and that some degree of interspecific competition is experienced.

### Intraspecific variation and overlap

For all species except corkwing and Baillon’s wrasse there was some evidence of a positive relationship between δ15N values and body size (Figure 5 & Figures S2-4). In the Isle of Skye, this relationship was not seen for ballan, and was weak for rock cook, but this is likely due to inter-site differences in the range of body sizes sampled (Table 1). Positive relationships between δ15N values and body size could suggest that these wrasse are feeding at higher trophic levels as they grow larger, as has been shown for many other fish species (e.g. Vander Zanden et al. 2000, Overman & Parrish 2001, Jennings et al. 2002); however, it is difficult to validate this inference with studies of the gut contents of wrasse due to their destructive feeding method (Liem & Sanderson 1986).

We also found a relationship between δ13C values and body size of goldsinny and rock cook, but this relationship varied between sample locations, potentially due to inter-site differences in the range of body sizes sampled (Figure 5e–f). There was also a decrease in δ34S values with increasing body size for cuckoo wrasse, which was consistent across sampling locations. Size-related changes in δ13C and δ34S could indicate ontogenetic shifts in foraging habitat and source materials (DeNiro & Epstein 1981, Currin et al. 1995, Inger & Bearhop 2008, Barros et al. 2010). There are a number of qualitative observations of shifts from shallower nursery grounds to deeper habitats as wrasse grow, and a new study shows quantitative evidence for these ontogenetic habitat shifts (Henly 2023). However, characterisation of isotopic baselines for potential foraging habitats would be needed to confirm whether this variation truly reflects such shifts.

Niche volume varied within species, with landed and returned individuals typically having quite distinct niches. The intraspecific variation in niche volume was greatest within the species that grow to the largest sizes (ballan, cuckoo and corkwing wrasse). Separation of niches with increasing size is thought to allow adults and juveniles of the same species to co-exist (Harmelin-Vivien et al. 1989). Furthermore, despite a broader range of food becoming available to larger species as they grow, evidence presented here suggests that the largest ballan wrasse (>28 cm in Dorset and >24 cm in the Isle of Skye) appear to be more specialised than their smaller conspecifics. Although there is a possibility that longer tissue turnover rates in larger individuals could have a compressing effect on isotopic niches, evidence from Dipper *et al.* (1977) supports our finding as they highlight that young ballan wrasse (0–10 cm) spend their first year in intertidal pools, where their diet is mainly limited to isopods and amphipods. When they grow older, the food groups available to them broadens as their jaws and teeth become stronger, and they start to shift their feeding into sublittoral areas. As they reach their largest sizes, and consequently can target even larger, and harder-bodied prey that smaller conspecifics cannot tackle they may exhibit greater dietary specialisation to reduce competition.

### Implications for fisheries management

Fisheries managers are increasingly taking an ecosystem-based approach in order to sustain the integrity, structure and function of ecosystems as well as the fisheries they support (Pikitch et al. 2004). Implementation of ecosystem-related information in fisheries assessments may be limited more by availability of relevant data than management structures (Marshall et al. 2019). Our assessment of variation and overlap in resource use among and within co-occurring temperate wrasse species provides a first step in predicting ecosystem-level impacts of live wrasse fisheries, demonstrates the utility of stable isotope analysis in informing an ecosystem-based approach to fisheries management, and highlights that the maintenance of functional diversity should be a priority when developing fishery management measures.

As wrasse are well-adapted to consume hard-bodied prey that many other groups are unable to exploit, and are well known for their facultative cleaning roles in which they remove parasites from other species in the system (Bjordal 1988), they are collectively likely to occupy relatively unique functional roles within temperate reef ecosystems. Among-species separation of trophic niches within this space therefore increases the risk that unsustainable removal of one or more wrasse species would ultimately destabilise trophic structure and/ or ecosystem function, and hence cause ecosystem-wide impacts within temperate reef ecosystems (Thompson et al. 2012). The low overall incidence of significant interspecific niche overlap among wrasse species could therefore lead to an overall low resilience of inshore rocky reef ecosystems to anthropogenic disturbance events such as fishing (Peterson et al. 1998, Thompson et al. 2012, Matich et al. 2017).

A number of previous studies have made similar predictions of ecosystem-wide effects following hypothetical overexploitation of one or more of these wrasse species. For example, Figueiredo *et al.* (2005) suggested that wrasse removal could result in a trophic cascade due to a reduction in predation and control of sea urchin populations, while Norderhaug *et al.* (2005) suggested that a significant removal of wrasse from kelp forests in Norway risks impacts to the surrounding community structure, through an increase in grazing invertebrates and a resultant decrease in algae. The isotope data presented here adds another layer of evidence supporting these predictions as, although studies have drawn similar conclusions, the level of interspecific trophic redundancy of wrasse had not previously been characterised, so the overall risk level of ecosystem-wide impacts of the removal of wrasse(s) was previously unclear.

Low interspecific niche overlap caused by resource partitioning does not always represent a lack of resilience to disturbance. If there is high competition among species with similar fundamental niches, competitively inferior species may achieve niche expansion, and hence maintain stability, if competition is reduced under environmental disturbance (Pianka 1976, Bolnick et al. 2010). However, it is difficult to foresee the potential for niche expansion, particularly under novel conditions, and when there is limited prior knowledge of the fundamental niches and levels of competition between the focal species, as is the case here. Furthermore, except in scenarios exceeding carrying capacity, over-exploitation of any given species is likely to reduce overall resilience to future perturbations (Naeem 1998, Borrvall et al. 2000), so conservation and management approaches should seek to support diversity and redundancy within the system.

Commercially-targeted wrasse species are likely to vary in their levels of trophic redundancy and consequently their capacity to mitigate the trophic effects of fishery-induced declines of sympatric species (Thompson et al. 2012, Matich et al. 2017). The results presented here suggest that ballan wrasse in both locations and corkwing wrasse in Dorset are likely to provide the most redundancy for other sympatric species. In particular, it is the individuals of landable size that have the highest incidences of significant overlap with other species, but in each case they do not significantly overlap the full suite of other sympatric species. Assuming isotopic niche overlap indicates genuine trophic niche overlap, fishery-induced declines or local extinctions of isotopically-functionally redundant species (those with isotopic niches that are overlapped significantly by ballan and/or corkwing) are therefore less likely to result in ecosystem-wide impacts as the remaining species may be able to fill niche space and undertake these neglected ecological roles (Lawton & Brown 1994, Peterson et al. 1998). However, ballan wrasse in both locations (and corkwing in Dorset) are not sufficiently overlapped by any other species, suggesting that although they may provide adequate redundancy to other species, there is likely insufficient redundancy among other species to fulfil their entire niche if their populations are overexploited to such a level that they can no longer fulfil their niche/functional roles. Furthermore, ballan wrasse are one of the most sought-after wrasse species (and corkwing second-most): commercially (for use in salmon farms (Henly et al. 2021), and recreationally (for catch and release angling; Henly *et al.,* in prep). Taken together, this evidence suggests that these species are conservation priorities, and generates impetus to ensure that management measures effectively prevent significant fishery-induced declines.

Our results also highlight that there is limited significant (isotopic) niche overlap between landed and returned individuals of the same species, which is likely to be driven at least in part by size-related shifts in resource use. This further highlights the need to maintain the demographic structure of a population when developing management measures for these (and other) fisheries, as the unsustainable removal of one size group could have potential consequences that extend beyond the species-specific consequences of removal outlined in (Henly et al. 2021).

Live wrasse fisheries operate within various Special Areas of Conservation (SACs) across the south coast of England (e.g. Plymouth Sound and Estuaries SAC, Studland to Portland SAC, and Fal and Helford SAC), each with an overall conservation objective “*to ensure that, subject to natural change, the integrity of the site is maintained or restored as appropriate, and that the site contributes to achieving the Favourable Conservation Status of its qualifying features*” (European Commission 1992, UK Government 2017). One means by which this can be achieved is “*by maintaining or restoring the structure and function (including typical species) of qualifying natural habitats*” (European Commission 1992, UK Government 2017). In the absence of a clear definition for ‘typical species’ in the Habitats Regulations, Natural England have adopted an approach by which an attribute for the “abundance of key ‘structural’ and ‘influential’ species for habitat features” has been included in the Supplementary Advice on Conservation Objectives (SACOs) for these sites (Natural England 2023). The target relating to this attribute is to *“[Maintain, Recover, or Restore] the abundance of listed [structural and influential] species, to enable each of them to be a viable component of the habitat.*” (Natural England 2023). They define structural species as “*those that form part of the habitat structure or help to define a key biotope*”, and influential species as “*those that are likely to have a key role affecting the structure and function of the habitat (such as bioturbators (mixers of sediment), grazers, surface borers, predators or other species with a significant functional role linked to the habitat).*” (Natural England 2023). These ‘structural’ and ‘influential’ species are yet to be identified for the sites in which live wrasse fisheries are active, but will be defined at a national level in accordance with the relevant definitions (Natural England 2023). Our study provides some of the first quantitative evidence to support the classification of wrasses (particularly ballan and corkwing) as influential species within these protected areas, and demonstrates the utility of these methods for defining species of interest for designated features in marine protected areas.

## Conclusions

To our knowledge, this study represents the first application of stable isotope analysis to compare the relative isotopic niche metrics of multiple commercially-important temperate wrasse species. We assess the inter- and intra-specific variation in resource use of these wrasses, and the potential implications of these findings for fisheries management.

Our study provides evidence that trophic redundancy is likely to be limited, both within and between species of wrasse. Ballan wrasse (the most commercially sought-after species) likely provides the highest overall level of inter-species trophic redundancy, but we suspect that there is insufficient redundancy among other species to fulfil the entire niche of ballan wrasse if they were to be overexploited. Individuals of sizes that are retained by the live wrasse fisheries are also more likely to provide redundancy to conspecifics than those that are returned to the sea, and the overall incidence of significant trophic overlap (redundancy) is low between landable and non-landable conspecifics. Our results also highlight the importance of considering demographic structure as well as species’ abundance when implementing fisheries management measures. Overall, this study demonstrates the insights that can be gained from stable isotope studies and how these data can be used in a fisheries management context to help define species conservation priorities within the broader context of an ecosystem-based approach to fisheries management.

**Author contributions**

LH and CT conceived the ideas and designed the methodology, LH obtained the samples and assisted JN with mass spectrometry. LH analysed the data and led the writing of the article. All authors contributed critically to drafts and gave final approval for publication.

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Table 1: Summary information for wrasse species in each site including number and size range of individuals, mean (and standard error), and range of δ13C, δ15N, and δ34S values (in per mille ‰) for each grouping. Summary information is also presented for subsets of the data which represent wrasse within (landed) and outside (returned) of minimum and maximum size limits implemented by the respective management authorities in Dorset and the Isle of Skye. Returned fish are either ‘under’ or ‘over’ the respective conservation reference size ranges. All Baillon’s wrasse are presumed to be returned as they are not mentioned in management measures, and cuckoo wrasse are prohibited to be landed in Dorset.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Site** | **Species** | **n** | **Size (cm)** | **δ13C (‰)** | **δ13C range** | **δ15N (‰)** | **δ15N range** | **δ34S (‰)** | **δ34S range** |
| **Dorset** | **Baillon's** | 13 | 11.5–19.0 | -19.13 (0.21) | 2.50 | 13.61 (0.18) | 1.96 | 17.26 (0.09) | 1.15 |
| **Ballan** | 142 | 6.0–48.0 | -18.61 (0.06) | 4.10 | 14.82 (0.06) | 3.20 | 17.61 (0.05) | 3.23 |
| Returned (under) | 29 | 6.0–17.5 | 19.34 (0.85) | 3.80 | 14.50 (0.10) | 2.28 | 17.61 (0.08) | 1.85 |
| Landed | 75 | 18.0–28.0 | -18.55 (0.06) | 2.60 | 14.77 (0.08) | 3.20 | 17.68 (0.07) | 3.23 |
| Returned (over) | 38 | 28.5–48.0 | -18.16 (0.06) | 1.60 | 15.18 (0.12) | 2.60 | 17.49 (0.09) | 2.00 |
| **Corkwing** | 56 | 9.0–22.0 | -19.29 (0.12) | 5.70 | 13.81 (0.08) | 2.84 | 17.91 (0.10) | 5.25 |
| Returned (under) | 38 | 9.0–13.5 | -19.35 (0.11) | 3.10 | 13.86 (0.09) | 2.84 | 17.95 (0.11) | 4.35 |
| Landed | 18 | 14.0–22.0 | -19.18 (0.31) | 5.70 | 13.71 (0.16) | 2.30 | 17.81 (0.20) | 3.89 |
| **Cuckoo** | 12 | 12.0–25.0 | -18.05 (0.07) | 0.70 | 14.35 (0.18) | 1.73 | 17.60 (0.09) | 0.86 |
| **Goldsinny** | 63 | 6.0–15.0 | -18.68 (0.05) | 2.50 | 14.30 (0.06) | 2.12 | 17.26 (0.06) | 2.42 |
| Returned (under) | 43 | 6.0–11.5 | -18.85 (0.06 | 2.10 | 14.15 (0.07) | 1.58 | 17.28 (0.07) | 1.95 |
| Landed | 20 | 12.0–15.0 | -18.33 (0.06) | 1.20 | 14.64 (0.10) | 1.79 | 17.22 (0.11) | 2.14 |
| **Rock cook** | 17 | 4.5–12.0 | -18.42 (0.11) | 1.60 | 13.99 (0.17) | 3.02 | 17.37 (0.05) | 0.76 |
| Returned (under) | 16 | 4.5–11.5 | -18.44 (0.11) | 1.60 | 13.99 (0.18) | 3.02 | 17.39 (0.05) | 0.66 |
| Landed | 1 | 12.0 | -18.00 (0.00) | NA | 14.07 (0.00) | NA | 16.98 (0.00) | NA |
| **Isle of Skye** | **Ballan** | 60 | 14.0–30.0 | -17.11 (0.11) | 4.30 | 13.78 (0.08) | 2.54 | 18.37 (0.14) | 4.84 |
| Landed | 45 | 14.0–24.0 | -17.06 (0.13) | 4.30 | 13.81 (0.10) | 2.30 | 18.38 (0.18) | 4.84 |
| Returned (over) | 15 | 24.5–30.0 | -17.25 (0.20) | 3.20 | 13.71 (0.15) | 2.23 | 18.35 (0.16) | 1.91 |
| **Corkwing** | 39 | 12.5–20.0 | -17.24 (0.07) | 2.20 | 13.40 (0.06) | 1.76 | 18.36 (0.10) | 2.49 |
| Landed | 28 | 12.5–17.0 | -17.26 (0.07) | 1.50 | 13.35 (0.04) | 0.92 | 18.38 (0.12) | 2.49 |
| Returned (over) | 11 | 17.5–20.0 | -17.20 (0.21) | 2.00 | 13.50 (0.20) | 1.76 | 18.30 (0.17) | 1.78 |
| **Cuckoo** | 47 | 12.0–30.5 | -16.84 (0.05) | 1.70 | 14.66 (0.08) | 2.26 | 17.18 (0.10) | 3.88 |
| Landed | 37 | 12.0–24.0 | -16.81 (0.06) | 1.70 | 14.53 (0.08) | 1.67 | 17.19 (0.10) | 2.48 |
| Returned (over) | 10 | 24.5–30.5 | -16.95 (0.07) | 0.70 | 15.16 (0.14) | 1.58 | 16.86 (0.32) | 3.53 |
| **Goldsinny** | 58 | 11.0–15.0 | -17.20 (0.06) | 1.90 | 13.62 (0.06) | 1.79 | 17.69 (0.06) | 2.66 |
| Returned (under) | 2 | 11.0–11.5 | -17.00 (0.20) | 0.40 | 14.05 (0.31) | 0.61 | 17.34 (0.15) | 0.29 |
| Landed | 56 | 12.0–15.0 | -17.21 (0.06) | 1.90 | 13.61 (0.06) | 1.79 | 17.71 (0.06) | 2.66 |
| **Rock cook** | 52 | 9.5–14.5 | -17.24 (0.03) | 1.00 | 12.77 (0.05) | 2.17 | 18.24 (0.10) | 4.01 |
| Returned (under) | 7 | 9.5–11.5 | -17.21 (0.11) | 0.80 | 12.75 (0.11) | 0.69 | 18.34 (0.17) | 1.48 |
| Landed | 45 | 12.0–14.5 | -17.25 (0.04) | 1.00 | 12.78 (0.05) | 2.17 | 18.22 (0.12) | 4.01 |



Figure 1: δ13C values (a), δ15N values (b), and δ34S values (c) (in ‰) of muscle tissue from six species of wrasse in Dorset and five species of wrasse from the Isle of Skye. Within each box, horizontal bold lines denote median values; boxes extend from the 25th to 75th percentile of each group’s distribution of values; vertical extending lines denote adjacent values (i.e. the most extreme values within 1.5 interquartile range of the 25th and 75th percentile of each group); dots denote raw δ values for each group.

Table 2: Bayesian 75% ellipsoid volume (EVB; ‰3) estimates for wrasse sampled in Dorset and Isle of Skye, given as median with interquartile range (IQR).

|  |  |  |  |
| --- | --- | --- | --- |
| **Site** | **Species** | **Median** | **IQR** |
| **Dorset** | **Baillon's** | 5.88 | 4.67, 7.49 |
| **Ballan** | 9.27 | 8.65, 9.97 |
| Returned (under) | 7.44 | 6.37, 8.71 |
| Landed | 7.31 | 6.67, 8.05 |
| Returned (over) | 5.38 | 4.71, 6.18 |
| **Corkwing** | 14.46 | 12.95, 16.19 |
| Returned (under) | 9.56 | 8.48, 10.82 |
| Landed | 25.92 | 21.18, 31.54 |
| **Cuckoo** | 3.15 | 2.50, 3.99 |
| **Goldsinny** | 2.88 | 2.62, 3.21 |
| Returned (under) | 2.49 | 2.23, 2.84 |
| Landed | 2.83 | 2.38, 3.41 |
| **Rock cook** | 3.11 | 2.54, 3.84 |
| Returned (under) | 3.11 | 2.53, 3.84 |
| Landed | ― | ― |
| **Isle of Skye** | **Ballan** | 15.51 | 13.98, 17.21 |
| Landed | 18.07 | 16.10, 20.39 |
| Returned (over) | 9.11 | 7.46, 11.30 |
| **Corkwing** | 3.91 | 3.47, 4.49 |
| Landed | 2.54 | 2.17, 2.99 |
| Returned (over) | 7.88 | 6.23, 10.17 |
| **Cuckoo** | 4.07 | 3.61, 4.63 |
| Landed | 3.10 | 2.73, 3.53 |
| Returned (over) | 6.68 | 5.12, 8.66 |
| **Goldsinny** | 3.16 | 2.85, 3.55 |
| Returned (under) | ― | ― |
| Landed | 3.19 | 2.86, 3.56 |
| **Rock cook** | 2.74 | 2.44, 3.08 |
| Returned (under) | 3.80 | 2.79, 5.36 |
| Landed | 3.01 | 2.65, 3.38 |

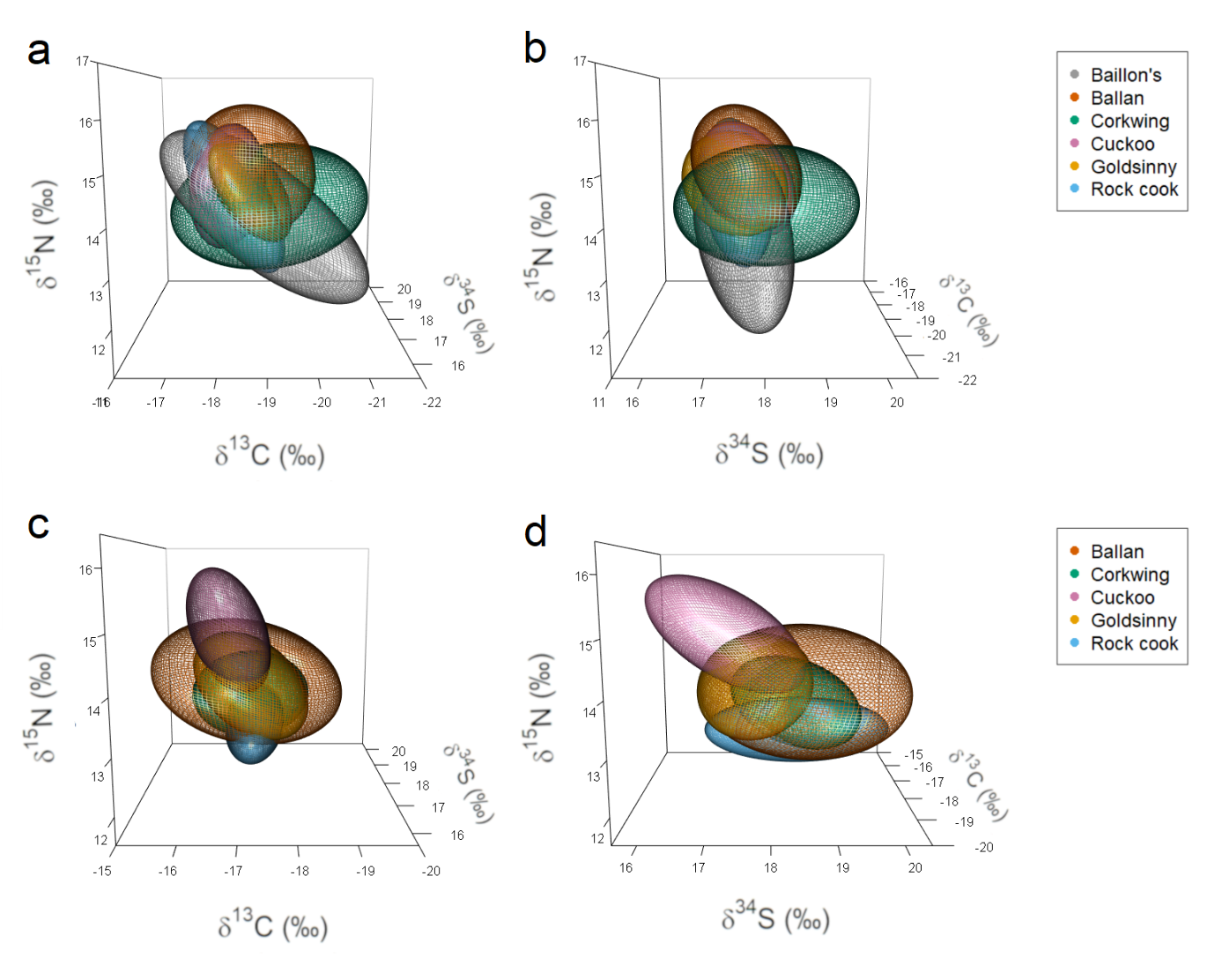


Figure 2: 75% ellipsoids corrected for sample size generated using δ13C, δ15N, and δ34S data for wrasse in Dorset (a & b), and the Isle of Skye (c & d).



Figure 3: Median percentage overlap in Dorset wrasse ellipsoids (Bayesian 75% ellipsoid generated using δ13C, δ15N, and δ34S data) with 95% credible intervals showing the uncertainty in the overlap estimates between (a) each pair of wrasse species. Overlap estimates are also shown between (b) returned/ landed ballan wrasse and other wrasse species, and (c) returned/landed corkwing wrasse and other wrasse species to identify which size ranges have the highest instances of significant niche overlap. The figure should be read so that the species of wrasse named in the facet headers are those that are overlapping those named on the x-axes. The horizontal red line represents the pre-determined 60% overlap threshold.



Figure 4: Median percentage overlap in Isle of Skye ellipsoids (Bayesian 75% ellipsoid generated using δ13C, δ15N, and δ34S data) with 95% credible intervals showing the uncertainty in the overlap estimates between (a) each pair of wrasse species. Overlap estimates are also shown between (b) returned/ landed ballan wrasse and other wrasse species to identify which size ranges have the highest instances of significant niche overlap. The figure should be read so that the species of wrasse named in the facet headers are those that are overlapping those named on the x-axes. The horizontal red line represents the pre-determined 60% overlap threshold.



Figure 5: Predicted effects (with shaded 95% confidence intervals) of total length (cm) on δ15N (a-d), δ13C (e-f), and δ34S (g) as estimated by LMs.

Table 3: Parameter estimates (and standard errors) for drivers of variation in a) δ15N, b) δ13C, and c) δ34S values in candidate and null models for each wrasse species. Mxx\_BEST represents the candidate model with the lowest AIC, Mxx\_FINAL represents the selected, most parsimonious model and Mxx\_NULL is the null model (containing only location as a predictor).k is the number of parameters in each model, LL is the log-likelihood, AIC is the absolute Akaike Information Criterion, and ΔAIC is the relative difference in AIC from the Mxx\_BEST. Dorset was used as the base level of the Location factor for all tables. BL: Baillon’s; BA: Ballan; CW: Corkwing; CK: Cuckoo, GO: Goldsinny; RC: Rock cook.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| a) | **β0** | **Location** | **Length (cm)** | **Length: Location** | **k** | **LL** | **AIC** | **ΔAIC** |
| **MBA\_FINAL** | 14.15 (0.19) | -0.39 (0.49) | 0.03 (0.01) | -0.03 (0.02) | 5 | -204.41 | 418.82 | 0 |
| **MBA\_NULL** | 14.82 (0.06) | -1.04 (0.11) | – | – | 3 | -211.16 | 428.32 | 9.5 |
| **MCK\_BEST** | 12.35 (0.35) | 0.86 (0.40) | 0.12 (0.02) | -0.04 (0.02) | 5 | -16.75 | 43.50 | 0 |
| **MCK\_FINAL** | 12.97 (0.17) | 0.09 (0.11) | 0.08 (0.01) | – | 4 | -18.88 | 45.77 | 2.27 |
| **MCK\_NULL** | 14.35 (0.16) | 0.31 (0.18) | – | – | 3 | -47.53 | 101.06 | 57.56 |
| **MGO\_BEST** | 12.52 (0.32) | 1.48 (1.03) | 0.17 (0.03) | -0.20 (0.08) | 5 | -67.10 | 144.20 | 0 |
| **MGO\_FINAL** | 12.79 (0.30) | -0.99 (0.10) | 0.14 (0.03) | – | 4 | -70.02 | 148.05 | 3.85 |
| **MGO\_NULL** | 14.30 (0.06) | -0.68 (0.09) | – | – | 3 | -82.01 | 170.02 | 25.82 |
| **MRC\_FINAL** | 11.22 (0.50) | 1.15 (0.84) | 0.28 (0.05) | -0.25 (0.07) | 5 | -30.35 | 70.70 | 0 |
| **MRC\_NULL** | 13.99 (0.11) | -1.22 (0.13) | – | – | 3 | -44.16 | 94.31 | 23.61 |
|  |  |  |  |  |  |  |  |  |
| b) | **β0** | **Location** | **Length (cm)** | **Length: Location** | **k** | **LL** | **AIC** | **ΔAIC** |
| **MGO\_FINAL** | -20.37 (0.27) | 4.14 (0.89) | 0.16 (0.02) | -0.23 (0.07) | 5 | -49.73 | 109.46 | 0 |
| **MGO\_NULL** | -18.68 (0.05) | 1.49 (0.08) | – | – | 3 | -67.60 | 141.19 | 31.73 |
| **MRC\_FINAL** | -19.83 (0.36) | 3.10 (0.60) | 0.14 (0.04) | -0.19 (0.05) | 5 | -7.63 | 25.26 | 0 |
| **MRC\_NULL** | -18.42 (0.07) | 1.17 (0.09) | – | – | 3 | -15.62 | 37.24 | 11.98 |
|  |  |  |  |  |  |  |  |  |
| c) | **β0** | **Location** | **Length (cm)** | **Length: Location** | **k** | **LL** | **AIC** | **ΔAIC** |
| **MCK\_FINAL** | 18.59 (0.29) | -0.32 (0.19) | -0.06 (0.01) | – | 4 | -48.33 | 104.67 | 0 |
| **MCK\_1** | 18.25 (0.60) | 0.11 (0.67) | -0.04 (0.03) | -0.03 (0.04) | 5 | -48.10 | 106.2 | 1.53 |
| **MCK\_NULL** | 17.60 (0.18) | -0.48 (0.21) | – | – | 3 | -56.34 | 118.69 | 12.49 |