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Feeding habits and trophic niche differentiation in three species of wolffish (*Anarhichas* sp.) inhabiting Newfoundland and Labrador waters

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The food and feeding habits of Northern Wolffish (*Anarhichas denticulatus*), Spotted Wolffish (*A. minor*), and Atlantic Wolffish (*A. lupus*) in Newfoundland and Labrador continental shelf waters were examined. A total of 1,451 stomachs were analysed for contents: 152 for Northern Wolffish; 262 for Spotted Wolffish; and 1,037 for Atlantic Wolffish. No particular prey item dominated the diet of any species. The two most important prey groups were pelagic fish and benthic fish (52 % of total fullness) for Northern Wolffish, shrimp and echinoderms (68 %) for Spotted Wolffish, and crabs and echinoderms (57 %) for Atlantic Wolffish. Diet overlap was highest between Spotted and Atlantic Wolffish (Schoener's Index; a = 0.52), and lowest among Northern and Atlantic Wolffish (a = 0.21). Ontogenetic shifts in dietary proportions of nine major prey groups were described for each species. Discriminant function analysis correctly classified species based on mean feeding habits (partial fullness index), with a 93-100 % success rate. Species differed significantly with respect to the relative proportions of nine major prey groups (mean PFI) in the diet (MANOVA; $p < 0.0001$), and percent contribution of benthic and piscivorous diet (MANOVA; $p < 0.01$). Based on all analyses, Northern Wolffish were described as "fish specialists" (piscivores), Spotted Wolffish as "echinoderm specialists" (benthivores), and Atlantic Wolffish as "mollusc specialists" (benthivores).

Différences dans les habitudes alimentaires et la niche trophique de trois espèces de loups de mer (*Anarhichas* sp.) présentes dans les eaux de Terre-Neuve-et-Labrador

RÉSUMÉ

On a étudié la nourriture et les habitudes alimentaires des loups à tête large (*Anarhichas denticulatus*), des loups tachetés (*A. minor*) et des loups atlantiques (*A. lupus*) dans les eaux du plateau continental de Terre-Neuve-et-Labrador. On a analysé le contenu de 1 451 estomacs : 152 estomacs de loups à tête large, 262 estomacs de loups tachetés et 1 037 estomacs de loups atlantiques. Aucune proie ne dominait particulièrement le régime alimentaire de ces trois espèces. Les deux espèces proies les plus importantes étaient les poissons pélagiques et benthiques (52 % de la plénitude totale) pour le loup à tête large, les crevettes et les échinodermes (68 %) pour le loup tacheté, et les crabes et les échinodermes (57 %) pour le loup atlantique. Le chevauchement le plus élevé (indice de Schoener; a = 0,52) a été constaté entre les régimes alimentaires du loup tacheté et du loup atlantique, et le plus faible entre ceux du loup à tête large et du loup atlantique (a = 0,21). On a décrit les variations ontogénétiques dans les proportions alimentaires de neuf principaux groupes de proies pour chaque espèce. L'analyse discriminante des données a permis de classer correctement les espèces selon leurs habitudes alimentaires moyennes (indice de plénitude partielle), avec un taux de succès de 93-100 %. Les proportions relatives des neuf principales espèces de proies (indice moyen de plénitude partiel) dans le régime alimentaire (analyse de la variance à plusieurs variables; $p < 0{,}0001$) et le pourcentage des proies benthiques et piscivores (analyse de la variance à plusieurs variables; $p < 0{,}01$) variaient considérablement d'une espèce de à l'autre. D'après les analyses, on a décrit le loup à tête large comme un « prédateur spécialiste du poisson » (piscivore). Pour ce qui est du loup tacheté et du loup atlantique, ils ont été désignés « prédateur spécialiste de l'échinoderme » (benthivore) et « prédateur spécialiste du mollusque » (benthivore) respectivement.

INTRODUCTION

An important component in understanding life history variation and population variability of wild fish is knowledge of their diet or feeding ecology. Diet can affect growth and condition of fish (Pazzia et al. 2002; Mello and Rose 2005*a*, 2005*b*) which, in turn, can affect fecundity and survival (Townsend and Winfield 1985; Rideout and Rose 2006). Such knowledge is particularly important to understanding variability in the population abundance of exploited fish species, as well as for those species that experienced high levels of abundance depletion. In Newfoundland and Labrador waters, the latter includes Northern Wolffish (*Anarhichas denticulatus*), Spotted Wolffish (*A. minor*), and Atlantic Wolffish (*A. lupus*): all having experienced major declines in abundance during the 1980s and early 1990s. Consequently, Northern Wolffish and Spotted Wolffish were designated as threatened on Schedule 1 of Canada's Species at Risk Act (SARA) in 2001 (recently upheld in November 2012), while Atlantic Wolffish was listed as a species of special concern (Simpson and Kulka 2002; Kulka et al. 2004). Although some signs of recovery for all three species have been recently detected (Simpson et al. 2011), many key aspects of wolffish life history and population dynamics remain only partially understood, including their diet and feeding ecology.

Studies of wolffish diet are not as numerous as those for economically important species in the North Atlantic; however, research has shown that they feed on a variety of organisms, including echinoderms, molluscs, polychaetes, crustaceans, and fish (Albikovskaya 1983; Templeman 1985, 1986*a*, 1986*b*; Hawkins and Angus 1986; Keats et al. 1986; Nelson and Ross 1992; Liao and Lucas 2000*a*, 2000*b*). Only one study compared feeding habits between all three species (Albikovskaya 1983). The others focused mainly on the feeding habits of Atlantic Wolffish.

This study addresses some of the knowledge gaps in wolffish diet and feeding ecology. An extensive analysis of feeding habits of all three species of wolffish inhabiting Newfoundland and Labrador waters was first conducted; then trophic niche differentiation between the three species was investigated by examination of diet overlap/separation, as well as ontogenetic and spatial variations in feeding habits. This knowledge is important to understanding variations in life history traits (e.g., growth, condition), is essential to designing effective conservation and management strategies for recovery of wolffish populations, and is critical to managing their local sustainability at sites perturbed by oil and gas exploration/production, bottom-contact fishing, marine transportation, mining, and hydroelectric projects.

METHODS

SAMPLE COLLECTION

Data were obtained during Canadian research bottom trawl surveys of NAFO Div. 2GHJ3KLMNO and Subdiv. 3Ps conducted in spring and fall (2001-04; Fig. 1). The surveys employed a stratified random design based on depth intervals and location. Kulka et al. (2006) provides a detailed description of survey design.

A total of 1,451 stomachs (Northern Wolffish: n = 152; Spotted Wolffish: n = 262; Atlantic Wolffish: n = 1,037) were sampled from Div. 2J3KLMNO and Subdiv. 3Ps. Sample sizes for Northern and Spotted Wolffish are relatively small and as such the findings of this study should be considered as preliminary for these species. Each stomach was extracted at sea and kept frozen until sampled in a laboratory at the Northwest Atlantic Fisheries Center (DFO-NL Region). Prey items were identified to the lowest taxon possible, and weighed to the nearest 0.1 gram. Excess mucous and fluids were removed prior to weighing stomach contents.

DATA HANDLING

Frequency of occurrence (FO), percent volumetric contribution (V), and mean partial fullness index (mean PFI) were used to assess the relative importance of each prey taxon to the diet of each species of wolffish. Frequency of occurrence (FO) (%) was calculated as

$$\mathrm{FO} = \frac{N_i}{N_{\mathrm{tot}}} \times 100$$

where N_i is the total number of stomachs with prey *i*, and N_{tot} is the total number of stomachs examined for each wolffish species. V (%) was calculated as

$$\mathrm{V} = \frac{w_i}{w_{\mathrm{tot}}} \times 100$$

where w_i is the total weight of prey *i* (g), and w_{tot} is the total weight of all prey (g) consumed by each wolffish species. Mean partial fullness index (mean PFI) is a length-standardized way of expressing relative volumetric prey importance (Bowering and Lilly 1992) and was calculated as

$$\text{mean PFI} = \frac{1}{n} \times \sum \frac{w_{ij}}{L_j^{\,3}} \times 10^4$$

where w_{ij} is the weight of prey *i* for fish *j* (g), L_j is the length of fish *j* (cm), and *n* is the total number of stomachs sampled for each wolffish species. Mean total fullness index (mean TFI) was also calculated as the sum of all mean PFI values. Frequency of occurrence (FO) V, and mean PFI were calculated for each prey taxon.

In addition, Schoener's Index (*a;* Schoener 1970) was used to measure the level of diet overlap between species (pairwise), and was calculated as

$$a = 1 - 0.5(\sum|pxi - pyi|)$$

where p_{xi} is the proportional contribution (mean PFI/mean TFI) of prey *i* to the diet of wolffish species *x*, and p_{yi} is the proportional contribution (volumetric) of the same prey to the diet of wolffish species *y.* Mean PFI and mean TFI values were used here (as opposed to V), in order to remove the effect of predator size on proportional prey importance. Values of *a* range between 0 and 1: low values indicate little diet overlap, and high values indicate a high level of diet overlap. Values of $a \geq 0.60$ are usually considered to represent a biologically significant level of diet overlap (Zaret and Rand 1971; Johnson and Ringler 1980).

Prey taxa were categorized into 9 major groups: pelagic fish (pf); benthic fish (bf); benthic invertebrates (bi); gastropods (gas); bivalves (biv); zooplankton (zoo); shrimp (shp); crabs (crb); and echinoderms (ech). Frequency of occurrence (FO) V, and mean PFI were recalculated for each major prey group for each wolffish species.

Mean PFI for each prey group, mean TFI, feeding intensity (FI; number of stomachs with food divided by total number of stomachs sampled), percent contribution (mean PFI values relative to mean TFI) of benthic (bf, bi, gas, biv, shp, crb, ech), fish (pf, bf) and hard-shelled prey (gas, biv, ech), and mean length-adjusted condition factor were also calculated by length class (10 cm intervals) and NAFO Division for each species of wolffish. Length-adjusted condition factor (K_{adj}) was calculated as

$$\mathrm{K}_{\mathrm{adj}} = \frac{W}{L^b} \times 100$$

where *W* is fish weight (g), *L* is standard length (cm), and *b* is the scaling coefficient from the length-weight power relationship given by

$$W = aL^b$$

STATISTICAL ANALYSIS

Discriminant Function Analysis (DFA; SPSS 10.0) was employed to test how well each wolffish species could be distinguished based on the relative importance (mean PFI) of the 9 major prey groups to wolffish diet. DFA was performed separately on length-class, and NAFO Division-specific mean PFI values. DFA was not used on individual-based PFI data, because of the predominance of zeros (i.e., empty stomachs), which violates the assumption of normality. Significance of DFA groupings was verified by Multiple Analysis Of Variance (MANOVA). It was assumed *a priori* that: (i) variability in diet between wolffish species would be larger than that between length-classes (i.e., ontogenetic variation); and (ii) variability in diet between species would be larger than that between NAFO Divisions (i.e., spatial variation).

Average feeding habits of each wolfish species were also ordinated using mean percent contribution of fish and benthic prey, and plotted in 2-dimensional trophic niche space by length class and NAFO Division separately. Differences in both variables (mean % benthic; mean % piscivorous) between wolffish species were tested simultaneously by MANOVA. TFIs (individual values; including zeros) were compared between species by length class and NAFO Division using non-parametric statistics (Kruskal-Wallis; Mann-Whitney). Mean NAFO Division K_{adj} was compared to mean NAFO Division TFI by Analysis of Covariance (ANCOVA); with K_{adj} as the dependent variable, mean TFI as the covariate, and species as a fixed factor.

RESULTS

DIET DIFFERENCES BETWEEN SPECIES

Stomach content analyses indicated that the most frequent prey (FO) found in Northern Wolffish stomachs were euphausiids (7.2 %) and Northern Shrimp (6.6 %; Table 1). However, in terms of volumetric contribution (V), fish was the largest component of the diet: primarily American Plaice (17.5 %), and redfish (14 %). In addition, molluscs (i.e., gastropods, bivalves) were absent from the diet of Northern Wolffish, and were infrequently observed in the diet of the other two species (FO and V < 4 %); except for the bivalve Ocean Quahog (*Arctica islandica;* see below). For Spotted Wolffish, FO and V were highest for Northern Shrimp (21.4 %; 27.2 %, respectively), followed by brittlestars (9.5 %; 14.4 %). Similarly, for Atlantic Wolffish, FO was highest for brittlestars (7.6 %) and Northern Shrimp (4.9 %); while V indicated that the main diet components were Sand Dollars (8.8 %) and Northern Shrimp (6.3 %).

The proportional contribution of each prey taxon (mean PFI as a fraction of mean TFI) similarly showed that the most important prey for Northern Wolffish was redfish, followed by shrimp (*Pandalus* sp.; Fig. 2). For Spotted Wolffish, the two most important prey taxa were shrimp and brittlestars; while brittlestars and crabs (various species) were such for Atlantic Wolffish.

When prey taxa were grouped into 9 major groups (Table 2), the most important prey for Northern Wolffish were benthic fish and pelagic fish (52 % of mean TFI); shrimp and echinoderms for Spotted Wolffish (68 %); and crabs and echinoderms for Atlantic Wolffish (57 %). Volumetric data (V) gave similar results to mean PFI data. One exception was the importance of bivalves to the diet of Atlantic Wolffish: volumetric contribution of bivalves was high (36.4 %); whereas proportional mean PFI was comparatively smaller (9.6 % of mean TFI). The source of this discrepancy was a high biomass of Ocean Quahogs in the diet of eight large

Atlantic Wolffish (> 70 cm). This example highlighted the importance of correcting for predator size (e.g., using mean PFI) when comparing relative importance of different prey to the diets of fish across a broad size range. Therefore, mean PFI values were considered to be a more accurate descriptor of wolffish diet, and were used for further comparisons.

Mean PFI data (Table 1) were used to calculate Schoener's Index of diet similarity (*a*). This index suggested that the wolffish species with the most similar diets were Spotted and Atlantic Wolffish ($a = 0.52$); although the highest in this study, *a* was below the threshold of 0.60 (i.e., usually not considered indicative of significant diet overlap). The species with the least similar diets were Northern and Atlantic Wolffish ($a = 0.21$; representing very little diet overlap). Diet overlap between Northern and Spotted Wolffish was also quite low ($a = 0.32$). These results are in good agreement with a previous study of Newfoundland and Labrador wolffish diet (Albikovskaya 1983).

DIET DIFFERENCES BETWEEN SPECIES BY LENGTH CLASS

Ontogenetic changes in diet proportions were evident for all three species of wolffish (sampling overlapped in the predator size range of 30-99 cm). The estimation of mean PFI by 10 cm length-class indicated that Northern Wolffish were mostly planktivorous until 30-39 cm, mostly benthivorous (feeding on shrimp and echinoderms) from 40 cm to 69 cm, and mostly piscivorous at lengths greater than 70 cm (Fig. 3). Crabs and shrimp were also present in the diet of large Northern Wolffish. Spotted Wolffish were mostly planktivorous only until 9 cm, and mostly benthivorous thereafter. Shrimp began to dominate Spotted Wolffish diet at lengths of 20-29 cm, while echinoderms became important at 40-49 cm. Although piscivory began at relatively small sizes for this species (20-29 cm), it remained relatively unimportant at all lengths. Atlantic Wolffish were mostly benthivorous throughout their lives: feeding on crabs and echinoderms at small sizes (< 30 cm); then on echinoderms, shrimp, and crabs at medium sizes (30-69 cm); and on bivalves at large sizes (> 70 cm). Piscivory was also unimportant for Atlantic Wolffish; regardless of predator length.

Length-adjusted condition factor (K_{adj}; Table 3, 4) of Northern Wolffish decreased over medium sizes (40-69 cm), and corresponded to a decline in mean TFI and an increase in benthivory (Fig. 3). K_{adj} (and mean TFI) subsequently increased with length once piscivory became important (> 70 cm). For Spotted Wolffish, K_{adj} decreased only over small lengths (20-29 cm) when planktivory prevailed, and during the early transitional period to benthivory. K_{adj} increased once shrimp became predominant in the diet of 30-49 cm Spotted Wolffish; prior to leveling out for larger sizes (50-79 cm) at which echinoderms became the main prey. Trends in mean TFI corresponded well with K_{adj}; except for fish > 80 cm. For the latter, mean TFI decreased as K_{adj} increased (coinciding with an increase in piscivory). For Atlantic Wolffish, K_{adj} decreased for small sizes (< 29 cm), but increased for medium (30-59 cm) and large fish (60-90 cm); albeit benthivory prevailed across lengths. K_{adj} decreased for Atlantic Wolffish > 90 cm. In most cases, trends in mean TFI corresponded well with K_{adj}.

TFI varied significantly between length-classes for all wolffish species (Kruskal-Wallis; $p < 0.001$), and was only significantly different between species over medium length-classes (Fig. 4). K_{adj} also varied significantly among length-classes (ANOVA; Northern Wolffish: $F_{9,148} = 2.96$, $p < 0.01$; Spotted Wolffish: $F_{10,255} = 5.28$, $p < 0.0001$; Atlantic Wolffish: $F_{10,1002} = 12.24$, $p < 0.0001$).

Discriminant Function Analysis of feeding habits (mean PFI by length-class; Table 3) was successful (93.1 %) in differentiating between the three wolffish species (Fig. 5). Consistent with results from previous analyses, the major discriminant factors were fish for Northern Wolffish; shrimp and echinoderms for Spotted Wolffish; and molluscs (bivalves, gastropods) and crabs for

Atlantic Wolffish. Depicting the ontogenetic range of trophic niche space occupied by each wolfish species, length-class based mean % piscivorous and mean % benthic diet indicated, on average, that Northern Wolffish occupied the least benthic and most piscivorous trophic niche; although trophic niche seemed highly variable ontogenetically (Table 3; Fig. 6). Atlantic Wolffish occupied the most benthic and least piscivorous trophic niche, and appeared highly stable ontogenetically. The latter was also noted for Spotted Wolffish; except for one length-class. Species groupings based on % benthic and % piscivorous were significant (MANOVA; Wilks' Lambda = 0.531, $F_{4,50} = 4.70$, $p < 0.01$).

DIET DIFFERENCES BETWEEN SPECIES BY NAFO DIVISION

Sampling of the three wolffish species overlapped only in NAFO Div. 2J3KLN (Table 5). The analysis of mean PFI indicated that Northern Wolffish were most piscivorous at the northern (Div. 2J) and southern limits (Div. 3NO) of their distribution, while shrimp, crabs, and echinoderms were relatively more important in Div. 3KLM (Fig. 7). For Spotted Wolffish, shrimp was the most important prey in northerly areas (Div. 2J3KL), but echinoderms dominated further south (Div. 3N). Similarly, shrimp declined in importance for Atlantic Wolffish from more northerly (Div. 2J3KL) to more southerly areas (Div. 3NOPs), while echinoderms increased in importance; crabs were relatively important in all areas, except in Subdivision 3Ps.

High mean K_{adj} appeared to correlate with high mean TFI values in all cases (Fig. 7). TFI varied significantly between NAFO Divisions only for Atlantic Wolffish (Kruskal-Wallis; $p < 0.05$); TFI varied significantly between species in Div. 3KLN (Fig. 8). Analysis of Covariance (ANCOVA) indicated that mean TFI was significantly correlated to mean K_{adj} between Divisions and species (Fig. 9). This relationship may reflect spatial differences in food availability and feeding success, or may have a seasonal component (i.e., not included in this analysis).

Discriminant analysis was successful 100 % of the time in discerning between the three wolffish species, based on mean feeding habits by NAFO Division (Fig. 10). Species groupings were statistically significant (MANOVA; Wilks' Lambda = 0.01, $F_{10,18} = 4.18$, $p < 0.01$). The major discriminant factors were fish for Northern Wolffish; shrimp and echinoderms for Spotted Wolffish; and molluscs (bivalves, gastropods) and crabs for Atlantic Wolffish.

Similarly, species groupings based on mean % piscivorous and mean % benthic diet confirmed the results based on length class means (Fig. 6). Northern Wolffish were found to occupy the least benthic and most piscivorous trophic niche (trophic niche was highly variable spatially); Atlantic Wolffish occupied the most benthic and least piscivorous trophic niche (trophic niche was highly stable spatially); and Spotted Wolffish occupied a trophic niche space similar to that of Atlantic Wolffish (Fig. 11). However, species groupings based on these two variables (% piscivorous and % benthic) were not significant (MANOVA; $F_{4,24} = 1.95$, $p = 0.135$).

DISCUSSION

For the three wolffish species inhabiting Newfoundland and Labrador waters, estimated indices of wolffish diet coupled with Discriminant Function Analysis were successful in: (i) characterizing feeding habits and the importance of specific prey taxa and prey groups to their diets; (ii) differentiating between species according to both size-dependent and area-specific feeding habits; and (iii) identifying trophic niches, as well as characterizing trophic niche space variability, which were related to wolffish ontogeny and geographic distribution.

Diet analysis indicated that Northern Wolffish can best be described as "fish specialists", Spotted Wolffish as "echinoderm specialists", and Atlantic Wolffish as "mollusc specialists" (for length-classes > 70 cm). Shrimp and crabs were frequently found in the diet of all three species, and probably reflects a large increase in these components of the food web since the mid1990s; particularly in the more northerly areas of the Newfoundland shelf (DFO 2003*a,* 2003*b*).

Despite showing preference for specific prey groups, wolffish ontogeny resulted in considerable variability in diet. In fact, both TFI and K_{adj} varied significantly between length-classes for all three wolffish species. In terms of feeding ecology, length-adjusted condition factor (K_{adj}) provided appropriate metrics for foraging success. For example, under optimal feeding conditions, K_{adj} should be a flat line (i.e., no local size-dependency); while a negative tendency of K_{adj} over a specific size range may indicate decreasing foraging success (Sherwood and Rose 2005), in addition to a feeding “bottleneck” (i.e., limitation on food or foraging habitat during critical growth and survival periods) in that size range (Sherwood et al. 2002).

Consistent with a feeding bottleneck argument, K_{adj} of Northern Wolffish decreased over medium lengths (40-69 cm); corresponding to a decline in mean TFI, and an increase in benthivory (from planktivory). K_{adj} subsequently increased with length once piscivory became important (> 70 cm). Such patterns suggest that piscivory is ‘optimal’, while benthivory is ‘sub-optimal’ for Northern Wolffish longer than 40 cm. A similar pattern of K_{adj} (i.e., a decline over medium sizes) had been observed in Northern Cod (*Gadus morhua*) by Sherwood and Rose (2005), employing stable carbon isotope analysis ($\delta^{13}C$), and was correlated to a distinct absence of Capelin (*Mallotus villosus*) in the diet of medium-size (40-69 cm) Atlantic Cod. The decline of prey species such as Capelin and redfish in Newfoundland and Labrador shelf waters since the 1990s (Gomes et al. 1995; Rose and O’Driscoll 2002) may also be negatively affecting Northern Wolffish. Echinoderms and bivalves appear to be ‘optimal’ for medium-size Spotted Wolffish and large Atlantic Wolffish, respectively. Future application of stable isotope analysis should elucidate relationships between life history variation (e.g., growth, condition, fecundity) and diet for each wolffish species.

Results of the present study also suggested significant trophic niche differentiation between Northern Wolffish, Spotted Wolffish, and Atlantic Wolffish. Schoener’s Index of diet similarity indicated no (biologically) significant level of diet overlap between the three wolffish species. Upon closer examination, wolffish diet was found to be different between species with respect to: proportional contribution of 9 major prey groups (by length-class and NAFO Division); and 2-dimensional trophic niche space (by length-class only). The significant diet differences found between Spotted Wolffish and Atlantic Wolffish in this study constitute the first reported evidence of trophic niche separation between these two closely-related species.

Understanding trophic niche differences between wolffish species may be crucial in setting ecologically meaningful targets for their recovery, and effectively managing the sustainability of local wolffish populations under environmental perturbations (i.e., anthropogenic, or otherwise). For example, low Capelin abundance is currently believed to be a potential limiting factor to the recovery of Northern Cod (Rose and O’Driscoll 2002). Similarly, the recovery of Northern Wolffish may depend, to some extent, on the return of Capelin and other prey species (e.g., redfish) to significantly higher abundance levels in Newfoundland and Labrador waters. In contrast, given their reliance on relatively bountiful benthic resources (i.e., echinoderms, shrimp, crabs, molluscs), future strategies for Spotted Wolffish and Atlantic Wolffish recovery should focus on issues other than prey availability; such as benthic habitat disturbances due to bottom-contact fishing gears or anthropogenic pollution (e.g., oil spills; hydroelectric effluents; mining tailings run-off), and wolffish bycatch mortality in commercial fisheries (Simpson and Kulka 2002). Lastly, this study highlights the importance of considering changes in ecosystem carrying capacity when designing recovery strategies for depleted fish populations in general, and for wolffish species in particular.

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Table 1. Frequency of occurrence (FO), percent volumetric contribution to the diet (V) and mean partial fullness index (mean PFI) of all prey taxa found in the diets of all individuals of Northern (Anarhichas denticulatus), Spotted (A. minor), and Atlantic Wolffish (A. lupus).

Pelagic fish

	A. denticulatus			***A. minor***			***A. lupus***		
Prey Taxa	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**
Capelin (*Mallotus villosus*)			4.6	4.6	0.101	0.3	1.7	0.005	
Lanternfishes (Family Myctophidae)	3.9	2.3	0.012	0.4	0.1	0.001			
Sand lances (Family Ammodytidae)						0.1	0.03	0.00004	
Redfishes (*Sebastes* sp.)	1.3	9.9	0.041				0.2	0.2	0.002
Deep water redfish *(Sebastes mentella*)	1.3	14.0	0.034	0.8	1.5	0.005	0.2	0.7	0.002
Unidentified fish (larvae)	3.9	5.4	0.021	0.8	0.1	0.001	1.4	0.2	0.009

Benthic fish

	A. denticulatus			***A. minor***			***A. lupus***		
Prey Taxa	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**
Atlantic cod (*Gadus morhua*)	0.7	6.7	0.017						
Common grenadier (*Nezumia bairdi*)	0.7	7.5	0.015	0.4	0.1	0.0004			
Striped wolffish (*A. lupus*)						0.1	0.4	0.003	
Spotted wolffish (*A. minor*)			0.4	0.4	0.01				
Snakeblenny (*Lumpenus lumpretaeformis*)				0.8	0.4	0.014			
Daubed shanny (*Lumpenus maculatus*)			0.4	0.03	0.005	0.1	0.2	0.001	
Eelpouts (Family Zoarcidae)	0.7	5.6	0.013						
Sculpins (Family Cottidae)						0.1	0.1	0.001	
Hookear sculpins (*Artediellus* sp.)			0.4	1.7	0.016				
Mailed sculpins (*Triglops* sp.)			1.1	0.5	0.006	0.2	0.4	0.001	
Longhorn sculpin (*Myoxocephalus octodecemspinosus*)				0.2	0.8	0.002			
Northern alligatorfish (*Agonis decagonus*)				0.4	0.05	0.001	0.1	0.2	0.001
Lumpfishes (Family Cyclopteridae)						0.1	0.1	0.001	
Seasnails (*Liparis* sp.)	0.7	0.1	0.006						
Righteye flounders (Family Pleuronectidae)				0.8	6.0	0.039	0.1	1.0	0.001
American plaice (*Hippoglossoides platessoides*)	0.7	17.5	0.037						

Benthic invertebrates

	A. denticulatus			*A. minor*			*A. lupus*		
Prey Taxa	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**
Invertebrates (unidentified)	0.7	0.01	0.0001				0.1	0.003	0.001
Sponges (Phylum Porifera)	0.7	0.1	0.002	1.9	0.3	0.048	0.3	0.5	0.001
Sea anemone (Subclass Actinaria)	0.7	0.1	0.0003	0.8	0.6	0.007	0.1	0.4	0.001
Bryozoan (Phylum Ectoprocta)	0.7	0.003	0.00001	1.1	0.0	0.002	0.6	0.02	0.003
Lamp shell (Phylum Brachiopoda)			0.4	0.1	0.0004				
Marine worms (Class Polychaeta)	2.0	0.02	0.0004	3.1	0.2	0.016	1.3	0.1	0.007
Sea mouse (Family Aphroditidae)						0.2	1.2	0.002	

Gastopods

	A. denticulatus			*A. minor*			*A. lupus*		
Prey Taxa	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**
Gastropods (snails) (Class Gastropoda)			0.4	0.001	0.00002	2.0	0.2	0.006	
Topshells (Family Trochidae)						3.4	0.1	0.005	
Solariella sp.					0.1	0.5	0.005		
Northern rosy margarite (*Margarites costalis*)							0.1	0.01	0.002
Moon snails (Family Naticidae)			0.4	0.003	0.00001	0.5	0.6	0.003	
Arctic natica (*Natica clausa*)						0.5	0.1	0.001	
Boreotrophons (*Boreotrophon* sp.)						0.2	0.003	0.0001	
Whelks (Family Buccinidae)			0.4	0.03	0.0001	1.2	1.2	0.005	
Buccinum whelk (*Buccinum* sp.)						0.9	2.7	0.007	
Neptunea whelk (*Neptunea* sp.)						0.4	2.6	0.003	
Colus whelk (*Colus* sp.)						0.7	1.3	0.004	
Turrids (Family Turridae)						0.6	0.0	0.001	
Giant or canoe bubble shell (*Scaphander punctorostriatus*)							0.1	0.0	0.0001
Bubble shell (*Cylichna alba*)			0.4	0.001	0.001				
Sea slugs (Order Nudibranchia)			0.4	0.02	0.007				

Bivalves

	A. denticulatus			*A. minor*			*A. lupus*		
Prey Taxa	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**
Bivalve (Class Bivalvia)			0.4	0.03	0.0004	1.8	0.6	0.019	
Little black mussel (*Musculus niger*)						0.1	0.2	0.002	
Scallops (Family Pectinidae)			0.4	0.3	0.001	1.3	0.3	0.006	
Iceland scallop (*Chlamys islandica*)			0.4	0.7	0.007	1.3	0.8	0.006	
Sea scallop (*Placopectin magellanicus*)							0.3	0.2	0.0005
Astartes (*Astarte* sp.)			0.4	0.02	0.0001				
Ocean quahog (*Arctica islandica*)						1.6	29.0	0.028	
Greenland cockle (*Serripes groenlandica*)							0.1	0.1	0.0003
Iceland cockle (*Clinocardium cilatum*)						0.3	0.1	0.002	
Stimpson's surf clam (*Mactromeris polynyma*)							0.3	2.5	0.004
Chalky macoma (*Macoma calcarea*)			0.8	0.1	0.0005				
Atlantic razor clam (*Siliqua costata*)						0.1	0.8	0.002	
Propellor clam (*Cyrtodaria siliqua*)			0.4	0.1	0.002	0.3	1.8	0.002	

Zooplankton

	A. denticulatus			*A. minor*			*A. lupus*		
Prey Taxa	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**
Crustaceans (Subphylum Crustacea)	3.9	0.04	0.0004	4.2	0.2	0.015	5.5	0.2	0.021
Calanoid copepods (Order Calanoida)						0.2	0.003	0.0002	
Amphipods (Order Amphipoda)						0.7	0.02	0.002	
Hyperiids (Family Hyperiidae)	3.9	0.5	0.029	1.9	0.1	0.111	0.4	0.1	0.0003
Gammarids (Suborder Gammaridea)				0.4	0.001	0.00003	1.0	0.1	0.009
Caprellids (Family Caprellidae)						0.2	0.02	0.004	
Mysids (Family Mysidae)	0.7	0.0	0.001	0.4	0.02	0.0001			
Euphausids (Order Euphausiacea)	7.2	0.7	0.01	1.1	0.1	0.001	0.1	0.001	0.00001

Shrimp

	A. denticulatus			*A. minor*			*A. lupus*		
Prey Taxa	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**
Decapods (Order Decapoda)						0.1	0.001	0.001	
Shrimp (Suborder Natantia)	2.0	0.04	0.0003	1.1	0.1	0.031	1.3	0.6	0.015
Acanthephyra pelagica	1.3	0.3	0.001	0.4	0.1	0.004			
Eualus sp.					0.1	0.1	0.001		
Pink shrimp (*Pandalus* sp.)	3.3	3.4	0.012	10.7	7.0	0.157	1.4	1.5	0.02
Northern Pink shrimp (*Pandalus borealis*)	6.6	6.8	0.039	21.4	27.2	0.469	4.9	6.3	0.081
Striped Pink shrimp (*Pandalus montagui*)	0.7	0.2	0.001	2.7	0.9	0.026	0.6	0.3	0.005
Argis dentata			0.4	0.1	0.0002	0.2	0.1	0.0003	

Crabs

	A. denticulatus			*A. minor*			*A. lupus*		
Prey Taxa	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**
Hermit crabs (Family Paguridae)						1.0	1.9	0.005	
Spiny red crab, porcupine crab (*Neolithodes grimaldii*)	1.3	2.7	0.007						
Crab (Infraorder Brachyura)	0.7	0.3	0.001	1.9	0.4	0.011	4.8	4.0	0.106
Snow crab (*Chionoecetes opilio*)	1.3	10.3	0.031	2.3	12.2	0.1	1.3	4.2	0.025
Toad crabs (*Hyas* sp.)			2.3	0.9	0.022	1.4	5.5	0.037	
Toad crab (*Hyas araneus*)			0.4	0.01	0.012	0.2	0.6	0.008	
Toad crab (*Hyas coarctatus*)			0.8	0.3	0.006	0.2	0.8	0.01	

Echinoderms

	A. denticulatus			*A. minor*			*A. lupus*		
Prey Taxa	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**
Echinoderms (Phylum Echinodermata)			0.4	0.003	0.007	0.3	0.1	0.001	
Sea cucumber (Class Holothuroidea)						0.1	0.4	0.001	
Sea urchin (*Strongylocentrotus* sp.)	2.0	1.0	0.006	6.1	7.7	0.072	4.4	5.0	0.039
Sand dollar (*Echinarachnius parma*)	0.7	0.01	0.0001	2.7	7.7	0.087	2.1	8.8	0.074
Heart urchin (*Brisaster fragilis*)	0.7	0.02	0.0001						
Sea star (Subclass Asteroidea)			0.8	0.03	0.0005	0.2	0.004	0.00004	
Mud star (*Ctenodiscus crispatus*)						0.1	0.3	0.001	
Spiny sun star (*Crossaster papposus*)							0.3	0.04	0.0001
Brittlestar (Subclass Ophiuroidea)	2.6	0.1	0.001	9.5	14.4	0.304	7.6	5.2	0.114
Basketstar (*Gorgonocephalus* sp.)	3.9	4.3	0.035	2.3	2.7	0.036			
Brittlestar (*Ophiura sarsi*)						0.1	0.1	0.0002	

	A. denticulatus			*A. minor*			*A. lupus*		
Prey Taxa	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**
Total stomachs analysed (Ntot)	152			262			1037		
Total stomachs with food (Nfull)	65			129			387		
Feeding intensity (Ntot/Nfull × 100)	42.8			49.2			37.3		
Mean TFI	0.373			1.765			0.736		

Table 2. Frequency of occurrence (FO), percent volumetric contribution, and mean partial fullness index (mean PFI) of 9 major prey groups to the diet of all individuals of Northern (Anarhichas denticulatus), Spotted (A. minor), and Atlantic Wolffish (A. lupus). Values in ***bold*** *indicate the 2 most important prey groups (based on mean PFI) to the diet of each species.*

		A. denticulatus			***A. minor***			***A. lupus***	
Prey Group	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**	**FO (%)**	**V (%)**	**Mean PFI**
Pelagic fish	10.5	31.7	**0.087**	6.5	6.2	0.108	2.2	2.9	0.009
Benthic fish	3.3	37.4	**0.108**	4.6	9.1	0.092	1.0	3.1	0.020
Benthic invertebrates	4.6	0.2	0.002	7.3	1.2	0.073	2.5	2.1	0.015
Gastropods	0.0			1.9	0.1	0.008	10.5	9.3	0.042
Bivalves	0.0			2.7	1.2	0.011	7.4	36.4	0.071
Zooplankton	15.8	1.3	0.041	8.0	0.4	0.127	8.0	0.4	0.037
Shrimp	13.8	10.8	0.054	36.6	35.4	**0.687**	8.6	8.9	0.123
Crab	3.3	13.3	0.039	7.6	13.7	0.151	8.8	17.0	**0.190**
Echinoderms	9.9	5.4	0.042	21.8	32.6	**0.508**	15.2	19.9	**0.230**

Table 3. Mean partial fullness index (mean PFI) of 9 different prey groups to the diet of Northern (Anarhichas denticulatus), Spotted (A. minor), and Atlantic Wolffish (A. lupus), by 10 cm length class. Mean total fullness index (mean TFI), percent contribution of benthic, piscivorous, and hard-shelled prey, total number of stomachs analysed (Ntot), total number of stomachs with food (Nfull), feeding intensity (FI) and mean length-adjusted condition factor (Kadj) for each species/length class combination are also shown.

Species	**Length class (cm)**										
Variable	**0-9**	**10-19**	**20-19**	**30-39**	**40-49**	**50-59**	**60-69**	**70-79**	**80-89**	**90-99**	**> 100**
A. denticulatus											
Mean PFI:											
Pelagic fish					0.005			0.522	0.169		0.917
Benthic fish				0.071			0.094		0.007	1.027	0.552
Benthic invertebrates									0.003	0.000	
Gastropods											
Bivalves											
Zooplankton				0.368	0.028	0.010	0.008				
Shrimp					0.017	0.096	0.037	0.031	0.036	0.224	
Crabs									0.451	0.047	
Echinoderms					0.064	0.020	0.047	0.107	0.038	0.019	
Mean TFI				0.439	0.123	0.126	0.187	0.659	0.704	1.317	1.469
% Benthic				16.1	72.4	91.9	95.6	20.8	76.0	100	37.6
% Piscivorous				16.1	4.4	0	50.6	79.2	25.1	78.0	100
% Hard-shelled				0	52.4	16.0	25.0	16.2	5.4	1.4	0
N_{tot}				12	39	35	21	14	12	11	4
N_{full}				2	11	11	9	11	8	8	2
FI (%)				16.7	28.2	31.4	42.9	78.6	66.7	72.7	50.0
Mean K_{adj}				1.84	1.88	1.80	1.78	1.84	1.94	2.04	2.06
A. minor											
Mean PFI:											
Pelagic fish				0.432			0.027	0.148	0.317	0.069	0.221
Benthic fish				0.112		0.148	0.192	0.230	0.007	0.443	0.073
Benthic invertebrates		0.244			0.045	0.057		0.062	0.018		
Gastropods			0.041							0.005	
Bivalves						0.024	0.112		0.020	0.023	
Zooplankton	0.919	0.240			0.045	0.009		0.010			
Shrimp	0.281		0.908	1.747	0.832	0.560	0.157	1.698	0.779	0.360	
Crabs		0.050	0.030	0.170	0.236	0.195	0.141	0.506	0.612		
Echinoderms		0.286	0.231	0.253	0.920	1.014	1.398	1.178	0.174	0.547	
Mean TFI	1.200	0.820	1.754	2.170	2.225	2.078	2.186	3.777	2.115	1.229	
% Benthic	23.4	70.8	75.4	100	98.0	98.3	93.2	91.4	96.7	82.0	
% Piscivorous	0	0	31.0	0	6.7	10.5	17.3	8.6	24.2	23.9	
% Hard-shelled	0	34.9	15.5	11.7	41.3	50.0	69.1	31.2	9.2	46.8	
N_{tot}	18	63	42	35	27	24	18	14	14	6	
N_{full}	3	14	19	21	17	17	11	12	10	5	
FI (%)	16.7	22.2	45.2	60.0	63.0	70.8	61.1	85.7	71.4	83.3	
Mean K_{adj}	1.16	0.98	0.92	0.96	1.04	1.04	1.06	1.04	0.97	1.03	
A. lupus											
Mean PFI:											
Pelagic fish					0.038			0.154	0.082		
Benthic fish	0.019	0.022			0.049	0.039	0.059	0.096			0.016
Benthic invertebrates	0.033	0.021	0.002	0.005	0.000	0.008	0.079	0.039	0.033	0.000	
Gastropods		0.039	0.029	0.041	0.044	0.118	0.070	0.151	0.007	0.145	0.218
Bivalves	0.078	0.049	0.008	0.021	0.039	0.021	0.204	0.441	1.026	1.921	0.486
Zooplankton	0.049	0.109	0.017	0.011							
Shrimp	0.006	0.105	0.116	0.221	0.238	0.121					

Species	Length class (cm)										
Variable	**0-9**	**10-19**	**20-19**	**30-39**	**40-49**	**50-59**	**60-69**	**70-79**	**80-89**	**90-99**	**> 100**
Crabs	0.233	0.142	0.185	0.312	0.110	0.062	0.286	0.148	0.051	0.108	0.295
Echinoderms	0.120	0.201	0.130	0.280	0.592	0.223	0.134	0.097	0.017	0.031	
Mean TFI	0.538	0.688	0.488	0.891	1.110	0.592	0.832	1.127	1.216	2.206	1.014
% Benthic	90.9	84.2	96.5	98.8	96.6	100	100	86.3	93.3	100	100
% Piscivorous	3.6	3.2	0	0	7.8	6.5	7.1	22.2	6.7	0	1.5
% Hard-shelled	36.8	42.0	34.1	38.3	60.8	61.2	49.0	61.2	86.4	95.1	69.4
N_{tot}	151	225	207	182	127	67	40	16	11	5	6
N_{full}	23	66	59	86	74	32	18	11	8	4	5
FI (%)	15.2	29.3	28.5	47.3	58.3	47.8	45.0	68.8	72.7	80.0	83.3
Mean K_{adj}	1.10	1.03	1.01	1.02	1.06	1.06	1.10	1.18	1.27	1.20	1.17

Table 4. Statistics for length–weight relationships (L = aWb) of three species of Northern (Anarhichas denticulatus), Spotted (A. minor), and Atlantic Wolffish (A. lupus)

Species	*a*	*b*	r^2	p	n
A. denticulatus	0.0160	3.000	0.983	< 0.0001	152
A. minor	0.0101	3.090	0.996	< 0.0001	262
A. lupus	0.0104	3.056	0.996	< 0.0001	1037

Table 5. Mean partial fullness index (mean PFI) of 9 different prey groups to the diet of Northern (Anarhichas denticulatus), Spotted (A. minor), and Atlantic Wolffish (A. lupus) by NAFO Division. Mean total fullness index (mean TFI), percent contribution of benthic, piscivorous, and hard-shelled prey, total number of stomachs analysed (N_{tot}), total number of stomachs with food (N_{full}), feeding intensity (FI) and mean length-adjusted condition factor (K_{adj}) for each species/NAFO Div. combination are also shown

Species Variable	NAFO Div. 2J	NAFO Div. 3K	NAFO Div. 3L	NAFO Div. 3M	NAFO Div. 3N	NAFO Div. 3O	NAFO Subdiv. 3Ps
A. denticulatus							
Mean PFI:							
Pelagic fish	0.094	0.009	0.007		0.172	0.384	
Benthic fish	0.350	0.001	0.138		0.047	0.354	
Benthic invertebrates	0.000	0.002	0.006	0.001	0.001		
Gastropods							
Bivalves							
Zooplankton	0.005	0.009	0.110	0.010	0.013	0.066	
Shrimp	0.053	0.124	0.082	0.050	0.003		
Crabs	0.044		0.102	0.037	0.015		
Echinoderms	0.015	0.166	0.024	0.046	0.004		
Mean TFI	0.560	0.311	0.469	0.144	0.254	0.804	
% Benthic	82.3	94.3	75.1	93.3	27.6	44.0	
% Piscivorous	79.2	3.0	31.0	0	86.1	91.8	
% Hard-shelled	2.6	53.5	5.2	32.2	1.5	0	
N_{tot}	14	26	41	14	42	11	
N_{full}	8	11	16	6	15	6	
FI (%)	57.1	42.3	39.0	42.9	35.7	54.5	
Mean K_{adj}	1.90	1.86	1.81	1.87	1.88	2.06	
A. minor							
Mean PFI:							
Pelagic fish		0.100	0.145				
Benthic fish	0.125	0.068	0.049		0.409		
Benthic invertebrates		0.012	0.129		0.006		
Gastropods			0.014		0.000		
Bivalves			0.015		0.038		
Zooplankton	0.001	0.084	0.166		0.002		
Shrimp	0.539	0.838	0.734		0.129		
Crabs	0.055	0.068	0.231		0.053		
Echinoderms	0.022	0.103	0.413		2.691		
Mean TFI	0.742	1.273	1.896		3.327		
% Benthic	99.9	85.5	83.6		99.9		
% Piscivorous	16.9	13.2	10.2		12.3		
% Hard-shelled	3.0	8.1	23.3		82.0		
N_{tot}	14	80	139		25		
N_{full}	6	31	73		17		
FI (%)	42.9	38.8	52.5		68.0		
Mean K_{adj}	0.94	0.96	1.01		1.05		
A. lupus							
Mean PFI:							
Pelagic fish	0.012	0.005	0.008		0.000	0.028	
Benthic fish	0.020	0.017	0.027		0.017	0.012	0.022
Benthic invertebrates	0.013	0.016	0.014		0.020	0.013	0.019
Gastropods	0.018	0.041	0.025		0.041	0.105	0.043
Bivalves	0.009	0.108	0.028		0.158	0.061	0.012
Zooplankton	0.054	0.038	0.044		0.019	0.044	0.005
Shrimp	0.184	0.270	0.171		0.017	0.010	0.004
Crabs	0.156	0.270	0.250		0.114	0.235	
Echinoderms	0.083	0.035	0.239		0.398	0.341	0.334
Mean TFI	0.548	0.799	0.807		0.782	0.849	0.439

Species Variable	NAFO Div. 2J	NAFO Div. 3K	NAFO Div. 3L	NAFO Div. 3M	NAFO Div. 3N	NAFO Div. 3O	NAFO Subdiv. 3Ps
% Benthic	88.0	94.7	93.5		97.6	91.6	98.9
% Piscivorous	5.8	2.7	4.4		2.2	4.7	5.0
% Hard-shelled	20.0	23.0	36.1		76.2	59.7	88.6
N_{tot}	170	176	250		232	145	50
N_{full}	50	66	88		105	62	13
FI (%)	29.4	37.5	35.2		45.3	42.8	26.0
Mean K_{adj}	1.01	1.08	1.07		1.07	1.04	0.95

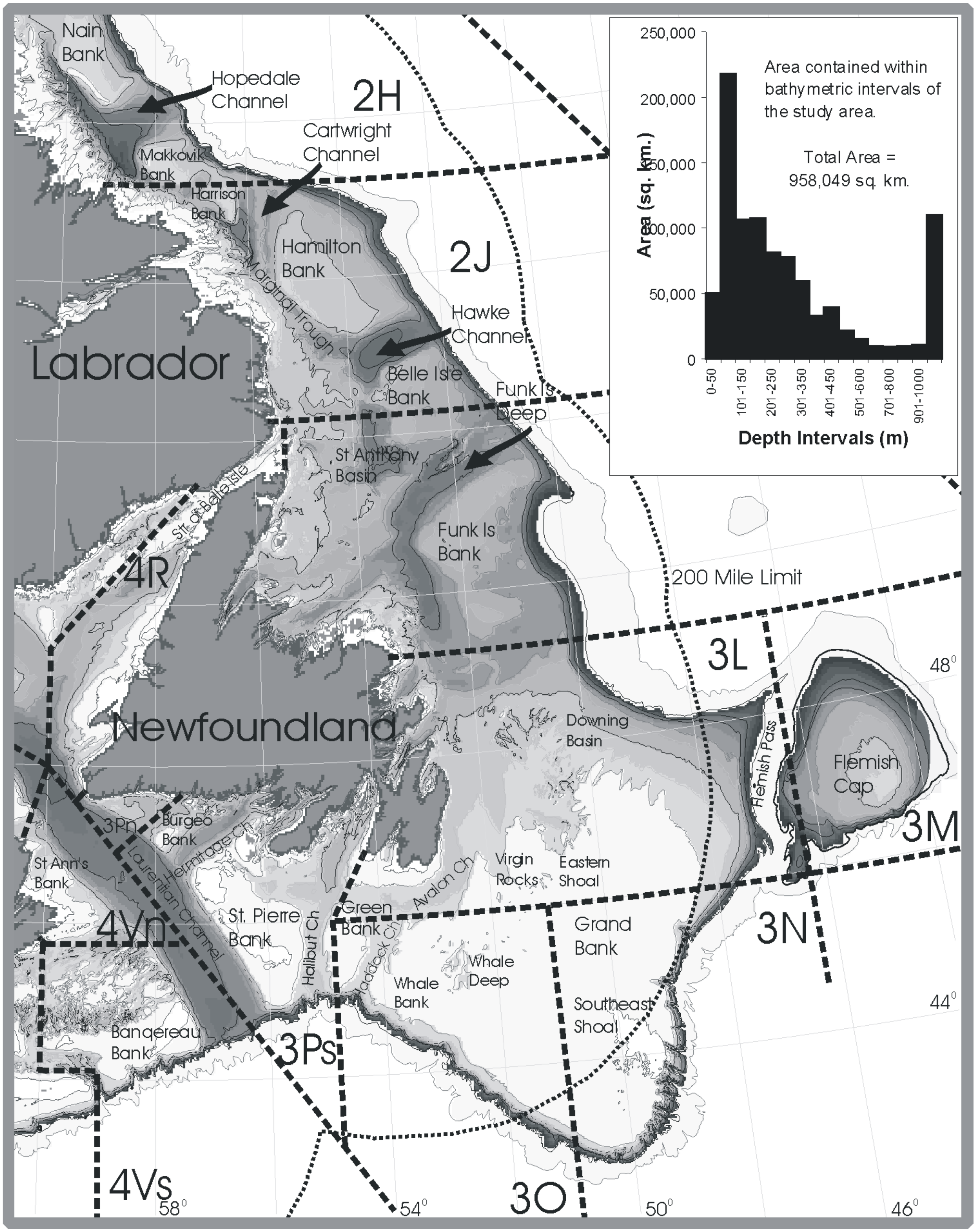

Figure 1. Map of the continental shelf off Eastern Canada and geographic features mentioned in the text. Depth range: <100 m (light grey) to >1000 m (dark grey). Canada's 200-Mile Limit is delineated by a thin dotted line, and NAFO Divisions by thick dotted lines

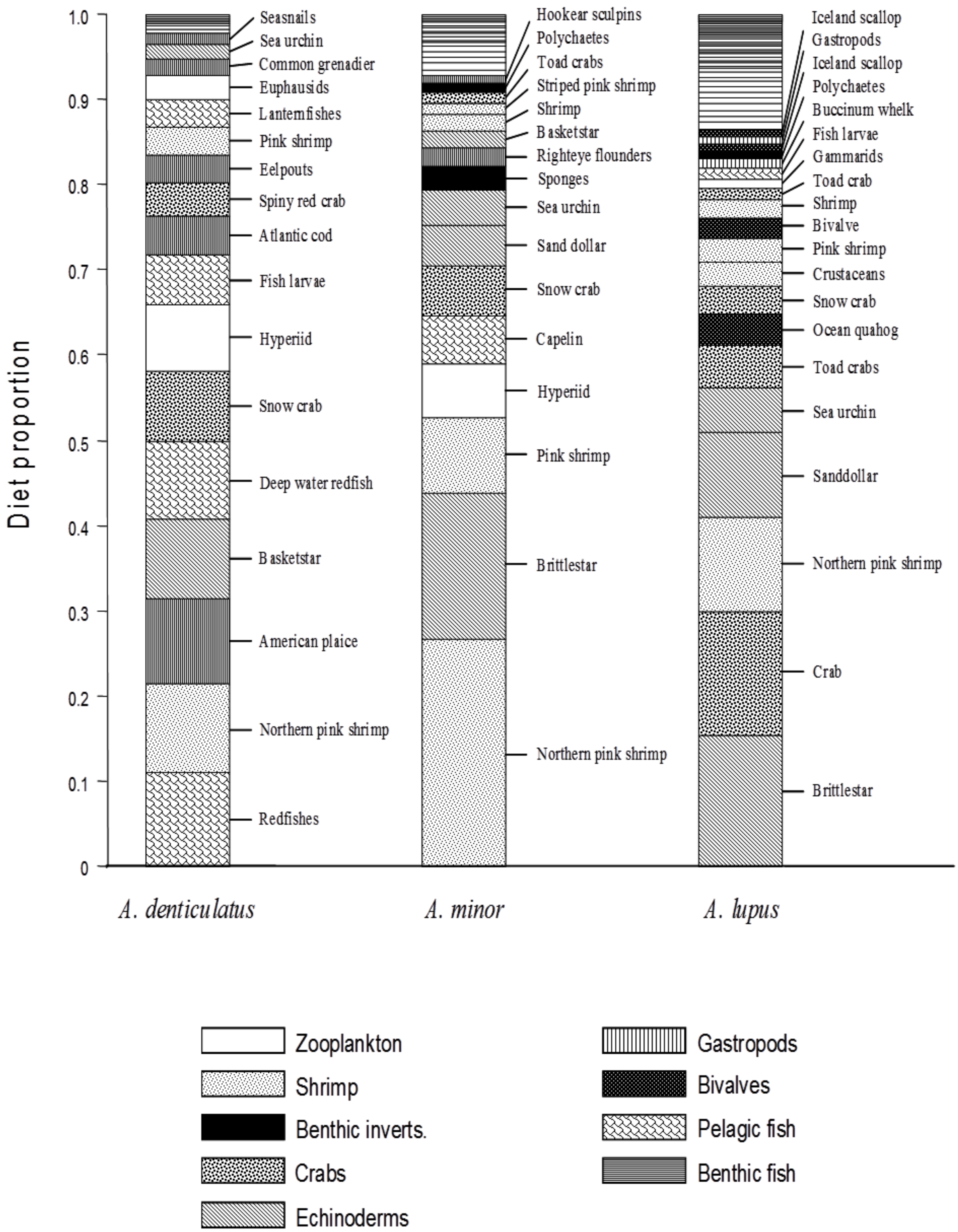

Figure 2. Proportional contribution (mean PFI as fraction of mean TFI) of the most important prey taxa to the diet of all individuals of three species of wolffish. Only prey taxa that make up at least 1 % of the total diet are listed. Bars with the same fill pattern belong to the same major prey group (see Legend).

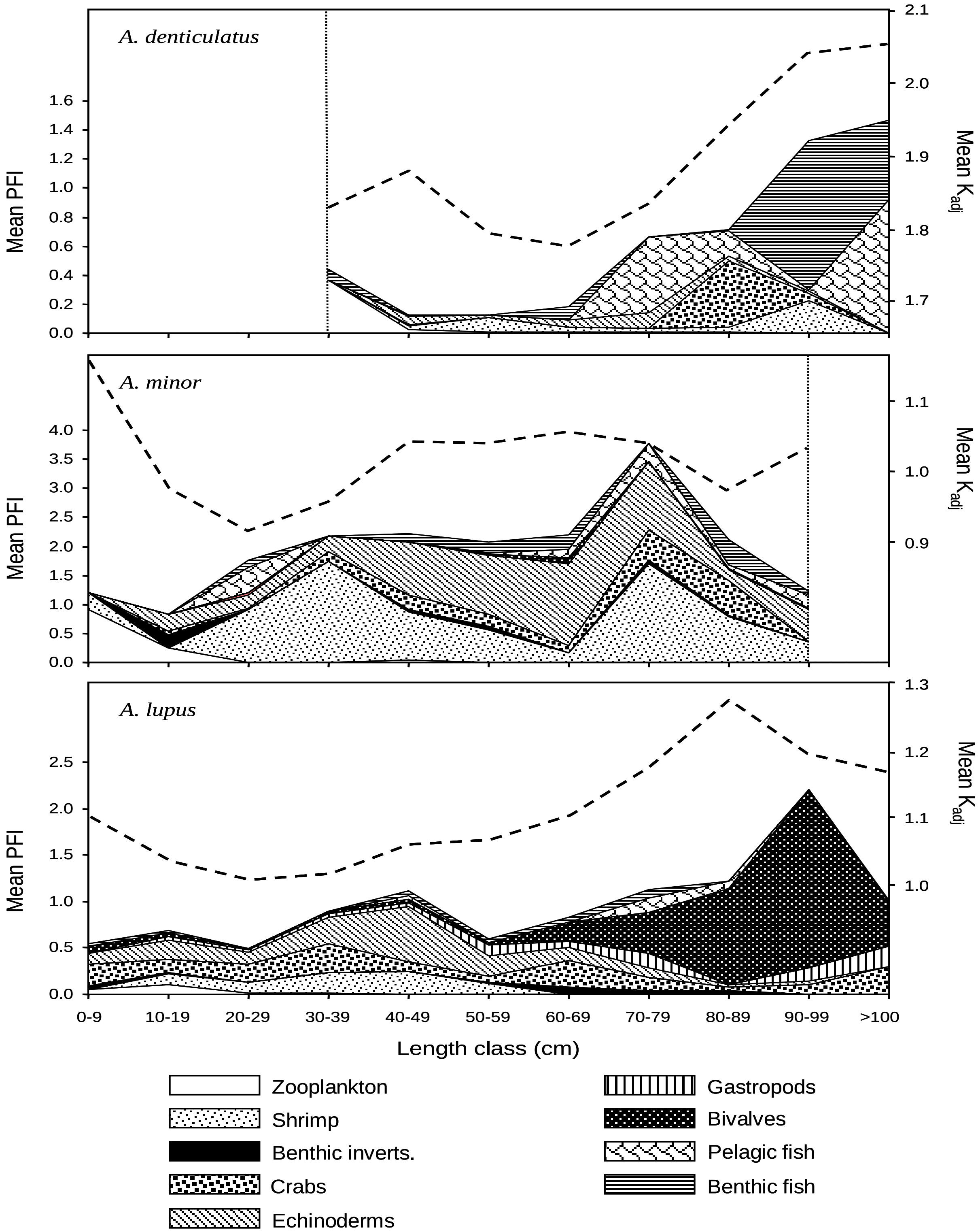

Figure 3. Mean partial fullness index (mean PFI) by length class for 9 major prey groups of three species of wolffish (see Legend). Note that the top line (of area graph) represents mean total fullness index (i.e, ean TFI = ∑ mean PFI). Dashed line indicates mean length-adjusted condition factor (K_{adj}). Sampling of the three wolffish species overlapped in the 30-99 cm size range.

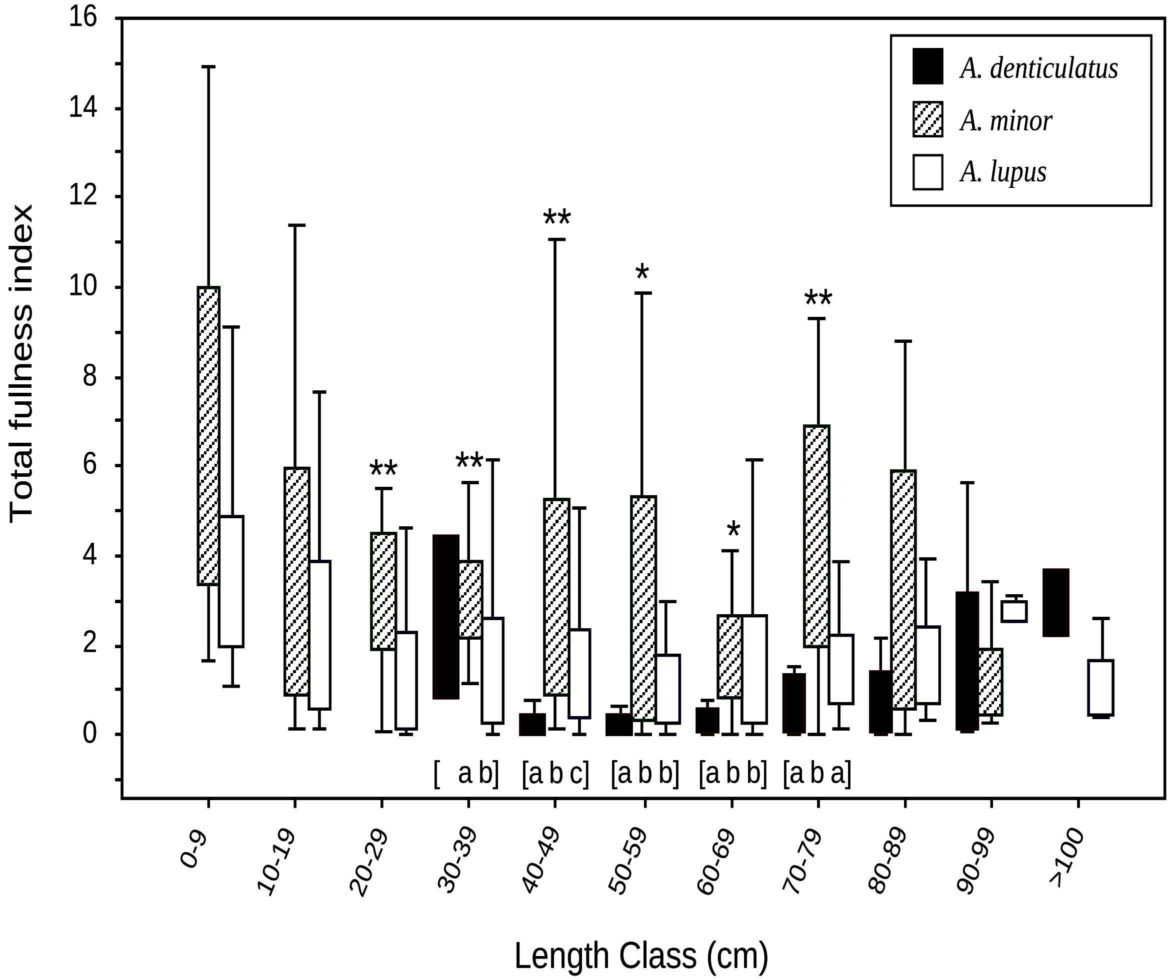

*Figure 4. Box and whisker plot of total fullness index (TFI) by length class for three species of wolffish. Boxes contain 50 % of TFI values; whiskers extend to minimum and maximum values (excluding outliers). Within length classes, asterisks indicate significant difference among species (Kruskal-Wallis: * $p < 0.05$; ** $p < 0.01$). Within length classes, bars with different letters (in square brackets) are significantly different (Mann-Whitney: $p < 0.05$).*

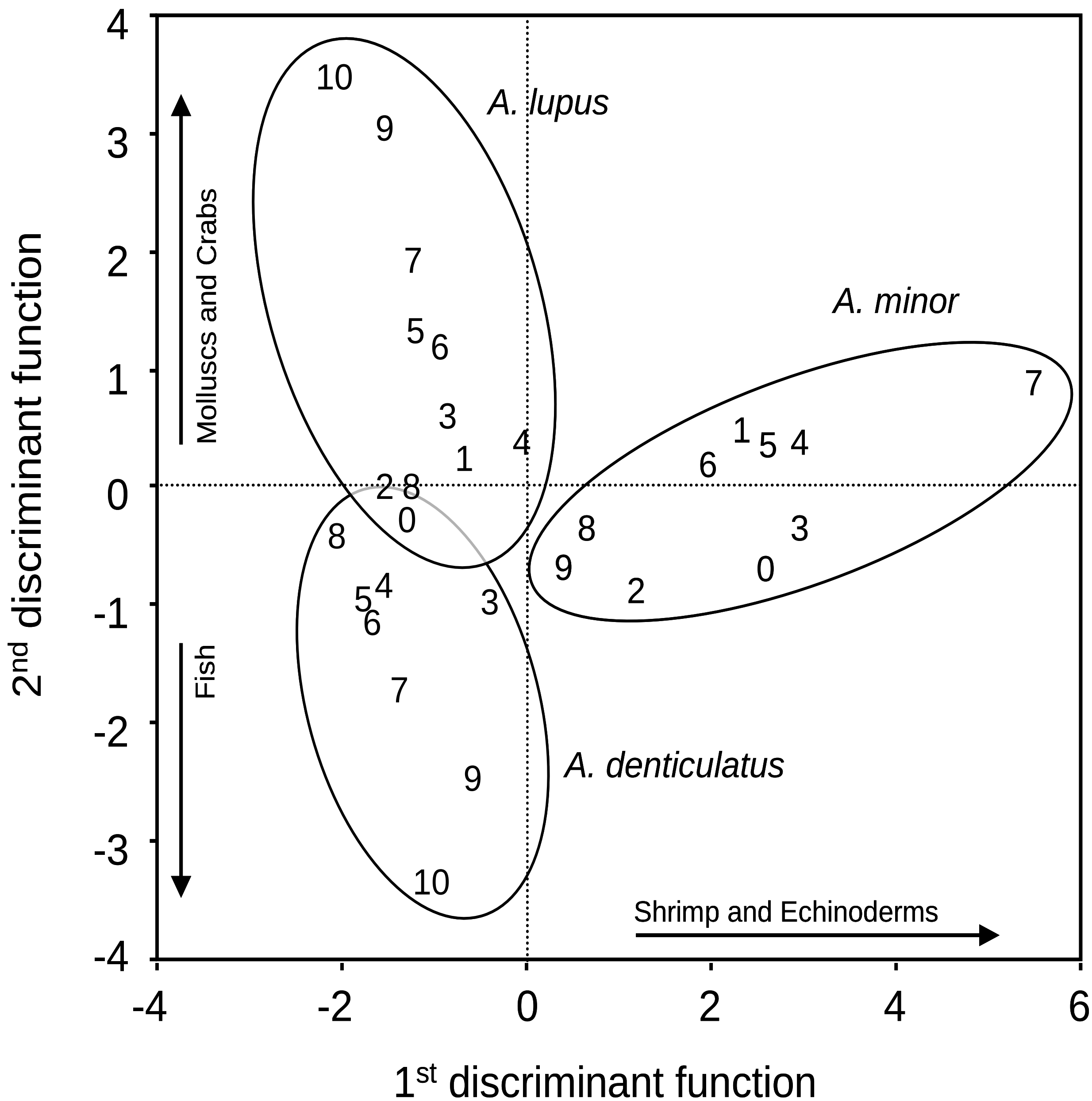

Figure 5. Discriminant analysis of mean feeding habits (mean PFI) by length class for three species of wolffish. Ellipses contain all data points (represented by numbers: 0 = 0-9 cm; 1 = 10-19 cm; etc.) for each species. Groupings were significant (MANOVA; Wilks' Lambda = 0.11; $F_{18,36} = 4.02$; $p < 0.0001$). 93.1 % of original grouped cases (8/8 A. denticulatus; 9/10 A. minor; 10/10 A. lupus) were correctly reclassified to species.

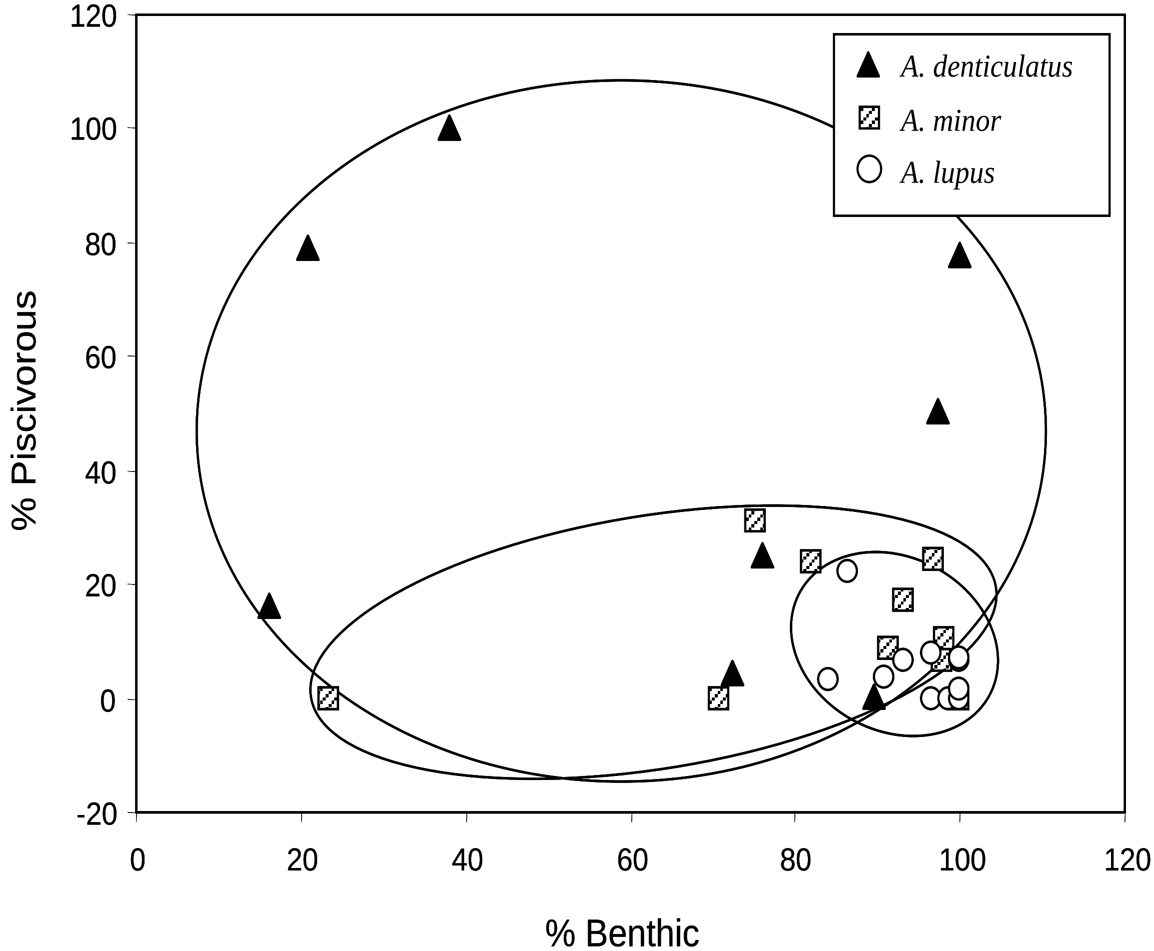

Figure 6. Length class mean percent piscivorous diet versus length class mean percent benthic diet (see Table 3) for three species of wolffish. Ellipses represent the ontogenetic range of mean 2-dimensional trophic niche space occupied by each species. Species groupings were significantly different (MANOVA; Wilks' Lambda = 0.531; $F_{4,50} = 4.71$*;* $p < 0.01$*).*

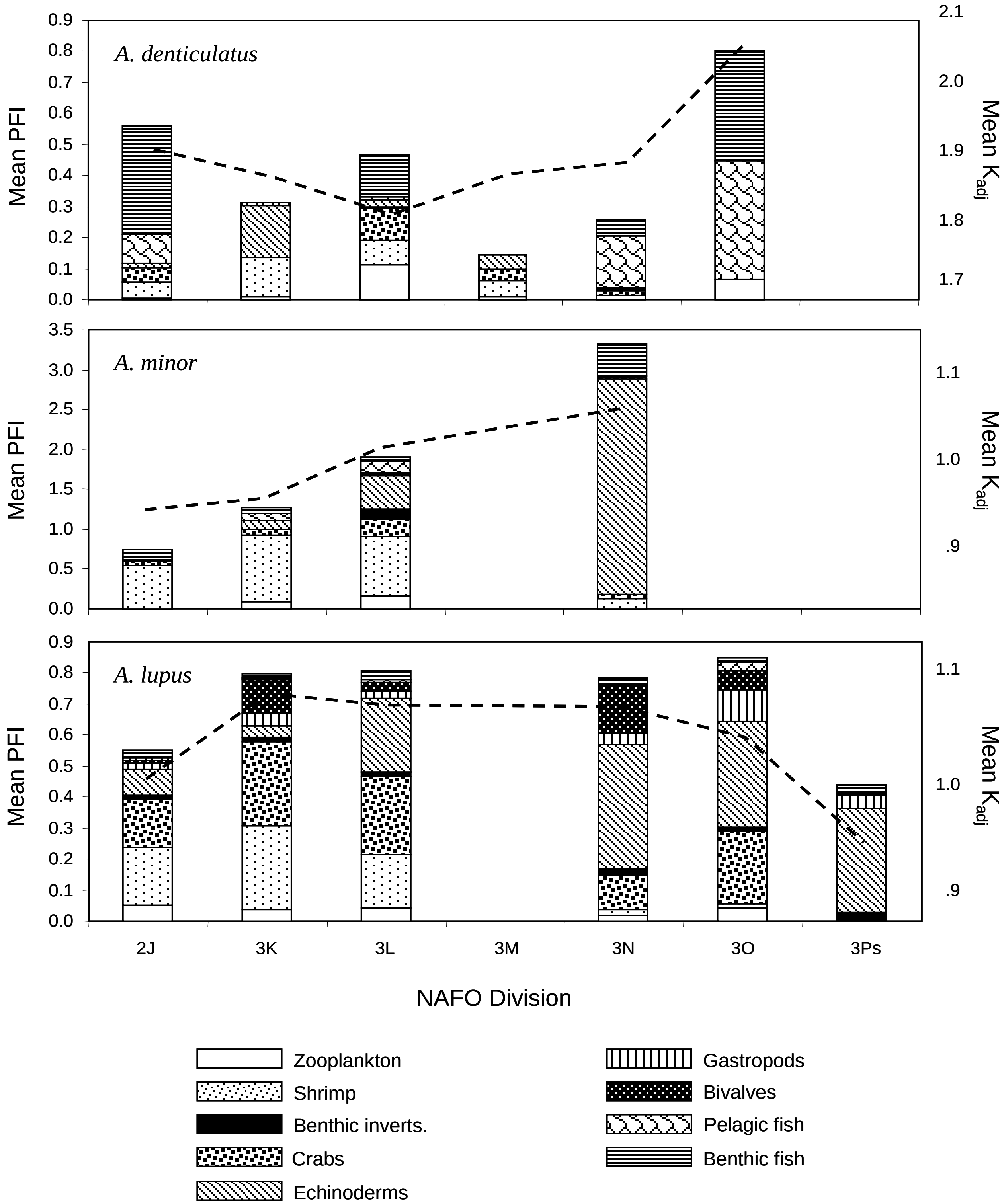

Figure 7. Mean partial fullness index (mean PFI) by NAFO Division for 9 major prey groups of three species of wolffish (see Legend). Note that the top of each bar represents total fullness index (i.e., mean TFI = ∑ mean PFI). Dashed line indicates mean length-adjusted condition factor (K_{adj}).

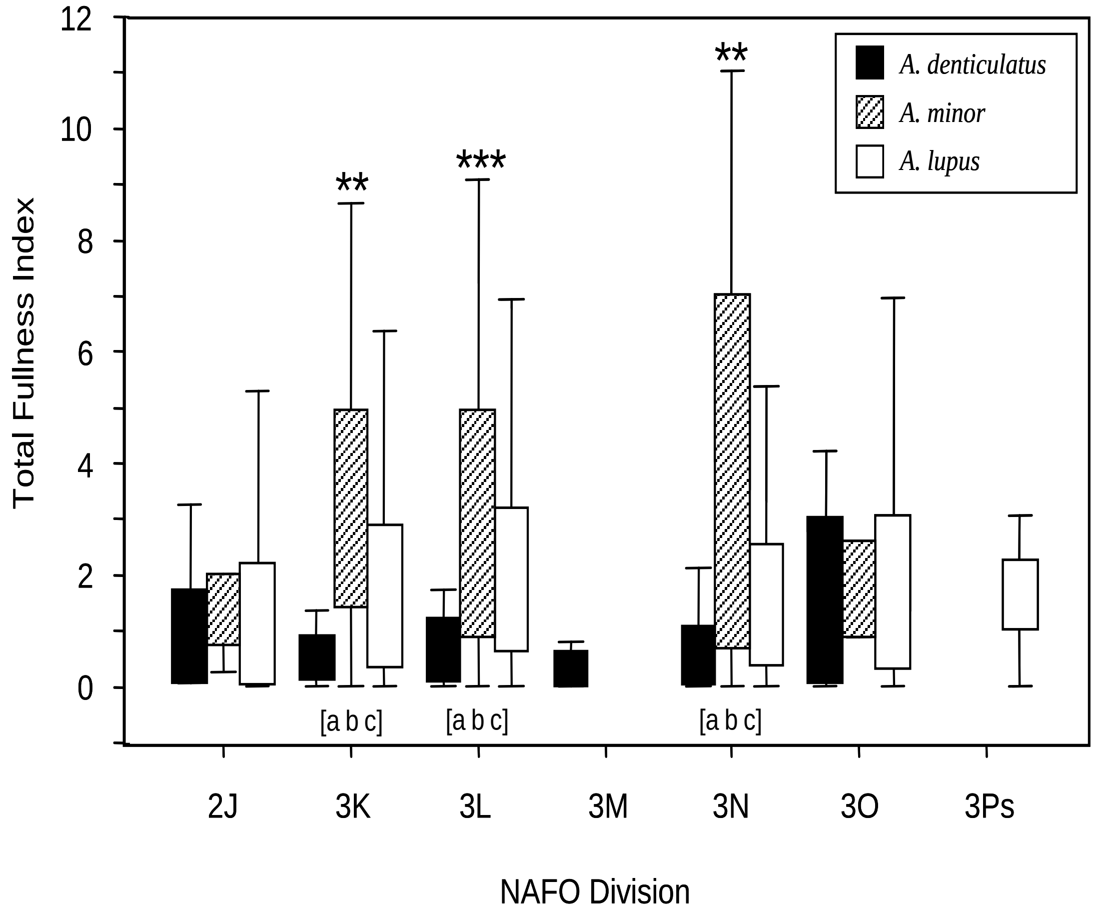

*Figure 8. Box and whisker plot of total fullness index by NAFO Division for three species of wolffish. Boxes contain 50 % of TFI values; whiskers extend to minimum and maximum values (excluding outliers). Within length classes, asterisks indicate significant difference among species (Kruskal-Wallis: ** $p < 0.01$; *** $p < 0.001$). Within length classes, bars with different letters (in square brackets) are significantly different (Mann-Whitney; $p < 0.05$).*

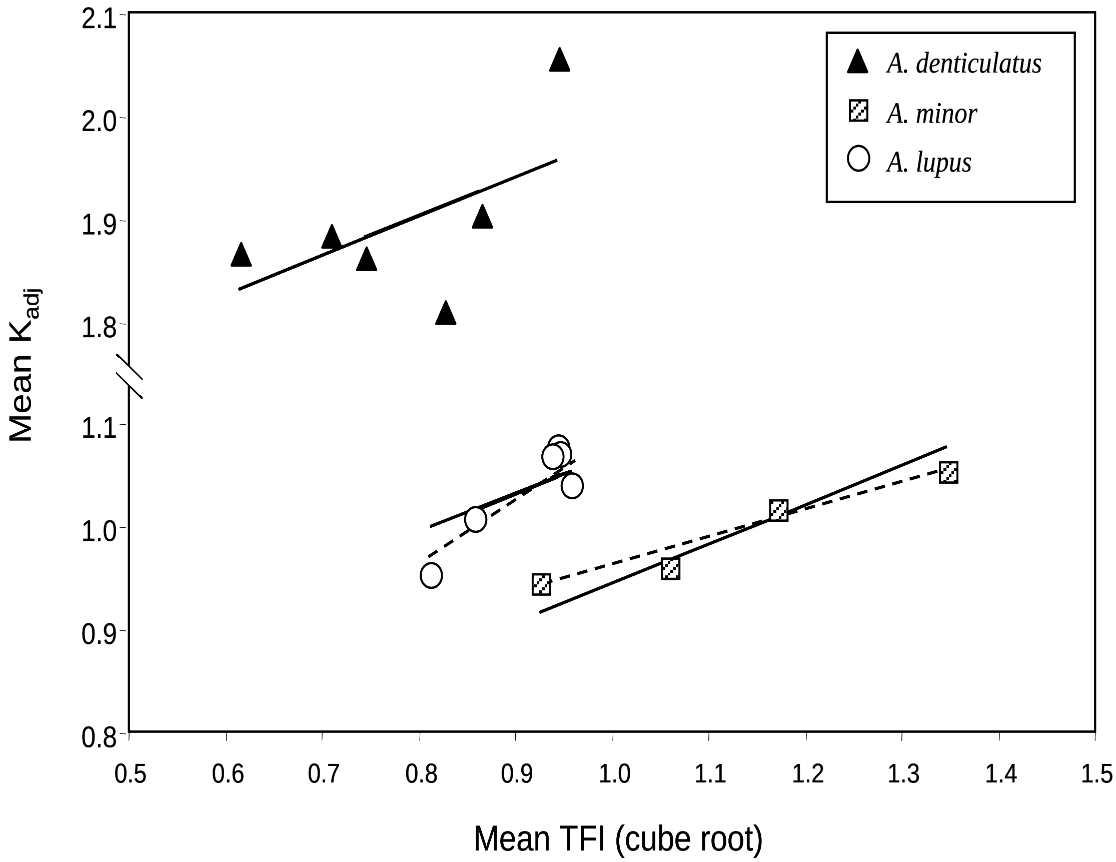

Figure 9. NAFO Division mean condition factor (K_{adj}; length-corrected) versus NAFO mean total fullness index (mean TFI; cube-root transformed) for three species of wolffish. Analysis of Covariance (ANCOVA) revealed a significant effect of mean TFI (cube-root transformed) on mean K_{adj} for all species combined (solid lines: $F_{1,16} = 11.2$; $p < 0.001$); mean K_{adj} was highly related to 'species' ($F_{2,16} = 427.0$; $p < 0.0001$). Within species, mean K_{adj} was significantly related (dashed lines) to mean TFI (cube-root transformed) for A. lupus ($r^2 = 0.86$; $p < 0.01$) and A. minor ($r^2 = 0.95$; $p < 0.05$). Note the break in the y–axis.

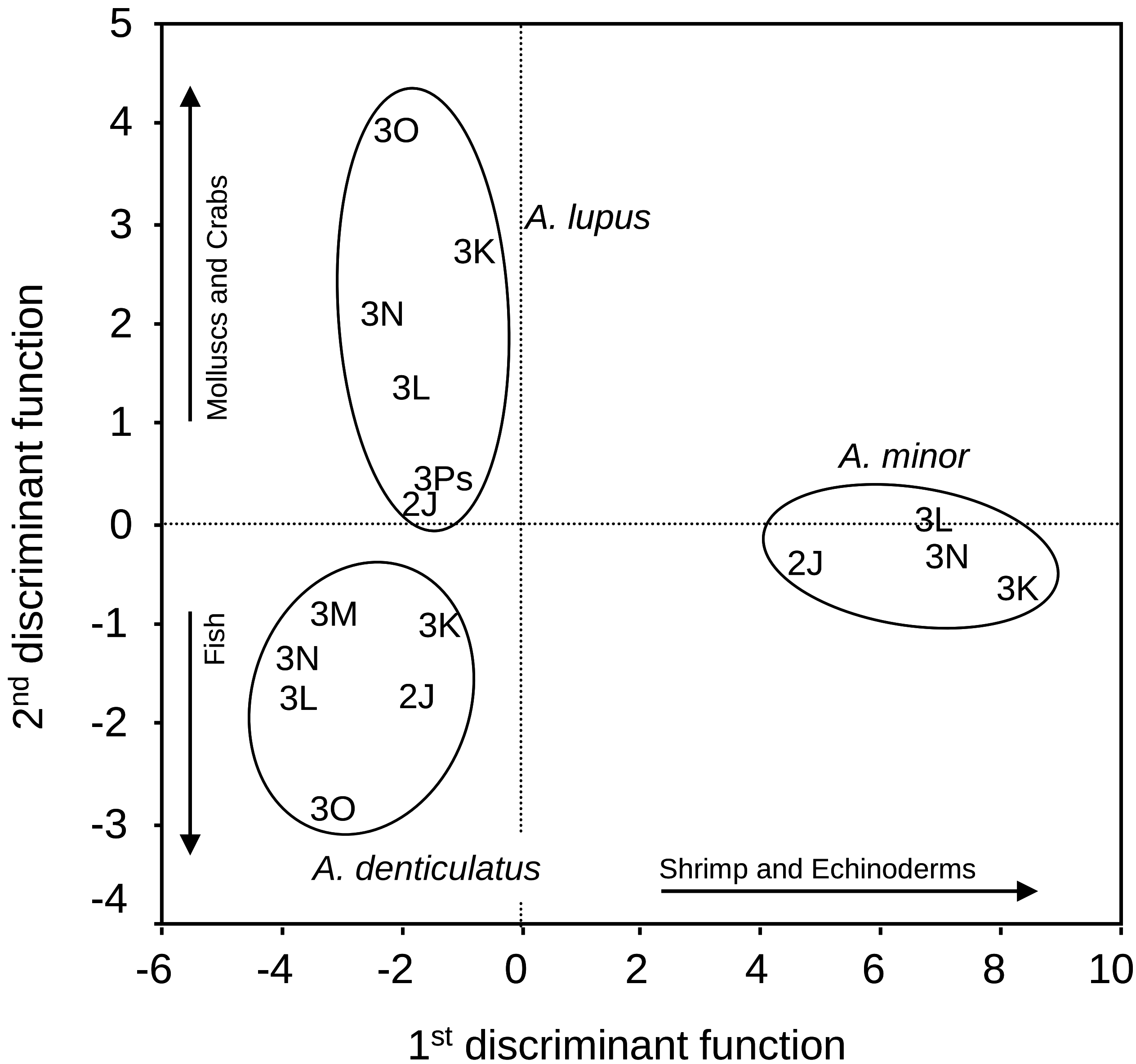

Figure 10. Discriminant analysis of mean feeding habits (mean PFI) by NAFO Division for three species of wolffish. Ellipses contain all data points (indicated as NAFO Division) for each species. Groupings were significant (MANOVA; Wilks' Lambda = 0.01; $F_{10,18} = 4.18$; $p < 0.0001$). 100 % of original grouped cases were correctly reclassified to species.

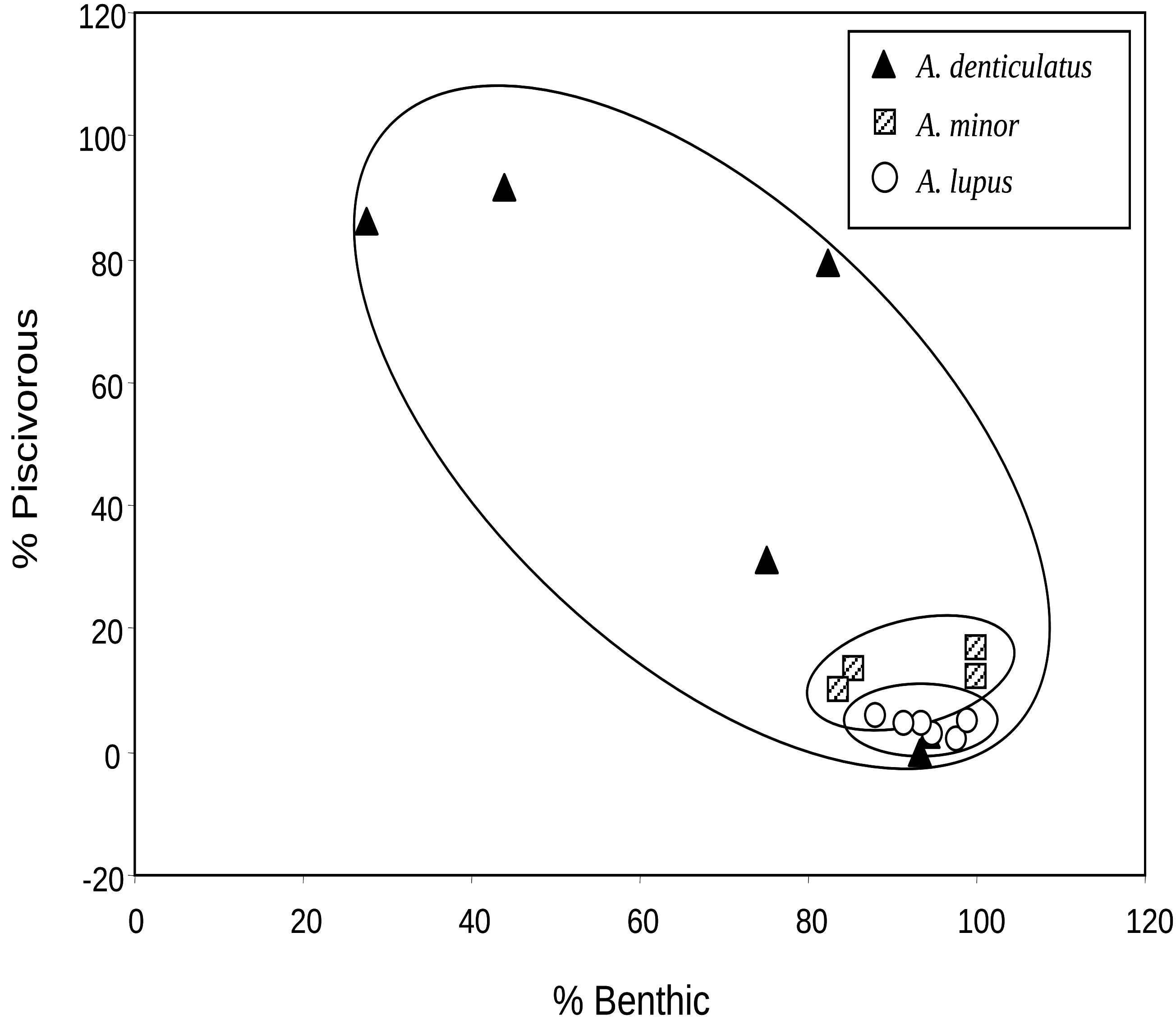

Figure 11. NAFO Division mean percent piscivorous diet versus NAFO Division mean percent benthic diet (see Table 5) for three species of wolffish. Ellipses represent the spatial range of mean 2-dimensional trophic niche space occupied by each species.