

# Diet composition and foraging ecology of U.S. Pacific Coast groundfishes with applications for fisheries management

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**Abstract** Determining the prey composition and foraging habitats of U.S. Pacific Coast groundfishes are specified management directives that have not received much scientific attention. To address this knowledge gap, we conducted a meta-analysis of the feeding ecology of 18 commercially important species and their life stages during a recent review of Pacific Coast groundfish essential fish habitat. A Major Prey Index was developed to evaluate relative importance among 47 prey taxa. Based on this metric, unidentified teleosts, euphausiids, and brachyuran crabs were the most important prey groups. When 14 generalized prey categories were used, fishes represented the dominant taxon (mean % weight or volume = 32.3) followed by shrimps (11.5), crabs (10.0), and euphausiids (9.5). PERMANOVA results indicated that species-specific

differences were the primary source of dietary variability among tested variables (life stage, functional group, taxonomic group). Pacific Coast groundfishes mainly were characterized as mesopredators with estimated trophic levels ranging from 3.4 to 4.2. Foraging habitats differed significantly among functional (benthic, demersal, pelagic) and taxonomic (elasmobranch, roundfish, rockfish, flatfish) groups. Using hierarchical agglomerative cluster analysis, we identified a significantly distinct trophic guild that consumes mainly polychaetes and hard-shelled molluscs (juvenile, juvenile–adult Dover Sole; juvenile–adult English Sole) and another that specializes on euphausiids (juvenile Pacific Hake; juvenile–adult Darkblotched Rockfish). Our findings filled substantial data gaps in the trophic ecology and habitat-based management of commercially important species and can be used to inform future reviews of Pacific Coast groundfish essential fish habitat.

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## Introduction

Ecosystem approaches to marine fisheries management require an ecological understanding of exploited species and their communities. One emerging technique is the use of food web models, which incorporate diet composition information, to examine a variety of trophic

dynamics. Because food web models can be used to determine and evaluate sources of variability in mortality and production that are not typically included in single-species stock assessments, their application may improve the management of exploited stocks (Gaichas et al. 2010, 2011; Link et al. 2011). One such application is the incorporation of steady-state mass-balance model outputs of the Gulf of Alaska food web for consideration in groundfish stock assessments (Zador 2014). However, a lack of ecological data, such as diet composition data needed for food web models, is a common limitation that has hampered our ability to implement ecosystem-based fishery management (EBFM; Essington and Punt 2011).

Determining the prey composition and foraging habitats of federally managed aquatic species in the U.S., such as Pacific Coast groundfishes, is a specified component of the Magnuson-Stevens Fishery Conservation and Management Act (United States Department of Commerce 1996). Food habits information has been used to assess consumption impacts (Overholz and Link 2007; Link and Sosebee 2008) and fishing effects (Garrison and Link 2000; Link and Garrison 2002) on the trophic dynamics Atlantic Coast groundfish stocks. This type of information is, however, limited for many regions, including the Pacific Coast. Ecological, multi-species approaches to Pacific Coast groundfish management currently focus on determining habitat associations and establishing restricted-take zones or marine protected areas (Pacific Fishery Management Council 2016). Ecosystem approaches to management that incorporate food web interactions are, however, currently being developed (Kaplan and Levin 2009; Kaplan et al. 2013).

The need for higher levels of taxonomic specificity in prey categories was a primary recommendation in a recent review of essential fish habitat (EFH) for Pacific Coast groundfishes (Pacific Fishery Management Council 2014), and can improve the accuracy of food web models. Federal regulations concerning EFH state that “fishery management plans should list the major prey species” of managed groundfishes, and that “actions that reduce the availability of a major prey species” may be considered adverse effects to EFH.<sup>1</sup> Once major prey species have been identified, potentially negative impacts (e.g., harvesting, habitat alteration) to them can be determined and monitored. However, no definition of what

constitutes a “major” prey species is provided in the EFH regulations, and syntheses of groundfish food habits literature are limited and highly generalized (e.g., DuFault et al. 2009; Szoboszlai et al. 2015).

In order to address these data limitations, we investigated aspects of trophic ecology for a variety of species and their life stages (species and/or life stages), and for the overall assemblage of Pacific Coast groundfishes. Five primary research questions were posed: 1) What are the diet compositions, trophic levels, and foraging habitats of Pacific Coast groundfish species and/or life stages? 2) What are the major prey taxa and foraging habitats of Pacific Coast groundfishes? 3) What are the main sources of dietary variation for Pacific Coast groundfish species and/or life stages? 4) Does diet composition, trophic level, and foraging habitat differ among functional or taxonomic groups? and 5) Can trophic guilds of Pacific Coast groundfish species and/or life stages be distinguished?

## Materials

### Data collection

We conducted a meta-analysis of the quantitative diet composition data of 18 federally managed Pacific Coast groundfish species (Table 1) from available food habits literature. Species were selected based on a combination of factors, including management priority, the relative amount of diet composition information, ecological and taxonomic diversity, and the relative number of species among established management categories. Selected groundfishes represent a small portion of the 117 species that are included in the fisheries management plan (Pacific Fishery Management Council 2014). Therefore, results should not be applied beyond the taxonomic or functional groups designated in this study.

Relevant literature (e.g., peer-reviewed publications, student theses, technical reports) was identified from summarized life history information in three publications (McCain et al. 2005; Love 2011; Pacific Fishery Management Council 2012), from a search of bibliographic databases (i.e., Aquatic Science and Fisheries Abstracts, BIOSIS, Web of Science, Zoological Record), and by cross-referencing citations in found literature. The geographic range of this analysis was restricted to the waters off the continental U.S. Pacific Coast; literature on groundfish diets specifically from other regions was not considered. However, studies that included some fish

<sup>1</sup> EFH Regulatory Guidelines in Code of Federal Regulations 50 CFR 600.815(a) (7).

**Table 1** Common name, scientific name, taxonomic group, and functional group (based on general occurrence in the water column) of 18 Pacific Coast groundfish species that were included in this study

| Common name           | Scientific name                   | Taxonomic group | Functional group |
|-----------------------|-----------------------------------|-----------------|------------------|
| Black Rockfish        | <i>Sebastes melanops</i>          | Rockfishes      | Demersal         |
| Brown Rockfish        | <i>Sebastes auriculatus</i>       | Rockfishes      | Demersal         |
| Copper Rockfish       | <i>Sebastes caurinus</i>          | Rockfishes      | Demersal         |
| Darkblotched Rockfish | <i>Sebastes crameri</i>           | Rockfishes      | Demersal         |
| Dover Sole            | <i>Microstomus pacificus</i>      | Flatfishes      | Benthic          |
| English Sole          | <i>Parophrys vetulus</i>          | Flatfishes      | Benthic          |
| Greenstriped Rockfish | <i>Sebastes elongatus</i>         | Rockfishes      | Demersal         |
| Lingcod               | <i>Ophiodon elongatus</i>         | Roundfishes     | Demersal         |
| Longspine Thornyhead  | <i>Sebastolobus altivelis</i>     | Rockfishes      | Benthic          |
| Pacific Hake          | <i>Merluccius productus</i>       | Roundfishes     | Pelagic          |
| Pacific Spiny Dogfish | <i>Squalus suckleyi</i>           | Elasmobranchs   | Pelagic          |
| Petrale Sole          | <i>Eopsetta jordani</i>           | Flatfishes      | Benthic          |
| Rosethorn Rockfish    | <i>Sebastes helvomaculatus</i>    | Rockfishes      | Demersal         |
| Sablefish             | <i>Anoplopoma fimbria</i>         | Roundfishes     | Demersal         |
| Sand Sole             | <i>Psettichthys melanostictus</i> | Flatfishes      | Benthic          |
| Sharpchin Rockfish    | <i>Sebastes zacentrus</i>         | Rockfishes      | Demersal         |
| Starry Skate          | <i>Raja stellulata</i>            | Elasmobranchs   | Benthic          |
| Yelloweye Rockfish    | <i>Sebastes ruberrimus</i>        | Rockfishes      | Demersal         |

sampled in Canada or Mexico were included when results from U.S. waters could not be differentiated.

The following information was extracted from each study and used as a basis for diet characterization and subsequent analyses: collection year, collection month, study region, sample size, collection method, collection depth, length range and maturity stage of fish, and diet metric. Only studies that reported quantitative estimates of prey weight or volume were included in our analysis because these metrics generally track energetic importance of prey taxa (Hyslop 1980; Cailliet et al. 1986). By contrast, frequency metrics (e.g., percent frequency of occurrence, %FO = number stomach samples in which a prey taxon occurs/total number of stomach samples \* 100) and relative number of a prey taxon typically are a proxy for feeding behavior, but do not necessarily represent the relative energetic contribution of each prey type in a fish's diet (Hyslop 1980; Cailliet et al. 1986). Weight or volume data, however, underestimate the relative contribution of easily digestible, soft-bodied prey (e.g., gelatinous zooplankton such as jellyfishes, ctenophores, and salps; polychaetes; small crustaceans or those with thin carapaces). Soft-bodied prey taxa therefore will be under-represented in diet composition calculations, as compared

to fishes and decapod crustaceans, which typically are more abundant in groundfish diets (Love 2011). Compound measures that incorporate weight or volume (such as Index of Relative Importance [IRI], Pinkas et al. 1971) were considered only if volume or weight were not individually reported.

#### Diet composition

Weight or volume of each prey category, as originally designated in a study, was converted to a percentage and then reclassified among 47 prey categories (Table 2; National Marine Fisheries Service 2013) to standardize diet composition estimates. Insufficient sampling can result in poor estimates of diet composition (Ferry and Cailliet 1996) and standard transformations can over-generalize relative variability among various sample sizes. A weighting scheme therefore was calculated to synthesize diet composition data when more than one study was available for a species and/or life stage. This scheme was developed by evaluating prey accumulation curves using individual-based diet data for five federally managed Pacific Coast skate species (Big, Longnose, California, Starry, Sandpaper; [Bizzarro 2015]), because

**Table 2** Abbreviations associated with high and low levels of taxonomic distinction among prey categories. Definitions are specific to high levels of taxonomic distinction

| Prey category   | High      | Low    |
|---|-----------|--------|
| Agnathan fishes                                       | AGNATH    | FISH   |
| Poachers  | AGON      | FISH   |
| Ammodytidae   | AMMO      | FISH   |
| Amphipods   | AMPH      | AMPH   |
| Axiidae   | AXIID     | CRUST  |
| Bivalves  | BIVAL     | MOLL   |
| Cephalopods, unidentified                             | CEPH      | CEPH   |
| Chondrichthyan fishes                                 | CHOND     | FISH   |
| Clupeidae   | CLUP      | FISH   |
| Gadiformes  | CODS      | FISH   |
| Copepods  | COPE      | COPE   |
| Crabs, unidentified                                   | CRAB      | CRAB   |
| Anomuran crabs  | CRAB A    | CRAB   |
| Brachyuran crabs                                      | CRAB B    | CRAB   |
| Other and unidentified crustaceans                    | CRUST     | CRUST  |
| Cuttlefishes  | CUTT      | CEPH   |
| Other Decapods  | DECA      | CRUST  |
| Echinoderms   | ECHINO    | ECHINO |
| Engraulidae   | ENGR      | FISH   |
| Euphausiids   | EUPH      | EUPH   |
| Pleuronectiformes                                     | FLAT      | FISH   |
| Gastropods  | GAST      | MOLL   |
| Herrings  | HERR      | FISH   |
| Hexagramidae  | HEX       | FISH   |
| Invertebrates, unidentified                           | INV       | INV    |
| Isopods   | ISO       | AMPH   |
| Jellyfishes and other unid.<br>Gelatinous zooplankton | JELL      | JELL   |
| Loligonidae   | LOLI      | CEPH   |
| Bivalves or Gastropods, unidentified                  | MOLL      | MOLL   |
| Myctophidae   | MYCT      | FISH   |
| Mysids  | MYSID     | MYSID  |
| Octopi  | OCTO      | CEPH   |
| Squids (Oegopsina)                                    | OEGO      | CEPH   |
| Osmeriformes  | OSMER     | FISH   |
| Polychaetes   | POLY      | POLY   |
| Rockfishes  | ROCK      | FISH   |
| Sardines  | SARD      | FISH   |
| Scorpaeniformes, other and identified                 | SCORP     | FISH   |
| Sculpins  | SCULP     | FISH   |
| Shrimps, unidentified                                 | SHRIMP    | SHRIMP |
| Caridean shrimps                                      | SHRIMP C  | SHRIMP |
| Penaeid and Sergestid shrimps                         | SHRIMP PS | SHRIMP |
| Squids, unidentified                                  | SQUID     | CEPH   |
| Other and unidentified Teleosts                       | TELE      | FISH   |
| Tunicates   | TUN       | INV    |
| Other marine worms<br>(e.g., Nematoda, Sipuncula)     | WORM      | POLY   |
| Zoarcidae   | ZOAR      | FISH   |

such data were unavailable for the teleost and shark species included in this study. Prey accumulation curves were generated for a variety of sample sizes using the 47 described prey categories (Table 2; Ferry and Cailliet 1996) and the Mao Tao expected richness function in Estimate-S (Colwell 2013). Linear regression was applied to calculate the slope ( $b$ ) of the curve terminus and determine if the curve approached an asymptote ( $b < 0.05$ ) (Bizzarro et al. 2007, 2009). The relative slopes of prey accumulation curves were compared at different sample sizes and among species. Based on these comparisons, the following weighting scheme was created and applied: if the number of samples =1, data were not weighted; 2–10 samples (weighted 2×); 11–25 samples (4×); 26–50 samples (8×); 51–100 samples (16×); 101–500 samples (32×); > 500 samples (64×). Sample size sufficiency typically was achieved at 101–500 samples; therefore, any studies with >500 samples were weighted equally.

When possible, diet composition data were calculated by life stage (i.e., juvenile or adult). Juveniles ranged from post-settlement individuals to subadults (i.e., immature). Mature individuals were considered adults. Life stages were directly assigned from the literature if maturity information was reported. In the absence of such information, life stage was assigned based on published size-at-maturity information for a species of interest (Appendix 1). When multiple size-at-maturity estimates were available, the cut-off value was chosen from the reproductive study that was conducted in closest proximity to the relevant food habits study. When assigned from the literature, juveniles were < length at first maturity and adults were  $\geq$  size at 100 % maturity. If size composition or life stage was not provided, or when reported sizes spanned the estimated range from first to 100 % maturity, diet was analyzed for combined juvenile-adult life stages.

#### Trophic level and foraging habitat

Trophic level and foraging habitat were calculated for each species and/or life stage using the synthesized diet composition data. Trophic levels were estimated using a formula provided by Cortés (1999):

$$TL_k = 1 + \left( \sum_{j=1}^n P_j * TL_j \right),$$

where  $TL_k$  = trophic level of species and/or life stage  $k$ ,  $P_j$  = proportion of prey category  $j$  in the diet of species  $k$ ,

$n$  = total number of prey categories, and  $TL_j$  = trophic level of prey category  $j$ . Trophic level estimates for prey categories were taken from Ebert and Bizzarro (2007). Foraging habitat was calculated using a modified version of the trophic level formula:

$$FH_k = \left( \sum_{j=1}^n P_j * H_j \right),$$

where  $FH_k$  = foraging habitat of species and/or life stage  $k$ ,  $P_j$  = proportion of prey category  $j$  in the diet of species  $k$ ,  $n$  = total number of prey categories, and  $H_j$  = habitat of prey category. Three categories were used to assign prey to a general region of occurrence (i.e., functional group): 1 = benthic (on or in the seafloor), 2 = demersal ( $\leq \sim 5$  m from the seafloor), 3 = pelagic ( $> \sim 5$  m from the seafloor). Prey taxa were assigned a primary and, when appropriate, secondary habitat designation based on a review of pertinent literature. Primary habitats were weighted twice as much as secondary habitats. These same classifications also were used to assign groundfishes to general regions of occurrence, or functional groups.

#### The Major Prey Index and its calculation

Five metrics were used to assess prey importance for our selected groundfish species, including: 1) Mean % Diet Composition (Mean), 2) Median % Diet Composition (Median), 3) Prey-Specific Abundance (PSA; Amundsen et al. 1996), 4) Minimum Diet Contribution (Minimum; Minimum  $\geq 20\%$ ), and 5) % Frequency of Occurrence (FO). These metrics were chosen because they are commonly used to summarize diet composition data and complement each other in collectively estimating prey importance.

To account for potential inaccuracies in diet composition estimates, the following data quality metrics were established: 1) Scientific Coverage, 2) Sample Size, 3) Spatial Coverage, and 4) Temporal Coverage. Scientific Coverage was the number of studies ( $n$ ) conducted on a species and/or life stage, weighted as follows:  $n = 1$  (unweighted),  $n = 2-3$  (weighted 2 $\times$ ),  $n = 4-6$  (3 $\times$ ),  $n = 7-9$  (4 $\times$ ),  $n \geq 10$  (5 $\times$ ) Sample Size ( $N$ , total number of stomach samples with prey items among all studies) was weighted as previously described. The distribution of each groundfish species was determined (Love et al. 2005), four regions were defined (Southern California, from the Mexican border to Monterey; Northern California, north of Monterey to the Oregon border; Oregon;

Washington), and Spatial Coverage was calculated as number of regions with diet information/number of regions in which a species occurs. Temporal Coverage was calculated in the same manner as Spatial Coverage, among the following categories: 1)  $\leq 1970$ , 2) 1971–1985, 3) 1986–2000, and 4) 2001–2015. Ranks of data quality for each category were standardized (0.00–1.00 scale) and summed. Overall data quality for a species ( $i$ ) was calculated as: value of summed data quality ranks for species  $i$ /greatest value of summed data quality ranks among all species. Overall data quality was presented on a relative scale, with the most robust data set assigned a value of 1.00. Relative abundance metrics (i.e., Mean, Median, PSA) for each species were adjusted for data quality using the overall data quality ranks and summed to produce overall Mean, Median, and PSA metrics for all groundfishes.

The five diet metrics were standardized (0.00–1.00) and evaluated for redundancy before being summed to create a Major Prey Index (MPI). Pearson's Correlation Coefficient ( $r$ ) was used to determine the degree of correlation, and redundant metrics ( $r > 0.70$  and  $P < 0.05$  with two or more other metrics) were removed from analyses. Raw values were ranked for each non-redundant metric, summed across metrics for each prey taxon, and scaled to a range of 0.00–1.00 using the maximum aggregate value ([aggregate value of a prey category – minimum aggregate value among all prey categories]/maximum aggregate value among all prey categories). This process precluded any overwhelming contributions by particular prey taxa and enabled the contribution of each taxon to be compared on relative terms. Although EFH legislation refers to major prey “species,” the MPI is used here to describe major prey “taxa” because available data did not lend itself to more specific taxonomic designations.

A randomization test (Manly 2006), iterated 9999 times, was used to determine the probability of generating the observed MPI values for each prey taxon. The ranked values among diet metrics constituted the set of observed values from which to draw, because ties limited the possible number of ranks among metrics to fewer than the number of prey categories. The expected values generated from the randomization test could fall outside the distribution of observed values; therefore, expected values were scaled by observed values. Prey taxa with MPI values significantly greater than expected by chance ( $P < 0.05$ ) were considered to be major prey. To facilitate accurate use of the MPI, all metric calculations and the

determination of major prey taxa were automated through the use of an R script and a reference data set that are provided (see [Online Resource](#)).

#### Sources of dietary variability

PERMANOVA was used to determine the best combination of response variables to explain the observed dietary variability in each assemblage. We summarized diet composition data among 14 generalized categories (Table 2), used a Bray-Curtis dissimilarity index (Bray and Curtis 1957) as the basis for matrix calculations, and permuted the model 9999 times. Variables (and their factors) included: SPECIES, LIFE STAGE (Juvenile, Juvenile–Adult, Adult), TAXONOMIC GROUP (elasmobranch, rockfish, roundfish, flatfish), and FUNCTIONAL GROUP (benthic, demersal, pelagic). PERMANOVA models were constructed independently for each variable to determine significant sources of dietary variability and their relative explanatory power. A final model then was calculated using forward, step-wise model selection to determine the best combination of variables to explain the observed variability in the data set. Interaction effects between variables and sample metrics also were tested to determine the influence of number of studies or number of samples among studies. Regional and temporal variables were not included in PERMANOVA models because data were insufficient to analyze the effect of their interactions with the selected variables. Including regional and temporal variables independently could yield misleading results because of dissimilar underlying species compositions.

Permutation tests of multivariate group dispersions were conducted to determine if variance differed significantly among categories for any response variable (Anderson 2006). Significant differences indicate high among-group variability that can bias *P*-value interpretations and increase the chance of Type-1 error. These, and all multivariate analyses, were conducted using the vegan package in R (v. 3.1.2) (Oksanen et al. 2013).

#### Trophic level and foraging habitat comparisons

Trophic level and foraging habitat indices of taxonomic and functional groups were compared using ANOVA. Index values for all groupings were homoscedastic and exhibited no extreme departures from normality. Differences in mean trophic level and foraging habitat values were compared among species groups using one-way

ANOVA on raw data because not all functional groups were represented for each taxonomic group.

#### Characterization of trophic guilds

We used hierarchical agglomerative cluster analysis to determine trophic guilds among species and/or life stages based on similar diet compositions. Calculations were conducted on the more generalized diet composition data set, using Ward's Minimum Variance technique (Ward 1963), and a Bray-Curtis similarity matrix. Cluster solutions were evaluated using agglomerative coefficients (to measure the clustering structure of the dataset), cophenetic correlations (a measure of how similar two objects must be in order to be grouped into the same cluster, which we used to evaluate the goodness-of-fit between the input data and cluster output), and randomization tests (to determine significant clusters). Trophic guilds comprised species and/or life stages that formed statistically significant clusters.

## Results

#### Diet composition

Forty-eight sources of quantitative diet composition information were used in this study of trophic ecology of 18 Pacific Coast groundfish species (Appendix 2). One-third of the species (Pacific Hake, Sablefish, Pacific Spiny Dogfish, English Sole, Dover Sole, Black Rockfish) accounted for 87 % of 17,611 total stomach samples. By contrast, there were <65 stomach samples for each of five rockfish (Darkblotched, Greenstriped, Rosethorn, Sharpchin, Yelloweye) and one flatfish (Petrale Sole) species. Standardized diet compositions were calculated for 31 species and/or life stages mostly from combined juvenile and adult samples (Table 3). Diet composition for juveniles was calculated for 12 species, but diet composition for the adult life stage was available only for three species and generally was represented by low sample sizes. Diet composition, trophic level, and foraging habitat were estimated for adult Copper Rockfish, but this species and/or life stage was not included in subsequent analyses because it was represented by a single stomach sample.

Most diet composition data for Pacific Coast groundfishes ranged from Northern California to Washington, more than half of the species-specific data were

**Table 3** Standardized diet compositions of 18 species of Pacific Coast groundfish and their life stages (when possible). Included are: the number of studies (*n*), total sample size among studies (*N*), trophic level (TL), and foraging habitat (FH). Table 2 indicates how the 47 high-resolution prey categories were grouped into the 14 low-resolution prey categories that are displayed

| Common name           | Life stage       | <i>n</i> | <i>N</i> | TL  | FH  | INV | JELL | ECHINO | POLY | MOLL | CEPH | COPE | MYSID | AMPH | EUPH | CRAB | SHRIMP | CRUST | FISH  |
|-----------------------|------------------|----------|----------|-----|-----|-----|------|--------|------|------|------|------|-------|------|------|------|--------|-------|-------|
| Black Rockfish        | Juvenile         | 2        | 793      | 3.9 | 1.5 | 0.3 | 0.0  | 0.0    | 0.8  | 0.2  | 0.0  | 12.6 | 18.2  | 61.6 | 0.0  | 2.6  | 2.2    | 1.2   | 0.3   |
| Black Rockfish        | Juvenile – Adult | 6        | 341      | 3.9 | 1.9 | 3.2 | 10.3 | 0.0    | 3.2  | 0.2  | 3.2  | 0.0  | 1.0   | 0.4  | 10.8 | 6.7  | 1.1    | 9.0   | 51.0  |
| Brown Rockfish        | Juvenile         | 1        | 206      | 3.7 | 1.4 | 7.1 | 0.0  | 0.0    | 2.3  | 0.6  | 0.1  | 0.9  | 0.0   | 7.6  | 0.0  | 45.4 | 11.5   | 1.0   | 23.5  |
| Copper Rockfish       | Juvenile         | 3        | 348      | 3.7 | 1.5 | 0.6 | 0.0  | 0.0    | 0.1  | 3.2  | 0.0  | 9.2  | 2.4   | 24.8 | 0.0  | 26.8 | 19.5   | 0.0   | 13.3  |
| Copper Rockfish       | Juvenile – Adult | 3        | 129      | 3.9 | 1.6 | 0.9 | 0.0  | 0.0    | 8.5  | 0.3  | 6.1  | 0.0  | 0.3   | 1.8  | 0.0  | 23.2 | 9.9    | 4.2   | 44.8  |
| Copper Rockfish       | Adult            | 1        | 1        | 4.2 | 2.0 | 0.0 | 0.0  | 0.0    | 0.0  | 0.0  | 0.0  | 0.0  | 0.0   | 0.0  | 0.0  | 0.0  | 0.0    | 0.0   | 100.0 |
| Darkblotched Rockfish | Juvenile         | 1        | 18       | 3.6 | 2.2 | 0.0 | 31.3 | 0.0    | 0.0  | 0.0  | 0.0  | 9.3  | 0.0   | 19.7 | 15.3 | 0.0  | 0.0    | 24.3  | 0.0   |
| Darkblotched Rockfish | Juvenile – Adult | 1        | 20       | 3.4 | 2.4 | 0.0 | 0.0  | 0.0    | 0.0  | 0.0  | 0.0  | 4.1  | 0.0   | 5.8  | 75.2 | 0.0  | 3.0    | 0.0   | 11.8  |
| Dover Sole            | Juvenile         | 1        | 23       | 3.5 | 1.0 | 0.0 | 0.0  | 4.1    | 83.8 | 11.4 | 0.0  | 0.2  | 0.0   | 0.4  | 0.0  | 0.0  | 0.0    | 0.0   | 0.0   |
| Dover Sole            | Juvenile – Adult | 5        | 1423     | 3.5 | 1.0 | 0.3 | 0.5  | 32.9   | 53.0 | 5.9  | 0.3  | 0.0  | 0.0   | 1.6  | 0.4  | 0.9  | 0.3    | 2.8   | 0.9   |
| English Sole          | Juvenile         | 2        | 303      | 3.6 | 2.0 | 0.0 | 0.0  | 0.0    | 26.7 | 0.3  | 0.0  | 46.0 | 0.0   | 17.6 | 0.0  | 0.0  | 0.0    | 9.4   | 0.0   |
| English Sole          | Juvenile – Adult | 9        | 1484     | 3.5 | 1.1 | 1.3 | 0.0  | 5.4    | 50.3 | 18.7 | 0.0  | 0.7  | 1.8   | 10.7 | 0.0  | 1.1  | 0.9    | 7.7   | 1.5   |
| Greenstriped Rockfish | Juvenile – Adult | 2        | 63       | 3.7 | 1.9 | 0.0 | 0.0  | 0.0    | 0.0  | 0.1  | 17.2 | 0.5  | 0.3   | 0.3  | 14.7 | 4.6  | 51.2   | 0.7   | 10.4  |
| Lingcod               | Juvenile         | 2        | 24       | 3.9 | 2.6 | 0.0 | 0.0  | 0.0    | 0.0  | 0.0  | 0.0  | 19.1 | 0.0   | 0.0  | 19.3 | 0.0  | 0.0    | 0.6   | 61.0  |
| Lingcod               | Juvenile – Adult | 4        | 478      | 4.2 | 1.9 | 0.0 | 0.0  | 0.0    | 0.0  | 0.2  | 2.2  | 0.0  | 0.0   | 0.0  | 0.1  | 0.0  | 4.9    | 0.0   | 92.6  |
| Longspine Thomyhead   | Juvenile – Adult | 1        | 281      | 3.8 | 1.5 | 1.2 | 0.0  | 5.5    | 6.5  | 1.1  | 9.1  | 0.0  | 0.4   | 1.9  | 0.0  | 19.5 | 10.2   | 13.1  | 31.4  |
| Pacific Hake          | Juvenile         | 5        | 1526     | 3.4 | 2.5 | 0.6 | 0.0  | 0.0    | 0.0  | 0.0  | 0.8  | 19.2 | 0.1   | 0.0  | 63.8 | 0.0  | 4.6    | 0.3   | 10.6  |
| Pacific Hake          | Juvenile – Adult | 7        | 2830     | 3.7 | 2.3 | 0.0 | 0.1  | 0.0    | 0.0  | 0.0  | 1.8  | 0.0  | 0.0   | 0.0  | 45.1 | 0.3  | 11.2   | 1.0   | 40.4  |
| Pacific Hake          | Adult            | 4        | 778      | 4.0 | 2.3 | 0.0 | 0.0  | 0.0    | 0.0  | 0.0  | 1.0  | 0.0  | 0.0   | 0.0  | 19.4 | 0.0  | 5.2    | 3.3   | 71.0  |
| Pacific Spiny Dogfish | Juvenile         | 1        | 128      | 3.5 | 2.6 | 0.0 | 70.4 | 0.0    | 0.0  | 0.0  | 0.0  | 0.0  | 0.0   | 0.0  | 0.0  | 0.0  | 0.0    | 29.6  | 0.0   |
| Pacific Spiny Dogfish | Juvenile – Adult | 8        | 2301     | 4.0 | 2.2 | 3.3 | 4.8  | 0.0    | 0.1  | 0.0  | 7.1  | 0.0  | 0.0   | 0.7  | 17.6 | 2.1  | 1.7    | 0.5   | 62.0  |
| Petrale Sole          | Juvenile – Adult | 2        | 43       | 4.0 | 1.5 | 0.0 | 0.0  | 0.0    | 0.0  | 0.0  | 1.8  | 0.0  | 8.0   | 0.0  | 2.8  | 0.0  | 11.3   | 9.4   | 66.8  |
| Rosehorn Rockfish     | Juvenile – Adult | 1        | 60       | 3.6 | 1.4 | 1.0 | 0.0  | 0.0    | 0.0  | 0.0  | 0.1  | 1.2  | 0.0   | 0.4  | 0.4  | 42.4 | 43.4   | 3.7   | 7.4   |
| Sablefish             | Juvenile         | 2        | 40       | 3.7 | 2.3 | 0.0 | 0.0  | 0.0    | 0.0  | 0.0  | 11.6 | 0.0  | 0.0   | 0.0  | 44.9 | 9.1  | 0.0    | 1.5   | 32.9  |
| Sablefish             | Juvenile – Adult | 5        | 3332     | 3.8 | 1.5 | 1.2 | 0.6  | 3.5    | 3.6  | 15.4 | 15.9 | 0.1  | 0.3   | 6.1  | 6.5  | 2.0  | 4.1    | 9.0   | 31.7  |
| Sand Sole             | Juvenile         | 2        | 33       | 4.0 | 1.4 | 0.0 | 0.0  | 0.4    | 9.5  | 2.8  | 0.0  | 0.0  | 3.6   | 33.9 | 0.0  | 1.2  | 10.3   | 5.4   | 32.9  |
| Sand Sole             | Juvenile – Adult | 4        | 414      | 3.4 | 1.9 | 0.0 | 0.0  | 0.0    | 0.1  | 0.0  | 0.0  | 0.0  | 52.1  | 5.4  | 0.0  | 0.1  | 9.4    | 0.1   | 32.7  |
| Sharpchin Rockfish    | Juvenile – Adult | 2        | 44       | 3.7 | 2.3 | 0.8 | 0.0  | 0.0    | 0.0  | 0.0  | 1.0  | 1.7  | 0.0   | 0.0  | 34.3 | 5.0  | 10.8   | 10.2  | 36.3  |
| Starry Skate          | Juvenile         | 1        | 78       | 3.9 | 1.5 | 0.1 | 0.0  | 0.0    | 0.1  | 0.1  | 22.4 | 0.0  | 0.0   | 1.2  | 0.2  | 9.6  | 33.7   | 0.0   | 32.6  |
| Starry Skate          | Adult            | 1        | 32       | 4.1 | 1.7 | 0.0 | 0.0  | 0.0    | 0.0  | 0.0  | 19.6 | 0.0  | 0.0   | 0.0  | 0.0  | 7.9  | 7.7    | 0.6   | 64.1  |
| Yelloweye Rockfish    | Juvenile – Adult | 2        | 37       | 4.0 | 1.4 | 0.0 | 0.0  | 0.0    | 0.0  | 0.0  | 1.0  | 0.0  | 0.0   | 0.0  | 0.0  | 26.7 | 9.3    | 0.0   | 63.0  |

published during 1971–1985, and diet data prior to 1971 were obtained for only four species (Appendix 1). Diet composition studies from Southern California were relatively rare, whereas all 18 species had diet composition information from Northern California and most species had food habits data from Oregon and Washington (Appendix 1).

Fishes were the most common and substantial dietary component of Pacific Coast groundfishes, with shrimps, crabs, and euphausiids also well represented (Table 3). Fishes were recorded in the diets of every species, with overall mean and median estimates of 32.3 % and 31.2 %, respectively. Primary fish taxa comprised unidentified species (mean = 11.9 %), flatfishes (3.7 %), myctophids (2.1 %), sculpins (2.0 %), and rockfishes (2.0 %). Shrimps also were consumed by every species, although in lesser mass/volume than fishes (mean = 11.5 %, median = 9.4 %). Within this category, caridean shrimps (FO = 94.4 %, mean = 6.9 %) were more common and abundant in groundfish diets than penaeid and sergestid shrimps (FO = 50.0 %, mean = 3.2 %). Crabs were an important prey group, occurring in the diets of 15 groundfishes with mean and median contributions of 10.0 % and 4.2 %, respectively. The contribution of brachyuran crabs (FO = 72.2 %, mean = 6.2 %) exceeded that of anomuran crabs (FO = 50.5 %, mean = 4.2 %). Euphausiids were ingested by 12 species, but only contributed substantially to the diets of half of these (mean = 9.5 %, median = 1.3 %; Table 3). Some prey taxa (e.g., cephalopods, hard-shelled molluscs, unidentified crustaceans) were present in the diets of several groundfishes, but occurred in low overall proportions (Table 3).

Juvenile groundfishes generally consumed a greater proportion of small crustaceans and fewer fishes than later life stages. Increased piscivory from juvenile to later life stages was pronounced for Black Rockfish, Copper Rockfish, Starry Skate, Pacific Hake, and Lingcod (Table 3). The diets of a few species, such as Sablefish and Sand Sole, exhibited similar proportions of fishes between juvenile and juvenile-adult stages. For species in which amphipods or copepods were a substantial food item, consumption always was considerably greater for juveniles than later life stages (Table 3). A similar trend was evident for gelatinous zooplankton. Consumption of shrimps was highly variable among species and/or life stages.

## Major prey taxa

Quality of diet composition data varied greatly among species. Pacific Hake ranked highest in overall data quality (1.00). Only English Sole ranked greater than Pacific Hake among any evaluation category (Table 4). Brown Rockfish ranked lowest (overall data quality = 0.32), and generally there was poorer quality diet data for the selected rockfishes than for the other groundfish species (Table 4). Spatial coverage of trophic studies was broad, and resulted in similar ranks among several species for this metric. Ranks of temporal data coverage also were similar, but only four species had diet composition data that spanned more than two time periods (Appendix 1). Scientific coverage and sample size were more variable and served to better distinguish data quality among species (Table 4).

After data quality ranks were applied, adjustments were made for highly correlated data and a significance value for major prey taxa was determined. Mean Diet Composition was found to be highly correlated with three other metrics ( $r = 0.855$  Minimum,  $0.849$  PSA,  $0.701$  FO;  $P < 0.001$ ) and was removed from analysis. Nine of the 47 prey taxa were considered major prey, as all observed values  $>0.707$  were significantly greater than expected ( $P < 0.05$ ).

Major Prey Index calculations indicated that unidentified teleosts, euphausiids, and brachyuran crabs were the most important prey taxa for the 18 species of groundfish (Table 5). Unidentified teleosts were noted among 17 species to varying degrees (mean = 0.1–39.8 %). Euphausiids were well represented in the diets of Darkblotched Rockfish (mean = 45.3 %), Pacific Hake (mean = 42.8 %), and Sharpchin Rockfish (mean = 34.3 %). Brachyuran crabs were substantial dietary components for Yelloweye Rockfish, Brown Rockfish, Copper Rockfish, and Longspine Thornyhead (mean = 19.3–25.5 %).

The next series of major prey (MPI = 0.82–0.84) included caridean shrimps, polychaetes, amphipods, and unidentified crustaceans. Caridean shrimps were eaten by all species except Darkblotched Rockfish but were not consumed in abundance by any species (maximum mean = 16.4 %, Starry Skate), moderating their relative importance among major prey. Polychaetes were especially important in the diets of two groundfish species with relatively robust data sets (Dover Sole, mean = 55.7 %; English Sole, mean = 37.9 %). Amphipods were a substantial dietary component (mean = 11.4–29.1 %) for



**Table 4** Ranking of data quality used as a basis to weight the contribution of species-specific diet composition data for Major Prey Index calculations for 18 species of Pacific Coast groundfish

| Common name           | <i>n</i> | <i>N</i> | Spatial | Temporal | Overall |
|-----------------------|----------|----------|---------|----------|---------|
| Pacific Hake          | 0.80     | 1.00     | 1.00    | 1.00     | 1.00    |
| Sablefish             | 0.60     | 1.00     | 1.00    | 1.00     | 0.95    |
| Pacific Spiny Dogfish | 0.80     | 1.00     | 0.75    | 1.00     | 0.93    |
| English Sole          | 1.00     | 1.00     | 1.00    | 0.50     | 0.92    |
| Black Rockfish        | 0.80     | 1.00     | 0.75    | 0.75     | 0.87    |
| Dover Sole            | 0.60     | 1.00     | 1.00    | 0.50     | 0.82    |
| Copper Rockfish       | 0.80     | 1.00     | 0.75    | 0.50     | 0.80    |
| Lingcod               | 0.60     | 1.00     | 0.75    | 0.50     | 0.75    |
| Greenstriped Rockfish | 0.40     | 0.25     | 1.00    | 0.50     | 0.57    |
| Sand Sole             | 0.60     | 0.50     | 0.75    | 0.25     | 0.55    |
| Darkblotched Rockfish | 0.40     | 0.13     | 0.75    | 0.50     | 0.47    |
| Yelloweye Rockfish    | 0.40     | 0.13     | 0.75    | 0.50     | 0.47    |
| Sharpchin Rockfish    | 0.40     | 0.13     | 0.75    | 0.50     | 0.47    |
| Longspine Thornyhead  | 0.20     | 0.50     | 0.75    | 0.25     | 0.45    |
| Petrals Sole          | 0.40     | 0.13     | 0.75    | 0.25     | 0.40    |
| Rosethorn Rockfish    | 0.20     | 0.25     | 0.75    | 0.25     | 0.38    |
| Starry Skate          | 0.20     | 0.50     | 0.33    | 0.25     | 0.34    |
| Brown Rockfish        | 0.20     | 0.50     | 0.25    | 0.25     | 0.32    |

Species are listed in order of descending data quality. Metric definitions and ranking criteria are provided in Methods  
*n* scientific coverage, *N* sample size, *Spatial* spatial coverage, *Temporal* temporal coverage

Black Rockfish, English Sole, Darkblotched Rockfish, and Copper Rockfish. Other and unidentified crustaceans were present in 17 groundfish diets but contributed <15 % to the mean diet composition of any species.

The final two major prey items were copepods and mysids, with MPI values of 0.77 and 0.71, respectively. Copepods only contributed substantially to the diet of English Sole (mean = 23.4 %) but were observed in 2/3 of the groundfish species. Similarly, mysids only were ingested in large quantities by Sand Sole (mean = 46.7 %) but were present in the diets of half of the studied species.

Major prey taxa generally were associated with benthic and demersal habitats (Table 5). Only one (copepods) of nine major prey taxa occupied pelagic habitats, and euphausiids were associated with pelagic and demersal habitats. By contrast, five major prey taxa were strongly associated with benthic or benthic-demersal habitats (Table 5).

#### Dietary variability

Species differences were the primary source of dietary variability for Pacific Coast groundfishes (Table 6). Independently, SPECIES explained 73.4 % of the variability in the overall data set. Two other variables, TAXONOMIC GROUP and FUNCTIONAL GROUP, exhibited significant differences among categories but explained far less overall dietary variability than SPECIES (Table 6). Although LIFE STAGE was not significant when analyzed independently, the final, best-fit model included SPECIES ( $r^2 = 0.735$ ) and LIFE STAGE ( $r^2 = 0.090$ ). Results of dispersion analysis were significant for both of these variables, indicating that variance was heterogeneous among constituent groups. Neither the number of studies nor the number of samples exhibited a significant interaction effect with SPECIES, TAXONOMIC GROUP, or LIFE STAGE. Both of these factors, however, significantly influenced the results for FUNCTIONAL GROUP ( $P < 0.05$ ).

**Table 5** Major Prey Index (MPI) values for 47 (high level) prey taxa as determined using standardized diet composition data for 18 Pacific Coast groundfish species

| High level      | Foraging habitat        | MPI          |
|-----------------|-------------------------|--------------|
| <b>TELE</b>     | <b>Demersal</b>         | <b>0.968</b> |
| <b>EUPH</b>     | <b>Pelagic-Demersal</b> | <b>0.911</b> |
| <b>CRAB B</b>   | <b>Benthic</b>          | <b>0.887</b> |
| <b>SHRIMP C</b> | <b>Benthic-Demersal</b> | <b>0.839</b> |
| <b>POLY</b>     | <b>Benthic</b>          | <b>0.831</b> |
| <b>AMPH</b>     | <b>Benthic</b>          | <b>0.823</b> |
| <b>CRUST</b>    | <b>Benthic-Demersal</b> | <b>0.823</b> |
| <b>COPE</b>     | <b>Pelagic</b>          | <b>0.774</b> |
| <b>MYSID</b>    | <b>Demersal</b>         | <b>0.710</b> |
| FLAT            | Benthic                 | 0.702        |
| JELL            | Pelagic                 | 0.637        |
| CRAB A          | Benthic                 | 0.629        |
| SHRIMP PS       | Benthic-Demersal        | 0.605        |
| SHRIMP          | Benthic-Demersal        | 0.573        |
| ECHINO          | Benthic                 | 0.524        |
| ROCK            | Benthic-Demersal        | 0.524        |
| SCULP           | Benthic                 | 0.508        |
| MYCT            | Pelagic                 | 0.500        |
| BIVAL           | Benthic                 | 0.468        |
| ENGR            | Pelagic                 | 0.419        |
| ISO             | Benthic                 | 0.419        |
| LOLI            | Demersal                | 0.403        |
| CLUP            | Pelagic                 | 0.395        |
| GAST            | Benthic                 | 0.379        |
| CODS            | Demersal                | 0.371        |
| OSMER           | Demersal                | 0.371        |
| SCORP           | Demersal                | 0.355        |
| OCTO            | Benthic                 | 0.347        |
| DECA            | Benthic-Demersal        | 0.339        |
| HERR            | Pelagic-Demersal        | 0.339        |
| ZOAR            | Benthic                 | 0.339        |
| HEX             | Demersal                | 0.331        |
| AXIID           | Benthic                 | 0.306        |
| AMMO            | Pelagic-Demersal        | 0.274        |
| CEPH            | Demersal                | 0.266        |
| TUN             | Benthic                 | 0.234        |
| SQUID           | Pelagic-Demersal        | 0.218        |
| INV             | Benthic-Demersal        | 0.194        |
| MOLL            | Benthic                 | 0.185        |
| OEGO            | Pelagic-Demersal        | 0.177        |
| CHOND           | Demersal                | 0.169        |
| CUTT            | Benthic-Demersal        | 0.113        |
| WORM            | Benthic                 | 0.113        |
| SARD            | Pelagic                 | 0.105        |
| AGON            | Benthic                 | 0.065        |
| CRAB            | Benthic                 | 0.048        |
| AGNATH          | Benthic                 | 0.032        |

Prey taxa are listed in order of descending MPI value. Major prey taxa are distinguished by bold type

**Table 6** PERMANOVA results of diet composition variability by species, taxonomic group, functional group, and life stage for 18 species of Pacific Coast groundfish, as calculated using low level prey categories (Table 2). Best-fit PERMANOVA model is shown first followed by individually-analyzed variables

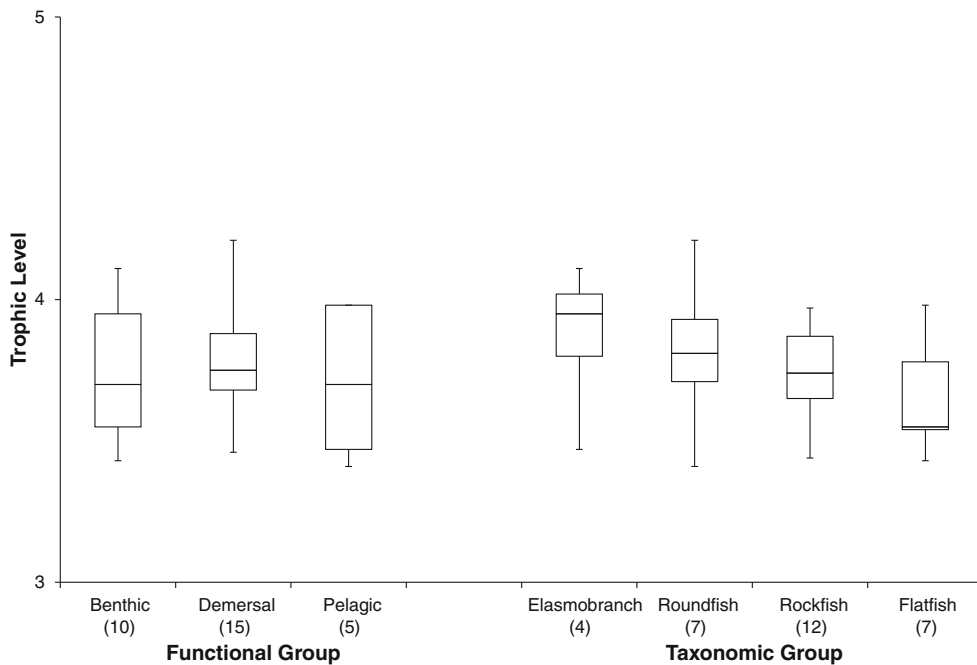
| Model(s)   | Variable(s)      | df | <i>F</i> | <i>r</i> <sup>2</sup> | <i>P</i> |
|------------|------------------|----|----------|-----------------------|----------|
| Best-fit   | Species          | 17 | 2.47     | 0.735                 | 0.001*   |
|            | Life stage       | 2  | 2.57     | 0.090                 | 0.009*   |
|            | Residuals        | 10 |          | 0.175                 |          |
| Individual | Species          | 17 | 1.95     | 0.734                 | 0.003*   |
|            | Taxonomic group  | 3  | 2.79     | 0.244                 | 0.001*   |
|            | Functional group | 2  | 2.00     | 0.129                 | 0.025*   |
|            | Life stage       | 2  | 1.59     | 0.105                 | 0.094+   |

Degrees of freedom (df), *F*-statistic, amount of variability explained. (*r*<sup>2</sup>), and *P*-value are presented. Statistically significant variables (\*) and heterogeneity of multivariate group dispersions (+) indicated. Data treatments and variable descriptions are provided in Methods

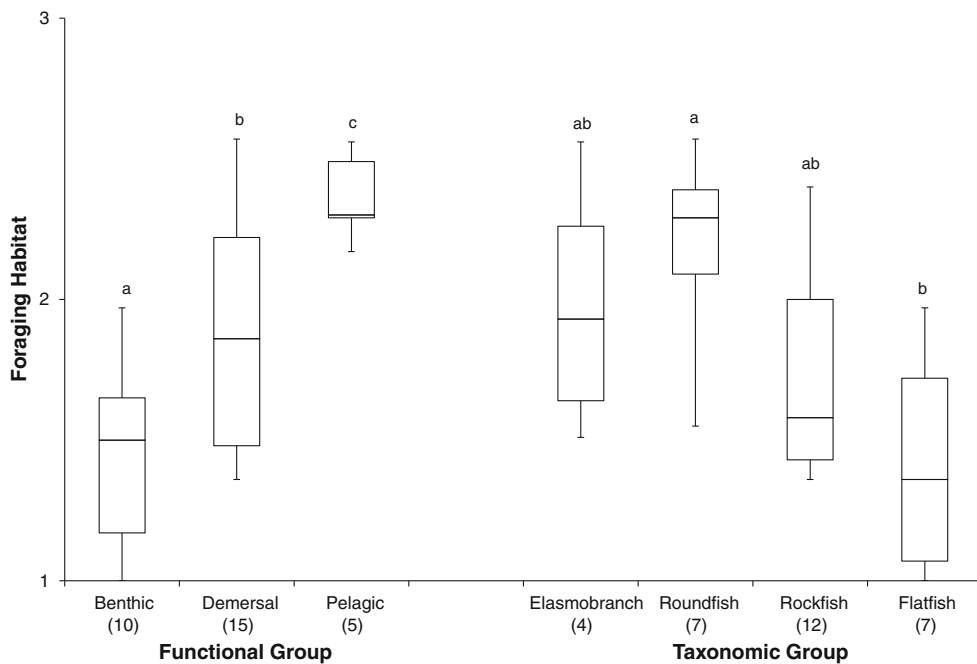
#### Trophic level and foraging habitat

Estimated mean trophic levels did not vary significantly among functional ( $F = 0.194$ ,  $P = 0.825$ ) or taxonomic ( $F = 1.106$ ,  $P = 0.364$ ) groups. Median and minimum trophic levels also were similar among functional groups, ranging from 3.70–3.75, but groundfishes inhabiting benthic and demersal regions had greater maximum trophic level estimates than pelagic species (Fig. 1). Variability around the median was greatest for species occupying pelagic regions and lowest for demersal species (Fig. 1). Median trophic levels differed among taxonomic groups (3.55–3.95), with considerable within-group variability. Mean trophic level estimates therefore were more similar (3.69–3.87) than median estimates. Minimum trophic level estimates also were similar among taxonomic groups, but considerably greater maximum and quartile values were determined for elasmobranchs and roundfishes (Fig. 1). Flatfishes had the lowest median trophic level.

Foraging habitat estimates varied greatly among species occupying different functional and taxonomic groups (Fig. 2). Mean foraging habitat differed significantly among functional groups ( $F = 10.280$ ,  $P < 0.001$ ) and was highly variable for groundfishes occurring in benthic and demersal regions. Pelagic species, by contrast, foraged mainly in demersal-pelagic regions (Fig. 2). Mean (and median) foraging habitat also differed substantially by taxonomic group ( $F = 5.014$ ,  $P = 0.007$ ), with roundfishes foraging significantly higher in the water



**Fig. 1** Box-and-whisker plot (median, first and third quartiles, minimum and maximum values) of trophic level for 30 Pacific Coast groundfish species and/or life stages, as calculated by Functional Group and Taxonomic Group. Numbers below labels indicate sample size



**Fig. 2** Box-and-whisker plot (median, first and third quartiles, minimum and maximum values) of foraging habitat (1 = benthic, 2 = demersal, 3 = pelagic) for 30 Pacific Coast groundfish species and/or life stages, as calculated by Functional Group and

Taxonomic Group. Letters indicate significantly different groups by ANOVA (when applicable). Numbers below labels indicate sample size

column than elasmobranchs and rockfishes, and all groups foraging farther off the bottom than flatfishes (Fig. 2). Flatfishes fed in benthic and demersal regions exclusively, whereas foraging habitats of elasmobranchs, roundfishes, and rockfishes ranged from benthic-demersal to demersal-pelagic regions (Fig. 2).

### Trophic guilds

Species and/or life stages were grouped into trophic guilds based on similar diet compositions (Fig. 3). An agglomerative cluster coefficient of 0.91 indicated a high degree of clustering throughout the dissimilarity range. Additionally, pairwise species and/or life stage dissimilarities and cophenetic distances associated with the cluster dendrogram were strongly correlated (0.79), indicating that the dendrogram is an appropriate summary of diet data for Pacific Coast groundfishes.

Two small, significant trophic guilds were detected at a level of  $P < 0.05$ , with four larger guilds established at a level of  $P < 0.10$  (Fig. 3). Dover Sole (juvenile, juvenile-adult) and English Sole (juvenile-adult) represented a significant guild with diets dominated by polychaetes (mean = > 50 %) and some hard-shelled molluscs, indicative of benthic foraging (Fig. 3). Juvenile Pacific Hake and juvenile-adult Darkblotched Rockfish formed a second significant guild, representing euphausiid predators feeding in the demersal-pelagic region (Fig. 3). Guilds formed at a level of  $P < 0.10$  included groundfish species that preyed (Fig. 3, from top to bottom): 1) on gelatinous zooplankton, copepods, amphipods, and other unidentified crustaceans, 2) mainly on fishes and assorted crustacean taxa (e.g., mysids, shrimps, amphipods), 3) on shrimps, crabs, and fishes, and 4) primarily on fishes and/or euphausiids.

### Discussion

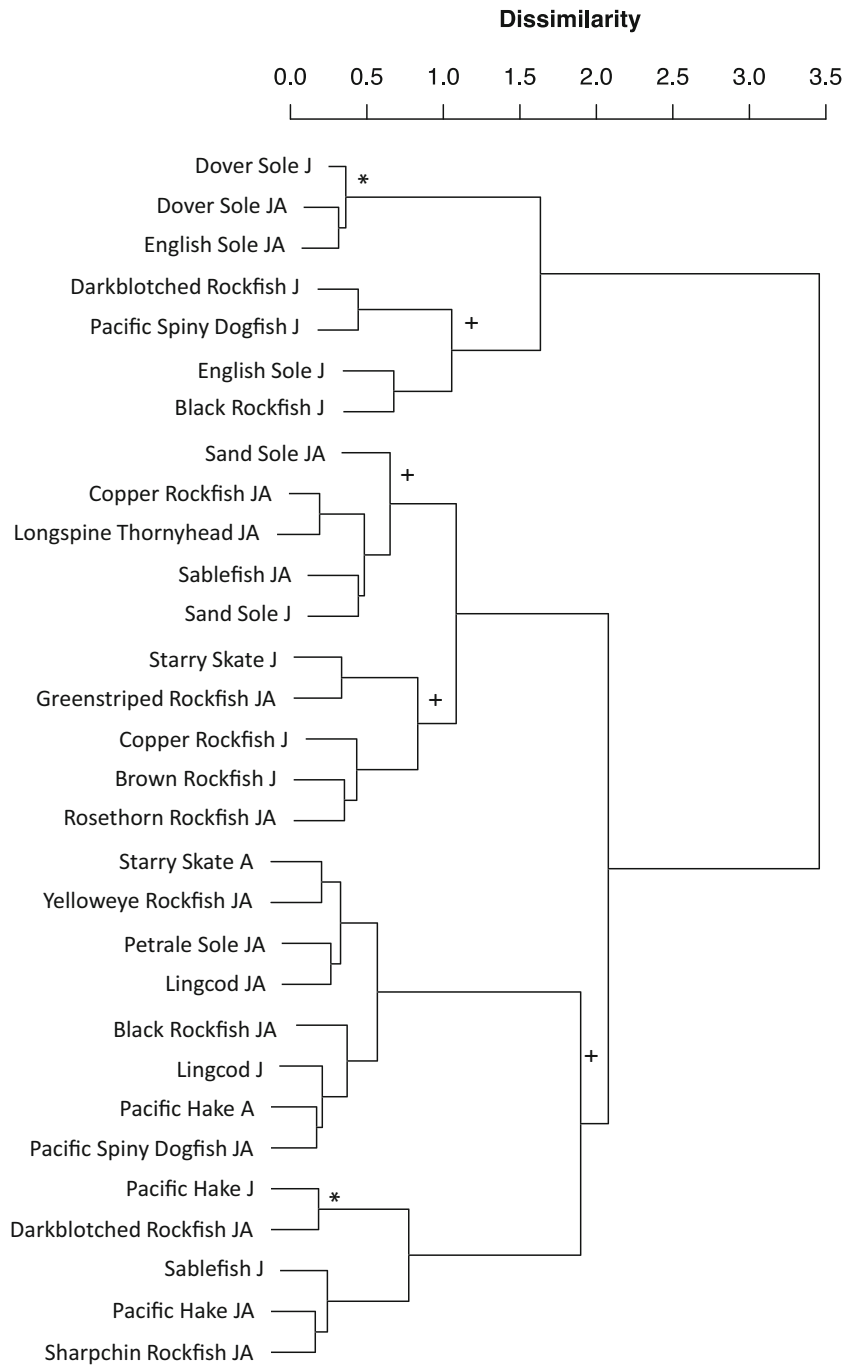
Determining the composition and habitats of major prey taxa for Pacific Coast groundfishes provided new insights into the trophic ecology of this group. Epifaunal organisms that typically are common and abundant on unconsolidated seafloors (polychaetes, amphipods, brachyuran crabs, caridean shrimps) were plentiful among major prey taxa. Two major prey taxa were, however, planktonic organisms in pelagic or demersal-pelagic environments (euphausiids, copepods), and mainly were ingested by juveniles of a variety of

groundfish species. The designation of common, abundant taxa in pelagic, demersal, and benthic environments as major prey indicates that groundfishes are trophic generalists, regardless of foraging habitat or life stage. Consequently, widespread and abundant prey with relatively high levels of taxonomic distinction but extremely low MPI values, for example benthic poachers or pelagic sardines, are decidedly insignificant in the diets of Pacific Coast groundfishes.

Most groundfish diets were dominated by varying amounts of fishes and crustaceans, but substantial species-specific variation was evident. Because species and functional group designations lacked variability (i.e., each species and/or life stage was assigned to a single functional group), an assessment of interaction effects in the comparative analysis of diet composition was not possible. Differential foraging locations among species, however, appears to be one of the main contributing factors to dietary differences. For instance, species (e.g., Sablefish, Pacific Hake, Darkblotched Rockfish, Spiny Dogfish) that foraged on pelagic prey such as euphausiids and gelatinous zooplankton had distinctly different diet compositions than some flatfishes (Dover Sole, English Sole) that fed on benthic polychaetes and bivalve siphons (Zebold 1970; Buckley et al. 1999) or rockfishes (e.g., Brown, Copper, Rosethorn) that foraged demersally for fishes, crabs, and shrimps. The estimates of standardized diet composition of groundfishes in this study were similar to those previously calculated for 60 skate species. Like Pacific Coast groundfishes, skates ate mostly decapods and fishes, with polychaetes and amphipods of secondary importance (Ebert and Bizzarro 2007). Euphausiids were less substantial prey for skates (Ebert and Bizzarro 2007) than for Pacific Coast groundfishes, probably because of the more narrowly subscribed benthic-demersal foraging habitats of skates.

The far greater power of species-specific differences in explaining dietary variability relative to that of taxonomic group, functional group, or life stage suggests that each species has a distinct trophic role. Although species-specific trophic differences were well supported by the available data, even using highly generalized prey categories, the studied groundfishes do not represent a sympatric assemblage that was sampled in the same place and time. Therefore, a direct link between observed dietary differences and trophic separation among species cannot be established. Compelling evidence for trophic separation is extremely sparse in marine fishes,

**Fig. 3** Hierarchical agglomerative cluster analysis of standardized diet composition among 30 Pacific Coast Groundfish species and/or life stages. Calculations were performed using 14 (low level) prey categories, Ward’s Minimum Variance technique, and a Bray-Curtis dissimilarity matrix. J = juvenile, JA = juvenile–adult, A = adult. \* = significant cluster ( $P < 0.05$ ), + =  $P < 0.10$



especially among generalist predators such as groundfishes. Even in field studies that infer resource partitioning from diet composition, sympatric fishes often exhibit dietary overlap when resources are abundant and only shift their prey spectrums when resources

are scarce (Hoines and Bergstad 1999; Feyer et al. 2003).

Spatio-temporal dietary differences such as these have been reported for many of the studied groundfishes (e.g., Brodeur and Pearcy 1984; Buckley and Livingston 1997;

Studebaker and Mulligan 2008; Reum and Essington 2013) and probably represent a substantial source of dietary variability. For example, the amount of rockfish consumed by lingcod was three times greater in marine reserves than in unprotected nearby waters (Beaudreau and Essington 2007). The timing and location of collection hauls represented the dominant source of dietary variability in eastern North Pacific skate assemblages, explaining an order of magnitude more variability than species or size differences (Bizzarro 2015). Brodeur and Percy (1984) reported seasonal, geographic, and diet variability in the diets of several groundfishes, and suggested that dietary variability seems to reflect differences in prey availability. Pooling data from different regions and time periods likely oversimplifies trophic relationships among species and/or life stages and may contribute to observed species-specific differences.

Identifying trophic guilds distinguishes fish species and/or life stages with similar predatory roles and prey taxa. Interpreting prey characteristics of the trophic guilds can provide an expanded ecological understanding of feeding relationships, foraging habitats, and improve EFH characterization for multiple life stages of exploited species. In this study, only two significant trophic guilds comprising five species and/or life stages were defined, indicating that there is broad overlap in diet composition among several prey categories for the selected groundfish species and/or life stages. These significant guilds ate large proportions of prey items (polychaetes and euphausiids) that were not abundant in the diets of most groundfish species and/or life stages. Furthermore, the members of these guilds exhibited marked spatial separation. Late juvenile and adult Dover Sole occupy much deeper habitats than comparable life stages of English Sole, though both eat large amounts of polychaetes and relatively high amounts of hard-shelled molluscs (Love 2011). Juvenile hake occur higher in the water column than Darkblotched Rockfish (Love 2011), and therefore do not use the same foraging grounds to consume euphausiids. Adding spatial associations to the specified cluster analysis would result in the assignment of ecological guilds that may differ substantially in structure and composition from the trophic guilds determined in this study.

Estimated trophic levels indicated that Pacific Coast groundfishes largely comprise meso- and upper-trophic level predators, and facilitated comparisons with trophic levels of other marine taxa. Trophic level increased with maturity for most species and reflected a shift from meso- to upper-trophic level predatory roles, typically

through increased piscivory. Mean ( $\pm$  SE) and ranges of trophic levels of Pacific Coast groundfishes ( $3.77 \pm 0.04$ ; 3.41–4.24) were similar to those of skates ( $3.80 \pm 0.02$ ; 3.44–4.24), owing to similar diet compositions (Ebert and Bizzarro 2007). Because the Starry Skate consumed mainly fishes and cephalopods, its trophic level estimates from our study (3.91 for juveniles, 4.11 for adults) were greater than those of four other species of sympatric Pacific Coast skates (Ebert and Bizzarro 2007). Trophic level estimates of rays (3.10–4.24) also were similar to those of Pacific Coast groundfishes. Approximately 80 % of ray species were mesopredators (trophic levels 3.0–4.0; Jacobsen and Bennet 2013), as compared to 74 % of groundfish species and/or life stages in our study. Trophic levels of Pacific Coast groundfishes generally were lower than those of the sharks, but were similar to those of some carcharhiniform families (Triakidae, Sphyrhinae, Scylliorhinae; Cortés 1999). Estimated trophic level of juvenile-adult Pacific Spiny Dogfish from our study (4.0) was comparable to that of combined Spiny Dogfish/ Pacific Spiny Dogfish (3.9; Cortés 1999); however, the trophic level estimate of juvenile Pacific Spiny Dogfish (3.5) was lower than both juvenile-adult estimates, reflecting a much greater reliance on gelatinous zooplankton instead of small, schooling fishes (Cortés 1999). Pacific Coast groundfish trophic levels estimated in our study were considerably greater than those of baleen whales or sea otters (3.2–3.4), but lower than those of pinnipeds and toothed whales (3.8–4.4) and orcas (4.5–4.6; Pauly et al. 1998).

#### Management applications

The creation and application of the MPI and the determination of foraging habitats directly address current limitations in EFH characterization of Pacific Coast groundfishes. Using the MPI, fisheries scientists and managers now can consider potential impacts (e.g., harvesting, habitat destruction) to prey in the design and implementation of spatial management regulations (National Marine Fisheries Service 2013). Furthermore, differences in foraging habitats among functional and taxonomic groups and in species-specific diet compositions indicate that important foraging areas are unlikely to overlap substantially among groundfishes. Such areas should be considered on a species-specific basis, when possible.

The framework developed in this study can be expanded and applied to determine trophic relationships for

evaluation and monitoring purposes, and as a precursor to the establishment of EBFM. Characterizing diet composition at high levels of taxonomic clarity can establish a comprehensive baseline condition for groundfish assemblages in a region of interest. Regular sampling in the same and nearby regions can facilitate an understanding of trophic dynamics that can be used to compare the effects of no take zones on marine communities. In addition, a food web model of the California Current (Field et al. 2006) that has been periodically updated and applied to evaluate the impacts of harvesting on food web structure (e.g., Kaplan and Levin 2009; Kaplan and Leonard 2012) can be further improved by incorporating the results of our study. Using an Atlantis model framework, it was predicted that intense fisheries exploitation would result in community replacement of relatively long-lived, *k*-selected species, such as skates, with short-lived, *r*-selected species, such as mackerel and anchovies (Kaplan and Levin 2009). A study by Dufault et al. (2009) modeled the food web of a diverse group of marine taxa (invertebrates, fishes, seabirds, whales) throughout the water column off the Pacific Coast, and is considered a key input to the Atlantis model (Kaplan et al. 2013). Marked species-specific differences in groundfish diets, however, suggest that higher taxonomic and functional groupings and generalized prey categories, such as those used by Dufault et al. (2009), might not accurately characterize the complexity of trophic relationships. Our study provides more specific and robust dietary information for groundfishes that can be used to evaluate model performance by comparing outputs generated from our data with those generated using the original data. The life-stage specific diet composition information from our study also can facilitate the creation of a specific food web model for groundfishes.

#### Caveats and considerations

Major, or key, ecosystem components often are distinguished through modeling exercises involving population dynamics of predators and prey, sometimes coupled with fishery interactions (Gaichas et al. 2010; Lassalle et al. 2011; Pikitch et al. 2012). Such an exercise was not possible in our study, given the nature and quality of the available diet composition data. An alternative method of prey evaluation therefore was required. Biological metrics and indices have been commonly and reliably employed to evaluate ecological data for research (Washington 1984; Krebs 1999; Abrantes et al. 2014) and fishery

management (Cury et al. 2005; Jennings 2005; Samhoury et al. 2009; Kaplan and Levin 2009). Therefore, the creation and application of an index was used as the basis for the determination of major prey in this study.

The MPI is intended to address current ambiguities regarding the designation of major prey in EFH regulations; however, the available diet composition data may be too general to produce accurate estimates of prey habitat for most species of Pacific Coast groundfish. For example, the taxonomic level of the nine major prey categories ranged from infraorder (Brachyura) to sub-phylum (Crustacea). Broad taxonomic categories, such as unidentified teleost, may contain more accurately identified prey (e.g., flatfishes, rockfishes). In these instances, MPI values will under-represent the true importance of these prey taxa. Data at higher resolution are needed to better resolve major prey taxa (ideally to species) so that their habitats can be effectively determined. In the absence of such data, a less conservative *P*-value of 0.10 may be considered more appropriate than the traditional 0.05 threshold to designate major prey, depending on the objectives and needs of the user.

Quality of diet composition data varied considerably among species and/or life stages and influenced trophic characterizations and comparisons. Rockfishes, which comprise the great majority of federally managed Pacific Coast groundfishes (Pacific Fishery Management Council 2016), were under-represented in MPI calculations because data on diets of the selected species in this group were of relatively poor quality. Prey taxa that are common to rockfish diets, such as decapod and fish taxa, therefore contributed unequally to MPI results as compared to those of other analyses that weighed the relative contribution of each species and/or life stage equally. In addition, most diet composition data on Pacific Coast groundfishes is historic in nature. Because an environmental regime shift occurred in the California Current during the late 1970s (Hare and Mantua 2000), diet composition data collected prior to this period may not accurately reflect current trophic relationships among groundfishes.

Insufficient sample size can bias results and subsequent analyses of diet composition. The number of studies and total number of stomach samples did not influence the results of PERMANOVA analysis, and no significant differences in variance were noted among species. These results indicate that species-specific differences were robust regardless of sample size, but the accuracy of synthesized diet composition information could not be tested and represents an unknown and

potentially major source of dietary variability. Additional quantitative studies with large (> 100) sample sizes, especially focused on rockfishes, are necessary to further refine estimates of major prey taxa and to facilitate more robust trophic analyses.

Differences in local prey availability may drive dietary dynamics in Pacific Coast groundfishes. Temporal and spatial factors therefore should be considered when collecting diet composition data for these generalist predators. Our study provides standardized, quantitative estimates of the diets of 18 groundfish species by life stage, which supports an improved characterization of EFH for these species. Further study that integrates spatio-temporal aspects of feeding ecology and habitat associations is a necessary step toward understanding comparative resource use by Pacific Coast groundfishes.

Because foraging habitat calculations were based on generalized prey habitats, our results should be further examined in relationship to the literature. For instance, although euphausiids were assigned to a pelagic-demersal habitat category, some marine organisms consume them when they become entrained on the benthos during vertical migrations (Isaacs and Schwartlose 1965; Genin et al. 1988; Ressler et al. 2005; Rinewalt et al. 2007; Genin 2014). Most euphausiid predators in this study, however, including some rockfishes (e.g., Greenstriped, Darkblotched, Sharpchin), are known to forage in pelagic regions (Love 2011). Therefore, the foraging habitat calculations for these species appear to be accurate. Copepods also were assigned to a pelagic-demersal functional group, and though most groundfishes foraged on pelagic copepod taxa, English Sole consumed harpacticoid copepods that are benthic (Toole 1980). In this instance, the foraging habitat for English Sole will overestimate pelagic-demersal foraging because of the generalized functional groups used in our study. Similarly, standardized diet composition should be examined in the context of fish feeding behavior. For instance, predation on bivalves by English Sole and Dover Sole is not an indication of prey excavation or durophagous feeding habits. Instead, these flatfishes nip the siphons off of bivalves as they protrude from the seafloor (Zebold 1970; Buckley et al. 1999).

## Conclusions

The findings of this study represent a necessary first step toward incorporation of trophic

information into the characterization of EFH of Pacific Coast groundfishes. Establishing objective, quantitative criteria for the determination of major prey taxa addresses a need in the development of spatial management plans for these species (National Marine Fisheries Service 2013). The identification of common and abundant taxa as major prey indicates that groundfishes are trophic generalists, regardless of foraging habitat or life stage. Dietary differences were, however, highly significant among species, with varying foraging locations greatly influencing these results. These differences are largely a consequence of differential use of crustacean and fish taxa, as there is broad dietary overlap of these prey categories among groundfish species. Pacific Coast groundfishes were mainly mesopredators, with diet compositions and trophic levels similar to those of skates (Ebert and Bizzarro 2007).

Future work should focus on collecting quantitative diet composition information and expanding analyses to include additional species and/or life stages of groundfishes and the evaluation of spatial and temporal dietary variability. Contemporary diet composition data are limited, especially for rockfishes and for most species off Southern California. The 18 selected species constitute a small portion of the 117 species of groundfishes included in the Pacific Coast Groundfish Management Plan (Pacific Fishery Management Council 2016). Diet studies on a greater number and diversity of species, and more research on poorly studied species, will help us better define major prey taxa and trophic ecology for Pacific Coast groundfishes. Adding a spatio-temporal component to analysis will enable a more complete assessment of the relative magnitude of different sources of dietary variability for each species and/or life stage and for the overall assemblage. The incorporation of spatial and temporal diet composition data also will facilitate a better understanding of the ecological relationships among Pacific Coast groundfishes.

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