***Target Journal – Proceedings of the Royal Society B: Biological Sciences***

*Proceedings of the Royal Society B: Biological Sciences (ProcB) publishes numerous articles on the stable isotope ecology, marine species, and ecological dynamics, including competition. Few published articles comine all three of these elements, with fewer still using pinnipeds as a model system. This study is thus of broad interest to biologists and other ecosystem stakeholders, as we integrate these three elements while using pinnipeds as a model system to illustrate changing ecostystem dynamics that necessitate management to adequately conserve two charismatic marine species. Additionally, ProcB has a relatively high impact factor for ecology, ensuring this study will be disseminated broadly.*

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| *Is fate Sealed? Stable isotopes reveal competitive ecosystem dynamics between two marine sentinel communities.* |

*I certify that this dissertation is entirely my own work and no part of it has been submitted for a degree or other qualification in this or another institution and give permission for a copy to held by my supervisor and distributed at their discretion.*

***Abstract:***

Interspecific competition is a driving force of natural selection, but is difficult to quantify in the marine realm. Comprehending competition necessitates understanding the feeding ecology of study species, which is critical to human management of marine predators, fish communities, and other marine resources. Here, we used stable isotope analysis (SIA) to quantify the feeding ecology of two sympatric pinniped species, grey (*Halichoerus grypus*) and harbour (*Phoca vitulina*) seals in the Shetland Islands, Scotland, UK. Using Bayesian isotopic ellipse and stable isotope mixing models, we identified diet overlap between the two species over multiple time domains, indicating probable competition. Further, we find that grey seals have a smaller isotopic niche than harbour seals, despite a higher number of probable prey components. Our results show that grey seals are likely outcompeting harbour seals for higher-quality food, forcing harbour seals to forage more broadly and/or spend more time foraging at sea. These results support hypotheses that grey seal populations rebounding from culls in the 20th century are contributing to an ongoing decline of harbour seal populations in this region. This assessment of competition between two marine predators demonstrates the complexity of the marine environment, and lays groundwork for adequate modelling to inform more comprehensive management.

***Introduction:***

Interspecific competition is a constant in many terrestrial and marine ecological systems (Crombie, 1947), however, it is seldom considered in marine management strategies (Morgan & Sulikowski, 2015). This is concerning, considering past and present anthropogenic effects on the marine environment (Jackson et al., 2001; Lotze et al., 2006) and difficulties associated with monitoring marine ecosystems. Species that forage across the food web, water column and large spatial domains integrate large masses of information, and can act as ecological sentinel species (sentinels (Hazen et al., 2019)). Sentinels present a cost-effective system to measure ecological change in the marine realm, as they can inform on many different parameters with relatively small amounts of sample (Hazen et al., 2019). Because of their large ranges, sentinels provide robust insights into environmental change (Fleming et al., 2016), anomalous events (Holser et al., 2022), and even future changes in ecosystem dynamics (Hückstädt et al., 2020). As wide-ranging animals that are either highly specialized or highly generalist, large marine vertebrates make excellent ecosystem sentinels (Fossi et al., 2012). Generalist foragers provide one model for measuring broad, unobservable ecosystem changes across spatiotemporal scales by integrating information on regime shifts and other changes in prey diversity (Horn & Whitcombe, 2015). Generally, large-scale marine ecological monitoring programs that could assess interspecific competition also take extractive tolls on communities through various anthropogenic stressors. Some of these include direct take, handling stress, and environmental stressors necessary to gain data for large-scale ecological models (Atkinson et al., 2015).

Naturally occurring stable isotopic variants of common atoms (e.g., carbon, nitrogen) provide a minimally invasive method to measure the ecology and physiology of large marine vertebrates (Hobson, 1999; S. D. Newsome et al., 2009; Seth D. Newsome et al., 2009; Vander Zanden et al., 2015), in a field generally termed Stable Isotope Analysis (SIA). SIA uses small amounts of samples from individuals to provide informative metrics including foraging behaviour (Newsome et al., 2007), diet variability at the individual and community levels (Hückstädt et al., 2012; Peters et al., 2020), and even changes in foraging habits over time (Hückstädt et al., 2017; Krause et al., 2020). Furthermore, SIA provides a cost-effective way to monitor and understand cryptic animals, such as marine vertebrates, in their otherwise unobservable systems (Hazen et al., 2019; Owen et al., 2011).

Despite the UK’s status as a high-income nation (IMF, 2022) with a history of environmental exploitation (Küpper & Kamenos, 2018) and numerous ongoing commitments to marine conservation (reviewed in Jackson et al., (2001)), there are significant gaps in the literature on the feeding ecology of many resident marine species. Extant studies that examine the feeding and foraging ecology of marine predators in the UK either lack long-term resolution (e.g., scat, stomach contents analysis (Wilson & Hammond, 2019)), or are phenologically dependant (i.e., studies of seabird diet at breeding colonies only (Bearhop et al., 1999; Thompson & Furness, 1995)). Both limitations provide a skewed lens for understanding the ecology of a given species. Using SIA over multiple time domains (e.g., using multiple tissue types (Caut et al., 2011)) provides one potential solution to this problem. Recent changes to the marine top predator regime in UK waters (Horton et al., 2021) have increased the need for SIA monitoring, as it will help inform if these changes are mediated by shifts in prey communities or changing water parameters affecting the physiology of these large top predators.

Pinnipeds are distinct among the UK’s marine ecological sentinels: their reliable haul-out behaviour increases the amount, diversity, and frequency of potential samples (e.g., scat, fur, blubber, vibrissae; reviewed in Hazen et al., (2019)) (Hindell M.A., 2003). Though the UK sees a variety of vagrant pinniped species, it has endemic populations of both grey (*Halichoerus grypus*) and harbour (*Phoca vitulina*) seals. Despite their utility as a sentinel species and top-down ecosystem controls (Aarts et al., 2019; Herreman et al., 2009), both grey and harbour seals were culled in the 20th century as they were seen as nuisance species and were interfering with fisheries activity (Brown et al., 2012; Thompson et al., 2007). Both species have shown incredible resilience, recovering rapidly to reach pre-cull levels in recent decades (SCOS, 2021). However, certain UK harbour seal Management Units (MU’s) across different regions of the UK have been in an unexplained persistent state of decline since the early 2000s (Hall et al., 2019; SCOS, 2021).

Numerous hypotheses attempt to explain these declines, including increased predation from grey seals and/or killer whales (*Orcinus orca*), long-term effects of Phocine Distemper Virus (PDV), other diseases (e.g., *Brucella*, avian influenza), or toxicity from harmful algal blooms (Thompson et al., 2019). Another hypothesised driver of the decline in harbour seals is competition with grey seals. In MU’s with declining harbour seal populations (e.g., Northern Scotland, Southeast England; declined to 40% the pre-2002 level and 25% the previous 5-year mean, respectively (SCOS, 2021)), grey seal populations have stabilised, apparently reaching carrying capacity (Thomas et al., 2019). Monitoring is critical to understand the dynamics driving declines in harbour seal populations while grey seal populations ostensibly stabilise (SCOS, 2021; Thomas et al., 2019). Such monitoring work will help determine whether declines in harbour seal populations are related to competition with grey seals, or driven by another pressure on the population. Furthermore, as harbour and grey seals have previously been shown to forage on similar prey (Wilson & Hammond, 2019), baseline monitoring efforts will also indicate how competition impacts prey species, providing more accurate implications for management.

Here, we use two stable isotope values (δ13C, δ15N) to analyse the trophic and spatial ecology of sympatric harbour and grey seal colonies in the Shetland Islands, Scotland, UK. δ13C is an established indicator of foraging strategy(Connolly et al., 2004; Szpak & Buckley, 2020), allowing us to map the foraging ecology of grey and harbour seals. δ13C benefits from the inclusion of δ15N data, as it indicates relative trophic position, allowing isotopes to show diet composition along two dimensions (Post, 2002). Because of their shared spatial domain and inferred trophic overlap from other studies, we expect to see isotopic niche overlap between these grey and harbour seals, indicating interspecific competition between them.

***Methods:***

*Seal Sample Preparation:*

Seals were captured on, or close to, haulout sites in the Shetland Islands, Scotland, UK using tangle or hand nets (Figure 1). Adult harbour seals (n = 29) were caught in March-April 2022 and September-October 2022, and grey seals (n = 10) were caught in June – July 2022. Seals were administered with intravenous Zoletil100 (Virbac, France) for immobilization during tagging and sample collection. All capture, handling and other licenced procedures were carried out under the Sea Mammal Research Unit (SMRU, St. Andrews, Scotland) UK Home Office project licence PF84B63DE under the Animals (Scientific Procedures) Act 1986, with specific licences from Marine Scotland. Appropriate site-specific approvals were obtained, with any associated mitigation measures observed for designated sites. Seal blood samples were allowed to sit at 4 ° until separate plasma and RBCs separated. RBC and plasma samples were then pipetted into separate containers, freeze-dried and prepared for stable isotope analysis.

A map of the united kingdom

Description automatically generated

B

A

**Geodetic CRS:** OSGB36/British National Grid

**EPSG:** 27700

**Projection:** Transverse Mercator

**Datum:** Ordinance Survey of Great Britain 1936

**Unit:** Meter

Figure 1: The study location. A) shows the Shetland islands and their location in the UK, with B) presenting fish tow locations and seal capture locations broken down by species. Size of seal capture location points corresponds to the number of seals caught in each region.

*Prey Sample Preparation:*

Whole fish and squid caught during net trawls (Figure 1) were debrided of skin and subdermal fat before sectioning a 2 cm2 section from both sides of the first dorsal fin. When more than three fish appeared in a trawl, a random subset of 3 were sectioned and prepared for SIA. Fish samples were freeze-dried for 24 hours and milled to a fine powder using a mortar and pestle. Mortars and pestles were washed with water followed by 70% ethanol and dried in a 70C oven for 24 hours after each use. Powdered samples were run in duplicates to minimize the adverse effects of lipid extraction. Lipid-extracted samples (below) ran for δ13C analysis to reduce erroneous results as a result of δ13C-depleted lipid relative to protein, while lipid-rich replicates ran for δ15N stable isotope analysis to conserve as much δ15N from proteins as possible (Sweeting et al., 2006).

*Lipid Extraction:*

Following previous lipid extraction protocols for fish muscle tissue (Chouvelon et al., 2014; Meier et al., 2017), 1 ml cyclohexane was added to 25 mg of freeze-dried fish tissue and agitated for 1 hour at 80 rpm. Following agitation, samples were centrifuged for 5 minutes at 3000 Xg, and the lipid-containing supernatant was decanted off. Samples were left to dry in a fume hood for 48 hours to evaporate any remaining cyclohexane and weighed for stable isotope analysis.

*Stable Isotope Analysis:*

Prepared samples were weighed in 4mm (C/N), or 6mm (S) tin capsules to 0.8 ± 0.05 mg and 6.0 ± 0.6 mg for C/N and S, respectively. Samples were run for bulk tissue stable isotope analysis at the Environmental and Sustainability Institute, University of Exeter, Penryn Campus. C/N samples were run on a Sercon Integra 2 Stable combination EA-IRMS system. Values are reported in reference to their accepted standards, Vienna PeeDee Belemnite (V-PDB) for δ13C, air (N2) for δ15N. Values for Sandeel (*Ammodytes spp.*) were taken from literature published (Bearhop et al., 1999; Thompson & Furness, 1995) in the same region and grouped into a benthic and pelagic group according to seasonal shifts in their foraging behaviour (Muus, 1999).

*Statistical Analysis:*

All statistical analyses were completed using R Statistical Software (v4.2.3 ; R Core Team 2023). Linear models were constructed to examine differences in δ13C and δ15N values between species (grey and harbour) and sample type (RBC and plasma), with effects included for capture date and location. Data and distributions satisfied all assumptions for parametric tests. Where linear models indicated significant difference, the difference in means was reported.

2D Niche isospace metrics (herein Layman metrics (Layman et al., 2007)) were computed using the SIBER package [39-40]. Total area (TA) represents the area of the minimum convex hull polygon of each study group in a two-dimensional space with δ13C as the x-axis and δ15N as the y-axis. Standard isotopic ellipse area (SEA) represents the maximum likelihood estimates of the means and covariance matrices of each study group, and SEAc represents these values corrected for small sample sizes.

Bayesian models with vague priors were fit to each species by sample type (Plasma or RBCs) using the SIBER package (Jackson et al., 2011) to calculate the Bayesian Standard Ellipse Area (SEAb) for each of four groups. Models consisted of five Markov-Chain Monte-Carlo (MCMC) chains of 1,000,000 iterations, a burn-in of 500,000, and a thinning rate of 500. Model convergence was checked against the Gelman-Rubin diagnostic, and burn-in length was verified by checking that ≤ 5% of the Geweke diagnostics were outside 1.96 standard deviations. Ellipse overlap between each species across sample type was calculated using SEAb.

The MixSIAR package (Stock et al., 2018) was used to create Bayesian Stable Isotope Mixing Models (SIMMs) to determine the relative contribution of different prey to the diets of grey and harbour seals across both time domains. SIMMs made in MixSIAR are robust tools for gleaning diet composition from isotopic data. MixSIAR SIMMs incorporate a suite of parameters, including trophic enrichment factors (TEFs) and informative prior distributions of prey composition (informative priors) while also using Bayesian methods (i.e., MCMC chains) to account for uncertainty. Outputs are aggregated as probable distributions of proportional diet contribution for any given fish in a study group model. Because SIMMs lose resolution with more source groups, we ran models in multiple iterations (figure 2): first with an uninformative prior to assess convergence and runtime, then with an informative prior to begin examining posterior distributions. After the first informative prior run, prey species with a median (50%) posterior density of 0.000 were removed from the model, and it was run again. This continued until all prey species left had >0.000 median posterior density. Then, any prey species with less than 0.050 median posterior density were removed from the model before final models were run.

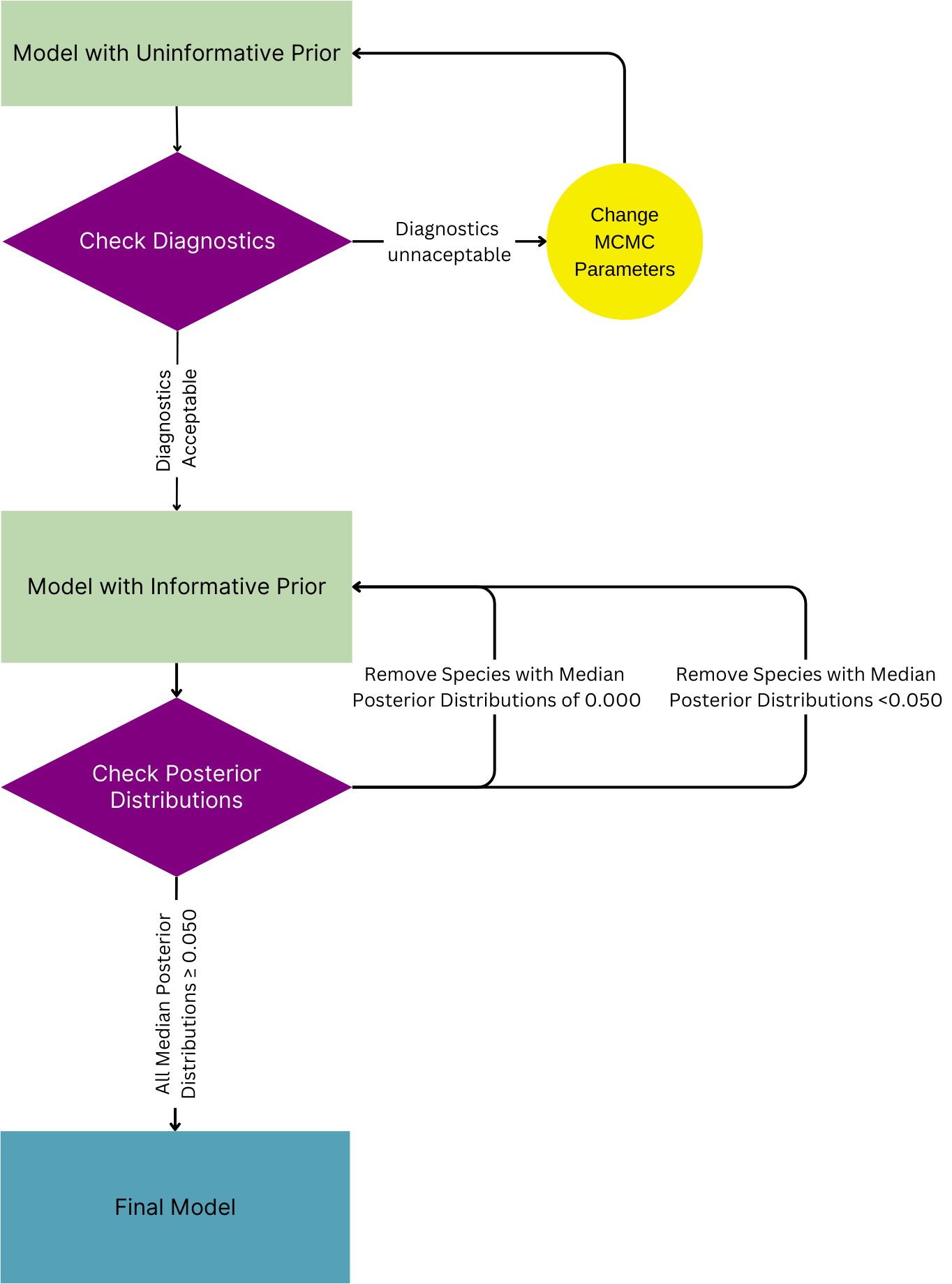


Figure 2: SIMM Model selection visualized as a flowchart.

Because SIMMs do not directly identify prey items, these prey were likely artifacts of the isotopic composition of other species that were identified with higher density in the diet. TEF values from controlled experiments in captive harbour, grey, ringed (*Pusa hispida*), and harp (*Pagophilus groenlandicus*) seals were used for both harbour and grey seals (Hobson et al., 1996; Lesage et al., 2002), as harbour seal TEFs were the closest published values to grey seals. Informative priors were constructed for SIMMs of each study group using values from published literature assessing the diet composition of the study populations via non-isotopic methods (i.e., scat analyses) (Wilson & Hammond, 2019). Due to the longer turnover time of RBC samples, we ran two sets of RBC models; one with informative priors from the spring/summer season, and one with informative priors from the autumn/winter season. MixSIAR MCMC SIMMs were run in various iterations until convergence was assured via the Gelman-Rubin diagnostics, with burn-in was further verified by ensuring 5% or less of Geweke diagnostics were outside 1.96 standard deviations (Fraleigh et al., 2023).

***Results:***

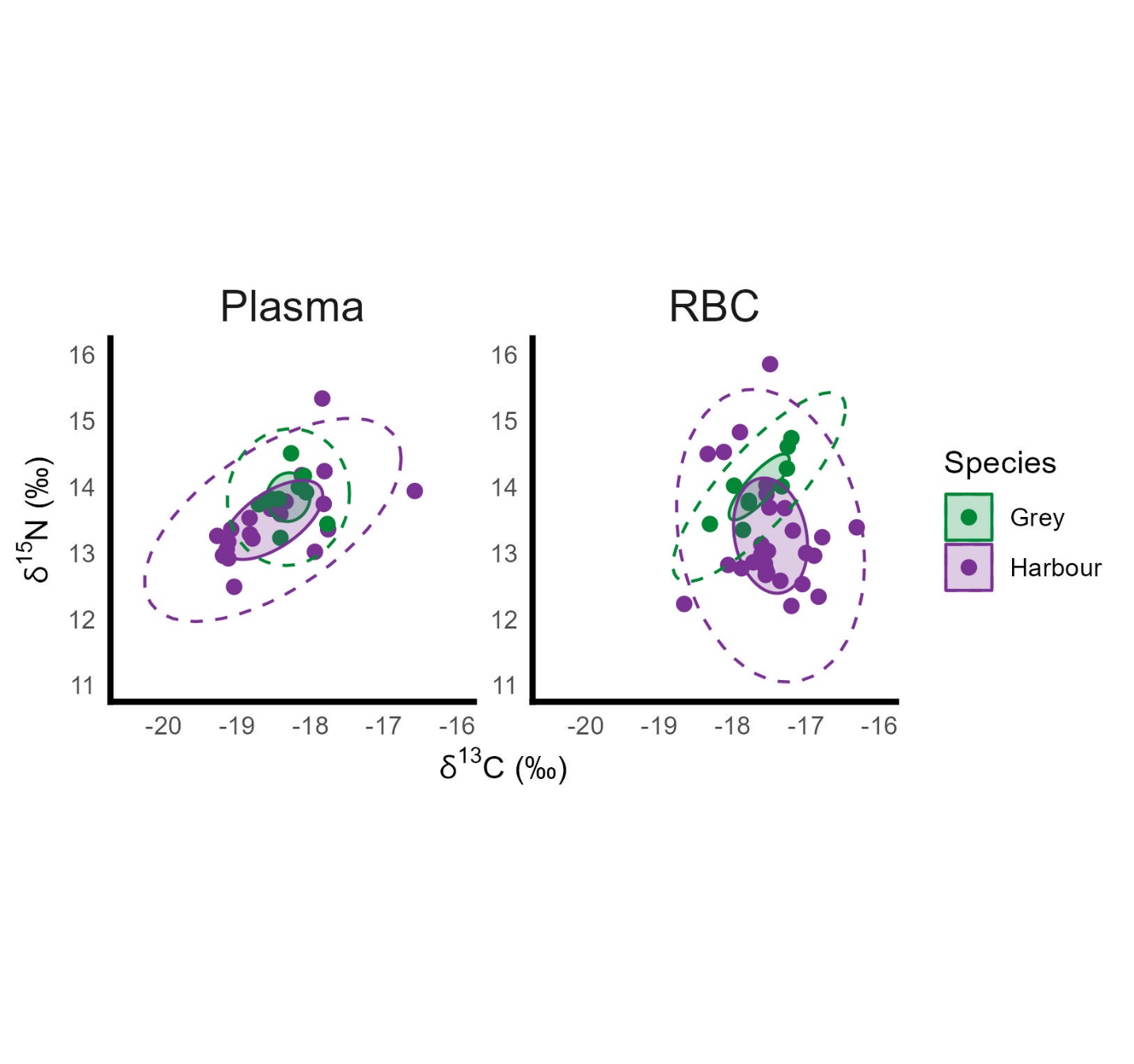
Grey and harbour seals exhibited no significant differences in δ13C values between species, sample type, capture date, or capture location. However, significant differences were observed in δ15N values (LM, T4,75,= -2.132, *p*=0.036), with grey seals 0.44 ± 0.21‰ (β ± SE) higher than harbour seals on average (Figure 3).

Figure 3: Plasma (left) and RBC (right) δ13C and δ15N values of Grey and Harbour seals in the Shetland Islands, Scotland. Green and purple points represent individual grey and harbour seals, respectively. The shaded areas represent the 40% standard isotopic ellipses, while dotted boundaries represent the 95% confident isotopic ellipses. Colour corresponds to species, and values are in ‰

Isotopic niche

Harbour seals showed a larger calculated isotopic niche area than grey seals: all Layman metrics showed a larger isotopic niche (ellipse) for harbour seal groups than grey seals, regardless of the tissue analysed (Table 1, Figure 3). Results of Bayesian models further indicated that harbour seals have a larger niche given by both sample types: the Bayesian Standard Ellipse Area (SEAb) for harbour seals was 2 times larger for plasma values, and 3 times larger for RBC values (Table 1, Figure 4). There was overlap in the Bayesian ellipse models for both sample types. Median overlap was higher in the plasma study groups (0.14 plasma overlap:0.09 RBC overlap), however the credible intervals were similar for both plasma and RBC groups (0.00, 0.37; 0.00, 0.40; respectively (Table 1))

Table 1: Layman metrics for each species by sample type. TA is the calculated convex hull total area. SEA is the maximum likelihood estimate of isotopic ellipse area based on the study group’s covariance matrix, and SEAc is the same estimate corrected for sample size. SEAb is a Bayesian estimate of isotopic ellipse area. Overlap is reported as the median overlap for study groups by sample type, with 95% credible intervals in parenthesis. All units are in ‰2.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Metric | Grey Seal Plasma | Harbour Seal Plasma | Grey Seal RBCs | Harbour Seal RBCs |
| TA | 0.62948 | 3.57455 | 0.6084 | 5.751449 |
| SEA | 0.317391 | 0.911631 | 0.33275 | 1.393351 |
| SEAc | 0.357065 | 0.949616 | 0.380286 | 1.435574 |
| SEAb | 0.354659 | 0.965615 | 0.450904 | 1.430523 |
| Overlap | .14 (0.00, 0.37) | | 0.091997 (0.00, 0.40) | |

A diagram of different types of species

Description automatically generated

Figure 4: Violin plots of the posterior draws of SEAb given for each species split by sample type. Colour corresponds to species, values are in ‰2.

Diet reconstructions

We caught a total of 13 fish species, and unidentified squid species that were preemptively grouped as squid. After running model iterations with uninformative and informative priors for each time domain, low-probability prey species were removed and final models were run (Table S1). Final model posterior distributions were extracted and analysed.

Final model posterior distributions from MixSIAR SIMMs indicate that grey seals likely predate on gadids, scorpaeniforms, and some sandeel in the spring/summer months and gadids and sandeel only in the autumn and winter. The same distributions indicate harbour seals likely predate on pelagic forage fish (i.e., Argentine), gadids, and sandeel throughout the year (Figure 5). Prey overlap from the SIMMs is evidenced in posterior densities for individual prey species. Furthermore, results from SIMMs indicate shifts in prey composition between sample types within species groups (Figure 6).A chart of different colored shapes

Description automatically generated

Figure 5: Violin Plots of scaled posterior density of each prey species in species diets separated by group for Plasma and RBC time domains. Note that a single value for scaled posterior density represents a single posterior from the MCMC model.

A diagram of different colors

Description automatically generated with medium confidence

B

A

Figure 6: Seal and Fish mapped in δ13C:δ15N isospace for Seal Plasma (A) and RBC (B) values. Fish means corrected for trophic discrimination factor by sample type are included as large points with error bars representing standard deviation, and effective isospace is created by drawing a minimum convex polygon around the standard deviation values. Seal are plotted by species in each sub-plot.

***Discussion:***

Studies of pinniped diet in the north sea (more so in the UK) are limited to analyses of hard parts found in scats and opportunistic stomach content analysis (Wilson & Hammond, 2019). Such studies provide an excellent estimate of diet composition, though only over a short time frame. Here, we used SIA to quantify the diet composition of two species endemic to the UK over multiple, larger time frames. Additionally, SIA allowed us to examine the overlap in diet between these species, allowing us to asses competition and other ecosystem dynamics with a single sampling draw. Data from this study will constitute a baseline for further SIA monitoring in the UK, allowing management agencies to better understand the implications of management decisions on species in dynamic, competitive systems.

Data from both the SIBER analyses and MixSIAR SIMMs support overlap in the diet composition of grey and harbour seals in the Shetland islands. The calculated SIBER overlap indicates overlap in the isotopic niche, while SIMM posterior distributions support these data, with evidence that grey and harbour seals have similar principal dietary components in a given season, likely reflecting the overall prey assemblages in preferred foraging grounds. Isolated, the SIBER overlap metrics could indicate that grey and harbour seals simply forage in similar environments at similar trophic levels (Fraleigh et al., 2023; Jackson et al., 2011). Likewise, SIMM posteriors alone simply indicate that these predators are foraging on similar prey species (Jackson-Ricketts et al., 2019; Sepúlveda et al., 2015; Stock et al., 2018). However, taken together SIBER and SIMM metrics of overlap indicate diet, trophic, and isotopic similarity, providing support for competition between grey and harbour seals.

Despite pressures from competition and more principal prey components, on average, grey seals have a smaller isotopic niche than harbour seals for both sample types (0.979619 and 0.610956 ‰2 for RBC and Plasma, respectively). A smaller niche may mean that an outcompeted species is forced onto one or two specific species (i.e., the “junk food” hypothesis (Österblom et al., 2008)). However, given the diversity in the grey seal diet and the habitats occupied by prey species in SIMMs, it is possible that grey seals are outcompeting harbour seals for species that are high-quality (i.e., high energy density), forcing harbour seals to forage on “junk” food with lower energy density, or in areas of lower prey density (e.g., pelagically).

This hypothesis is somewhat supported by an apparent shift in the long (RBC) and short (Plasma) time domains of the δ13C values for both species (Hobson et al., 1996). Plasma captures a time frame of days to weeks where RBCs integrate data from the preceding months (Lesage et al., 2002),so isotopic data reflects the partitioning of the foraging grounds by both species described in biologging literature (Jones et al., 2015), until their seasonal haul-outs for both moulting and feeding. Niche overlap in the plasma groups is thus likely a reflection of the isoscape local to the Shetland islands, while niche overlap in the RBC groups is more likely a reflection of the niches of the species during longer foraging trips.

Seasonal shifts in foraging behaviour are well documented across pinniped species (reviewed in (Carter et al., 2016). The observed shift from benthic to pelagic prey contrasts previous findings that harbour seals in north Scotland mostly forage on pelagic prey (Wilson & Hammond, 2019), and provides extra temporal resolution to earlier prey composition work. Our models included a fairly low number of pelagic prey species, meaning our SIMMs may be data-poor in the pelagic sphere. However, the observed differences in the δ13C (nearly 1‰) between time domains still support this as a shift in foraging behaviour. Ultimately, this observed shift alone serves as a baseline for future monitoring studies, and provides further resolution to work describing the food webs of northern Scotland, which should be taken into account when managing fisheries (Morgan & Sulikowski, 2015). This conclusion is further supported by diet component shifts as given by SIMM outputs, as plasma and spring/summer RBC values both differ from autumn/winter RBC values in component constitution and distribution. All δ13C data presented here would benefit from future δ34S SIA on the same species, tissues, and ideally, individuals. Evidence indicates δ34S can further stratify niche space (Szpak & Buckley, 2020), allowing us to map the foraging ecology of grey and harbour seals more accurately in 2D and 3D niche isospace.

Some (n=2 grey, 4 harbour) RBC values were high above the effective isospace mapped by the prey species we analysed (Figure S1). Because these individuals were not outliers on the δ13C plane, their δ15N values are particularly interesting. Of the 4 harbour seal outliers, there were 3 females and one male. As breeding, weaning pups, and moulting are all known causes of δ15N enrichment in pinnipeds, the three harbour seal females may have recently bred and been weaning a pup at the time of capture (Newsome et al., 2010). The single harbour seal male is a peculiar case, as it also had the highest recorded δ15N value in this study. Though moulting drives δ15N enrichment, without the added burden of weaning a pup, it is unlikely a healthy life history was the only driver of this individual’s high δ15N. Some alternative explanations of this high δ15N value include larger foraging distances or starvation (Hobson et al., 1996). Neither of the values were dramatically higher than isoscape values for the one each grey seal male and female outliers. The enriched δ15N here is thus likely driven by moulting in the months before capture, or prey species that we were unable to catch.

One drawback of a single set of informative priors for each seal species is that the prior distributions used may not accurately reflect the time domains of both tissues. Specifically, as we used scat analysis to construct priors, the RBCs may not be properly incorporated, as foraging behavior of both species may change before the effective season (e.g., spring/summer, autumn/winter). However, when run against uninformative priors, the informative priors provide more resolution to the data, and thus are still worth including until better priors become available. Further, the inclusion of an extra model with the off-season prior further mitigates this effect. An ideal model array would have priors grouped by time domain for each specific tissue, but such an effort would be time and labour-intensive.

Physiologically, grey and harbour seals look very similar. Their onboard oxygen storage, average/maximum dive durations, and muscle myoglobin concentrations are somewhat similar (Ponganis, 2015). However, grey seals have a much higher blood volume (213 ml/kg, compared to 132 ml/kg in harbour seals) and appear to be physiologically capable of longer bouts of diving, increasing their foraging time. This is supported by dive profiles from the region: grey seals in Scotland generally forage at depths of 50-90m (Mcconnell et al., 1999), while harbour seals dive to depths of 20-60m (Tollit et al., 1998). Importantly, both grey and harbour seals generally forage at or near the bottom of the water column, with exceptions at the individual level (Jones et al., 2015). Further, the at-sea usage of grey seals appears to be larger than the at-sea usage of harbour seals, suggesting that the increased size of grey seals enables them to forage across a larger area, while harbour seals’ size limits both movement and thermoregulatory capacity (Jones et al., 2015).

Grey seals and harbour seals coexist in many systems, but the observed decline in harbour seal populations is unique to specific MU’s within the UK. Concurrently, in these MU’s, grey seal populations have apparently reached carrying capacity, and PDV outbreaks have caustically damaged harbour seal populations in the last 30 years. While it is probable that the two populations are in competition, this competition must be considered in the context of human exploitation of seal prey species. Furthermore, with grey seal populations approaching pre-cull levels, harbour seal declines may in fact be attributable to exploitation of prey species driving direct competition, as such competition may not have existed before fishing pressure that ultimately led to culls (SCOS, 2021). While continuous monitoring is needed to determine whether harbour seals are declining due to competition, fish stocks (especially gadids and Sandeel) must be re-evaluated for human take, as in this case they likely support double the number of pinniped species as previously thought, in addition to a suite of other species (Howell et al., 2010; Jones et al., 2006).

The observed niche areas (0.354659, 0.965615, 0.450904, and 1.430523 ‰2 for grey and harbour Seal Plasma and RBC’s, respectively Table 1) and prey composition analyses herein provide support for grey seal competition as a driver of harbour seal decline. Ultimately, competition reduces the available prey for harbour seals, and may even force them to shift to lower quality prey, or expand their foraging range and prey items to meet energetic demand. Future prey quality analyses will help to understand if this is indeed the case, or if harbour seals’ broader niche is a consequence of differential foraging behaviour (Witteveen et al., 2011). In either case, the decline of harbour seals in UK MU’s warrants further monitoring, at least until harbour seal population stabilise, or a cause of decline is identified and halted.

This study examined the stable isotope ecology of two sympatric pinniped populations in the UK, and provided preliminary evidence for competition. While we recommend continued monitoring, these findings can be further contextualized by using SIA on historical samples (e.g., museum specimens of bone or teeth). Further, our findings set a baseline for future SIA studies that can monitor fish populations by proxy, using an inexpensive, minimally invasive technique. The management implications for this study are apparent: any protections for grey seals will likely also protect harbour seals, and vice versa. Though they are best managed as separate stocks, the carry-over effects of conservation efforts on one species (e.g., a marine protected area designed for grey seals) will have immediate positive impacts on the other. Additionally, adequate fisheries management strategies (e.g., the 2023 closure of the UK’s North Sea sandeel fishery (DEFRA, 2023)) will increase the available biomass in the water, allowing both species to thrive with reduced competitive pressure. Future responsible management of fish stocks must consider that humans actively compete with marine predators for prey, and ensure that anthropogenic pressures do cause undue harm on the marine environment.

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Table S1: Informative Prior distributions and posterior densities for each prey species grouped by SIMM. Informative prior distributions (informative priors) are in %, and posterior density values are rported as medians with 95% credible intervals in brackets as a proportion.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | RBC Autumn/Winter | | | Plasma | | | RBC Spring/Summer | | |
|  | Prey Spp. | Informative Prior | Posterior Density | Prey Spp. | Informative Prior | Posterior Density | Prey Spp. | Informative Prior | Posterior Density |
| Grey |  |  |  | Blue Whiting | 35.3 | 0.159 (0.010-0.534) | Blue Whiting | 35.3 | 0.218 (0.008-0.705) |
| Blue Whiting | 31.9 |  | Bluemouth | 33.6 | 0.225 (0.017-0.501) | Bluemouth | 33.6 | 0.227 (0.011-0.680) |
| Benthic Sandeel | 33.3 |  | Cod | 35.3 | 0.087 (0.005-0.330) | Cod | 35.3 | 0.093 (0.005-0.424) |
| Cod | 31.9 |  | Grey Gurnard | 33.6 | 0.154 (0.008-0.489) | Grey Gurnard | 33.6 | 0.087 (0.004-0.369) |
| Pelagic Sandeel | 33.3 |  | Pelagic Sandeel | 18.8 | 0.146 (0.002-0.407) | Pelagic Sandeel | 18.8 | 0.063 (0.000-0.331) |
|  |  |  | Red Gurnard | 33.6 | 0.107 (0.005-0.406) | Red Gurnard | 33.6 | 0.115 (0.005-0.473) |
| Harbour | Argentine | 20 | 0.129 (0.003-0.585) | Argentine | 31.4 | .307 (0.225-0.396) | Argentine | 31.4 | 0.205 (0.020-0.705) |
| Blue Whiting | 27.6 | 0.286 (0.008-0.840) | Benthic Sandeel | 23.7 | .207 (0.147-0.278) | Blue Whiting | 23.9 | 0.331 (0.009-0.888) |
| Cod | 27.6 | 0.250 (0.013-0.721) | Cod | 23.9 | 0.231 (0.160-0.313) | Cod | 23.9 | 0.181 (0.008-0.683) |
| Pelagic Sandeel | 31.5 | 0.188 (0.020-0.473) | Pelagic Sandeel | 23.7 | 0.250 (0.173-0.338) | Pelagic Sandeel | 23.7 | 0.106 (0.000-0.378) |

A diagram of different colors

Description automatically generated with medium confidenceA chart of different colors

Description automatically generated with medium confidence

Figure S1: An analogue of figure 4B; Seals in RBC isospace with shape mapped to sex. 4 Harbour seals exceed the isospace polygon formed by the aggregated values from prey species, while 2 harbour grey seals exceed the same polygon.