ICES Journal of Marine Science, 2025, Vol. 82, Issue 4, fsaf052
https://doi.org/10.1093/icesjms/fsaf052
Received: 9 October 2024; **revised:** 3 April 2025; **accepted:** 4 April 2025
Original Article

ICES CIEM
International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

Morphological traits distinguish feeding guilds in a Southern Ocean demersal fish community

Patrick Eskuche-Keith[1,2,*], **Simeon L. Hill**[2], **Michelle L. Taylor**[1], **Philip Hollyman**[2,3], **Martin A. Collins**[2], **Eoin J. O'Gorman**[1]

[1]School of Life Sciences, University of Essex, Wivenhoe Park, Colchester CO4 3SQ, United Kingdom
[2]British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, United Kingdom
[3]School of Ocean Sciences, Bangor University, Bangor, Gwynedd LL57 2DG, United Kingdom

*Corresponding author. School of Life Sciences, University of Essex, Wivenhoe Park, Colchester CO4 3SQ, United Kingdom. E-mail: patrickaekeith@gmail.com

Abstract

Morphological traits reflect an organism's ecological niche and role within ecosystems. Identifying how traits are associated with diet will therefore improve our understanding of the drivers of community structure. We combined individual morphological measurements with stomach contents from nine demersal fish species from the subantarctic island of South Georgia, where climate change is impacting the distribution of a key prey species, Antarctic krill. Cluster analysis identified five feeding guilds, with traits such as gape size proving especially useful for determining guild membership. Individuals feeding on fish had larger gapes and higher caudal and pectoral fin aspect ratios, enhancing their ability to capture and consume such large, fast prey. In contrast, benthic feeders had smaller gapes and lower fin aspect ratios, reflecting reliance on suction feeding and higher manoeuvrability. Random Forest analysis reliably predicted feeding guild membership based on these simple traits, highlighting the strong links between ecology and morphology. This study provides an important step forward in the application of trait-based approaches within the Southern Ocean. Continued research into links between morphology and diet will improve our understanding of niche partitioning in marine ecosystems and aid our ability to predict the effects of environmental change on community composition and structure.

Keywords: food webs; functional traits; marine ecosystems; ecomorphology; fisheries

Introduction

The field of ecology is increasingly focusing on how interactions between individuals shape the structure and functioning of ecosystems (Åkesson et al. 2021). A key component of this approach is the consideration of how functional traits, including physiological, morphological, behavioural and life history attributes, shape how organisms respond to each other and to their environment (Violle et al. 2007). This trait-based approach seeks to identify how the functional traits of organisms combine to determine their interactions and thus drive the organization of ecological communities (Savage et al. 2007). By describing the distribution of traits within ecosystems, one can generalize the mechanisms underlying complex ecological processes and predict the resilience of key ecosystem functions to perturbations (Kiørboe et al. 2018, Beukhof et al. 2019).

Ecomorphology is a key component of trait-based ecology, whereby an individual's body form is linked to its behaviour and interactions with others (Barr 2018). An organism's physical features represent adaptation to its environment; therefore, the combination of different morphological traits largely underlies its ecological niche (Violle et al. 2007, Barr 2018). As such, morphological traits may be strongly tied to the distribution and functional role of organisms within ecosystems (e.g. Gibb et al. 2015, Pigot et al. 2016, Thomas et al. 2020).

Marine ecosystems are often strongly size-structured due to gape limitations and the interplay between body size and feeding (Jennings et al. 2001, Potapov et al. 2019). In fish, gape size often reflects feeding mode, with ambush piscivores generally exhibiting large gapes, while suction feeding planktivores often have small gapes (Luiz et al. 2019). Gape size also often constrains the maximum size of prey that can be consumed, thus determining the structure of feeding relationships (Christensen 1996). Allometric scaling relationships have been identified for tropical and temperate fish species, whereby gape size, and thus also average and maximum prey size, generally increase with predator body size (Bachiller and Irigoien 2013, Dunic and Baum 2017). In many species maximum prey size increases faster than minimum prey size as fish become larger, resulting in a widening of their trophic niche (Scharf et al. 2000). Differences in allometric relationships for body size and gape morphology could also influence levels of resource partitioning and competitive interactions within the fish community (Schuckel et al. 2012, Barnes et al. 2021). Other traits may also be important, such as fin morphology, which is linked to habitat use and prey acquisition: for example, high aspect ratios (ARs) of the caudal and pectoral fins are linked with greater swimming efficiency and maximum speed (Sambilay 1990, Higham 2007) and generally found in more active species that feed on pelagic or mobile prey such as zooplankton and fish (Hobson 1979, Bridge et al. 2016). Lower ARs provide greater manoeuvrability and thrust at low speeds and may therefore be better suited to less active benthic or ambush feeding (Higham 2007, Bridge et al. 2016).

While marine studies increasingly use trait-based approaches, these often involve competition models focused primarily on basal groups and overlook trophic interactions between predators and their prey (Kiørboe et al. 2018). The few studies that have investigated the links between morphology and diet across whole fish communities generally support the differentiation of diets based on traits such as body size, while the relative importance of other morphological traits varies (Reecht et al. 2013, Podder et al. 2021; but see also Labropoulou and Markakis 1998). Further research is needed to better define the traits driving trophic relationships, particularly in remote and understudied marine ecosystems, including polar regions where trait-function relationships might differ from those identified in other regions (Degen et al. 2018). Here, we describe the relationships between morphology and diet for nine abundant fish species around the sub-Antarctic island of South Georgia in the Southern Ocean. These are primarily demersal taxa, with only three species considered to exhibit benthopelagic behaviour (www.fishbase.se, accessed 20/02/2025). Previous research on the diet and biology of these species has revealed a system largely dominated by consumption of Antarctic krill, *Euphausia superba*, in addition to fish and macrozooplankton such as amphipods, particularly in periods of low krill availability (Kock et al. 2012), with some evidence of interspecies dietary differentiation (Targett 1981, McKenna 1991).To date, however, there has been no comprehensive investigation of the links between morphological traits and dietary niches across the wider South Georgia demersal fish community. Such information will improve our understanding of the mechanisms underlying community structure and energy flow through this component of demersal food webs. Many marine species at South Georgia are at the northern edge of their distributions and may be vulnerable to ocean warming, which is particularly rapid in this region (Whitehouse et al. 2008, Hogg et al. 2011). A southward range contraction by *E. superba* has already been observed (Kawaguchi et al. 2024), and changes in the dynamics and distribution of other zooplankton groups might also occur (Whitehouse et al. 2008), ultimately driving significant changes in community composition and associated feeding interactions. One of these demersal fish species (*Notothenia rossii*) has shown initial signs of population recovery decades after previous overfishing (Hollyman et al. 2021), whereas inferred population declines in two species (*Chaenocephalus aceratus* and *Pseudochaenichthys georgianus*) led to IUCN classifications of vulnerable and endangered, respectively (Williams 2024a, 2024b). These apparently conflicting responses and the reliance on inference highlight the need for more information on community structure and dynamics. Identifying how morphological traits influence prey selection will provide insight into the possible consequences of such shifts in prey availability for community structure. The relationships between feeding ecology and morphology identified here will provide an important addition to wider literature around fish morphology-diet relationships (e.g. Reecht et al. 2013, Podder et al. 2021), which together provide greater understanding of the drivers of marine ecosystem structure. Extending the geographical coverage of research on this topic into understudied regions such as this will also aid the identification of generalizable relationships across communities.

We hypothesize that dietary differences between and within species are explained by differences in their functional traits. We expect that predators with larger gape sizes and higher fin ARs primarily consume fish and krill, due to their ability to capture and consume such larger, mobile prey. Those feeding on smaller, less mobile prey, such as benthic invertebrates or amphipods, will display smaller gape sizes and lower fin ARs to provide the necessary manoeuvrability for benthic foraging.

Materials and methods

Sample collection

The demersal fish community was sampled from the FV *Robin M Lee* over the South Georgia and Shag Rocks shelves between the 1st and 10th of February 2023 as part of the biennial groundfish survey conducted by the British Antarctic Survey and the Government of South Georgia and the South Sandwich Islands (under Regulated Activity Permit no. 2022/065). The survey utilized a random stratified design across five shelf areas and two depth strata (100–200 m and 200–350 m), with 76 bottom trawls completed using an FP-120 net (Caedmon Nets, UK; Fig. 1). See Hollyman et al. (2023) for further details on sampling methodology. For this study, fish were opportunistically sampled from 47 catches, with efforts made to choose specimens representing a range of body lengths for each species. Selected individuals were frozen at -20°C for later analysis at the King Edward Point research station, South Georgia.

Morphological measurements and stomach contents dissection

We focused on a set of broad, key traits that can be easily measured in the field, namely body size, gape size, and ARs of the caudal and pectoral fins. Each fish was thawed before being weighed using either a small (Kern, PCB1000-2, ±0.01 g) or large (M3, WPL industries, ±1 g) top-loading scale depending on the size of the fish. For large fish (>400 mm total length, TL), measurements of TL were recorded using a fish board and dissecting ruler. All other specimens were photographed using a Sony RX100i digital camera mounted on a copy stand (Kaiser R2N), with length later measured in ImageJ software (Schneider et al. 2012). Gape measurements to the nearest mm were taken for each specimen using Vernier callipers for maximum vertical gape (G_{height}) and a dissecting ruler for maximum horizontal gape (G_{width}). The gape height and width of each fish were then combined to estimate the maximum oral gape area (G_{area}) using the following equation (Ward-Campbell et al. 2005):

$$G_{\text{area}} = \pi\left(0.5G_{\text{height}} \times 0.5G_{\text{width}}\right).$$

Photographs were also taken of each specimen's caudal and pectoral fins, with the latter excised at the fin base and laid flat. The AR of each fish's caudal and pectoral fins was estimated using the following equation:

$$\text{AR} = \frac{h^2}{a},$$

where a is the fin area (in mm) and h is either the caudal fin height or length of the leading edge of the pectoral fin, measured in ImageJ (Pauly 1989).

Each fish stomach was dissected, with non-empty stomachs weighed to the nearest 0.01 g. Stomach contents were grouped according to the lowest identifiable taxonomic level, weighed, and counted, excluding fish prey displaying no evidence of digestion (probably the result of net feeding). Where stomachs contained many individuals of a prey group, 30 individuals were subsampled and weighed to obtain an average individual weight, which was then compared to the total weight of

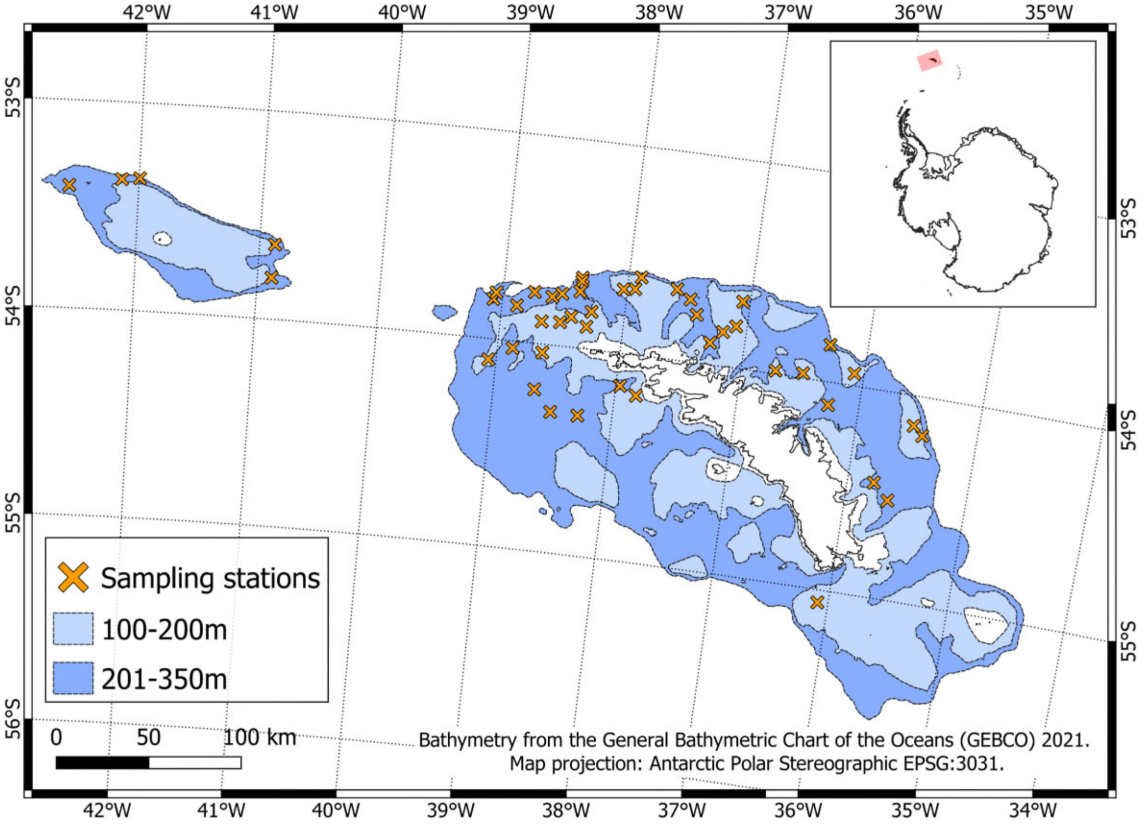

Figure 1. Distribution of haul locations from which specimens were taken, identifying the two depth zones sampled. Map generated in QGIS 3.28.0-Firenze.

those prey to estimate the total number of individuals in the stomach.

To investigate potential changes in diet with size, each individual fish was assigned to a size class, estimated by splitting the range of sampled TL across the community into four size bins of 175 mm. These were numbered 1–4 in ascending size order (1 = 93–269 mm; 2 = 269–444 mm; 3 = 444–620 mm; 4 = 620–795 mm). This split, whilst arbitrary, provided the best balance of sample sizes across size classes for most species. We defined size classes at the community level rather than at the species level to ensure that size classes were comparable across species. The relative importance of each prey group in the diet of each species-size class combination was estimated from three separate measures of importance using the % index of relative importance (%IRI), calculated as

$$\%\mathrm{IRI}_i = \frac{(\%N_i + \%W_i) \times \ \%\mathrm{FO}_i}{\sum_{i=1}^{n} (\%N_i + \ \%W_i) \ \times \ \%\mathrm{FO}_i} \times 100,$$

where %FO is the percentage frequency of occurrence, %N is the proportional abundance, and %W is the proportional weight of each prey group in the diets of each species-size class (Pinkas et al. 1970). We set a minimum sample size of five non-empty stomachs, resulting in the exclusion of the largest *Parachaenichthys georgianus* (size class 3) and smallest *C. aceratus* (size class 1) ($n = 2$ in both cases).

Identification of feeding guilds

All analyses were conducted using R statistical software version 4.3.0 (R Core Team 2023; see Table S1 for an overview of the various packages used). Species-size classes were grouped into feeding guilds with hierarchical cluster analysis, using Bray–Curtis dissimilarities calculated from the prey %IRI values. A cutoff of 50% dissimilarity was used, as this captured the primary dietary differences within the community whilst avoiding the creation of single species-size-class groups (cutoffs of 0.4 and below) and the over-grouping of taxa with relatively contrasting diets (cutoffs of 0.6 and above) (Fig. S1).

Prey were grouped into broad taxonomic groups: krill (all members of the Euphausiidae); *Themisto gaudichaudii* (an abundant swarming amphipod); other non-swarming amphipods (primarily *Vibilia* sp., *Primno macropa*, and individuals of superfamily Lysianassoidea); isopods; fish; mysids; benthic decapods (*Notocrangon* sp. and *Chorismus* sp.), and miscellaneous benthos (including polychaetes, annelids, bivalves, gastropods, and echinoderms which were sporadically found in stomachs). A reanalysis combining both amphipod groups established that this has negligible impact on the overall conclusions of this study; therefore, we present the original results with separated amphipod groups here (see Tables S11–S13 and Figs. S6–S7 for the reanalysis results). Prey accumulation curves fitted for each fish species-size class combination showed a generally adequate level of sampling at this resolution, with 18 out of 20 combinations including at least 80% of predicted diet items and >70% (mean 89%) of the predicted prey items described in all cases. Nevertheless, increased sampling for some fish species-size class combinations would have ensured a more complete description of the diet, providing context for the interpretation of our results (Fig. S2). Differences between assigned feeding guilds were then identified using the similarity percentage routine.

Table 1. Species sampled in this study, including the Food and Agriculture Organization identification code for each species, the number of individuals sampled, the range of total lengths (TL mm) of individuals sampled, and the number of non-empty stomachs.

Species	Common name	Code	*N* fish	TL range (mm)	Size classes	*N* stomachs
Family Channichthyidae (icefish)						
Champsocephalus gunnari	Mackerel icefish	ANI	135	154–573	1, 2, 3	88
Chaenocephalus aceratus	Scotia Sea icefish	SSI	119	164–622	2, 3	30
Pseudochaenichthys georgianus	South Georgia icefish	SGI	117	187–523	1, 2, 3	75
Family Nototheniidae (rockcod)						
Notothenia rossii	Marbled rockcod	NOR	75	336–795	2, 3, 4	66
Trematomus hansoni	Striped rockcod	TRH	69	169–383	1, 2	61
Lepidonotothen squamifrons	Grey rockcod	NOS	101	100–462	1, 2	86
Lepidonotothen larseni	Painted notie	NOL	81	93–216	1	67
Gobionotothen gibberifrons	Humped rockcod	NOG	104	150–572	1, 2	95
Family Bathydraconidae (dragonfish)						
Parachaenichthys georgianus	South Georgia dragonfish	PGE	92	123–434	1, 2	58

The number of stomachs by size group is shown in Fig. 4.

Predator–prey size relationships

We explored the relationship between predator mass and prey mass using a linear mixed effects model. This model included the count-weighted average prey body mass ($\log_{10}$-transformed to reduce skew and heteroscedasticity and better fit assumptions of normality) of each prey type within each stomach as a response, and predator body mass ($\log_{10}$ g) and feeding guild plus their interaction as predictors, to identify predator–prey size relationships specific to different dietary groups. Average prey masses were used to minimize the potential effects that large differences in the number of individual prey items per stomach might have on the analyses. Prey type was included as a random effect to account for potential differences in size relationships across prey taxa, and different covariate weighting structures were investigated to account for any systematic variance in the residuals (e.g. exponential, fixed, constant). Model selection by AIC comparison was used to identify the best random effects, variance weighting, and fixed effects structures (in that order).

Morphological trait distributions

We first explored inter- and intra-specific trait variation to provide context for later trait analyses. This included non-parametric Kruskal–Wallis analysis of variance (due to non-normality of residuals) and pairwise comparisons of trait distributions from the post-hoc Dunn's test with Bonferroni correction. We also plotted trait-body size relationships to describe size-related trends across species.

To identify relationships between morphological traits and feeding guild membership, the distribution of trait values (gape area, caudal fin AR, and pectoral fin AR) across individuals within each feeding guild was compared using Kruskal–Wallis analysis of variance and Dunn's test. We also used a principal components analysis (PCA) based on Euclidean distance to explore the distribution of feeding guilds in multi-dimensional trait space. To minimize the influence of individual body size on the ordination, we standardized each measurement to the TL of the individual using the following equation:

$$Y_i^* = Y_i \left| \frac{TL_0}{TL_i} \right|^b ,$$

where Y_i^* is the standardized predicted value of trait Y for individual i, Y_i is the measured value of the trait for individual i, TL_i is the measured TL of individual i, TL_0 is the mean TL for all individuals, and the parameter b is the slope from an ordinary least-squares regression of log-transformed Y and TL (Lleonart et al. 2000). This standardization effectively adjusts the trait measurements to values they would have if the individuals were of the average body size for the sampled population (Lleonart et al. 2000). We conducted this standardization for all individuals of the same species that were assigned to the same feeding guild to reduce allometric effects while still reflecting situations where different size classes of a given species were assigned to separate guilds.

We then implemented a Random Forest (RF) model to assess whether feeding guild membership could be predicted from the standardized morphological traits. RF modelling is a classification tool that uses bootstraps for the prediction of group membership and provides an indication of the relative importance of predictor variables for partitioning individuals into clusters (Cutler et al. 2007). We implemented cross-validation by randomly sub-sampling 70% of the data to calibrate the model and then using the remaining 30% for prediction and repeated this 100 times to investigate the variability around classification accuracy and relative importance of each trait. We assessed the predictive ability of the RF model through the true skill statistic (TSS), with values of 1 and 0 indicating perfect and completely random predictions, respectively (Allouche et al. 2006).

Results

A total of 893 individuals from nine demersal fish species were sampled for this study (Table 1). In most species, stomach contents were present for the majority of individuals, although for Scotia Sea icefish (*Chaenocephalus aceratus*) only 25% of stomachs were non-empty (Table 1).

Species trait relationships

The sampled fish displayed various interspecific differences in their traits. The icefish *Ps. georgianus* and *C. aceratus* and rockcod *N. rossii* had the largest gapes, while the remaining rockcods, particularly *L. larseni*, had the smallest gapes (Fig. S3a). The intercepts of the species-specific gape-size relationships showed a similar rank order (with the icefish *Ps. georgianus* highest and *G. gibberifrons* and *L. larseni* lowest) with consistent slopes across species (Fig. S3b). *Champsocephalus gunnari gunnari* and *C. aceratus* displayed the

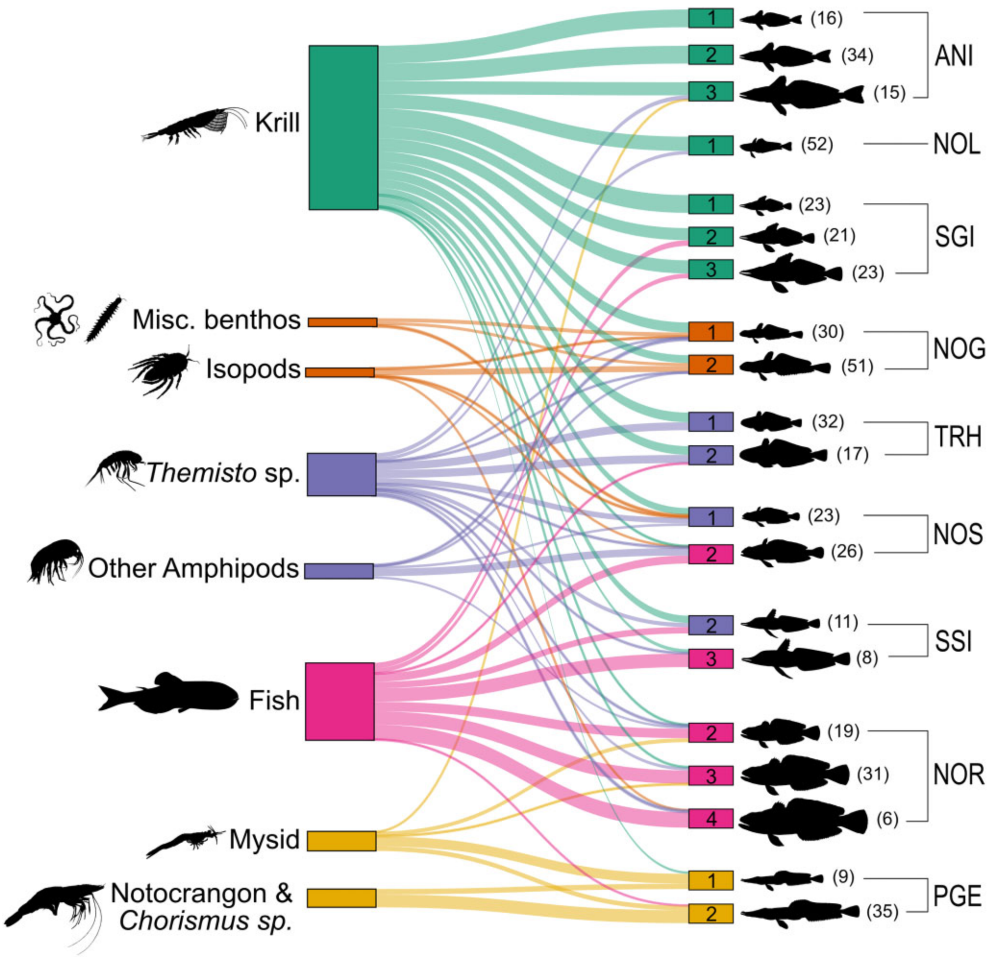

Figure 2. Sankey diagram depicting the trophic interactions between prey groups (left) and predators (right). Link thickness is proportional to %IRI (links representing <1% are omitted for clarity). Node colours represent the feeding guilds determined by cluster analysis (from top to bottom: 'krill feeders'; 'benthos feeders'; 'Themisto and krill feeders'; 'fish feeders'; 'benthic shrimp feeders'). Numbers within boxes indicate the size class (also represented by silhouette size), numbers in brackets indicate sample size (number of non-empty stomachs). Species codes are: ANI = *Champsocephalus gunnari*; NOL = *Lepidonotothen larseni*; SGI = *Pseudochaenichthys georgianus*; NOG = *Gobionotothen gibberifrons*; TRH = *Trematomus hansoni*; NOS = *Lepidonotothen squamifrons*; SSI = *Chaenocephalus aceratus*; NOR = *Notothenia rossii*; PGE = *Parachaenichthys georgianus*.

highest caudal ARs, and *N. rossii* and the icefish *Ps. georgianus* exhibited the highest pectoral ARs, while the dragonfish *Pa. georgianus* had the lowest caudal and pectoral ARs (Fig. S3c, e). The relationships between fin AR and body size varied considerably between species (Fig. S3d, f).

Feeding guilds

The cluster analysis identified five feeding guilds at a 50% dissimilarity level (Fig. 2; Fig. S4; Table S2): (i) 'krill feeders' included all size classes of the icefish *C. gunnari* and *Ps. georgianus* (classes 1–3), and the rockcod *L. larseni* (which was only represented by the smallest size class 1); (ii) 'benthos feeders' consumed miscellaneous benthos and isopods, and represented all size classes of *G. gibberifrons* (1 and 2); (iii) '*Themisto* and krill feeders' contained all size classes of *T. hansoni* (1 and 2), in addition to the smallest *L. squamifrons* (1) and size class 2 *C. aceratus*, though fish were also important in their diet; (iv) 'fish feeders' contained the larger *C. aceratus* (3) and *L. squamifrons* (2), and all *N. rossii* (2–4); and (v) 'benthic shrimp feeders', represented by the dragonfish *Pa. georgianus* (classes 1 and 2), which fed primarily on mysids and the decapods *Notocrangon* sp. and *Chorismus* sp. See Table S3 for an overview of the %IRI values of each predator species-size class by prey group combination.

The final linear mixed effects model of prey mass as a function of predator mass included a random intercept for prey type (reflecting different average body sizes for prey taxa) and a combination of fixed variance weighting structure for predator body mass and constant variance weighting structure for prey type (Table S4). The fixed effect structure included predator body mass and feeding guild as additive predictors, with no significant interaction identified (Table S5). Overall, the model identified a significant increase in prey size with predator size, with a consistent slope but different intercepts of the relationship across feeding guilds ($F_{6,599} = 134.80$, $P < .001$; Fig. 3; Table S6).

Distinguishing feeding guilds with functional traits

Significant differences in trait values between feeding guilds were observed for all traits (Fig. 4; Tables S7–S8). 'Fish feeders' had the largest gape areas, while 'krill feeders' and 'benthic shrimp feeders' generally had intermediate gape areas, with 'benthos feeders' and '*Themisto* and krill feeders' having the smallest gape areas (Fig. 4a). There were only small dif-

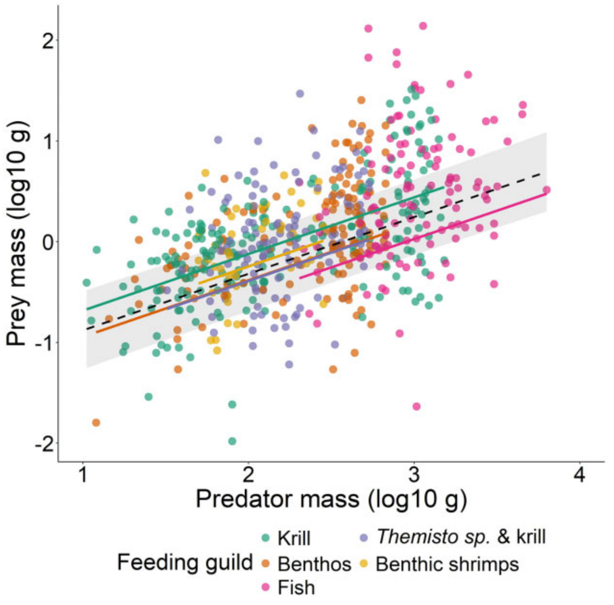

Figure 3. Partial residuals plot from a linear mixed effects model of the relationship between predator body mass and count-weighted average prey mass consumed across feeding guilds. Each point represents one predator. Dashed line represents the overall model fit, with shading representing 95% confidence intervals. Solid lines represent fits for each feeding guild. Model coefficients are provided in Table S5.

ferences in caudal fin AR across guilds, with the largest values observed in the 'fish feeders' and 'krill feeders' and the smallest observed in the 'benthic shrimp feeders' (Fig. 4b). Similarly, the 'fish feeders' had the highest pectoral fin ARs, while the 'benthic shrimp feeders' had significantly lower values compared to other groups (Fig. 4c). These differences between feeding guilds were captured by the PCA of length-standardized fish traits, which consisted of three dimensions with Dim1 and Dim2 together explaining 86% of the variance (Table S9). Dim1 was strongly correlated with gape area and pectoral fin AR ($r = 0.62$ and $r = 0.59$, respectively), while Dim2 was strongly correlated with caudal fin AR ($r = 0.84$; Fig. 5a; Table S10). The PCA indicated substantial overlap in trait space for each feeding guild, with the primary differentiation being between the 'fish feeders', which generally had positive Dim1 scores, and the 'benthic shrimp feeders', '*Themisto* and krill feeders', and 'benthos feeders', which generally had negative Dim1 scores and overlapped considerably with one another (Fig. 5a). Additionally, 'benthic shrimp feeders' were separated from the '*Themisto* and krill feeders' guild along Dim2 (Fig. 5a). The 'krill feeders' were spread across most of the trait space (Fig. 5a).

Despite the high levels of overlap in trait space for some feeding guilds, the RF model could predict feeding guild membership relatively well, with an average TSS score of 0.77 ± 0.12 over 100 cross-validation runs. The most important trait for predicting guild membership was gape area (84% relative importance), followed by caudal and pectoral fin AR (both 8% relative importance; Fig. 5b).

Discussion

We investigated the role of morphological traits in driving prey selection at the community level, providing insight into the partitioning of energy flows across species and size classes of demersal fish. Such a trait-based understanding of trophic interactions can ultimately be used to model community structure and function (Kiørboe et al. 2018) and could thus elucidate how future environmental change will alter the structure and stability of food webs.

Our analyses suggest that members of this community display differing levels of dietary specialization, with the diets of some groups dominated by specific taxa while others are clearly more opportunistic and generalist. The observed feeding relationships are broadly consistent with previous dietary research in the region (e.g. Targett 1981, McKenna 1991, Reid et al. 2007, Clarke et al. 2008, Main et al. 2009, Hollyman et al. 2021), indicating that we successfully described the broad summer dietary niches of the studied fish. The large proportion of empty stomachs observed for *C. aceratus* is a common observation in other studies and may be due to a combination of sporadic feeding and regurgitation during capture (Flores et al. 2004).

There can, however, be interannual variability in diets (e.g. Main et al. 2009, Hollyman et al. 2021), possibly driven by changes in krill availability, and it is notable that the %IRI of krill in *C. gunnari* diets in 2023 was the third highest in 14 years of data (see Fig. S5). Thus, our data may represent a situation in which krill were more readily available to the demersal fish community than usual. Overall, the utilization of krill by all feeding guilds highlights the key role this group plays in maintaining energy flow within Southern Ocean food webs. Demersal fish are themselves a major dietary component of albatrosses, petrels, gentoo penguins, and Antarctic fur seals (Hill et al. 2005, Reid et al. 2005, Waluda et al. 2017), indicating that these fish are a key link between krill and many top predators in the Southern Ocean.

Size-based feeding

Average prey mass increased with predator mass with consistent scaling across all feeding guilds regardless of prey type, suggesting strong size-structuring. This supports the generalizability of predator–prey size relationships across feeding guilds, suggesting that allometric scaling could be applied more broadly to predict feeding interactions. Previous research on coral reef fishes found that predator–prey size scaling relationships vary with diet type, with piscivores exhibiting positive allometric relationships but benthic invertivores displaying no significant change in prey size with predator size (Dunic and Baum 2017). The contrast with our results may be due to methodological differences, as we used log10 masses rather than untransformed TLs and count-averaged rather than individual prey size. Indeed, another study on coral reef fish which employed a similar approach to ours found significant increases in prey size with predator size for both piscivores and benthic invertivores, supporting our conclusions (Coghlan et al. 2022).

The variation in the intercepts of the relationship between predator and prey size for different feeding guilds may reflect differences in the dietary specialization of their constituent members. Surprisingly, the 'fish feeders' had the smallest intercept, which could be due to their generalist diets consisting of a broad range of prey sizes, including numerous very small prey items in addition to fewer large fish prey. As fish grow, minimum prey sizes often increase less steeply than maximum prey sizes, resulting in a broadening of their trophic niche, which may be the case for members of this guild (Scharf et al. 2000).

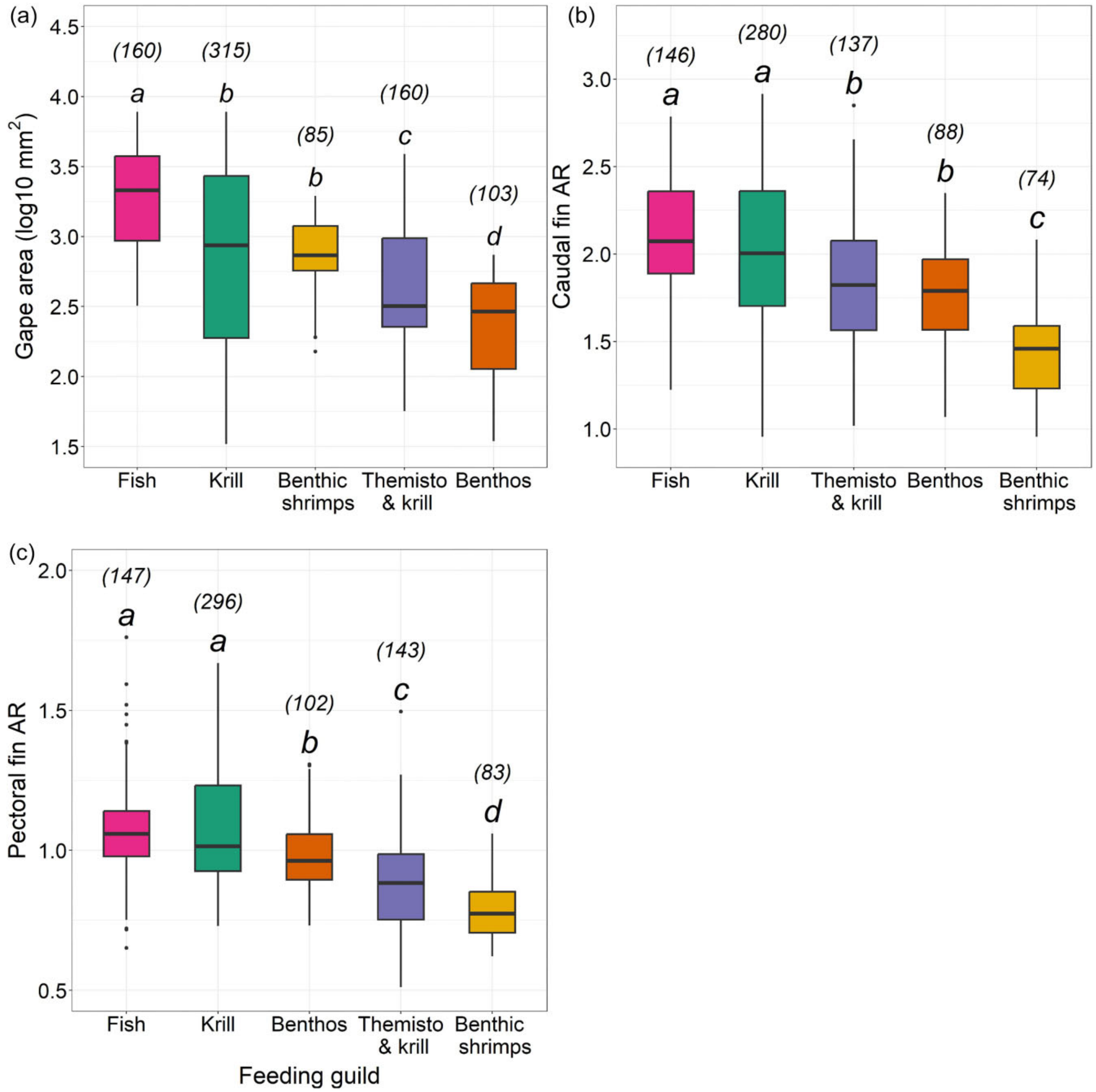

Figure 4. Boxplots of the distribution of absolute traits for each feeding guild, organized in decreasing order of median trait value: (a) gape area; (b) caudal fin AR; (c) pectoral fin AR. Letters indicate groupings assigned by a Dunn's test with Bonferroni correction (groups with a letter in common are not significantly different), numbers in brackets represent sample sizes. Note the log scale in panel (a).

In contrast, the apparent high dependence of the 'krill feeders' on such a relatively large-bodied prey, with minor contributions from other prey groups, may lead to a low trophic niche breadth which ultimately drives the higher intercept for this feeding guild. There were also some size-related changes in prey selection, e.g. *C. aceratus* switched from a mixture of krill, *Themisto* sp., and limited fish consumption to a fish-dominated diet as they became larger, while *G. gibberifrons* moved from small and relatively immobile taxa like bivalves and gastropods to large, more mobile isopods as they grew. These shifts indicate that these fish are potentially gape limited at smaller sizes or that their foraging behaviour changes as they grow.

Functional traits and feeding guilds

We found that some easily measured morphological traits can be used to distinguish feeding guilds. Gape area was the best predictor of guild membership, and 'fish feeders' generally had the largest gapes, reflecting the influence of gape limitation on the diets of fish. However, the icefish *Ps. georgianus* (a krill feeder) had absolute and standardized gape areas of similar or even greater dimensions to those of 'fish feeders', which suggests that prey selection by this species is not driven solely by gape limitation. Thus, the combination of multiple traits is important in determining trophic niches in ecological communities. It has been proposed that the elongated head, non-protractile jaw, and large gape of channichthyids, includ-

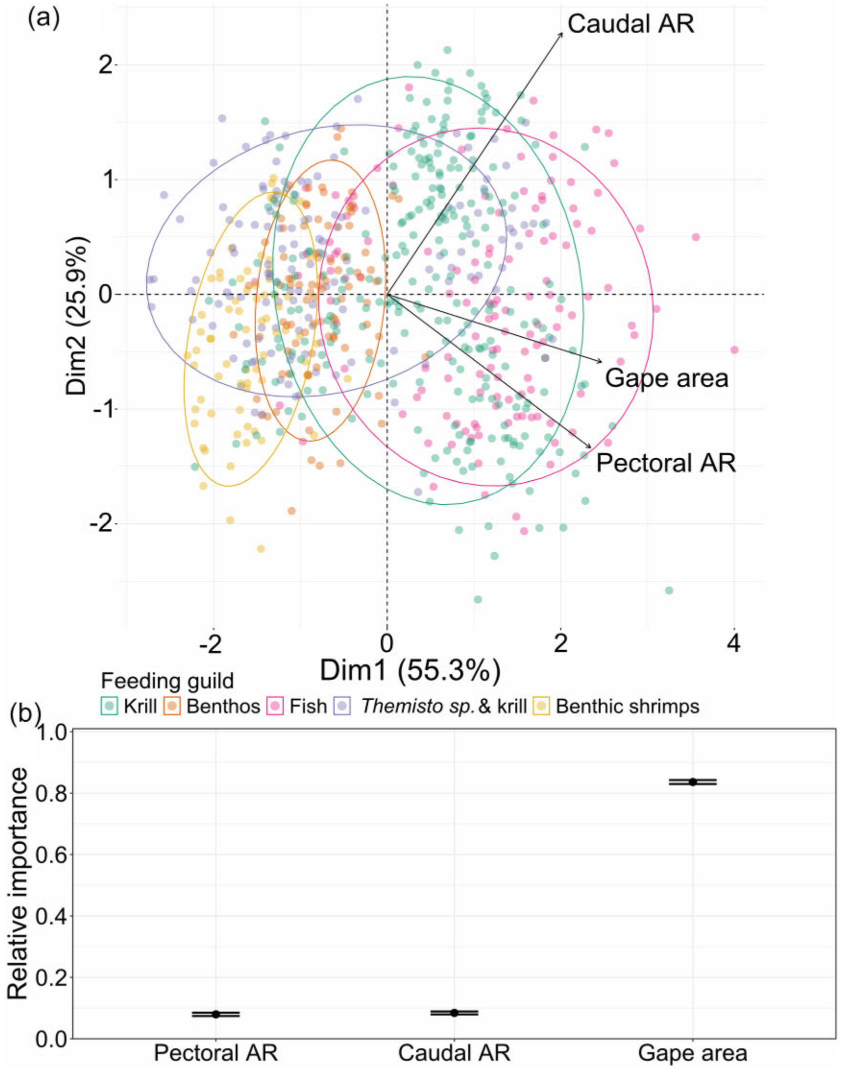

Figure 5. (a) PCA plot of individual fish based on the length-standardized morphological traits, coloured by feeding guild. Ellipses encompass 80% of the points from that guild; (b) relative importance of length-standardized traits (as proportion of the summed importance of all traits) for classifying individuals into feeding guilds. Error bars are the 95% confidence intervals from 100 cross-validations of the model.

ing *Ps. georgianus* facilitates a ram feeding mode (Bansode et al. 2014), and this might aid zooplanktivores that feed on swarming prey, as they can efficiently capture many prey items simultaneously. The diets of larger *Ps. georgianus* also contained some fish, and both *Ps. georgianus* and *C. aceratus* ('fish feeder') are morphologically very similar, which indicates that there may be further factors driving prey selection in these species, such as possible differences in their distribution within the water column or variation in opercular structure (Wilson et al. 2013). At the other end of the scale, the 'benthos feeders' had the smallest absolute and relative gape areas of all the feeding guilds. Possession of a relatively small mouth aperture correlates inversely with flow velocity (Wainwright et al. 2007) and may benefit these fish, which likely use suction feeding to capture benthic epi- and infauna.

Interestingly, *L. larseni* had an extremely small gape area despite being a member of the 'krill feeders' guild, which normally utilize large mouths to consume many prey items simultaneously, and the average size of krill consumed did not differ from other larger members of the 'krill feeders'. This suggests that *L. larseni* may target individual krill despite their sub-optimal trait configuration, highlighting the adaptability of the demersal fish community to incorporate such ubiquitous, high energy content prey in their diet.

The fin ARs measured across this community are quite low for fish in general (Sambilay 1990). This reflects the demersal nature of these fish, as low AR typically corresponds with lower swimming efficiency but higher manoeuvrability at low speeds, suited to fish that inhabit benthic environments (Pauly 1989, Bridge et al. 2016). Despite the narrow range of AR values, it was possible to distinguish some species and feeding guilds based on this trait. For example, *C. gunnari* are known to feed pelagically, which may explain their relatively high caudal AR, as this facilitates sustained swimming (Higham 2007). Similarly, the high pectoral fin AR of the 'fish feeders' likely aids in capturing mobile prey, providing greater potential for efficient, lift-based swimming (Pauly 1989, Bridge et al. 2016). The extremely low fin AR observed for the 'benthic shrimp feeders' may be closely tied to the ecology of their main prey (mysids and the decapods *Notocrangon* spp. and *Chorismus* spp.), which spend much of their time either partially buried in substrate or perched on sponges (Gutt et al. 2004). Low pectoral fin AR, representing greater manoeuvrability and stability at low speeds (Higham 2007), may provide this group with the mobility required to position themselves rapidly and accurately in relation to these individual prey items. Additionally, malacostracan crustaceans, including shrimps, are capable of rapid 'tail-flip' antipredator escape responses (Arnott et al. 1998); therefore, the high acceleration potential provided by very low caudal AR may allow the 'benthic shrimp feeders' to strike and capture their prey before they are able to flee. The remaining guilds are more difficult to distinguish by their fin morphology alone, suggesting either that similar swimming capabilities are required for feeding on krill, amphipods, and benthic taxa, or that their fin morphology is not tied strongly to their diet.

Further considerations

While our simple morphological traits proved useful for differentiating some feeding guilds, we also conclude that there is a significant region of shared trait space between certain guilds, which could hinder efforts to identify generalizable trait-diet relationships in this community. In particular, the 'krill feeders' guild displayed a broad range of morphologies which overlapped with all other guilds, suggesting that krill were readily available to fish regardless of their morphology and behaviour. *Euphausia superba* is traditionally considered a pelagic species which spends most of its time in epipelagic waters, but there is evidence that krill-benthos interactions are common, with large krill swarms often observed close to the seabed and krill found in the diet of strictly benthic species like the benthic skate *Amblyraja georgiana* (Main and Collins 2011, Schmidt et al. 2011). Plasticity in krill behaviour may mean they act as both a swarming prey in the water column for bentho-pelagic predators to feed on and also come into contact with the epibenthos, where they become available to benthic feeders. The combination of such widespread accessibility and the high energetic value and general abundance of krill makes them a suitable prey item for fish displaying a wide variety of trait configurations. This further highlights the key role of krill within Southern Ocean food webs, indicating that they effectively bridge the ecological niches otherwise imposed by longer-term morphological evolution.

The density and availability of krill to shelf predators around South Georgia varies interannually (Fielding et al. 2014) and, as noted above, availability may have been high during sampling for the current study. Competition theory holds that niche partitioning should increase as resources become limited, with predators focusing on the prey they are best suited to exploit, thereby promoting coexistence (Schoener 1982). The link between morphology and diet might therefore become clearer in periods of krill scarcity when levels of dietary segregation within the groundfish community may increase as species match their longer-term evolutionary niches. Continued monitoring of diets across the whole demersal community, including over different seasons, would provide insight into such competitive dynamics and could reveal temporal shifts in the importance of different prey taxa. For example, amphipods such as *T. gaudichaudii* are widely consumed by Southern Ocean fish, squid, seabirds, and marine mammals (Padovani et al. 2012, Havermans et al. 2019), and our results highlight their role in supplementing the diets of many demersal species around South Georgia. These amphipods might therefore provide an alternative resource for demersal fish around South Georgia during periods of low krill availability, although the extent to which they could support the total energy requirements of the groundfish community requires further study (Kock et al. 1994).

Further studies on the links between morphological traits and diet will help elucidate the evolutionary constraints on prey selection. The traits used in this study represent broad and easily measurable morphological features expected to influence feeding, but there are likely to be further fine-scale morphological features that could be investigated in future studies. For example, jaw length is linked to stealth and jaw closing speed and may therefore influence prey selection (Ferry et al. 2015), mouth position relates to feeding mode and habitat association (Helfman et al. 2023), and gill raker morphology determines feeding mode and minimum prey size (Macnuson and Heitz 1971). Ultimately, predator–prey interactions are determined by the combination of traits exhibited by both predator and prey individuals, including mobility, body size, physical and chemical defences, camouflage, visual acuity, feeding method, and habitat association (Spitz et al. 2014, Weigel and Bonsdorff 2018). It will therefore be important to consider the traits of prey alongside those of their predators when further investigating the drivers of feeding interactions. Detailed predator–prey trait matching could also facilitate analyses of the drivers of predation at the individual level by capturing the fine-scale variation in trait space across predator diets. By describing the distribution of traits across the available prey assemblage, it is also possible to investigate how environmental change alters the suitability of the prey field for different predators (Weigel and Bonsdorff 2018), which will be a powerful tool for predicting the ecological consequences of climate change.

Conclusion

This study provides a baseline understanding of how morphological traits underlie the ecology of Southern Ocean demersal fish. We identified gape size and, to a lesser degree, fin ARs as key predictors, with individuals that feed primarily on fish exhibiting larger gapes and ARs, while those feeding on benthic invertebrates and amphipods had smaller trait values. We also found that fish with diets dominated by krill exhibited a variety of morphological trait combinations, highlighting the key role that krill play in supporting the food web regardless of predator morphology. Continued investigation of the links between functional traits and prey selection will aid the production of generalizable community models to answer questions regarding trophic dynamics in marine food webs and the implications of abiotic change.

Acknowledgements

Many thanks to the officers and crew of the FV *Robin M Lee* for their help in collecting the samples used in these analyses. Thanks also to the staff at King Edward Point research station for supporting this research and to Dr Sophie Fielding for providing insights into krill ecology at South Georgia.

Author contributions

Conceptualization: P.E-K., S.L.H., M.L.T., P.H., and E.J.O. Methodology and Investigation: P.E-K., S.L.H., P.H., and M.A.C. Data curation, Formal analysis and Visualisation: P.E-K. Writing – original draft: P.E-K. Writing – review & editing: all authors.

Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

Conflict of interest: None declared.

Funding

This work was supported by the Natural Environment Research Council (NERC) funded ARIES Doctoral Training Partnership [NE/S007334/1] (PEK) and the NERC British Antarctic Survey (BAS) CONSEC project (SH). Groundfish survey work was supported by NERC core funding to the BAS Ecosystems programme and facilitated by the Government of South Georgia and the South Sandwich Islands (GSGSSI) and the BAS King Edward Point Research Programme.

Data availability

The data and code used in this study are available through Zenodo (https://doi.org/10.5281/zenodo.15120691).

References

Åkesson A, Curtsdotter A, Eklöf A *et al.* The importance of species interactions in eco-evolutionary community dynamics under climate change. *Nat Commun* 2021:**12**;4759 . https://doi.org/10.1038/s41467-021-24977-x

Allouche O, Tsoar A, Kadmon R. Assessing the accuracy of species distribution models: prevalence, Kappa and the true skill statistic (Tss). *J Appl Ecol* 2006;**43**:1223–32. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Arnott SA, Neil DM, Ansell AD. Tail-flip mechanism and size-dependent kinematics of escape swimming in the brown shrimp *Crangon Crangon*. *J Exp Biol* 1998;**201**:1771–84. https://doi.org/10.1242/jeb.201.11.1771

Bachiller E, Irigoien X. Allometric relations and consequences for feeding in small pelagic fish in the Bay of Biscay. *ICES J Mar Sci* 2013;**70**:232–43. https://doi.org/10.1093/icesjms/fss171

Bansode MA, Eastman JT, Aronson RB. Feeding biomechanics of five demersal Antarctic fishes. *Polar Biol* 2014;**37**:1835–48. https://doi.org/10.1007/s00300-014-1565-z

Barnes CL, Beaudreau AH, Yamada RN. The role of size in trophic niche separation between two groundfish predators in Alaskan waters. *Mar Coast Fish* 2021;**13**:69–84. https://doi.org/10.1002/mcf2.10141

Barr AW. Ecomorphology. In: D Croft, D Su, S Simpson (eds), *Methods in Paleoecology: Reconstructing Cenozoic Terrestrial Environments and Ecological Communities*. 2018, Springer: Cham, Switzerland, 339–49. https://doi.org/10.1007/978-3-319-94265-0_15

Beukhof E, Dencker TS, Pecuchet L *et al.* Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change. *Mar Ecol Prog Ser* 2019;**610**:205–22. https://doi.org/10.3354/meps12826

Bridge TCL, Luiz OJ, Coleman RR *et al.* Ecological and morphological traits predict depth-generalist fishes on coral reefs. *Proc R Soc B Biol Sci* 2016;**283**:20152332. https://doi.org/10.1098/rspb.2015.2332

Christensen B. Predator foraging capabilities and prey antipredator behaviours: pre- versus postcapture constraints on size-dependent predator–prey interactions. *Oikos* 1996;**76**:368–80. https://doi.org/10.2307/3546209

Clarke S, Reid WDK, Collins MA *et al.* Biology and distribution of south Georgia icefish (*Pseudochaenichthys georgianus*) around South Georgia and Shag Rocks. *Antarct Sci* 2008;**20**:343–53. https://doi.org/10.1017/S0954102008000990

Coghlan AR, Blanchard JL, Heather FJ *et al.* Community size structure varies with predator–prey size relationships and temperature across Australian reefs. *Ecol Evol* 2022;**12**:e8789. https://doi.org/10.1002/ece3.8789

Cutler DR, Edwards TC, Beard KH *et al.* Random forests for classification in ecology. *Ecology* 2007;**88**:2783–92. https://doi.org/10.1890/07-0539.1

Degen R, Aune M, Bluhm BA *et al.* Trait-based approaches in rapidly changing ecosystems: a roadmap to the future polar oceans. *Ecol Indic* 2018;**91**;722–36. https://doi.org/10.1016/j.ecolind.2018.04.050

Dunic JC, Baum JK. Size structuring and allometric scaling relationships in coral reef fishes. *J Anim Ecol* 2017;**86**:577–89. https://doi.org/10.1111/1365-2656.12637

Ferry LA, Paig-Tran EM, Gibb AC. Suction, ram, and biting: deviations and limitations to the capture of aquatic prey. *Integr Comp Biol* 2015;**55**:97–109. https://doi.org/10.1093/icb/icv028

Fielding S, Watkins JL, Trathan PN *et al.* Interannual variability in Antarctic Krill (*Euphausia superba*) density at South Georgia, Southern Ocean: 1997–2013. *ICES J Mar Sci* 2014;**71**:2578–88. https://doi.org/10.1093/icesjms/fsu104

Flores H, Kock KH, Wilhelms S *et al.* Diet of two icefish species from the South Shetland Islands and Elephant Island, *Champsocephalus gunnari* and *Chaenocephalus aceratus*. *Polar Biol* 2004;**27**:119–29. https://doi.org/10.1007/s00300-003-0570-4

Gibb H, Stoklosa J, Warton DI *et al.* Does morphology predict trophic position and habitat use of ant species and assemblages? *Oecologia* 2015;**177**:519–31. https://doi.org/10.1007/s00442-014-3101-9

Gutt J, Gorny M, Arntz W. Spatial distribution of antarctic shrimps (Crustacea: Decapoda) by underwater photography. *Antarct Sci* 1991;**3**:363–9. https://doi.org/10.1017/S0954102091000469

Havermans C, Auel H, Hagen W *et al.* 2019. *Predatory Zooplankton on the Move: Themisto Amphipods in High-Latitude Marine Pelagic Food Webs*. Elsevier: Amsterdam.

Helfman GS, Collette BB, Facey DE *et al.* 2023. *The Diversity of Fishes: Biology, Evolution and Ecology*. John Wiley & Sons Ltd: Chichester, UK.

Higham TE. The integration of locomotion and prey capture in vertebrates: morphology, behavior, and performance. *Integr Comp Biol* 2007;**47**:82–95. https://doi.org/10.1093/icb/icm021

Hill SL, Reid K, North AW. Recruitment of mackerel icefish (*Champsocephalus gunnari*) at South Georgia indicated by predator diets and its relationship with sea surface temperature. *Can J Fish Aquat Sci* 2005;**62**:2530–7. https://doi.org/10.1139/f05-157

Hobson ES. Interactions between Piscivorous Fishes and Their Prey. *Predator–prey systems in fisheries management*, 1979:231–42.

Hogg OT, Barnes DK, Griffiths HJ. Highly diverse, poorly studied and uniquely threatened by climate change: an assessment of marine biodiversity on South Georgia's continental shelf. *PLoS One* 2011;**6**:e19795. https://doi.org/10.1371/journal.pone.0019795

Hollyman P, Hill SL, Gunn C *et al.* Report of the UK groundfish survey at South Georgia (CCAMLR Subarea 48.3) in February 2023. 2023. *CCAMLR WG-FSA 2023/45*.

Hollyman PR, Hill SL, Laptikhovsky VV *et al.* A long road to recovery: dynamics and ecology of the marbled rockcod (*Notothenia rossii*, family: nototheniidae) at South Georgia, 50 years after overexploitation. *ICES J Mar Sci* 2021;**78**:2745–56. https://doi.org/10.1093/icesjms/fsab150

Jennings S, Pinnegar JK, Polunin NVC *et al.* Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *J Anim Ecol* 2001;**70**:934–44. https://doi.org/10.1046/j.0021-8790.2001.00552.x

Kawaguchi S, Atkinson A, Bahlburg D *et al.* Climate change impacts on Antarctic krill behaviour and population dynamics. *Nat Rev Earth Environ* 2024;**5**:43–58. https://doi.org/10.1038/s43017-023-00504-y

Kiørboe T, Visser A, Andersen KH *et al.* A trait-based approach to ocean ecology. *ICES J Mar Sci* 2018;**75**:1849–63. https://doi.org/10.1093/icesjms/fsy090

Kock KH, Barrera-Oro E, Belchier M *et al.* The role of fish as predators of krill (*Euphausia superba*) and other pelagic resources in the Southern Ocean. *CCAMLR Science* 2012;**19**:115–69.

Kock KH, Wilhelms S, Everson I *et al.* Variations in the diet composition and feeding intensity of mackerel icefish *Champsocephalus gunnari* at South Georgia (Antarctic). *Mar Ecol Prog Ser* 1994;**108**:43–57. https://doi.org/10.3354/meps108043

Labropoulou M, Markakis G. Morphological-dietary relationships within two assemblages of marine demersal fishes. *Environ Biol Fishes* 1998;**51**:309–19. https://doi.org/10.1023/A:1007445112309

Lleonart J, Salat J, Torres GJ. Removing allometric effects of body size in morphological analysis. *J Theor Biol* 2000;**205**:85–93. https://doi.org/10.1006/jtbi.2000.2043

Luiz OJ, Crook DA, Kennard MJ *et al.* Does a bigger mouth make you fatter? Linking intraspecific gape variability to body condition of a tropical predatory fish. *Oecologia* 2019;**191**:579–85. https://doi.org/10.1007/s00442-019-04522-w

Macnuson JJ, Heitz JG. Gill raker apparatus and food selectivity among mackerels, tunas, and dolphins. *Fish Bull* 1971;**69**:361–70.

Main CE, Collins MA. Diet of the Antarctic starry skate *Amblyraja georgiana* (Rajidae, Chondrichthyes) at South Georgia (Southern Ocean). *Polar Biology* 2011;**34**:389–96. https://doi.org/10.1007/s00300-010-0894-9

Main CE, Collins MA, Mitchell R *et al.* Identifying patterns in the diet of mackerel icefish (*Champsocephalus gunnari*) at South Georgia using bootstrapped confidence intervals of a dietary index. *Polar Biol* 2009;**32**:569–81. https://doi.org/10.1007/s00300-008-0552-7

Mckenna JE. Trophic relationships within the Antarctic demersal fish community of South Georgia Island. *Fishery Bull* 1991;**89**:643–54.

Padovani LN, Viñas MD, Sánchez F *et al.* Amphipod-supported food web: *T hemisto gaudichaudii*, a key food resource for fishes in the southern Patagonian Shelf. *J. Sea Res.* 2012; **67**: 85–90. https://doi.org/10.1016/j.seares.2011.10.007

Pauly D. Food consumption by tropical and temperate fish populations: some generalizations. *J Fish Biol* 1989;**35**:11–20. https://doi.org/10.1111/j.1095-8649.1989.tb03041.x

Pigot AL, Trisos CH, Tobias JA. Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. *Proc R Soc B Biol Sci* 2016; **283**: 1–9. https://doi.org/10.1098/rspb.2015.2013

Pinkas L, Oliphant MS, Iverson ILK. Food habits of albacore, bluefin tuna, and bonito in California Waters. *Fish Bull.* 1970;**152**:**1**–105.

Podder A, Panja S, Chaudhuri A *et al.* Patterns of morphological traits shaping the feeding guilds in the intertidal mudflat fishes of the Indian Sundarbans. *J Fish Biol* 2021;**99**:1010–31. https://doi.org/10.1111/jfb.14800

Potapov AM, Brose U, Scheu S *et al.* Trophic position of consumers and size structure of food webs across aquatic and terrestrial ecosystems. *Am Nat* 2019;**194**:823–39. https://doi.org/10.1086/705811

R Core Team. 2023. *R: Language and Environment for Statistical Computing*. R Foundation for Statistical Computing: Vienna, Austria. https://www.R-project.org

Reecht Y, Rochet MJ, Trenkel VM *et al.* Use of morphological characteristics to define functional groups of predatory fishes in the Celtic Sea. *J Fish Biol* 2013;**83**:355–77. https://doi.org/10.1111/jfb.12177

Reid WDK, Clarke S, Collins MA *et al.* Distribution and ecology of *Chaenocephalus aceratus* (Channichthyidae) around South Georgia and Shag Rocks (Southern Ocean). *Polar Biol* 2007;**30**:1523–33. https://doi.org/10.1007/s00300-007-0313-z

Reid WDK, Hill SL, Diniz TC *et al.* Mackerel icefish *Champsocephalus gunnari* in the diet of upper trophic level predators at South Georgia: implications for fisheries management. *Mar Ecol Prog Ser* 2005;**305**:153–61. https://doi.org/10.3354/meps305153

Sambilay VC. Interrelationships between swimming speed, caudal fin aspect ratio and body length of fishes. *Fishbyte* 1990;**8**:16–20.

Savage VM, Webb CT, Norberg J. A general multi-trait-based framework for studying the effects of biodiversity on ecosystem functioning. *J Theor Biol* 2007;**247**:213–29. https://doi.org/10.1016/j.jtbi.2007.03.007

Scharf FS, Juanes F, Rountree RA. Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar Ecol Prog Ser* 2000;**208**:229–48. https://doi.org/10.3354/meps208229

Schmidt K, Atkinson A, Steigenberger S *et al.* Seabed foraging by Antarctic krill: implications for stock assessment, bentho-pelagic coupling, and the vertical transfer of iron. *Limnol Oceanogr* 2011;**56**:1411–28. https://doi.org/10.4319/lo.2011.56.4.1411

Schneider CA, Rasband WS, Eliceiri KW. Nih Image to Imagej: 25 Years of Image Analysis. *Nat Methods* 2012;**9**:671–5. https://doi.org/10.1038/nmeth.2089

Schoener TW. The controversy over interspecific competition: despite spirited criticism, competition continues to occupy a major domain in ecological thought. *Am Nat* 1982;**70**:586–95.

Schuckel S, Sell AF, Kroncke I *et al.* Diet Overlap among flatfish species in the southern North Sea. *J Fish Biol* 2012;**80**:2571–94. https://doi.org/10.1111/j.1095-8649.2012.03309.x

Spitz J, Ridoux V, Brind'amour A. Let's go beyond taxonomy in diet description: testing a trait-based approach to prey–predator relationships. *J Anim Ecol* 2014;**83**:1137–48. https://doi.org/10.1111/1365-2656.12218

Targett TE. Trophic ecology and structure of coastal Antarctic fish communities. *Mar Ecol Prog Ser* 1981;**4**:243–63. https://doi.org/10.3354/meps004243

Thomas KN, Gower DJ, Bell RC *et al.* Eye size and investment in frogs and toads correlate with adult habitat, activity pattern and breeding ecology. *Proc R Soc B Biol Sci* 2020;**287**:20201393. https://doi.org/10.1098/rspb.2020.1393

Violle C, Navas M-L, Vile D *et al.* Let the concept of trait be functional! *Oikos* 2007;**116**:882–92. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Wainwright P, Carroll AM, Collar DC *et al.* Suction feeding mechanics, performance, and diversity in fishes. *Integr Comp Biol* 2007;**47**:96–106. https://doi.org/10.1093/icb/icm032

Waluda CM, Hill SL, Peat HJ *et al.* Long-term variability in the diet and reproductive performance of penguins at Bird Island, South Georgia. *Mar Biol* 2017;**39** :164. https://doi.org/10.1007/s00227-016-3067-8

Ward-Campbell BMS, Beamish FWH, Kongchaiya C. Morphological characteristics in relation to diet in five coexisting Thai fish species. *J Fish Biol* 2005;**67**:1266–79. https://doi.org/10.1111/j.1095-8649.2005.00821.x

Weigel B, Bonsdorff E. Trait-based predation suitability offers insight into effects of changing prey communities. *PeerJ* 2018;**6**:e5899. https://doi.org/10.7717/peerj.5899

Whitehouse MJ, Meredith MP, Rothery P *et al.* Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century: forcings, characteristics and implications for lower trophic levels. *Deep Sea Res Part I* 2008;**55**:1218–28. https://doi.org/10.1016/j.dsr.2008.06.002

Williams JT. 2024a. *Chaenocephalus aceratus. The IUCN Red List of Threatened Species 2024: e.T241133178A241133181*. https://doi.org/10.2305/IUCN.UK.2024-1.RLTS.T241133178A241133181.en (20 February 2025, date last accessed).

Williams JT. 2024b. *Pseudochaenichthys georgianus. The IUCN Red List of Threatened Species 2024: e.T241133167A241133169*. https://doi.org/10.2305/IUCN.UK.2024-1.RLTS.T241133167A241133169.en (20 February 2025, date last accessed).

Wilson LA, Colombo M, Hanel R *et al.* Ecomorphological disparity in an adaptive radiation: opercular bone shape and stable isotopes in Antarctic icefishes. *Ecol Evol* 2013;**3**:3166–82. https://doi.org/10.1002/ece3.708

Handling Editor: Francis Juanes