

Breaking with tradition: redefining measures for diet description with a case study of the Aleutian skate *Bathyraja aleutica* (Gilbert 1896)

Simon C. Brown · Joseph J. Bizzarro ·
Gregor M. Cailliet · David A. Ebert

Received: 1 September 2010 / Accepted: 27 October 2011
© Springer Science+Business Media B.V. 2011

Abstract Characterization of fish diets from stomach content analysis commonly involves the calculation of multiple relative measures of prey quantity (%N,%W,%FO), and their combination in the standardized Index of Relative Importance (%IRI). Examining the underlying structure of dietary data matrices reveals interdependencies among diet measures, and obviates the advantageous use of underused prey-specific measures to diet characterization. With these interdependencies clearly realized as formal mathematical expressions, we proceed to isolate algebraically, the inherent bias in %IRI, and provide a correction for it by substituting traditional measures with prey-specific measures. The resultant new index, the Prey-Specific Index of Relative Importance (%PSIRI), is introduced and recommended to replace %IRI for its demonstrated more balanced treatment of the relative measures of prey quantity, and less erroneous behavior across taxonomic levels of identified prey. As a case study, %PSIRI was used to examine the diet of the

Aleutian skate *Bathyraja aleutica* from specimens collected from three ecoregions of the northern Gulf of Alaska (GOA) continental shelf during June–September 2005–2007. Aleutian skate were found to primarily consume the commonly abundant benthic crustaceans, northern pink shrimp *Pandalus eous* and Tanner crab *Chionoecetes bairdi*, and secondarily consume various teleost fishes. Multivariate variance partitioning by Redundancy Analysis revealed spatially driven differences in the diet to be as influential as skate size, sex, and depth of capture. Euphausiids and other mid-water prey in the diet were strongly associated with the Shelikof Strait region during 2007 that may be explained by atypical marine climate conditions during that year.

Keywords Skate · *Bathyraja aleutica* · Diet · Gulf of Alaska · Food habits · Index of relative importance

S. C. Brown (✉) · J. J. Bizzarro · G. M. Cailliet ·
D. A. Ebert
Pacific Shark Research Center,
Moss Landing Marine Laboratories,
8272 Moss Landing Road,
Moss Landing, CA 95039, USA
e-mail: simoncbrown@gmail.com

Present Address:
J. J. Bizzarro
School of Aquatic and Fishery Sciences,
University of Washington,
PO Box 355020, Seattle, WA 98195-5020, USA

Introduction

Diet information is crucial to our understanding of species ecology, trophic interrelationships, food webs, and ultimately, the flow of energy through ecosystems. Stomach content analysis remains a universal technique for sampling the diets of fishes and these studies contribute large amounts of species-specific diet data for potential use in trophic ecosystem modeling that provide ecosystem-based fishery management advice (Ainsworth et al. 2010). Although

there has been an arguably successful call (294 citations in Web of Science) for consistency in reporting diet compositions of elasmobranchs with percent number (%N), percent weight (%W), frequency of occurrence (%FO), and the standardized Index of Relative Importance or %IRI (Cortès 1997), there remain critical unresolved weaknesses in this widely used and accepted methodology (Cortès 1998; Hansson 1998). There are, in fact, not only weaknesses, but also serious unrecognized mathematical flaws in the presentation of diet data both graphically and by indices that have gone largely unnoticed in the published literature. These methodological problems are a direct consequence of diet researchers' incorrect mathematical understanding of diet measures. A deeper understanding of the structure of dietary data and the resulting mathematical relationships between diet measures not only resolves current methodological weaknesses, but also leads to increased extraction of information about food habits in graphical displays and diet composition tables.

Proper metrics are necessary to characterize diets of abundant, data-poor species, to avoid faulty or incomplete conclusions about their trophic roles. Skates as abundant mesopredators (Ebert and Bizzarro 2007) likely play important trophic roles in demersal fish communities and may be able to overtake the resource niche left open by depleted teleost stocks (Stevens et al. 2000; Link and Sosebee 2008). For large marine ecosystems with large industrial fisheries, like the northern Gulf of Alaska (GOA) shelf, attaining trophic information on skates is beneficial for consideration in ecosystem based modeling and management. In the GOA, skates contribute substantially to the bycatch (retained and discarded) of directed fisheries such as those for Pacific Halibut *Hippoglossus stenolepis* and other commercially valuable groundfish species (Ormseth and Matta 2009), but their ecology is poorly understood.

Skates of the genus *Bathyraja* are widely distributed in the North Pacific. In the GOA the Aleutian skate *Bathyraja aleutica* (Gilbert 1896) is one of the most abundant skate species (Ormseth and Matta 2009). The Aleutian skate ranges from the northern Sea of Japan into the Sea of Okhotsk and Bering Sea to the eastern GOA, but has been reported as far south as Cape Mendocino, California, U.S.A. (Hoff 2002), typically occupying shelf and slope depths of 100–800 m (Mecklenburg et al. 2002). It is a relatively

large skate, reaching a maximum size of 150 cm total length (TL). Diet data reported from the western North Pacific and Aleutian Islands indicate that Aleutian skates consume primarily decapod crustaceans, with fishes and cephalopods also represented (Orlov 1998; Yang 2007); however, scant dietary information is available for the Aleutian skates in the northern GOA. The findings of this study represent the first detailed trophic information on the Aleutian skate population from the northern GOA shelf ecosystem.

To improve current data reporting methods for stomach contents analysis of elasmobranchs, our objectives for this study are to: 1) define the structure of diet data; 2) elucidate mathematical relationships between diet measures; 3) demonstrate how appropriate operationalization of these relationships can correct current flaws in compound diet indices and graphical displays and; 4) illustrate the application of this approach in reporting the diet composition on dietary data from the Aleutian skate. Additionally, we provide an in-depth statistical analysis of ontogenetic, regional, and interannual variation in the diet of the Aleutian skate from the northern GOA ecosystem during 2005–2007.

The structure of diet data

Stomach content analysis typically incorporates measurements of numerical abundance (i.e. aggregate counts of individual prey items in each designated prey category), gravimetric (or volumetric) abundance (i.e. aggregate weights or volumes of prey items in each designated prey category), and the frequency of occurrence of prey categories among all stomach samples (Hyslop 1980). The resulting diet data matrix, by numerical abundance or biomass, is composed of columns of prey categories (i) by rows of individual stomach samples (j) standardized to proportion by total individual stomach content (i.e. by row):

$$\text{stomach sample } (j) \begin{bmatrix} & \text{prey category } (i) \\ & 1 & 0 & 0 & 0 \\ 0 & 0.25 & 0.5 & 0.25 \\ 0 & 0 & 0.5 & 0.5 \\ 0 & 0.75 & 0 & 0.25 \end{bmatrix}$$

This stomach sample by prey item diet matrix is well-suited for multivariate statistical analysis

(de Crespin de Billy et al. 2000), but also conveniently serves in calculation of diet measures. The average percent number (%N) and average percent weight (%W) for each prey item are column averages of this matrix and are additive, meaning that they sum to 100% for all different prey items of a prey category. For example, in the dietary data matrix provided above, the average percent value for each prey category (i.e. each column) is 25%, and the aggregate values for all prey categories sum to 100%.

The Percent Frequency of Occurrence (%FO) can be calculated as the column averages from the same diet matrix, but translated to discrete conditions of presence/absence (i.e. binary data). From the example diet matrix above, the %FO for each prey category (from left to right) is: 25%, 50%, 50%, and 75% and sums to an indeterminate value which, is 200% in this example. Because different prey categories occur together within a single stomach sample, %FO is specific to each category, meaning that its value can range from >0% to 100%, independent of the %FO values of all other prey items.

Relationship to relative measures of prey quantity

There is a specific mathematical relationship between %N and %W, with %FO embedded in the structure of diet matrices from which these measures are calculated. Either a prey is absent in a stomach sample, thereby receiving a value of zero for all three diet measures, or it is present, ranging from >0 to 1 by proportion of numerical or gravimetric abundance. The meaning of the zero value is the same regardless of which diet measures it is incorporated into: *a discrete condition of absence*. This obfuscation of discrete absences with numerical and gravimetric abundance has profound consequences for the graphical display of diet compositions and compound diet indices that incorporate two of more individual measures (e.g., %FO, %N, %W).

Relationship to graphical displays

If %N or %W is plotted against %FO, as suggested for some graphical displays of diet data (Costello 1990; Cortès 1997) exactly one-half of the plot space is non-existent; it is mathematically impossible for any prey to occur at coordinates above the 1:1 line of %N, or %W, and %FO. This is because a value

of %N or %W cannot exceed its corresponding %FO value for any prey category. The determined value of %FO represents an upper limit to %N and %W values because discrete absences are averaged into all measures, this creates a mathematical dependence between diet measures whose strength increases with the increasing frequency of zero values in a diet data matrix. Amundsen et al. (1996), fully realizing this graphical limitation of diet measures in constructing feeding strategy diagrams (Costello 1990), proposed a new measure termed *prey-specific abundance*. Prey-specific abundance is defined as the percent numerical abundance of a prey item averaged over the stomach samples in which it occurs (i.e. excluding zero values). Like %FO, the value of the prey-specific abundance for a prey item may take any value >0% to 100% independent of the values for all other prey items. For example, from the diet data matrix above from left to right the prey-specific abundance is 100%, 50%, 50%, and 33.3%. We adopt the terminology of Amundsen et al. (1996) and extend it to weight (prey-specific weight) for the remainder of this study.

Although prey-specific abundance was originally proposed as a modification to the Costello (1990) feeding strategy diagram, it should actually be applied to correct any graphical method attempting to plot %N or %W against %FO. For example, IRI diagrams, in which %N and %W are plotted against %FO to produce rectangular surfaces representing each prey category's relative importance, where the unit area is equal to the unit IRI, represent a false geometry. The measures representing each rectangle's sides are not actually at right angles unless the diet data matrix contains no zero values, thus a rectangle is an incorrect representation, falsely implying that %FO is orthogonal to %N and %W.

Relationship to compound diet indices

The IRI and %IRI, like the aforementioned graphical methods, are also flawed by the inherent redundancy in combining mathematically dependent measures. A major weakness in the %IRI resulting from this combination is that it is non-additive across taxonomic levels (or other nested prey categories), an attribute of %IRI that has been incorrectly attributed to the inclusion of %FO in its calculation. This means, despite being standardized to 100% for any given

taxonomic level, there is disagreement in %IRI values from one taxonomic level to the next. The %IRI therefore has an intrinsically arbitrary property since its values are dependent upon the taxonomic level or the designated prey categories chosen by a researcher, largely defeating its purpose as a standardized measure of prey importance to facilitate comparisons. Because it is not likely that all prey will be consistently identified to the same taxonomic level within a study, let alone between studies, this is a serious weakness in %IRI that results from its flawed calculation. The flaws in the most commonly used contemporary dietary indices can be described through simple algebra. Each diet measure is defined:

Prey-specific abundance (%PN_i, %PW_i):

$$\%PA_i = \frac{\sum_{j=1}^n \%A_{ij}}{n_i} \tag{1}$$

Average percent abundance (%N_i, %W_i):

$$\%A_i = \frac{\sum_{j=1}^n \%A_{ij}}{n} \tag{2}$$

Frequency of Occurrence (FO):

$$FO_i = \frac{n_i}{n} \tag{3}$$

where %A_{ij} is the abundance (by counts or weights) of prey category *i* in stomach sample *j*, *n_i* is the number of stomachs containing prey *i*, and *n* is the total number of stomachs. It is evident that Eq. 2 is the multiplicative product of Eq. 1 and Eq. 3:

$$\frac{\sum_{j=1}^n \%A_{ij}}{n_i} \times \frac{n_i}{n} = \frac{\sum_{j=1}^n \%A_{ij}}{n}$$

which is proof of the theorem that the average percent abundance (%N and %W) is *already a compound index containing %FO*. Because of their direct mathematical dependence, %N and %W should not be redundantly combined with %FO in a compound diet index such as the Index of Relative Importance (IRI) whose intended purpose is to provide a more balanced estimate of dietary importance. The resulting bias in IRI from combining these measures can be isolated by mathematical expression. Simple algebraic re-

arrangement of the IRI using the equivalencies above results in the following:

$$\begin{aligned} IRI &= \%FO \times (\%N + \%W) \\ &= \%FO \times [(\%PN \times \%FO) + (\%PW \times \%FO)] \\ &= \%FO^2 \times (\%PN + \%PW) \end{aligned}$$

It is now revealed %FO is unknowingly squared in the calculation of IRI which, among other undesired behaviors, accounts for the empirically observed bias in %IRI to over-emphasize frequently occurring prey and under-emphasize rare prey with respect to the %FO (Ortiz et al. 2006). Having isolated this bias in IRI, we can now modify it by substituting %N and %W with their corresponding prey-specific abundances, %PN and %PW:

$$\%PSIRI_i = \frac{\%FO_i \times (\%PN_i + \%PW_i)}{2}$$

This Prey-Specific IRI (%PSIRI) sums to 200% and therefore dividing by 2 results in a version of the standardized %IRI, with an important distinction: the %PSIRI is additive with respect to taxonomic levels, such that the sum of %PSIRI for species will be equal to the %PSIRI of the family containing those species, and so forth. This characteristic enhances %PSIRI for comparisons between predators and studies because its values are not dependent upon taxonomic level or prey categories designated by a researcher. Additionally, because of the mathematical relationships between diet measures the %PSIRI is also a generalized form of the standardized Geometric Importance Index (Assis 1996) where only %N and %W are considered:

$$\%PSIRI_i = \frac{\%FO_i \times (\%PN_i + \%PW_i)}{2} = \frac{\%N + \%W}{2} = \%GII$$

It is preferable, however, to express %PSIRI in terms of prey-specific measures and %FO such that there is less obfuscation of presence/absence and abundance, or biomass. If only numerical abundance, or biomass, is recorded then %N and %W may act themselves as compound indices:

$$\%N = \%FO \times \%PN \text{ and } \%W = \%FO \times \%PW$$

This last expression demonstrates another useful point; if a researcher does not wish to combine numerical abundance with biomass in an index like %PSIRI, they may still present prey-specific measures

with the %FO and use %N and %W as separate compound indices to summarize relative importance.

Material and methods

Study area

The study area was located on the northern GOA continental shelf, extending from the Kenai Peninsula westward to the Shumagin Islands along Alaska Peninsula. The northern GOA shelf extends far offshore, encompassing Kodiak Island and ranging to 200 m depth, and is crosscut with deeper canyons and gullies (Weingartner 2005). This region contains the highest biomass of skates in the GOA and is the regional center of abundance for the Aleutian skate (Stevenson et al. 2007; Ormseth and Matta 2009).

Specimen collection

Skate stomachs were obtained by participation aboard fishery-independent bottom trawl surveys conducted by the National Marine Fisheries Service's Alaska Fisheries Science Center (AFSC) in June-July of 2005, and the Alaska Department of Fish and Game (ADFG) in June-September of 2006 and 2007. In 2005, haul stations were spaced across the entire northern GOA shelf. In 2006 and 2007, however, haul stations were stratified into distinct regions contained within the larger study area, including: Alaska Peninsula (AKP), Shelikof Strait (SHS), and the shelf adjacent to the southeastern side of Kodiak Island (KOD). We therefore examined spatial variation in 2005 across the shelf for evidence of regional correspondence in the diet, and then made regional comparisons in 2006 and 2007.

Skates were sexed and total length (TL) was measured (± 1 mm). The foregut (esophagus and stomach to the pyloric sphincter) was excised, fixed in 10% neutral buffered formalin, and then preserved in 70% ethanol for subsequent analysis. The stomach was not taken from any skate that showed signs of stomach eversion or regurgitation of prey in the buccal cavity.

Stomach contents analysis

Stomach contents were sorted, identified, enumerated, and weighed. An index of vacuity was used to express

the number of empty stomachs encountered as a percentage of the total stomachs examined. Any highly digested material that could not be placed in a taxonomic category, stomach parasites, and inorganic material were noted but excluded from further analysis. Identification of prey was performed to the lowest possible taxonomic level primarily using taxonomic keys, field guides, consultation with experts, and museum collections. The number of each prey item in a stomach sample was estimated using the most conservative count when the detached components of prey were present. Prey items were then weighed (0.01 g) after excess moisture was blotted away.

Sample size sufficiency

To assess whether the number of sampled skate stomachs was sufficient to describe the diet, cumulative prey curves (Ferry and Cailliet 1996) were computed with EstimateS (Version 8.2, R. K. Colwell, <http://purl.oclc.org/estimates>). The estimated number of unique prey categories and associated 95% CIs were plotted against the cumulative number of stomach sample examined. Because visual examination of prey curves for an asymptote is unreliable, the slope of the linear regression (b) through the ultimate five sub-samples was used as an objective criteria where $b \leq 0.05$ signified acceptable leveling off of the prey curve for diet characterization (Bizzarro et al. 2009).

Statistical analysis of diet variation

For the purpose of statistical analysis, prey categories were designated for different prey types at higher taxonomic levels (e.g. polychaetes) and for common prey taxa (e.g. Tanner crab *Chionoecetes bairdi*). Highly digested fishes were often difficult to identify, as skates appeared to digest hard parts, like otoliths and bones that aid in identification. Therefore, a majority of the prey category "Fish" contains highly digested fishes, but also several infrequently encountered species (e.g. sockeye salmon *Oncorhynchus nerka*, three-spined stickleback *Gasterosteus aculeatus*). Because of regular occurrence of some fish species in skate stomachs, Pacific walleye pollock *Theragra chalcogramma*, capelin *Mallotus villosus*, flatfishes (Order Pleuronectiformes), Pacific sandlance

Ammodytes hexapterus, dwarf wrymouth *Cryptacanthodes aleutensis*, eelpouts (Family Zoarcidae), and pricklebacks (Family Stichaeidae) were assigned to separate prey categories.

The numerical diet composition was chosen for statistical analysis because this measure best reflects feeding behavior (Hyslop 1980; Amundsen et al. 1996) and there was high measurement error in the weights of prey found in various stages of digestion in skate stomachs. Furthermore, distance matrices of the diet composition by number and by weight were strongly (rank) correlated indicating similar results from statistical analysis would be obtained by either measure.

Redundancy Analysis (RDA) was chosen as an appropriate multivariate statistical technique because it allows for components of dietary variation chosen *a-priori* to be examined and tested for statistical significance and was performed in the software CANOCO v4.5 (ter Braak and Smilauer 2002). Euclidean distance, upon which RDA is calculated, is not an appropriate resemblance measure for prey abundances because it is possible that the joint absence of a prey in two samples will produce less distance between the samples than two samples that share the same prey species in differing abundances (Orloci 1978). For this reason, prior to analysis, the diet data was transformed using the Hellinger transformation, in this case the square root of the proportional abundance of a prey category in a stomach sample, or:

$$y'_{ij} = \sqrt{\frac{y_{ij}}{y_{i+}}}$$

where y_{ij} is the abundance of prey items of category j in sample i , and y_{i+} is the total abundance of all prey items in sample i (Legendre and Gallagher 2001). A matrix of Euclidean distances calculated on y'_{ij} translates directly to a matrix of Hellinger distances:

$$D_{Hellinger}(x_1, x_2) = \sqrt{\sum_{j=1}^p \left[\sqrt{\frac{y_{1j}}{y_{1+}}} - \sqrt{\frac{y_{2j}}{y_{2+}}} \right]^2}$$

that range from a minimum distance of zero when two samples are identical in species abundances, to a maximum distance of $\sqrt{2}$ when two samples share no species in common (Legendre and Legendre 1998).

Intraspecific and spatial diet variation

Variance partitioning procedures were performed using RDA to differentiate significant spatial and intraspecific components of dietary variation in 2005 (Borcard et al. 1992). Continuous variables included haul coordinates, skate size (TL), and depth (m). Sex (male, female) was the only categorical variable.

To account for potential non-linear relationships of prey with space, such as prey patches, haul coordinates (x, y) were entered as variables into a spatial matrix using the nine terms of the cubic surface trend regression (Borcard et al. 1992) of the form:

$$S = x + y + xy + x^2 + y^2 + x^2y + xy^2 + x^3 + y^3$$

Likewise, intraspecific variables were entered into a matrix along with 1st degree interaction terms:

$$I = TL + Depth + Sex + TL \times Depth + TL \times Sex + Depth \times Sex$$

Forward selection of each set of explanatory variables was then performed by Monte Carlo permutations (10 000) to select only the variables explaining statistically significant components of variation in the diet. Multiple partial RDAs were then used to partition the variance unique to, and shared between, each set of variables as described in Borcard et al. (1992).

Regional diet variation

Homogeneity of multivariate dispersion in regional diet composition was statistically tested by permutation ANOVA (Anderson 2006; Oksanen et al. 2011). The response variable was the dietary dispersion, calculated as the Hellinger distance between each sample and the spatial median of all samples in principal coordinates analysis (PCoA) space. If statistically significant heterogeneity of variance was detected in the diet among regions, these results were interpreted qualitatively, using %PSIRI diagrams, since a permutation test on regional diet difference would fail to produce the correct null hypothesis. If heterogeneity of variance in the diet among regions was not strong, then redundancy analysis (RDA) was computed with region as a factor and Monte Carlo permutations (10 000) were performed to indicate significance of the resulting model.

Results

Sampling results

In total, 270 Aleutian skate were sampled from 2005 to 2007. The index of vacuity was 6.6% indicating non-selective opportunistic foraging on various available prey resources. Only the stomachs containing prey were analyzed further. Females were caught more frequently than males (1.73:1.00). The size distribution was left-skewed for females (-0.657) and males (-1.028), with greater frequencies of larger-sized individuals (Fig. 1). Male and female Aleutian skate, however, exhibited significantly different size distributions ($K-S Z=2.075$, 2-tailed, $p=0.0003$), with females being larger. Smaller size classes of Aleutian skate ($< \sim 80$ cm TL) were largely absent from the sampled GOA shelf area, only beginning to appear at depths $> \sim 200$ m and were predominantly male (Fig. 1).

Diet description

Crustaceans were the dominant prey taxa of Aleutian Skate, followed by fishes (Table 1). Among the crustaceans, Pandalid shrimps and Tanner crab were

most frequently consumed (67.7% FO and 55.5% FO respectively) and comprised 33.7% PSIRI and 20.0% PSIRI of the total 74.6% PSIRI of all crustacean prey. Euphausiids, when consumed (24.0% FO), contributed modestly (53.4% PN and 14.3% PW) to the diet composition. Hippolytid and crangon shrimp were regularly consumed prey items (27% FO and 39% FO) but never occurred in great relative abundance within stomach contents.

Among identified fish prey, Pacific walleye pollock and capelin were the only two species consumed with any regularity (17.7% FO and 16.5% FO). The remaining identified fish prey was composed of various small forage species, i.e., Pacific sandlance, dwarf wrymouth, pricklebacks, eelpouts, Pacific sandfish *Trichodon trichodon*, and flathead sole *Hippoglossoides elassodon*. A single large sockeye was recovered from the distended stomach of an individual skate. Cephalopods were tertiary prey (16.9% FO) and did not contribute substantially to overall diet by weight or number (3.1% W and 2.3% N respectively) but did contribute modestly to the diet of those skates that consumed them (18.1% PW and 13.4% PN).

Comparison to %IRI

For comparison, %IRI was calculated at the taxonomic level of Class (%IRI_{CLASS}) and Family (%IRI_{FAMILY}) (Table 1). These taxonomic levels represent conceivably realistic prey categories that two independent researchers might choose in order to assess relative importance in the diet of Aleutian skates. The discrepancy between %IRI_{CLASS} and the sum of the corresponding %IRI_{FAMILY} categories contained therein ($\Sigma\%IRI_{FAMILY}$) reflects the erroneous behavior of %IRI. Notably, Class Crustacea displayed an increase from 85.5%IRI_{CLASS} to 94.3 $\Sigma\%IRI_{FAMILY}$, and Class Teleostei correspondingly decreased from 13.9%IRI_{CLASS} to 5.1 $\Sigma\%IRI_{FAMILY}$. %PSIRI is additive with respect to taxonomic level (i.e. %PSIRI_{CLASS}= $\Sigma\%PSIRI_{FAMILY}$ within rounding errors) and more balanced with respect to %FO. For example, the relative contributions of Class Crustacea to diet composition by %PSIRI_{CLASS} and $\Sigma\%PSIRI_{FAMILY}$ were 74.6% and 74.5%, respectively. Corresponding values of Class Teleostei were 22.1% when calculated using either taxonomic level of teleosts (Teleostei).

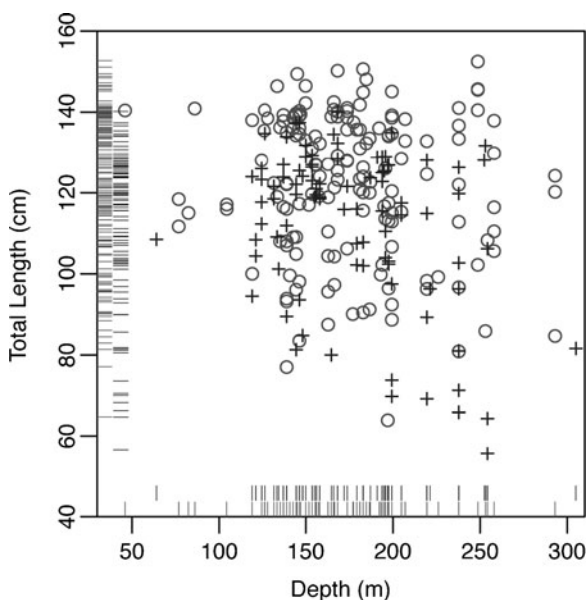


Fig. 1 Size-depth distribution of female (circles) and male (crosses) skates. Rug charts display the frequency distributions for total length (cm) and depth (m) of each sex (female=outside, male=inside)

Table 1 Diet composition of *Bathyrāja aleutica* by percent frequency of occurrence (%FO), percent prey-specific number (%PN), percent number (%N), percent prey-specific weight (%PW), percent weight (%W), and prey-specific index of relative importance (%PSIRI)

| Class | Order | Family | Species | %FO | %PN | %N | %PW | %W | %PSIRI | | | | |
|------------------------------|--------------------------|--------------------------------------|-------------------------------|-------------------|-------------------------------------|--------------|---------------------------|------|--------|------|------|------|------|
| Polychaeta | | | | 3.1 | 12.0 | 0.4 | 4.4 | 0.1 | 0.3 | | | | |
| | | Nephtyidae | Unidentified | 1.2 | 9.1 | 0.1 | 8.4 | 0.1 | 0.1 | | | | |
| | | Pectinariidae | Unidentified | 0.4 | 5.0 | 0.02 | 1.7 | <0.1 | <0.1 | | | | |
| | | Polynoidae | Unidentified | 1.2 | 14.2 | 0.2 | 2.0 | <0.1 | 0.1 | | | | |
| | | Unidentified Polychaeta | Unidentified | 0.8 | 10.4 | 0.1 | 1.0 | <0.1 | <0.1 | | | | |
| Bivalvia | | | <i>Nuculana spp.</i> | 2.0 | 18.4 | 0.4 | 2.2 | <0.1 | 0.2 | | | | |
| Gastropoda | | | <i>Cryptonatica affinis</i> | 0.4 | 7.7 | <0.1 | 7.0 | <0.1 | <0.1 | | | | |
| Cephalopoda | | | | 16.9 | 13.4 | 2.3 | 18.1 | 3.1 | 2.7 | | | | |
| | Octopoda | Octopodidae | | 2.4 | 14.8 | 0.3 | 17.2 | 0.4 | 0.4 | | | | |
| | | | <i>Benthoctopus leioderma</i> | 1.2 | 21.7 | 0.3 | 1.4 | <0.1 | 0.1 | | | | |
| | | | <i>Enteroctopus dofleini</i> | 0.4 | 6.3 | <0.1 | 98.2 | 0.4 | 0.2 | | | | |
| | | | Unidentified Octopodidae | 0.8 | 8.7 | 0.1 | 0.5 | <0.1 | <0.1 | | | | |
| | Teuthida | | | | 15.0 | 12.9 | 1.9 | 17.7 | 2.7 | 2.3 | | | |
| | | | | Octopodoteuthidae | <i>Octopoteuthis deletron</i> | 0.4 | 2.2 | <0.1 | 2.8 | <0.1 | <0.1 | | |
| | | | | Gonatidae | | 7.9 | 17.4 | 1.4 | 31.2 | 2.5 | 1.9 | | |
| | | | | | <i>Berryteuthis magister</i> | 3.9 | 24.2 | 1.0 | 24.6 | 1.0 | 1.0 | | |
| | | | | | <i>Gonatopsis borealis</i> | 2.0 | 10.5 | 0.2 | 69.4 | 1.4 | 0.8 | | |
| | | | | | <i>Gonatus onyx</i> | 0.8 | 11.7 | 0.1 | 9.9 | 0.1 | 0.1 | | |
| | | | | | <i>Gonatus madokai/middendorffi</i> | 2.8 | 4.7 | 0.1 | 1.9 | 0.1 | 0.1 | | |
| | | | | | Unidentified | Unidentified | 7.5 | 7.3 | 0.5 | 2.4 | 0.2 | 0.4 | |
| | | | | Crustacea | | | | 93.7 | 83.3 | 78.1 | 75.8 | 71.1 | 74.6 |
| | | | | | Isopoda | Aegidae | <i>Rocinela angustata</i> | 8.7 | 8.4 | 0.7 | 5.9 | 0.5 | 0.6 |
| | | 4.3 | 11.2 | | | | 0.5 | 3.5 | 0.2 | 0.3 | | | |
| | Amphipoda | Melitidae | <i>Wimvadocus torreli</i> | | 2.0 | 16.5 | 0.3 | 3.1 | 0.1 | 0.2 | | | |
| Unidentified Gammaridea | | Unidentified | 2.4 | | 6.7 | 0.2 | 3.7 | 0.1 | 0.1 | | | | |
| Euphausiacea | Euphausiidae | | 24.0 | | 53.4 | 12.8 | 14.3 | 3.4 | 8.1 | | | | |
| | | <i>Thysanoessa inermis/spinifera</i> | 21.7 | | 57.3 | 12.4 | 15.9 | 3.4 | 7.9 | | | | |
| | | Unidentified Euphausiidae | 2.4 | | 17.4 | 0.4 | 0.1 | <0.1 | 0.2 | | | | |
| Mysidacea | | | 2.0 | | 7.1 | 0.1 | 4.4 | 0.1 | 0.1 | | | | |
| Decapoda | | | | | 91.7 | 69.7 | 63.9 | 72.9 | 66.9 | 65.4 | | | |
| | Pasiphaeidae | <i>Pasiphaea pacifica</i> | 7.9 | | 13.4 | 1.1 | 10.5 | 0.8 | 0.9 | | | | |
| | | Crangonidae | | | 39.0 | 16.7 | 6.5 | 8.3 | 3.2 | 4.9 | | | |
| | <i>Argis dentata</i> | | 3.1 | | 37.2 | 1.2 | 26.4 | 0.8 | 1.0 | | | | |
| | <i>Argis spp.</i> | | 2.0 | 20.5 | 0.4 | 6.9 | 0.1 | 0.3 | | | | | |
| | <i>Crangon communis</i> | | 32.7 | 14.5 | 4.7 | 6.8 | 2.2 | 3.5 | | | | | |
| | Unidentified Crangonidae | | 3.1 | 6.6 | 0.2 | 1.3 | <0.1 | 0.1 | | | | | |
| | Hippolytidae | | | 27.2 | 16.3 | 4.4 | 7.9 | 2.2 | 3.3 | | | | |
| | | | <i>Eualus avinus</i> | 23.2 | 15.6 | 3.6 | 7.2 | 1.7 | 2.6 | | | | |
| | | <i>Eualus barbatus</i> | 0.4 | 50.0 | 0.2 | 86.2 | 0.3 | 0.3 | | | | | |
| | | <i>Eualus berkeleyorum</i> | 0.4 | 4.3 | 0.1 | 2.7 | <0.1 | 0.1 | | | | | |
| | <i>Eualus biunguis</i> | 0.4 | 2.7 | 0.1 | 1.1 | <0.1 | 0.1 | | | | | | |
| <i>Eualus macrophthalmus</i> | 0.79 | 3.9 | 0.1 | 3.8 | <0.1 | 0.1 | | | | | | | |

Table 1 (continued)

| Class | Order | Family | Species | %FO | %PN | %N | %PW | %W | %PSIRI |
|-------------|-------------------|-------------------|-----------------------------------|------|-------|------|-------|------|--------|
| | | | <i>Heptacarpus decorus</i> | 0.8 | 9.4 | 0.1 | 3.0 | <0.1 | <0.1 |
| | | | <i>Heptacarpus spp.</i> | 0.4 | 8.3 | 0.1 | 0.9 | <0.1 | 0.1 |
| | | | <i>Spirontocaris spp.</i> | 0.8 | 7.2 | 0.1 | 0.6 | <0.1 | <0.1 |
| | | | <i>Spirontocaris truncata</i> | 0.4 | 2.0 | 0.1 | 1.5 | <0.1 | 0.1 |
| | | | <i>Lebbeus groenlandicus</i> | 0.4 | 2.9 | 0.1 | 1.3 | <0.1 | 0.1 |
| | | | Unidentified Hippolytidae | 2.4 | 14.8 | 0.4 | 2.5 | 0.1 | 0.2 |
| | | Pandalidae | | 67.7 | 53.2 | 36.0 | 46.5 | 31.5 | 33.7 |
| | | | <i>Pandalopsis dispar</i> | 21.7 | 11.1 | 2.4 | 6.2 | 1.3 | 1.9 |
| | | | <i>Pandalus eous</i> | 53.5 | 46.4 | 24.9 | 48.0 | 25.7 | 25.3 |
| | | | <i>Pandalus jordani</i> | 0.4 | 20.0 | 0.1 | 45.3 | 0.2 | 0.1 |
| | | | <i>Pandalus spp.</i> | 15.7 | 35.0 | 5.5 | 18.5 | 2.9 | 4.2 |
| | | | Unidentified Pandalidae | 15.4 | 20.7 | 3.2 | 8.6 | 1.3 | 2.2 |
| | | Galatheidae | <i>Munida quadrispina</i> | 1.6 | 95.3 | 1.5 | 82.4 | 1.3 | 1.4 |
| | | Paguridae | | 4.7 | 14.2 | 0.7 | 17.4 | 0.8 | 0.7 |
| | | | <i>Ellasochirus tenuimanus</i> | 0.4 | 33.3 | 0.1 | 2.3 | <0.1 | 0.1 |
| | | | <i>Pagurus aleuticus</i> | 0.8 | 27.4 | 0.2 | 49.5 | 0.4 | 0.3 |
| | | | <i>Pagurus confragosus</i> | 0.4 | 2.2 | <0.1 | 2.1 | <0.1 | <0.1 |
| | | | <i>Pagurus kenerlyi</i> | 0.4 | 9.1 | <0.1 | 31.6 | 0.1 | 0.1 |
| | | | <i>Pagurus spp.</i> | 1.2 | 7.1 | 0.1 | 7.7 | 0.1 | 0.1 |
| | | | Unidentified Paguridae | 2.0 | 10.0 | 0.2 | 10.2 | 0.2 | 0.2 |
| | | Pinnotheridae | <i>Pinnixa occidentalis</i> | 2.0 | 10.0 | 0.2 | 5.7 | 0.1 | 0.2 |
| | | Majidae | | 55.9 | 24.2 | 13.5 | 48.2 | 26.9 | 20.2 |
| | | | <i>Chionoecetes bairdi</i> | 55.5 | 24.1 | 13.4 | 48.0 | 26.6 | 20.0 |
| | | | <i>Hyas lyratus</i> | 1.2 | 14.6 | 0.2 | 26.7 | 0.3 | 0.2 |
| Urochordata | | | | 0.8 | 27.5 | 0.2 | 7.3 | 0.1 | 0.1 |
| Teleostei | | | | 63.8 | 29.2 | 18.7 | 40.2 | 25.6 | 22.1 |
| | Gasterosteiformes | Gasterosteidae | <i>Gasterosteus aculeatus</i> | 0.4 | 8.3 | <0.1 | 13.1 | 0.1 | <0.1 |
| | Clupeiformes | Clupeidae | <i>Clupea pallasii</i> | 1.6 | 38.0 | 0.6 | 54.7 | 0.9 | 0.7 |
| | Osmeriformes | Osmeridae | <i>Mallotus villosus</i> | 16.5 | 24.6 | 4.1 | 25.7 | 4.2 | 4.2 |
| | Salmoniformes | Salmonidae | <i>Oncorhynchus nerka</i> | 0.4 | 100.0 | 0.4 | 100.0 | 0.4 | 0.4 |
| | Perciformes | | | 16.9 | 37.5 | 6.4 | 49.8 | 8.4 | 7.4 |
| | | Ammodytidae | <i>Ammodytes hexapterus</i> | 2.8 | 27.8 | 0.8 | 26.9 | 0.7 | 0.8 |
| | | Cryptacanthodidae | <i>Cryptacanthodes aleutensis</i> | 5.5 | 33.1 | 1.8 | 33.9 | 1.9 | 1.8 |
| | | Stichaeidae | | 5.5 | 33.4 | 1.8 | 53.4 | 2.9 | 2.4 |
| | | | <i>Lumpenus spp.</i> | 1.6 | 52.4 | 0.8 | 65.2 | 1.0 | 0.9 |
| | | | <i>Poroclinus rothrocki</i> | 1.6 | 49.6 | 0.8 | 75.9 | 1.2 | 1.0 |
| | | | Unidentified Stichaeidae | 2.4 | 10.0 | 0.2 | 30.5 | 0.7 | 0.5 |
| | | Zoarcidae | | 3.9 | 47.2 | 1.9 | 69.1 | 2.7 | 2.3 |
| | | | <i>Lycodes brevipes</i> | 2.8 | 59.3 | 1.6 | 81.2 | 2.2 | 1.9 |
| | | | <i>Lycodes spp.</i> | 0.8 | 18.4 | 0.1 | 26.1 | 0.2 | 0.2 |
| | | | Unidentified Zoarcidae | 0.4 | 20.0 | 0.1 | 70.2 | 0.3 | 0.2 |
| | | Trichodontidae | <i>Trichodon trichodon</i> | 0.4 | 15.8 | 0.1 | 37.9 | 0.1 | 0.1 |
| | Scorpaeniformes | Scorpaenidae | | 1.2 | 14.8 | 0.2 | 24.5 | 0.3 | 0.2 |
| | | | <i>Sebastes alutus</i> | 0.4 | 2.6 | 0.0 | 31.1 | 0.1 | 0.1 |
| | | | <i>Sebastes spp.</i> | 0.8 | 20.8 | 0.2 | 21.1 | 0.2 | 0.2 |

Table 1 (continued)

| Class | Order | Family | Species | %FO | %PN | %N | %PW | %W | %PSIRI |
|-------|-------------------|------------------------|----------------------------------|------|------|-----|------|-----|--------|
| | Gadiformes | | | 19.3 | 19.9 | 3.8 | 43.3 | 8.4 | 6.1 |
| | | Merlucciidae | <i>Merluccius productus</i> | 1.2 | 25.0 | 0.3 | 63.6 | 0.8 | 0.5 |
| | | Gadidae | | 18.1 | 19.5 | 3.5 | 42.0 | 7.6 | 5.6 |
| | | | <i>Eleginus gracilis</i> | 0.4 | 33.3 | 0.1 | 67.2 | 0.3 | 0.2 |
| | | | <i>Theragra chalcogramma</i> | 17.7 | 19.2 | 3.4 | 41.4 | 7.3 | 5.4 |
| | Pleuronectiformes | Pleuronectidae | | 4.3 | 23.5 | 1.0 | 18.1 | 0.8 | 0.9 |
| | | | <i>Hippoglossoides elassodon</i> | 1.2 | 24.8 | 0.3 | 19.8 | 0.2 | 0.3 |
| | | | Unidentified | 3.1 | 23.0 | 0.7 | 17.4 | 0.5 | 0.6 |
| | | Unidentified Teleostei | Unidentified | 13.8 | 15.8 | 2.2 | 16.1 | 2.2 | 2.2 |

Values of %PSIRI are additive to 100% within nested taxonomic levels

2005 spatial and intraspecific diet variation

The cumulative prey curve generated from 2005 samples ($n=44$) reached a slope of $b=0.047$, indicating adequate sample size (Fig. 2a). The prey categories that composed ~90% PSIRI in 2005 were, in decreasing order of importance: Tanner crab, pandalid shrimps, unidentified fishes, Pacific walleye pollock, euphausiids, galatheid crab *Munida quadripisina*, and hippolytid shrimps (Fig. 3a). From the areas of the shaded boxes, for each prey category in the PSIRI diagram, we can see that Tanner crab, pandalid shrimps, and fishes contributed roughly equal amounts to the diet in 2005. Pacific walleye pollock and euphausiids were of secondary importance, contributing about equally by %PSIRI; however, Pacific walleye pollock contributed more by weight and euphausiids more by number because of their different sizes. It is also evident from the %PSIRI diagram that galatheid crabs were eaten infrequently, but in very high relative abundances. Conversely, hippolytid shrimps were eaten infrequently by Aleutian skate and consumed in low relative abundance by both number and weight.

The results of variance partitioning for space and intraspecific variables explained a combined ~46% of the variance in the diet, sharing ~5% of the variance explained. Spatial dependence explained 27.7% of the variance in the diet when treated independently and 22.9% of the variance while accounting for the effects of intraspecific variation. Intraspecific variation in the Aleutian skate population accounted for 23.6% of the variance in the diet when assessed alone and 18.6% of

the variance while accounting for the effects of spatial variation.

The results of the forward selection of the spatial variables produced four significant polynomial terms that together represent space as a curved surface (Table 2). The primary spatial gradient in the diet is displayed by ordination biplot (Fig. 4a) along with a plot of the first constrained polynomial axis displayed in the real geographic space (Fig. 4b) to aid in the interpretation of the ordination diagram that suffers from introduced polynomial distortion. The spatial variation in the diet of Aleutian skate along the GOA shelf coincides with ecoregional designations (Fig. 4b). Tanner crab in the diet was strongly associated with AKP, located furthest southwest in our study area indicating its high relative abundance in this area. Euphausiids and pandalid shrimps were associated with the central parts of the study area, within SHS and adjacent to the eastern side of Afognak/Kodiak Islands. Lastly, galatheid crab was strongly associated with several haul locations on the outer shelf of the eastern extent of the study area, contributing almost the entire stomach contents of skates (95.3% PN, 82.4% PW) captured there.

The intraspecific terms remaining after forward selection, in order of the diet variation explained, included: TL, depth, their interaction (TL*depth), and sex, which explained a combined 23.6% of the variation in the diet, and 18.6% of dietary variation when accounting for the effects of space (Table 3). The effects of intraspecific predictors on the diet, when accounting for spatial variation, are displayed in the correlation biplot (Fig. 5). Consumption of fishes

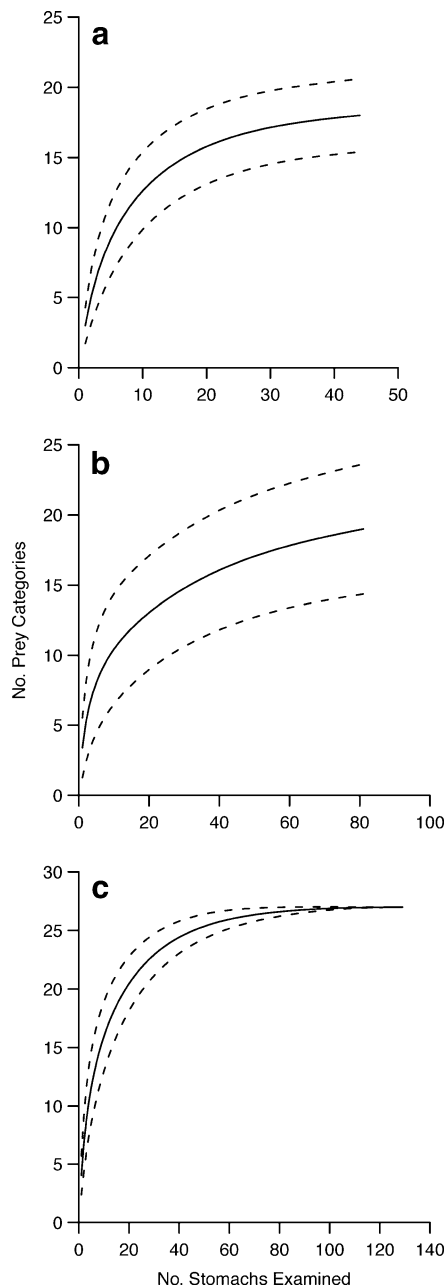


Fig. 2 Cumulative number of prey categories (solid line) and 95% CIs (dashed lines) for the diet of *Bathyraja aleutica* during (a) 2005, (b) 2006, and (c) 2007

(unidentified and infrequently encountered species) was associated with larger skates in shallower depths, whereas consumption of Pacific walleye pollock was associated with larger skates in deeper depths. Consumption of euphausiids, amphipods, and mysids, all small sized prey, were inversely related to TL.

Octopods were consumed only at deeper depths. The effects of sex indicate that larger sized female skates consumed more fish than male skates (Fig. 5).

2006 regional diet variation

The cumulative prey curve generated from 2006 data achieved a linear slope of $b=0.050$ in the ultimate five sub-samples, indicated sufficient sample size (Fig. 2b). The wide 95% CIs around the cumulative prey curve is attributed to the large differences in the regional multivariate dispersion (*see below*) from which subsamples were drawn.

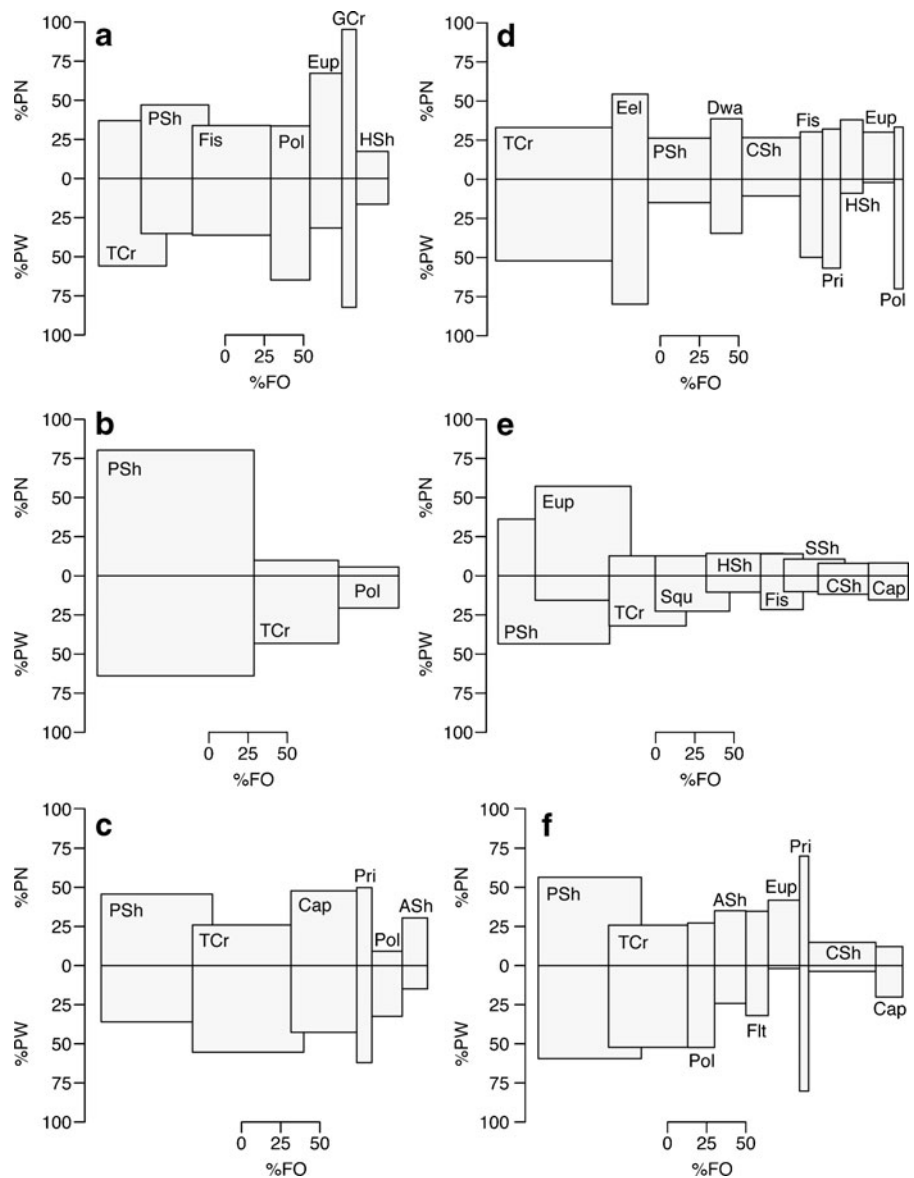
Strong heterogeneity of multivariate dispersion in the diet of Aleutian skate during 2006 indicates differences in regional foraging ($F_{\text{DISP}}=101.9$, $p=0.0001$), but precludes any further statistical testing of regional dietary differences by permutation. Pandalid shrimps and Tanner crab in both regions were the primary and secondary prey categories in terms of importance, but the relative contribution of each category differed between areas. The dispersion in SHS (0.3391) was significantly less than that of AKP, indicating a narrow diet and cursory examination of the diet indices for this region (Fig. 3b) indicated that pandalid shrimps dominated the diet composition, followed by Tanner crab and Pacific walleye pollock. The dispersion in AKP was much greater (0.7359) indicating a substantially broader diet. In addition to pandalid shrimps and Tanner crab, skates in AKP also fed on a more even diet of capelin, pricklebacks, Pacific walleye pollock, and argid shrimps (Fig. 3c).

2007 regional diet analysis

The cumulative prey curve generated for 2007 data (Fig. 2c) reached a linear slope of $b=0$ for the ultimate five subsamples of the dataset ($n=129$). Homogeneity of multivariate dispersion was marginally significant ($F_{\text{DISP}}=3.1954$, $p=0.0445$) among the three regions sampled in 2007 (SHS, AKP, KOD). Because the dispersion was not strongly heterogeneous between SHS (0.7077), AKP (0.7709), and KOD (0.8245), we proceeded with statistical testing of regional diet differences.

The diet of Aleutian skate in 2007 was significantly different among regions (Trace=0.102, $F_{\lambda}=7.805$, $p=0.0001$). The effects of regional diet variation are displayed by a constrained ordination biplot (Fig. 6).

Fig. 3 Graphical depiction of the diet composition (~90% PSIRI by surface area) by year and study region: **a** 2005/Central shelf, **b** 2006/ Shelikof Strait, **c** 2006/ Alaska Peninsula, **d** 2006/ Kodiak Island shelf, **e** 2007/ Shelikof Strait, **f** 2007/ Alaska Peninsula (f). *Ash* argid shrimps, *Cap* capelin, *CSh* crangon shrimps, *Dwa* dwarf wrymouth, *Eel* eelpouts, *Eup* euphausiids, *Fis* unidentified fishes, *Flt* flatfishes, *GCr* galatheid crab, *HSh* hippolytid shrimp, *Pol* Pacific walleye pollock, *Pri* prickleback, *PSh* northern pink shrimp, *SSH* side-striped shrimp, *Squ* squid, *TCr* Tanner crab



Pairwise comparisons further revealed that SHS was most different from both AKP (Trace=0.085, F_{λ} = 8.452, $p < 0.001$) and KOD (Trace=0.101, F_{λ} = 10.345, $p < 0.001$), and that AKP and KOD were least different (Trace=0.042, F_{λ} = 2.973, $p < 0.010$).

Tanner crab, eelpouts, and dwarf wrymouth distinguished the diet in KOD from that of other regions (Fig. 4d). KOD and AKP skates shared crangon shrimps in common, which differentiated diets in both regions from that of SHS. The diet in SHS was differentiated from the other two regions by the presence of midwater prey: Pacific glass shrimp *Pasiphaea pacifica*, euphausiids, squids, and very

small (<10 mm carapace length) side-striped shrimp *Pandalopsis dispar* (Fig. 4e). Capelin and northern pink shrimp, however, were common in diets of skates from SHS to AKP, which resulted in dietary differences between these two regions and KOD. Finally, skate diet in AKP was distinguished from that of the other two regions by flatfishes and argid shrimps (Fig. 4f).

Discussion

We have demonstrated by algebraic proof that: 1) when each calculated on a stomach sample by prey

Table 2 Marginal effects of the terms of the cubic surface trend regression in explaining spatial variation (λ) in the diet of *Bathyraja aleutica* by Redundancy Analysis. Conditional effects of the terms selected step-wise by Monte Carlo permutation and the significance (p) of the pseudo-F ratio (F_λ)

| Marginal effects | | | |
|---------------------|-----------|--------|-------------|
| Variable | λ | | |
| x | 0.09 | | |
| y ² | 0.09 | | |
| y*x | 0.08 | | |
| y ³ | 0.08 | | |
| x*y ² | 0.08 | | |
| x ² | 0.08 | | |
| y | 0.08 | | |
| x ³ | 0.07 | | |
| y*x ² | 0.07 | | |
| Conditional effects | | | |
| Variable | λ | p | F_λ |
| x | 0.09 | 0.001 | 3.87 |
| +x ² | 0.09 | 0.0001 | 4.36 |
| +y ² | 0.06 | 0.009 | 3.07 |
| +y | 0.04 | 0.047 | 2.13 |

item data matrix, %N and %W are mathematically dependent on %FO and 2) that this dependence translates bias and subjectivity to %IRI, greatly weakening its applicability as a generalized index for diet studies despite its wide use among diet studies. The %IRI places undue emphasis on %FO as proven by algebraic re-arrangement, shown actually to be equivalent to a squared term (i.e. %FO²) in the calculation of IRI. Additionally, %IRI behaves erroneously when calculated at different taxonomic levels of prey identification or nested prey categories as demonstrated in comparison to %PSIRI with the case study diet data for the Aleutian skate. Thus, IRI and %IRI are not as balanced, or less biased, with regards to individual diet measures as has been widely assumed.

By separating the information contained in prey counts and prey weights with prey-specific measures from the frequency of occurrence, we have provided a solution to these weaknesses in IRI and %IRI through the creation of %PSIRI. Graphical displays plotting %N and %W against %FO are flawed in the same manner as the %IRI, with half of the graphical plotting space being mathematically impossible for any point value to occupy because %N and %W can mathematically not

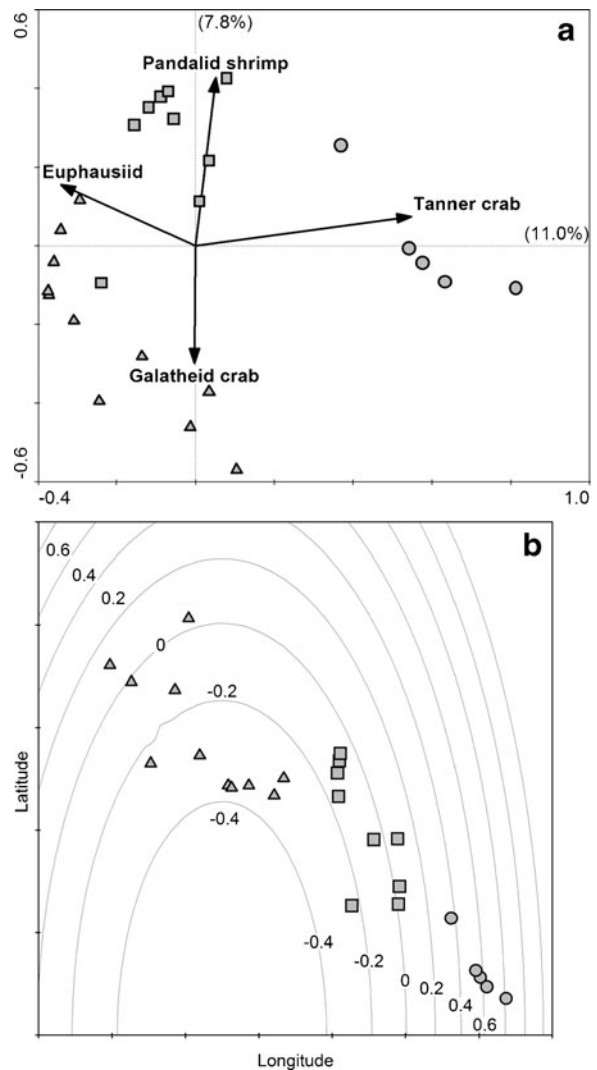


Fig. 4 Redundancy Analysis (RDA) biplot displaying spatial variation in (a) the diet of *Bathyraja aleutica* in 2005 and (b) the first RDA axis represented by contours in geographic space to aid in interpretation of the introduced polynomial distortion. Regional designations are represented by symbol shape: Alaska Peninsula (circles), Shelikof Strait (squares), southeastern Kodiak Island (triangles)

exceed the corresponding value of %FO. We therefore recommend that researchers should instead use and report %PN, and or %PW, and %FO in both diet composition tables and in graphical displays, as has already been done for feeding strategy diagrams (Amundsen et al. 1996). Furthermore, the %PSIRI is recommended to replace %IRI as a standardized index of relative importance for diet studies. %PSIRI is the mathematically correct version of %IRI, and more closely achieves its original intent: ‘to promote

Table 3 Marginal effects of the terms of the cubic surface trend regression in explaining size-sex-depth variation (λ) in the diet of *Bathyraja aleutica* by Redundancy Analysis. Conditional effects of the terms selected step-wise by Monte Carlo permutation and the significance (p) of the pseudo-F ratio (F_λ). TL total length. * $p < 0.1$, ** $p < 0.01$

| Marginal effects | |
|---------------------|-----------------------------|
| Predictor | λ |
| TL | 0.09 |
| TL*Sex | 0.08 |
| Depth | 0.07 |
| Depth*Sex | 0.06 |
| Sex | 0.05 |
| TL*Depth | 0.05 |
| Conditional effects | |
| Predictor | λ p F_λ |
| TL | 0.09 0.001** 3.93 |
| +Depth | 0.06 0.004** 2.82 |
| +TL*Depth | 0.05 0.012* 2.54 |
| +Sex | 0.04 0.08* 1.79 |

consistency and facilitate comparisons among studies, and to obtain a robust estimate of relative importance of the prey' (Cortès 1997). For comparisons to previously published diet studies that reported %IRI, one only needs to apply the mathematical relationships between diet measures to extract prey-specific information from a diet composition table to then calculate %PSIRI. This conversion is demonstrated as

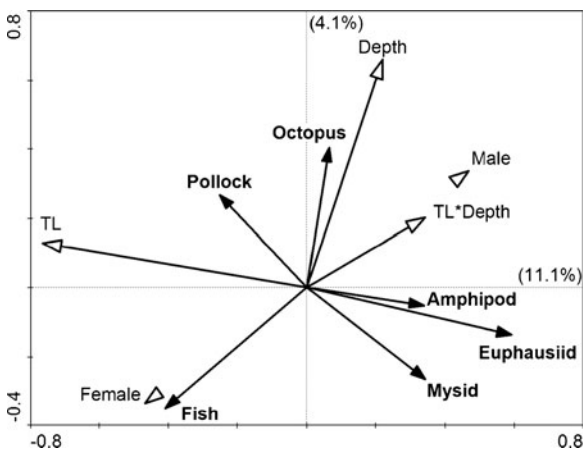


Fig. 5 Redundancy Analysis biplot of dietary variation in *Bathyraja aleutica* explained by total length (TL), depth, and sex while accounting for spatial variation in the diet

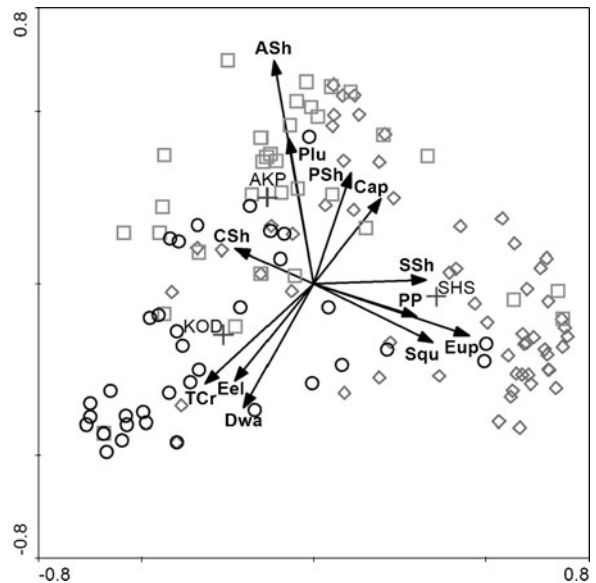


Fig. 6 Redundancy Analysis biplot of regional diet variation in 2007 among Alaska Peninsula (AKP, squares), Shelikof Strait (SHS, diamonds) and southeastern Kodiak Island (KOD, circles) in *Bathyraja aleutica*. Prey vectors pointing in the direction of a centroid contribute to a regional difference in the diet, where as prey vectors pointing in between two centroids contribute to the difference between those two regions versus the other. ASh argid shrimps, Plu flatfishes, PSh northern pink shrimp, Cap capelin, SSh side-striped shrimp, PP Pacific glass shrimp, Eup euphausiids, Squ squid, Dwa dwarf wrymouth, Eel eelpouts, TCr Tanner crab, CSh crangon shrimps

follows from a hypothetical excerpt of a pre-existing diet composition table:

| Prey | %FO | %N | %W | %IRI |
|------|-----|----|----|------|
| i | 75 | 50 | 25 | |

$$\%PN_i = \frac{0.50}{0.75} = 0.667 = 66.7\%$$

$$\%PW_i = \frac{0.25}{0.75} = 0.333 = 33.3\%$$

$$\%PSIRI_i = \frac{0.75 \times (0.667 + 0.333)}{2} = 0.375 = 37.5\%$$

Case study

Aleutian skate from the northern GOA shelf was found to forage primarily on northern pink shrimp and Tanner crab by all diet indices examined. Both species are important lower trophic level prey for

commercially important gadids and flatfishes in the GOA shelf ecosystem (Yang et al. 2006). Additionally, the abundance of these prey species in the northern GOA has been documented to respond strongly to shifts in the dominant marine climate regime (Anderson and Piatt 1999). The high consumption of this prey by Aleutian skate raises the potential for resource competition with both commercially important groundfish species (e.g. Pacific Cod, Pacific Halibut) and historical commercial shellfish fisheries. It also raises questions about how fluctuations in relative and absolute abundances of these prey species with changing climate may alter the trophic interactions of Aleutian skate.

Within the duration of the study (2005–2007), the Pacific Decadal Oscillation (PDO) displayed atypical conditions of the long-term trend shifting from positive (warmer) to negative (cooler) conditions (Fig. 7), which are suspected to have influenced the observed interannual differences in the diet of Aleutian skate. The abundance of pandalid shrimps in the diet was exceptionally high during 2006 in the Shelikof Strait region, which then shifted towards mid-water prey including euphausiids and squids in 2007. Locally in the northern GOA in 2007 demersal near-shore water column temperatures measured at the mooring station GAK1 (<http://www.ims.uaf.edu/gak1/>) were anomalously cold (Fig. 8). The observed changes in the PDO and, locally, in demersal water column temperatures in the northern GOA seems to indicate the confluence of marine climate, currents, and unique bathymetry affects the local abundance and availability of euphausiids and other mid-water prey to Aleutian skate within Shelikof Strait.

The consumption of fishes by Aleutian skate was secondary to the consumption of crustaceans, and

Fig. 7 Time averaged series of the Pacific Decadal Oscillation Index (data from <http://jisao.washington.edu/pdo/>) with shading indicating the periods of diet sampling during 2005–2007

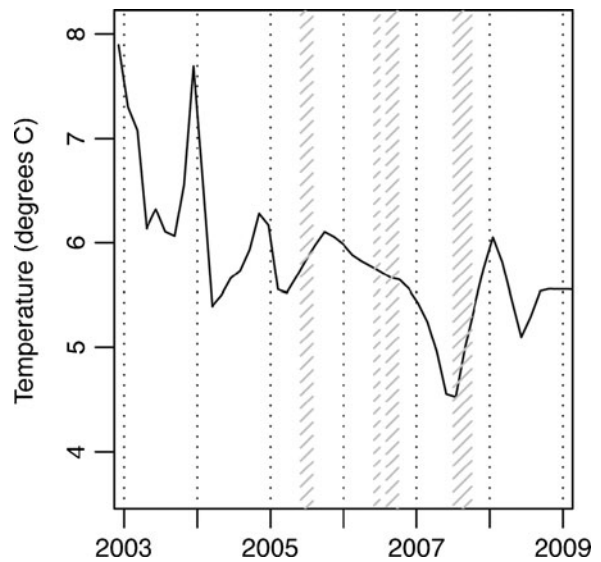
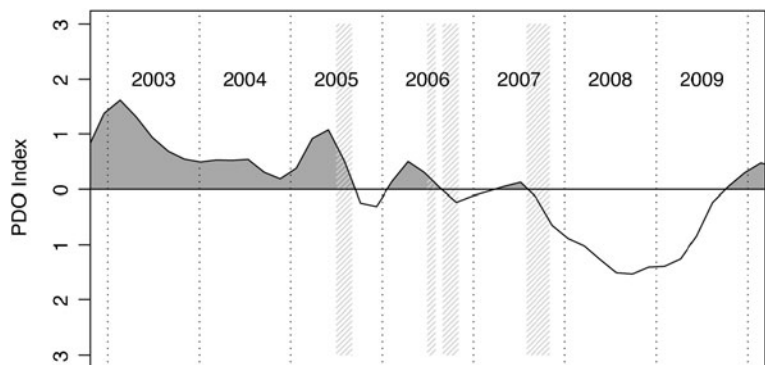


Fig 8 Time averaged series of the temperature of the bottom layer (200 m) of the Alaska coastal current from the GAK1 mooring station (data from <http://www.ims.uaf.edu/gak1/>). Shading indicated periods of diet sampling

consisted of forage fishes and small individuals of other demersal fish species. Even though smaller size classes (<80 cm TL) of Aleutian skate was largely absent from our study area, the results of our analysis of intraspecific variation in the diet of Aleutian skate supports the recurring findings from other studies of the increased consumption of fishes with increasing skate size, and the consumption of various small invertebrate prey including mysids, amphipods, and euphausiids with decreasing skate size (Brickle et al. 2003; Robinson et al. 2007; Barbini et al. 2010). Body size and gape limitation are likely explanations for this pattern. In one of the few documented

laboratory observations of skate feeding behavior it was noted that skates use their entire bodies to ambush fish prey, forcefully pressing the fish against the substrate until immobilized, and then coercing it into the buccal cavity (Berestovskiy 1989). This feeding behavior is dependent on the use of bottom substrate to capture and immobilize fishes and therefore seems to limit skates to fishes found on or near the sea floor. The presence of capelin, a pelagic fish, in the diet of Aleutian skate can be attributed to scavenging on the postspawn mortalities, as noted by Berestovskiy (1989) in the diets of *Raja radiata* and *R. fyllae* in the Barents and Norwegian Seas. Alternatively, recent movement studies in other skate species have identified extensive nocturnal vertical migration patterns in large sized individuals (Wearmouth and Sims 2009), but it is not conclusively known whether skates actively forage during these excursions off of the sea floor.

Examination of spatial variation in diet across the northern GOA shelf elucidated the spatial dependence of important prey species corresponding to geographic sub-regions of known ecological significance (Piatt and Springer 2007). Further examination of dietary variation within these ecoregions revealed Shelikof Strait to be unique from other regions because of the presence of mid-water prey (euphausiids, squid, Pacific glass shrimp) in 2007. The unique bathymetry of Shelikof Strait, at the head of a long narrow sea valley may help to concentrate mid-water prey near the sea floor under certain oceanographic conditions. A similar mechanism has been proposed for *B. kincaidii* which was found to feed on euphausiids near the edge of the Monterey Bay submarine canyon (Rinewalt et al. 2007). The notable addition of mid-water prey to the diet in Shelikof Strait directly links Aleutian skate to the pelagic foodweb. In the other regions examined, the diet of Aleutian skate was constrained largely to benthic crustaceans and demersal fishes.

Seasonal variation in the diet of Aleutian skate within the northern GOA shelf ecosystem was not examined in this study. We suspect, however, that during winter months the Aleutian skate's distribution, similar to other skate species, is contracted to deeper slope habitats (Antonenko et al. 2007). When in these regions, it likely consumes a different fauna consisting of locally abundant crustaceans, cephalopods, and fishes.

Although we were able to extract ecologically meaningful information from the number of stomach samples analyzed each year, this study would no doubt have benefited in resolution from additional samples. Skates were sampled aboard fishery independent surveys, as is often the case in diet studies, and thus our sample size was limited to the number of individuals caught during each survey. Cumulative prey curves are useful for estimating prey richness in diet description and for assessing sample size sufficiency; however, comparing such curves to a true asymptote as an evaluation criterion for achieving sample size sufficiency in diet studies of demersal elasmobranchs is overly-prohibitive. This is because only rare prey species with little influence on subsequent statistical analyses are typically encountered after the slope of the cumulative prey curve begins to decline rapidly. The criteria of attaining a linear slope (b) of ≤ 0.05 in the five ultimate subsamples to assess the sufficiency of stomach samples for diet description as proposed by Bizzarro et al. (2009) is therefore further recommended as a reasonable cut-off point for diet studies of demersal elasmobranchs.

This study provides the first detailed information on the diet composition of the Aleutian skate from the northern GOA shelf. Although marine climate is currently regarded as the dominant force influencing community structure of the northern GOA shelf-ecosystem, Aleutian skate may influence lower trophic levels between multi-decadal shifts in the North Pacific climate regime. We therefore emphasize the need for species-specific population assessments and continued food habits monitoring of Aleutian skate, and other abundant demersal predators, to better understand the trophic structure of the northern GOA shelf ecosystem.

Acknowledgements This manuscript benefited enormously from two anonymous reviewers and from previous comments received from Sturre Hansson and Lara Ferry. We would like to thank the many people from the National Marine Fisheries Service Alaska Fisheries Science Center (NMFS/AFSC) and Alaska Department of Fish and Game (ADFG) in Homer and Kodiak who provided invaluable assistance on various portions of this study. In particular, we thank Eric Brown, Sarah Gaichas, Christopher Gburski, Dan Kimura, Ned Laman, Bob Lauth, Frank Shaw, and Jim Stark from NMFS-AFSC in Seattle for their input and cooperation in allowing us to participate on survey cruises in the Gulf of Alaska. Lynne Mattes, Kally Spalinger, and Ken Goldman coordinated our participation in ADFG surveys in the northern Gulf of Alaska. Funding for this

work was provided by the North Pacific Research Board project 621, the National Oceanic and Atmospheric Administration's National Marine Fisheries Service through the Pacific Shark Research Center and the National Shark Research Consortium, and the David and Lucile Packard Foundation. This is North Pacific Research Board contribution 306.

References

- Ainsworth CH, Kaplan IC, Levin PS, Mangel M (2010) A statistical approach for estimating fish diet compositions from multiple data sources: Gulf of California case study. *Ecol Appl* 20:2188–2202
- Amundsen PA, Gabler HM, Staldvik FJ (1996) A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello (1990) method. *J Fish Biol* 48:607–614
- Anderson MJ (2006) Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62:245–253
- Anderson PJ, Piatt JF (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar Ecol Prog Ser* 189:117–123
- Antonenko D, Pushchina O, Solomatov S (2007) Distribution and some biological features of skate *Bathyraja parmifera* (Rajidae, Rajiformes) in the northwestern part of the Sea of Japan. *J Ichthyol* 47:279–287
- Assis C (1996) A generalised index for stomach contents analysis in fish. *Sci Mar* 60:385–389
- Barbini SA, Scenna LB, Figueroa DE, Cousseau MB, de Astarloa JMD (2010) Feeding habits of the Magellan skate: effects of sex, maturity stage, and body size on diet. *Hydrobiologia* 641:275–286
- Berestovskiy EG (1989) Feeding in the skates, *Raja radiata* and *Raja fyllae*, in the Barents and Norwegian Seas. *Voprosy Ikhtologii* 29:994–1002
- Bizzarro JJ, Smith WD, Márquez-Farías JF, Tyminski J, Hueter RE (2009) Temporal variation in the artisanal elasmobranch fishery of Sonora, Mexico. *Fish Res* 97:103–117
- Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055
- Brickle P, Laptikhovskiy V, Pompert J, Bishop A (2003) Ontogenetic changes in the feeding habits and dietary overlap between three abundant rajid species on the Falkland Islands' shelf. *J Mar Biol Assoc UK* 83:1119–1125
- Cortès E (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Can J Fish Aquat Sci* 54:726–738
- Cortès E (1998) Methods of studying fish feeding: reply. *Can J Fish Aquat Sci* 55:2708
- Costello MJ (1990) Predator feeding strategy and prey importance: a new graphical analysis. *J Fish Biol* 36:261–263
- de Crespín de Billy V, Doledec S, Chessel D (2000) Biplot presentation of diet composition data: an alternative for fish stomach contents analysis. *J Fish Biol* 56:961–973
- Ebert DA, Bizzarro JJ (2007) Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environ Biol Fishes* 80:221–237
- Ferry LA, Cailliet GM (1996) Sample size and data analysis: are we characterizing and comparing diet properly? *Gut Shop*, American Fisheries Society
- Hansson S (1998) Methods of studying fish feeding: a comment. *Can J Fish Aquat Sci* 55:2706–2707
- Hoff GR (2002) New records of the Aleutian Skate, *Bathyraja aleutica* from Northern California. *California Fish Game* 88:145–148
- Hyslop EJ (1980) Stomach contents analysis—a review of methods and their application. *J Fish Biol* 17:411–429
- Legendre P, Legendre L (1998) Numerical ecology. Elsevier
- Legendre P, Gallagher E (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280
- Link JS, Sosebee K (2008) Estimates and implications of skate consumption in the Northeast U.S. continental shelf ecosystem. *N Am J Fish Manag* 28:649–662
- Mecklenburg C, Mecklenburg T, Thorsteinson L (2002) Fishes of Alaska. American Fisheries Society, Bethesda, p 1037
- Oksanen J, Blanchet F, Kindt R, Legendre P, O'Hara R, Simpson G, Solymos P, Henry M, Stevens M, Wagner H (2011) Vegan: community ecology package. R package version 1.17-6. <http://CRAN.R-project.org/package=vegan>
- Orloci L (1978) Multivariate analysis in vegetation research. Dr. W. Junk B.V, The Hague
- Orlov AM (1998) The diets and feeding habits of some deep-water benthic skates (Rajidae) in the Pacific Waters Off the Northern Kuril Islands and Southeastern Kamchatka. *Alaska Fish Res Bull* 5:1–17
- Ormseth OA, Matta B (2009) Assessment of the skate complex in the Gulf of Alaska SAFE Report, North Pacific Fisheries Management Council
- Ortiz M, Von Bach PB, Candia R (2006) The diet of the neotropical insectivorous fish *Creagrutus bolivari* (Pisces: Characidae) according to the “graphic” and “relative importance” methods. *Rev Biol Trop* 54:1227–1239
- Piatt JF, Springer AM (2007) Marine ecoregions of Alaska. In: Spies R (ed) Long-term ecological change in the Northern Gulf of Alaska. Elsevier, Amsterdam, pp 522–526
- Rinewalt CS, Ebert DA, Cailliet GM (2007) Food habits of the sandpaper skate, *Bathyraja kincaidii* (Garman, 1908) off central California: seasonal variation in diet linked to oceanographic conditions. *Environ Biol Fishes* 80:147–163
- Robinson HJ, Cailliet GM, Ebert DA (2007) Food habits of the longnose skate, *Raja rhina* (Jordan and Gilbert, 1880), in central California waters. *Environ Biol Fishes* 80:165–179
- Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES J Mar Sci* 57:476–494
- Stevenson DE, Orr JW, Hoff GR, McEachran JD (2007) Emerging patterns of species richness, diversity, population density, and distribution in the skates (Rajidae) of Alaska. *Fish Bull* 106:24–39

- ter Braak CJ, Smilauer P (2002) CANOCO reference manual and CanoDraw for windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithica
- Wearmouth VJ, Sims DW (2009) Movement and behaviour patterns of the critically endangered common skate *Dipturus batis* revealed by electronic tagging. *J Exp Mar Biol Ecol* 380:77–87
- Weingartner T (2005) Chapter 4 physical and geological oceanography: coastal boundaries and coastal and ocean circulation. In: Mundy PR (ed) *The Gulf of Alaska: biology and oceanography*, Alaska sea grant college program. University of Alaska, Fairbanks
- Yang M-S (2007) Food habits and diet overlap of seven skate species in the Aleutian Islands. In: Commer USD (ed) NOAA Tech. Memo, p 46
- Yang M-S, Dodd K, Hibpshman R, Whitehouse A (2006) Food habits of groundfishes in the Gulf of Alaska in 1999 and 2001. In: Commer USD (ed) NOAA Tech. Memo, p 199