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Forage species in predator diets: Synthesis of data from the California Current

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ABSTRACT

Characterization of the diets of upper-trophic pelagic predators that consume forage species is a key ingredient in the development of ecosystem-based fishery management plans, conservation of marine predators, and ecological and economic modeling of trophic interactions. Here we present the California Current Predator Diet Database (CCPDD) for the California Current region of the Pacific Ocean over the past century, assimilating over 190 published records of predator food habits for over 100 predator species and 32 categories of forage taxa (species or groups of similar species). Literature searches targeted all predators that consumed forage species: seabirds, cetaceans, pinnipeds, bony and cartilaginous fishes, and a predatory invertebrate. Diet data were compiled into a relational database. Analysis of the CCPDD highlighted differences in predator diet data availability based on geography, time period and predator taxonomy, as well as prominent prey categories. The top 5 forage taxa with the most predators included juvenile rockfish, northern anchovy, euphausiid krill, Pacific herring and market squid. Predator species with abundant data included Pacific hake, common murre, and California sea lion. Most diet data were collected during the summer; the lack of winter data will restrict future use of the CCPDD to understand seasonal patterns in predator diet unless more such data become available. Increased synthesis of historical information can provide new resources to understand patterns in the role of forage species in predator diet. Increased publication and/or accessibility of long-term datasets and data-sharing will further foster the synthesis of information intended to inform the management, conservation and understanding of marine food webs.

1. Introduction

Ecosystems are complex systems in which small-scale interactions may shape large-scale processes (Cowan et al., 2012; Levin and Lubchenco, 2008). In marine ecosystems this complexity may limit the understanding of food web dynamics and predator-prey interactions (Frid et al., 2006). For example, forage fish fisheries account for over 30% of marine landings globally (Alder et al., 2008), but knowledge is limited on how removals of these fish affect marine ecosystem functions (Pikitch et al., 2014; Smith et al., 2011). Food web models that examine the impacts of forage fisheries on marine ecosystems rely on detailed information on predator food habits and diet composition, information that is rarely available at the desired high-resolution spatial and temporal scales. Spatial details are needed to account for large-scale delineation of bio-physical features (Fujioka et al., 2014; Sherman, 1995). Temporally explicit data provide key information on seasonal or inter-annual variation that can affect predators via changes in prey energetic content (Rojbek et al., 2014) or prey availability (Ainley et al., 1996; Becker et al., 2007). Importantly, when data are averaged across space and time the reduced resolution can mask high local diet dependencies (Pikitch et al., 2014). Thus, enhancing knowledge of spatial and temporal detail in pelagic food webs is required to improve our abilities to assess forage fisheries, as well as climatic impacts, within and across marine ecosystems.

In contrast to many marine ecosystems, information on food habits and diet composition of marine middle- and upper-trophic-level predators in the California Current System (CCS) is rich. In this ecosystem, observational studies of pelagic predator diets have been conducted over the past 100 years, but assimilation of this information in food web models has been hindered by: 1) the high species diversity of middle- to upper-trophic-level predators (>160 species) that eat a diversity of forage species, 2) the large spatial domain of the CCS that spans Canada, the United States, and Mexico, and 3) the relatively short-term nature of the majority of these studies. To address the need for greater spatial and temporal detail for inclusion in ecosystem models of the CCS, we designed and populated the *California Current Predator Diet Database* (CCPDD). In this paper, we describe the database,

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identify gaps in food web knowledge, and review how we compiled disparate information from the peer-reviewed and technical literature to enhance understanding of food webs in this region. To meet this objective, we compiled existing research on predators of 32 focal taxa, expanding the traditional definition of small schooling pelagic fishes to include invertebrate taxa <50 cm in length and juvenile stages of larger fishes, which are also important components of predator diet in this system. We assessed the limitations of this synthesis in taxonomic, spatial, and temporal terms, as well as the use of different measurement units for predator consumption. With this database, we address the following questions: 1) Which forage species are commonly eaten by upper-trophic-level pelagic predators in the CCS? 2) What is the taxonomic, spatial, and temporal resolution of data on various forage species in predator diets?

2. Methods

2.1. Literature search and selection

We conducted a systematic review of the literature by querying the BIOSIS search engine for articles on predators occurring in the CCS from the northern tip of Vancouver Island, Canada, to the southern tip of Baja California, Mexico. Queries included topical keywords for diet and CCS geography, and taxonomic terms for each major taxonomic group of predators (Table 1). For bony fishes, taxonomic searches were for families and genera of marine fish known in the CCS (Eschmeyer and Herald, 1983), including both current and synonymous taxonomic names (based on the Integrated Taxonomic Information System [ITIS]).

Paper titles and abstracts returned from the search were screened by multiple expert reviewers (Table 1) to include only those with 1) middle- or upper-trophic-level predators, 2) CCS geographic region[1] (nearshore to ~200 nmi offshore, Baja to Vancouver Island), 3) indicator forage taxa identified to species, genus or family (those not denoted by * in Table 2), and 4) numerical or proportional diet data (e.g., not raw fatty acid data, and rarely stable isotope data). This list was supplemented by "citation chasing" (searching within existing articles, reviews, and books to avoid "availability bias", or including only easily-available studies; Collaboration for Environmental Evidence, 2013, p. 41), and querying subject experts for different taxonomic groups, Google's online search engine, subject-specific databases (Washington Seabird Diet Database, S. Pearson/WDFW; Northern CCS Fish Diet Database, R. Brodeur/NMFS), and government websites (National Oceanographic and Atmospheric Association, National Marine Fisheries Service, Canadian Department of Fisheries and Oceans, and state wildlife management departments). This screening sequence returned 285 relevant citations (Appendix A).

We entered data from 193 of the relevant citations in peer-reviewed journal publications and books (n = 161), technical reports (n = 19), and theses (n = 13). We prioritized data entry to achieve a broad perspective on predator diet, but could not enter every citation given time limitations. First we entered a minimum of one citation for each predator species, then we included as many regions as data were available for each predator (Canada, Washington, Oregon, northern California, central California, southern California, Mexico), and finally we filled in temporal gaps where possible with at least one citation for more recent data from the year 2000 forward. Additionally, we entered as much data as were available for those predators and prey with limited diet data (e.g., cetaceans as predators, sardines as prey). This approach ensured we had strong taxonomic, spatial and temporal resolution for predator diet. Of the remaining 92 citations not in the database, 75 were filed for future use because some data for the predator had already been entered in each region for the more recent time period or because data from a time-series was redundant with a more recent citation. The remaining 17 citations were either impossible to locate by interlibrary loan, or were acquired after analysis began.

The exclusion of additional citations due to time limitations was primarily for well-studied predators with many citations, e.g., for common predators in regions or time periods already represented in the CCPDD, including salmon, Pacific cod, Pacific hake, Caspian tern, Cassin's auklet, common murre, pigeon guillemot, rhinocerous auklet, California sea lion, and harbor seal. Supplements 1 and 2 provide a grid that portrays the citations included in the CCPDD, highlighting excluded citations that overlap in time (Supplement 1) and space (Supplement 2), as well as those not entered because the data were collected prior to 2000 or the citation was not yet published or difficult to locate. This first version of the CCPDD was developed to include broad scale spatial representation of diet data for each predator species, with an emphasis on more recent data from 2000 forward. Future iterations of the project will focus on entering newly published datasets, and enhancing the spatio-temporal resolution for data-rich predator species. In order to capture the best possible representation of which predators consume forage taxa among different regions, we occasionally include data from beyond the boundaries of the CCS (e.g., inland seas), when it improves the resolution of the diet data. We feel the benefits of characterizing the potential for consumption of forage taxa outweigh the cost of including data from slightly outside the CCS domain. For example, although lingcod occurs throughout the CCS, the only published diet data in WA comes from Puget Sound (Beaudreau and Essington, 2007). Likewise, the only copper rockfish, and coho and chum salmon diet data available in Canada are from inlets in British Columbia (Murie 1995, King and Beamish, 2000). When seabird colonies occur slightly inland, such as Caspian terns near the mouth of the Columbia River (e.g., Roby et al., 2002), an inference of at-sea foraging from diet composition supports inclusion in the database. Data from these studies are valuable because they improve geographic variation in diet data for predators otherwise lacking information in individual regions or in some cases at all. Future analyses can query the CCPDD for studies from varying spatial areas.

2.2. Database structure and data entry

We developed the database by reviewing each citation to characterize the range of methodological information (e.g., consumption unit types, predator metadata, prey metadata) and used this list to build a web-based data-entry form as well as database tables. Data were extracted by annotating PDF files and the data were entered just as they occurred in the citation (i.e., numeric quantities were not transformed, used given taxonomic names). Graphical data were extracted with GraphClick (Arizona Software, 2010) when original data could not be obtained directly from the text. The relational database stores individual occurrences of a predator eating a prey. Each record includes information on the citation, study location, study date, observation type (e.g., stomach content, visual observation), predator (taxonomy, life-history stage, sample size), and prey (taxonomy, life-history stage, amount consumed (e.g., percent mass, number, or frequency of occurrence; or non-proportional data)). Location information was extracted from written descriptions and maps in the original text and was entered by drawing polygons in a Geographic Information System (QGIS Development Team, 2013; Szoboszlai et al., 2015). Additional information housed in the database but not included here will be reported in future publications and includes: study time of day, study depth, predator size/age/sex, prey size/age/sex, and values for the amount of prey consumed.

[1] For a few wide-ranging predator species we included data from the Eastern Tropical Pacific, North Pacific, inland seas, river mouths, and Gulf of California due to limited data from the CCS (annotated in Appendix B).