A critical review of methods of studying fish feeding based on analysis of stomach contents: Application to elasmobranch fishes

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Abstract: Using real data sets of elasmobranch fishes as examples, this paper presents a critical review of selected methods and statistical approaches used in fish feeding studies and makes recommendations on the application of such methodology. The percent index of relative importance is proposed as a standardized measure in dietary analyses, and a three-dimensional graphical representation of the diet is introduced. Multiway contingency table (log–linear) analysis is recommended to test for dietary variations. Caution is advised when using rank correlation to study dietary overlap and parametric tests when stomach content data do not satisfy parametric assumptions. Sampling gear type, experimental design, and statistical tests can affect results on diel feeding chronology, and stomach content weights do not suffice to interpret diel feeding chronology. On the basis of sampling requirements and model assumptions, the Diana and Olson–Mullen methods appear to be the most appropriate approaches for estimating daily ration in sharks. Use of resampling techniques is highly desirable because they provide a measure of the error in daily ration estimates. Using several criteria to evaluate the best-fitting model of gastric evacuation in fishes is also strongly advocated. Overall, increased consolidation of methods and analyses is recommended to facilitate comparative studies.

Résumé : En prenant pour exemples des séries de données réelles sur des poissons élasmobranches, nous présentons une analyse critique de certaines méthodes et approches statistiques utilisées dans les études sur l'alimentation des poissons, et nous faisons des recommandations sur l'application de cette méthodologie. Nous proposons un indice de l'importance relative en pourcentage comme mesure normalisée pour les analyses alimentaires, et nous introduisons une représentation graphique tridimensionnelle du régime alimentaire. L'analyse (log–linéaire) de tableaux multidimensionnels est recommandée pour étudier les variations dans l'alimentation. Nous conseillons la prudence dans l'emploi de la corrélation de rangs pour étudier les chevauchements dans le régime alimentaire et des tests paramétriques quand les données sur le contenu stomacal ne satisfont pas les hypothèses paramétriques. Le type d'engin utilisé pour l'échantillonnage, le protocole expérimental et les tests statistiques peuvent avoir un effet sur les résultats de la chronologie de l'alimentation nycthémérale, et le poids du contenu stomacal ne suffit pas à interpréter cette chronologie. D'après les besoins de l'échantillonnage et les hypothèses des modèles, les méthodes de Diana et d'Olsen–Mullen semblent être les plus appropriées pour estimer la ration quotidienne chez les requins. L'emploi de techniques de rééchantillonnage est très souhaitable car cette démarche donne une mesure de l'erreur dans les estimations de la ration quotidienne. Nous recommandons aussi fortement d'avoir recours à plusieurs critères pour évaluer le modèle qui offre le meilleur ajustement pour l'évacuation gastrique chez les poissons. Globalement, il est recommandé de regrouper de plus en plus les méthodes et les analyses pour faciliter les études comparatives.
[Traduit par la Rédaction]

Introduction

The study of diets and food habits of fish and other marine vertebrates through the examination of stomach contents has become standard practice (Hyslop 1980). However, a review of dietary, food habit, and food consumption studies of fish reveals a lack of consistent methodological approaches and application of statistical tests to analyze results. The present study was prompted by a perceived need to promote consis-

tency, facilitate comparisons, and verify the proper application of methodological approaches in feeding studies.

The purpose of this study is to examine some selected methods and statistical approaches commonly used in diet, food habit, and food consumption studies of fish and, with the help of illustrative examples, present recommendations on how to obtain, analyze, and report data. Specifically, the objectives are to (*i*) review the most commonly used indices of dietary importance and propose the use of a standardized index and a new graphical method to illustrate prey importance and predator feeding strategy and homogeneity at the population level; (*ii*) reemphasize the need for reporting precision and determining sample size sufficiency in dietary descriptions; (*iii*) review the use of multivariate statistics, log–linear analysis, and multiway contingency table analysis to detect seasonal, ontogenetic,

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Table 1. Relative importance of food type by different indices for two species of sharks.

Food type	%N	%W	%O	IRI	%IRI
Lemon shark (*Negaprion brevirostris*)					
Fishes	75.4	98.4	131.2 (86)	22 802 (14 947)	97.2 (96.6)
Molluscs	1.5	0.9	3.1 (3.1)	7 (7)	0.03 (0.05)
Crustaceans	7.7	0.4	14.1 (12.5)	114 (101)	0.5 (0.6)
Bonnethead shark (*Sphyrna tiburo*)					
Crustaceans	63.4	82.9	97.4 (88.9)	14 250 (13 006)	82.2 (84.9)
Molluscs	0.8	0.8	3.5 (2.3)	6 (4)	0.03 (<0.01)
Teleosts	0.5	0.7	1.5 (1.5)	2 (2)	0.01 (<0.01)
Angiosperms	26.7	7.0	78.4 (56)	2 642 (1 888)	15.2 (12.4)
Miscellaneous	8.6	8.6	25.4 (24.8)	437 (427)	2.5 (2.8)

Note: %N, percent by number; %W, percent by weight; %O, percent frequency of occurrence; IRI, index of relative importance; %IRI, percent index of relative importance. Values for %O in parentheses are observed nonadded values (i.e., corresponding to a particular food type, not the sum of its components). Values for IRI and %IRI in parentheses were calculated using observed nonadded %O values.

or other differences in feeding among predators, and the use of the most common measures of dietary overlap to detect differences between diets; (*iv*) comment on the reporting of stomach content data and discuss the influence of sampling gear type, experimental design, and statistical analysis when studying diel feeding chronology; (*v*) review the main approaches for estimating daily ration in fishes, identify those most appropriate for sharks, and emphasize the need for including error analyses of the estimates; and (*vi*) discuss the appropriateness of the statistical criteria used to evaluate the fit of mathematical curves in studies of gastric evacuation in fishes.

Owing to the diversity of topics covered, separate sections addressing each of the objectives listed above will be presented. Although many of the recommendations and conclusions are applicable to fishes and other marine vertebrates, examples will be drawn using real data sets of stomach contents of sharks and special attention paid to this group of aquatic predators whose study presents unique difficulties.

Quantitative diet analysis

Traditional methods of dietary analysis include counts, frequency of occurrence, and volume or weight of individual prey items (Hynes 1950; Hyslop 1980). Each of these measures provides different insight into the feeding habits of a predator. Numerical abundance is informative regarding feeding behavior (Macdonald and Green 1983), volume or weight measures reflect dietary nutritional value (Macdonald and Green 1983), and occurrence represents population-wide food habits (Cailliet 1977).

A number of compound indices incorporating one or more of these measurements also have been developed. Although the decision of which method to use for determining the relative importance and dominance of the prey is generally subjective (Hyslop 1980), one of the more widely used compound indices in fish diet studies is the index of relative importance (IRI; Pinkas et al. 1971). In this method, the percent frequency of occurrence of each prey category is multiplied by the sum of the percentage volume (or weight) and percentage number. The rationale for using this method lies in that it seems to cancel out biases in its individual components (Bigg and Perez 1985). By incorporating bulk, amount, and occurrence into a single measure it appears to provide a more accurate description

of dietary importance and is also intended to facilitate comparative studies. Macdonald and Green (1983), however, argued that compound indices may be redundant, adding little new information to single measures.

Generally, results of dietary analyses are given in tabular form and include one or more of the above-mentioned indices: percentage by number (%N), percentage by volume (%V) or by weight (%W), percentage frequency of occurrence (%O), and IRI. Some studies fail to report %O and IRI for the higher taxonomic levels, complicating or impairing diet comparisons among species. This lack of reporting arises because %O (the proportion of stomachs containing a specific prey category) is a nonadditive index (several different categories of a specific prey type, e.g., several families of teleosts, can occur simultaneously in the same stomach, be counted more than once, and yield a total for the taxonomically higher prey type (all teleosts) >100%). Furthermore, if these values of %O are used in the calculation of IRI, the IRI value itself is also affected. For example, the sum of %O values corresponding to each of 14 families or categories of fishes in stomachs of young lemon sharks (*Negaprion brevirostris*) (Cortés and Gruber 1990) is 131.2%, equivalent to an absolute IRI value of 22 802 (Table 1). However, recalculation of %O and IRI for teleosts as a higher taxonomic group yields values of 86% and 14 947 for %O and IRI, respectively (Table 1).

Because they are not expressed as a percentage, IRI values make comparisons difficult among food types. Although IRI has been expressed occasionally on a percent basis (e.g., Carrassón et al. 1992; Barry et al. 1996; Cortés et al. 1996), this is not yet standard practice. It is therefore suggested that IRI be expressed on a percent basis, such that %IRI for a specific food category i (IRI_i) becomes

$$\%IRI_i = 100\ IRI_i / \sum_{i=1}^{n} IRI_i$$

where n is the total number of food categories considered at a given taxonomic level. Percent IRI values calculated with added %O values (the sum of %O values for all prey categories at a given taxonomic or grouping level) and nonadded %O values (%O value for the higher taxonomic or grouping level) in the above example yield 97.2 and 96.6%, respectively. Similarly, %IRI values calculated with both methods

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for crustaceans in the diet of the bonnethead shark (*Sphyrna tiburo*) yield 82.2 and 84.9%, respectively, whereas absolute IRI values calculated with both methods yield 14 250 and 13 006, respectively (Table 1). On the basis of this limited analysis of the relative performance of IRI and %IRI, the latter seems more robust to changes in %O values and could be used as a standardized index to facilitate diet comparisons.

Thus, to promote consistency and facilitate comparison among studies, and to obtain a robust estimate of relative importance of the prey, whenever possible results of dietary analyses should be reported as %N, %W (or %V), %O, and %IRI for all taxonomic levels considered.

A new graphical representation of the diet

Graphical representation of diet analysis has been used as an alternative to summary tables, because results are easier to interpret (Cailliet et al. 1986; Mohan and Sankaran 1988; Cailliet and Ebeling 1990; Costello 1990). Costello (1990) presented a graphical method that uses the frequency of occurrence and a percent measure of abundance (%W, %V, or %N) and provides a good depiction of prey importance (dominant or rare), predator feeding strategy (specialized or generalized), and the degree of homogeneity of feeding in the predator population. Tokeshi (1991) proposed the use of diversity indices to illustrate feeding strategies also at the population level. In contrast, Bridcut and Giller (1995) proposed an individual-based method that utilizes individual prey type diversity and consumption levels to characterize feeding strategies.

I propose a modification of Costello's method, which uses %O, %N, and %W (or %V) in a three-dimensional graphical representation of population-level stomach content data. Each point on the graph represents the percent occurrence and abundance (in weight or volume and numbers) for a prey category (Fig. 1). Any prey point located close to 100% O, 100% W, and 100% N is the dominant food taxon or category (*a* in Fig. 1). Conversely, points located near the origin of the three axes represent rare prey types (*b* in Fig. 1). Any point located closer to the %N axis than to the %W axis along the horizontal plane indicates that counts contribute more than weight to the abundance of that item. Conversely, any point located closer to the %W axis than to the %N axis along the horizontal plane indicates that weight contributes more than counts to the abundance of that item.

The other six vertices of the cube in Fig. 1 can be regarded as extreme cases pointing to either specialized or generalized diets. Thus, a cluster of points located close to 100% O and the origin of the other two axes (%W and %N) would indicate a generalized diet (most predators take several different prey taxa in low abundance; *c* in Fig. 1). In contrast, a point close to 1% O, 100% W, and 100% N (*d* in Fig. 1) would indicate a specialized diet by a few predators, which would take large numbers of heavy items or items that make up a very large proportion of the total number and weight of stomach contents. A point located close to 100% O, 100% N, and 1% W would be indicative of a light food item consumed by most predators (*e* in Fig. 1). Conversely, a point close to 1% O, 1% N, and 100% W would indicate a specialized diet by a few predators, which would take a few very heavy items or items that make up a very large proportion of the total weight of stomach contents (*f* in Fig. 1). A point located near 100% O, 100% W, and

Fig. 1. Proposed three-dimensional graphical representation of stomach content data. D, dominant food category; R, rare food category; G, generalized diet; S, specialized diet. See text for definitions of *a*, *b*, *c*, *d*, *e*, *f*, *g*, and *h* and explanation of lines.
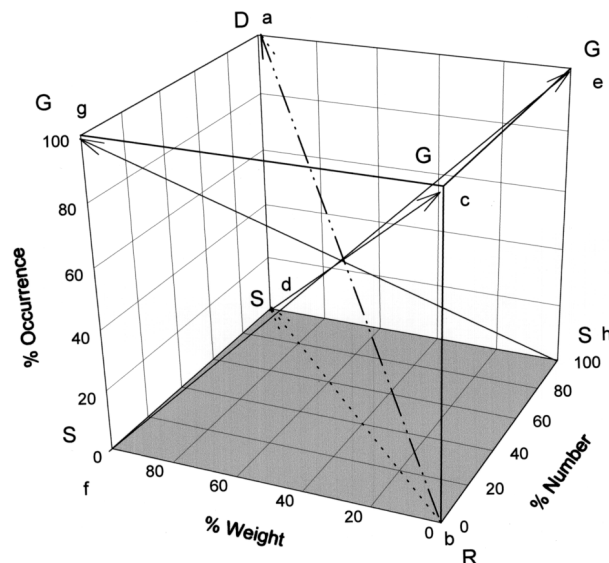
1% N (*g* in Fig. 1) would indicate that most predators take a few heavy items or items that make up a very large proportion of the total weight of stomach contents. In contrast, a point close to 1% O, 1% W, and 100% N (*h* in Fig. 1) would indicate a specialized diet by a few predators, which would take very large numbers of light items.

As proposed by Costello (1990) for his two-dimensional graphical analysis, diagonals can also be drawn on the three-dimensional plot for the present method to help visualize prey importance (dominant versus rare prey taxa) and predator feeding strategy (generalized versus specialized feeding). Thus, a line uniting points *b* and *a* in Fig. 1 would indicate increasing prey importance, and lines uniting points *d* and *c*, *f* and *e*, and *h* and *g* would all indicate a shift from a specialized to a more generalized feeding strategy.

Illustrative examples
The graphical framework presented in Fig. 1 can be illustrated with several examples of shark diets. The diet of the lemon shark (Cortés and Gruber 1990; Fig. 2*a*) is dominated by teleosts, while crustaceans, molluscs, and plants are rare. Weight contributes more to the overall abundance of teleosts (point situated to the left of the floor diagonal), while counts contribute more to the overall abundance of plants. Feeding in the lemon shark is homogeneous, with most predators specializing in teleost prey. In contrast, the diet of the blue shark (*Prionace glauca*) (Harvey 1989; Fig. 2*b*) is much more heterogeneous. Teleosts are consumed by about half of the predators in small numbers but constitute half the total weight of stomach contents. Some blue sharks specialize on crustaceans, which they consume in very large numbers, while most of the blue sharks eat a few molluscs (cephalopods). Elasmobranchs and plants are rare items. Overall, the diet of blue sharks is generalized.

The proposed graphical method can also be used to show ontogenetic, seasonal, geographic, or habitat-related dietary

Fig. 2. Four examples of shark diets used to illustrate the three-dimensional graphical representation of stomach content data: (*a*) lemon shark (*Negaprion brevirostris*), (*b*) blue shark (*Prionace glauca*), and (*c*) juvenile and adult leopard shark (*Triakis semifasciata*). T, teleosts; P, plants; C, crustaceans; M, molluscs; E, elasmobranchs; Ech, echinoderms; Pol, polychaete worms.
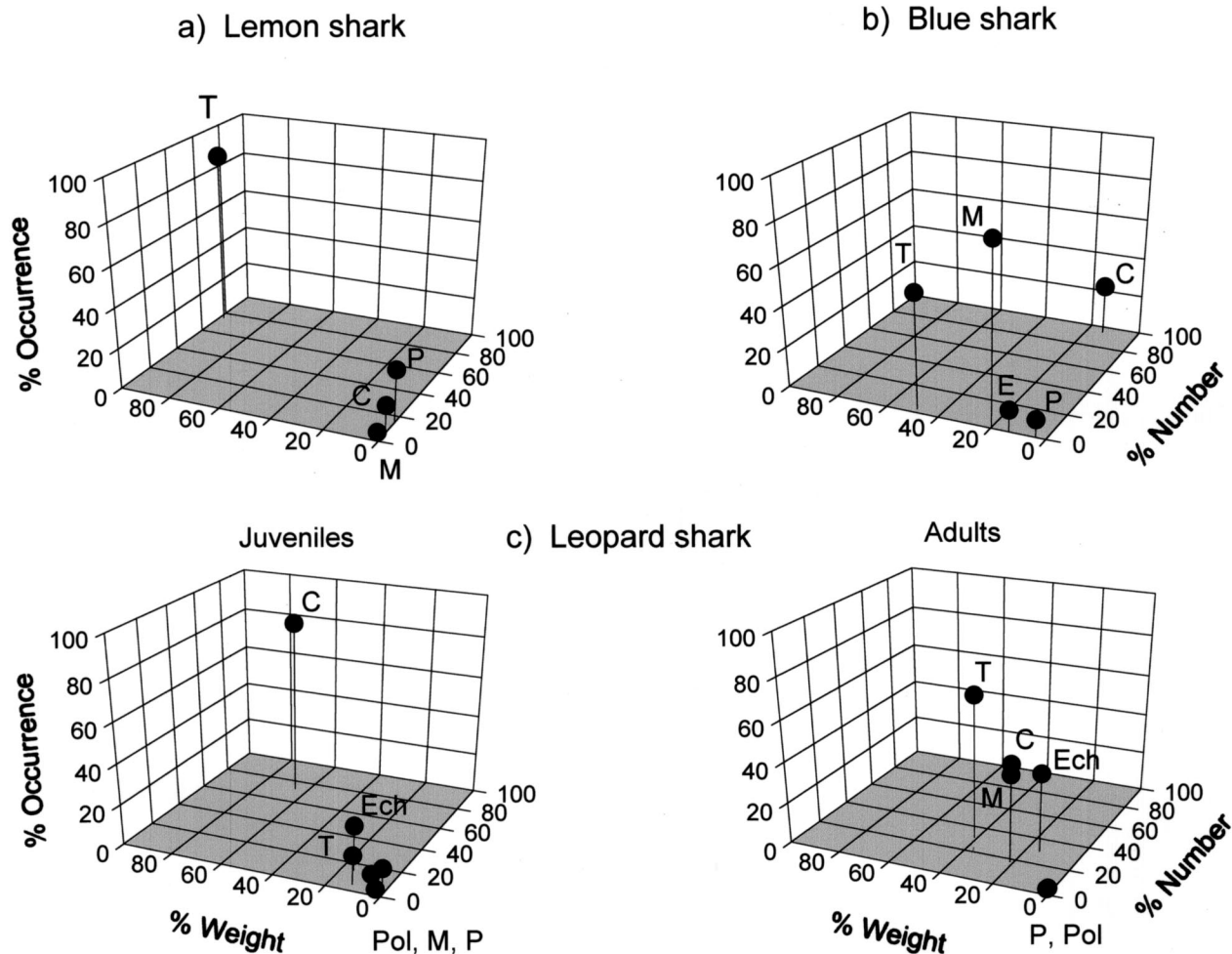
differences in a predator population or species. For example, the leopard shark (*Triakis semifasciata*) (Talent 1976; Figs. 2*c* and 2*d*) exhibits an ontogenetic dietary shift. The dominant prey item in the diet of juvenile leopard sharks is crustaceans, while echinoderms, teleosts, polychaete worms, molluscs, and plants are only rarely found (Fig. 2*c*). Adult leopard sharks have a more generalized diet (Fig. 2*d*). Teleosts and molluscs become more important, and crustaceans less important, in the diet of the adult sharks. This graphical representation of the diet allows us to easily identify the dominant and rare prey items, generalized versus specialized feeding, and homogeneous versus heterogeneous diets.

Statistical description of feeding habits

Precision in diet description, sample size sufficiency, and dietary comparisons

Ferry and Cailliet (1996) recently reported that, from the over 200 dietary studies they reviewed, none provided any estimates of precision in describing diet. These and other authors (Huturbia 1973; Cailliet 1977; Hoffman 1979; Karpov and Cailliet 1979; Barry et al. 1996, among others) have advocated

the use of cumulative prey curves or trophic diversity curves to determine whether a sufficient number of samples has been collected to precisely describe the diet of a particular predator. Essentially, in these approaches the cumulative number of (preferably) randomly pooled stomachs (X axis) is plotted against the cumulative number of prey types or a cumulative measure of trophic diversity (Y axis), with the asymptotic stabilization of the curve indicating the minimum number of stomachs that have to be analyzed to obtain precise and thus more reliable results.

For subsequent dietary comparisons between species or other factors, Ferry and Cailliet (1996) strongly advocated the use of a priori power analysis (Cohen 1988) to determine sample size sufficiency, a technique that apparently has not been used in fish food habit studies.

Many studies of fish diets attempt to describe variations in stomach contents owing to season, age, size, location, habitat, or other factors but often include only qualitative comparisons, with no statistical support for their conclusions. Crow (1979) first proposed the use of multivariate statistical methods, in which prey categories are treated as separate variates, to test for dietary differences when stomach contents are expressed as gravimetric proportions. Somerton (1991) further proposed

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a nonparametric randomized test for a one-way multivariate analysis of variance (MANOVA) to test for differences in diets between two samples also expressed in terms of weight. In this latter approach, significance was tested with Hotelling's T^2 and post-hoc univariate t tests run to detect differences owing to individual prey categories. Similarly, 1-, 2-,. . ., n-way MANOVA can be applied to stomach content weights or volumes (not proportions) with the weight or volume of each food category as a dependent variable and seasons, sizes, locations, or other factors as treatments. For example, in a one-way MANOVA testing for differences in diet composition among seasons, if the F statistic in the multivariate test is found to be significant, then univariate F tests can reveal the dependent variable(s) (weight of food categories) responsible for the significance. Alternatively, canonical discriminant analysis (Manly 1994) can further detect the individual food categories responsible for the variation in each particular season.

When stomach contents are expressed numerically or as occurrences, an analogous approach is to use multiway contingency table analysis based on log–linear models. The significance of the interaction terms (e.g., food type × season) can be tested by individually deleting them from the model and a post-hoc test then can be run to detect specific differences. One constraint of multiway log–linear analysis that limits its applicability is that very large sample sizes are required to have less than 20% of the cells with values <5. Crow (1982) advocated the use of simpler $R \times C$ contingency table analysis to test for independence between food categories and predators or predator characteristics (such as seasons or other factors) when stomach contents are expressed numerically or as occurrences. The advantage of this technique is that it allows one to readily identify the rows (prey types) and columns (e.g., predators) most responsible for the dietary differences. Despite its simplicity this technique is seldom used in fish food studies.

Illustrative example

The results of a three-way contingency table (log–linear) analysis testing for seasonal variations in the diet of four size-classes of bonnethead sharks reveal that all two-factor interactions are significant (Table 2). The significance of each interaction term is determined by testing the significance of the χ^2 value obtained by subtracting the likelihood ratio χ^2 statistic of the original model from the χ^2 of the model without the interaction.

A 4×4 contingency table (modified from Cortés et al. 1996) that includes both the χ^2 and G statistics (Sokal and Rohlf 1981; Table 3) is then applied to examine the interaction food type × season. Cell values in this case are numbers of each prey type, but could also be occurrences. To avoid too many cells having expected frequencies <5 (Sokal and Rohlf 1981; Crow 1982; and references therein), some of the prey types were pooled into a larger category (miscellaneous). However, as pointed out by Crow (1982), some expected frequencies <5 should not affect the analysis. The χ^2 and G values were calculated for each row and column. The grand total χ^2 and G statistics indicated a significant difference ($p < 0.001$, df = 9) in the proportions of prey types being consumed seasonally. The rows and columns contributing most to the variability, i.e., those with the largest χ^2 and G marginal values, can readily be identified by examining Table 3. Among seasons (columns), the main source of variation comes from winter;

Table 2. Three-way contingency table (log–linear) analysis testing for seasonal differences in diet composition among four size-classes of bonnethead sharks.

Factor deleted	Likelihood ratio χ^2 statistic	df	Test of interaction	p
None	27.4	27	na	0.444
Food type × season	76.4	36	49.0	<0.001
Food type × size	165.5	36	138.1	<0.001
Season × size	97.8	36	70.4	<0.001

Note: Each two-factor interaction is examined and tested for significance by deleting it from the model. Factor 1, food type (four levels); factor 2, season (four levels); factor 3, size-class (four levels). na, not applicable.

among prey types, the main source of variation comes from digested food, followed by plants to a lesser extent. Expected values (in parentheses) are also included in Table 3 to allow one to readily identify those cells contributing most to the variation.

Post-hoc tests (Table 4) reveal that eliminating the main source of variability among rows (digested food) or among columns (winter) does not suffice to yield a nonsignificant χ^2 or G statistic. Nonsignificance is achieved, however, after further eliminating the second largest source of variation among rows (plants) in both cases. Reexamining Table 3, we would conclude that the seasonal dietary differences were mainly the result of a larger than expected amount of digested food in winter and a smaller than expected amount of plants in fall.

Dietary overlap

The degree of overlap in the diet of fish species has often been measured using parametric or non parametric correlation coefficients or other measures of dietary overlap, such as Morisita's measure (Morisita 1959; C), the simplified Morisita index (Horn 1966; C_H), percentage overlap (Renkonen 1938; P_{jk}), and Horn's index of overlap (Horn 1966; R_o).

Cailliet and Barry (1979) and Krebs (1989) discussed the advantages and disadvantages of the most widely used indices of overlap and similarity and Krebs (1989) recommended using Morisita's index as the best measure to minimize bias, and Horn's index if prey types cannot be expressed as numbers. Numerous studies still use rank correlation to compare fish diets. However, the choice of how many food categories to use in the comparisons is left to the investigator. Both the number of food categories considered and the degree of decimal precision can influence the analysis, since rank correlation is a semiquantitative measure that assigns ranks to food categories. Thus, when using rank correlation, different groupings of food categories should be attempted to assess the effects of those grouping choices on the results. In contrast, R_o and C_H, two of the most commonly used indices when resources are expressed as proportions (Cailliet and Barry 1979), are quantitative measures not influenced by the number of food categories considered because they use the relative proportions of each food type rather than assigning ranks. R_o and C_H vary between 0 (no categories in common) and 1 (identical categories). For C_H, Zaret and Rand (1971) considered values >0.60 to indicate significant overlap; no formal statistical testing of C_H or R_o has been developed (Cailliet and Barry 1979).

Table 3. Contingency table analysis of the seasonal variation of four different categories of food items found in the stomachs of bonnethead sharks.

Prey type	Winter	Spring	Summer	Fall	N_i	χ_i^2	G_i
Crabs	13 (24)	348 (322)	191 (213)	50 (44)	602	10.05	10.99
Miscellaneous	1 (2)	25 (23)	11 (16)	7 (3)	44	6.27	5.32
Plants	13 (11)	128 (148)	124 (98)	11 (20)	276	14.24	14.58
Digested food	12 (3)	30 (38)	25 (25)	4 (5)	71	32.32	18.68
N_j	39	531	351	72	993		
χ_j^2	35.92	6.47	10.72	9.78		62.95***	
G_j	23.10	6.67	10.39	9.40			49.57***

Note: Values are observed numbers, with expected values given in parentheses. The χ^2 and G statistics are highly significant (***, $p < 0.001$).

Table 4. Results of post-hoc contingency table analyses of the seasonal variation of four different categories of food items found in the stomachs of bonnethead sharks after eliminating selected rows and (or) columns.

Row(s) or column(s) eliminated	Significance of χ^2 or G statistic	Sample size
Digested food	$p < 0.001$	922
Digested food, plants	ns	646
Winter	$p < 0.001$	954
Winter, plants	ns	691

Note: ns, not significant.

Table 5. Diet overlap in male and female bonnethead sharks using the Spearman rank correlation coefficient (r_s), the simplified Morisita index (C_H), and Horn's index of overlap (R_o) for different groupings of food categories and varying decimal precision (in parentheses).

No. of food categories	r_s	Critical value	C_H	R_o
7	0.929	0.929[a]	0.992	0.978
17	0.922 (1)	0.711[b]	0.995 (1)	0.947 (1)
17	0.812 (2)	0.711[b]	0.995 (2)	0.946 (2)
17	0.722 (3)	0.711[b]	0.995 (3)	0.946 (3)

[a]Critical value at 1% significance.
[b]Critical value at 0.2% significance.

Illustrative example

Cortés et al. (1996) used the Spearman rank correlation coefficient (r_s) corrected for ties (Fritz 1974), C_H, and R_o to calculate overlap in the diet of male and female bonnethead sharks. If the stomach content data are grouped into seven categories, the null hypothesis (H_o) of no correlation ($\rho = 0$) is rejected at the 0.01 level of significance (Table 5). If, instead, 17 categories are used in the calculation of r_s, H_o is rejected at the 0.002 level of significance and the fewer decimal points considered, the larger our confidence in rejecting H_o, i.e., the more similar the diet becomes. In contrast, results obtained with the quantitative indices C_H and R_o are very homogeneous, relatively unaffected by the number of food categories considered and by decimal precision (Table 5). All C_H and R_o values indicate a very high degree of similarity in the diet.

Stomach content data transformations

Stomach content weight distributions frequently do not satisfy

Table 6. Evaluation of relative performance of several transforms for normalizing stomach content weight data of lemon sharks, expressed as percentage of wet body weight (%BW).

Transform	Normality test results	p	Kolmogorov–Smirnov statistic (D)	Mean	Back-transformed mean
None (Y)	Failed	<0.001	0.305	0.515	—
$\ln(Y+1)$	Failed	<0.001	0.249	—	0.350
$Y^{1/2}$	Failed	<0.001	0.185	—	0.231
$(Y+1)^{1/2}$	Failed	<0.001	0.269	—	0.418
$\arcsin(Y/100)^{1/2}$	Failed	<0.001	0.185	—	0.232

the assumptions of parametric tests (i.e., independence, normality, homogeneity of variances, and additivity). In that case, the original data should be transformed to attempt to satisfy those assumptions. Several transformations have been applied to stomach content weight data: the logarithmic (natural or base 10) transform, the arcsine transform, and the square-root transform (Sokal and Rohlf 1981). Because stomach content weights are generally reported as a percentage of fish body weight (%BW), the arcsine transform, indicated for percentages and proportions (Sokal and Rohlf 1981; Krebs 1989), seems appropriate. Data should be reported as back-transformed means in those cases where transformations were applied. Alternatively, if the parametric statistical assumptions are still not met after the data transformation, especially in those cases where the assumptions are grossly violated, nonparametric techniques should be used and median values reported.

Illustrative example

The distribution of stomach content weights (expressed as percentage of wet body weight) in a sample of 86 lemon sharks was found not to be normal (Table 6). Visual inspection of the data plotted graphically as a histogram and probit analysis (Sokal and Rohlf 1981) further revealed substantial deviations from normality. Some of the more common transformations were then used to attempt to normalize the original data and a Kolmogorov–Smirnov test of goodness of fit (Sokal and Rohlf 1981) was run on each transformed data set, yet none of the data transforms yielded normality ($p < 0.001$ in all cases; Table 6). By noting the magnitude of the Kolmogorov–Smirnov statistic (D) and comparing it with the tabulated 1% critical value (0.111), the least significant values (smaller D values) were obtained with the square-root and arcsine transforms, although data were still far from being normally

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Fig. 3. The influence of experimental design on studies of diel feeding chronology in teleost and elasmobranch fishes. In elasmobranch studies, grouping sampling times of stomachs collected throughout 24-h periods during a sampling campaign into successive 3-h intervals adds variability along the horizontal axis. In teleost studies, stomachs can generally be collected at specific sampling times. Vertical and horizontal error bars are simulated ±SEs.
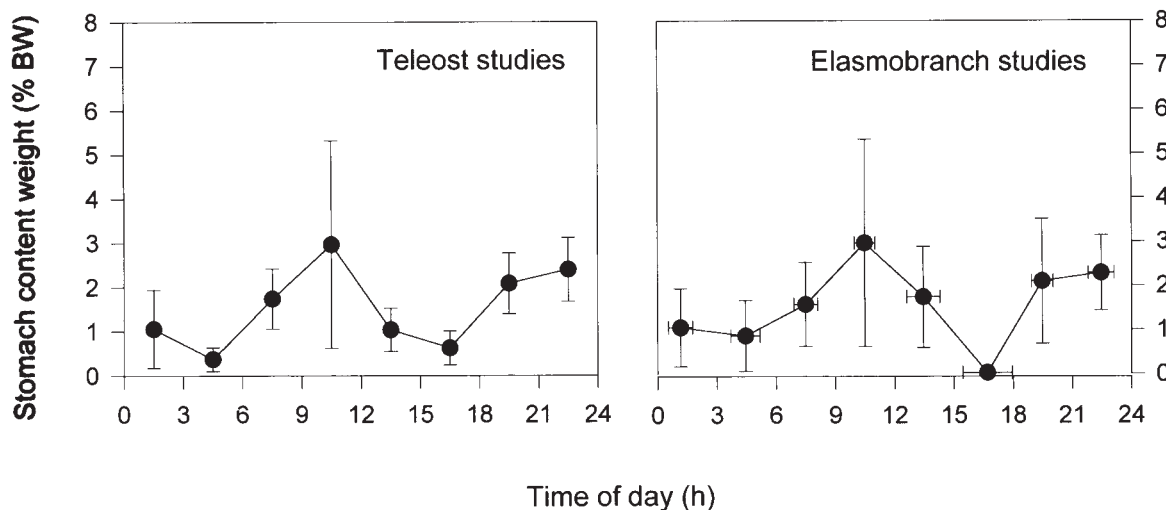
distributed. Had we found that any of the transformations satisfied the normality assumption, we should still have tested for homoscedacity if we were to compare our sample with other data sets. In this particular example, the median should probably be calculated and nonparametric techniques applied for comparisons with other data sets.

Diel feeding chronology: influence of sampling gear, experimental design, and statistical analysis

Discontinuity of feeding activity over time of day is investigated in fishes by randomly collecting samples at regular intervals throughout the 24-h period (Jenkins and Green 1977). To account for differences in fish size, stomach content weights are usually expressed as a percentage of the fish weight (%BW). Mean %BW values for each sampling time are then calculated and plotted against sampling time in the X axis, with ±SE, 95% confidence intervals (CI), or range generally placed around the mean at each sampling time (Fig. 3). Jenkins and Green (1977) showed that visual inspection of these plots was misleading because apparent peaks in stomach fullness detected by eye are often not corroborated by statistical analyses. These authors proposed one-way analysis of covariance (ANCOVA) of fish weight versus stomach content weight to test statistically for temporal feeding continuity, indicating that the test of intercepts given common slopes is the test of among-time differences in stomach content weights adjusted for fish size.

Diel feeding continuity is more often examined using one-way analysis of variance (ANOVA). This test allows detection of discontinuity in stomach content weight among the sampling intervals when applied to original or transformed stomach content weight data. To further determine which sampling times are responsible for the difference(s), post-hoc Student–Newman–Keuls or similar tests can be applied to perform pairwise comparisons of means. Alternatively, a nonparametric one-way ANOVA (Kruskal–Wallis test) and corresponding

post-hoc nonparametric comparisons (Dunn's or similar tests) can be applied. Cortés et al. (1996) compared ANCOVA and ANOVA tests to determine feeding (dis)continuity in bonnethead sharks, finding that the results from the two approaches agreed in <50% of the cases (Table 7).

Sampling gear and experimental design can also affect results for diel feeding chronology and food consumption estimates. Studies dealing with teleost fishes generally use electrofishing, beach seines, traps, otter trawls, or similar gear to sample at regular intervals throughout the day. This type of gear allows the investigator to collect most of the samples for each interval in a short time period and thus obtain a good representation of stomach content weights at each sampling time. In contrast, elasmobranchs are much less abundant than teleost fishes and more difficult to collect. Passive gear, such as gill nets, is generally set throughout the day and retrieved at regular intervals. The exact time of capture of each sampled specimen is generally unknown. In some cases, owing to the difficulty of collecting a substantial sample of stomach contents in a 24-h period, instead of collecting samples at regular intervals (typically 3 h) throughout the 24-h period, sampling times of stomachs collected at different times throughout the day and night during a sampling campaign are grouped into successive (generally 3 h) intervals (Medved et al. 1988; Cortés and Gruber 1990; Cortés et al. 1996), adding variability along the horizontal axis (Fig. 3). Cortés et al. (1996) showed that in this type of experimental design the length (3 versus 4 h) and starting time of the interval yielded different results on diel feeding chronology within and between statistical tests (Table 7).

The effect of active versus passive gear in studying diel feeding chronology and estimating food consumption has not been investigated in elasmobranchs. Hayward et al. (1989) found significantly higher median amounts of food in stomachs of yellow perch (*Perca flavescens*) caught with passive gear (gill net) versus active gear (otter trawl). They concluded that active gear produced more accurate estimates of food consumption because it samples both low-activity or nonforaging

Table 7. Summarized results from a study by Cortés et al. (1996) showing the influence of the statistical test and the length and starting point of the time interval on the determination of diel feeding chronology.

Time interval length (h)	Time interval starting point	Statistical test results (p)	
		ANOVA	ANCOVA
3	11:00	<0.05	ns
3	12:00	<0.05	ns
3	13:00	ns	ns
4	10:00	<0.05	ns
4	11:00	<0.05	<0.05
4	12:00	<0.05	<0.01
4	13:00	ns	ns

Note: ns, not significant.

Table 8. Main requirements of the most common in situ methods used to estimate daily ration in fishes.

Model	Gastric evacuation requirements	Periodic sampling	Applicability to elasmobranchs
Elliott–Persson	Exponential	Yes	Yes, if TI ≤ 3 h
Eggers	Exponential	No	Yes
Diana	Any	No	Yes
Olson–Mullen	Any	No	Yes
Pennington	Nonlinear	Yes	Yes

Note: TI, time interval.

fish and actively feeding fish, whereas passive gear only effectively samples those individuals in a population that are actively feeding. Active gear, such as otter and bottom trawls, has been used in dietary studies of skates, rays, and bottom-dwelling sharks but is not appropriate for sampling most coastal and oceanic shark species. To sample these species, gill nets are the most commonly used type of gear, largely preferable over longlines because the latter tend to attract individuals with empty stomachs (Wetherbee et al. 1990). Passive versus active gear bias in field estimation of diel feeding chronology and food consumption could probably be investigated in some species of skates and rays but this does not appear to be feasible for most species of sharks.

An important consideration when interpreting results obtained through the standard methods based on sampling at regular intervals throughout the 24-h period is that the terms continuity and discontinuity are often misapplied or misunderstood. Considering only the weight of stomach contents does not allow one to draw any conclusions on feeding (dis)continuity; only conclusions on feeding intensity and chronology can be drawn at best. For example, when an investigator concludes that feeding is continuous after analyzing stomach content weight versus time of collection data, all that can actually be concluded is that there were no significant differences in the weight of food in the stomach over a diel period. However, feeding may still be discontinuous or, rather, intermittent, in the species under study. Similarly, if, for example, the mean weight of stomach contents of a given fish species is found to be significantly higher at 10:30 (Fig. 3), this does not necessarily mean that feeding activity increases at that time in that species, unless we can determine that all food items were consumed very recently.

Stomach content weights alone do not suffice to assess feeding continuity or to interpret diel feeding chronology. We also need to consider the percentage of empty stomachs in the sample and the dietary composition and stage of digestion of each individual item in each individual stomach at each sampling interval. If the digestion rate of each different prey item is known or can be approximated, meal sizes and ingestion times can be reconstructed. The distribution of ingestion times among time intervals then can be tested with a goodness of fit test to detect preferred feeding times in the population studied. These considerations are especially important in large carnivorous predators such as sharks, most of which only feed intermittently and not necessarily every day (Wetherbee et al.

1990). Diel feeding activity is a complex process influenced by environmental, behavioral, and physiological constraints. Thus, in addition to considering sampled stomach content weights, a better understanding of all these integrated factors is required.

Daily ration

The adequacy of the most common models used to estimate daily ration and of the associated types of gastric evacuation curves in fishes has been discussed at length (Elliott and Persson 1978; Mullen 1986; Persson 1986; Boisclair and Leggett 1988; Ruggerone 1989; Boisclair and Marchand 1993; Bromley 1994; and references therein). However, the extent to which the most common models used to estimate daily ration in teleost fishes are applicable to elasmobranchs has not been investigated in depth. Surprisingly, only two published studies to date have used multiple in situ methods to estimate daily ration in elasmobranchs (Medved et al. 1988; Cortés and Gruber 1990). Medved et al. (1988) used the Elliott and Persson (1978) and the Diana (1979) models to calculate the daily ration of the sandbar shark (*Carcharhinus plumbeus*), whereas Cortés and Gruber (1990), in addition, used the Olson and Mullen (1986) model to estimate the daily ration of the lemon shark. Results from these two studies indicated that despite the nonfulfillment of several of the model assumptions, the models used in each study yielded similar estimates of daily ration.

Elliott and Persson (1978) originally proposed two methods for nonpiscivorous fishes, one that assumes constant feeding and another that assumes a decreasing feeding rate with time. Both methods assume an exponential gastric evacuation rate. The second method, in addition, requires an estimate of satiation ration and that the larger fish feed to satiation, making it inadequate or difficult to apply in most situations. The Elliott–Persson method generally referred to in the literature is thus the simpler method that assumes constant feeding rate. Elliott and Persson (1978) empirically determined using the brown trout (*Salmo trutta*) that this method is applicable to intermittent feeders if the sampling interval is kept short (≤3 h). Indeed, despite the violation of the major assumptions of continuous and constant rate of feeding implicit in this method, it seems to yield reasonable results when applied to elasmobranch studies if sampling intervals are kept ≤3 h (Medved et al. 1988; Cortés and Gruber 1990; Table 8).

Another commonly used model to estimate daily ration is that of Eggers (1979). This method also requires an exponential evacuation rate, but only an estimate of the mean weight

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Table 9. Point, jackknife, and bootstrap estimates of daily ration for lemon sharks through the Eggers and the Elliott–Persson models using transformed and original (percent wet body weight) data.

Estimate	Recombi-nations	Eggers			Elliott–Persson		
		Arithmetic mean	Geometric mean	BT arcsine mean	Arithmetic mean	Geometric mean	BT arcsine mean
Point		2.16	1.47	1.01	2.18	1.56	3.53
Jackknife		2.21 (1.29–3.13)	1.46 (0.95–1.97)	0.44 (0–3.95)	2.23 (1.18–3.28)	1.48 (0.81–2.15)	3.56 (3.08–4.04)
Bootstrap	100	2.27 (2.17–2.37)	1.51 (1.46–1.56)	1.85 (1.52–2.17)	2.25 (2.16–2.33)	1.66 (1.60–1.71)	3.99 (3.83–4.14)
	200	2.20 (2.13–2.27)	1.79 (1.75–1.84)	1.78 (1.55–2.01)	2.29 (2.23–2.35)	1.69 (1.65–1.73)	3.97 (3.86–4.09)
	300	2.17 (2.11–2.23)	1.89 (1.85–1.92)	1.69 (1.50–1.87)	2.26 (2.21–2.31)	1.70 (1.66–1.73)	4.02 (3.92–4.11)
	400	2.15 (2.10–2.20)	1.93 (1.91–1.96)	1.67 (1.51–1.83)	2.23 (2.19–2.27)	1.73 (1.70–1.76)	4.15 (4.07–4.23)
	500	2.14 (2.10–2.19)	1.96 (1.94–1.99)	1.65 (1.51–1.79)	2.22 (2.19–2.26)	1.72 (1.69–1.74)	4.12 (4.05–4.20)
	600	2.14 (2.11–2.18)	1.98 (1.96–2.00)*	1.63 (1.50–1.75)	2.23 (2.20–2.27)	1.71 (1.69–1.73)	4.10 (4.04–4.17)
	700	2.14 (2.11–2.18)	2.00 (1.98–2.02)*	1.66 (1.54–1.78)	2.23 (2.20–2.27)	1.70 (1.68–1.72)	4.09 (4.03–4.15)
	800	2.14 (2.11–2.17)	2.01 (1.99–2.03)*	1.64 (1.53–1.75)	2.24 (2.21–2.27)	1.70 (1.68–1.72)	4.07 (4.02–4.13)
	900	2.14 (2.11–2.17)	2.02 (2.00–2.03)*	1.61 (1.51–1.72)	2.25 (2.22–2.28)	1.70 (1.68–1.72)	4.04 (3.98–4.09)
	1000	2.14 (2.11–2.16)	2.02 (2.01–2.04)**	1.61 (1.51–1.71)	2.25 (2.22–2.27)	1.69 (1.67–1.71)	4.03 (3.98–4.08)

Note: Values in parentheses are 95% confidence intervals. Asterisks indicate significant differences from the point estimate (*, $p < 0.05$; **, $p < 0.01$). BT arcsine mean is the back-transformed mean of data transformed using arcsin $(\%BW/100)^{1/2}$. See text for details.

of stomach contents over a 24-h period (Table 8). Although not calculated by Cortés and Gruber (1990), daily ration by the Eggers method for the lemon shark yields almost identical results to the Elliott–Persson method (2.16 versus 2.18% BW).

The reconstructive method of Diana (1979) seems more appropriate for top predators such as sharks because it assumes that feeding is asynchronous and intermittent, feeding bouts are short, and the interval between meals is longer than digestion time. In addition, gastric evacuation can be of any form (Table 8). The Olson and Mullen (1986) model was also conceived for predatory fish, such as tuna, and assumes that fish feed on mixed prey items at random intervals. Like the Diana model, the Olson–Mullen model is less restrictive than the two exponential models, because any type of gastric evacuation function is acceptable (Table 8). Finally, the Pennington (1985) model assumes that the rate of evacuation at any given time depends only on the stomach contents at that moment, and not on initial meal size. For exponential evacuation rates, the Pennington model simplifies into the Eggers model. The only restriction of this method is that it does not allow for a linear rate of gastric evacuation (Table 8).

The Elliott–Persson and Pennington models allow estimation of the diurnal feeding cycle (Mullen 1986) but are logistically more demanding than the other methods because they require periodic sampling (Table 8). On the basis of fulfillment of assumptions and sampling requirements, it appears that the less restrictive Diana and Olson–Mullen methods are more appropriate for top predators such as sharks.

Analysis of statistical variability in daily ration estimates is usually absent from fish food consumption studies because the models traditionally used to estimate daily ration are deterministic. As an alternative approach, numerous studies have attempted to determine daily ration through different methods and then compare the various estimates derived. Worobec (1984) and Pennington (1985) first proposed equations to estimate an approximate standard error of the daily ration when using the Elliott–Persson and Eggers models, respectively. As discussed by Boisclair and Leggett (1988), the formulae presented by these two authors are restricted by their complexity, combination of transformed and nontransformed variables, and lack of replicated estimations of daily ration. More

recently, several studies have used resampling techniques, such as the jackknife or the bootstrap, or Monte Carlo simulations, to provide a measure of the error associated with daily ration estimates (Boisclair and Leggett 1988; Hayward 1991; Hayward et al. 1991; Boisclair and Marchand 1993).

An illustrative example of the measurement of variation in daily ration estimates of elasmobranchs

No error analysis dealing with the daily ration of elasmobranchs has been published, and thus no statistical testing of differences between daily ration estimates has been possible. To provide a first measure of the uncertainty associated with estimating daily ration in sharks, I used the jackknife and bootstrap methods on transformed and original (standardized as percent wet body weight) stomach content data of lemon sharks and compared the estimates obtained through the Eggers and Elliott–Persson models (Table 9).

For the Eggers model, the bootstrap arithmetic mean, geometric mean, and back-transformed mean of arcsin $(\%BW/100)^{1/2}$ (back-transformed arcsine mean) converged on a value of 2.14, 2.02, and 1.61% BW after 500, 900, and 900 recombinations, respectively. Precision (measured as the magnitude of the CI) was higher for the bootstrap estimates than for the jackknife estimate in all cases and increased with number of recombinations. Significant differences with the point estimate were only found for the bootstrap estimates after 600 recombinations when using geometric means (Table 9).

For the Elliott–Persson model, only the bootstrap arithmetic mean converged on a stable value, after 900 iterations (Table 9). Precision was higher for the bootstrap estimates than for the jackknife estimate in all cases, increasing with number of recombinations. No significant differences were found between the jackknife or bootstrap estimates and the point estimate when using any of the three means.

Point, jackknife, and bootstrap (for 1000 recombinations) estimates were compared between the two models for each of the three types of means. Using the overlap of the 95% CI as the significance criterion, significant differences were found between the bootstrap estimates for arithmetic, geometric, and back-transformed arcsine means. Additionally, for geometric means, the Eggers bootstrap estimate was significantly different

Table 10. Goodness of fit of several mathematical models fitted to gastric evacuation data ($n = 52$) for the lemon shark.

Model	r^2	F	p	RSS	SD of residuals	Y intercept	CV of residuals	Residual analysis[a]		
								N	H	A[b]
Linear	0.607	79.88	<0.001	7046	11.6	96.6	0.177	P ($p = 0.122$)	F ($p < 0.001$)	2.198
Exponential[c]	0.492 (0.615)[d]	50.38	<0.001	2.93	0.24	103.0	0.059	F (p = 0.002)	F ($p < 0.001$)	2.273
Exponential	0.615			6902	11.5	102.2	0.176	P ($p = 0.198$)	F ($p < 0.001$)	2.259
Square root[c]	0.561 (0.613)[d]	66.14	<0.001	33.77	0.81	99.1	0.102	F (p =0.048)	F ($p < 0.001$)	2.243
Square root	0.613			6938	11.5	99.3	0.176	P ($p = 0.176$)	F ($p < 0.001$)	2.239
Logistic	0.670			6643	11.3	54.7	0.172	P ($p = 0.100$)	F ($p < 0.001$)	2.391
Gompertz	0.663			6747	11.4	60.7	0.174	P ($p > 0.2$)	F ($p < 0.001$)	2.338

[a]N, normality test; H, homoscedacity test; A, autocorrelation test; P, pass; F, fail.

[b]Autocorrelation tested by Durbin–Watson statistic (values closer to 2 indicate lower autocorrelation of residuals).

[c]Linearized models.

[d]Values are r^2 between back-transformed fitted values ($\hat{Y}_i$) and untransformed observed values (Y_i).

($p < 0.05$) from the Elliott–Persson point estimate, and, for back-transformed arcsine means, the Eggers point estimate was significantly different from both the Elliott–Persson jackknife ($p < 0.001$) and bootstrap ($p < 0.001$) estimates (Table 9).

In all, there was little variation in daily ration estimates among estimation procedures or between models when using arithmetic means. However, there was more substantial variation when using back-transformed means, especially in the case of back-transformed arcsine means (Table 9). This indicates that there are potentially important differences in the accuracy of daily ration estimates obtained from different models and (or) estimation procedures. The present exercise, however, was not designed to identify which estimates are more accurate.

Resampling techniques provide a picture of the variability associated with estimating daily ration because they allow calculation of CIs and comparison of estimates obtained through different models. For the data set studied, a greater precision was achieved with the bootstrap than with the jackknife method in all cases, and precision always increased with increasing number of recombinations. On the basis of precision alone, the bootstrap method seems preferable over the jackknife to provide a measure of the error associated with estimating daily ration.

Gastric evacuation

Knowledge of gastric evacuation rates in fishes is essential to estimate daily ration through in situ methods. In elasmobranchs, especially in sharks, measurement of evacuation rates under controlled laboratory or field conditions has been severely impaired by the difficulty of collecting and keeping large or adult specimens in captivity. Thus, researchers have opted for a more pragmatic approach and concentrated on small species (Jones and Geen 1977) or juvenile specimens of larger species (Medved 1985; Cortés and Gruber 1992). In all, knowledge of gastric evacuation dynamics in elasmobranchs remains very fragmentary.

The adequacy of the most common models used to describe gastric evacuation patterns in fishes (linear, exponential, square root, and surface area) is still a matter of research and debate (Bromley 1994; Gerking 1994). In general, no single model appears to fit equally well the evacuation dynamics of different species consuming different prey items under varying

environmental conditions. While the physiological rationale of the different curves has been reviewed (Jobling 1981, 1986, 1987; Persson 1986; Gerking 1994), the appropriateness of the criteria used to select the best model of evacuation from a statistical standpoint has only been partially discussed (Bromley 1994). Some of the most commonly used criteria include comparison of r or r^2 (Macdonald et al. 1982; Persson 1982, 1984; Brodeur and Pearcy 1987; Bromley 1987; Ruggerone 1989; Dos Santos and Jobling 1991; Russell and Wooton 1993; Bromley 1994), residual sum of squares (RSS) or residual mean squares (RMS; Medved 1985; Jobling 1987), standard deviation (SD) or variance of the residuals (Longmuir et al. 1971; Jobling 1986), and the coefficient of variation of the residuals (CV; Somerton 1980; Cortés and Gruber 1992).

A problem typically arises when exponential and square-root models are linearized to perform least-squares regression, because the magnitudes of the above criteria are no longer comparable. One way to circumvent this problem is to apply nonlinear regression and use the above criteria to compare fits. Preferably, a criterion adjusted for the number of observations and parameters in the model (adjusted linear r^2) and the magnitude of the dependent variable (adjusted nonlinear r^2 (Dos Santos and Jobling 1991) or CV (Somerton 1980)) should be used. An alternative is to calculate an adjusted r^2 between the back-transformed fitted values ($\hat{Y}_i$) and the untransformed observed values (Y_i) for the linearized model, since it yields the same result as the nonlinear r^2 value calculated for the corresponding nonlinear model.

Additional criteria that should be used to compare model fits include determination of the Y-axis intercept (Persson 1982; Jobling 1986, 1987; Brodeur and Pearcy 1987; Ruggerone 1989; Cortés and Gruber 1992) and an examination of residual plots (Medved 1985; Ruggerone 1989) or formal residual analysis (Olson and Mullen 1986). Compliance of each model to regression assumptions is important not only as a comparative criterion but also to determine whether a weighting factor needs to be applied to the data.

Illustrative example

Gastric evacuation data for the lemon shark were fitted with several common models and their goodness of fit was evaluated with several criteria (Table 10). The fit of the linear model cannot be compared with that of the linearized exponential or square-root models using r^2, RSS, SD of residuals, or CV as criteria because linearization has altered their magnitudes

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(Table 10). All *F* values from the ANOVA table are highly significant, indicating that the models explain most variance. When comparing the linear with the linearized models, the most accurate estimate of *Y*-axis intercept is given by the square-root model, but residual analysis reveals that only the linear model passes the normality assumption of least squares regression and has the lowest autocorrelation of residuals. However, if we consider the nonlinear exponential and square-root models, both have slightly better fits than the linear model according to r^2, RSS, SD of residuals, and CV and predict more accurately the *Y* intercept, while also conforming to the normality assumption of nonlinear least squares regression. The fit of the nonlinear exponential and square-root models has thus changed in relation to that of the linearized forms. Note that the adjusted r^2 value between back-transformed fitted values and observed values of the linearized exponential and square-root models equals the adjusted nonlinear r^2 value of the corresponding nonlinear form (Table 10). While the logistic and Gompertz models show a better fit than all of the other models according to r^2, RSS, SD of residuals, and CV, they severely underestimate the *Y* intercept and are thus inadequate.

Because none of the models passed the homogeneity of variances assumption of least squares regression and on the basis of the direct relationship between σ_i^2 and X_i observed in the analysis of residuals, a weight $w_i = 1/X_i$ (Neter et al. 1990) was applied to the data and the fits were reexamined. In this particular example, weighting does not improve the fit; it actually worsens it because the normality assumption of regression is not met. Overall, considering the unweighted fits (Table 10), it does not seem practical to select a best-fitting model on the basis of the criteria used, probably as a result of insufficient experimental data.

Inconclusive outcomes following efforts to identify a best-fitting gastric evacuation model may arise quite commonly. If the gastric evacuation model is to be further used in the estimation of daily ration through in situ methods, a prudent approach is to use several in situ methods with different gastric evacuation requirements or methods that accommodate any form of gastric evacuation and then compare the outcomes corresponding to each gastric evacuation form used.

Summary

Published studies of diets, food habits, and food consumption of fish show a lack of standardization in the use of indices and of consistency in methods, experimental design, data reporting, and statistical analysis, all of which hinder comparative studies.

The need for consolidation of methods is especially critical in elasmobranch feeding studies, owing to the added difficulty of obtaining large sample sizes and the limited ability to conduct controlled experiments with large or adult specimens. A pragmatic approach is recommended in food consumption studies of elasmobranchs to predict diel feeding chronology and feeding and gastric evacuation rates. To advance our knowledge in these areas, we may have to compromise between the rigorous application of experimental design and adherence to model assumptions and other approaches that require fewer parameter estimates and are logistically less demanding. Emphasis should then be placed on maximizing the information derived from examining stomach contents of field-caught fish. For example, when attempting to predict daily ration, multiple models should be applied and resampling techniques, such as the bootstrap, should be used to provide a measure of the error associated with parameter estimates. Results from gastric evacuation studies also should be fully incorporated into attempts to describe diel feeding chronology. New food consumption models more akin to the feeding activity of large predators such as sharks may well have to be developed. Setting aside logistical considerations, the main needs in feeding studies of elasmobranch fishes remain a more quantitative approach and the consolidation of methodology and data analysis.

Acknowledgements

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