

A statistical approach for estimating fish diet compositions from multiple data sources: Gulf of California case study

CAMERON H. AINSWORTH,^{1,4} ISAAC C. KAPLAN,² PHILLIP S. LEVIN,² AND MARC MANGEL³

¹*Marine Resources Assessment Group (MRAG) Americas Inc., Northwest Fisheries Science Center (NWFSC-NOAA), 2725 Montlake Blvd. E., Seattle, Washington 98112 USA*

²*National Marine Fisheries Service, Northwest Fisheries Science Center (NWFSC-NOAA), 2725 Montlake Blvd. E., Seattle, Washington 98112 USA*

³*Center for Stock Assessment Research and Department of Applied Mathematics and Statistics, Jack Baskin School of Engineering, University of California–Santa Cruz, 1156 High Street, Santa Cruz, California 95064 USA*

Abstract. Trophic ecosystem models are one promising tool for providing ecosystem-based management advice. Diet and interaction rate parameters are critical in defining the behavior of these models, and will greatly influence any predictions made in response to management perturbations. However, most trophic ecosystem models must rely on a patchwork of data availability and must contend with knowledge gaps and poor quantification of uncertainty. Here we present a statistical method for combining diet information from field samples and literature to describe trophic relationships at the level of functional groups. In this example, original fieldwork in the northern Gulf of California, Mexico, provides gut content data for targeted and untargeted fish species. The field data are pooled with diet composition information from FishBase, an online data repository. Diet information is averaged across stomachs to represent an average predator, and then the data are bootstrapped to generate likelihood profiles. These are fit to a Dirichlet function, and from the resulting marginal distributions, maximum-likelihood estimates are generated with confidence intervals representing the likely contribution to diet for each predator–prey combination. We characterize trophic linkages into two broad feeding guilds, pelagic and demersal feeders, and explore differentiation within those guilds. We present an abbreviated food web for the northern Gulf of California based on the results of this study. This food web will form the basis of a trophic dynamic model. Compared to the common method of averaging diet compositions across predators, this statistical approach is less influenced by the presence of long tails in the distributions, which correspond to rare feeding events, and is therefore better suited to small data sets.

Key words: *Atlantis; Dirichlet; FishBase; fish diet; Gulf of California, Mexico; gut content; maximum-likelihood estimation; predator–prey interactions; Sea of Cortez; stomach content.*

INTRODUCTION

Nearly every modern treatise on the management of marine natural resources contains some endorsement of ecosystem-based management (EBM). EBM is place-placed, considers connections within and among ecosystems, and focuses on maintaining the long-term ability of ecosystems to deliver a range of goods and services (Rosenberg and McLeod 2005). EBM differs from single-sector or single-species management in that it defines management portfolios for entire systems instead of focusing solely on individual parts of the system. Around the world, EBM is increasingly being adopted as a preferred approach for managing ocean resources (Brodziak and Link 2002, FAO 2003, Garcia et al. 2003, NOAA 2003, U.S. Commission on Ocean

Policy 2004). Development of tools for EBM has lagged behind the requirements of formal mandates, but an invigorated political will is spawning rapid progress (Pitcher 2000, Smith et al. 2007, Levin et al. 2009).

Management of marine resources has long relied on the synthesis of diverse information into a coherent whole (e.g., Methot 2005). Data from marine ecosystems are often limited in their spatial and temporal extent, and in the processes they are able to capture. To produce management advice at the ecosystem level, fisheries stock assessors have developed methods to represent larger systems by combining multiple disparate data sets. These combined data sets provide a more precise evaluation of the status and trends of fish stocks than would be possible with any single data source (Methot 1989). As EBM tools are developed, researchers must confront the same problem that single-species modelers have already considered: how to merge information and data from a wide assortment of sources of varying scope and quality.

Manuscript received 9 April 2009; revised 4 December 2009; accepted 2 February 2010. Corresponding Editor: K. Stokesbury.

⁴ E-mail: cameron.ainsworth@noaa.gov

Trophic ecosystem models are one of the most widely used EBM tools in marine systems, and in this paper, we develop a novel approach for synthesizing diet information from diverse sources to inform these models. Although we use trophic ecosystem models as an example, our approach is applicable to any situation in which the synthesis of data is required. Trophic ecosystem models consider population dynamics of many ecosystem components simultaneously and make predictions concerning the interactions of fish, habitat, and fisheries in ways not possible through classical single-species and multispecies methods. Despite their immense data requirements, scientists have successfully applied these tools to data-poor regions through creative use of available data. Various studies have utilized unconventional information sources such as archeology (Lozano 2006) and local ecological knowledge (Ainsworth et al. 2008a), or have drawn on centralized databases (Pauly et al. 2009) and have relied on directed field studies to target specific data gaps (Ainsworth et al. 2008b, Pinkerton et al. 2008).

A key to any trophic model is to portray accurately the diet and interaction rate parameters because they greatly influence any predictions made in response to management perturbations (Pinnegar et al. 2005). Despite their importance, most trophic ecosystem models must rely on a patchwork of data and must contend with knowledge gaps. Consequently, modelers are required to integrate empirical data with information from a variety of sources, including literature values and online data repositories. Thus, proper synthesis of diet information is crucial to any trophic ecosystem model. An accurate representation of the uncertainty surrounding input data is also paramount, as this has been a barrier to the implementation of ecosystem models as practical tools in EBM (Hill et al. 2007, Plagányi 2007).

In this paper, we focus on these problems for the northern Gulf of California ecosystem, Mexico (Fig. 1). We present a new statistical technique for assimilating diet information from field studies with literature-derived information, and for quantifying uncertainty surrounding the diet values. We characterize feeding relationships in the ecosystem of the northern Gulf and develop a preliminary food web with the intent to parameterize an Atlantis ecosystem model (Fulton et al. 2004). Atlantis is a modeling platform that integrates physical, chemical, ecological, and socioeconomic dynamics in a spatially explicit domain.

Our approach is especially helpful in modeling study areas with data deficiencies, because it is in those situations that information synthesis has the potential to improve models greatly.

METHODS

Sampling

We collected fish stomachs in the northern Gulf of California between February and August 2008. Protocol for the diet sampling is provided by Ainsworth (2007).

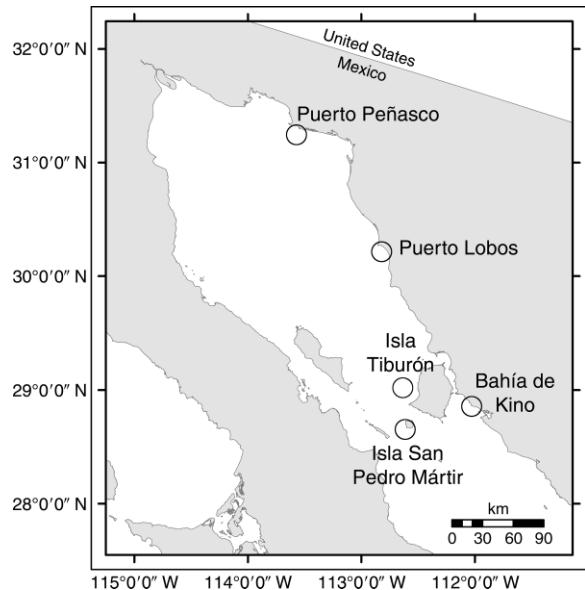


FIG. 1. Northern Gulf of California (Mexico) study area showing sites of fish stomach collections.

Briefly, fish stomachs were obtained for common commercial and bycatch species of the northern Gulf of California from local markets, directly from fishermen, or by retaining fish from a concurrent trawl sampling study (see Plate 1). In initial collections made of longline catch and bycatch species, we found many stomachs empty; therefore, we expanded the collection to include fish caught by a variety of baited and unbaited gear types: 40.6% of samples were taken from gill net fisheries, 25.6% were from longline, 17.2% were from trap, 8.4% were from shrimp and nearshore trawl, 6.1% were from hook and line, and 2% were from diving. We sampled 444 stomachs, of which 209 had identifiable stomach contents. The variety of gear types used to capture specimens and the varied capture locations should help to reduce intra-haul correlation as a source of error, a problem for predators that concentrate on patchy prey distributions (Tirasin and Jørgensen 1999). Using a variety of gear types will also introduce an uncontrolled bias, as the characteristics of each gear type will influence the kinds of prey found in stomachs (i.e., species and life stages) and the digestion state of prey, which relates to our ability to identify prey taxa.

The origins of the fish stomachs were from areas surrounding Puerto Peñasco in the north (113°34'57.7" W, 31°14'44.6" N), on the east coast near Puerto Lobos (112°49'13.7" W, 30°12'56.5" N) near Bahía de Kino (112°1'38.5" W, 28°50'44.8" N), and in the central gulf near Isla San Pedro Mártir (112°37'29.2" W, 28°39'37.3" N) and off Isla Tiburón (112°37'29.2" W, 28°39'37.3" N); see Fig. 1. Stomachs were frozen prior to dissection in the laboratory.

TABLE 1. Taxa sampled in field collection in the northern Gulf of California (Mexico) study area.

Scientific name	Common name	Functional group
<i>Atractoscion nobilis</i>	white seabass	drums and croakers
<i>Balistes polylepis</i>	finescale triggerfish	large reef fish
<i>Calamus brachysomus</i>	Pacific porgy	small demersal fish
<i>Caulolatilus affinis</i>	bighead tilefish	small demersal fish
<i>Caulolatilus princeps</i>	ocean whitefish	small reef fish
<i>Dasyatis dipterura</i>	diamond stingray	skates, rays, and sharks
<i>Epinephelus acanthistius</i>	gulf coney	Gulf coney
<i>Micropogonias megalops</i>	bigeye croaker	drums and croakers
<i>Mycteroperca jordani</i>	gulf grouper	Gulf grouper
<i>Paralabrax maculatofasciatus</i>	spotted sand bass	groupers and snappers
<i>Raja inornata</i>	California ray	skates, rays, and sharks
<i>Scomberomorus sierra</i>	Pacific sierra	mackerel
<i>Semicossyphus pulcher</i>	California sheephead	large reef fish
<i>Sphoeroides annulatus</i>	bullseye puffer fish	small reef fish
<i>Cynoscion</i> spp.	weakfishes	drums and croakers
<i>Mustelus</i> spp.	smooth-hound sharks	small migratory sharks
<i>Paralabrax</i> spp.	rock-basses	groupers and snappers
<i>Paralichthys</i> spp.	southern flounders	flatfish
<i>Sphoeroides</i> spp.	common puffers	small reef fish

Due to our data requirements for the ecosystem model, we were able to simplify the laboratory component of the analysis using a method similar to that of Ainsworth et al. (2008c). We identified prey items only to the level of functional groups and weighed them in aggregate. We did not consider differential digestion or gastric evacuation rates, so it is possible that the contribution of soft-bodied organisms (e.g., cnidaria) and high-energy-content organisms are underestimated relative to chitinous organisms, e.g., crustaceans (Jackson et al. 1987). However, determining appropriate correction factors is not straightforward, because predators show interspecific variability in digestion rates, but digestion and evacuation models are available for relatively few species (Berens and Murie 2008). We were interested in obtaining the widest possible representation across taxa, because the Atlantis ecosystem model that we are designing implicitly or explicitly includes a large number of fish species (576) occurring in the study area. However, the availability of samples restricted our focus to common species. We sampled 18 species and obtained usable gut content information for 13 species and 7 more generic taxa (Table 1).

Trophic ecosystem models typically reduce the complexity of the ecosystem by aggregating living components into broad functional groups, combining species similar in trophic role, morphology, behavior, physiology, or other niche characteristics. Aggregating species introduces a strong set of assumptions (Chalcraft and Resetarits 2003), but it is a necessary computational and conceptual tool in order to make the models operational. For the models we require

$$p_{ij} = \text{proportion of species } i \text{ in the diet of species } j \quad (1)$$

where species are identified at the resolution of the functional group, and proportion is measured in terms of biomass. Note that we must have $\sum_i p_{ij} = 1$, because when summed over all of the species eaten, the

proportions consumed by predator species j must total 1.0. These studies lead to a matrix of results:

$$p_{ijk} = \text{fraction of species } i \text{ in the stomach of individual } k \text{ of species } j \quad (2)$$

that we treat as random variables. For example, suppose that the functional group “large pelagic fish” (say, $j = 1$) ate only mackerel ($i = 1$), small pelagics ($i = 2$), and squid ($i = 3$), and that we sampled two stomachs. In the first stomach, we found 10% mackerel, 60% small pelagics, and 30% squid by mass; in the second stomach, we found 20% mackerel, 60% small pelagics, and 20% squid. Then we have

$$P_{ilk} = \begin{bmatrix} 0.1 & 0.6 & 0.3 \\ 0.2 & 0.6 & 0.2 \end{bmatrix} \quad (3)$$

where i indexes columns (prey species) and k indexes rows (stomach samples).

In order to expand the database, we augmented our diet data from the northern Gulf with diet information derived from FishBase, a global archive of diet and life history information (Froese and Pauly 2008). FishBase contains information on 82 species that are found in the northern Gulf of California, of which we observed only three during field sampling. We took references from 60 studies, covering 101 species, and 23 functional groups of the Atlantis model’s 27 fish functional groups (Appendix: Tables A1 and A2). Although these FishBase data usually originated from other world areas, the comparison with the Gulf of California may be accurate to the predator/prey functional group levels based on the assumption of similar predator-to-prey size ratios and physiological feeding constraints across ecosystems (White et al. 2007). Although this assumption introduces a potential source of error, it is necessary to account for logistical limitations in sampling, especially prevalent in developing countries, and envi-

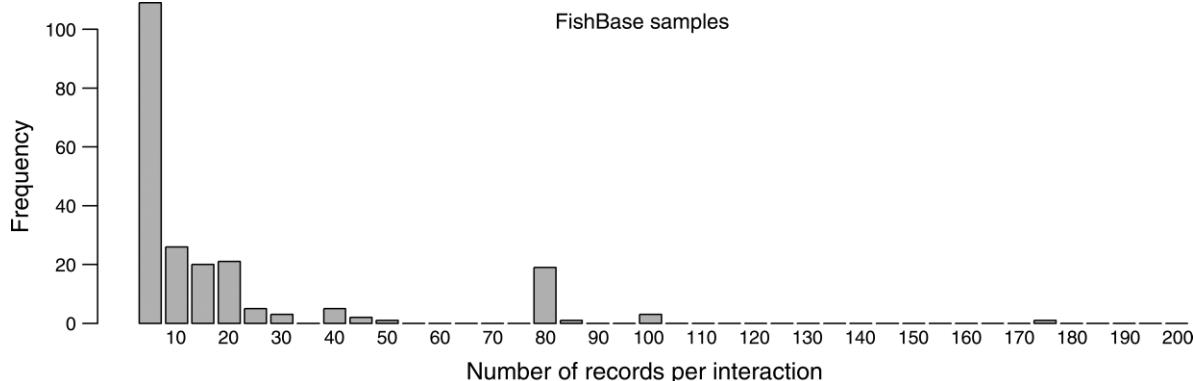


FIG. 2. Number of diet records available from FishBase per predator-prey feeding interaction.

ronmental and physiological stochasticity affecting gut content studies (Deb 1997).

FishBase prey item categories are general and poorly standardized, so we assigned prey items listed for predators to corresponding Atlantis functional groups (Appendix: Table A3). In some cases, we could assign FishBase prey items to specific prey functional groups, depending on the predator in question (Appendix: Table A4). We treated each diet value from FishBase (i.e., a value defining the percentage contribution of prey to the diet of a given predator, resulting from a single study) as a single observation of a “stomach,” regardless of how many stomachs contributed to that FishBase observation. In this way, our field observations numerically dominate the FishBase observations. A large number of predator-prey interactions described in FishBase are based on a small number of studies (Fig. 2), but when combined with our sample data, they allow us to achieve adequate representation across a large number of model functional groups. All diet information reported in Fishbase is provided in terms of percentage of mass or percentage of volume (Froese and Pauly 2008), which we assumed to be equivalent. One could also apply the present methodology to evaluate frequency of occurrence or numbers of prey, but the results would not be useful for trophic dynamic modeling because the energy contribution to the diet of predators could not be determined.

Our goal is to make inferences about p_{ij} from P_{ijk} . We will discuss this procedure in the following section. For researchers who may be interested in using this technique to analyze diet information, please note that we have included an online Supplement containing a simple worked example, the MATLAB source code, and instructions.

Data processing

Even when we included the diet data from FishBase, the mode of the contribution of a prey species to the diet of a predator species was usually zero because there were always a large number of observations that did not contain any of a given prey group (Fig. 3). To deal with this issue, we randomly selected groups of 10 predator stomachs,

averaged their diet compositions, and re-normalized to create proportions. We required that the stomachs be within same functional group, but not necessarily the same species. We then bootstrapped 100 000 samples with replacement following this procedure, and this resulted in a distribution of diet proportions (Fig. 4).

Fitting the data with a multivariate beta (Dirichlet) distribution

We fitted these bootstrapped diet compositions to a Dirichlet distribution. The Dirichlet is a multivariate generalization of the beta distribution (Gelman et al. 2004). The beta distribution is appropriate for estimating diet proportions because it is defined on the interval [0, 1] and can take a variety of shapes.

In what follows, we ignore the subscript on predator (j) because we treat the predators independently in the analysis. To motivate our approach, imagine a situation in which a predator was an obligate predator on only two prey species. Then our goal is to estimate the proportions of species 1 (p_1), and species 2, ($p_2 = 1 - p_1$) in the diet. A natural choice for the probability density of a proportion is the beta density (Hilborn and Mangel 1997, Mangel 2006):

$$f(p_1|\alpha, \beta) = \frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)} p_1^{\alpha-1} (1 - p_1)^{\beta-1} \quad (4)$$

with parameters α and β and where $\Gamma(z)$ is the gamma function (for introductory discussions about the gamma function, see Hilborn and Mangel 1997, Mangel 2006).

If we assume that P_{ik} follows the beta density given by Eq. 4, then

$$E\{P_{ik}\} = \frac{\alpha}{\alpha + \beta}$$

and

$$\text{Var}\{P_{ik}\} = \frac{\alpha\beta}{(\alpha + \beta)^2(\alpha + \beta + 1)} \quad (5)$$

(DeGroot 1970), which can be viewed as a method of moments estimator for the two parameters, given the

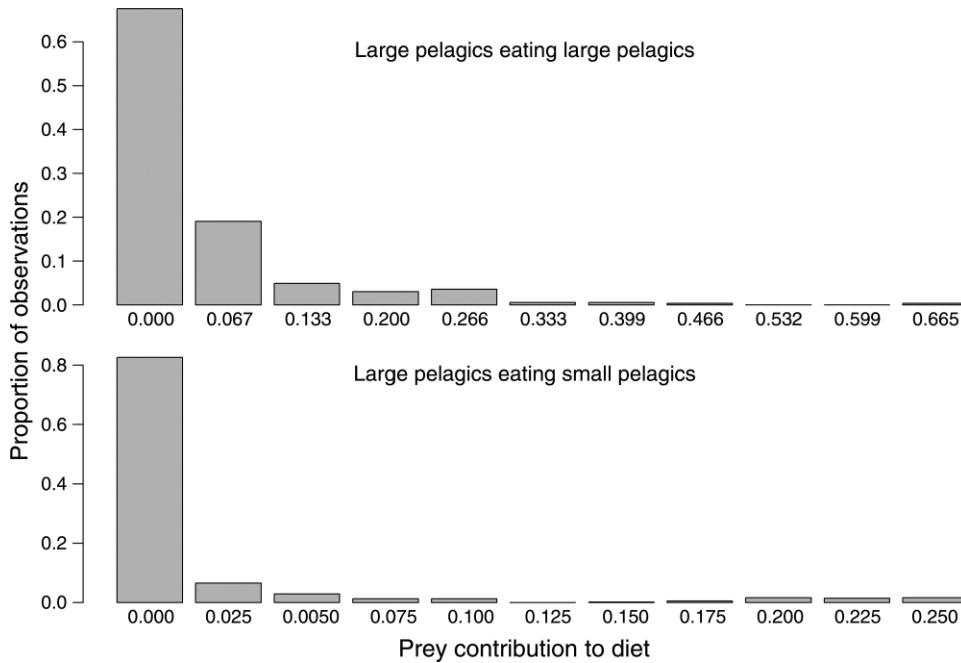


FIG. 3. Proportional diet composition for two predator-prey interactions used as input to the Dirichlet fitting routine. The left-most column indicates the proportion of stomachs with zero large pelagic (upper panel) or small pelagic (lower panel) prey items.

data. Note, too, that we could write

$$f(p_1, p_2 | \alpha, \beta) = \frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)} p_1^{\alpha-1} p_2^{\beta-1} \quad (6)$$

but we would be in error to think of this as a function

with two independent variables, because of the constraint that $p_2 = 1 - p_1$.

The beta density is commonly used in ecological settings as a prior probability density for binomial trials in which the probability of success is unknown (Hilborn

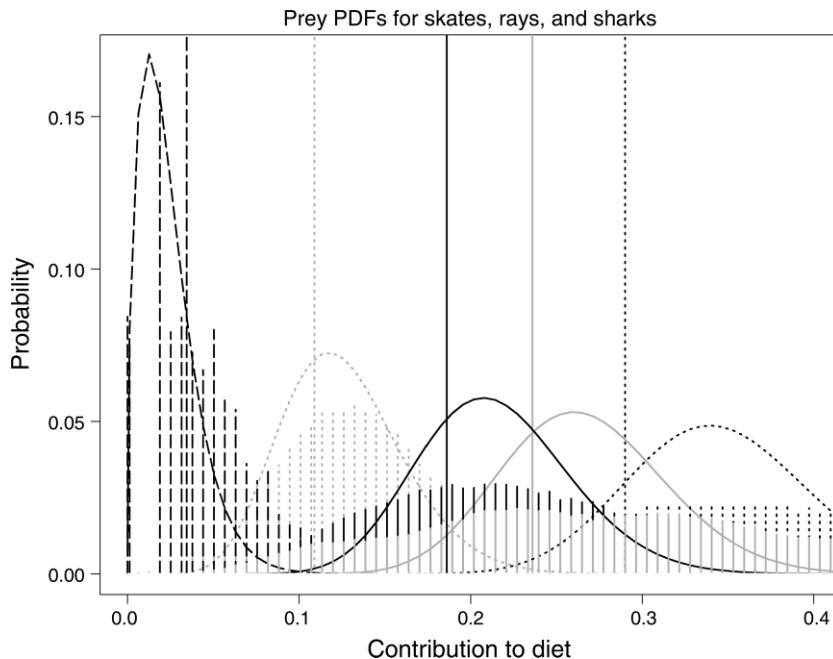


FIG. 4. Bootstrapped diet composition data with fitted probability density functions (PDFs). The top five prey items are shown for the predator group skates, rays, and sharks. From right to left these are: bivalves (black dotted), crabs and lobsters (gray solid), infaunal/epifaunal meiobenthos (black solid), carnivorous macroinvertebrates (gray dotted), and large zooplankton (black dashed). Histograms show bootstrapped data; long vertical lines show the simple average of the diet proportions across stomachs.

and Mangel 1997, Mangel 2006, Clark 2007, Bolker 2008) in the beta-binomial model. We shall generalize and use the beta density in a very different way.

Because we have more than two prey species, we generalize Eq. 6 to the multivariate beta or Dirichlet density:

$$f(p_1, p_2, \dots, p_I | \alpha_1, \alpha_2, \dots, \alpha_I) = \frac{\Gamma(\alpha_1 + \alpha_2 + \dots + \alpha_I)}{\Gamma(\alpha_1)\Gamma(\alpha_2)\dots\Gamma(\alpha_I)} p_1^{\alpha_1-1} p_2^{\alpha_2-1} \dots p_I^{\alpha_I-1} \quad (7)$$

where we are constrained by all $p_i \geq 0$, $\sum_{i=1}^I p_i = 1$ (because the predator species of interest must eat something), and all $\alpha_i > 0$. It is also helpful to define

$$\alpha_0 = \sum_{i=1}^I \alpha_i.$$

Before discussing how we estimate the α_i from the data P_{ik} , it is helpful to briefly discuss the Dirichlet distribution itself. First, integration over any of the $I - 1$ variables in Eq. 7 leads to a beta density for the remaining variable so that the marginal density for the proportion of species l in the diet of the predator is

$$f(p_l | \alpha_l, \alpha_0) = \frac{\Gamma(\alpha_0)}{\Gamma(\alpha_l)\Gamma(\alpha_0 - \alpha_l)} p_l^{\alpha_l-1} (1 - p_l)^{\alpha_0 - \alpha_l - 1}. \quad (8)$$

The Dirichlet distribution also has an extremely natural interpretation for ecological settings, which is worthwhile to consider now. Imagine that the focal predator encounters prey species type i according to a Poisson process with parameter λ_i so that if $N_i(t)$ is the number of prey items encountered in 0 to t :

$$\Pr\{N_i(t) = n | \lambda_i\} = e^{-\lambda_i t} \frac{(\lambda_i t)^n}{n!}. \quad (9)$$

It is well known to ecologists (e.g., Southwood 1966, Hilborn and Mangel 1997, Mangel 2006) that if λ_i has a gamma density,

$$f_\gamma(\lambda_i | c, \alpha_i) = \frac{c^{\alpha_i}}{\Gamma(\alpha_i)} e^{-c\lambda_i} \lambda_i^{\alpha_i-1} \quad (10)$$

then the resulting distribution of encounters follows a negative binomial distribution (found by multiplying the right-hand sides of Eqs. 9 and 10 together and then integrating over λ_i). The mean encounter rate is α_i/c and coefficient of variation of the encounter rate is $1/\sqrt{\alpha_i}$ (Mangel 2006). Thus, c is a measure of time between encounters and α_i is a measure of dispersion (i.e., deviation of encounters from random).

It is less well known (but known by those in the know for a long time; see Johnson [1960] and Mosimann [1962, 1963]) that if we define

$$p_i = \frac{\lambda_i}{\sum_{i'=1}^I \lambda_{i'}} \quad (11)$$

then the proportions have the Dirichlet distribution given by Eq. 7. In summary, if the rate of including prey species i in the diet follows a gamma density with mean α_i/c and coefficient of variation $1/\sqrt{\alpha_i}$ (Mangel 2006), then the relative rate at which species i is included in the diet follows the Dirichlet distribution. Goodhardt et al. (1984) call this the NBD-Dirichlet model. Because our data are biomasses, Eq. 11 should be understood as building intuition, rather than a precise derivation of the Dirichlet.

The moments of the Dirichlet generalize those of the beta given in Eq. 5 (Kotz et al. 2000: Chapter 49):

$$E\{P_i\} = \frac{\alpha_i}{\alpha_0}$$

and

$$E\{P_i^2\} = \frac{\alpha_i(\alpha_i + 1)}{\alpha_0(\alpha_0 + 1)}. \quad (12)$$

Fielitz and Myers (1975) recommend that a method of moments estimate of the parameters is best obtained using the $k - 1$ equations from the expected value and the first equation for the second moment. Thus, if n is the number of stomach samples, we have the following for the first and second moments (\hat{P}_{i1} and \hat{P}_{i2} , respectively) of the proportion of species in the diet i (Kotz et al. 2000:504–505):

$$\hat{P}_{i1} = \frac{1}{n} \sum_{k=1}^K P_{ik}$$

and

$$\hat{P}_{i2} = \frac{1}{n} \sum_{k=1}^K P_{ik}^2. \quad (13)$$

The moment estimators for the parameters are as follows (Fielitz and Myers 1975, Narayanan 1992):

$$\hat{\alpha}_i = \frac{(\hat{P}_{11} - \hat{P}_{12})\hat{P}_{i1}}{\hat{P}_{12} - (\hat{P}_{11})^2}$$

for

$$i = 1, 2, \dots, I - 1 \quad (14)$$

and

$$\hat{\alpha}_I = \frac{(\hat{P}_{11} - \hat{P}_{12}) \left(1 - \sum_{i=1}^{I-1} \hat{P}_{i1} \right)}{\hat{P}_{12} - (\hat{P}_{11})^2}. \quad (15)$$

Eqs. 14 and 15 provide an estimate for the parameters of the Dirichlet, and also a starting point for maximum-likelihood estimation. In light of Eq. 7, the likelihood for a set of data is

$$\begin{aligned}
 L(\alpha_1, \alpha_2, \dots, \alpha_I | \{P_{ik}\}) &= \left(\frac{\Gamma(\alpha_1 + \alpha_2 + \dots + \alpha_I)}{\Gamma(\alpha_1)\Gamma(\alpha_2)\dots\Gamma(\alpha_I)} \right)^n \left(\prod_{k=1}^n P_{1k} \right)^{\alpha_1-1} \\
 &\times \left(\prod_{k=1}^n P_{2k} \right)^{\alpha_2-1} \dots \left(\prod_{k=1}^n P_{Ik} \right)^{\alpha_I-1} \tag{16}
 \end{aligned}$$

where we understand that

$$P_{Ik} = 1 - \sum_{i=1}^{I-1} P_{ik}$$

because of the constraint that the proportions must sum to 1. Taking logarithms, we have

$$\begin{aligned}
 \log\{L(\alpha_1, \alpha_2, \dots, \alpha_I | \{P_{ik}\})\} &= n \log(\Gamma(\alpha_0)) - n \sum_{i=1}^I \log(\Gamma(\alpha_i)) \\
 &+ \sum_{i=1}^I (\alpha_i - 1) \sum_{k=1}^n \log(P_{ik}). \tag{17}
 \end{aligned}$$

Clearly, we cannot make the transition from Eq. 16 to Eq. 17 if any of the proportions are zero. Narayanan (1992) notes that we can write

$$\sum_{k=1}^n \log(P_{ik}) = n \log\left(\prod_{k=1}^n P_{ik}\right)^{1/n}$$

and that $(\prod_{k=1}^n P_{ik})^{1/n} = P_i^{GM}$ is the geometric mean of the stomach proportions for prey type i . We are thus able to rewrite Eq. 17 as

$$\begin{aligned}
 \log\{L(\alpha_1, \alpha_2, \dots, \alpha_I | \{P_{ik}\})\} &= n \log(\Gamma(\alpha_0)) - n \sum_{i=1}^I \log(\Gamma(\alpha_i)) \\
 &+ n \sum_{i=1}^I (\alpha_i - 1) \log(P_i^{GM}). \tag{18}
 \end{aligned}$$

Differentiating the log-likelihood in Eq. 18 with respect to each of the α_i and setting the derivative equal to 0 gives a set of equations for the parameters. Unfortunately, these equations involve the digamma function (the derivative of the gamma function) and the second derivatives of the log-likelihood involve the trigamma function (the second derivative of the gamma function); see Narayanan (1972) or Ronning (1989) for further details. Although these are well-understood functions of classical applied mathematics (Abramowitz and Stegun 1964), they are insufficiently familiar to most ecologists (or statisticians, for that matter); thus we cannot recommend use of analytical maximum-likelihood methods. A possible alternative would be Bayesian methods. Castillo et al. (1997) derive conjugate priors for the Dirichlet, but that involves exponentials of gamma functions.

In consequence, we numerically maximized the likelihood and estimated the $\{\alpha_i\}$. We used the Fastfit Toolbox for MATLAB 6.1 (MathWorks 2003). This package is based on a non-quadratic generalized Newton iteration procedure (Minka 2003, 2004). After estimating all of the parameters, we recovered the marginal beta distribution probability density functions (PDFs), $P_i \sim \text{Beta}(\alpha_i, \alpha_0 - \alpha_i)$, and recorded the maximum-likelihood estimates (MLEs) of mean diet proportions for each interaction along with the uncertainty. We computed the 95% likelihood intervals by integrating under the curve at $(p = 0.025)$ and $(p = 0.975)$. Maximum likelihoods were then normalized for each predator.

We used the Dirichlet fitting procedure for functional groups represented by at least 10 observations; that is, stomachs containing food in the case of field results, individual studies in FishBase, or a combination of field observations and literature values. These functional groups are: drums and croakers, extranjero, flatfish, herbivorous fish, large reef fish, mackerel, skates/rays/sharks, small demersal fish, small migratory sharks, small reef fish, large pelagic fish, and large pelagic sharks. Here, we present diet results for these functional groups only.

As a sensitivity analysis, we also used a simple averaging method for comparison. In particular, the diet mean contributions (\overline{DC}_i) for prey item i , averaging across the set of stomachs (K), can be calculated as

$$\overline{DC}_i = \frac{\sum_{k=1}^K DC_{ik}}{\sum_{k=1}^K \sum_{i=1}^I DC_{ik}}. \tag{19}$$

There is a large (and unknown) amount of uncertainty on these simple averages. We present them here for comparison only, because this simple method is used often within this class of trophic ecosystem model to compute diet values. In our Atlantis model, we have used this simple averaging method only where data were insufficient to apply the Dirichlet method, but results for those groups are not presented here.

RESULTS

The bootstrapped data form distributions that are fitted to the PDFs. We present the predator functional group skates, rays, and sharks as an example because it showed relatively clear prey distributions (Fig. 4). Over 97% of the diet for this group consists of these five prey items, although 28 prey groups were identified in total. These weak linkages may be important, because a rare prey group can be heavily affected by predation of an abundant predator. Simple averages of the proportional diet data, relative to the MLE method, underestimate the four largest contributing prey items and overestimate the minor prey item. Considering all predator-prey interactions studied, the means from these two methods

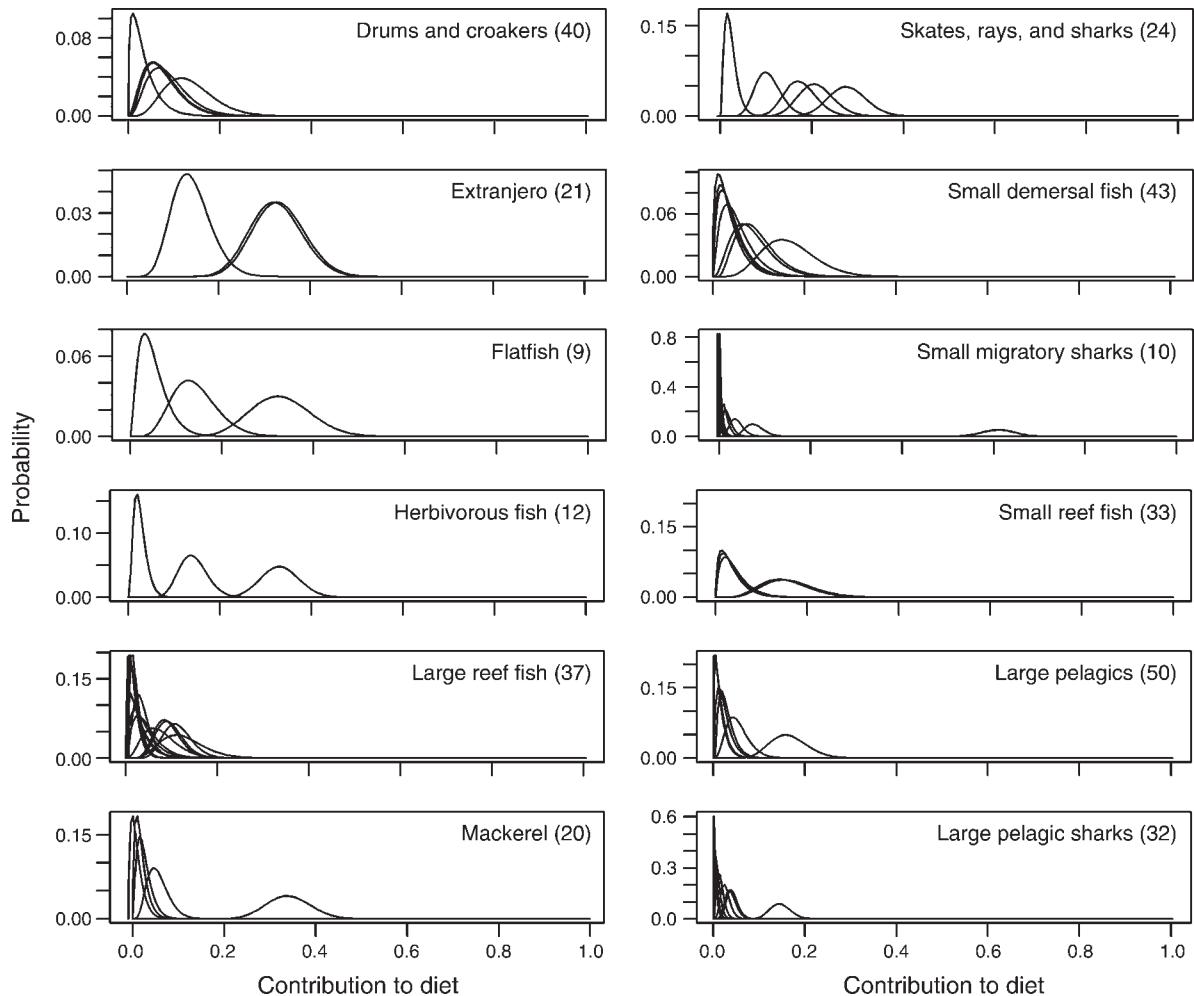


FIG. 5. Marginal beta probability distributions for prey item contribution to the predator diet. The x-axis values have been staggered slightly to show overlapping distributions. Distributions may overlap for some prey items because we have allotted generic FishBase prey categories to multiple prey item functional groups in equal proportions, resulting in identical PDFs. The values in parentheses show the number of observations available for each predator. One observation corresponds to one stomach in the case of field samples, and one study in the case of FishBase data.

(MLE vs. the simple average) are statistically similar (paired t test; $P = 0.91$), but there is significantly greater variance using the MLE method (F test; $P < 0.001$).

The recovered PDFs for all predator functional groups are presented in Fig. 5. Highly aggregated functional groups, such as small demersal fish (consisting of 130 member species), show many more feeding linkages than functional groups representing fewer species, such as the group extranjero. Diversity of prey items measured using the Shannon index (Shannon and Weaver 1949) generally increases with the number of species represented in the predator functional group. However, well-sampled groups with a large number of diet records (e.g., large pelagic fish and large reef fish) show relatively greater diversity in their diets, whereas poorly sampled groups (e.g., small reef fish) show less diversity (Table 2). This is an unavoidable sampling bias that we may need to correct in applications.

Fig. 6 shows the resulting diet composition of the skates, rays and sharks predator group. Diet compositions for 11 other predator groups are provided in accompanying online materials. Of the 246 predator-prey interactions studied, in only four cases does the averaging method yield diet contribution estimates that fall outside of the 95% confidence intervals predicted by the MLE method. The MLE method consistently predicts higher contributions to the predator diet than the averaging method for major prey items (more than ~12% of predator diet as indicated in Fig. 7) and lower contributions for minor prey items.

Fig. 8 compares among predators the relatedness of the final diet compositions derived from the MLE method. Two main predator feeding guilds are evident: a pelagic guild and a demersal guild. Members of the pelagic feeding guild (large pelagics, mackerel, extranjero, and flatfish) all consume the following prey: small

TABLE 2. Shannon diversity of diet composition, number of prey groups, and number of species in the predator functional group for fish in the northern Gulf of California study area.

Predator functional group	Shannon diversity	Number of prey groups	Number of species in predator group	Number of diet records
Large pelagic fish	2.76	23	37	82
Large reef fish	2.71	8	58	37
Small demersal fish	2.14	9	130	43
Drums and croakers	2.02	19	29	40
Herbivorous fish	1.72	49	14	12
Small reef fish	1.71	35	106	33
Skates, rays, and sharks	1.58	20	23	24
Flatfish	1.34	28	33	9
Small migratory sharks	1.23	25	4	10
Mackerel	1.20	17	5	20
Extranjero	1.07	25	2	21

pelagics, hake, penaeid shrimp, blue shrimp, and crabs and lobsters. Although flatfish are demersal, shrimp and small pelagic prey were the largest contributors to their diet, possibly owing to the fact that all of our samples were captured in nearshore areas by gill nets. The diet of flatfish may more closely resemble a demersal feeding guild if we could expand the representation to include older individuals found in deep water.

A demersal feeding guild consists of large reef fish, skates/rays/sharks, small migratory sharks, small demersal fish, herbivorous fish, and small reef fish. All of these groups consume the following prey in some amount: blue shrimp, penaeid shrimp, herbivorous

echinoderms, crabs and lobsters, carnivorous macrobenthos, meiobenthos, bivalves, sessile invertebrates, and sea grass. The demersal elasmobranchs, skates/rays/sharks, and small migratory sharks show a close degree of similarity in feeding habits. The small migratory shark group is composed entirely of the genus *Mustelus*. These animals are demersal feeders that prefer crustaceans (Compagno 1984), so this grouping is consistent with known ecology: crabs and lobsters constitute 70% of their diet, while an additional 17% comes from macro- and meiobenthos groups. The feeding habits of herbivorous fish most closely resemble those of small reef fish, an aggregated group containing some faculta-

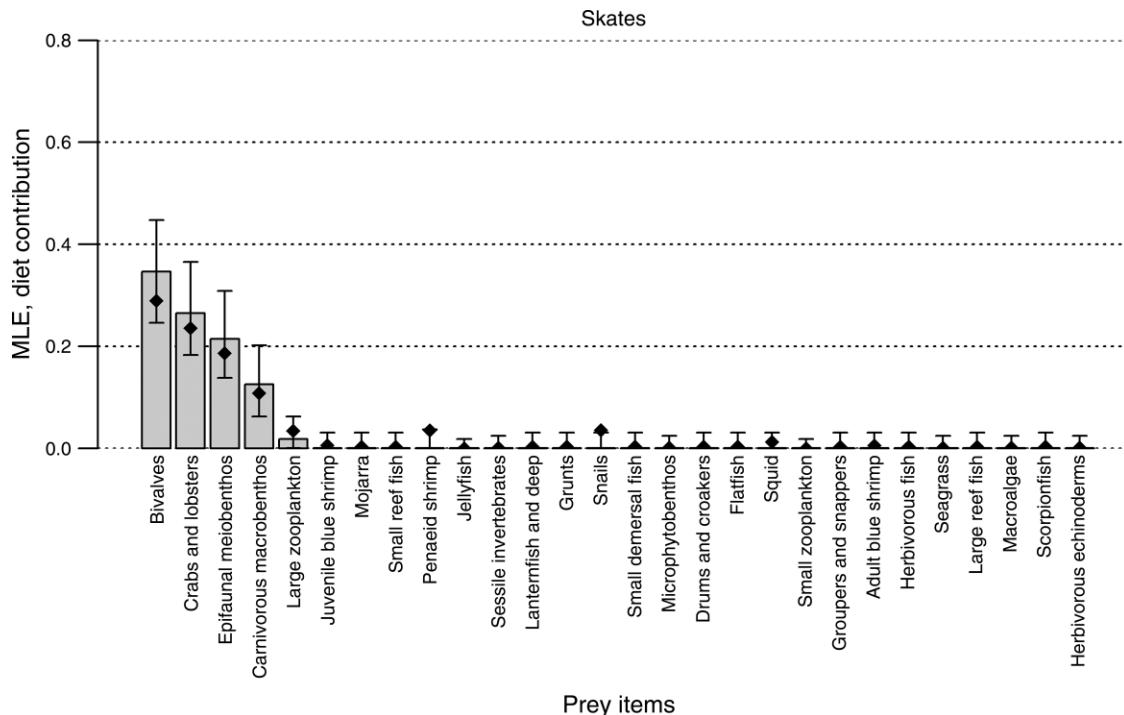


FIG. 6. Maximum-likelihood estimates (MLE) of diet contributions for the predator functional group skates, rays, and sharks derived from marginal beta distributions. Error bars show upper and lower 95% confidence intervals. The figure is arranged from left to right in the order of decreasing contribution to the diet of the predator. Bullet points show results of the simple averaging method. For other predator groups, see Appendix: Fig. A1.

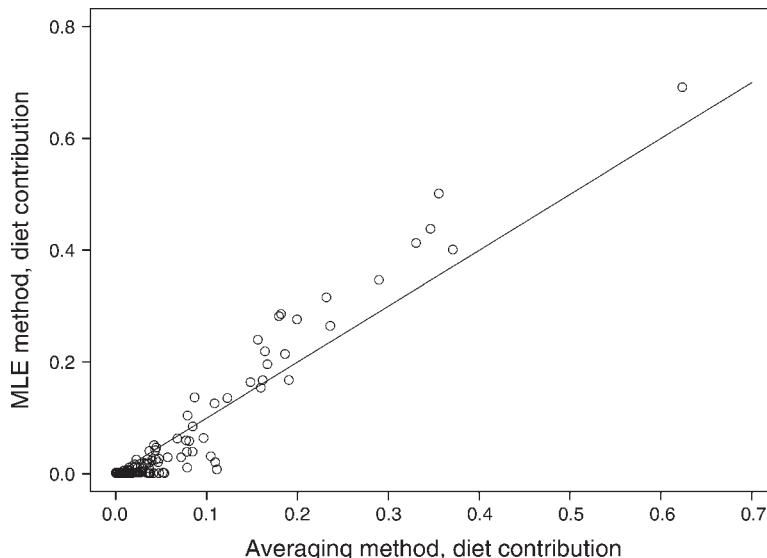


FIG. 7. Contribution to diet for each predator–prey interaction predicted by MLE method (y-axis) and averaging method (x-axis). The line shows the 1:1 ratio.

tive grazers. The outliers, large pelagic sharks and drums/croakers, show similarity in feeding habits to both pelagic and demersal guilds. Drums/croakers were also the most thoroughly sampled functional group in the current field study, so their uniqueness here may reflect more comprehensive seasonal diet data.

We were able to construct a partial food web for the northern Gulf of California using the results of this study (Fig. 9). Only a fraction of the connectances is shown in this figure, yet a dense network of feeding relationships is evident. Also indicated are some instances of cannibalism, which depend strongly on the species aggregation pattern used in functional groups. Stomach sampling was conducted in winter and summer, so this network represents something close to an average annual approximation. In our planned application, as a diet matrix for an ecosystem model, we will gain back most of those seasonal differences, as

interaction rates change in response to seasonal concentrations of predator and prey.

Certain prey groups occur widely in the diets of predators; these universal favorites can be considered the forage base of the ecosystem. Ordered by total volume, the most popular invertebrate prey groups include crabs and lobsters (including stomatopods), penaeid shrimp, meiobenthic invertebrates (e.g., amphipods, annelids, small shrimp), carnivorous macrobenthos (e.g., octopus, sea stars, chitons), and blue shrimp. Popular vertebrate prey items include hake, small pelagics, small reef fish, flatfish, and small demersal fish.

DISCUSSION

Previous trophic models of the Gulf of California (e.g., Arreguín-Sánchez et al. 2002, Morales-Zárate et al. 2004, Lozano 2006, Díaz-Uribe et al. 2007, Rosas-Luis et al. 2008) and other world regions have relied on

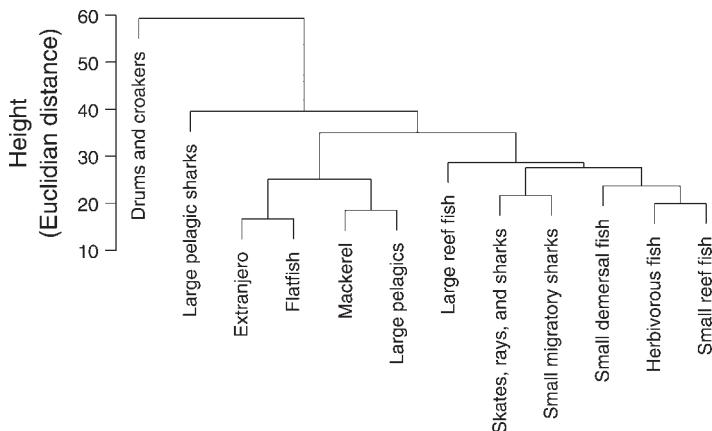


FIG. 8. Hierarchical clustering of maximum-likelihood diet values. Clustering shows feeding guilds based on the relatedness of the final diet composition vectors. The method uses complete linkage clustering. Height represents relative distance in Euclidean space separating clusters (diet dissimilarity).

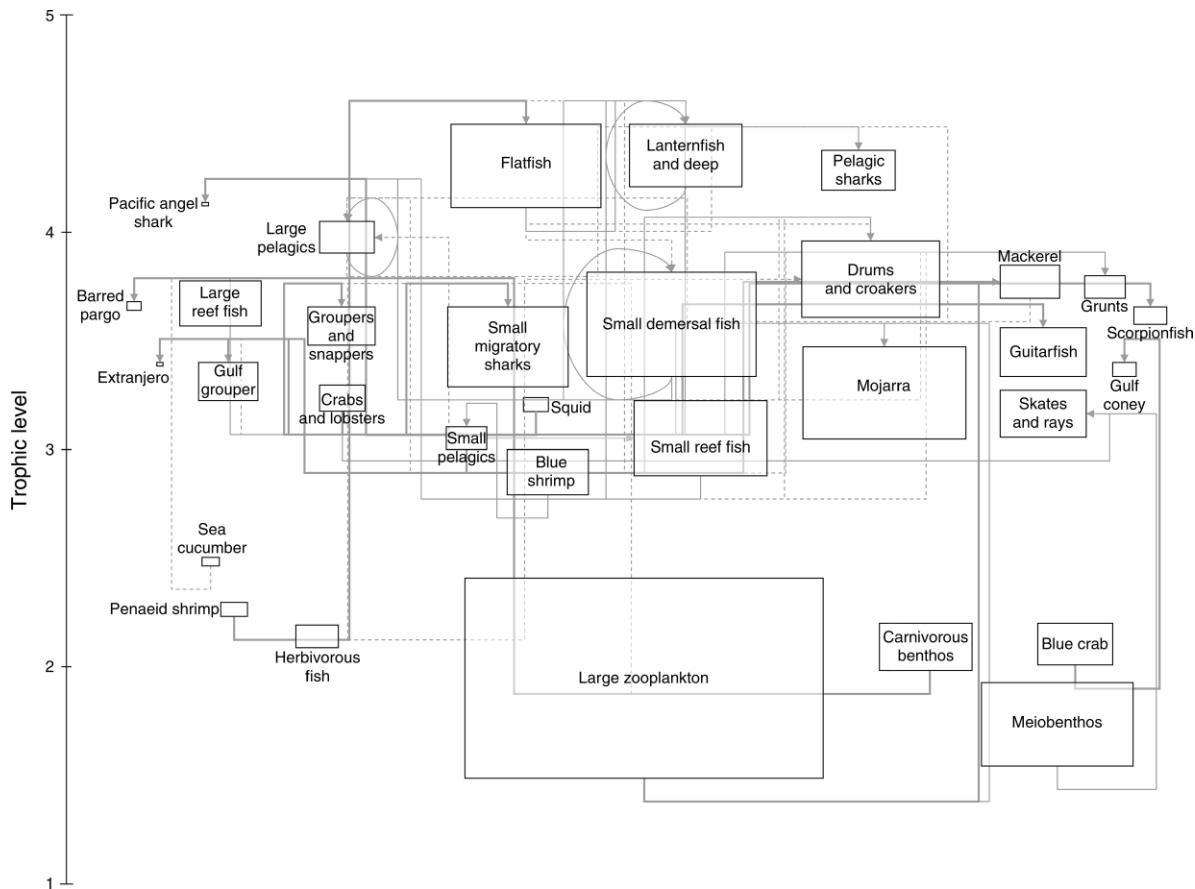


FIG. 9. Food web interactions in the northern Gulf of California informed by the current study. Diet contributions are shown: dashed gray lines, 20–40% of predator diet; thin black lines, 40–60%; thick gray lines, >60%. Connections less than 20% of the diet are not shown. Groups are arranged in the horizontal direction for clarity. The area of each box is directly proportional to the biomass concentration averaged over all areas in the northern Gulf of California (C. Ainsworth, unpublished data). The trophic level of each functional group is presented from literature values (Morales-Zárate et al. 2004, Lozano 2006; also see references in Appendix: Table A1). Aggregation of species into functional groups results in some amount of cannibalism for three groups.

averaging diet compositions across species for aggregate functional groups: the standard method described by Eq. 19. For the predator-prey interactions that we analyzed, the estimates from the simple averaging method are lower than estimates derived from the maximum-likelihood method for major prey items (i.e., those constituting more than ~12% of the predator’s diet, according to Fig. 7), and higher for minor prey items. The averaging method is more influenced by the presence of long tails in the distributions, corresponding to rare instances in which stomachs are full of a single prey item, as may result from opportunistic feeding on prey with patchy spatial distributions, or when potentially important prey are rare in predator stomachs. The maximum-likelihood method discounts these rare events and so it may be a more robust way of analyzing data containing fewer observations.

The difficulty of using sample data containing long tails and many zeros has been long recognized in ecology (e.g., Martin et al. 2005), although aggregating species by functional group alleviates some of these problems.

Nevertheless, in applying these diet data to ecosystem models, it is important to provide an accurate representation of weak links (i.e., minor diet contributions) buffered, if possible, against the random variation found in stomachs and high intra-sample correlation. Any nonzero interaction rate represents a qualitative difference over a zero interaction rate. Atlantis, like Ecopath with Ecosim (EwE: Christensen and Pauly 1992, Walters et al. 1997), will never initiate new diet linkages, so all potential prey items must be accounted for in model construction. Unfortunately, the use of nonlinear functional responses, like those described by the Holling equations to model compensatory/depensatory dynamics and prey switching, makes it difficult for modelers to envisage the strength of interaction once the simulation has varied far from initial conditions. The same can be said for EwE’s foraging arenas (Walters et al. 1997) or Atlantis’ gape-size feeding restrictions (Fulton et al. 2004). A seemingly unimportant prey item can become important to a predator as species’ concentrations change. Moreover, a weak diet link that



PLATE 1. Technicians from CEDO (A. Sánchez-Cruz and R. Loaliza-Villanueva) prepare stomach samples of *Micropogonias megalops*. Photo credit: H. Morzaria Luna.

represents a negligible fraction of a predator's diet may represent a significant source of mortality for the prey. Accurately representing the interaction strength of weak links also plays into model stability and the capacity to assess extinction risk and resilience to perturbation in real systems (McCann et al. 1998, Pinnegar et al. 2005).

The ability to characterize error distributions of diet information will offer a significant advance in the field of trophic marine ecosystem models. Diet relationships are often the most poorly known aspect of ecosystem functioning (Christensen and Walters 2004, Kavanagh et al. 2004); especially when compared to abundance and biomass information, which may be supported by formal sampling or stock assessment, and consumption and production rates, which may be consistent between ecosystems or empirically predictable. The confidence intervals provided by this new statistical method can help to bracket the trophic relationships and constrain ecosystem functioning to within a plausible range. Confidence intervals on our diet estimates also offer heuristic advantage when evaluating seasonal or ontogenetic shifts in diet, as the degree of overlap between periods or groups can help put the differences into perspective. Having the likelihood profile on hand also allows us to make sensible choices for sensitivity analysis.

As computing power continues to increase, more ecosystem models probably will be built to accommodate input of likelihood profiles in the diet matrix. Even

now, several marine ecosystem modeling systems are able to incorporate uncertainty explicitly in this critical area. These systems could directly use the error distributions generated by this statistical method. Examples are Ecoranger, part of EwE (Christensen and Walters 2004), Minimum Realistic Models (Punt and Butterworth 1995), GADGET (Begley and Howell 2004, Begley 2005), and multispecies statistical models (Kinzey and Punt 2009). The new method presented here could also be used in modeling terrestrial food webs in mass-balance models (Krebs et al. 2002, Ruesink et al. 2002), contaminant transport models (Whicker and Kirchner 1987), and bioaccumulation models (Armitage and Gobas 2007). The statistical technique, in fact, may be more useful for simple terrestrial food webs, where each interaction has the potential to influence system behavior, as is the case with marine food webs featuring wasp-waist structure or keystone species. In these cases, small numbers of interaction rate parameters have overriding influence on ecosystem dynamics.

The maximum-likelihood method presented here has some disadvantages compared to the simple averaging method in Eq. 19. First, statistically estimating the mean and variance of each prey contribution to a predator group's diet requires a larger sample size than the simple averaging method. This could necessitate the use of data from literature to supplement field sampling. In using literature values, additional assumptions may be required to reconcile different species groupings and

imprecise taxonomies, as was done here. However, such data requirements are common in sophisticated methods for estimating diet compositions, such as Bayesian mixing models (Moore and Semmens 2008, Parnell et al. 2008), particle-size relationships (Silvert 1993, Begley 2005), and gape-size models (Fulton et al. 2004, Ainsworth et al. 2007). Second, the Dirichlet function is subject to assumptions similar to those of a Poisson or negative binomial distribution (Mangel 2006). Finally, this method assumes that functional groups are homogeneous, that differential digestion and evacuation rates of prey can be ignored, and that the probability of prey capture follows the uniform, unimodal, or bimodal forms of the beta distribution (an important consideration when aggregating species).

We have investigated only a small portion of the food web in the northern Gulf of California, and have identified a dense network of connections. Because of logistic limitations in sampling, we have restricted the analysis to the level of functional groups. In doing so, and in using relatively coarse species aggregations, we may have underestimated the true connectivity of the system (Paine 1988), potentially missing critical links to ecosystem function. Likewise, focusing on adult age classes was a sampling convenience, but expanding the analysis to include different life stages would reveal new connections and links potentially occurring during sensitive periods of organism development.

Identifying feeding relationships can help us to predict ecosystem effects of fisheries and management schemes. For example, the efficacy of vertical zoning policies in marine protected areas depends greatly on the degree of linkage between the demersal and pelagic realms (Grober-Dunsmore et al. 2008), so the presence of generalist predators (such as large pelagic sharks and, potentially, sciaenids in the case of the northern Gulf of California) could impact the success of such measures. Similarly, removing specialists through the activity of fisheries could lead to trophic cascades that have far-reaching impacts (Lilly et al. 2000, Daskalov 2002). Eroding the forage base of the ecosystem is also risky. The two most significant fisheries in the Gulf of California pursue shrimp and sardines (Mexico 2006), both of which occur widely in the diets of predators and may be critical to ecosystem functioning. Unfortunately, knowledge of diet relationships alone may not be sufficient to forecast human effects. Quantitative ecosystem responses must be estimated using trophic dynamic modeling to account for synergistic activity and nonlinear feeding relationships.

CONCLUSION

Trophic ecosystem models are designed to generate advice that will improve ecosystem-based management (EBM). Even in data-poor regions such as the northern Gulf of California, our work shows that it is possible to construct a detailed representation of the food web through targeted acquisition of data, and by relying on

tools that can integrate data collected from other world regions. The products of ecosystem models have only recently been used by managers (e.g., Fulton et al. 2007). One of the key limitations has been an inadequate characterization of uncertainty (Plagányi 2007). There are, of course, many sources of uncertainty in complex ecosystem models; however, the methods presented here for characterizing the uncertainty of diet estimates are an important step forward. Our specific approach is applicable to numerous modeling systems; it should help us to move toward broader application of trophic modeling as a way of satisfying the technical requirements of EBM. We are reminded of E. O. Wilson's (1998:269) observation that "we are drowning in information" and that successful conservation and resource management depend ultimately on the rigorous synthesis of information. We hope the approach that we have developed here provides a template for others attempting to integrate other kinds of information for use in a wide variety of applications.

ACKNOWLEDGMENTS

We gratefully acknowledge Brice Semmens at Northwest Fisheries Science Center (NWFS) for helpful discussions and for providing MATLAB code to fit gut content data to the Dirichlet distribution. We also thank Bethann Pflugeisen for discussions on the Dirichlet distribution and Nick Tolimieri at NWFS for discussions on the statistical analysis. Researchers from Centro Intercultural de Estudios de Desiertos y Océanos (CEDO) conducted field and laboratory work (Ángeles Sánchez-Cruz, Rene Loaiza-Villanueva, Sergio Pérez-Valencia, and Verónica Castañeda Fernández de Lara) as well as researchers from Comunidad y Biodiversidad (COBI) (Nabor Encinas, Mario Rojo, and Cesar Moreno) and the Centro de Investigaciones Biológicas de Noroeste (CIBNOR-Guaymas). This study was funded by a grant from the David and Lucille Packard Foundation.

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APPENDIX A

Maximum-likelihood estimates by species and additional references cited from FishBase (*Ecological Archives* A020-082-A1).

SUPPLEMENT

Maximum-likelihood estimation procedure for diet composition based on the Dirichlet function: a simple example (*Ecological Archives* A020-082-S1).