Comparative resource utilization of eastern North Pacific skate assemblages with applications for fisheries management

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Abstract

Comparative resource utilization of eastern North Pacific skates with applications for fisheries management

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Skates (Rajiformes: Rajoidei) are an extremely diverse group of cartilaginous, marine fishes that are common mesopredators in benthic communities. Population declines, shifts in assemblage structure, and ecological interactions with exploited groundfishes have focused increased scientific and management attention on skates. The main purpose of this study was to address a knowledge gap in the ecology of eastern North Pacific (ENP) skates, and thereby inform the development of improved monitoring and management strategies for exploited skate stocks off the U.S. West Coast and in the Gulf of Alaska. Chapter 1 investigated spatial associations of ENP skates in continental shelf and upper continental slope waters of each study region. Chapter 2 focused on the other aspect of the traditional niche by examining trophic relationships within each skate assemblage and among distant populations of big and longnose skates. The goal of this chapter was to address the paradox of ecological redundancy in skates (i.e., skates occupy similar habitats and eat similar prey). Chapter 3 utilized an improved understanding of ENP skate ecology to establish baseline information for the development of fisheries management strategies. Space appears to be more important than food in structuring ENP skate assemblages. Spatial segregation among sympatric skate species and their life stages was demonstrated off central California and in the western Gulf of Alaska. In contrast, ENP skate assemblages displayed a high degree of trophic redundancy, with the timing and location of collection trawls explaining the great majority of dietary variation. Species-level and length-based differences were highly significant, but explained a relatively minor portion of the observed dietary variability, especially in the western Gulf of Alaska. Big and longnose skates had different predatory roles in each region, with a greater reliance on decapods in the Gulf and fishes off California. Distribution and abundance patterns of U.S. West Coast skate species and their life stages were modeled and can be used to characterize essential fish habitat. Updates to a Gulf of Alaska food web model indicated that skates (especially big skate) are major predators of Tanner crab and may considerably influence regional trophodynamics.

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General Introduction

Skates are represented by nearly 300 species of benthic, egg-laying cartilaginous fishes that constitute one-quarter of all extant chondrichthyans (sharks, rays, and chimaeras). Although they are extremely speciose, skates have conservative morphology, consisting of a dorso-ventrally flattened body and a limited color pallet that includes shades of brown, grey, and black. Skate identification is therefore difficult, and skate species have been historically misidentified or grouped into generalized categories by fishery scientists and managers for convenience.

Although species-specific identification has been problematic, some general characteristics of skate biology have emerged. Skates are extremely widespread, ranging throughout the globe from intertidal regions to the abyssal plain. They typically have k-selected life histories, a trait that is especially pronounced in species that attain relatively large sizes and those that inhabit deep-water. The ecological interactions of skates are not well understood, but they are considered to be generalist predators that occur on soft-bottom regions. This suggested ecological redundancy in a speciose group of sympatric fishes presents a paradox. How can there be so many skate species if they all perform the same ecological function? It is likely that, instead, historical beliefs regarding skate ecology are a result of misidentification and a lack of focused quantitative research.

Skates are exploited in commercial groundfish fisheries throughout the world's temperate and boreal regions, primarily as bycatch in other fisheries. Despite this incidental take, fishery mortality has altered species composition of skates and caused substantial declines in the populations of many large, nearshore species. Skates were afforded little scientific or management attention in the past because they have not supported lucrative or sustained fisheries. However, this situation is changing because skates are predators and competitors of other commercially important groundfishes, and because dramatic changes in the population sizes of exploited species have occurred.

In Alaskan waters, stocks of the two dominant, shallow water (< 200 m) species, the big skate (*Beringraja binoculata*) and longnose skate (*Raja rhina*), are federally managed on a species-specific basis, whereas skates occurring in deeper waters (e.g., Aleutian skate, *Bathyraja aleutica*; Bering skate, *B. interrupta*) or in low relative abundance (e.g., Alaska skate, *B. parmifera*) are managed in aggregate. Skates in the Gulf of Alaska assemblage include species that range to the Western North Pacific (Aleutian skate, Alaska skate), those with widespread, eastern North Pacific (ENP) distributions (big skate, longnose skate), and one species that is restricted to boreal regions of the ENP (Bering skate). Most of these are relatively large species, exceeding 1.3 m total length (TL), with the smallest species (Bering skate) reaching 86 cm TL. Skates in the Gulf of Alaska are reliably identified to species, and general aspects of their distribution and abundance recently have been determined. However, spatial associations of individual species, and the degree of spatial overlap among species remain unknown. In addition, there are no published diet studies on skates from Alaskan waters. Outputs from a steady-state mass-balance model are included in stock assessments for Gulf of Alaska groundfishes, but trophic information needed to model managed skate taxa are lacking or extrapolated from distant regions. This situation is problematic for generalist predators such as skates and may not be representative of local trophic relationships. More accurate data inputs are needed to refine food web models for skates in the Gulf of Alaska, and a greater understanding of spatial ecology is necessary to evaluate inter- and intraspecific ecological interactions within the assemblage.

Only one skate species, the longnose skate (*R. rhina*) is recognized among approximately 90 federally managed groundfishes off the U.S. West Coast. Populations of four skates that commonly occur on the continental shelf and upper continental slope of the U.S. West Coast are considered ecosystem components and not directly managed: Big skate (*B. binoculata*), California skate (*R. inornata*), starry skate (*R. stellulata*), and sandpaper skate (*B. kincaidii*). Unlike the Gulf of Alaska assemblage, most species are relatively small, with only the big (to 2.4 m total length, TL) and longnose (to 1.9 m TL) Skates exceeding 76 cm TL. These two larger species occur in the Gulf of Alaska and off the U.S. West Coast, but the other, smaller West Coast skates are largely distributed from the US/Canadian border to subtropical Mexican waters. Recent, quantitative diet composition and trophic information is available for some West Coast skate species off central California, and suggests dietary variation as a function of a variety of factors (e.g., size, sex, depth) based on species-specific studies or generalized diet composition information. A more detailed synthesis of regional skate trophic ecology is needed to properly evaluate the main sources of dietary variation and assess the degree of dietary overlap among species. Management of U.S. West Coast skates lags behind that of Alaskan species, and is focused on spatial associations and the establishment of no-take zones rather than food web dynamics. West Coast skate landings still are largely unidentified, however, precluding the establishment of a baseline condition for the dominant species. Determining species composition and spatial associations of the species in the West Coast skate assemblage is therefore a necessary precursor for effective management of these fishes.

The main purpose of this study was to address a knowledge gap in the ecology of ENP skates, and thereby provide baseline information that can be used to more effectively monitor and manage exploited skate stocks in the Gulf of Alaska and off the U.S. West Coast. Chapter 1 investigated spatial associations within each assemblage to answer the following questions: 1) Are there areas within the broader study region(s) that are of differential importance to skates and their life stages?, 2) Is there spatial segregation among skate species and their life stages and, if so, at what scale(s)?, and 3) If distributions of skate species within an assemblage overlap, do they differ in size (i.e., TL)? Chapter 2 focused on the other aspect of the traditional (i.e., Hutchinsonian) niche by examining trophic relationships within each skate assemblage and among distant populations of big and longnose skates. The goal of this chapter was to address the paradox of ecological redundancy in ENP skates. Specific objectives were to: 1) determine the magnitude and primary sources of dietary variability in ENP skate assemblages, 2) compare diet composition and trophic level between big and longnose skate populations, and 3) investigate morphological relationships that may influence prey spectrums of some species.

Chapter 3 utilized an improved understanding of ENP skate ecology, provided by Chapters 1 and 2, to establish baseline information for the development of fisheries management strategies for skates. Specific objectives for the Gulf of Alaska portion of this chapter were to: 1) characterize diet composition of each skate species based on the main sources of variability (spatio-temporal, length-based) that were identified in Chapter 2, 2) estimate per capita daily consumption and consumptive removals of commercially important taxa for each skate species and the entire assemblage, and 3) incorporate diet composition and consumptive removal results for skates to update the current Gulf of Alaska food web model. The goals of the West Coast portion of Chapter 3 were to: 1) estimate distribution and abundance patterns of juveniles and adults of all soft-bottom associated skate species, 2) determine the relative importance of each factor (i.e., depth, latitude, habitat) in predicting distribution and abundance patterns, and 3) update essential fish habitat data on geographic, depth, habitat, and temperature associations of each species in the assemblage.

Chapter 1: SPATIAL SEGREGATION IN EASTERN NORTH PACIFIC SKATE ASSEMBLAGES

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Skates (Rajiformes: Rajoidei) are common mesopredators in marine benthic communities. The spatial associations of individual species and the structure of assemblages are of considerable importance for effective monitoring and management of exploited skate populations. This study investigated the spatial associations of eastern North Pacific (ENP) skates in continental shelf and upper continental slope waters of two regions: central California and the western Gulf of Alaska. Long-term survey data were analyzed using GIS/spatial analysis techniques and regression models to determine distribution (by depth, temperature, and latitude/longitude) and relative abundance of the dominant species in each region. Submersible video data were incorporated for California to facilitate habitat association analysis. We addressed three main questions: 1) Are there regions of differential importance to skates?, 2) Are ENP skate assemblages spatially segregated?, and 3) When skates co-occur, do they differ in size? Skate populations were highly clustered in both regions, on scales of 10s of kilometers; however, high-density regions (i.e., hot spots) were segregated among species. Skate densities and frequencies of occurrence were substantially lower in Alaska as compared to California. Although skates are generally found on soft sediment habitats, *Raja rhina* exhibited the strongest association with mixed substrates, and *R. stellulata* catches were greatest on rocky reefs. Size segregation was evident in regions where species overlapped substantially in geographic and depth distribution

(e.g., *R. rhina* and *Bathyraja kincaidii* off California; *B. aleutica* and *B. interrupta* in the Gulf of Alaska). Spatial niche differentiation in skates appears to be more pronounced than previously reported.

1.1. INTRODUCTION

Determining distribution and abundance patterns of sympatric organisms and the mechanisms driving these patterns are fundamental aspects of ecological research. Estimating species composition and relative abundance within an assemblage and a better understanding of ecosystem processes provide a scientific basis for effective monitoring and management of exploited marine fishes. For fishes that share a close association with the benthos, a detailed understanding of spatial associations can inform the designation of no-take zones or marine protected areas (MPAs). These tools are in widespread use to conserve and rebuild multiple sympatric fish stocks. For example, the density and mean length of four reef fishes were significantly greater in a no-take zone compared to adjacent fished regions in the southwestern Indian Ocean [1]. Off California, substantial recent advancements in the knowledge of rockfish (*Sebastes* spp.) habitat associations have been a driving force in the development of a spatial fishery management strategy that has led to the establishment of nearly 200 MPAs [2], [3]. Benefits of spatial closures are not restricted to reef fishes on rocky habitats. The establishment of a no-take zone for flatfishes in the Baltic Sea resulted in increased densities of two exploited species and a net larval export to fished areas [4].

Skates (Rajiformes: Rajoidei) are represented by nearly 300 species of benthic, egg-laying, cartilaginous fishes that constitute one-quarter of all chondrichthyan species [5]. They are common meso- and upper-trophic level predators in temperate and boreal regions, at depths ranging from the intertidal to the abyss [6], [7], [8]. Skates are among the most common bycatch in groundfish fisheries, and have been subjected to periodic direct exploitation [9], [10]. Skates present a suite of difficulties for determining accurate distribution and abundance patterns. They are remarkably morphologically conservative with a narrow palette of coloration, and therefore are challenging to identify for all but the specifically trained observer. Their habit of concealing themselves beneath the substrate leads to generalized taxonomic designations (i.e., "unidentified skate") or missed sightings on submersible transects. Finally, although skates typically are associated with soft bottom, some species are found on mixed sediments or rocky substrates, so they are not adequately sampled in bottom trawl surveys. Developing spatial models for skates will require a synthesis of sampling techniques and data sources, as well as careful verification of species for some sampling modalities.

Fishery exploitation has affected the abundance, distribution, and species composition of skates and skate assemblages. However, the impact of fishing on skate populations is variable in magnitude and direction, and cannot be precisely predicted because most skate life histories are poorly known. For example, substantial increases in the biomass of skates have been reported in some heavily exploited regions whereas declines have been noted in others [11], [12], [13], [14]. Conflicting estimated population trends of some skate stocks could be due to a poor understanding of distribution and spatial associations that lead to erroneous interpretation of survey or fishery catch rate data [15], [16], [17], [18]. Even when overall skate biomass trends appear to be stable, substantial population fluctuations may occur among individual skate stocks [19], [20], [21], [22], [23]. Where species-specific data are available, the typical response of skate assemblages to exploitation has been a decline in the abundance of relatively large, long-lived species (some of which are endangered) and an inverse trend among small, short-lived species [24], [25], [26]. However, misidentification and taxonomic uncertainty are common problems that complicate understanding skate population dynamics [9], [27], [28], [29], [30], [31].

Recent spatial studies of skates suggest complex ontogenetic and seasonal dynamics, including aggregating behavior and shifts in local abundance in association with depth changes and periodic migrations [23], [32], [33]. Skates, like other elasmobranchs, are known to exhibit different distribution patterns throughout ontogeny, with juveniles often occurring in deeper (i.e., *Bathyraja* spp.) or shallower (i.e., *Raja* spp.) waters than egg cases or adults [32], [33], [34], [35]. Although historically considered to inhabit unconsolidated, soft-bottom habitats, recent video data has indicated that several species are primarily associated with rocky substrates, including high-relief regions (Kuhnz et al., unpublished data). In addition to variable substrate associations, sympatric skate species are known to exhibit distinct depth zonation which limits their spatial overlap [36]. This depth zonation may actually be a function of variable temperature preferences among species, as temperature appears to be a key factor in determining distribution patterns and seasonal movements [16], [37]. Abundance and diversity of skates tend to reach a peak at the continental shelf break, where the shallower dwelling *Raja* species and deeper *Bathyraja* species typically overlap [36], [38]. Skates often are spatially aggregated, and the composition of these aggregations may temporally vary by sex and life stage [23], [37]. Migration patterns are poorly understood, but most appear to coincide with seasonal movements to breeding grounds and/or egg deposition sites [23].

Spatial studies of skates in the eastern North Pacific (ENP) have begun to clarify patterns of distribution and abundance among species. Five species dominate skate biomass in continental shelf and upper continental slope waters ($\leq$ 600 m) off central California and in the Gulf of

Alaska (GOA) [38], [39]. Two of these species, the big skate (*Beringraja binoculata*, formerly *Raja binoculata*; [40]) and longnose skate (*Raja rhina*), co-occur between regions. Spatial studies of skates off the U.S. West Coast consist of large-scale investigations of the composition of skate and demersal teleost assemblages [13], [41]. These studies demonstrated that *R. rhina* and, to a lesser extent, the sandpaper skate (*Bathyraja kincaidii*) are among the most abundant groundfish species by biomass, with peaks in abundance on the upper continental slope. Large-scale distribution and abundance patterns of skates in the GOA recently were described and indicated that *R. rhina* is the most abundant species by biomass, followed by *B. binoculata* [38]. Spatial segregation of skate species and assemblage composition was documented off southeastern Alaska [42]. In addition, nursery grounds of several skate species recently have been found in the Bering Sea, and suggest that skates regularly migrate to these areas to deposit their eggs [32], [43].

Recent U.S. management decisions and data needs highlight the importance of understanding spatial structure of skate stocks and guilds. A directed fishery developed for *B. binoculata* and *R. rhina* in 2003 off Kodiak Island but was considered unsustainable and curtailed in 2005 [10]. However, this fishery demonstrated that skate landings are lucrative, and retention of incidentally captured skates in the GOA has increased as a result [44]. Recognizing their variable life histories and vulnerability to exploitation, skates in the GOA were separated from a catch-all management group termed “Other Species” in 2005. Since then, separate fishing quotas have been established for the dominant, shallow water (< 200 m) species, *B. binoculata* and *R. rhina*, whereas skates occurring in deeper water (e.g., Aleutian skate, *Bathyraja aleutica*, Bering skate, *B. interrupta*) or in low relative abundance (e.g., Alaska skate, *B. parmifera*) are managed as a complex [38]. Directed fishing has been prohibited for all skate species in federal waters of the GOA since 2005. A second directed fishery for *B. binoculata* and *R. rhina* was attempted in the state waters of Prince William Sound during 2009 and 2010 by the Alaska Department of Fish and Game (ADFG), but also was terminated because of a lack of profitability and observed declines in the landings of large females (K. Goldman, ADFG, Homer; pers. comm.). However, retention of incidental skate catch in regions such as Kodiak Island, Lower Cook Inlet, and Prince William Sound remains a management concern [10], [38]. Locating aggregation sites (or hot spots) for individual skate species and for the overall GOA skate assemblage can help determine likely areas of high bycatch, which can inform fishery management.

Off the U.S. West Coast, only one skate species, *R. rhina*, is included in federal groundfish management plans. In contrast to Alaska, delineation of essential fish habitat (EFH) for individual species and associating species with habitat guilds are fundamental to groundfish management along the West Coast, typically through the designation of MPAs and other no-take zones [45]. However, skate landings along the West Coast historically have not been identified to species and misidentification of recently reported landings has further complicated an understanding of assemblage structure and stability [9]. Therefore, a baseline condition for West Coast skate assemblages must be established as a necessary first step toward spatial management.

Comprehensive, species-specific spatial studies are needed to determine distribution patterns of ENP skates, and the structure of regional skate assemblages. Improvements in skate identification by fisheries scientists have enabled this type of research for skate assemblages off central California and in the western GOA. Our initial question of interest was (Q1): Are there areas within the broader study regions that are of differential importance to skate species and their life stages? This question was evaluated by: a) determining broad-scale (regional) patterns of distribution and abundance in both study areas, b) using regression analysis to predict geographic and depth preferences on regional and local (i.e., inshore waters of the west-central GOA, Monterey Bay) scales in both study areas, and c) assessing habitat associations across a variety of scales off central California. Collectively, these results enabled an investigation of potential inter- and intraspecific variation in spatial associations, framed by the following question (Q2): Is there spatial segregation among skate species and their life stages and, if so, at what scale(s)? Finally, we asked (Q3): If distributions of skate species within an assemblage overlap, do they differ in size (i.e., total length, TL)? This question was addressed by: a) developing a randomization test to evaluate observed vs. expected species richness among regional bottom trawl hauls, and b) comparing mean sizes of species that exhibited substantial spatial overlap in trawl landings.

In summary, the overall aim of this study was to use existing, fishery-independent data to determine and compare spatial associations of the primary species and their life stages in two ENP skate assemblages. The determination of geographic, depth, and substrate associations broadens the current understanding of skate ecology, enables comparisons of assemblage structure with other skate and benthic marine teleost assemblages, and allows us to make recommendations to improve management of ENP skates based on a greater understanding of distributional patterns. Investigations of spatial and size segregation also contribute to the broader body of such literature concerning benthic and demersal marine fishes.

1.2. METHODS

1.2.1. *Data Collection: Central California*

Data and specimens necessary for megascale (1-10s of km) spatial studies [46] of the five indicated skate species off central California were collected from bottom trawl and longline surveys conducted by regional offices of the U.S. National Marine Fisheries Service (NMFS) (Table 1). The inception of all data sets corresponds to the first year of reliable, species-specific skate identifications, as determined by personal communication with survey personnel. The study site ranged from 36.0º N to 37.5º N, and corresponded to the spatial extent of published and ongoing life history and ecological research by the Pacific Shark Research Center (PSRC) (Moss Landing Marine Laboratories, California State University, Moss Landing, CA). The depth range extended from the shallowest sampled regions to the 600 m isobath. A truncated depth range was used for consistency with NMFS–Southwest Fisheries Science Center–Fisheries Ecology Division (SWFSC–FED) surveys conducted in the greater Monterey Bay area and to avoid overlap with a similar, deep-water study underway by Monterey Bay Aquarium Research Institute (MBARI) researchers in the same region. SWFSC–FED bottom trawl surveys targeted soft substrate regions, whereas bottom longline surveys were conducted on areas of extensive rock outcrop (Figure 1). All skates from these surveys were identified and sampled for biological information (e.g., TL, sex, maturity stage = juvenile, transitional, adult) by PSRC personnel. Maturity was determined using criteria established by [47]. Maturity status of skates was not determined for the coast-wide NMFS–Northwest Fisheries Science Center (NWFSC) and NMFS–Alaska Fisheries Science Center (AFSC) surveys that spanned the study range (Table 1). Instead, maturity of unsampled skates was assigned from TL data and corresponding length-at-maturity estimates, which were available for the skate populations within the study region [48], [49], [50], (Ebert, unpublished data).

Manned and unmanned submersible data were used to investigate meso- (10s of m to <1 km), macro- (1 to 10s of m), and microscale (< 1 m) habitat associations [46] of the central California skate assemblage. All skates observed during manned submersible dives of the *Delta*, conducted by NMFS personnel, and unmanned, remotely operated vehicle (ROV) dives of the *Tiburon* and *Ventana*, conducted by MBARI personnel, were identified by the authors (Bizzarro, Ebert, and Kuhnz) from archived video (Table 1). Identifications were ranked (1 = positive identification, 2 = uncertain identification) and only positive, species-level identifications were utilized. Transect data from *Delta* dives were available from long-term groundfish habitat association studies conducted on the shelf and upper slope throughout the study region and facilitated quantitative analysis (Table 1). ROV dives extended to the 600 m limit, with the great majority occurring within the Monterey Bay Canyon System at depths > 300 m (Table 1). Life stage was determined for ROV data, but too few observations were available to utilize maturity data for *Delta* dives. Whenever possible, lasers set at a fixed distance apart were used to estimate TL from ROV and manned submersible video data, which was compared to established length-at-maturity data [48], [49], [50], (Ebert, unpublished data). In some cases pelvic fins were clearly visible and the presence/absence and size of the paired copulatory organs (claspers) revealed an individual to be a mature or immature male or a female.

1.2.2. *Data Collection: Western Gulf of Alaska*

Trawl data from NMFS–AFSC and ADFG were utilized for megascale spatial analysis in the western GOA. The study site was substantially larger than that off central California, ranging from 144.0º W to 164.0º W, but also corresponded to the spatial extent of published and ongoing PSRC life history and ecological research. Trawl sets were generally fished on soft substrate regions. Regional trawl surveys of ADFG, Kodiak (Alaska Peninsula, Kodiak Island, Shelikof Strait) and ADFG, Homer (Kamishak Bay) offices were conducted within the larger study site (Figure 2). NMFS trawls reached considerably deeper depths, but the majority of the effort for the NMFS and ADFG surveys was focused on the continental shelf (Table 1). Maturity stage of each species was estimated from TL data and corresponding length-at-maturity estimates for individuals collected within the study region [51], [52], [53], [54], or in close proximity [55].

1.2.3. *Spatial Analysis*

Spatial analyses were conducted using NMFS–AFSC and NMFS–NWFSC bottom trawl data sets in California, and NMFS–AFSC data in the western GOA. Data sets encompassed the entirety of each study region, and were collected regularly over several years (Table 1). Spatial analyses addressed Q1 (i.e., areas of differential importance?) and Q2 (i.e., spatial segregation?) by determining and comparing the distribution and abundance patterns of species and their life stages, when possible.

Skate numerical and weight data, expressed as catch-per-unit-effort (#individuals/km^2; kg/km^2), were pooled across years to investigate long-term trends in abundance and biomass for every species in each skate assemblage. For this and all subsequent analyses, haul-specific mean depth data (taken from temperature-depth recorders or averaged from minimum and maximum depths) and gear midpoint locations (either provided or averaged from gear start and end points) were used whenever possible. However, only a starting location and depth were available for some of the analyzed hauls.

Spatial data analysis tools were used to link distribution and abundance patterns with the underlying process (or processes; e.g., depth, latitude) driving these patterns and the associated scale of the process. Autocorrelation and clustering were investigated on local (trends within the study region) and global (overall trend across the entire study region) scales [56]. All analyses were conducted in ArcMap v. 10.1 on data sets projected in UTM Zone 10N (WGS 1984) or Teale Albers (NAD 1927) for California and Alaska, respectively [57]. Incremental Spatial Autocorrelation (ISA), which uses Moran's I measure to test for spatial autocorrelation across a series of distances throughout a pre-defined region (i.e., study site) [57], was conducted to determine the distance associated with peak clustering of skate biomass (e.g., ISA = peak clustering at 60 km). The value obtained from ISA was then used as the incrementing distance for iterative Multi-Distance Spatial Clustering (K-Function) [58], which assessed whether skate biomass exhibited statistically significant clustering or dispersion over a range of distances (e.g., K = significant clustering at a range of 40-100 km). Global spatial autocorrelation (Global Moran's I) [59] was conducted to evaluate if skate biomass was clustered, dispersed, or randomly distributed within the overall study site. This measure ranges from -1 to 1, with values close to -1 indicating extreme dispersion, values close to 1 indicating extreme clustering, and values near zero indicating complete spatial randomness. High-Low Clustering (General G) [60], [61] was used to determine if there was significant spatial clustering of high or low values within the overall study region. The local version of the General G statistic (Gi*) was used to map and identify statistically significant regions of high (hot spots) and low (cold spots) values of skate abundance or biomass. I, G, and Gi* are indices that are used to generate an observed value for comparison with an expected value in order to evaluate statistical significance (p-value) and indicate the degree of autocorrelation or clustering (negative z-score = dispersed; positive z-score

= clustered). Iterative randomization of CPUE values among the spatially fixed observational points (i.e., haul locations) was used to test the statistical significance of the observed pattern; therefore, the introduction of simulated locations was not required.

1.2.4. *Comparison of Size Distributions*

Randomization tests were used to investigate species-specific spatial segregation (Q2), and one-way ANOVA (with Tukey's HSD post-hoc tests) and t-tests were used to determine if skate species that commonly occurred in trawls differed in size (Q3). The NMFS–NWFSC and NMFS–AFSC bottom trawl data sets were used for analysis off California and in the western GOA, respectively, and hauls with 0, 1, 2, 3, 4, or 5 skate species were recorded. For the randomization tests, an expected distribution of hauls containing 0-5 species was created to compare with the observed distribution. Because species occurrences were influenced by spatial location of hauls, binomial probabilities of occurrence were generated for each species in order to estimate the expected distribution. This step was accomplished by constructing generalized linear models with species richness (presence/absence) as the response variable and depth, latitude, and longitude as covariates. Akaike's information criterion was used to select the best models for each species. Binomial probability models for each species were combined and the expected distribution of species richness among hauls was randomized 999 times to form the expected distribution. Contingency tables with Chi-square statistics were used to determine if the observed species richness among hauls was significantly different than expected on an overall basis and, subsequently, for each level of species richness. Mean total length of species that commonly co-occurred in hauls was then compared to determine if size segregation was evident. Data for these comparisons were restricted to hauls in which both species were captured.

Normality was assessed using histograms and residuals, and power analyses were conducted when significant differences were not found.

1.2.5. *Regression Models*

Regression analysis was conducted using bottom trawl and bottom longline data sets to address Q1 and Q2, thereby complementing the previously described spatial analyses. Regression models were fit to data to determine variables that were associated with predicted numerical counts (response variable) of skate species and their life stages, and to estimate depth, geographic, and (indirectly) temperature ranges of common and maximum occurrence. Depth-temperature relationships for both regions were constructed using generalized additive models fit to data from the most expansive (global) data sets in each area, with depth as the response variable and temperature as the explanatory variable. Other covariates were not incorporated because model fits were robust, and so that established depth ranges could be isolated to predict temperature preferences directly.

The California NMFS-NWFSC data from 2003-2010 were modeled using zero-inflated Poisson (ZIP) regression, with effort (i.e., area swept) as an offset [62], because of an abundance of zero-catch data and dispersion issues with basic Poisson regression. The full model was fit for each sex-life stage of all species. Backwards model selection, with a cut-off of $p = 0.05$ was used to determine if regression coefficients significantly affected the distribution of a sex-life stage. The final life-stage specific models (without the inclusion of error terms) were then used to predict the magnitude of occurrence across the entire sampled depth and latitudinal ranges. The distribution of predicted maximum counts for sampled depth and latitude ranges were compared between transitional and adult males and females and combined if no significant covariates were found, or if the predicted depths and latitudes of maximum occurrence were within approximately 5% of the overall range of values. When individuals of a particular life stage were too few or too infrequently captured to construct robust models, transitional and adult males and females were first pooled, and then further combined with juveniles, if necessary. Covariates (depth, depth^2, latitude, latitude^2) were scaled to avoid computational problems in the optimization of regression models. Temperature was not included as a covariate because it was not consistently recorded and was highly correlated with depth. Longitude also was omitted because it was highly correlated with latitude ($\rho = 0.91$). Depth was log-transformed and the other covariates were scaled by their means and standard deviations. “Common” depth and geographic ranges were created as the locations where more than the median predicted counts were expected from the regression results. Regression model construction was generally consistent for SWFSC–FED trawl data, but oceanographic season (i.e., Davidson, December-February; Upwelling, March-July; Oceanic, August-November; after [63]) also was included, and tows were standardized by duration because no area-swept data were available.

Because skate catches were extremely low or absent in most western GOA AFSC trawl sets, these data were reduced to presence-absence and analyzed using logistic regression. Covariates included: depth, depth^2, longitude, and longitude^2 because skate distributional extents are generally oriented on longitudinal gradient in the GOA [38].

The ADFG data were analyzed using ZIP models, similar to the California data. However, length data were unavailable for the ADFG data set, precluding life-stage specific calculations. Numerical CPUE data were therefore analyzed with ZIP regression on a species-specific basis. Covariates included: ADFG fishery management region, depth, and depth^2.

ZIP models also were fit to the SWFSC–FED longline data for *R. stellulata*, and manned submersible data for *R. rhina*. All sex and age classes were combined for each species because low sample size precluded more detailed analysis. Longline data were not appropriate for analysis of other California skate species because they exhibited extremely low sample sizes relative to trawl data. Similarly, *R. rhina* was the only species for which sufficient manned submersible data were available to model distribution and habitat associations using multiple variables (mean depth, mean depth^2, latitude, habitat type, area swept) and previously described regression techniques.

The MBARI and NMFS–AFSC data for California were not analyzed with regression models because of inherent deficiencies and biases. No estimates of area swept were available for MBARI ROV data, precluding quantitative analysis. The timing and design of NMFS–AFSC continental shelf and continental slope surveys were inconsistent with those more recently conducted by NMFS–NWFSC and therefore were not included.

1.2.6. *Habitat Association Analysis*

Species-specific determination of habitat associations was possible for the central California region, using the ROV and manned submersible data, to further investigate areas of differential importance (Q1) and potential spatial segregation (Q2) among skate species and their life stages. Analytical methods varied for *Delta*- and ROV-collected data sets because of inherent differences in their methods of data collection. SWFSC–FED personnel used the *Delta* to conduct quantitative, strip transects that could be used to determine densities of fishes among different habitat types, and thereby to facilitate spatial analysis (see [2], [64]). By contrast, ROV video data were collected opportunistically during a variety of seafloor operations, which varied substantially in their objectives and in the amount of seafloor surveyed. Therefore, these data could not be standardized to produce density estimates for skates, and were instead limited to presence-only data and treated qualitatively. ROV and manned submersible data were useful, however, in providing unambiguous depth records, observing behavior under natural conditions, and examining habitat characteristics. Habitat patches of specific substrate types and general composition within a *Delta* transect were collapsed to form three habitat categories for transects: 1) Hard ($\geq$ 67% of area swept is rock), 2) Soft ($\geq$ 67% of area swept is soft sediment), and 3) Mixed (< 67% of area swept is rock and < 67% of areas swept is soft sediment). Habitat preferences were then analyzed using Pearson's chi-squared tests to compare observed and expected distributions of skates among transects of different habitat types, and an index of habitat electivity (summing to 1.0) was calculated to determine the relative magnitude of habitat preferences (after [65]).

ZIP regression model outputs were used to resolve inaccuracies in the spatial models used by NMFS to determine EFH for skates off the U.S. West Coast [66]. A habitat suitability probability (HSP) model was developed by NMFS and outside contractors to describe and identify EFH for each life stage of federally managed groundfishes [66]. HSP is a measure of the likelihood that a particular habitat (i.e., depth, latitude, and substrate type) is suitable for a fish species or life stage. This model requires prior knowledge or estimation of habitat suitability indices (HSIs) for depth (Z), latitude (Y), and substrate type (ST). HSP is then calculated from separate probabilities derived from HSIs for each habitat characteristic (Z, Y, ST) as HSP = $HSI_{yz} * HSI_{st}$. Latitude and depth HSI (HSI_{yz}) are combined and represented as a continuous variable (0-1) in the HSP model using binary presence/absence data. The midpoints of a species' latitude and depth ranges were assigned a value of 1, and then a linear relationship was established between the midpoints and the spatial extents (i.e., endpoints) of each range. HIS_{st} was determined from the literature and given a value of 0, 0.33, 0.66, or 1.00, depending on perceived preference. Results are presented graphically as an HSP profile that spans the West Coast. Because only the static HSP profiles are available, the original HSP models were recreated following strict adherence to described procedures [66] to generate consistent maps for comparison with new model outputs.

The structure of the HSP model was retained to maintain consistency with the NMFS' methods of determining EFH, but the inputs were improved to create more accurate model outputs. Minimum and maximum depth distributions were updated through a literature review, which resolved several inaccuracies. Preferred minimum and maximum depths were set to the common depth ranges established by NMFS–NWFSC ZIP models, as previously described. When available, the NMFS method used the 5th and 95th percentiles of the surveyed depth range as extents to establish preferred depths. However, such values were typically extrapolated from data rich to data poor species, such as skates. We used the optimal depths predicted with the ZIP models, instead of averaging them from preferred depth ranges. For both techniques, curves were fit through the five possible data points to generate suitability values (0-1). NMFS HSP models generate an optimal latitude by averaging latitude values at the preferred minimum and maximum depths. Because the study site was restricted to the central California coast, latitudinal distribution estimates were updated by averaging and scaling species-specific CPUE estimates from 2003-2008 NMFS-NWFSC trawl surveys among five consecutive, non-overlapping regions that spanned the West Coast [67], and then fitting a curve through these five points. Distributional extents were updated, when possible, from a literature review and used to establish zero values. Updated substrate preference information was taken directly from preference indices established from manned submersible data (after [65]). Using these updated methods, a new HSP profile was created for transitional/adult specimens of *R. inornata* as an example, and compared to a recreation of the original model for this species.

1.3. RESULTS

1.3.1. *Central California Skate Assemblage: Spatial Analysis*

Generally, skate distributions were clustered on a global scale (i.e., within the extents of the study region) significantly more than expected by chance. Global spatial autocorrelation (i.e., results of Global Moran's I analyses) was most evident for *R. rhina* and *R. inornata*, with the distribution of numerical- and weight-specific CPUE values exhibiting highly significant spatial clustering (Table 2). The distribution of *B. kincaidii* was strongly clustered by abundance, but not by biomass (Table 2). Numerical and weight values for *B. binoculata* and *R. stellulata* each were globally clustered, but the complementary values were not significant (K; Table 2). All the hardnose skates (*Raja* and *Beringraja* spp.) exhibited significant high-low clustering (General G; Table 2) by abundance and/or biomass, with results driven by high-density aggregations. For *B. kincaidii*, spatial clustering of high abundance and biomass values displayed a significant departure from spatial randomness, but clustering was more pronounced in numerical catch data. When all skates were combined for analysis, global clustering was significant (Global Moran's I; Table 2); but local clustering of high or low values was not (General G; Table 2).

Spatial processes promoting local clustering exhibited significant, maximum peaks for all species by both measures (CPUE N, CPUE WT), but the degree of clustering varied among species at broader spatial scales. ISA results indicated consistent values of maximum peak clustering between measures for *R. inornata*, *R. stellulata*, and *B. kincaidii*, as a result of consistent magnitudes between measures among fixed haul locations (Table 2). Maximum peak clustering occurred at scales ranging from 8.26 km (*B. kincaidii*) to 23.04 km (*B. binoculata*, CPUE WT) (ISA; Table 2). An opposite trend in max peak clustering was observed between *R. rhina* (greater distance by number) and *B. binoculata* (greater by weight) (ISA; Table 2). Although significant clustering was observed at specific distance intervals, broad-scale spatial clustering (K) was not significant for *R. rhina* or the two hardnose species with low sample sizes (*B. binoculata*, *R. stellulata*). The central California population of *R. inornata* was clustered at distances up to > 50 km, whereas that of *B. kincaidii* was clustered over a considerably shorter distance range (K; Table 2). For both species, multi-distance spatial clustering results were consistent between measures (K; Table 2). When species were combined, significant peak clustering was observed at 6.91 km, and skates were clustered at distances of up to 33.93 km.

Significant, largely distinct hot spots were observed for central California skate species, with clear cold spots also evident when overall skate distribution was analyzed. Significant aggregations of the two largest species, *B. binoculata* and *R. rhina*, were spatially segregated. The region of greatest *B. binoculata* clustering extended from south-central Monterey Bay northward to > 37° N, with results of lower significance at the outer edge of the surveyed area (Getis-G z-scores; Figure 3a). Isolated aggregations of *R. rhina* extended from the northern edge of Monterey Bay, and were situated at the outer continental shelf and upper slope, often in association with the headward parts of submarine canyon systems (Figure 3b). The center of *R. inornata* aggregation was located on the broad, inner continental shelf north of Monterey Bay and extended to the edge of the study region (Figure 4a), whereas that of *R. stellulata* was confined to a more limited region of the inner continental shelf to the south of Monterey Bay

(Figure 4b). *Bathyraja kincaidii* biomass exhibited a single, highly significant hot spot cluster on the outer edge of the continental shelf from ~37’ 10” N–37’ 15” N (Getis-G z-scores; Figure 4c).

Two skate species typically were caught in a tow (%FO = 52.8%, *n* = 124), but only 12.8% of tows (*n* = 30) contained three species, none contained four species, and a single haul caught all five (0.4%, *n* = 1) species. Observed and expected species richness values did not differ significantly, however, indicating that skates were not more clustered or segregated than expected among hauls ($\chi^2 = 4.62$, $p = 0.463$, df = 4). The haul with all five species was observed at 114 m, to the south of the Monterey Bay Peninsula. Catches of three species generally were scattered throughout the continental shelf from the northern axis of Monterey Bay to the northern extent of the study site, and were most commonly composed of *R. rhina*, *B. binoculata*, and *R. inornata* co-occurrences. Significant hot spots for species richness were found on the outer continental shelf in the northern part of the study region, in outer Monterey Bay, and just south of the Monterey Peninsula (Figure 5). The largest and most significant cold spot for species richness was nearly adjacent to the southernmost hot spot cluster, and other spatially restricted cold spots were noted on the continental shelf off the northern and southern mainland coast (Figure 5).

1.3.2. *Central California Skate Assemblage: Comparison of Size Distributions*

When species commonly co-occurred in central California trawls, they consistently differed in size. Among 19 hauls that captured at least one *B. binoculata*, *R. rhina*, and *R. inornata*, mean TL differed significantly among species ($F = 102.87$, $p < 0.001$). Mean TL of *B. binoculata* (88.3 ± 28.6 cm, *n* = 33) in these hauls was significantly greater than that of *R. rhina* (51.9 ± 19.0 cm, *n* = 92; Tukey’s HSD, $p < 0.001$) and *R. inornata* (39.4 ± 13.9 cm, *n* = 155; Tukey’s

HSD, p < 0.001), and specimens of *R. rhina* were significantly larger than those of *R. inornata* (Tukey's HSD, p < 0.001). When two species were caught in a haul, they were primarily composed of *R. rhina-B. kincaidii* (*n* = 69) and *R. rhina-R. inornata* (*n* = 45) co-occurrences. Mean size of *R. rhina* (47.8 ± 17.5 cm TL, *n* = 232) was significantly greater than that of *R. inornata* (41.7 ± 14.6 cm TL, *n* = 262; *t* = -4.20, *p* < 0.001). Because the NMFS–NWFSC database did not contain length information for *B. kincaidii*, length data were instead culled from the more spatially restricted SWFSC–FED trawl data set for comparative purposes (Figure 1, Table 1). Among 53 hauls in Monterey Bay that captured both species, mean TL of *R. rhina* (56.4 ± 16.4 cm, *n* = 912) was significantly greater than that of *B. kincaidii* (48.3 ± 4.9 cm, *n* = 156; *t* = -6.16, *p* < 0.001).

1.3.3. *Central California Skate Assemblage: Regression Models*

The central California skate assemblage exhibited depth zonation based on regression models constructed using NMFS–NWFSC data throughout the study range. Common distributional ranges and distribution of maximum catches were determined for *B. binoculata* and *B. kincaidii* on a species-specific basis, and for juvenile and transitional/adult life stages of *R. rhina* and *R. inornata*. The distribution of *R. stellulata* was not analyzed because captures were extremely infrequent and of small magnitude. The common latitudinal ranges of all species spanned the study region. *Beringraja binoculata* and *R. inornata* juveniles and transitional/adult individuals typically were found from the inner continental shelf to the outer continental shelf or upper continental slope, respectively (Table 3). Common depth ranges and depth at maximum occurrence were similar between *R. inornata* life stages (Table 3). The distributions of *Raja rhina* and *B. kincaidii* were shifted to deeper water, with *B. kincaidii* occurring from the outer continental shelf to the maximum depth of the study region, and *R. rhina* extending from the mid-shelf to maximum depth (Table 3). The common depth range was equivalent between *R. rhina* life stages, but the maximum count of juveniles was found approximately 45 m shallower than that of adults (Table 3). Typical temperature ranges were warmer, and much more restricted for the two shallower-dwelling species (Table 3). *Raja rhina* was (numerically) the most abundant species among non-zero hauls, whereas *B. binoculata*, by contrast, was the least abundant (Table 3).

Seasonal shifts in depth and abundance were evident in the central California skate assemblage from the greater Monterey Bay region. *Raja stellulata* catches were too low and infrequent in the SWFSC–FED trawl data set to enable modeling. The longline survey, however, exhibited much greater catch numbers and frequencies and was therefore used to estimate the distribution of this species on an overall basis (i.e., combined life stages). For all other skate species, predicted catches were greater for juveniles than transitional/adult specimens (Table 4). This trend was consistent for each species among all seasons, with the exception of *R. rhina*, and was most pronounced for *B. kincaidii*. Depth zonation was similar to that determined from the more expansive NMFS-NWFSC data set, with *B. binoculata* and *R. inornata* commonly found on the continental shelf during all seasons and *R. rhina* and *B. kincaidii* distributions extending to much deeper waters (Table 4). *Raja stellulata* typically occurred on the mid-shelf and its predicted seasonal depth of maximum counts ranged from 92-135 m. Juvenile *B. kincaidii* and, to a lesser extent, *B. binoculata* were found shallower than adults, whereas depth zonation between life stages was not evident for *R. rhina* or *R. inornata* (Table 4). Median and maximum predicted counts of juvenile *B. binoculata* and *B. kincaidii*, transitional and adult male *R. inornata*, and both life stages of *R. rhina* were most abundant during the Oceanic season. The common depth range of *B. binoculata* juveniles and transitional/adults deepened throughout the year (Davidson < Oceanic < Upwelling), whereas juvenile and transitional/adult male *R. inornata* exhibited the opposite trend (Table 4). No seasonal differences in depth zonation were evident for life stages of the deeper dwelling *R. rhina* and *B. kincaidii* (Table 4). Sample sizes were low for all species and life stages. Therefore, though these results from Monterey Bay are useful for comparative purposes with the more expansive NMFS–NWFSC data set, they should be considered preliminary.

1.3.4. *Central California Skate Assemblage: Habitat Associations*

Skates were infrequently observed during manned submersible operations off central California, with only 190 occurrences documented among 1203 dive transects totaling 0.593 km^2 of seafloor. Transect habitat composition was as follows: Hard (0.190 km^2, n = 389), Mixed (0.298 km^2, n = 618), and Soft (0.105 km^2, n = 196). *Raja rhina* was the most numerically abundant species among transects, and was significantly more abundant on mixed and soft habitat than on hard habitat (Chi-square; Table 5). Based on ZIP model results, occurrence was significantly greater on mixed sediment submersible transects as compared to soft habitat transects (z = 1.99, p = 0.046), and latitude at the maximum predicted count (36.69º N) was consistent with ZIP model results calculated from NMFS–NWFSC trawl survey data (Table 3). The depth associated with the predicted maximum count (221 m) was considerably shallower when calculated using submersible data, as a consequence of the much shallower distribution of submersible transects compared to NMFS–NWFSC bottom trawls (Table 1). Although far less commonly observed, *R. stellulata* also was encountered significantly more often on soft and mixed substrate transects (Chi-square; Table 5). *Raja inornata* and *B. kincaidii* displayed strong associations with soft substrate, whereas the few *B. binoculata* observed were all on transects of predominantly mixed substrates. All skate species displayed substantial variation in coloration, which they appeared to modify to match the surrounding seafloor. This variability was most evident in *R. rhina*, *B. binoculata*, and *R. stellulata*, all of which were more commonly observed on heterogeneous seafloors, and could exhibit black or white spotting, mottling, or markings or be of uniform coloration (browns to greys), depending on their surroundings.

Of 1002 skates observed in 3775.1 hours of bottom time during ROV dives, 977 were identified to species, including: 771 *R. rhina*, 197 *B. kincaidii*, 6 *B. binoculata*, 1 *R. stellulata*, 1 roughtail skate (*B. trachura*), and 1 deepsea skate (*B. abbysicola*). With the notable exception of *R. rhina*, hardnose skates were largely absent from this data set. *Beringraja binoculata* individuals ranged from 30-243 m and were observed resting on flat, sand- (*n* = 4) or mud-covered (*n* = 1) seafloors or swimming demersally (*n* = 1), typically within larger regions of uniform habitat type. One *R. stellulata* was observed at 103 m on a flat, lower portion of a heavily sedimented rock wall. The maximum depths recorded for the deeper dwelling species among all ROV dives performed by MBARI throughout the West Coast are: *R. rhina* (931 m), and *B. kincaidii* (786 m). There were no verified sightings of *R. inornata*.

Off central California, *R. rhina* was observed at depths of 74-599 m, with a median depth of 340 m (Q_1 = 279 m, Q_3 = 388 m). Most (94.6%, *n* = 686) individuals were found on mud, but a small percentage was found on rock, including pebble, cobble, scarps and outcrops in particular. Two specimens were observed swimming demersally. Most associated microhabitats were of low-relief (91.0%). Macrohabitat types were of greater relief (medium = 13.2%, high = 20.4%) and contained a higher percentage of rock (26.6%) than microhabitats. No obvious sexual segregation was observed. Instead, subadult and adult males and females and juveniles were found throughout the canyon system, especially on the upper slope, and were frequently encountered at the shelf break. Median depth of juveniles (276 m, $n = 196$) was substantially shallower than that of subadults and adults (361 m, $n = 255$). *Raja rhina* commonly employs its walking legs (anterior lobes of pelvic fins) for locomotion, especially at short distances, and exhibited considerable dexterity. Several individuals were observed performing traditional punting for fairly rapid, small-scale movements, with one specimen using this technique to hurdle a detached giant kelp (*Macrocystis pyrifera*) holdfast. *Raja rhina* also used its walking legs individually to pivot in place, or alternately to slowly walk across the sediment. It was observed fluidizing sediment to enable partial burying for resting and/or refuge.

Bathyraja kincaidii was found from depths of 46-596 m, with a median depth of 400 m ($Q_1 = 320$ m, $Q_3 = 455$ m). Individuals were typically found on mud (92.9%, $n = 183$), but a small percentage was associated with rock, including cobble, boulder fields, scarps and especially outcrops. Correspondingly, most associated microhabitats were of low relief (91.5%). Macrohabitat types displayed a greater association with medium- (8.5%) and high-relief (12.8%) seafloors, and contained a higher percentage of rock (17.5%), but generally were consistent with microhabitat findings. No obvious sexual segregation was observed. An aggregation of juveniles ($n = 20$) was noted between 451-564 m on a single dive conducted during March 2007 on the central portion of the northern canyon system. *Bathyraja kincaidii* was occasionally observed using its walking legs to punt; however, its primary form of locomotion is undulatory swimming with an exaggerated, flapping motion. *Bathyraja kincaidii* often skims the benthos as it swims, burst swimming and relocating quickly when startled, as indicated by a trailing plume of sediment. Like *R. rhina*, *B. kincaidii* was observed fluidizing sediment to enable partial burying.

The HSP profile of *R. inornata* adults was substantially modified based on the results of this study (Figure 6a). Sizes were generally consistent between adult designations of *R. inornata* as defined by NMFS from anecdotal data (> 52 cm TL), and transitional/adult designations as defined in this study from unpublished size-at-maturity information (males > 50.1 cm TL, females > 54.5 cm TL). All of the general input parameters (latitude, depth, benthic habitat) were updated, resulting in a new HSP map that bears little resemblance to the original (Figure 6b). The most notable difference between the two profiles is the significant reduction in suitable habitat in the updated profile (Figure 6). Maximum verified depth for *R. inornata* was reduced from 1600 m to 318 m, with the prior depth record consisting of a misidentification. This correction moved the distribution of this species considerably inshore (Figure 6). In addition, highly suitable habitat (HSP > 0.80) was greatly reduced and restricted to a region of central California off San Francisco Bay (Figure 6b). Habitat suitability also showed a much more pronounced latitudinal gradient in the updated map, with all HSP values > 0.2 contained entirely within California and poor habitat quality located off the Oregon and Washington coasts (Figure 6b).

1.3.5. *Western Gulf of Alaska Skate Assemblage: Spatial Analysis*

Clustering of skate distributions in the western Gulf of Alaska was highly significant at the global scale, driven by the greater intensity of highly clustered high catch rates over lows. Global spatial autocorrelation was marked for both measures of all species (Global Moran’s I; Table 6). Z-scores for all General G statistic calculations were positive, indicating that spatial highs were of significantly greater influence than spatial lows for this data set. When individuals of all species were considered, the results mirrored those of single species (Table 6).

Local clustering was significant at peak intervals and over broad spatial scales for four skate species in the western GOA. ISA yielded significant results by both measures for all species but *R. rhina* (Table 6). Clustering exhibited similar significant maximum peaks among species by weight, at distances ranging from 34.34-40.36 km. Numerical CPUE results of ISA were more variable and typically occurred at greater distances (Table 6). Clustering was highly significant at scales ranging from 20.06 km (*B. binoculata*, number) to 41.87 km (*B. parmifera*, biomass) but was quite similar between measures for all species (K; Table 6). In each case, cluster distance was comparable or slightly larger by weight (K; Table 6). When individuals of all species were combined, there were no significant peak clusters. Skates distribution was significantly more clustered than random, however, at distances of up to 24.26 km.

Significant hot and cold spots were observed for skates in the western GOA, with several clusters and/or expansive, highly clustered areas located within the study region. Significant aggregations of *B. binoculata* and *R. rhina* were spatially segregated. Highly significant, long-term regions of *B. binoculata* aggregation were located along the mainland coast (especially lower Cook Inlet), on the continental shelf southwest of Kodiak Island, and off the Island's east coast (Figure 7a). By contrast, cold spots were less significant and located in regions of relatively deep water at the outer edge of the survey region and just south of the Kenai Peninsula (Figure 7a). The same general region south of the Kenai Peninsula contained the greatest concentration of clustered *R. rhina* biomass values, with a smaller, more diffuse region extending from northeastern Shelikof Strait to the offshore waters north of Kodiak Island (Figure 7b). Additional, localized hot spots were scattered throughout the eastern and central portion of the study region, whereas the greatest concentration and most highly significant low values occurred at the western extent (Figure 7b). The *B. aleutica* population was highly significantly concentrated from the greater Shelikof Strait region to the continental shelf region southwest of Kodiak (Figure 8a). A similarly expansive region of clustered low biomass values extended from southern Cook Inlet directly offshore and from the southern coast of the Kenai Peninsula to deeper, offshore regions (Figure 8a). The primary region of *B. interrupta* aggregation also was located throughout Shelikof Strait (Figure 8b). Spatially restricted, positive clustering was observed on the outer shelf in the east-central portion of the study region, and similar, isolated cold spots were located in the central and especially western part of the study site (Figure 8b). Highly significant hot spots were observed for *B. parmifera* at the western extent of the study region, with more spatially restricted, less significant clustering occurring on the continental shelf south and east of Kodiak, in southern Cook Inlet, and at the outer edge of the continental shelf at ~158ºW–159ºW (Figure 8c).

The great majority of tows contained no skates (57.0%, $n = 2241$) or one species (30.6%, $n = 1202$). Tows with multiple species were infrequently observed. Only ten tows (0.3%) contained four species and no tows contained all five species. Observed and expected values differed significantly, with tows of zero, four, and five species occurring less often than expected by chance and tows with one species occurring more often ($\chi^2 = 65.40$, $p < 0.001$, df = 4). Tows with multiple species mainly were located in the central and north-eastern part of the study region, with the region of greatest species richness occurring in the greater Shelikof Strait region and waters south and west of Kodiak Island. In all cases, hauls with four species did not contain *B. parmifera*.

Highly significant clustering of highs and lows was evident throughout the study region for combined skates of all species. An expansive, contiguous cluster of highly significant positive values for species richness was located in the greater Shelikof Strait region, with more restricted regions evident throughout the central and north-eastern portion of the study site (Fig 9). Cold spots were largely clustered in the western and outermost central portion of the region (Figure 9).

1.3.6. *Western Gulf of Alaska Skate Assemblage: Comparison of Size Distributions*

When species commonly co-occurred in trawls conducted in the western Gulf of Alaska, they typically differed in size. Among the 10 hauls that captured four species, mean TL differed significantly among species (Table 7). Mean TL of *B. binoculata* was significantly greater than that of all other species, whereas *B. interrupta* was significantly smaller (Table 7). No difference was noted between mean TL of *R. rhina* and *B. aleutica*, but the power to detect a difference was extremely low (Table 7, Power = 0.04). The majority (60%) of tows with three species ($n = 55$) caught *R. rhina*, *B. aleutica*, and *B. interrupta*. Mean TL of these species differed significantly, as did all post-hoc comparisons (Table 7). Among co-occurring species pairs, mean size of (larger indicated first) *R. rhina–B. interrupta* ($n = 141$ tows), *B. aleutica–B. interrupta* ($n = 44$ tows), and *B. binoculata–B. interrupta* ($n = 24$ tows) differed significantly (Table 7). *Raja rhina–B. binoculata* ($n = 42$ tows) and *R. rhina–B. aleutica* ($n = 82$ tows) mean TL did not differ significantly (Table 7). Relatively high standard deviations resulted in low power for these comparisons (Power = 0.13, 0.05; respectively).

1.3.7. *Western Gulf of Alaska Skate Assemblage: Regression Models*

The western GOA skate assemblage exhibited depth and spatial zonation based on results of regression models constructed using NMFS–AFSC data throughout the study range. Skates in the GOA were far less frequently encountered and exhibited much lower catch rates than those off central California (Table 2, Table 6). Individuals of all life stages of *B. binoculata* exhibited very similar common depth and longitudinal ranges, and depths of maximum occurrence (Table 8). Distribution of *R. rhina* life stages was variable. Transitional specimens had the widest (and deepest) typical depth range, and the distribution of adults was shifted to more shallow waters than that of juveniles (Table 8). Depth of maximum occurrence, however, decreased with ontogeny, and juveniles commonly occurred over a much broader longitudinal range than transitionals or adults (Table 8). The typical temperature range for *R. rhina* was more restricted and slightly lower in the GOA than off central California (Table 3, Table 8). *Bathyraja aleutica* exhibited the same trend in maximum occurrence as *R. rhina*, with juveniles found at deepest depths and adults at shallowest. The depth ranges of maximum occurrence, as well as the common depth ranges, were shifted to deeper water for life stages of this species, and the center of distribution occurred more westward than that of *R. rhina* (Table 8). Correspondingly, *B. aleutica* commonly occurred across a temperature range that was slightly warmer than that of *R. rhina* (Table 8). Depth and spatial zonation differed somewhat between life stages of *B. interrupta*, but differences were not of substantial magnitude or consistent across ontogeny (Table 8). The depth range of this species overlapped considerably with that of *R. rhina* (slightly shallower) and *B. aleutica* (slightly deeper), but the longitudinal range of common occurrence was shifted west of *R. rhina*, and the longitude at maximum occurrence was distinct (Table 8). *Bathyraja parmifera* was captured infrequently and in very low numbers, but was encountered over the widest depth range of all species (Table 8). Transitional individuals commonly were found both shallower and substantially deeper than juveniles, at temperatures ranging from (2.7ºC–8.0º C). However, results should be considered preliminary for this species because of extremely low and infrequent counts. The maximum predicted occurrence of this species was at the western extent of the study region. For all species, median predicted occurrences of juveniles were greater than that of older life stages, and maximum predicted occurrences were always greatest for juveniles (Table 8).

Predicted depths of occurrence and magnitude of catches varied considerably among skate species and ADFG management regions. The largest predicted counts of *B. binoculata* were in Shelikof Strait, with lowest values associated with the Alaska Peninsula region. Predicted depth at maximum occurrence was consistent among regions and occurred in shallow shelf waters (Table 9). Predicted common depths, however, varied considerably among regions at depths ≤ 155 m. *Raja rhina* occurrence was greatest at Kodiak and Shelikof, with the maximum count (3.92/tow) predicted at 176 m off Kodiak Island. When compared with *B. binoculata* distribution, greater counts of *R. rhina* were evident at Kodiak and Kamishak, with greater median but smaller maximum values at Shelikof, and fewer *R. rhina* off the Alaska Peninsula (Table 9). Depths of common *R. rhina* occurrence extended from the mid-shelf to the outer shelf or upper slope. Like *B. binoculata*, predicted maximum depths of *R. rhina* occurrence were consistent among regions (176-178 m), but predicted common depth ranges were highly variable (Table 9). *Bathyraja interrupta* was relatively common, with median and maximum predicted catches exceeding those of *B. binoculata* and *R. rhina* in each management region. Depth ranges were similar to those of *R. rhina* in each region but Shelikof, where *B. interrupta* extended into considerably deeper waters (Table 9). Depths of maximum predicted catches, however, were considerably deeper than those of *R. rhina* at all locations except Kamishak (Table 9).

Bathyraja aleutica and *B. parmifera* were rare in Kamishak surveys and their distributions were therefore only modeled for three management regions. *Bathyraja aleutica* was relatively abundant in Shelikof Strait, where it had the greatest maximum predicted catch of any species (Table 9). The common depth range of *B. aleutica* overlapped substantially with that of *R. rhina* and *B. interrupta*, whereas the maximum predicted depths mirrored that of *B. interrupta*. As previously indicated, however, mean sizes of these specimens differed significantly. *Bathyraja parmifera* occurrence was infrequent among all management regions, but common and maximum predicted catches were greatest at Kodiak and least at Shelikof (Table 9). This species was primarily distributed on the outer continental shelf with only slight variability among regions (Table 9).

1.4. DISCUSSION

Spatial segregation among ENP skates was pronounced (Q2), and supports a general conclusion that comparably sized skate individuals of different species do not typically co-occur (Q3). In both study regions, species distributions exhibited temporally consistent areas of high aggregation that were largely distinct among species (Q1, Q2). Skate species in the North Atlantic and off South Africa have similar, patchy distribution patterns with little spatial overlap between dominant species [36], [68], [69]. When abundant species do overlap considerably in distribution, it is consistently reported among species of differing size. In the western GOA, the core regions of *B. aleutica* and *B. interrupta* overlapped substantially in Shelikof Strait, but early life stages of the larger species, *B. aleutica*, were absent. When a third species of intermediate size (*B. parmifera*) was present, its TL mode occurred between that of the other two congeners [70]. Off California, the core regions of *B. kincaidii* and *R. rhina* distribution overlapped, especially in association with headward parts of submarine canyons. *Raja rhina* grows to 1.80 meters [29], nearly three times the maximum size of *B. kincaidii* (66 cm TL) [71]. Among seven skates that constitute a skate assemblage between Nova Scotia and Cape Hatteras, North Carolina, most exhibited little spatial overlap; however, two species pairs (*Leucoraja erinacea–L. ocellata*; *Malacoraja senta–Amblyraja radiata*) had complementary distributions [72]. Each pair consisted of one species that attained a maximum size that was nearly twice that of the other [73]. A similar relationship has been demonstrated among demersal rockfish congeners in the ENP that are sympatric with *R. rhina* and *B. kincaidii*. *Sebastolobus alascanus* occupies shallower depths than similar sized *S. altivelis*, but moves down slope to shared habitats after attaining larger sizes [74].

Limited competition for prey resources may be a primary factor driving the observed co-occurrence of some skate species pairs. Diet composition of skates generally is consistent among size classes: small skates and early life stages of large species (< ~50 cm TL) consume amphipods, small decapods, and polychaetes; medium-sized skates (< ~100 cm TL) consume decapods with some small fishes; and large skates (≥ 100 cm TL) consume fishes and large decapods [75]. Dietary differences, therefore, may facilitate coexistence among skates of different sizes by limiting exploitative competition. For instance, diets of *R. rhina* > 60 cm TL differed markedly from those of *B. kincaidii* collected in the same habitats off central California [39]. Intraspecific competition typically is more intense than interspecific competition because individuals within a species are more ecologically similar to those of other species. Intraspecific competition among similar sized individuals may therefore further structure the distribution and abundance of the studied skate populations. A detailed examination of dietary variability will be necessary for a complete assessment of resource utilization in ENP skate assemblages, and to determine the extent of niche differentiation within and among species.

Spatial variability was evident by life stage and season for some ENP skates, but transitional and adult male and female distributions were similar within species. Some studies have reported sympatric occurrences of juveniles and adults (e.g., [76]), whereas others report segregation (e.g., [77]). It has been further suggested that juvenile hard-nosed skates (*Raja* spp.) occur at shallower depths than adults, whereas the opposite situation is described for *Bathyraja* spp. [32], [33], [51]. The results of this study provided only limited support for the suggested ontogenetic differences in distribution (e.g., *B. binoculata* off California, *B. aleutica* in the western GOA), and in some cases an opposite trend was observed (e.g., *B. kincaidii* off California). Complex seasonal immigration and emigration patterns of juveniles and adults also have been reported for some species of skates, resulting in spatial segregation by sex and life stage [77], [78], [79], [80]. It is possible that seasonal migrations and intraspecific segregation patterns are more widespread than reported because of inconsistencies in the methods and timing of specimen collection. For instance, sex ratios obtained from a limited time period or during multiple seasons may be insufficient to reliably infer sexual segregation [36], [45]. In this study, seasonal variability in distribution and abundance was typical among Californian skates, suggesting seasonal movements and possible immigration/emigration from the study region. Adult and transitional individuals of all species in both regions displayed very similar distribution patterns between sexes. Since the primary surveys used in this study occurred during summer months, it is suggested that sexual segregation is not apparent among mature and maturing individuals at this time. However, year-round surveys, and (ideally) telemetry studies are necessary to resolve ambiguity in these and similar results to better understand intraspecific spatial relationships of skates throughout ontogeny.

Spatial analysis of ENP skates has yielded new insights into skate spatial associations and assemblage structure. Investigation of autocorrelation and clustering in ENP skate distributions enabled the determination of regions of aggregation and relative scarcity for skates within the larger seascape. Skate populations were highly clustered off central California and in the western GOA, with the distances of maximum peak clustering substantially greater for Alaskan species. This difference may be reflective of the greater relative abundance of California skates. Fishing pressure, environmental characteristics, geographic location and faunal composition differ substantially between study regions. The design and gear specifications of NMFS surveys also differed between study regions (e.g., [67], [81]), as did the relative size of the study regions. Therefore, any conclusions about the reasons for these perceived differences are largely speculative. Each assemblage contained five primary species of variable sizes. Differences in size composition are typical, but species richness in the study regions is depauperate compared to most continental shelf and upper continental slope assemblages [36], [72], [82]. In Alaska, several deep-water species venture above 600 m, and when these are considered, regional skate diversity is relatively high [38], [71]. However, off California only one such deepwater vagrant, *B. trachura*, is present. It is not known if this discrepancy in skate diversity between ENP regions is a result of tropical submergence in California skates or a result of variable benthic community structure between locations. As is typically noted, the assemblages contained endemics (i.e., *R. inornata*, *R. stellulata*, *B. parmifera*) as well as wide-ranging species (*B. binoculata*, *R. rhina, B. aleutica*) [7] [71]. *Bathyraja interrupta*, which was originally believed to range from the Bering Sea to southern California, appears to be a species complex consisting of *B. kincaidii* off the West Coast and potentially several Alaskan species (J. Orr, NMFS–AFSC;

pers. comm.). The largest species were the most widespread, which may indicate increased mobility, broader environmental tolerances, or possibly competitive dominance [75], [83], [84].

Considerable advances have been made in understanding spatial relationships of skates and the processes that drive observed distribution patterns. Based on a review of the available literature, the primary process at work appears to be temperature; with depth and substrate association serving to further define habitat niches. Temperature differences were noted among ENP skate species, especially between *B. binoculata* populations, which inhabited much colder waters at comparable depths in the GOA. A similar situation was exhibited by *Leucoraja erinacea* populations in the North Atlantic [76], demonstrating that: 1) allopatric skate populations may exhibit highly variable temperature associations, and 2) some species may have extremely broad temperature tolerances that enable large potential distributions. Skate populations may be concentrated at temperatures that are known to be suboptimal for growth and maintenance even when other, more favorable temperature regimes are locally available [37]. Temperature also appears to be a major driving force in determining the structure and dynamics of skate assemblages [23], [78], [82]. The common skate, *D. batis*, and a recently discovered cryptic species have overlapping depth and substrate associations, but distributions are largely dictated by variable thermal limits, resulting in considerable interspecific spatial segregation [31]. Migrations to spawning grounds cause additional temporal variability in skate assemblage structure [80], [82]. Inter- and Intraspecific depth zonation was observed among ENP skates and is a common condition within skate assemblages (e.g., [36], [85]). Off California, observed seasonal differences in depth distribution likely tracked temporal variation in bottom temperatures. Skate assemblages, and constituent species, appear to exhibit different sediment associations that may further differentiate habitat niches among sympatric skates [82], [85], [86].

Off California, habitat associations differed substantially among all species, with *R. rhina* exhibiting the most general characteristics and having the most widespread distribution. Based on these results, spatial niche differentiation appears to be more pronounced in skates than previously reported [6], [7].

Advances in knowledge of ENP skate biology include resolved depth distributions, new information on substrate and temperature preferences, and the determination of spatial associations at a variety of scales. In Alaska, depth distributions were largely consistent with previously reported information [38], although the depth information was expanded from predictions of common depth ranges and depths of maximum occurrence. In California, where skate identification has been less reliable, considerable confusion in skate depth distributions was resolved. *Raja inornata* has been reported to 1600 m [71]. Results of this study, however, indicate that it is largely a shelf species that ranges to the upper slope, with a predicted maximum occurrence in waters < 75 m. Sporadic occurrences of skates well beyond their normal depth range have been reported but a discontinuity of this magnitude can only result from identification error [72], [82]. Smaller discontinuities are evident for *B. binoculata* and *R. stellulata*, which are largely distributed on the inner and mid shelf but have maximum reported depths of 800 m and 732 m, respectively. Verified specimens are necessary to resolve potential misidentification of these species in deep water.

Depth information was used to create temperature profiles for each species, which represents the first such reported information for ENP skates and enables a more nuanced understanding of skate distributions and comparisons among systems. Habitat associations were determined for several California species for the first time. *Raja stellulata* was most commonly associated with rocky reef habitats. This species has dermal denticles on its ventral side, perhaps to protect it from abrasion in these regions, a phenomenon that could be more widespread and warrants further attention. *Raja rhina* mainly was distributed on mixed and, to a lesser extent, soft habitats at a variety of spatial scales, whereas *B. kincaidii* was largely observed on mud. Since habitat associations of most groundfishes are spatially consistent (e.g., [87]), *R. rhina* also can be expected to occupy mixed and soft habitats in the GOA. Direct substrate associations of *R. inornata* could not be determined, but its center of aggregation was largely restricted to the wide continental shelf region between Monterey and San Francisco. This region consists mainly of mud, with sands confined to inner and outer shelf waters [88]. All ENP skate species but the California population of *R. rhina* exhibited long-term areas of high aggregation. Instead, *R. rhina* distribution was generally ubiquitous from the mid shelf to upper slope off central California.

Skate management in the GOA has advanced to consider individual quotas for commonly exploited skate species (i.e., *B. binoculata*, *R. rhina*) and to establish a precautionary closure to directed fishing, but we offer some suggestions to enable continued progress. Habitat areas of particular concern (HAPCs), subsets of EFH that are considered to be vital to the long-term sustainability of particular species, have been established to protect six skate nursery grounds in the Bering Sea [32]. Results of hot spot analysis can be used to distinguish areas that are especially important to particular skate species, life stages, or the overall GOA assemblage, as a basis for the creation of HAPCs or to delineate fishery management areas and establish regional quotas. *Beringraja binoculata* is a large, nearshore species and therefore may be particularly vulnerable to fisheries exploitation [26]. Within two years of the inception of a *B. binoculata* fishery in Prince William Sound, a notable decline was observed in the overall abundance and relative proportion of subadult and adult females, contributing to the termination of the fishery

(K. Goldman, ADFG, Homer; pers. comm.). By determining the common depth, temperature, and geographic distribution of this species, populations in the western GOA can be better monitored and managed. Detailed distribution and relative abundance information provided from this study also can inform food web models (e.g., [89]) by estimating the degree of spatial overlap among species, which may impact the intensity of their trophic interactions. Regional differences in the relative abundance of skates were noted among ADFG management regions. Length data should be analyzed to determine whether ontogenetic composition is consistent or variable among regions to better understand observed differences and possible causation. Survey data were grouped for the purposes of this study, but can be assessed on a yearly basis to determine how environmental variability may affect species composition and relative abundance between management regions.

Although the efficacy of California's MPA experiment is still largely unknown, spatial management has been embraced along the West Coast and accurate, species-specific spatial data are the foundation of this strategy [90]. Identification of skate landings remains a major problem in California, with over 99% of all such landings classified as "unspecified skate" [9]. *Raja inornata* is highly sexually dimorphic and may contain a cryptic species (*R. inornata inermis*) [28]. Based on recent NMFS–NWFSC surveys that record this species from the mid slope [67], it probably continues to be misidentified. Morphometric and genetic techniques should be combined to resolve any taxonomic issues with *R. inornata* and establish a reliable means of identification. The probability of a skate species occurring at a particular depth can be predicted from the regression models created for this project, and should be used to assess the reliability of extreme depth records. A synthesis of results regarding habitat associations, and depth and geographic distributions was used to update the HSP profile for adult *R. inornata*, which considerably reduced the amount and spatial distribution of highly suitable habitat regions. Since HSP profiles are used to distinguish EFH, the updated profile of *R. inornata* can directly inform the development of improved management plans for this species along the West Coast. Updated HSP profiles for *B. binoculata* and *R. rhina* also can be constructed from the results of this project for the same purpose.

Skates are a remarkably speciose group of fishes that are distributed throughout the world's oceans. Project findings indicate that ENP skates: 1) occupy regions of differential importance (e.g., hot and cold spots) within the study regions, 2) are spatially segregated by species and often also by life stage, and 3) differ in size when they commonly co-occur. Skates therefore appear to have much more complex spatial associations than were previously described [6], [7]. Although they are morphologically conservative, skates may exhibit the greatest distribution of any fish group, occurring from pole to pole, at depths ranging from ≤ 2 m (*B. binoculata*, *R. stellulata*) [71] to 4156 m (*Rajella bigelowi*) [91]. Reliable identification, measurements, and life history research can facilitate relatively inexpensive, detailed spatial studies such as this one, which can provide a more nuanced understanding of skate distributions and assemblage structure. Seasonal surveys and telemetry studies are necessary to provide greater resolution to results of this project and to expand knowledge of skate migrations and habitat use. Coupled spatial and trophic studies can better assess the degree of niche differentiation among sympatric species and are an important next step in building a greater ecological understanding of skates. An improved ecological understanding of skates may in turn help explain their observed diversity patterns and can contribute to the formation of effective fishery management plans for benthic marine communities.

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1.6. TABLES

Table 1.1. Number (N) of trawl tows, longline sets, and submersible dives (MBARI) or dive transects (NMFS–SWFSC–FED); and temporal occurrence [Month(s), Year(s)] and depth (Median, Range, Quartiles) of sampling efforts conducted by regional offices of federal (NMFS) and state (ADFG) management agencies, and by an independent research institution (MBARI) throughout and in local areas of the western Gulf of Alaska and off central California.

Region	**Organization**	**Sampling Method**	**N**	**Month(s)**	**Year(s)**	**Depth Range**	**Median Depth**	**Depth Quartiles**
						m	**m**	**m**
Central California	NMFS–AFSC*	Bottom Trawl	98	June–Oct	1998–2004	59–477	118	90–335
Central California	NMFS–AFSC**	Bottom Trawl	24	June–Oct	1997–2001	190–602	422	245–465
Central California	NMFS–NWFSC	Bottom Trawl	235	June–Oct	2003–2010	58–598	118	94–268
Monterey Bay	NMFS–SWFSC–FED	Bottom Longline	106	Jan–Dec	2002–2005	5–503	93	88–136
Monterey Bay	NMFS–SWFSC–FED	Bottom Trawl	80	Jan–Dec	2002–2003	9–614	144	66–294
Monterey Bay	MBARI	ROV	219	Jan–Dec	1997–2007	30–600	354	261–424
Monterey Bay	NMFS–SWFSC–FED	Manned Submersible	1203	Aug–Nov	1992–2009	24–316	107	73–193
Western GOA	NMFS–AFSC	Bottom Trawl	3931	May–Aug	1999–2011	13–984	121	80–180
Kamishak Bay	ADFG–Homer	Bottom Trawl	160	May–Aug	2003–2012	49–326	128	45–139
Alaska Peninsula	ADFG–Kodiak	Bottom Trawl	1368	July–Aug	2003–2012	18–210	101	45–72
Kodiak Island	ADFG–Kodiak	Bottom Trawl	1836	June–Sept	2003–2012	15–253	121	40–80
Shelikof Strait	ADFG–Kodiak	Bottom Trawl	278	Sept	2003–2012	59–289	156	65–100

Note: Data were collected yearly for the indicated ranges, with the following exceptions: NMFS–AFSC* = 1998, 2001, 2004; NMFS–AFSC** = 1997, 1999, 2001; NMFS–SWFSC–FED (submersible) = 1992–1994, 1997, 1998, 2002–2004, 2007–2009; western GOA = biennially; Kamishak Bay = 2003–2007, 2010, 2012. * = effort was focused on continental shelf, ** = effort was focused on continental slope; NMFS = National Marine Fisheries Service, AFSC = Alaska Fisheries Science Center, NWFSC = Northwest Fisheries Science Center, SWFSC–FED = Southwest Fisheries Science Center–Fisheries Ecology Division, MBARI = Monterey Bay Aquarium Research Institute, ADFG = Alaska Department of Fish and Game, ROV = remotely operated vehicle, N = number of samples for each method, Oct = October, Jan = January, Dec = December, Aug = August, Nov = November, Sept = September, m = meters.

Table 1.2. Results of spatial analysis of catch–per–unit-effort (CPUE) by number (N) and weight (WT) for the five most abundant skate species collected during National Marine Fisheries Service, Northwest Fisheries Science Center and Alaska Fisheries Science Center trawl surveys (*n* = 422) conducted during 1997–2010 on the continental shelf and upper slope of central California. Abundance (N), biomass (WT, kg), and frequency of occurrence (%FO) are presented. Statistics include: Incremental Spatial Autocorrelation (ISA), Autocorrelation (Moran's I), Multi-Distance Spatial Clustering (K-Function), and High-Low Clustering (General G).

Species	**N**	**WT**	**%FO**	**Measure**	**ISA km**	**Moran's I**	**K km**	**General G**
Beringraja binoculata	73	504	10.0	CPUE (N)	15.00*	0.091**	NS	0.730*
				CPUE (WT)	23.04*	0.033	NS	0.712
Raja rhina	2787	4706	72.3	CPUE (N)	21.68*	0.086**	NS	0.028*
				CPUE (WT)	8.26*	0.082**	NS	0.032*
Raja inornata	697	465	28.0	CPUE (N)	13.63*	0.218**	52.25*	0.045**
				CPUE (WT)	13.63*	0.239**	51.28*	0.050**
Raja stellulata	30	40	3.1	CPUE (N)	16.31*	0.009	NS	0.056
				CPUE (WT)	16.31*	0.036*	NS	0.126*
Bathyraja kincaidii	1663	923	45.3	CPUE (N)	8.26*	0.238**	15.89*	0.050**
				CPUE (WT)	8.26*	0.005	18.83*	0.055*
All Species	5250	6,638	89.1	Species Richness	6.91*	0.069**	33.93*	0.023

Significant *p*-value thresholds are indicated as follows: * = < 0.05, ** = < 0.001, NS = not significant. N = number, WT = weight (kilograms), %FO = frequency of occurrence among hauls, ISA = incremental spatial autocorrelation, K = K Function, km = kilometers.

Table 1.3. ZIP model predictions of median and maximum count, and associated depth and latitude ranges, and GAM model predictions of temperature for central California skate species/life stages throughout the study site.

Model Outputs	***B. binoculata***	***R. rhina* (juv)**	***R. rhina* (t-a)**	***R. inornata* (j)**	***R. inornata* (t-a)**	***B. kincaidii***
Non–Zero Hauls (N)	30	149	138	97	66	80
Median Count	0.2	3.3	1.7	0.9	0.4	0.1
Common Depth (m)	58–182	124–598	124–598	58–231	58–242	173–598
Common Temp (C)	8.6–9.6	5.4–9.1	5.4–9.1	8.2–9.6	8.2–9.6	5.4–8.7
Common Lat	36.00–37.50	36.10–37.50	36.00–37.50	36.03–37.50	36.00–37.50	36.00–37.50
Max Count	1.3	12.3	6.0	8.2	3.3	18.1
Max Depth (m)	58	293	338	67	58	354
Max Latitude	36.00	36.80	36.74	37.13	37.01	36.92

Juv = juvenile, t-a = transitional and adults, N = number of hauls, m = meters, C = degrees Celcius, Max = maximum. Results were calculated from National Marine Fisheries Service–Northwest Fisheries Science Center trawl data collected during 2003–2010 among 235 tows throughout the study region. Common depth, temperature, and latitudinal range are included (see methods), as well as the depth and latitude at which the maximum number of skates were predicted.

Table 1.4. ZIP model predictions of median and maximum count, and associated depth ranges, and GAM model predictions of temperature for life stages of central California skates in Monterey Bay.

Species	Life Stage	Season	Catches	Hauls N	Median Count	Common Depth m	Common Temp m	Pred. Max Count	Pred. Depth	Pred. Temp C
B. binoculata	J	Davidson	22	46	6.3	14–85	9.4–9.9	7.9	18	9.9
B. binoculata	J	Oceanic	22	46	13.7	14–113	9.2–9.9	21.2	35	9.8
B. binoculata	J	Upwelling	22	46	6.3	38–164	8.8–9.7	9.2	79	9.4
B. binoculata	TR, A	Davidson	14	46	1.5	21–152	8.9–9.9	2.8	59	9.5
B. binoculata	TR, A	Oceanic	14	46	0.9	30–164	8.8–9.8	1.5	68	9.5
B. binoculata	TR, A	Upwelling	14	46	0.8	63–318	7.6–9.5	1.3	141	9.3
R. rhina	J	Davidson	28	35	23.0	113–342	7.4–9.2	40.3	204	8.5
R. rhina	J	Oceanic	28	35	33.6	32–532	5.9–9.8	54.1	426	6.7
R. rhina	J	Upwelling	28	35	10.4	91–368	7.2–9.3	13.7	176	8.7
R. rhina	TR, A	Davidson	24	35	9.6	91–459	6.5–9.3	11.2	204	8.5
R. rhina	TR, A	Oceanic	24	35	28.3	98–532	5.9–9.3	37.7	396	7.0
R. rhina	TR, A	Upwelling	24	35	13.8	73–532	5.9–9.5	17.6	204	8.5
R. inornata	J	Davidson	21	46	5.9	24–318	7.6–9.8	8.5	98	9.3
R. inornata	J	Oceanic	21	46	5.3	44–190	8.6–9.7	7.1	98	9.3
R. inornata	J	Upwelling	21	46	15.7	32–113	9.2–9.8	28.8	59	9.6
R. inornata	TR, AM	ALL	18	46	1.4	30–176	8.7–9.8	1.7	91	9.3
R. inornata	TR, AM	Davidson	18	46	1.3	26–220	8.3–9.8	1.8	79	9.4
R. inornata	TR, AM	Oceanic	18	46	8.8	30–176	8.7–9.8	20.1	73	9.5
R. inornata	TR, AM	Upwelling	18	46	3.7	35–141	8.9–9.8	7.1	68	9.5
R. stellulata	ALL	Davidson	24	106	1.8	84–123	9.1–9.4	5.9	102	9.3
R. stellulata	ALL	Oceanic	24	106	0.9	70–260	8.0–9.5	1.9	135	9.0
R. stellulata	ALL	Upwelling	24	106	0.9	70–112	9.2–9.5	1.9	92	9.2
B. kincaidii	J	Davidson	13	58	23.0	113–342	7.4–9.2	40.3	204	8.5
B. kincaidii	J	Oceanic	13	58	33.6	32–532	5.9–9.8	54.1	426	6.7
B. kincaidii	J	Upwelling	13	58	10.4	91–368	7.2–9.3	13.7	176	8.7
B. kincaidii	TR, AF	ALL	22	58	1.8	78–614	5.3–9.4	3.5	309	7.6
B. kincaidii	TR, AM	Davidson	22	58	2.9	143–614	5.3–8.9	4.2	400	6.9
B. kincaidii	TR, AM	Oceanic	22	58	1.2	47–614	5.3–9.7	10.8	614	5.3
B. kincaidii	TR, AM	Upwelling	22	58	1.1	72–614	5.3–9.5	2.6	614	5.3

J = juvenile, TR = transitional, A = adult, M = male, F = female, ALL = combined life stages, N = number of hauls, m = meters, C = Celsius. Results were calculated from NMFS–SWFSC–FED trawl and longline data (*R. stellulata*, only) collected during 2002–2005 in the greater Monterey Bay region. Oceanographic season, catches with skates (Catches) and the total number of trawl or longline catches (Hauls) are included, as well as common depth and temperature ranges, and depth and temperature at which the maximum number of occurrences was predicted. Predicted median count was used as the cut–off value to determine common ranges.

Table 1.5. Number (*n*), frequency of occurrence (%FO), density (#/km^2), depth range and mesoscale habitat electivity (after Manly et al. 1993) of the California skate assemblage among 1203 submersible dive transects conducted at depths of 24−316 m. Significant habitat types ($p < 0.05$), as calculated by Chi-square tests, are indicted (*).

Species	***n***	**%FO**	**Density #/km^2**	**Depth Range m**	**Hard**	**Mixed**	**Soft**
Beringraja binoculata	4	0.33	6.8	89-275	0.00	1.00*	0.00
Raja rhina	137	7.73	232.2	79-313	0.15	0.43*	0.42*
Raja inornata	5	0.42	8.5	91-290	0.00	0.15	0.85*
Raja stellulata	16	1.33	27.1	58-138	0.18	0.37*	0.45*
Bathyraja kincaidii	10	0.83	16.9	79-301	0.11	0.09	0.80*

n = sample size, %FO = frequency of occurrence, km = kilometers, m = meters. * = $p < 0.05$ for Chi-square test.

Table 1.6. Results of spatial analysis of catch–per–unit-effort (CPUE) by number (N) and weight (WT) for the five most abundant skate species collected during National Marine Fisheries Service, Alaska Fisheries Science Center trawl surveys (*n* = 3931) conducted during 1999–2011 on the continental shelf and slope of the western Gulf of Alaska. Abundance (N), biomass (WT, kg), and frequency of occurrence (%FO) are presented. Statistics include: Incremental Spatial Autocorrelation (ISA), Autocorrelation (Moran's I), Multi–Distance Spatial Clustering (K-Function), and High-Low Clustering (General G).

Species	**N**	**WT**	**%FO**	**Measure**	**ISA km**	**Moran's I**	**K km**	**General G**
Beringraja binoculata	883	14,195	10.6	CPUE (N)	40.36*	0.083**	20.06*	0.048**
				CPUE (WT)	40.36*	0.091**	24.85*	0.057**
Raja rhina	1340	9128	21.6	CPUE (N)	NS	0.127**	26.87*	0.011**
				CPUE (WT)	NS	0.090**	27.47*	0.011**
Bathyraja aleutica	768	5961	11.1	CPUE (N)	76.52*	0.072**	29.82*	0.124**
				CPUE (WT)	37.51*	0.098**	29.48*	0.047**
Bathyraja interrupta	720	1386	12.1	CPUE (N)	58.44*	0.081**	29.57*	0.070**
				CPUE (WT)	34.34*	0.069**	30.30*	0.033**
Bathyraja parmifera	128	541	2.7	CPUE (N)	46.39*	0.020**	36.83*	0.064**
				CPUE (WT)	37.35*	0.021**	41.87*	0.050**
All Species	3839	31,211	43.0	Species Richness	NS	0.209**	24.26*	0.009**

Significant *p*-value thresholds are indicated as follows: * = < 0.05, ** = < 0.001, NS = not significant. N = number, WT = weight (kilograms), %FO = frequency of occurrence among hauls, ISA = incremental spatial autocorrelation, K = K Function, km = kilometers.

Table 1.7. ANOVA and t–test comparisons of mean total length among co–occurring skates in the western Gulf of Alaska.

Species Comparison	n	TL (cm)	SD	F/t–Statistic	p–value
B. binoculata	10	136.9	22.3	18.54	< 0.001
B. interrupta	17	67.5	10.0		
R. rhina	19	108.7	25.0		
B. aleutica	17	107.2	34.0		
B. interrupta	96	65.6	14.3	83.87	< 0.001
R. rhina	117	96.6	26.3		
B. aleutica	114	106.1	25.4		
R. rhina	101	105.4	23.9	0.818	0.414
B. aleutica	143	108.2	27.8		
B. interrupta	69	65.9	14.5	14.373	< 0.001
B. aleutica	95	111.2	25.5		
B. interrupta	193	66.0	12.3	-19.579	< 0.001
R. rhina	252	104.4	25.0		
B. binoculata	61	110.4	40.5	0.294	0.769
R. rhina	69	108.8	20.3		
B. binoculata	54	108.9	37.0	-5.308	< 0.001
B. interrupta	29	71.3	12.0		

n = number of individuals, TL (cm) = mean total length, SD = standard deviation. Comparisons are based on co-occurrence among NMFS-AFSC trawls conducted in the western Gulf of Alaska during 1999–2011.

Table 1.8. Logistic model predictions of median and maximum count, and associated depth and longitude ranges, and GAM model predictions of temperature for life stages of skates in the western Gulf of Alaska.

Species	**Life Stage**	**Catches**	**Hauls N**	**Median Count**	**Common Depth m**	**Common Temp C**	**Common Longitude W**	**Max Count**	**Depth m**	**Temp C**	**Pred. Long W**
B. binoculata	J	208	3908	0.10	13–91	5.4–8.0	144.01–164.00	0.87	13	8.0	-144.01
B. binoculata	TRF	26	3908	0.10	13–58	6.2–8.0	144.01–159.92	0.86	13	8.0	-144.01
B. binoculata	TRM	157	3908	0.05	13–83	5.5–8.0	144.01–164.00	0.14	29	7.4	-164.00
B. binoculata	A	149	3908	0.05	13–91	5.4–8.0	144.01–163.18	0.22	22	7.6	-152.57
R. rhina	J	306	3894	0.20	129–373	4.5–5.1	144.01–151.35	0.35	219	5.2	-144.01
R. rhina	TR	479	3894	0.10	58–407	4.4–6.2	144.01–157.88	0.26	154	5.2	-148.49
R. rhina	A	218	3894	0.05	58–286	4.7–6.2	145.23–157.47	0.12	129	5.1	-151.35
B. aleutica	J	261	3900	0.10	141–755	3.5–5.1	148.90–164.00	0.27	341	4.6	-157.47
B. aleutica	TR	159	3900	0.05	99–486	3.9–5.2	149.72–160.33	0.12	219	5.2	-155.02
B. aleutica	A	85	3900	0.02	91–373	4.5–5.4	149.31–161.14	0.07	184	5.3	-155.43
B. interrupta	J	168	3905	0.05	129–444	4.1–5.4	146.05–159.92	0.16	240	5.0	-152.98
B. interrupta	TRF	199	3905	0.05	108–373	4.5–5.1	145.23–160.33	0.15	201	5.3	-152.57
B. interrupta	TRM	173	3905	0.05	91–530	4.0–5.4	148.09–157.88	0.11	219	5.2	-152.98
B. parmifera	J	45	3922	0.02	91–407	4.4–5.4	155.84–164.00	0.04	184	5.3	-164.00
B. parmifera	TR	42	3922	0.02	13–984	2.7–8.0	162.37–164.00	0.02	13	8.0	-164.00

J = juvenile, TR = transitional, F = female, M = male, A = adult, N = number of hauls, m = meters, C = degrees Celsius, W = West. Data were collected during 1999–2011 throughout the study region. Catches with skates (Catches) and the total number of trawl hauls (Hauls) are included, as well as common depth, temperature, and longitude ranges, and depth, temperature, and longitude at which the maximum number of occurrences was predicted. Predicted median count was used as the cut–off value to determine common ranges.

Table 1.9. Logistic model predictions of median and maximum count, and associated depths for skates among surveyed regions in the western Gulf of Alaska.

Species	Region	Catches	Hauls	Median	Common Depth m	Max Count	Max Depth m
B. binoculata	Kamishak	76	160	1.39	33–78	1.44	51
B. binoculata	Kodiak	608	1834	1.50	22–121	1.94	49
B. binoculata	Peninsula	354	1363	0.86	26–101	1.11	51
B. binoculata	Shelikof	109	277	1.94	59–155	4.13	59
R. rhina	Kamishak	68	159	2.33	68–178	2.55	178
R. rhina	Kodiak	1242	1834	3.71	121–252	3.92	176
R. rhina	Peninsula	218	1363	0.45	102–210	0.5	176
R. rhina	Shelikof	225	277	3.57	146–208	3.61	177
B. aleutica	Kodiak	453	1834	0.81	132–252	2.52	252
B. aleutica	Peninsula	229	1363	0.57	106–210	1.75	210
B. aleutica	Shelikof	127	277	3.52	155–289	8.44	289
B. interrupta	Kamishak	95	153	5.66	66–178	6.32	178
B. interrupta	Kodiak	756	1834	3.05	121–252	3.81	252
B. interrupta	Peninsula	612	1363	3.62	101–210	4.32	210
B. interrupta	Shelikof	149	277	4.54	155–289	5.57	289
B. parmifera	Kodiak	301	1834	0.57	124–219	0.61	165
B. parmifera	Peninsula	160	1363	0.36	104–210	0.42	166
B. parmifera	Shelikof	42	277	0.20	139–199	0.2	166

m = meters. Data were collected from ADFG trawl surveys conducted in the west–central portion of the study region during 2003–2012. Sampling areas (Region), catches with skates (Catches) and the total number of trawls (Hauls) are included as well as common depth ranges, and depth at which the maximum number of occurrences was predicted. Median count was used as the cut–off value to predict common ranges.

1.7 FIGURES

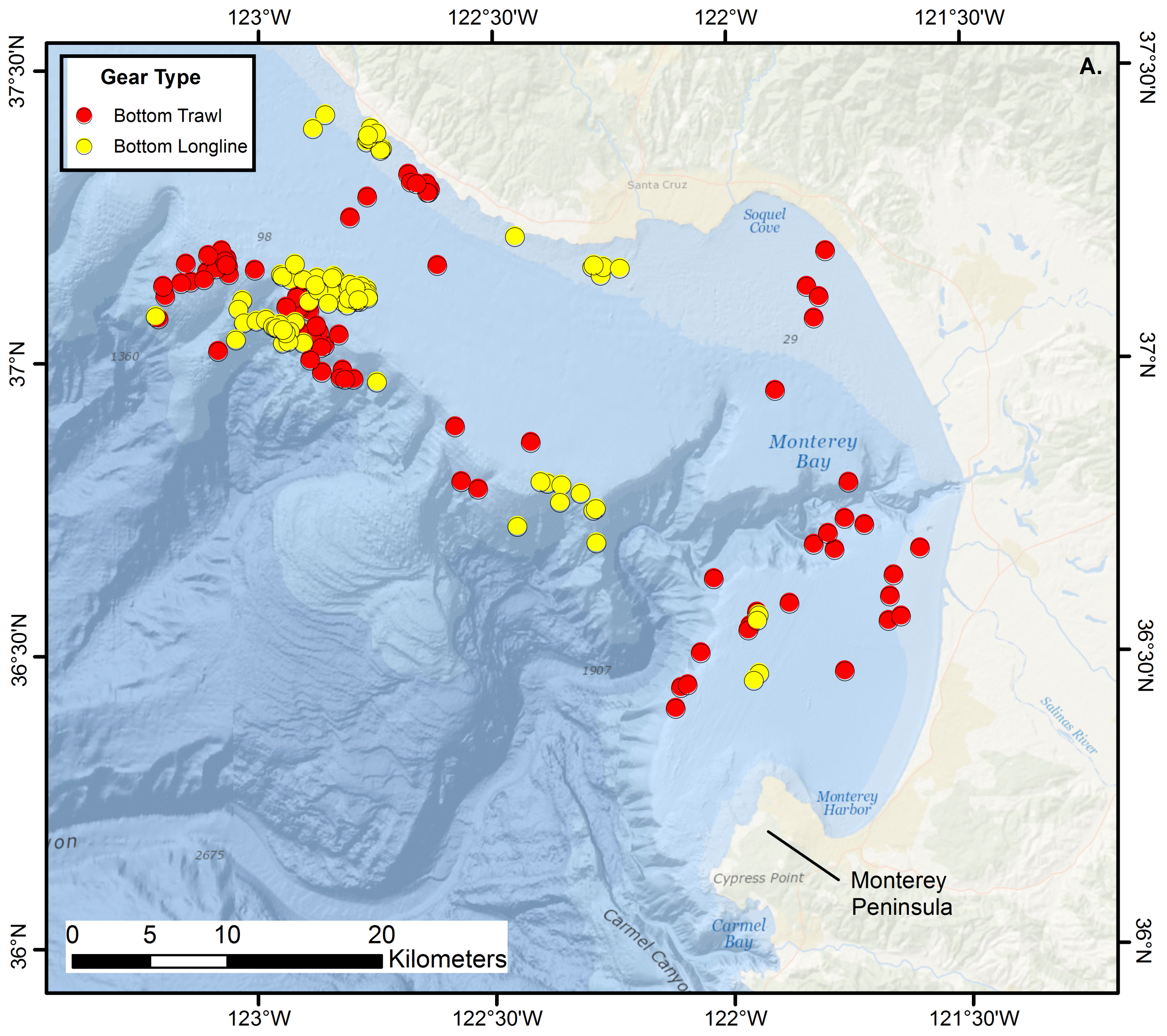

Figure 1.1. National Marine Fisheries Service–Southwest Fisheries Science Center–Fisheries Ecology Division bottom set trawl (*n* = 80) and longline (*n* = 106) survey locations in the greater Monterey Bay region.

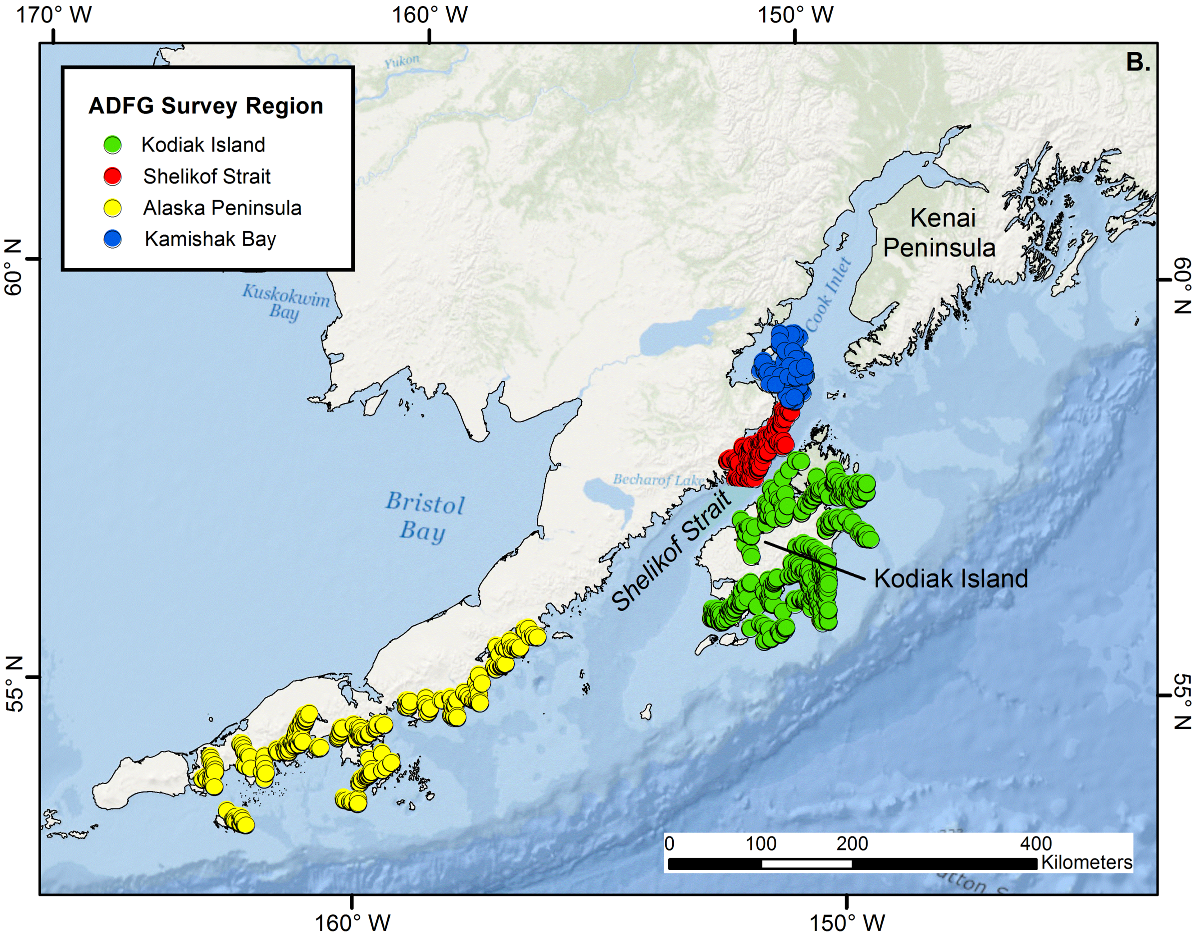

Figure 1.2. Alaska Department of Fish and Game trawl survey regions located within the larger study site in the western Gulf of Alaska. The total number of trawls conducted during 2003–2012 among regions was, as follows: Kodiak Island (*n* = 1836), Shelikof Strait (*n* = 278), Alaska Peninsula (*n* = 1368), and Kamishak Bay (*n* = 160).

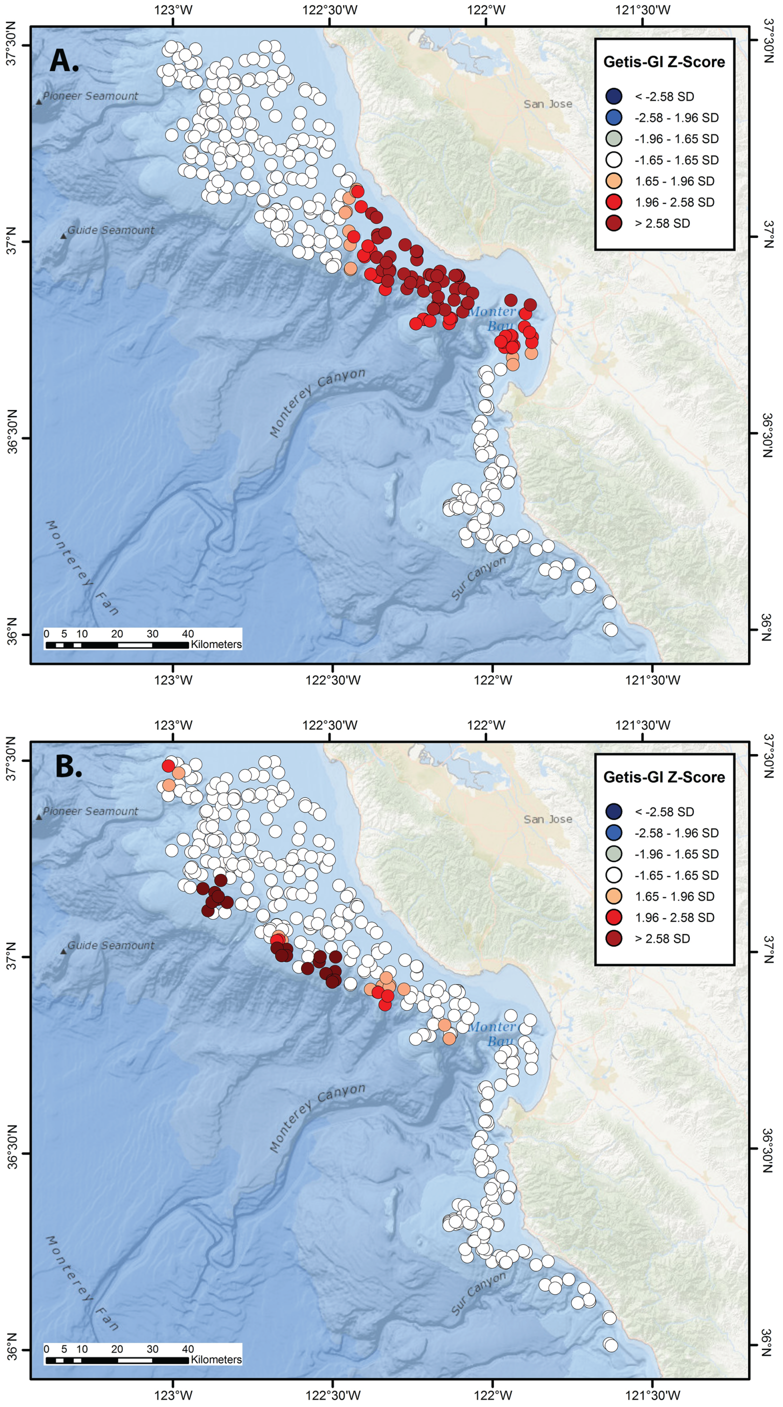

Figure 1.3. Getis-GI Hot Spot Analysis Z-score plots of catch-per-unit-effort (kg/km) for the hardnose skates, *Beringraja binoculata* (A) and *Raja rhina* (B), off central California, as calculated from NMFS–AFSC and NMFS–NWFSC trawl surveys conducted during 1997–2010.

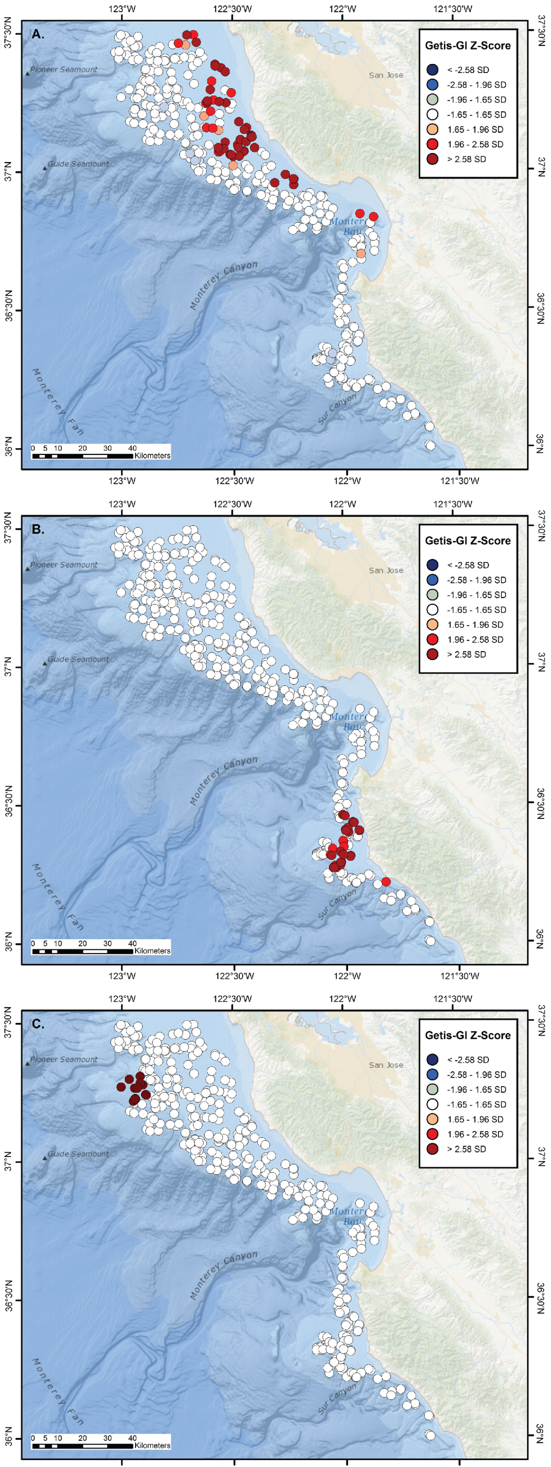

Figure 1.4. Getis-GI Hot Spot Analysis Z-score plots of catch-per-unit-effort (kg/km) for the California skate, *Raja inornata* (A); starry skate, *R. stellulata* (B), and sandpapaer skate, *Bathyraja kincaidii* (C) off central California, as calculated from NMFS–AFSC and NMFS–NWFSC trawl surveys conducted during 1997–2010.

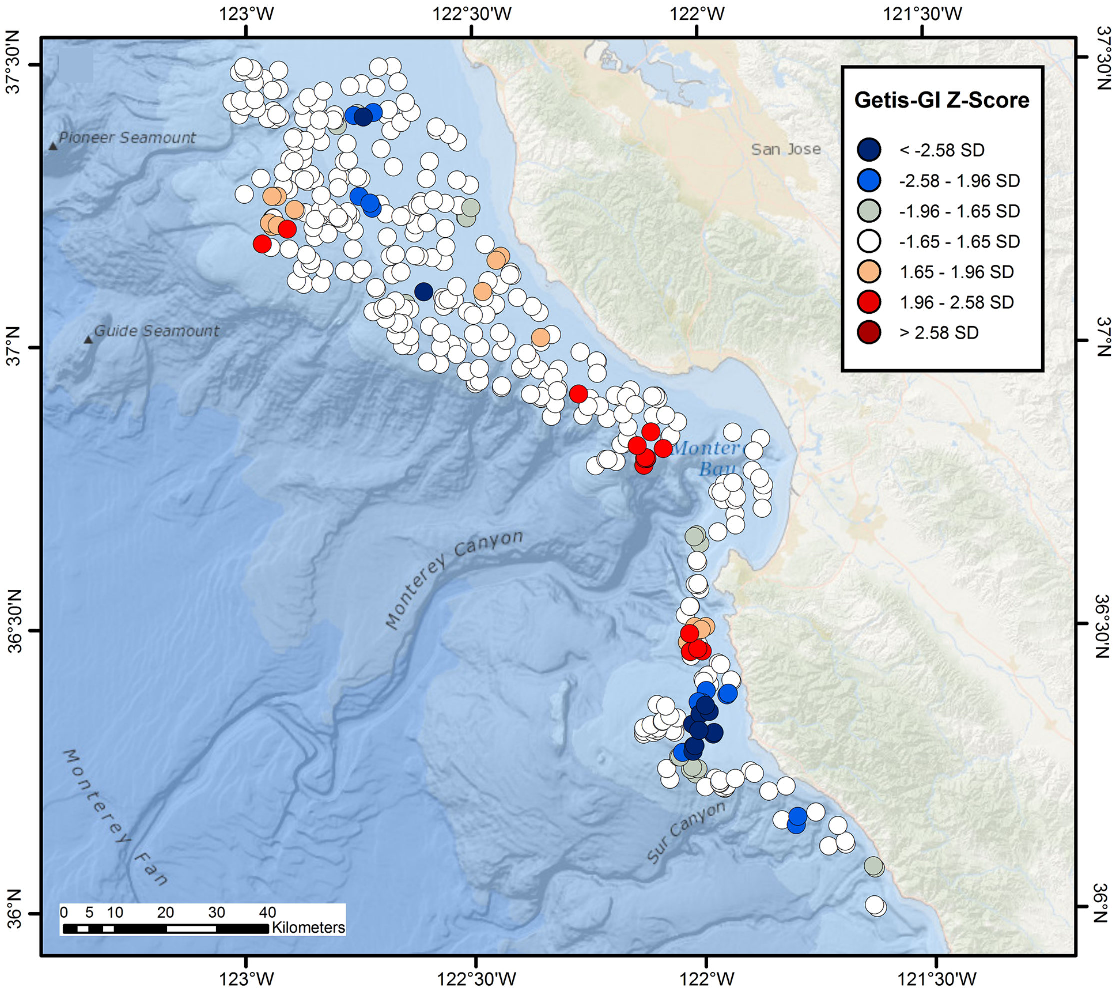

Figure 1.5. Getis-GI Hot spot Analysis Z-score plot of species richness of skates collected from NMFS–AFSC and NMFS–NWFSC trawl surveys conducted during 1997–2010.

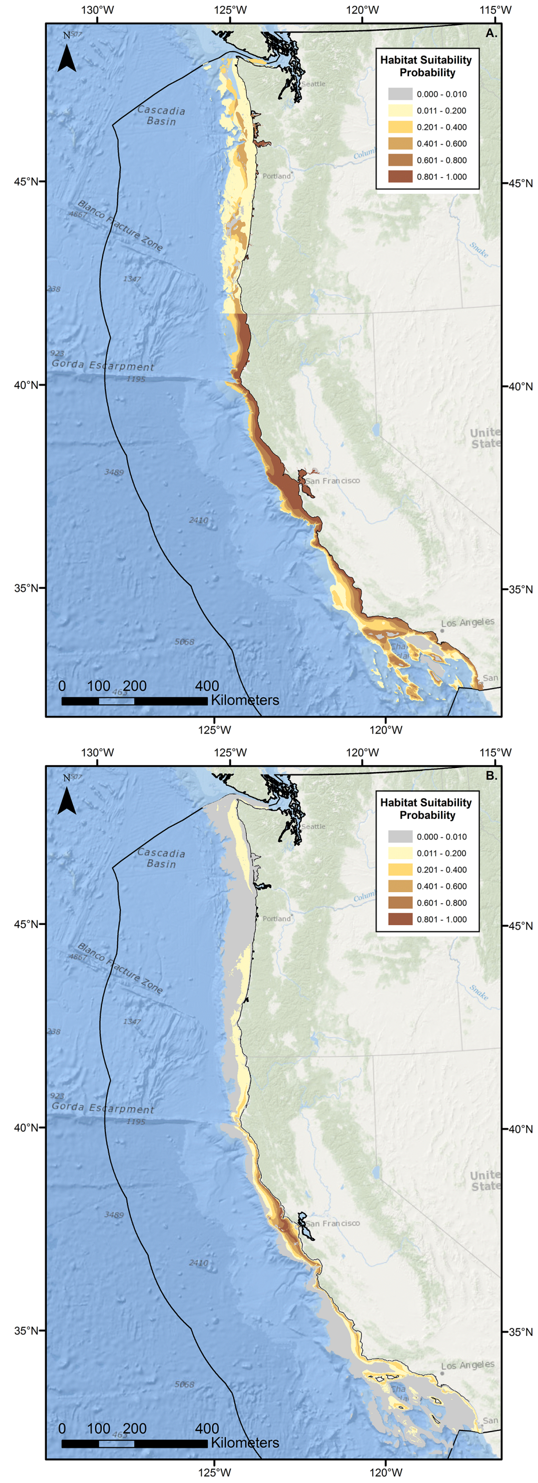

Figure 1.6. Reconstruction of original (A) and updated (B) habitat suitability probability profiles for adult and transitional/adult *Raja inornata* throughout the U.S. West Coast. The original profile (A) was depicted in the 2005 Essential Fish Habitat Amendment to the Pacific Coast Groundfish Fishery Management Plan (Anonymous 2005). The black line offshore depicts the limit of the U.S. EEZ.

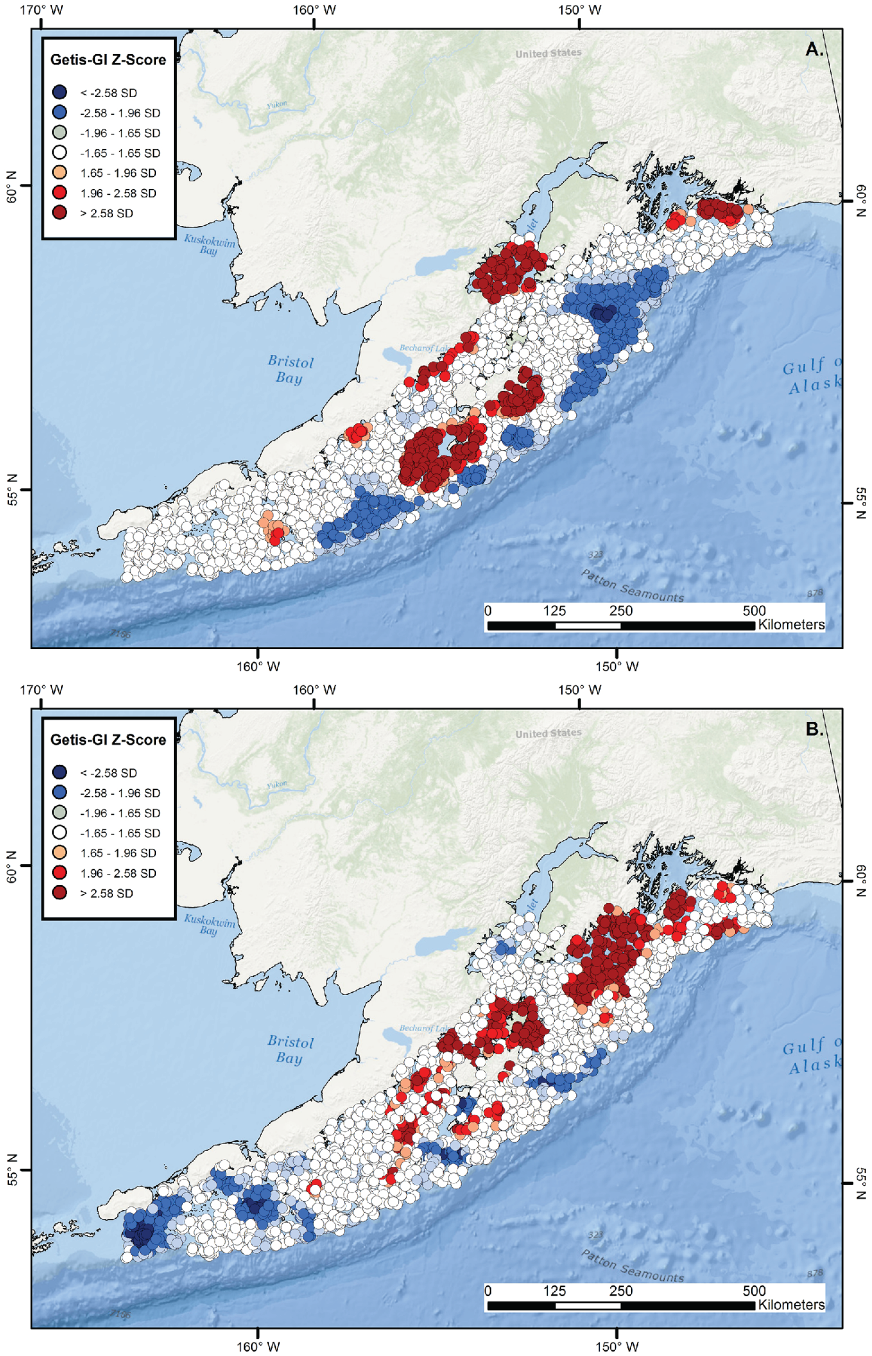

Figure 1.7. Getis-GI Hot Spot Analysis Z-score plots of catch-per-unit-effort (kg/km) for the hardnose skates, *Beringraja binoculata* (A) and *Raja rhina* (B), in the western Gulf of Alaska, as calculated from NMFS–AFSC trawl surveys conducted during 1999–2011.

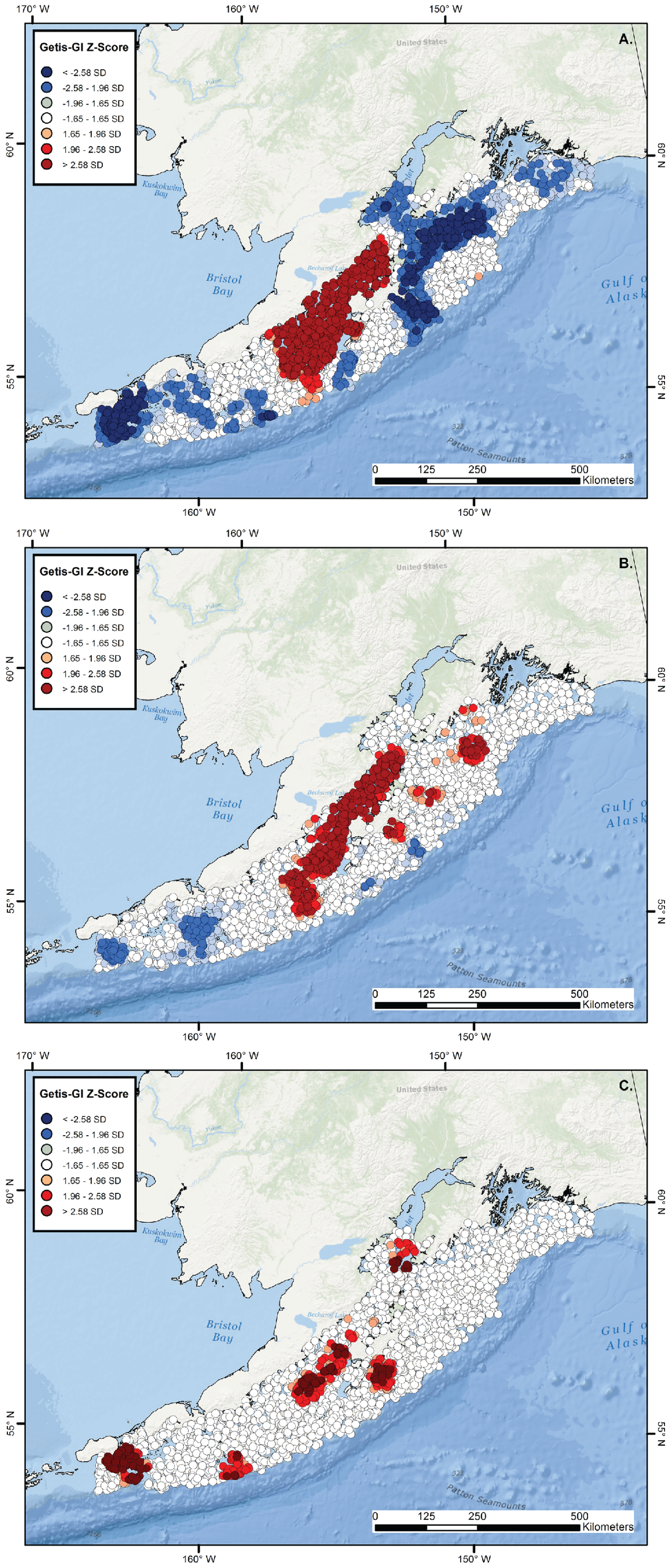

Figure 1.8. Getis-GI Hot Spot Analysis Z-score plots of catch-per-unit-effort (kg/km) for the softnose skates, *Bathyraja aleutica* (A), *B. interrupta* (B), and *B. parmifera* (C), in the western Gulf of Alaska, as calculated from NMFS–AFSC trawl surveys conducted during 1999–2011.

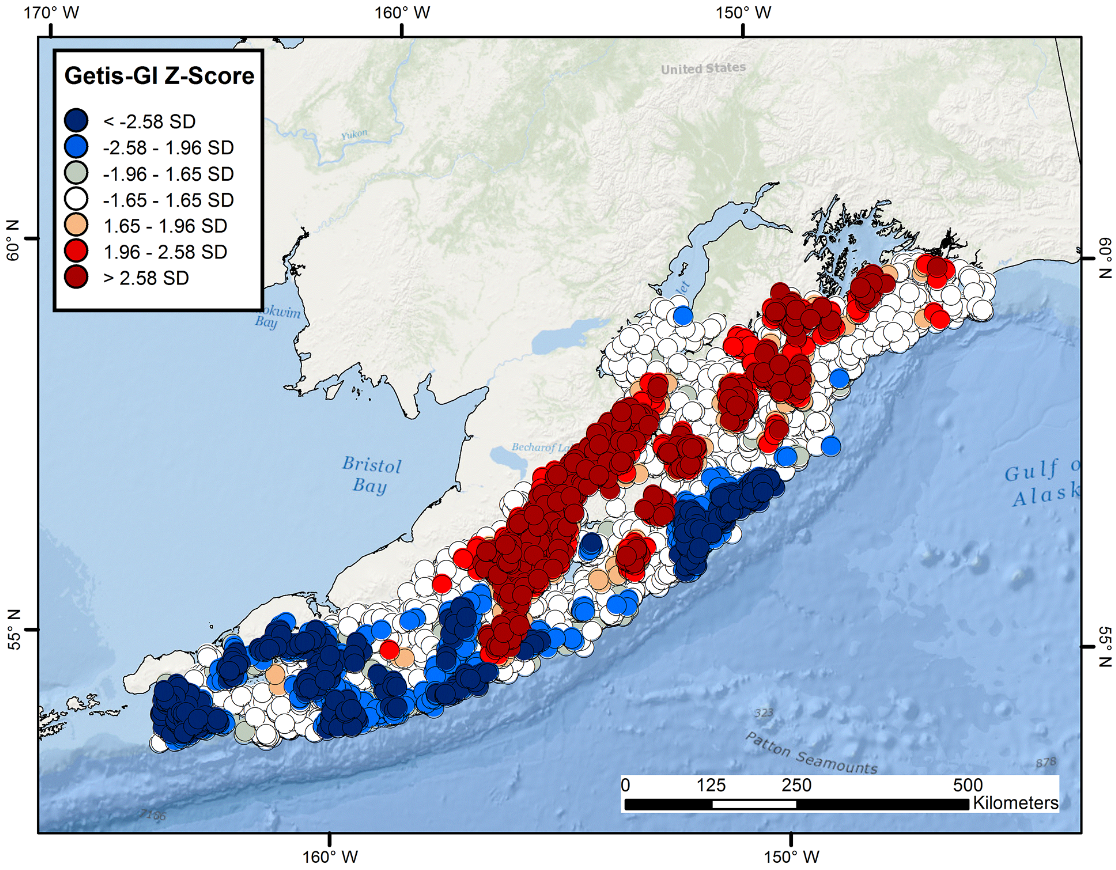

Figure 1.9. Getis-GI Hot Spot Analysis Z-score plot of species richness of skates collected during combined NMFS–AFSC trawl surveys conducted in the western Gulf of Alaska during 1999–2011.

Chapter 2: HOW CAN THERE BE SO MANY SKATE SPECIES?

Skates (Rajiformes: Rajoidei) are an extremely diverse group of cartilaginous, marine fishes that historically have been considered to occupy unconsolidated habitats and serve similar trophic roles. This presents a paradox: how can there be so many skates if they are ecologically redundant? The hypothesis of trophic redundancy in skates was evaluated using diet composition data from two eastern North Pacific skate assemblages (central California, western Gulf of Alaska). Diet compositions differed significantly by species (SPECIES) and total length (TL), but the location and timing of hauls (HAUL) was the most important consideration in explaining the substantial dietary variability in each assemblage. This finding reinforces the perception that skates are generalist predators, and largely supported the null hypothesis of trophic redundancy in skates. Dispersion analyses also were highly significant, indicating additional extreme within-group variability in skate diet among these variables. Canonical correspondence analysis was used to associate specific variable factors (e.g., juvenile, subadult, adult) with prey taxa and substantiated the general concept of greater piscivory and less reliance on small crustaceans (e.g., amphipods and polychaetes) with increasing total length. Diet composition and trophic level of *Beringraja binoculata* and *Raja rhina* differed considerably between regions and indicated a greater reliance on crustaceans (Tanner crab and shrimps, respectively) in Alaska and fishes in California. The different geographic predatory roles of these species may reflect ecosystem-level differences in prey compositions and competitive interactions. These results, coupled with those of a complementary study of spatial relationships, demonstrate that skates are more ecologically diverse than previously reported, and that space appears to be more important than food in structuring skate assemblages. Pronounced differences in core resource use across broad, overlapping spectrums of trophic and spatial tolerances: 1) probably facilitate the coexistence of speciose skate assemblages, and 2) may explain the remarkable taxonomic diversity in this group. Ecological studies and fishery management plans that incorporate ecosystem considerations should include species-specific spatial information for skates. Diet composition data can be pooled among sympatric skate species, however, unless the timing and locations of hauls and TL of individuals are available for analysis.

2.1. INTRODUCTION

The concept of the niche is considered one of the fundamental tenets of community ecology. It was first introduced by Grinnell (1917), based on his observations of the limited range and habitat specificity of the California thrasher (*Toxostoma redivivum*), later expanded to include trophic relationships (Elton 1927), and developed into the modern concept (e.g., no vacant niches, fundamental vs. realized niche) by Hutchinson (1957). Niche differentiation (sometimes termed niche or resource partitioning) is a process by which competition among species results in differential resource use. This process represents a manifestation of Grinell's concept that no two species can occupy the same realized niche over a protracted period of time. Coexistence is, instead, enabled by differentiation of species' realized niches.

The complexity of the niche concept creates a fundamental problem in demonstrating niche differentiation in natural systems, and especially among marine fishes. Observations of differential resource use between or among sympatric species are not sufficient evidence of niche differentiation. Experimentation also is necessary to determine if competition is the driving factor in observed differential resource use. Niche partitioning is demonstrated when differential use of resources is observed after a competitor is removed (fundamental niche) compared to when it is present (realized niche). Experimental manipulations are common in intertidal regions and have demonstrated niche partitioning among marine invertebrates (e.g., Connell 1961; Vance 1972). However, comparable studies of marine fishes are rare, and evidence for niche partitioning in this group is extremely limited (e.g., Larson 1980, Holbrook et al. 1990; Munday et al. 2001). This situation results partially from the difficulty in performing field manipulations and has historically confined such studies to shallow, nearshore regions.

Experimental and theoretical studies also suggest that most evidence for niche differentiation in marine fishes comes from closed systems and structured habitats. Even in field studies that infer resource partitioning from diet composition, fishes often show considerable dietary overlap at times when resources are abundant and only shift their prey spectrums during relative times of scarcity (Hoines and Bergstad 1999; Feyrer et al. 2003). These findings indicate that realized niches may be quite broad and plastic in marine fishes, and could enable the long-term co-occurrence of species that occasionally compete for limiting resources. Dynamic realized niches in marine fishes may be a function of the openness and lack of specialists evidenced in some marine systems that result in high connectivity and weak species interactions (Link 2002). In addition, trophic interactions in marine fishes often are structured by size. A good example is provided by Atlantic cod (*Gadus morhua*) in the Baltic Sea, which are preyed upon by sprat (*Sprattus sprattus*) during early life stages, but later consume sprat as adults (Köster et al. 2005). Therefore, in contrast to intertidal, freshwater, or terrestrial systems where much of the foundational work on development of traditional niche theory was based, niche theory may not be generally applicable to most marine fish populations.

The lack of demonstrable niche differentiation in marine fishes does not preclude the importance of determining resource use (trophic relationships, spatial associations) of individual species and comparing niche overlap within fish assemblages. Such information is fundamental to understanding marine community structure and change. It also provides necessary information for the development of fishery management plans that increasingly consider environmental and biological effects (Essington and Punt 2011). Predator-prey interactions are one of the main forces that determine the structuring and dynamics of marine communities (Hunsicker et al. 2011). They form the basis for trophodynamic models that attempt to capture and understand variability in marine ecosystem function and inform integrated fisheries management policies (Fu et al. 2012; Pranvovi et al. 2012). However, a poor understanding of the underlying function and dynamics of marine ecosystems limits progress towards this goal (Essington and Punt 2011). Commercially important marine fishes often garner the most scientific attention, but sympatric species may have a substantial or even dominant influence on structure and function of marine fish assemblages (Link 2007). Trophic relationships of teleost groundfishes (e.g., gadids, pleuronectids) are relatively well studied; however, the trophic ecology of an abundant group of widely sympatric fishes, the skates (Rajiformes: Rajoidei) are poorly understood.

Skates are a widespread, speciose group of meso-trophic level predators that commonly co-occur with commercially important groundfishes (Ebert and Bizzarro 2007). Although they are morphologically conservative, skates exhibit extraordinary taxonomic diversity, comprising nearly 25% of all elasmobranch species (Eschmeyer 2014). This number is likely to increase, as 60% of the 296 extant skate species have been described in the last 60 years because of the historical difficulty in sampling their common, deep-water habitats (D.A. Ebert, Pacific Shark Research Center, Moss Landing, CA, pers. database, March 2015). Despite their ubiquity and predatory roles in marine benthic communities, skates historically have been considered to be ecologically redundant. This viewpoint has developed because: 1) skates have not been afforded much direct ecological attention, 2) the accumulated scientific literature regards skates as generalist predators on unconsolidated substrates, and 3) skate species are difficult to differentiate and of low historical economic values; therefore, they have been grouped together by fisheries managers for convenience (e.g., Haas 2009; Ormseth and Matta 2010). The only notable differences in resource use are attributed to size-based dietary differences, with the consumption of fishes increasing with total length, and that of crustaceans decreasing (Wetherbee et al. 2012). This presents a paradox: How can there be so many skates if they perform the same ecological function (sensu Hutchinson 1961)? It is quite possible that the historical beliefs regarding skate ecology are a result of misidentification and a lack of detailed, quantitative research. These potential misconceptions about skates are problematic because they: obscure a true understanding of ecological relationships among marine benthic communities, preclude species-specific monitoring for population changes, and can impact the effectiveness of modeling efforts and fishery management plans.

In this study we take advantage of two skate assemblages in the eastern North Pacific (ENP) that have similar compositions and characteristics. Off central California, five species dominate numerical abundance and biomass of the skate assemblage of the continental shelf and upper continental slope (< ~600 m): longnose skate (*Raja rhina*), sandpaper skate (*Bathyraja kincaidii*), California skate (*R. inornata*), big skate (*Beringraja binoculata*), and starry skate (*R. stellulata*) (Chapter 1). Two of these species, the longnose and big skate, are also components of the western Gulf of Alaska skate assemblage at comparable depths. Three additional species, Bering skate (*B. interrupta*), Aleutian skate (*B. aleutica*), and Alaska skate (*B. parmifera*) complete the western Gulf assemblage. Off central California, one other skate, the black skate (*B. trachura*), rarely ventures into waters < 600 m (Chapter 1). Five species of *Bathyraja*, including *B. trachura*, occur in very low numbers throughout the Gulf of Alaska (< 2.5% by numerical abundance, Stevenson et al. 2008), and are even scarcer on the continental shelf and upper slope of the western Gulf (Chapter 1). The two co-occurring species are the largest in each assemblage (Love et al. 2005). In addition, the two smallest species (sandpaper skate; Bering skate) are substantially smaller than the rest, and were considered synonyms until recently (Ebert

2003). The other two skates in the California assemblage reach total lengths of < 1 m (California skate, 75 cm; starry skate, 76 cm), whereas those of the Alaska assemblage are much larger (Alaska skate, 130 cm; Aleutian skate, 161 cm). Spatial segregation is pronounced in each assemblage (Chapter 1) and skates are generalist predators (Ebert and Bizzarro 2007), which suggests that perhaps competition for prey resources may be relaxed among sympatric species in each region.

The goal of this study was to address the paradox of ecological redundancy in a widespread, speciose group of marine fishes, the skates. Prior work indicated that sympatric ENP skates were spatially segregated (Bizzarro 2014). This study builds upon that work to investigate the other aspect of the niche, use of trophic resources. Together, these studies will provide a comprehensive description of comparative resource use in skate assemblages that can promote a better understanding of benthic community ecology and inform fishery management plans. The working hypothesis was that skates are tropichally redundant and that dietary differences among sympatric species are insignificant. The alternative hypothesis is that skate species exhibit significant trophic separation and each species is therefore distinctive. If the working hypothesis is true, co-occurring skates can be generalized and grouped for ecological studies and fishery management. If not, such groupings are artificial and obscure substantial interspecific differences in the skate ecology. The diet composition and trophic ecology of the central California and western Gulf of Alaska assemblages were used as case studies to test this hypothesis. Specific objectives were to: 1) determine the magnitude and primary sources of dietary variability in ENP skate assemblages, 2) compare diet composition and trophic level between populations of skate species that occur in each study region, and 3) investigate morphological relationships that may influence their prey spectrums of some species.

2.2. METHODS

2.2.1. *Data Collection*

Data and specimens for trophic studies of the dominant skate species off central California and in the western Gulf of Alaska were obtained from research surveys (Table 1). For central California, skates were collected during 2002–2005 from bottom trawl and longline surveys conducted by the National Marine Fisheries Service, Southwest Fisheries Science Center, Fisheries Ecology Division (NMFS–SWFSC–FED). Bottom trawl surveys targeted soft substrates, whereas bottom longlines were set in areas of extensive rock outcrop. All species except *R. stellulata* were primarily obtained from monthly trawl surveys conducted during late 2002 and throughout 2003. However, because *R. stellulata* occurs mainly on rocky reefs (Bizzarro et al., 2014), these specimens were derived from episodic longline surveys conducted in 2004 and 2005. The central California study site extended from ~36.0º N to 37.5º N, and the average haul depth ranged from 14–581 m (median = 155 m) for trawl surveys ($n = 57$), and 80–379 m (median = 95 m) for longline surveys ($n = 24$). All skates were identified to species and sampled for biological information (e.g., total length (TL, to the nearest 1.0 cm), sex, weight (to the nearest 0.01 kg), maturity stage = juvenile, subadult, adult). Maturity was determined using criteria established by Ebert (2005).

In the western Gulf of Alaska, skates were sampled during fishery-independent trawl surveys conducted by the Alaska Department of Fish and Game (ADFG; 2006, 2007). The western Gulf of Alaska study site was substantially larger than that off central California, ranging from 151.7º W to 162.2º W. All Alaska surveys were restricted to summer months (June–September). Trawl sets were generally fished on soft substrates. Local trawl surveys of ADFG, Kodiak (Alaska Peninsula, Kodiak Island, Shelikof Strait) and ADFG, Homer

(Kamishak Bay) offices were conducted throughout the study region (22–254 m, median = 132, *n* = 301; Fig. 1). Biological information was collected for all skates sampled in the western Gulf of Alaska as previously described; however, weight was not measured and mouth width (MW, to the nearest 1.0 mm) was collected for a subset of the skates sampled in Shelikof Strait.

Stomach samples were collected opportunistically from individuals of all species in each described skate assemblage. Newly captured specimens were provided by NMFS–SWFSC–FED surveys and stored frozen until processing. In the western Gulf of Alaska, all skates were sampled at sea. The stomach and foregut were excised from each sampled individual and the mouth and gill rakers were checked for regurgitation. Skates with regurgitated prey items were not sampled. Stomach samples of all California specimens were stored frozen after excision; whereas those of Alaska specimens were fixed in 10% buffered formalin at sea, and then switched to 70% ethanol for long-term storage. Prey items were identified to the lowest possible taxonomic level, enumerated, and weighed under laboratory conditions. When the exact number of individuals of a prey taxon could not be positively determined, a conservative count was estimated. All specimens of each prey type were blotted dry and weighed collectively to the nearest 0.01 g. Incidentally ingested materials (e.g., plant matter, sediment, detritus) and parasites were discarded. Unidentified organic matter was not included in calculations of diet composition but was incorporated into estimates of total mass of consumed prey.

Prey items were grouped into generalized categories (after NMFS 2013) to minimize redundancy among identifications of different taxonomic resolution (e.g., Teleostei, Scorpaeniformes, Scorpaenidae, *Sebastes* spp. *Sebates saxicola*). The 47 NMFS categories were then augmented to better match the prey spectrum consumed by each skate assemblage and to account for prey items of high taxonomic resolution that contributed substantially to diet composition (e.g., Tanner crab, *Chionoecetes bairdi* for the Alaska assemblage; Table 2).

2.2.2. *Data Analysis*

PERMANOVA analysis was used to determine the best combination of response variables to explain the observed dietary variability in each assemblage. PERMANOVA is directly analogous to MANOVA in that it is a multivariate technique that partitions sums of squares. However, it is a non-parametric technique that uses semi-metric or metric distance matrices in these calculations, and significance tests are based on permutations of the raw data (Anderson 2001). For this study, the Bray-Curtis dissimilarity index was utilized as the basis for matrix calculations and the model was permuted 9999 times (Bray and Curtis 1957). The following variables (and their factors, for categorical variables) have been demonstrated to be sources of dietary variability in elasmobranchs (Wetherbee et al. 2012) and were analyzed for the California skate assemblage: SPECIES, TL (cm), SEX, MATURITY (Juvenile, Subadult, Adult), HAUL, (OCEANOGRAPHIC) SEASON (Davidson, Upwelling, Oceanic; after Rinewalt et al. 2007), and DEPTH (m). The same variables were analyzed for the Alaska assemblage with slight modifications based on the available data (added: REGION (Kamishak Bay, Shelikof Strait, Kodiak Island, Alaska Peninsula), YEAR; dropped: SEASON). PERMANOVA models were constructed for each variable and for some likely interactive effects (e.g., HAUL x SPECIES, SPECIES x TL), and then a final (best) model was calculated for each assemblage using forward, step-wise model selection. Although its depth range overlaps that of the other California skate species, *R. stellulata* occurs primarily on rock reefs (Chapter 1), and was caught with longline gear during a later time period. Therefore, a second PERMANOVA was conducted for the trawl-caught California species, in order to: 1) assess the influence of *R. stellulata* on the relative and total amount of variability explained by the overall model, and 2) determine sources of dietary variability for skate species with similar habitat characteristics.

Permutation tests of multivariate group dispersions also were conducted to determine if variance differed significantly between or among categories for any response variable (Anderson 2006). Significant differences indicate high within-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) (Oaksanen 2013).

Raw diet composition data were used to determine the choice of dietary metric(s) and to investigate the influence of rare prey categories as precursors to PERMANOVA analysis. Four individual-based dietary metrics were calculated for each skate species in the California data set: percentage by number (%N), percentage by weight (%W), prey weight/predator weight, and prey weight/(predator weight)$^{0.77}$ (scaled to account for size-based differences in consumption rates; Essington et al. 2001). Numerical data are typically associated with feeding behavior, whereas weight data are considered a proxy for energetic value (Hyslop 1980). Because skate weight was not collected during Alaska surveys, only two of the four prey metrics (%N, %W) could be calculated for the western Gulf of Alaska assemblage. Evaluation of dietary metrics was therefore limited to the California species. Species-specific PERMANOVAs were conducted using each metric and then evaluated for consistency and the amount of variability explained. The three weight-based metrics performed very similarly within and among species. %N-based model outputs generally were consistent with those of weight-based measures but explained a smaller amount of dietary variability. In addition, gravimetric metrics have been shown to be more representative of known diet composition than numerical metrics (Ahlbeck et al. 2012).

Therefore, since it is the most commonly used of the weight-based metrics, %W was advanced for analysis.

Rare species were eliminated from analysis or grouped into broader categories based on their frequency of occurrence because they can disproportionately affect the outcome of multivariate analyses (Legendre and Gallagher 2001). Four occurrence thresholds (None, 1%, 2%, 4%) were evaluated to determine the most parsimonious model, using the percentage of variability explained by the best-fit PERMANOVA model as the primary criterion of evaluation. Based on a comparison of results, a 2% threshold was used for the California data set, whereas a 1% threshold was used for the Alaska data set (Appendix 1).

Canonical correspondence analysis (CCA) was conducted to complement and expand upon the results of PERMANOVA analysis, by determining the degree of association between diet composition data and response variables. CCA uses chi-square distance as a basis for matrix calculations and is the appropriate analysis when species responses are not linear (ter Braak 1986). The variable, HAUL, highly influenced results and confused visual interpretation of ordination plots because of the extremely high number of categories relative to other variables. HAUL therefore was removed from the model prior to analysis and its association with diet composition was assessed using GIS mapping techniques in ArcMap v 10.2.2. CCA outputs are highly influenced by inclusion of rare species. However, no further modifications were made to the dietary data sets, as the goal of this analysis was to determine what prey groups were most strongly associated with each variable, not to maximize the explanatory power of the model. Significance of the overall model, each canonical axis, and each response variable was determined by permutation (9999 simulations), and a biplot of response variables and prey groups along the first two canonical axes was constructed for interpretation.

Diet composition and trophic level were compared between California and Alaska populations of *B. binoculata* and *R. rhina* to determine if the predatory role of these species varied between regions. Diet composition data were grouped into seven general categories (polychaetes, bivalves and gastropods, cephalopods, crabs, shrimps, other and unidentified crustaceans, and fishes) to account for differences in the distribution and abundance of prey taxa between regions and analyzed using PERMANOVA. Trophic level was calculated using the formula provided by Cortés (1999), and the trophic level estimates reported by Ebert and Bizzarro (2007) for common prey taxa of skates. Data were assessed for homoscedasticity and extreme departures from normality. Regional regional trophic estimates then were compared intraspecifically using two-sample t-tests on raw or log-transformed data, as appropriate.

2.3. RESULTS

2.3.1. *Central California Skate Assemblage*

PERMANOVA of diet composition data for the overall California assemblage indicated that SPECIES, TL, and MATURITY were highly statistically significant, but were relatively meaningless, biologically. HAUL explained nearly an order of magnitude more dietary variability than the next most important explanatory factors, SPECIES and TL, in the final model, supporting the null hypothesis that skates are trophically redundant (Table 3). In addition, there were highly significant multivariate interactions between HAUL, SPECIES, and TL (Table 3). These three variables, alone and in combination, accounted for the great majority of the variability explained by the final model ($r^2 = 0.390$). When each variable was analyzed independently, the observed model was significantly less dissimilar than any of the 9999 expected models for all variables except SEX (Table 3). Results of dispersion analysis were highly significant for all variables except SEX (Table 3). These findings indicate that diet composition data are inconsistent both among and within variables.

The timing of collection, gear type used, and sampled habitat differed for *R. stellulata*; however, removing this species did not alter the constituent elements of the best-fit PERMANOVA model, nor the amount or distribution of the total variability explained among variables (Table 3). The final, reduced model explained slightly less variability in the data set ($r^2 = 0.381$) than the full (five-species) model ($r^2 = 0.390$). The variability explained by independent and interaction variables also was highly consistent with the full model. Dispersion analysis indicated significant within-group variability for all variables except SEX, as in the full model (Table 3).

CCA results were consistent with those of PERMANOVA analysis and indicate trophic separation associated with dissimilar diets among size and species of skates, and depth of capture. The overall model was highly significant ($F = 11.17$, $P < 0.001$) but only explained 9.0% of the variability in the data set, further reinforcing the strong association between HAUL and diet composition, and the inherent variability within the data set. The first and second CCA axes explained 29.4% and 22.6% of the total variation in the final CCA model. Four of the 13 tested factors were omitted from the final model: *R. stellulata* (SPECIES), Upwelling (SEASON), Male (SEX), and Adult (MATURITY). CCA 1 represents a general gradient of increasing proportions of fishes and crabs in the diet, and decreasing proportions of small crustaceans, such as amphipods, isopods, and euphausiids (Fig. 2). The diet of *Bathyraja kincaidii* and the variable DEPTH are most strongly associated with small crustaceans, whereas the other three species in the model and TL are most strongly associated with a diet of crabs and fishes (Fig. 2). The second CCA axis indicates a change in diet composition from one consisting mostly of amphipods, crabs, and other crustaceans to one consisting primarily of fishes and cephalopods (especially octopods and cuttlefishes) (Fig. 2). Juvenile skates, *R. inornata*, and *R. binoculata* are most strongly associated with crustacean diets and TL, *R. rhina*, and DEPTH are most associated with fish and cephalopod diets along this axis (Fig. 2). Distinct trophic separation is evident among species, with the exception of, *B. binoculata* and *R. inornata*, which have very similar diet compositions (Fig. 2).

The substantial proportion of dietary variability explained by HAUL in the PERMANOVA model is attributed mainly to spatio-temporal differences in specimen collection. Because *R. stellulata* did not influence the behavior of the overall PERMANOVA model and was collected with longline gear, it was removed from the data set and only trawl-caught species and their diet composition were investigated. Differences in diet composition likely reflect differences in local prey composition at the time of trawl collections. For example, hauls that were dominated by *R. rhina* in the southeastern portion of the study site displayed diets consisting mainly of shrimps and fishes, whereas hauls of similar size that were dominated by *R. rhina* in the deeper, northeastern part of the study site exhibited a much broader diet composition (Fig. 3). Several hauls fished in similar regions with comparable species composition had different prey compositions (Fig. 3).

Differences in size and species composition of the catch, and variable numbers of skates/tow contributed substantially to the high variability explained by HAUL in the PERMANOVA model. *Raja rhina* was collected throughout the study site, whereas *R. inornata* was mainly caught in the northeastern portion. *Beringraja binoculata* individuals largely were taken in nearshore waters, whereas *B. kincaiidi* was collected in deeper, offshore waters, especially in association with submarine canyon heads in the northwestern part of the region.

Size differences are evident among these species and contribute further to diet variability/haul (Table 1). The contribution of fishes and cephalopods to the diet composition of the assemblage increases with depth, whereas that of crabs and shrimps shows the opposite trend. Uneven sample sizes were evident among hauls, and many hauls had low sample sizes (30 of 57 hauls contained 10 or fewer individuals). There was an overall trend of increasing number of prey categories and greater variability (SD) among prey categories with increasing sample size (#skates/haul). These conditions create considerable differences in within-haul diet composition variability that also contributes to the overall “Haul-effect.”

2.3.2. *Western Gulf of Alaska Skate Assemblage*

PERMANOVA analysis of the western Gulf of Alaska skate assemblage detected highly significant interspecific differences in diet composition. Results generally were consistent with those calculated for the central California skate assemblage and suggest distinctive trophic relationships among species and extreme dietary variability. SPECIES explained more than twice the dietary variation of any other independent factor except HAUL (Table 4). HAUL was, by far, the most important factor, explaining 55.6% of the total variability in the final model (Table 4). For all variables except SEX, the observed model was more dissimilar than any of the 9999 expected models (Table 4). Highly significant multivariate interactions were evident between HAUL, SPECIES, and TL, and between SPECIES and REGION (Table 4). HAUL, SPECIES and TL, alone and interactively, accounted for 76.9% of the total variability in the data set. MATURITY, DEPTH, and SEX were included in the final model, but explained only 0.6% of the observed dietary variability. Results of dispersion analysis were (highly) significant for all variables except YEAR and SEX (Table 4).

CCA results generally were consistent with those of PERMANOVA analysis and indicate trophic separation by species, size, and depth. The CCA model was highly significant ($F = 7.22$, $P < 0.001$), but explained only 7.5% of the variability in the data set. The first and second CCA axes explained 27.9% and 24.0% of the total variation in the CCA model. Five of the 16 factor-groups were omitted from the final model: *R. rhina* (SPECIES), 2007 (YEAR), Shelikof Strait (REGION), Male (SEX), Subadult (MATURITY). CCA 1 represents a general gradient of increasing proportions of shrimps, euphausiids, and mysids in the diet, and decreasing proportions of fishes and crabs (Fig. 4). The diet of *B. interrupta*, DEPTH, and juvenile skates loaded positively on CC1, indicative of a diet that is most strongly associated with shrimps and shrimp-like crustaceans. Conversely, *B. binoculata* and TL are most strongly associated with a diet of fishes and crabs (Fig. 4). The second CCA axis indicates a change in diet composition from one characterized by pandalid shrimps, gonatid squids, and other fish and shrimp taxa to one incorporating relatively rare prey taxa, such as polychaetes, isopods, ammodytid fishes, euphausiids, and mysids (Fig. 4). *Bathyraja aleutica*, DEPTH, and TL are associated with the former diet composition, whereas *B. interrupta* and, to a lesser extent, *B. binoculata* are associated with the latter (Fig. 4). Distinct trophic separation is evident among species, although *B. parmifera* does not contribute substantially and *R. rhina* was not included in the final CCA model (Fig. 4).

The considerable power of HAUL in explaining dietary variability is a function of several inherent factors, including spatio-temporal differences in specimen collection, and the relatively low number of samples/tow. Samples were derived from over 300 hauls in the western Gulf of Alaska, of which more than 30% contained only one skate, 57% contained three or fewer skates, and hauls with more than 10 sampled specimens were extremely rare (5%; Fig. 1). The low number of replicates/haul results in a situation where within-haul dietary variability is artificially reduced. Hauls were collected over a broad region during summer months of two consecutive years, and are therefore highly spatio-temporally variable. As in the California data set, mulitiple hauls fished in the same region exhibited variable prey compositions (Appendix 2). The contribution of crabs, shrimps, and fishes to the diet composition of the western Gulf of Alaska skate assemblage varied considerably throughout the study region on small and large scales Appendix 2, B, D, E). Cephalopods and euphausiids, however, were largely consumed in the relatively deep waters of Shelikof Strait (Appendix 2, A, C).

Species- and size-specific differences in catch composition further contributed to the explanatory power of HAUL for Alaskan skates. *Beringraja binoculata* and *B. interrupta* were collected throughout the study site, largely in relatively shallow and deep water, respectively (Appendix 3, A, D). *Raja rhina* mainly was restricted to the Kodiak Island and Shelikof Strait regions, were it was the most abundant species sampled (Appendix 3, B). Most of the *B. parmifera* individuals included in this study were collected in the Kodiak Island region (Appendix 3, E). *Bathyraja aleutica* was captured throughout the study site, but most specimens were collected in deep regions of Shelikof Strait and off the Alaska Peninsula (Appendix 3, C). The species composition of Kamishak Bay was almost exclusively comprised of *B. binoculata* individuals (Appendix 3, A). Size-specific dietary differences were found to be a highly significant by PERMANOVA, and size composition of skates differed considerably among species and hauls (Table 1).

Because *B. aleutica* and *B. interrupta* exhibit a high degree of spatial overlap in the Shelikof Strait region and share some common prey taxa, the relationship of MW to TL was compared between individuals of these species to assess gape as a possible source of trophic separation. ANCOVA was applied, and the slope of the best fit linear regression models of MW-TL for each species did not differ significantly ($F = 0.24$, $P = 0.626$; Fig. 5). Therefore, at similar sizes, these species have similar gapes.

2.3.3. *Regional Comparisons of B. binoculata and R. rhina Populations*

Diet composition and trophic level differed substantially between *B. binoculata* populations, indicating regional variation in the predatory role of this species. Although California specimens had greater mean trophic level estimates ($t = -7.78$, $P < 0.001$; Fig. 6a), their mean TL was only half that of Alaska specimens (CA = 56.1 cm, $n = 211$; AK = 112.6 cm, $n = 336$; $t = 18.11$, $P < 0.001$). In both regions, there was a significant, positive relationship between TL and trophic level, although there was considerable scatter in each data set (CA, $t = 7.41$, $r^2 = .208$, $P < 0.001$; AK, $t = 6.49$, $r^2 = 0.112$, $P < 0.001$). Diet composition differed significantly between regions ($F = 90.06$, $P < 0.001$), and was not related to differences in TL ($F = 0.27$, $P = 0.823$). Diet composition of Alaska specimens largely consisted of crabs, especially Tanner crab, whereas California specimens were more piscivorous, with similar proportions of crabs and shrimps (Fig. 6a). Individual dietary variability was extreme both populations (Fig. 6a). Dispersion analysis indicated significant differences in within-group dietary variability by TL ($P < 0.001$) but not by region ($P = 0.38$).

Size-specific differences were evident in the consumption of Tanner crabs by *B. binoculata* in the western Gulf of Alaska. The relationship between number, total weight, and mean weight of Tanner crabs and TL was compared using linear regression, after raw data were plotted and assessed for linearity and homoscedasticity. Total and average weight data were subsequently log-transformed prior to analysis. Tanner crab dominated the diet of *B. binoculata* in this region, occurring in 78.9% of sampled *B. binoculata* individuals, and contributing 61.7% to diet composition by mean weight and 80.1% by median weight. The relationship between the number of Tanner crabs and TL of *B. binoculata* ($n = 265$) was not significant ($t = 0.596$, $P = 0.552$). However, the (log-transformed) total ($t = 10.21$, $P < 0.001$) and (log-transformed) mean ($t = 13.20$, $P < 0.001$) weight of Tanner crabs exhibited positive, significant relationships with TL. These results indicate that, in the western Gulf of Alaska, *B. binoculata* is a Tanner crab specialist, with larger specimens consuming larger crabs.

Diet composition and trophic level differed significantly between *R. rhina* populations, indicating geographic variability in the trophic role of this species. General diet composition differed between regions ($F = 227.87$, $P < 0.001$), and there was a significant interaction between region and TL ($F = 32.24$, $P < 0.001$). Alaska specimens ($n = 341$) exhibited diets consisting largely of shrimps, whereas California specimens ($n = 544$) were largely piscivorous (Fig. 6b). Supplemental prey contributions also differed, with crabs and cephalopods consumed almost exclusively by Alaska and California populations, respectively. Individual dietary variability was extreme in both populations (Fig. 6b). Dispersion analysis indicated significant differences in within-group dietary variability by TL ($P < 0.001$) but not by region ($P = 0.24$).

Comparative trophic level results of *R. rhina* were similar to those of *B. binoculata*, with larger, Alaska individuals (mean TL = 84.9; CA mean TL = 57.3 cm; $t = 14.37$, $P < 0.001$) occupying lower trophic levels than California individuals ($t = -15.09$, $P < 0.001$; Fig. 6b). In both regions, there was a significant, positive relationship between TL and trophic level, although there was substantial variability in each data set (CA, $t = 18.51$, $r^2 = .256$, $P < 0.001$; AK, $t = 7.53$, $r^2 = 0.112$, $P < 0.001$).

2.4. DISCUSSION

Spatio-temporal variation in prey availability, as evidenced by the timing and location of hauls, was the strongest determinant of diet composition among sympatric ENP skates. This finding indicates that the skates are highly adaptable to differences in the local composition of prey resources. Other spatio-temporal variables (e.g., YEAR, REGION, and DEPTH in AK; SEASON and DEPTH in CA), which incorporated broader regions and longer time scales than hauls, were not important in explaining observed variability in diet composition of either assemblage. Intra-haul correlation previously has been reported as an important source of variability in diet composition data for marine fishes (Tirasin and Jorgensen 1999). This is especially true of generalist predators, such as skates, whose diets are highly influenced by fluctuations in local prey abundance. Indeed, at broad spatial and temporal scales, skate diet composition has been posited as a useful, indirect method to infer benthic community dynamics (Link 2004).

Based on these findings, it is unlikely that sympatric ENP skates are in direct competition for prey resources or that trophic specialization has been a driving force in creating or maintaining skate diversity. Instead, it appears that the realized spatial niches of these species are the main source of segregation, and may dictate the observed interspecific differences in diet composition. Skates exhibit several characteristics that may promote speciation, including: marked spatial segregation (Chapter 1), a high degree of endemism (McEachran 1990; Compagno and Ebert 2007) and relatively small ranges compared to other elasmobranchs (McEachran 1990, McEachran and Miyake 1990). Sexual selection by mate recognition also can result in rapid speciation (West-Eberhard 1983), and skates have complex mate recognition systems which are highly conservative within species (McEachran 1990, Morson and Morrissey 2007).

Collection surveys of skates should be designed to account for the high likelihood of intra-haul dietary similarity within and among species. In this study, samples were collected opportunistically, and within-group variability of important response variables (e.g., SPECIES, HAUL, TL) was extremely high, somewhat tempering analytical results. The opportunistic collection of extreme generalist predators, such as skates, may complicate or preclude fine-scale explorations of dietary variability. In addition, the low samples sizes and taxonomic diversity evident in the most tows, especially those in Alaska, may have over-emphasized the importance of HAUL in explaining dietary variability in this study.

Species-specific differences in diet composition were evident in both study regions, but were relatively trivial as compared to spatio-temporal dietary variation. This result indicates that trophic separation among species is largely driven by differences in spatial occurrence, and that, when species overlap in foraging habitats, they generally eat the same prey species. Many comparative studies of skate diet composition have demonstrated variable trophic relationships (e.g., Bizzarro et al. 2007; Treloar et al. 2007) or claimed to demonstrate resource partitioning (Muto et al. 2001; Barbini and Lucifora 2012). However, most studies focus on only one or two potential sources of dietary variation, and rarely incorporate spatio-temporal variables. Much of the historic, comparative skate diet literature may therefore over-accentuate the importance of species-level dietary differences while underestimating the true magnitude and complexity of trophic interactions among other potential sources of variability. Although, in isolation, specific dietary differences did not explain much variability in the final model, the interaction between HAUL and SPECIES was an important source of dietary variability in both ENP assemblages. Therefore, haul-specific diet composition data should not be generalized across skate species for scientific study or fishery management purposes.

Size-related differences were another highly significant, but rather trivial source of dietary variability in each studied assemblage. A general pattern of dietary shifts among relatively small (< ~50 cm), medium (~50–100), and large (> ~100 cm) skates recently has been reported (Ebert and Bizzarro 2007; Wetherbee et al. 2012), and is substantiated by this study. Skates with small maximum sizes and early life stages of larger specimens typically eat diets consisting of small crustaceans, such as amphipods, isopods, and euphausiids, and polychaetes. In this study, this characteristic diet composition was associated with *B. kincaidii* and *B. interrupta*, the smallest skates in the California and Alaska assemblages, respectively. Medium-sized individuals incorporate more decapods and, to a lesser degree, small fishes, with large specimens eating a mixed diet of fishes and decapods (Ebert and Bizzarro 2007; Wetherbee et al. 2012). Increasing total length was associated with increasing contributions of fishes to the diet in both ENP assemblages. Furthermore, diets characterized by large decapods and fishes were limited to those of the largest species included in regional CCA models (CA; *R. rhina*; AK*; B. aleutica*, *B. binoculata*). Trophic levels, calculated from diet composition data, also showed a positive association with increasing total length in distant, allopatric populations of *B. binoculata* and *R. rhina*. Interactions between HAUL and TL and HAUL and SPECIES greatly increased the explanatory power of PERMANOVA models in each region. Therefore, these variables, at a minimum, should be recorded during sampling and incorporated into diet analysis of skates.

Ontogenetic dietary differences commonly have been reported for skates and are considered nearly universal in fishes (Gerking 1994), and sex-based dietary variation also has been documented (e.g., Rinewalt et al. 2007). In this study, neither of these variables contributed substantially to the observed dietary variability in either skate assemblage. Ontogenetic and sex-specific dietary variables are difficult to isolate, however, and are often inappropriately used as a proxy for size-based or spatial differences in diet composition. Female skates consistently attain larger sizes than males of the same species and sexual segregation of elasmobranch life stages, including those from ENP assemblages, has been widely reported (Sims 2005; Chapter 1). In addition, the attribution of sex-based dietary differences to sexual heterodonty in adult batoids has largely been debunked. Such differences are associated with mating behavior (e.g., Kajiura and Tricas 1996), where males grip females during copulation with the assistance of more angular, elongate teeth, but do not appear to influence food habits (McEachran 1977; Taniuchi and Shimizu 1993). Dietary differences by maturity stage and sex may exist, but they are more likely related to intraspecific size and spatial differences. Maturity determination requires internal examination of females and, ideally, males and can be quite time consuming and costly during survey operations (Ebert 2005). A lack of maturity or sex-specific data probably will not hamper the determination of the primary sources of dietary variability for skate species or assemblages.

Diet compositions and trophic levels of *B. binoculata* and *R. rhina* populations varied substantially, indicating that these species serve different predatory roles in each study region. Results were consistent between species in demonstrating a greater reliance on decapods in the Gulf of Alaska and fishes off central California. The extent of regional trophic variability is surprising, especially considering that the sampled specimens from Alaska were substantially larger than those from California. The general conclusion that piscivory and thereby trophic level show positive relationships with size may consequently only be applicable to sympatric skate populations. Function and structure of the California Current and Gulf of Alaska ecosystems differ markedly (Di Lorenzo et al. 2013); however, complex ecosystem dynamics, different benthic community structure, and variable fishing histories make it difficult to relate differences in ecosystem characteristics to observed variation in the trophic function of *B. binoculata* and *R. rhina* populations. Furthermore, populations of several co-occurring groundfishes from the western Gulf of Alaska demonstrate ontogenetic and spatial differences in trophic position (Marsh et al. 2012). It is therefore apparent that incorporating species-specific dietary data from different regions is inappropriate for *R. binoculata* and *R. rhina*, and probably most marine fishes that are trophic generalists. Diet composition data from California have been used to model *R. rhina* predation effects in Alaska (Gaichas et al. 2010), a situation that is likely to arrive in erroneous model outputs given the observed geographic variability in diet and trophic position.

Gape, measured as mouth width, represents a feeding constraint that influenced trophic relationships of some study species. Intraspecific trophic separation was not apparent for the Alaska population of *B. binoculata* based on diet composition but was instead facilitated by difference in size-based choice of Tanner crab prey. *Bathyraja aleutica* (max size = 161 cm TL; Love et al. 2005) and *B. interrupta* (max size = 86 cm TL; Love et al. 2005) populations exhibit considerable spatial overlap, with regions of high abundance co-occurring in Shelikof Strait (Chapter 1). However, early life stages on *B. aleutica*, which have nearly identical gape limitations as comparably sized *B. interrupta*, are largely absent from Shelikof Strait. Instead, *B. interrupta* occurs at sizes ranging from neonates to adults (Ainsley et al. 2011; Chapter 1). The spatial segregation of small and large specimens of *B. aleutica* may represent a mechanism to reduce intraspecific competition for prey resources, which is generally considered to be more intense than interspecific competition.

Directed resource utilization studies have considerably advanced knowledge of skate ecology in recent years. This increase in scientific attention largely is a result of widespread declines in populations of large and/or long-lived skate species (Dulvy et al. 2014), changes in the species composition of skate assemblages (Frisk 2010), and an increased awareness of the important predatory role of skates in benthic communities. Skates can have a notable impact on consumptive removals of common prey species (Link and Sosbee 2008). Large individuals forage in the water column at night in addition to consuming typical benthic and demersal prey, and therefore serve as a source of energy transfer between habitats (Wearmouth and Sims 2009). Long considered to be restricted to soft bottom habitats, recent findings suggest that skates can also occupy mixed and rocky regions (Methrata and Link 2006, Chapter 1). Their habit of sheltering beneath this benthos is a source of disturbance that may provide feeding opportunities for other organisms or influence local epifaunal and infaunal dynamics. These findings have added considerable depth and complexity to the body of information on skate ecology and have begun to build a theoretical bridge between observed taxonomic diversity and ecological diversity within this group of fishes.

The notion that skates are redundant, generalist predators, restricted to unconsolidated substrates is an oversimplification. Instead, skates appear to have highly distinctive yet relatively plastic niches, and complex ecological interactions that likely facilitate their coexistence. Skates exhibit markedly variable temperature, depth, and substrate associations, as well as daily movements and seasonal migrations. In regions where skate populations exhibit a high degree of spatial overlap, competition for prey resources is likely minimized, as demonstrated by the combined results of this chapter and Chapter 1. Most skates are meso–trophic level, generalist predators with diets that reflect the dominant benthic organisms within their prey spectrums (Link 2004; Ebert and Bizzarro 2007). Generalist food habits enable a degree of trophic variability and a focus on resources that may typically not be limited, which can facilitate coexistence of ecologically similar species. For example, during rockfish recruitment events or localized entrainment of euphausiids in Monterey Bay, skates of all species may feed on episodically plentiful prey resources. Considerable dietary overlap may occur, however, among comparably sized skates, at least at generalized levels of prey differentiation (Bizzarro et al. 2007). Skate populations that overlap substantially in size may, therefore, exhibit distinct spatial zonation to reduce competition for food resources when such resources are limiting, expanding their ranges when food is plentiful. Because most skates seem to have broad potential niches, populations can respond to dynamic conditions by contacting or expanding their realized niches. This process may facilitate the long–term persistence of even highly diverse skate assemblages and account for the remarkable taxonomic diversity within this group.

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2.6 TABLES

Table 2.1 Number of stomach samples for each species in the central California (n = 1254) and Gulf of Alaska (n = 1419) skate assemblages and descriptive information for continuous dietary variables (TL = total length).

Region	Species	Samples (n)	Median TL (cm)	TL Range (cm)	Median Depth (m)	Depth Range (cm)
California	*Beringraja binoculata*	211	38	18–169	31	14–532
	Raja rhina	544	56	23–109	183	29–532
	Raja inornata	264	46	22–66	132	16–194
	Raja stellulata	110	58	41–74	92	44–207
	Bathyraja kincaidii	125	50	35–59	309	128–581
Alaska	*Beringraja binoculata*	357	113	22–199	42	18–212
	Raja rhina	411	94	21–145	121	42–286
	Bathyraja aleutica	252	120	56–162	155	46–313
	Bathyraja interrupta	347	68	17–88	166	42–307
	Bathyraja parmifera	52	87	17–111	141	77–249

Table 2.2. Prey categories added to those originally created by NMFS (2013) for U.S. West Coast Groundfishes and their use in diet composition calculations for the central California and western Gulf of Alaska skate assemblages.

Category	Definition	California	Alaska
ARGIS	crangonid shrimps of the genus *Argis*		X
BAT	Batrachoididea (toadfishes)	X	
BER	*Berryteuthis magister* (armhook squid)		X
CAPE	*Mallotus villosus* (capelin)		X
CGON	crangonid shrimps of the genus *Crangon*		X
COM	*Neocrangon communis* (twospine crangon)		X
CRAN	crangonid shrimps	X	X
CUSK	Ophidiidae (cusk eels)	X	
DWRY	*Cryptacanthodes aleutensis* (dwarf wrymouth)		X
EUAL	hippolytid shrimps of the genus *Eualus*		X
EUCAR	Eucarida (shrimps, mysids, and euphausiids)	X	
FISH	chondrichthyan and teleost fishes	X	X
GONAT	squids of the family Gonatidae		X
HERM	Paguoroidea (hermit crabs)		X
HIPPO	hippolytid shrimps	X	X
MAJID	crabs of the family Majidae		X
PAND	pandalid shrimps	X	X
PANDOP	pandalid shrimps of the genus *Pandalopsis*		X
PANDUS	pandalid shrimps of the genus *Pandalus*		X
PASIPH	pasiphaeid shrimps	X	X
POLL	*Theragra chalcogramma* (walleye pollock)		X
STICH	Sitchaeidae (pricklebacks)		X
TANN	*Chionoecetes baridi* (tanner crab)		X
THYS	euphausiids of the genus *Thysanoessa*		X

Table 2.3. PERMANOVA models of diet composition among several explanatory variables for the skate assemblage off central California with all species included, and with only trawl-caught species (excluding *Raja stellulata*). Degrees of freedom (df), F-statistic, amount of variability explained (r^2), P-value, and results of dispersion analysis ($^{A} = P < 0.05$, $^{B} = P < 0.01$, $^{C} = P < 0.001$) are included. TL = total length. See Materials and Methods for data treatment and variable descriptions.

		ALL SPECIES				TRAWL-CAUGHT SPECIES			
Model(s)	Variable(s)	df	F	r^2	P	df	F	r^2	P
Full Model	Haul	80	4.68	0.217	0.0001	56	5.85	0.206	0.0001
	Species	3	13.06	0.023	0.0001	3	13.17	0.025	0.0001
	TL	1	42.33	0.025	0.0001	1	40.92	0.026	0.0001
	Maturity	2	3.38	0.004	0.0001	2	3.99	0.005	0.0001
	Haul x TL	63	2.04	0.074	0.0001	46	2.29	0.066	0.0001
	Haul x Species	48	1.49	0.041	0.0001	49	1.50	0.045	0.0001
	Species x TL	3	3.72	0.006	0.0001	3	3.72	0.007	0.0001
	Total	200		0.390		160		0.381	
	Residuals	1053		0.610		1143		0.619	
Independent Variables	Haul	80	4.06	0.217	0.0001^{C}	56	5.05	0.206	0.0001^{C}
	Species	4	28.83	0.085	0.0001^{C}	3	33.83	0.082	0.0001^{C}
	TL	1	55.43	0.042	0.0001^{C}	1	52.74	0.044	0.0001^{C}
	Depth	1	43.89	0.034	0.0001^{C}	1	46.26	0.039	0.0001^{C}
	Maturity	2	18.00	0.028	0.0001^{A}	2	17.72	0.030	0.0001^{B}
	Season	2	10.54	0.017	0.0001^{C}	2	11.89	0.020	0.0001^{C}
	Sex	1	1.92	0.002	0.0289	1	2.23	0.002	0.0133
Interaction Effects	Haul	80	4.29	0.217	0.0001	56	5.36	0.206	0.0001
	Species	3	11.96	0.023	0.0001	3	12.05	0.025	0.0001
	Haul x Species	49	1.68	0.052	0.0001	49	1.69	0.057	0.0001
	Haul	80	4.44	0.217	0.0001	56	5.52	0.206	0.0001
	TL	1	38.36	0.023	0.0001	1	37.02	0.025	0.0001
	Haul x TL	63	2.11	0.081	0.0001	46	2.43	0.075	0.0001
	Species	4	30.81	0.085	0.0001	3	36.24	0.082	0.0001
	TL	1	59.41	0.041	0.0001	1	56.92	0.043	0.0001
	Species x TL	4	7.92	0.022	0.0001	3	9.46	0.021	0.0001

Table 2.4. PERMANOVA models of diet composition among several explanatory variables for the western Gulf of Alaska skate assemblage. Degrees of freedom (df), *F*-statistic, amount of variability explained (r^2), *P*-value, and results of dispersion analysis (A = $P < 0.001$) are included. TL = total length. See Materials and Methods for data treatment and variable descriptions.

Model(s)	Variable(s)	df	*F*	r^2	*P*
Full Model	Haul	300	3.34	0.449	0.0001
	Species	4	28.02	0.050	0.0001
	TL	1	34.86	0.016	0.0001
	Maturity	2	4.36	0.004	0.0001
	Depth	1	2.87	0.001	0.0049
	Sex	1	2.72	0.001	0.0131
	Haul x TL	205	1.69	0.155	0.0001
	Haul x Species	149	1.43	0.095	0.0001
	Species x TL	4	2.35	0.004	0.0002
	Total	667		0.775	
	Residuals	502		0.225	
Independent Variables	Haul	300	2.36	0.449	0.0001^{A}
	Species	4	48.17	0.142	0.0001^{A}
	Depth	1	78.10	0.063	0.0001^{A}
	Region	3	22.77	0.055	0.0001^{A}
	TL	1	64.26	0.052	0.0001^{A}
	Maturity	2	13.31	0.022	0.0001^{A}
	Year	1	5.64	0.005	0.0001
	Sex	1	2.14	0.002	0.0390
Interaction Effects	Haul	300	2.88	0.449	0.0001
	Species	4	24.14	0.050	0.0001
	Haul x Species	168	1.59	0.139	0.0001
	Haul	300	2.79	0.449	0.0001
	TL	1	50.32	0.027	0.0001
	Haul x TL	205	1.54	0.169	0.0001
	Species	4	50.45	0.142	0.0001
	TL	1	28.13	0.020	0.0001
	Species x TL	4	8.01	0.023	0.0001
	Species	4	50.86	0.142	0.0001
	Region	3	14.95	0.031	0.0001
	Species x Region	9	3.58	0.022	0.0001

2.7 FIGURES

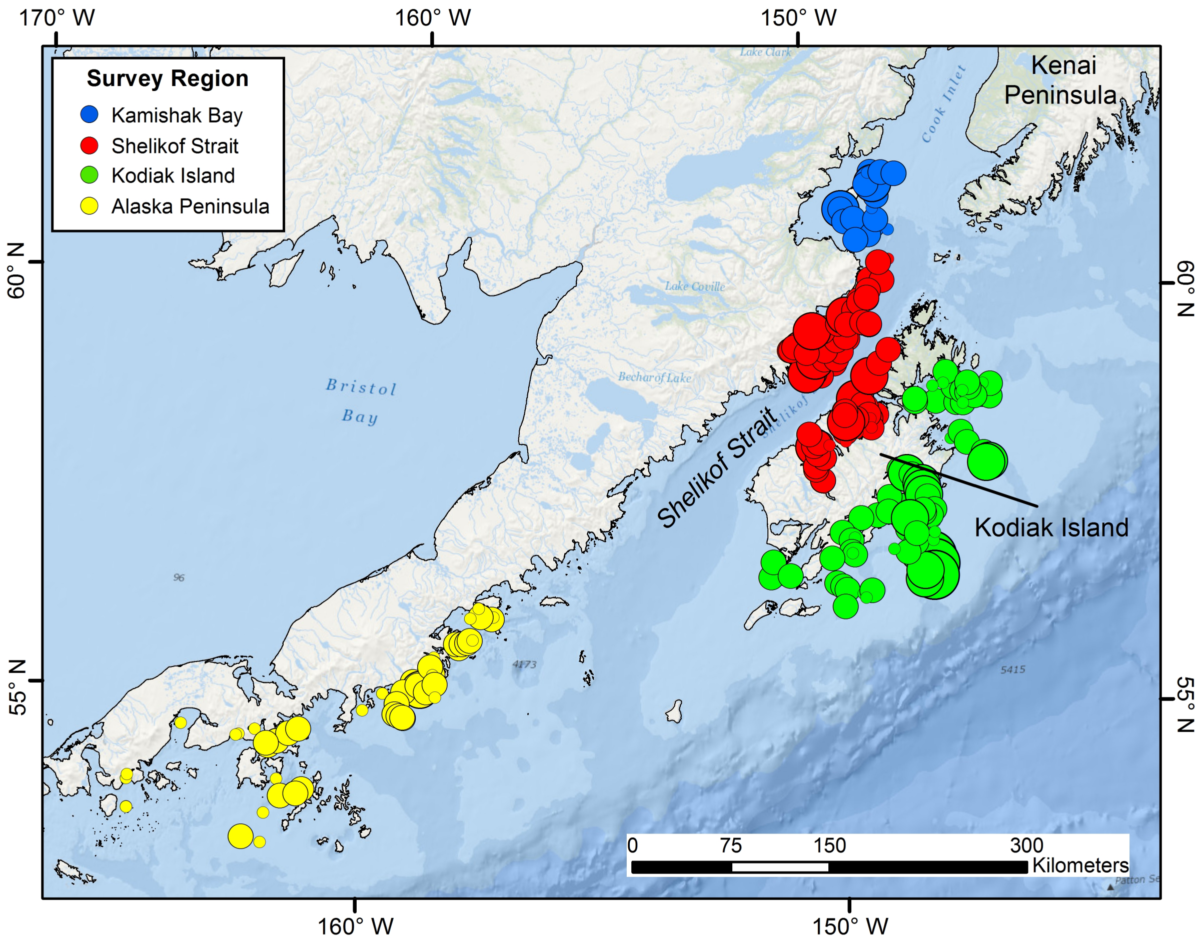

Figure 2.1. Number of stomach samples/haul among regional trawl surveys conducted by the Alaska Department of Fish and Game during 2006 and 2007. Graduated symbols indicate relative sample size among the following categories: 1, *n* = 93; 2–8, *n* = 182; 9–16, *n* = 23; 17–24, *n* = 3. Total number of hauls/region = Kamishak Bay (*n* = 27), Kodiak Island (*n* = 93), Shelikof Strait (*n* = 112), Alaska Peninsula (*n* = 69).

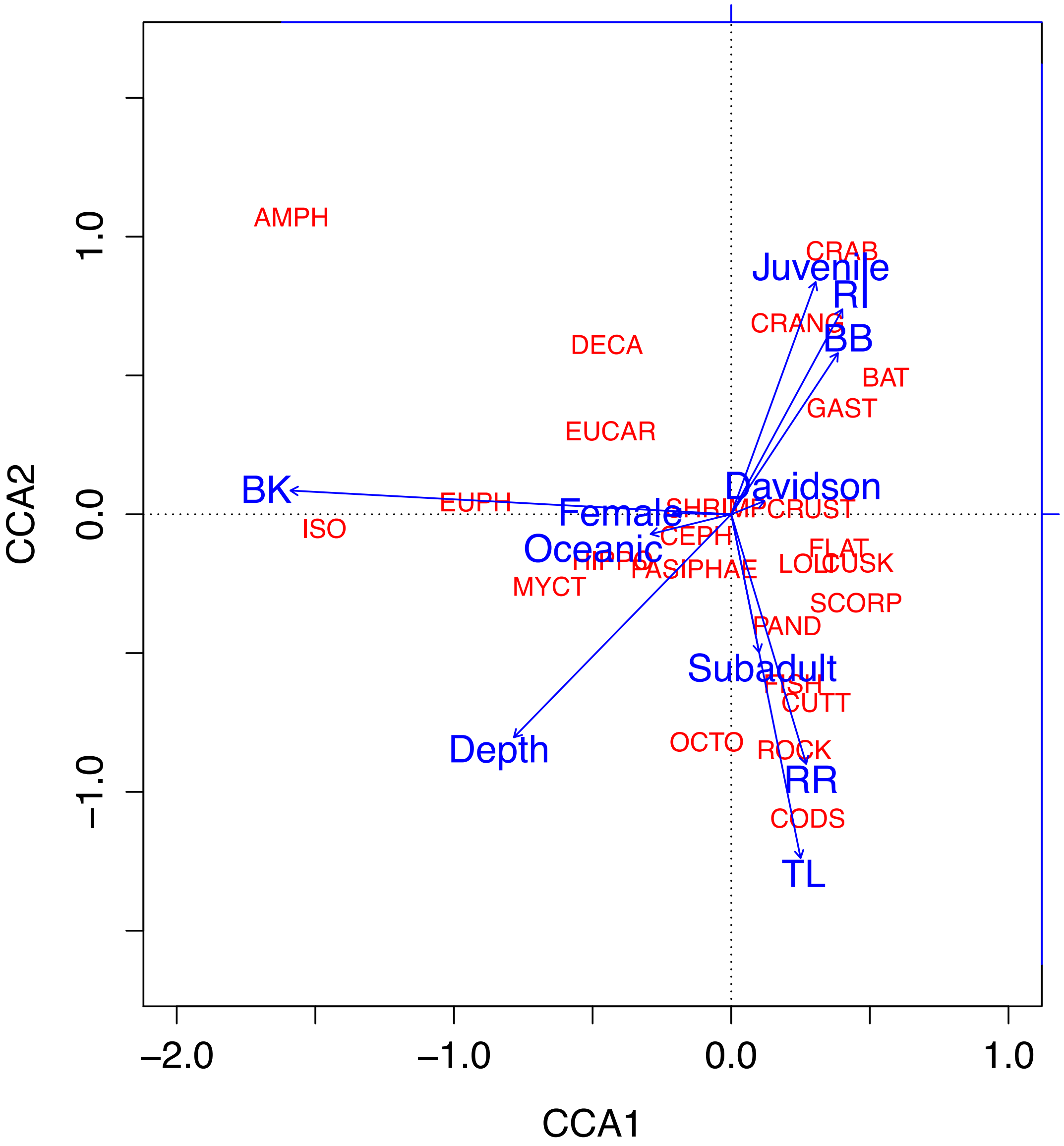

Figure 2.2. CCA biplot of the relationships between response variables (blue) and prey categories (red) for the central California skate assemblage. Length and direction of arrows indicate the relative amount of dietary variation explained by each variable on each canonical axis, whereas the spatial association between response variables and prey category labels indicates the strength of the relationship between them. BB = *B. binoculata*, BK = *B. kincaidii*, RI = *R. inornata*, RR = *R. rhina*. Prey category definitions are provided in Table 2 and NMFS (2013).

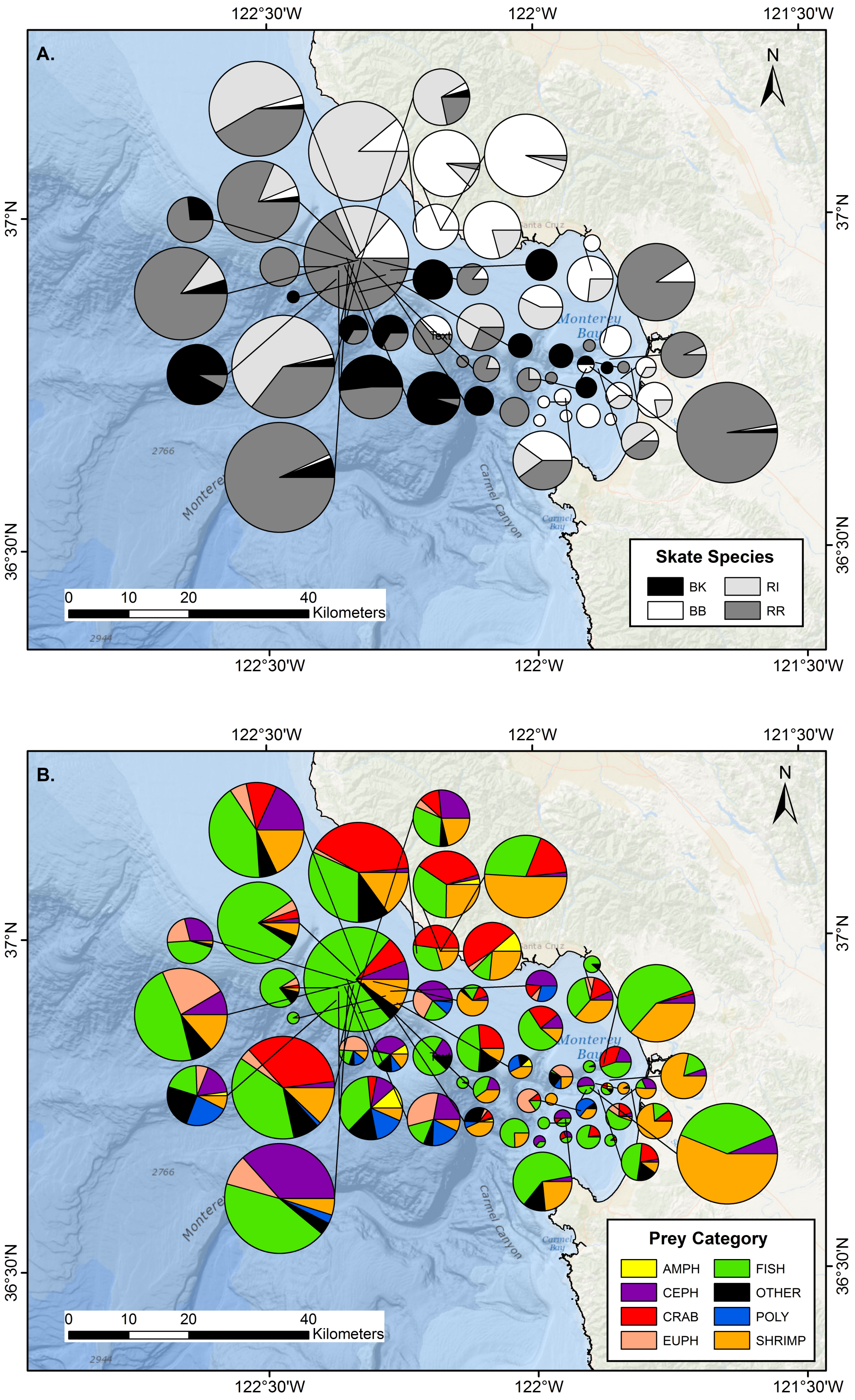

Figure 2.3. Species (A) and diet (B) composition of trawl-collected skates off central California. Relative size of pie indicates sample size (*n* = 1–87 individuals/haul) grouped into 10 categories. BK = *Bathyraja kincaidii*, BB = *Beringraja binoculata*, RI = *Raja inornata*, RR = *R. rhina*. AMPH = amphipods, CRAB= crabs, CEPH = cephalopods, FISH = fishes, SHRIMP = shrimps, POLY = polychaetes, OTHER = all other prey items, EUPH = euphausiids. Lines indicate trawl locations.

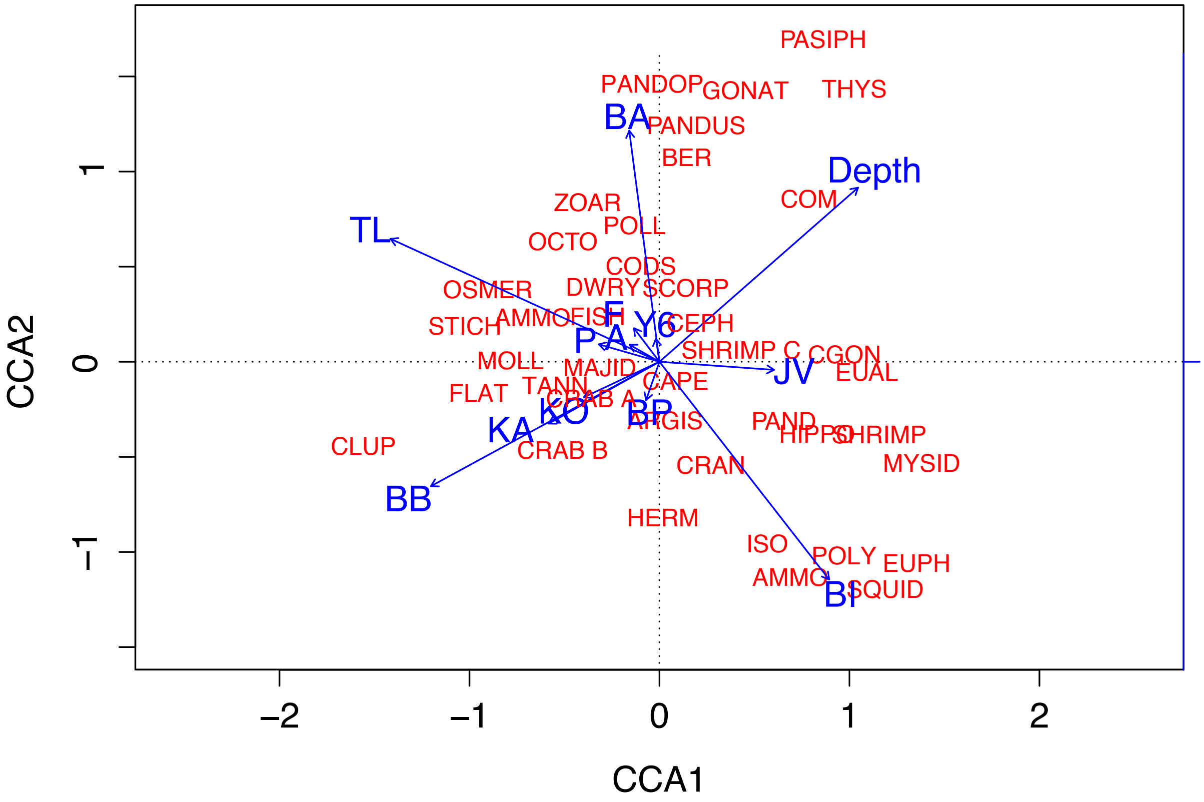

Figure 2.4. CCA biplot of the relationships between response variables (blue) and prey categories (red) for the western Gulf of Alaska skate assemblage. Length and direction of arrows indicate the relative amount of dietary variation explained by each variable on each canonical axis, whereas the spatial association between response variables and prey category labels indicates the strength of the relationship between them. BA = *B. aleutica*, BB = *B. binoculata*, BI = *B. interrupta,* BP = *B. parmifera*, KA = Kamishak Bay, KO = Kodiak Island, P = Alaska Peninsula, Y6 = 2006, JV= juvenile, A = adult, F = female. Prey category definitions are provided in Table 2 and NMFS (2013).

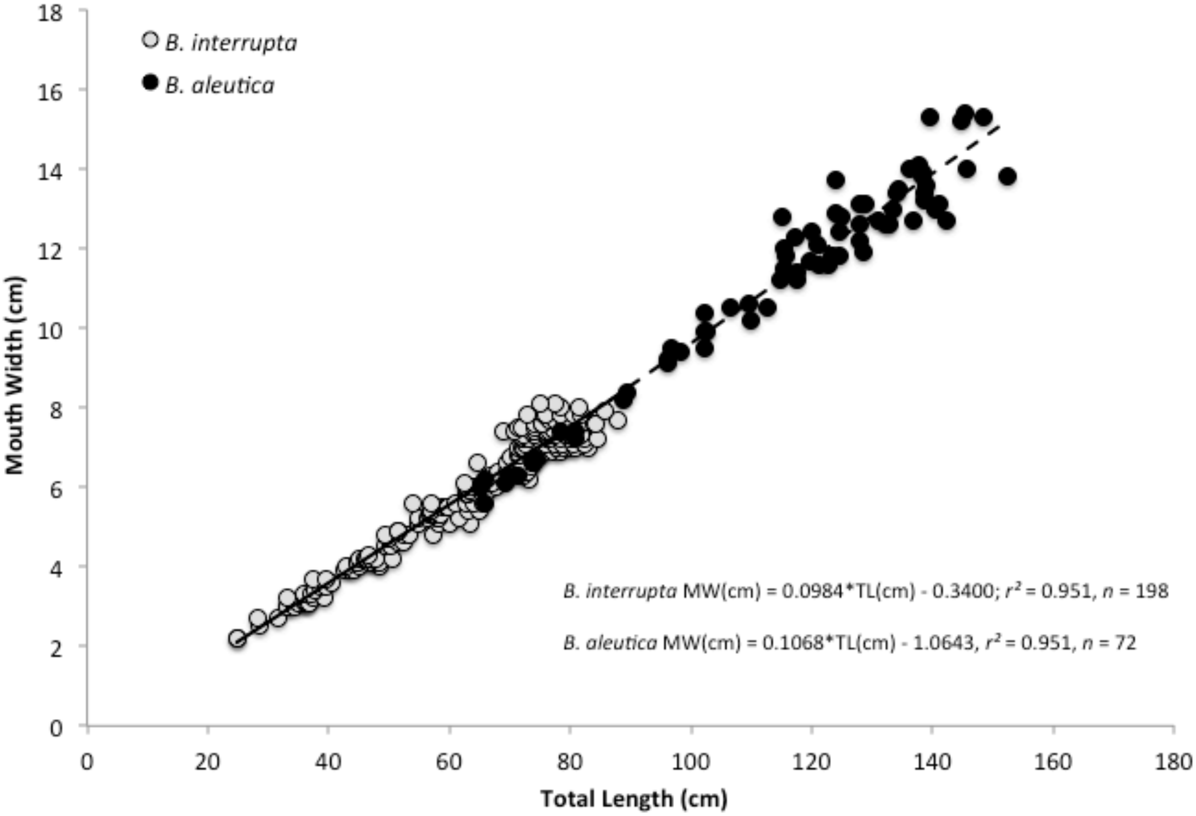

Figure 2.5. Relationship of mouth width to total length for *Bathyraja aleutica* and *B. interrupta.* individuals captured in Shelikof Strait during 2007. Solid line = line of best fit for *B. interrupta*, dashed line = line of best for *B. aleutica*.

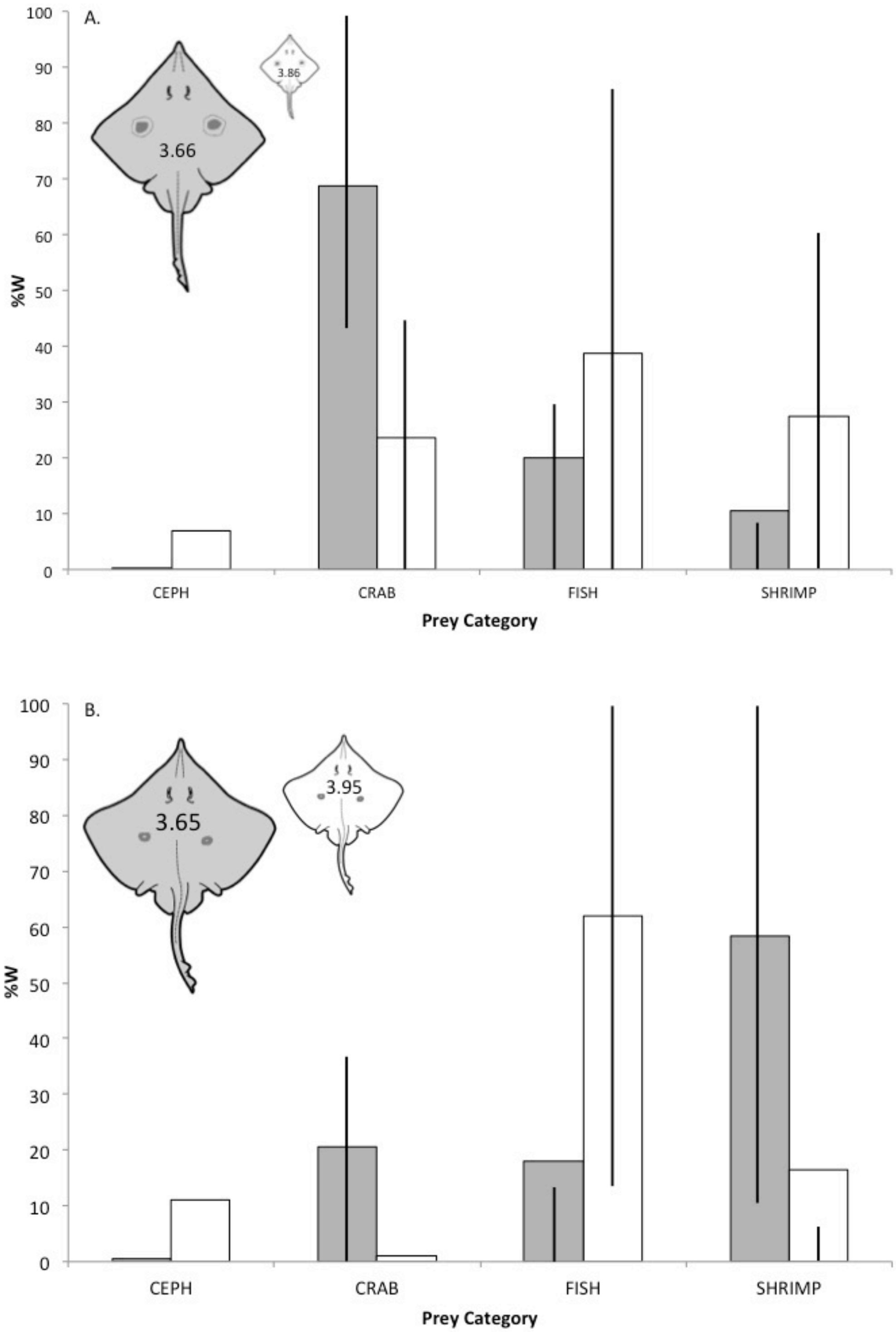

Figure 2.6. Comparative general diet composition of (A) *Beringraja binoculata* and (B) *Raja rhina* from the western Gulf of Alaska (grey) and off central California (white). Histograms indicate mean %W values, whereas black lines depict first and third quartiles. Skate images are scaled to reflect relative differences in median total length between regions and include median trophic level values.

Chapter 3: ECOLOGICAL CONSIDERATIONS FOR IMPROVED MANAGEMENT OF EASTERN NORTH PACIFIC SKATES

Population declines, shifts in assemblage structure, and ecological interactions with exploited groundfishes have focused increased scientific and management attention on skates (Rajiformes: Rajoidei). Skates are common components of exploited groundfish assemblages in the Gulf of Alaska (GOA) and off the U.S. West Coast, but a better understanding of skate ecology is necessary for the development of effective, ecosystem approaches to skate management in these regions. Diet composition and consumption of big, longnose, and softnosed skate (*Bathyraja* spp.) were determined and applied to a GOA food web model. Diets of big and Alaska skates consisted primarily of Tanner crab, pandalid shrimps were the main prey of the Aleutian skate, and longnose and Bering skates ate a mixture of pandalid, crangonid, and hippolytid shrimps. During 2006 and 2007, consumptive removals of Tanner crab (~85,000 t/year) and pandalid shrimps (~84,000 t/year) by skates in the GOA exceeded commercial landings of these decapods throughout Alaskan waters. Updating diet compositions and annual consumption to biomass ratios of skates in the GOA food web model substantially altered trophic interactions and system dynamics. In the original model, total skate predation mortality on Tanner crab was estimated at 0.2%. Skates (especially big skate) were the most important predatory group of Tanner crabs in the updated model, accounting for 28.3% of Tanner crab predation mortality, followed by cods (27.2%) and flatfishes (16.0%). Off the U.S. West Coast, distribution and abundance patterns of juvenile and adult life stages of federally managed (longnose) and other common (California, longnose, sandpaper, starry) skates were determined as a potential basis for spatial management. Depth was the primary factor responsible for predicting distribution and abundance patterns, followed by latitude and habitat type. The variable influence of these factors served to define core regions of common occurrence for juvenile and adult life stages. Spatial segregation was evident among species, but adults of relatively large species often overlapped in distribution with juveniles and adults of smaller species (e.g., adult big skate, California skate; adult longnose skate, sandpaper skate). Results of trawl analysis and predictive modeling were used to resolve inaccuracies and update information in the National Marine Fisheries Service (NMFS) Habitat Use Database, which is used as a basis for habitat analysis and management considerations for West Coast groundfishes, including skates. Habitat Suitability Probability maps, which estimate essential fish habitat (EFH) for managed groundfishes, are deterministic and over-emphasize the importance of habitat. Maps based on regression model predictions, like those developed in this study, provide a more objective, quantitative option for estimating EFH.

3.1. INTRODUCTION

Fisheries managers recently have embraced the development and implementation of more holistic strategies (i.e., ecosystem-based fisheries management, EBFM) that, in addition to incorporating economic and societal goals, integrate ecological considerations and related environmental factors that influence the structure and dynamics of marine ecosystems (Essington and Punt 2011; Link et al. 2012). EBFM represents a fundamental ideological shift in strategy by considering impacts to marine ecosystems as well as target species, with the goal of maintaining the sustainability of exploited stocks while reducing the ecological footprint of fisheries (Pikitch et al. 2004). Although the philosophy driving this paradigm shift has progressed rapidly, the development and implementation of EBFM has lagged behind because of the inherent complexity of the concept, our rather poor understanding of marine ecosystem structure and dynamics, and the logistical constraints involved in modifying established management plans

(Essington and Punt 2011). In regions where an ecosystem approach has been proposed (e.g., New England groundfish; Link et al. 2011) or incorporated (Southern Ocean krill; Watters et al. 2013) into management strategies, ecological information that describes spatial associations and trophic relationships are fundamental to the process.

Skates, cartilaginous fishes of the suborder Rajoidei, are exploited in commercial groundfish fisheries throughout temperate and boreal regions of the world. Although mainly taken incidentally, fishery mortality has altered species composition of skate assemblages and caused substantial declines in the populations of many large, nearshore species (Walker and Hislop 1998; Dulvy et al. 2000, 2014). Skates were afforded little scientific attention or management consideration in the past because they have not supported lucrative or sustained fisheries. However, because they are predators and competitors of other commercially important, sympatric groundfishes (Link et al. 2002), and because dramatic changes in population sizes of exploited species have been documented (Frisk 2010), this situation is changing.

Skates are common components of exploited groundfish assemblages in Alaskan waters and off the U.S. West Coast. Federal groundfish management techniques differ substantially between these regions, partially as a result of different spatial associations, movement patterns, and life history traits of regional fisheries stocks. EBFM efforts off Alaska are focused on modeling trophic relationships and food web dynamics (Zador 2014). The primary demersal fishery targets in Alaskan waters, cods (Gadiformes) and flatfishes (Pleuronectiformes), are either highly mobile or do not display strong habitat associations, and therefore appear to be well suited for this type of management approach. Off the U.S. West Coast, an abundant and speciose component of the regional groundfish assemblage, rockfishes (Sebastidae), are typically associated with hard-bottom habitats. In addition, many exploited rockfish stocks have k-selected life history traits that make them vulnerable to overfishing. Of the ten groundfish stocks that have been declared overfished since the passage of the Sustainable Fisheries Act in 1996, seven are rockfishes. Contemporary management approaches off the West Coast typically involve spatial closures and marine protected areas (MPAs), which are intended for demersal species with strong habitat associations such as rockfishes (National Marine Fisheries Service, NMFS 2013).

In Alaskan waters, stocks of the two dominant, shallow water (< 200 m) species, the big skate (*Beringraja binoculata*) and longnose skate (*Raja rhina*), are managed on a species-specific basis, whereas skates occurring in deeper waters (e.g., Aleutian skate, *Bathyraja aleutica*; Bering skate, *B. interrupta*) or in low relative abundance (e.g., Alaska skate, *B. parmifera*) are managed in aggregate (Ormseth 2014). Directed fishing of skates has been prohibited in federal waters of the Gulf of Alaska since 2005 because target fisheries established during 2003 were unsustainable (Ormseth 2014). However, the retention of incidental skate catch in regions such as Kodiak Island, Lower Cook Inlet, and Prince William Sound remains a management concern because the Acceptable Biological Catch (ABC) of big and longnose skates routinely has been exceeded since 2005 (Stevenson et al. 2008; Ormseth 2014).

Food web models of commercially important species can improve fisheries management by determining and evaluating sources of variability in mortality and production that are not typically included in single-species stock assessments (Gaichas et al. 2010). An application of food web models to fisheries management is evident in the Gulf of Alaska, where outputs derived from steady-state mass-balance models are included in groundfish stock assessments. However, trophic information necessary to effectively model the food web of the two managed hardnosed (*Raja*) stocks and the aggregate softnosed (*Bathyraja* spp.) skate stock, and for inclusion in the overall Gulf of Alaska food web model are lacking. Diet composition data from other regions therefore were used as model inputs (Gaichas et al. 2010). This practice, however, is not appropriate for generalist predators such as skates, as evidenced by the highly variable prey spectrums and predatory roles of disjunct big and longnose skate populations in the eastern North Pacific (Chapter 2). More accurate data inputs are needed to refine food web models for skates in the Gulf of Alaska.

Only one skate species (longnose skate) is included in the current Federal Management Plan (FMP) for U.S. West Coast groundfishes (NMFS 2013). Populations of four other species that commonly occur on the continental shelf and upper continental slope, the big skate (*B. binoculata*), California skate (*R. inornata*), sandpaper skate (*B. kincaidii*), and starry skate (*R. stellulata*) are considered ecosystem components and not managed directly (Chapter 1). Management of U.S. West Coast skate stocks lags behind that of Alaska. West Coast skate landings are still largely unidentified or misidentified, and a baseline condition for the distribution and relative abundance of the dominant species on the continental shelf and upper slope only recently has been established (Chapter 1). Coastwide habitat suitability maps that were developed as a possible precursor to spatial management of the three FMP skate species do not appear to accurately reflect their distribution and abundance patterns (PFMC 2005). For example, by simply providing more accurate model inputs, the amount of highly suitable habitat for the California skate was reduced to 5% of that originally predicted (Chapter 1). More accurate predictions of distribution and abundance patterns are necessary before effective spatial management strategies can be developed for West Coast skates

The primary objective of this study was to provide a better understanding of skate ecology in the U.S. eastern North Pacific as a basis for the development of improved EBFM strategies for these species. Efforts focused on trophic interactions of skates in the Gulf of Alaska, and spatial associations of skates along the U.S. West Coast, in accordance with the current regional managerial strategies in effect. The most abundant skate species occurring on the continental shelf and upper continental slope of each region constituted the study species. Specific objectives for the Alaska portion of the study were to: 1) characterize diet composition of each skate species based on the main sources of variability (spatio-temporal, length-based) that were identified in Chapter 2; 2) estimate per capita daily consumption and consumptive removals of commercially important taxa for each skate species and the entire assemblage; and, 3) incorporate diet composition and consumptive removal results for skates to update the current Gulf of Alaska food web model. The goals of the West Coast portion of the study were to: 1) estimate distribution and abundance patterns of juveniles and adults of all soft-bottom associated skate species, 2) determine the relative importance of each factor (depth, latitude, habitat) in predicting distribution and abundance patterns, and 3) update essential fish habitat (EFH) data on geographic, depth, habitat, and temperature associations of each species in the assemblage.

3.2. METHODS

3.2.1. *Gulf of Alaska: Spatio-Temporal and Length-Based Diet Composition*

Stomach samples and data necessary for diet composition estimates of the five most common skate species in the Gulf of Alaska (Stevenson et al. 2008) were obtained from research bottom trawl surveys. All skates were sampled at sea during Alaska Department of Fish and Game (ADFG) surveys that were conducted in the west-central Gulf of Alaska during May–September of 2006–2007 (Fig. 1). Trawl sets generally were fished on soft substrates on the continental shelf (22–254 m). All skates were identified to species and measured (total length, TL, to the nearest 1.0 cm). Stomach samples were collected opportunistically from individuals of all species and processed as described in Chapter 2. Prey items were grouped into 47 generalized categories, developed by the NMFS during a recent 5-year review of EFH legislation for West Coast groundfishes, to minimize redundancy among identifications of different taxonomic resolution (NMFS 2013). These prey categories were then augmented to better match the prey spectrum consumed by skates in the western Gulf of Alaska, and to account for more specific prey taxa that contributed substantially to diet composition (e.g., Tanner crab, *Chionoecetes bairdi*; see Chapter 2, for additional prey categories).

Diet composition was estimated by calculating a single, commonly used metric (%Weight, %W) that is considered to be a general proxy for energetic value (Hyslop 1980). %W was computed on an individual-basis (mass of a prey category in a stomach sample/total mass of all prey categories in a stomach sample), which enabled measures of central tendency and variability. Mean values of diet composition (sum of %W for all non-empty stomach samples of a prey category/total number of non-empty stomach samples) are often inappropriate estimators for generalist predators (such as skates) because of extreme intraspecific variability in diet composition (see Bizzarro et al. 2007). To mitigate this bias, median values (midpoint of %W values when arranged from lowest value(s) to highest value(s)) also were computed, as well as the first and third quartiles. %W was estimated for the 68 referenced prey categories, and taxa were subsequently grouped such that all final categories occurred in at least 1% of non-empty stomach samples. A 1% cut-off value was used to minimize redundancy among minor prey taxa and because it resulted in the most parsimonious PERMANOVA model of dietary variability explained for this assemblage (Chapter 2).

Diet composition data were grouped based on known sources of variability and analyzed for each Alaska skate species. Prior study indicated extreme spatio-temporal variability in diet composition of the Gulf of Alaska skate assemblage, and significant dietary differences across a TL gradient (Chapter 2). Therefore, diet composition was calculated by region (Alaska Peninsula, Kamishak Bay, Kodiak Island, Shelikof Strait) for each sample year (2006, 2007), and separately by size (< 50 cm TL, 50–99 cm TL, 100–149 cm TL, 150–199 cm TL). TL categories were chosen to reflect the general sizes of observed dietary shifts in skates from prior studies (Ebert and Bizzarro 2007; Wetherbee et al. 2012), and to minimize low data density (i.e., number of stomach samples) among size categories. Diet composition was calculated for all spatio-temporal or size groupings with $\geq$ 25 samples. To evaluate sample size sufficiency of diet composition results, the estimated number of unique prey taxa was plotted against the cumulative number of stomach samples examined (Ferry and Cailliet 1996; Gotelli and Colwell 2001) using the Mao Tao expected richness function (Colwell et al. 2012). The resultant curve was determined to approach an asymptote, indicative of sample size sufficiency, if the best-fit regression line of the last five estimated values had a slope < 0.05 (after Bizzarro et al. 2009).

3.2.2. *Gulf of Alaska: Per Capita Daily Consumption and Consumptive Removals*

Per capita daily consumption was calculated using the gastric evacuation rate method (Eggers 1977; Elliot and Persson 1978), as advocated by Link and Sosebee (2008) for its relative ease of calculation and widespread usage. By this method, per capita consumption rate of species i (C_i) = $24 * E_i * \bar{S}$, where C_i = per capita consumption rate for species i, 24 = number of hours in a day, E_i = evacuation rate = $\alpha e^{\beta T}$, and $\bar{S}$ = mean weight (g) of prey items among all (empty and non-empty) stomach samples. In the formula for evacuation rate, the parameters α and β were set to values of 0.02 and 0.11, and T = mean temperature at depth among all trawl sets. These values have been advocated as appropriate for skates based on studies conducted for the Northeastern Atlantic assemblage (see Link and Sosebee 2008); however, unpublished data suggest that using these parameter values may result in substantial underestimates of per capita consumption rates, or that there may be significant variation in such rates among species (Sarah G. Gaichas, , NMFS–Alaska Fisheries Science Center, pers. comm.) Results should therefore be considered to represent conservative estimates. Per capita daily consumption rates were computed by year (2006, 2007) and size class (as previously indicated) for the NMFS Central management region (147–159º W). All calculations were made on an individual basis, and then combined to compute descriptive statistics (i.e., median, quartiles, range) for each species/group.

Median per capita daily consumption rate estimates were scaled up to estimate total consumption (C) for each species and the entire assemblage in the Central Region during the five sampled months (May–September), as follows: $C = 153 * C_i * N_i$, where 153 = number of days in the sampling period, C_i = per capita consumption rate, and N_i = estimated numerical abundance of skate species i. Numerical abundance, as estimated by year and NMFS management region, was provided for 2007 from a survey-based stock assessment (Olav Ormseth, NMFS–Alaska Fisheries Science Center, pers. comm.). Because no bottom trawl survey was conducted in the Gulf of Alaska during 2006, the numerical abundance estimate for 2006 was averaged from 2005 and 2007 stock assessment estimates.

Total consumption of each species was calculated on an overall basis and then partitioned among common prey taxa of commercial importance to estimate consumptive removals. Consumptive removals by skates can exceed fishery removals and may have a significant effect on the population dynamics of some prey species (Link and Sosebee 2008). These totals were therefore compared to fishery removals to evaluate the relative magnitude of skate removals and potential competition between skates and fisheries for prey taxa. Commercially important prey of skates in the Gulf of Alaska include: pandalid shrimps, Tanner crab, walleye pollock (*Theragra chalcogramma*), and flatfishes (Pleuronectiformes) (Chapter 2). Upper and lower bounds were created for consumptive removal using the ± SD of numerical abundance values.

3.2.3. *Gulf of Alaska: Food Web Model*

Diet composition and consumption estimates were included in an existing steady-state food web model for the Gulf of Alaska continental shelf (Gaichas et al. 2010, Ormseth 2014) to improve model accuracy and compare outputs. The use of static food web models to assess trophic relationships and mortality sources: 1) provides ecological considerations to existing single-species management approaches and, 2) enhances the opportunity for EBFM of skates and their competitors, predators, and prey by enabling an evaluation of the simplifying assumptions of single-species models (constant natural mortality, density-dependent growth) and their suitability in an ecosystem context. An independently implemented version of the Ecopath model (Polovina 1984) was developed and used to estimate the Gulf of Alaska continental shelf food web, as described in Gaichas et al. (2010). Fisheries removals were incorporated in this model, and fisheries can therefore be considered as potential competitors or predators. Three skates species groups were included: big skate, longnose skate, and other skates, which is an aggregate category of softnosed skate species, with inputs blended based on relative biomass.

Literature values from distant regions and related taxa were used for skates in the construction of the original Gulf of Alaska food web model because local information was extremely limited (Gaichas et al. 2010). For example, historical diet composition data for the longnose skate were incorporated from a study conducted off the Oregon coast (Wakefield 1984) and modified based on observations made during a 1993 Gulf of Alaska bottom trawl survey. Updated data inputs included: 1) numerical abundance and biomass estimates from Gulf-wide stock assessments, 2) new, detailed diet composition data, and, 3) an updated estimate of consumption/biomass (Q/B). Abundance and biomass data for 2007 were taken directly from trawl survey estimates and stock assessments (Ormseth 2014; O. Ormseth, pers. comm.). Since no survey was conducted during 2006, data from 2005 and 2007 surveys were averaged to produce estimates for 2006. Estimates from 2006 and 2007 were then averaged to produce a single estimate of numerical abundance and biomass for each skate species group. Diet composition data (%W) from 2006 and 2007 were averaged for each of the three ADFG survey regions that are included in the NMFS Central Region (Kamishak Bay, Kodiak Island, Shelikof Strait), then scaled based on the predicted relative abundance of each species group among regions (Chapter 1). Scaled regional diet composition estimates were then summed and converted back to proportional data (%W) to create an overall diet composition estimate for the Central Region. Because more widespread diet composition data are not available, estimates from the Central Region were extrapolated to the entire Gulf. All dynamic outputs (i.e., estimated trophic level, total number of pathways, mortality rates, magnitude of biomass flows, overall structure of the food web) were compared between the original and updated model to assess the effect of incorporating more representative model inputs.

3.2.4. *West Coast: Trawl Survey Data*

Data necessary for determining distribution and abundance patterns of the four most common skate species on unconsolidated and mixed seafloors off the U.S. West Coast (Chapter 1) were collected from research bottom trawl surveys. Surveys were conducted by the NMFS–Northwest Fisheries Science Center (NMFS–NWFSC) during May–October of 2003–2013. The inception of the data sets corresponds to a change in the coverage and design of NMFS surveys along the U.S. West Coast. In 2003, the function of three former surveys was collapsed into a single West Coast Bottom Trawl Survey (WCBTS) that samples continental shelf and slope regions (55–1,280 m) between Cape Flattery, Washington (48º 10' N) and the U.S.–Mexico border (32º 30' N). A stratified-random sampling design is executed using commercial trawlers to monitor long-term trends in distribution and abundance of West Coast groundfishes among five geographic areas and three depth strata (Keller et al. 2007). Stations are chosen randomly among all towable regions in each area and depth strata. An Aberdeen-style net with a 1.5" codend liner is used to sample groundfish abundance and biomass. Each tow is fished for approximately 15 minutes. The WCBTS is conducted in two non-overlapping legs that progress from north to south, separated by a short break during August. Data were limited to those with geographic coordinates that were derived from tow midpoints, resulting in a data set of 4,593 hauls that were fished at depths of 56–1271 m from 32.01–48.45° N (Fig. 2A). Depth and temperature ranges of the analyzed data set were consistent with those of the larger data set (*n* = 6923), and the distribution of tows was similar (Median, Q1–Q3; truncated data set: 288 m, 125–575 m; 41.3º, 35.4º–45.0º N; full data set: 273 m, 120–591 m; 41.3º, 35.5º–45.0º N).

Skates from the WCBTS were identified and sampled for biological information (e.g., TL and sex) at sea by NMFS personnel. Maturity status of skates was not determined during the surveys. Instead, maturity of WCBTS-collected skates was assigned from TL data and corresponding length-at-maturity estimates, which were available for skate populations sampled independently off central California (D.A. Ebert, Pacific Shark Research Center, Moss Landing, CA, unpublished data). Juveniles measured less than the median size at 50% maturity, whereas larger specimens were considered adults. Maturity stages could not be distinguished for sandpaper skate because length information was not typically recorded.

3.2.5. *West Coast: Statistical Modeling of Habitat Use*

As a precursor to modeling distribution and abundance patterns of skates along the U.S. West Coast, a temperature-depth relationship was constructed and a contiguous habitat map was created. It was necessary to establish a temperature-depth relationship because these variables were highly correlated (ρ = -0.86), and because temperature was not consistently recorded during the WCBTS. A coast-wide temperature-depth relationship was estimated using a generalized additive model (GAM), with temperature as the response variable and depth as the explanatory variable. The best-fit GAM model, Log(Temp) ~ s(Depth) + s(Latitude), explained 91.1% of the variability in temperature. Habitat type was derived from an updated, raster version of the West Coast substrate map that was created for the recent 5-year EFH review (NMFS 2013; Fig. 2B). Habitat types follow seabed induration (Greene et al. 1999) and were translated from polygon format to a 25 m by 25 m raster image by selecting the habitat type with the maximum combined area within each cell. A circular buffer, set to the length of the tow, was created around each tow midpoint to include all potentially trawled seafloor. Three habitat types (soft, mixed, hard) were distinguished because of the limited availability of more specific habitat characterizations (e.g., grain size). The compound scoring method of Stein et al. (1992) was used to characterize habitat types, with primary habitats covering $\geq$ 50% of the potential towed region, and secondary habitats accounting for $\geq$ 20%. For species with too few occurrences to facilitate inclusion of multiple habitat variables in model calculations (big skate, California skate), a simplified habitat variable was created based on the dominant habitat type (i.e., Hard, Mixed, Soft).

Zero-inflated Poisson (ZIP) regression models were fit to trawl and seafloor habitat data to: 1) determine which variables were associated with predicted numerical counts (response variable) of skate species and their life stages and, 2) estimate depth, habitat, geographic, and (indirectly) temperature ranges of occurrence. ZIP models were used to model WCBTS data from 2003–2013, with effort (i.e., area swept) as an offset (Maunder and Punt 2004), because of an overabundance of zero-catch data and dispersion issues compared with that expected under an Poisson distribution. Numerical covariates (e.g., depth, depth^2, latitude, latitude^2) were scaled by their means and standard deviations to avoid computational problems in the optimization of regression models. Longitude was omitted because it was highly correlated with latitude (ρ = -0.89). The full model was fit for juveniles and adults of each species, and for the sandpaper skate. Distribution and abundance patterns of the starry skate were not modeled because WCBTS are conducted in trawlable (i.e., soft sediment) habitats and starry skates are found primarily on rocky reefs (Chapter 1).

ZIP models with different variable combinations were evaluated and a final model was chosen for each species/life stage and used to predict expected counts among explanatory variables. Stepwise model selection, with a cut-off of $p = 0.05$. was conducted to determine if regression coefficients significantly affected the distribution of a life stage or species. Aikaike’s Information Criterion was used to evaluate the relative fit of different regression models (Aikaike 1974). If the Habitat variable resulted in a substantially improved fit, it was included in final ZIP models even if no individual factors (e.g., hard-mixed, soft-hard) were significant. Potential spatial autocorrelation in variables was visually assessed using residual plots. The final life-stage (or species) specific models, without the inclusion of error terms, were used to predict the magnitude of occurrence across the entire sampled depth and latitudinal ranges. Three metrics were calculated for numerical data: 1) overall range = minimum value–maximum value, 2) common range = locations where counts > median counts, and 3) maximum occurrence = largest value(s) + any values within 10% of the maximum value. Significant habitat factors in the final model were identified.

3.2.6. *West Coast: Trawl Survey Analysis and Habitat Use Database Updates*

Predicted distribution and abundance patterns from ZIP model outputs were compared to observed patterns derived from the WCGBTS to determine actual values associated with overall, common and maximum counts and to evaluate model performance. These results then were compared to those contained in NMFS–NWFSC's groundfish Habitat Use Database (HUD) to resolve inaccuracies and augment existing knowledge. The HUD was developed from a literature review conducted for each designated life stage (egg/larvae, juvenile, adult) of all FMP groundfish species and is used as a basis for habitat analysis and management considerations (NMFS 2005). It provides absolute, common, and optimal ranges for depth, temperature, and latitude, in addition to documenting habitat associations. Absolute range is considered as the minimum and maximum occurrence values for all explanatory variables. Common ranges of modeled West Coast skates were considered as previously described and are analogous to preferred ranges in the HUD. Optimal ranges were those associated with predicted maximum occurrence. Absolute, common, and maximum depth and temperature ranges also were updated for the starry skate. Habitat associations were calculated for each species and life stage using G-Tests, conducted from a comparison of observed and expected densities among habitat types.

3.3. RESULTS

3.3.1. *Gulf of Alaska: Spatio-Temporal and Length-Based Diet Composition*

Gulf of Alaska skates consumed mainly shrimps (Pandalidae, Crangonidae, Hippolytidae) and Tanner crab during 2006 and 2007, with fishes ingested supplementally and other taxa (Polychaeta, Mollusca) contributing trivially to diet composition. Interspecific dietary variation was reflected in the differential relative proportions of decapod crustaceans and fish prey among species. Diets of big and Alaska skates consisted primarily of Tanner crab, whereas pandalid shrimps were the main prey of the Aleutian skate, and longnose and Bering skates ate a mixture of pandalid, crangonid, and hippolytid shrimps. The relative dietary contribution of fishes increased with size for all species, and those attaining the greatest TLs (big, longnose) were more piscvivorous. By contrast, consumption of polychaetes and amphipods only was notable in the diet of the smallest species (Bering skate). Diet composition of most species reflected the ingestion of a wide prey spectrum, but spatio-temporal dietary differences were evident. For instance, a greater proportion of euphausiids was observed in the diet of softnosed skates in Shelikof Strait during 2007 as compared to 2006, and Tanner crab consumption was greatest in the Kodiak region among species with available data.

Tanner crab dominated big skate diet composition in all sampled regions during 2006 and 2007 (Table 1); therefore, spatio-temporal dietary differences were relatively minor compared to those of sympatric skates. Crangonid shrimp consumption was elevated in Kamishak Bay during both sample years, whereas *Argis* spp. were preyed upon mainly along the Alaska Peninsula (Table 1). The greatest dietary contribution of Tanner crab (80%) occurred in the Kodiak region during 2007. Fish consumption was greater during 2006 (mean %W = 21.3; 2007 mean %W = 10.0) in Kamishak Bay and off Kodiak, but never totaled more than 23% among any spatio-temporal groupings. Hard-shelled molluscs and octopods were consistent, but trivial dietary components (Table 1).

Tanner crab dominated diet composition of all big skate length classes, but the relative proportion of fishes:shrimps increased with length (Table 2). Individuals measuring 50–99 cm TL ate diets consisting of 17.7% shrimp and 7.7% fishes, whereas specimens ranging from 150–199 cm TL consumed proportions of 2.9% and 41.5%, respectively. Intermediate-sized individuals (100–149 cm TL) ate nearly 75% Tanner crab by weight. Fishes (14.9%) and shrimps (3.7%) were relatively minor prey taxa for skates measuring 100–149 cm TL. Crangonids were the primary shrimp prey regardless of size (Table 2). The dietary contribution of flatfishes increased with increasing length (Table 2), and constituted 74% of identified fish prey in specimens $\geq$ 150 cm TL.

Longnose skate diet was relatively diverse, with most spatio-temporal and length-based dietary variation reflected in the relative proportions of shrimps and fishes (Table 3). Off the east side of Kodiak Island, shrimps were more abundant in the diet during 2007, whereas fishes were more abundant during 2006 (Table 3). The opposite trend was observed in Shelikof Strait, and shrimp were consumed in greater proportions in this region, dominating diet composition during both sample years (Table 3). The dietary proportion of fish to shrimp increased with length. Shrimp taxa composed 91.8% of diet in specimens < 50 cm TL, but only 39.1% in specimens measuring 100–149 cm TL. A substantial decline in consumption of relatively small shrimps (crangonids, hippolytids) was responsible for this trend, as consumption of larger, pandalid shrimps slightly increased with length (Table 3). Fishes, by contrast, were negligible in the diet of the smallest specimens (0.1%) but accounted for 30.1% of diet composition in the largest size class.

Diet composition of the Aleutian skate was relatively diverse but exhibited notable spatio-temporal and length-based variation in core prey taxa (Table 4). The presence of euphausiids and cephalopods (e.g., gonatid squids) in Shelikof Strait diets was restricted to 2007, when they were common supplemental prey items (Table 4). Diet composition also was more evenly distributed among prey taxa during 2007 in Shelikof Strait, as shrimps contributed 67% to regional diet composition during 2006. Fishes contributed much more substantially to diet composition in the Peninsula region than in Shelikof Strait (Table 4). Capelin (*Mallotus villosus*) and Tanner crab were consumed in greater abundance off the Peninsula during 2006, whereas *Pandalus* spp. were more common in diet composition during 2007 (Table 4). Aleutian skate diet off Kodiak consisted primarily of fishes (44.5%) and Tanner crab (39.0%), although a wide variety of other taxa were ingested in small amounts. A clear dietary distinction was evident between specimens measuring 50–99 cm TL and those measuring 100–149 cm TL . Smaller specimens consumed less fish and cephalopod prey, and ate greater proportions of smaller shrimps and euphausiids than larger specimens (Table 4).

Pronounced differences were evident in Bering skate diet composition by year, region and length class (Table 5). Off Kodiak, consumption of hermit crabs (Paguroidea) and fishes was elevated during 2006, whereas a greater proportion of Tanner crab and isopods were ingested during 2007 (Table 5). In Shelikof Strait, more shrimps, crabs, and fishes were consumed during 2006, whereas euphausiids, a trivial prey item during 2006 (0.4%), constituted 42.2% of diet composition in 2007. Regional differences were more pronounced than inter-annual differences within regions for the Bering skate. Cephalopods, euphausiids, and shrimps were more abundant in the diet of the Shelikof population, whereas Kodiak specimens ate more Tanner crab and fishes. Individuals < 50 cm TL had diets containing a larger proportion of small crustaceans (e.g., mysids, euphausiids, crangonids, hippolytids) and fewer large (pandalid) shrimps, Tanner crab, and fishes (Table 5). A greater diversity of fishes also was observed among larger individuals.

Tanner crab was the dominant prey taxon in the diet of Alaska skate based on samples collected off Kodiak during 2007, and for individuals measuring 50–99 cm TL (Table 6). *Crangon* spp., hermit crabs, and fishes (especially flatfishes) were the primary supplemental prey off Kodiak (Table 6). Euphausiids, pandalids, hermit crabs, and fishes (e.g., pollock, flatfishes) contributed substantially to diet composition of specimens ranging from 50–99 cm TL (Table 6).

3.3.2. *Gulf of Alaska: Per Capita Consumption and Consumptive Removals*

Per capita daily consumption estimates of Gulf of Alaska skates increased markedly among length classes but exhibited considerable variability within and between species-groups (Fig. 3). The smallest length class of skates, represented by Bering and longnose skates, had uniform estimated (median) daily consumption values of 1.0 g., with maximum rates greatest for Bering skate during 2006. No differences in mean per capita consumption were determined for this group ($F = 2.37$, $P = 0.986$). Among medium-sized skates (50–99 cm TL), the relatively large, shallow-dwelling big skate exhibited significantly greater per capita consumption rate estimates during both years ($F = 26.35$, $P < 0.001$; Tukey's, $P < 0.05$; Fig. 3A). No other differences in mean per capita consumption rates were detected among medium-sized species-groups (Tukey's, $P > 0.05$). Median per capita consumption estimates of big skate were nearly 3–4 times greater than those of longnose and Aleutian skates, and increased during 2007, when prey removals of 38.3 g/day (maximum = 223.9 g/day) were estimated. Relatively small (Bering) and deep-dwelling (Aleutian) skates exhibited the lowest estimated median per capita consumption rates among skates measuring 50–99 cm TL (Fig. 3A). Median per capita consumption estimates of medium-sized longnose skates were consistent between years, and similar to those of Alaska skate (Fig. 3A).

Per capita consumption rates of large (100–149 cm TL) specimens varied among species and between sample years ($F = 11.55$, $P < 0.001$). Mean per capita consumption of big skate during 2007 was significantly greater than that of all other large-sized species-groups, whereas big skate consumption during 2006 was significantly greater than all species-groups except longnose skate during 2006 (Tukey's, $P < 0.05$) Median per capita consumption by large Aleutian skate was estimated to be slightly greater than that of large longnose skate, and estimates for both species were somewhat elevated during 2006 (Fig. 3B). Higher maximum per capita rates for these species were reported during 2007, although mean per capita consumption rates did not differ significantly between these species during either year (Tukey's, $P > 0.05$). (Fig. 3B). Big skate median per capita consumption estimates dwarfed those of Aleutian and longnose skates, reaching 94.7 g/day during 2007. Maximum per capita consumption was, however, comparable among large individuals of all three species. Only big skates collected during 2006 occupied the extra-large size class. Median per capita consumption values for these individuals were estimated to be 224.4 g/day, with maximum values of nearly 1 kg./day.

During May–September of 2006 and 2007, consumptive removals of Tanner crab and pandalid shrimps by skates in Central Region the Gulf of Alaska exceeded annual commercial landings of these taxa from throughout the Gulf of Alaska and Bering Sea (Fig. 4). No pandalid shrimp fisheries operated in the Central Region during 2006 or 2007, and Tanner crab fisheries were limited to 2006 (141 t landed). Skates consumed an estimated 35,173 t of pandalid shrimps in the Central Region during May–September, 2006, with the great majority taken by Aleutian and longnose skates (Fig. 4A). Skates consumed less biomass of pandalids during the same time period in 2007, largely as a result of reduced predation by Aleutian skate (Fig. 4B). Tanner crab consumption in the Central Region exceeded that of pandalids during 2006 and was nearly three times greater during 2007 (Fig. 4). During both years, this trend was largely driven by big skate, which consumed an estimated 26,869 t of Tanner crab during 2006 and 46,571 t during 2007. Longnose and Alaska skate consumption of Tanner crab was similar during 2006 (Fig. 4A), and slightly greater by longnose skate during 2007 (Fig. 4B). Total annual consumption of big, longnose, and softnosed skates throughout the Gulf of Alaska was estimated at approximately 136,000 t during 2006 and 152,000 t during 2007. Of these totals, 59.1% and 58.4%, respectively, were estimated to consist of Tanner crab and pandalid shrimps.

Gulf of Alaska skates commonly ingested two commercially important fish taxa, flatfishes (Pleuronectiformes) and walleye pollock. Among the skates sampled in the Central Region big skate accounted for most estimated flatfish consumption during May–September of both years (2006 (84.1%) and 2007 (58.1%)), with longnose skate predation accounting for most of the remaining removals (Fig. 4). Consumptive removals of flatfishes by skates in the Central Region exceeded those of commercial landings during May–September of 2006 (4,232 t) and 2007 (1,797 t) (Fig. 4). However, in contrast to relative removals of pandalids and Tanner crab, skate consumptive removals during these time periods represented minor fractions of flatfishes landed throughout Alaskan waters (Fig. 4). Commercial landings of pollock were considerably greater than consumptive removals of skates in the Central Region during May–September (2006 = 26,711 t; 2007 = 19,123 t; Fig. 4). Annual pollock landings from throughout Alaskan waters dwarfed consumptive removals of skates in the Central Region of the Gulf of Alaska during May–September of both years (Fig. 4).

3.3.3. *Gulf of Alaska: Food Web Model*

Incorporating quantitative, local trophic data for big, longnose, and (combined) softnosed skates substantially altered two principal inputs in the Gulf of Alaska food web model, annual consumption to biomass ratios (Q/B) and diet compositions. In addition, updating skate biomass estimates from the original time period of the model (1990–1993) to coincide with newer trophic inputs (2006–2007) resulted in a considerable increase in overall skate biomass (56,000 t to 108,000 t). Softnosed skate (193%), longnose skate (149%), and big skate (25%) biomass all increased between modeled time periods. Combined softnosed skate inputs were highly influenced by the Aleutian skate, which accounted for 82.3% of biomass. Q/B of the relatively large, shallow-dwelling big skate (2.35) was greater than the generalized value of 2.0 that had been used previously. Q/B values decreased with increasing size and depth distribution of the skate species/group (longnose Q/B = 1.72; softnosed Q/B = 1.61). Diet composition data, synthesized from skate populations that were surveyed in the Central Region during 2006 and 2007, differed markedly from previous estimates for all species groups: Percentage Dietary Similarity = 20.0 (big skate), 16.2 (longnose skate), and 17.4 (softnosed skates). Big skate dietary differences largely were related to much greater estimated Tanner crab consumption from this study (66.3% of diet composition), and a near total reliance on fishes (52.7%) and nonpandalid shrimps (44.1%) in the original model. The most pronounced difference between longnose skate diet composition estimates was the contribution of fishes. The original model considered longnose skate to be almost entirely piscivorous (97.9% fishes), whereas fishes only constituted 19.2% of diet composition in this study. In the original softnosed skate model, benthic amphipods constituted 67.5% of diet composition, and polychaetes and other worms contributed 9.7%. However, these prey groups were minor dietary components based on local, contemporary estimates (0.8% combined), with shrimps (47.2%) and Tanner crab (24.8%) instead dominating diet composition.

Updating the skate data inputs in the Gulf of Alaska food web model with the results of this study substantially altered trophic interactions and system dynamics. Marked changes in estimated trophic level were found for longnose (by -0.58) and softnosed skates (by 0.48) (Fig. 5). Big skate trophic level increased slightly (by 0.05). The overall number of predator-prey linkages among skate species groups decreased (big = -11, longnose = -3, softnosed = -11), but several new linkages also were established (Fig. 5). Altering skate abundance and trophic parameters resulted in system-wide biomass changes. Substantial biomass increases were estimated for Tanner crab (54%), other rockfishes (22%), and hydroids (12%). The greatest overall gains in biomass were noted among bivalves (0.45 t/km^2), Tanner crab (0.36 t/km^2), pandalid shrimps (0.27 t/km^2) and polychaetes (0.25 t/km^2), whereas declines were relatively less severe (sandlance = -0.04 t/km^2, eelpouts = -0.03 t/km^2, misc. shallow fishes = -0.01 t/km^2, other sculpins = -0.01 t/km^2). Fishery mortality on longnose (-0.06) and other skates (-0.08) decreased between model runs, whereas unexplained mortality increased (0.09; 0.09). By contrast, fishing (-0.01) and unexplained mortality (0.02) rates of big skate remained consistent.

The addition of updated diet and consumption data led to substantial changes in the estimated predation pressure on Tanner crab. In the original model, skate predation on Tanner crab was limited to softnosed species, which consumed 0.2% of yearly Tanner crab biomass. The primary predators of Tanner crab were gadids (especially Pacific Cod, 49.9%) and flatfishes (especially Pacific halibut, 20.1%), which together accounted for 83.9% of predation mortality. In contrast, skates are the most important predatory group of Tanner crabs in the updated model, accounting for 28.3% of Tanner crab predation mortality, followed by cods (27.2%) and flatfishes (16.0%). The primary predator of Tanner crab remains Pacific cod (25.7%), followed by big skate (20.1%). Longnose (4.1%) and other skates (4.1%) are estimated as the fifth and sixth most significant Tanner crab predators in the updated Gulf food web model.

In addition to the noted effects of big skate consumption on Tanner crab, increased big skate consumption on flatfish altered mortality estimates in the updated model. Flatfishes totaled 11.6% of diet composition by weight in this study, whereas they were only 0.2% of big skate diet in the original model. These differences, in addition to increased biomass and Q/B rates, caused considerable increased mortality in the following groups: Alaska plaice (167.8%), juvenile Pacific halibut (121.7%), miscellaneous flatfishes (86.9%), northern rock sole (58.5%), yellowfin sole (41.3%), and southern rock sole (25.%). The only notable drop in mortality rate was evidenced in the rex sole (-57.5%). Predation mortality rates on skates also dropped as a result of increased biomass estimates: softnosed skates (-66.6%), longnose skate (-59.9%), big skate (-19.8%).

3.3.4. *West Coast: Distribution and Abundance*

Big skate primarily was distributed at mid shelf depths throughout the study site, with life stages exhibiting slight differences in depth and latitudinal (or geographic) range (Table 7). Juveniles were reported to depths of 459 m, whereas adult depth distribution was limited to waters ≤ 250 m. Common depth ranges were similar, but the depth at maximum occurrence was deeper in adults (Table 7). Geographic distributions were comparable between life stages, with common ranges extending approximately from San Francisco (juveniles) or northern California (adults) to northern Oregon (Table 7; Fig. 6A, 7A). Individuals were found at temperatures of 5.0–12.7° C, with very similar common ranges between life stages (Table 7). Big skate were the least commonly encountered species among those inhabiting predominantly soft and mixed bottom habitats. Juveniles occurred in 6.0% of tows (*n* = 274) and were adults captured in 4.5% of tows (*n* = 206). Only 2,095 total big skate (*n* = 1,600 juveniles, 76.4%) were collected during the 11-year study period. Maximum counts and catch-per-unit-effort (#individuals/km^2, CPUE) of juveniles (*n* = 49, 46; CPUE = 0.29, 0.30) were substantially greater than those of adults (*n* = 11, CPUE = 0.07).

Depth was the most significant factor in predicting big skate count for juveniles and adults, with latitude relatively less important and habitat only included in the juvenile model. The final models of each life stage included the following depth and latitude parameters: Depth, Latitude, Latitude^2, Latitude^3. Significantly greater counts of juvenile big skate occurred on soft bottom rather than on mixed or hard substrate based on model results (*df* = 14, *P* = 0.002). G-Tests, conducted independently of the regression model, also indicated a strong preference for soft substrate among juveniles (*G* = 92.2, df = 2, *P* < 0.001), but no preference among adults (*G* = 4.5, *df* = 2, *P* = 0.11). Predicted geographic distributions generally were consistent with those observed from trawl surveys, although maximum values were predicted to occur at higher latitudes (Table 7, Fig. 6, 7). Predicted depth ranges, however, were inconsistent at deeper extents. The juvenile depth range was truncated, whereas adults were predicted to 639 m, nearly 400 m deeper than they were reported from trawl survey (Table 7). Predicted and observed common and maximum depth values were similar for juveniles, but shifted to much deeper waters for adults (Table 7). Temperature predictions were similar to those observed, but more limited in range (Table 7). The model predicted a much greater frequency of occurrence of skates among tows (%FO = 42.8% juvenile, 37.8% adult; n_{total} = 4559 tows). Predicted third quartile values exceeded those observed for both life stages (Fig. 6, 7).

Longnose skate occurrence was widespread, extending throughout the geographic and depth range of the study (Table 7). The common distribution of adults was more restricted than that of juveniles, however, and shifted northward (Table 7, Fig. 8A, 9A). Juveniles were much more commonly observed (%FO = 58.9, n = 2616 tows, 21,858 individuals) than adults (%FO = 7.7, n = 344 tows, 494 individuals). Maximum observed counts (n = 86) and CPUE (0.54 individuals/km^2) of juveniles also were far greater than those of adults (n = 6, CPUE = 0.03–0.04). Although the adult depth range did not exceed 787 m, adult common and maximum depths occurred in deeper water than those of juveniles (Table 7). Longnose skate were found across a broad temperature range, but locations of maximum occurrence were associated with lower temperatures for adults (5.8–6.9º C, juveniles = 7.9–8.8º C).

Depth, latitude, and habitat, listed in order of relative importance, were the most significant factors in predicting juvenile and adult longnose skate counts. The final model for juveniles contained 9 terms (Depth, Depth^2, Depth^3, Depth^4, Latitude, Latitude^2, Latitude^3, Latitude^4, Habitat), whereas that of adults contained 5 terms (Depth, Depth^2, Depth^3, Latitude, Habitat). There were highly significant differences between observed and expected juvenile (G = 72.1, df = 5, $P < 0.001$) and adult (G = 250.2, df = 5, $P < 0.001$) habitat distributions. Juveniles and adults displayed a preference for mixed-soft habitats, but adult preferences were stronger and adults also were strongly associated with soft-mixed and soft-hard habitats. The mixed-soft habitat term was significant in the juvenile longnose skate model, but no habitat types were significant in the final adult model. Predicted depth distributions of juveniles and adults were similar to those observed (Table 7). Predicted geographic distributions also were similar, but common geographic distributions were shifted slightly to the south (Table 7). Temperature predictions were consistent with those observed, but more limited in range (Table 7). The models predicted skates to occur more frequently (%FO = 90.2, juveniles; 19.2, adults) and in greater abundance (*n* = 27,764 juveniles, *n* = 920 adults) than results of trawl surveys. Predicted quartile and median counts of juvenile longnose skates exceeded those observed (Fig. 8 A, B), whereas the distribution of adult counts was comparable (Fig. 9A, B). Predicted and actual maximum counts were located in relatively close proximity (Fig. 8, 9).

Both life stages of California skate exhibited restricted depth and geographic distributions, with more limited and stray occurrences reported far outside of common ranges (Table 7, Fig. 10A, Fig. 11A). The common depth ranges of juveniles (78–108 m) and adults (75–108 m) were located on the mid-shelf, with depths of maximum counts occurring far deeper for adults (Table 7). Temperature range and common temperatures were consistent between juveniles and adults (Table 7). California skates primarily were distributed between Point Conception and San Francisco, with adults occupying a slightly more restricted, northern-oriented geographic range. Maximum occurrence was located off south-central California for juveniles but northern California for adults (Fig. 10A, Fig. 11A). Frequency of occurrence was low for juveniles (8.2%, *n* = 375 tows) and adults (5.5%, *n* = 248 tows), and relatively few California skates were captured overall when compared to other skates (*n* = 2645). Maximum densities and numerical abundance of juveniles (0.27 individuals/km^2, *n* = 1,963) was must greater than that of adults (0.13 individuals/ km^2, *n* = 682). Catches of up to 47 juveniles and 21 adults were reported, but all occurrences of both life stages were restricted to the upper quartile (Fig. 10A, 11A).

Depth and latitude were the most significant factors in predicting counts of juvenile and adult California skates, with depth relatively more important. The final model of juveniles included seven parameters (Depth, Depth^2, Latitude, Latitude^2, Latitude^3, Latitude^4, Habitat).

The adult model had identical depth and latitude variables but lacked a habitat term. G-Tests indicated that observed and expected habitat distributions differed significantly for juveniles (G = 24.1, df = 4, $P < 0.001$) and adults (G = 127.8, df = 2, $P < 0.001$). Juveniles were preferentially associated with soft-hard and soft-mixed habitats, whereas adults were found in significantly greater densities on soft habitats. The lower limits of predicted depth ranges and depths of maximum occurrence were much shallower than observed, but common ranges were shifted slightly deeper (Table 7). Predicted temperature ranges were more restricted than observed (Table 7). Although the predicted and actual geographic ranges of juveniles were generally consistent (Fig. 10B), the predicted range of adults was shifted much farther to the north (Fig. 11B). In addition, maximum adult count was predicted at the northern extent of the survey footprint, whereas that of juveniles was located off central California (Fig. 10B, 11B). The model predicted a much greater frequency of occurrence of juveniles (23.6%, $n = 1075$) and adults (40.8%, $n = 1855$ tows) than were observed. Predicted maximum and upper quartile counts of adults also were overestimaed; however, those of juveniles were underestimated and similar, respectively (Fig. 10B, 11B).

Sandpaper skate occurrence spanned nearly the entire geographic and depth extents of the survey, with the common range reported from northern California to southern Washington at depths of 160–400 m (Table 8, Fig. 12A). Maximum counts and catch-per-unit-effort (0.43–0.51 individuals/km^2) were located near the California-Oregon border at depths of 246–309 m (Table 8, Fig. 12A). Sandpaper skates were collected across a broad temperature range (Table 8), with maximum catches corresponding to temperatures of 5.5º and 9.0º C. Sandpaper skates were captured in 33.7% of tows ($n = 1543$ tows, 8,512 individuals). The great majority of tows contained zero or one individual (Fig. 12A). Although catches of up to 73 skates were reported, only 18% of tows contained more than two sandpaper skates, and 5% of tows contained more than ten individuals.

Depth was the most significant factor in predicting sandpaper skate count, followed by latitude and habitat. The final model included seven parameters (Depth, Depth^2, Latitude, Latitude^2, Latitude^3, Latitude^4, Habitat), with significantly greater numbers of sandpaper skates occurring on mixed-soft and soft-mixed habitats than on exclusively soft, hard, or a mixture of soft and hard bottom habitats. G-Tests, conducted independently of the regression model, indicated that observed habitat distribution differed significantly from expected ($G = 468.4$, $df = 5$, $P < 0.001$), with a clear preference for soft-mixed habitats and substantially more individuals than expected occurring on mixed-soft habitats. The predicted distribution generally was consistent with that observed from trawl surveys (Table 8). The predicted depth range was truncated at approximately 800 m, however, and the predicted common depth range was broader (Table 8). Predicted and observed latitudinal ranges were consistent, but the predicted common range extended farther to the south (Table 8). In addition, the location of maximum occurrence was considerably farther north and somewhat deeper than observed (Table 8; Fig. 12B). Temperature predictions were similar to those observed, with the exception of a lower maximum. A significant mismatch was noted in that the model predicted a much greater frequency of occurrence of skates among tows (81.9%, $n = 3{,}639$ tows), and therefore, quartile and median counts that substantially exceeded those observed (Fig. 12B).

Starry skates were collected infrequently ($\%\text{FO}_{\text{juveniles}} = 1.9$, $\%\text{FO}_{\text{adults}} = 0.4$; total number of tows = 4593) and in low numbers during the WCGBTS ($n_{juveniles} = 141$, $n_{adults} = 27$). The greatest number of juveniles collected in a tow was 14, corresponding to a CPUE of 0.9 individuals/km^2. Only five tows captured more than one adult starry skate ($n_{max} = 4$, CPUE = 0.3

individuals/km^2). Common depth ranges of juveniles and adults were located on the mid-shelf, but maximum depth of juveniles extended to almost 1000 m (Table 8). Starry skates were distributed throughout the study range, but were most common between Point Conception (~34º N) and northern California (Table 8). Juveniles had depth, latitude, and temperature values associated with maximum occurrence that were near the midpoints of common ranges (Table 8). The relatively low amount of adults precludes definitive conclusions regarding their distribution and abundance patterns and limits comparisons with juveniles. Because of low sample size, life stages were pooled for habitat analysis and only sediments dominated by soft substrate could be included. Starry skate densities were significantly greater on soft-mixed and soft-hard habitats compared to uniformly soft substrates ($G = 127.3$, $df = 2$, $P < 0.001$).

3.4. DISCUSSION

3.4.1. *Gulf of Alaska Skates*

Application of new information on diet composition and feeding rates of skates indicates that they are major predators of Tanner crab in the Gulf of Alaska. Skate biomass and consumption estimates for the big skate, the principal skate predator on Tanner crab, increased substantially and strongly influenced model results. In the new model, skates consumed more Tanner crab biomass than any other group of predators, and overall predatory removals of Tanner crab nearly doubled. Tanner crab was once abundant in the Gulf of Alaska, but the stock collapsed during the early 1980s and has not recovered. Only small-scale, localized fisheries for Tanner crab have operated in the Gulf since the collapse, which appears to have occurred from a combination of changing environmental conditions and overfishing (Zheng and Kruse 2000; Litzow et al. 2013). Szuwalski and Punt (2013) found evidence to support “Oscillating Control” of related snow crab

(*Chionoecetes opelio*) in the eastern Bering Sea, by which recruitment control oscillates from female spawning biomass (during anomalously warm PDO periods) to environmental conditions (during anomalously cool PDO periods). However, Gulf of Alaska Tanner crab stocks have remained depressed through different climate regimes. It is therefore unclear if a similar relationship of alternating environmental (i.e., bottom up) and biological (i.e., top down) control exists in the Gulf, or if the Gulf Tanner crab stock has not recovered because of other factors, such as predation pressure. The elevated consumption estimates of Tanner crabs from the results of this study and the emerging predatory importance of skates may help scientists and fisheries managers better understand Tanner crab population dynamics in the Gulf of Alaska.

Updating biomass, consumption, and diet composition estimates for skates caused additional, system-wide changes in the Gulf of Alaska food web model. Flatfishes were minor dietary components of all studied species, and consumptive removals of flatfishes by skates were trivial when compared to fishery removals. However, greater consumption of juvenile halibut and Alaska plaice by big skate in the updated model increased predation mortality estimates on these flatfishes by more than 100%. Pacific halibut are one of the most important commercial species in the Gulf of Alaska, and a main predator in this region (Gaichas et al. 2010). Although the stock has remained relatively healthy, exploited halibut populations appear vulnerable to heavy fishing pressure (Gaichas et al. 2011). Increased consumption by skates may represent an added source of mortality on halibut that has bearing on biomass flows throughout the Gulf as well as management considerations for the halibut stock. By contrast, rex sole was estimated at 3.1% of longnose skate diet in the updated model, but 25.4% in the original model (Aydin et al. 2007). The new model therefore estimates less predation mortality on the Gulf rex sole population. Because the updated model indicates lower levels of piscivory, the trophic levels estimates of fisheries with high incidental skate catch (e.g., halibut longline, groundfish trawl, Pacific cod longline) decreased slightly. More reliable estimates of skate predation, afforded through this study, may provide an important considerations when determining population demographics and establishing quotas for commercially important flatfishes.

Consumption rates of skates in the Gulf of Alaska varied based on the TL and depth distributions of the species/groups. Consumption rates increase with size and temperature, and the big skate, which can reach TLs of 2.44 m (Love et al. 2005), inhabits the shallowest range of all Gulf of Alaska skates (Chapter 1). Consumption of big skate was greater than that of other skates at similar-sizes, and peaked at nearly 225 g/day in specimens $\geq$ 150 cm TL. The per capita consumption rates generated from this study were consistent with those reported from Link and Sosbee (2008), though the use of different size categories and measures of central tendency precluded direct comparisons. From combined results, skate less than 50–60 TL had per capita consumption rates of ~0.5–3.0 g/day (Link and Sosbee 2008), depending largely on the relative size and depth distribution of the species. Weight increases nonlinearly with TL in fishes. The substantial gains in consumption rates that were evident among increasing 50 cm TL size categories in this study are therefore consistent with expectations and indicate that large skates (> ~1m TL) have much greater predatory impacts. Total consumptive removals by seven skate species off the U.S. Northeast coast averaged 230 t/year (Link and Sosbee 2008), whereas those of the five species in this study averaged 145 t/year. Since per capita consumption rates are generally consistent, differences are likely due to the warmer temperatures off the U.S. Northeast coast, differences in relative biomass and/or size composition between studies, or imprecision of parameter estimates used in the Eggers (1977) model (Link and Sosbee 2008, Ormseth et al. 2014, Chapter 1). Consumption:biomass (Q/B) values used in this study refined the general estimates used in Link and Sosebee (2008) and enabled more reliable species-specific consumptive removal calculations. Q/B values increased with skate size and temperature preferences, but ranged from 1.61–2.35, providing support for the use of the generalized Q/B = 2.0 value when more specific data are unavailable.

Spatio-temporal and length-based variation was evident in big and longnose skate diets, but characteristic trends emerged. Big skate typically consume a mixture of crabs, shrimps, and fishes, with variable proportions reported among studies (Wakefield 1984; Bizzarro et al. 2007, Chapter 2), and a greater amount of fishes (especially flatfishes) associated with increasing size. At similar sizes, longnose were more piscivorous than big skates in the Gulf of Alaska, as has been reported off the U.S. West Coast (e.g., Wakefield 1984; Bizzarro et al. 2007). Consumption of decapod prey also differs between these species, with longnose skates consuming mainly shrimp (Wakefield 1984; Robinson et al. 2007). To some degree, this difference is a consequence of the variable availability of crabs and shrimp, as big skate (and true crabs) have a shallower depth distribution. However, even at similar depths, longnose skate eat a larger proportion of crab than big skate (Wakefield 1984; Bizzarro et al. 2007). This tendency therefore appears to be at least partially behavioral. Big and longnose skate diet composition inputs for the Gulf of Alaska food web model were compiled from a study conducted off the Oregon Coast in the early 1980s and modified with observations from the 1993 Gulf of Alaska trawl survey (Aydin et al. 2007; Gaichas et al. 2010). The incorporation of more robust, recent information from the study site has greatly altered the perceived trophic relationships of these large, predatory fishes. The mismatch between original and updated diet composition data used in the Gulf of Alaska food web model emphasizes the pitfalls of extrapolating data from distant regions, time periods, or based on low sample sizes for generalist predators such as skates.

Softnosed skates in the Gulf of Alaska had diet compositions that differed greatly from those of prior estimates (Aydin et al. 2007). Because local diet information was lacking for softnosed skates when the Gulf of Alaska model was created, studies from the Russian waters were incorporated (Orlav 1998, 1999). However, diet compositions of Aleutian, Bering, and Alaska skates from the western North Pacific differ substantially from those reported here and in related, baseline food habit studies in the Gulf of Alaska (Brown 2010; Brown et al. 2012). Extrapolated diets of Aleutian and Alaska skate consisted of greater proportions of fishes and squids and less reliance on decapods than those of Gulf populations (Orlov 1998, 1999). Diet of the Bering skate in Russian waters was dominated by amphipods (49%), with polychaetes also of considerable importance (14%; Orlov 1998, 1999). However, these prey combined to total < 10% of Alaska skate diet composition in the Gulf during 2006–2007. Softnosed skates are not as abundant or valuable as hardnosed skates to commercial groundfish fisheries in the Gulf of Alaska, and therefore are afforded less management attention. However, Aleutian skate constitutes the great majority of regional softnosed skate biomass and greatly influence food web modeling results for the group. In addition, overall biomass estimates for softnosed skates in the updated model were averaged from species-specific biomass estimates for 2006 and 2007 and should not be extrapolated to periods of differing species composition (Ormseth 2014). For these reasons, it may be beneficial to treat the Aleutian skate separately from other softnosed skates for modeling purposes.

Food web models, such as the one developed for the Gulf of Alaska (Aydin et al. 2007), are gaining use as fishery scientists increasingly incorporate ecosystem considerations into strategy evaluation (Gaichas et al. 2012). In the Gulf of Alaska, there appears to be no single, shared driver of biomass trajectories among species/groups, but rather alternative control among predator-prey relationships, environmental factors, and fishing mortality (Gaichas et al. 2011). Whereas light (baseline fishing levels) and moderate (2x baseline fishing) levels of fishing pressure are unlikely to result in ecosystem restructuring, heavy pressure (3x baseline fishing levels) may have these effects (Gaichas et al. 2012). The use of representative model inputs is especially important in complex systems such as the Gulf of Alaska to produce reliable simulations for evaluation. Because predator-prey interactions of groundfishes typically are unknown or inferred from a few, localized studies, important inputs for these models (e.g., consumption rates, diet composition) may necessarily be generalized. Extrapolations from other regions, as evidenced by this study, can fundamentally alter estimates of predation mortality and biomass flows in a system. When the Gulf of Alaska food web model was originally constructed, one of the recognized goals was to address this deficiency by improving biomass, consumption, and diet information for skates, which were recognized as important predators (Aydin et al. 2007). Large, continental shelf species, such as big and longnose skates, are responsible for the greatest consumptive removals among skates and are particularly vulnerable to overfishing (Dulvy et al. 2014). Although they are not key species in the biomass flow of energy on the Gulf of Alaska continental shelf, the predatory impact of skates in this system has been likely underestimated. Refining food web model inputs with local, species-specific information for skates can enable a more accurate assessment of the importance of skates to the trophodynamics of the Gulf.

It is difficult to accurately determine the expected diet composition of skate populations. Although skates typically consume a core group of prey species in abundance, their overall diets are quite diverse and variable relative to those of other fishes (Link 2004; Wetherbee et al. 2012). Intraspecific diet composition also is highly variable, even among individuals of similar sizes that were collected concurrently (Bizzarro et al. 2007; Chapter 2). As a result, many stomach samples are needed to accurately characterize the diet composition of a population of interest at low levels of taxonomic (prey) identification. Furthermore, stomach samples for dietary analysis usually are collected during general trawl survey operations and may therefore not be readily amenable to research focused at a priori hypothesis testing. Most species groups used in this study were insufficiently sampled for diet composition using augmented NMFS prey categories (NMFS 2013). However, diet composition for such groupings can be considered reliable at higher levels of prey identification (e.g., families but not genera or species) for the great majority of species groups. Given the time and cost constraints of collecting and processing stomach samples from skates and their typical dietary variability, it may not be feasible to precisely quantify the diet of populations of interest at low taxonomic levels. If this is the objective, however, surveys should be designed to ensure that sufficient sample sizes are collected across at least a length and spatio-temporal gradient. Prey taxa can be grouped into more generalized categories to ensure representative diet composition estimates if sample size remains insufficient following prey identification.

Some aspects of the Gulf of Alaska food web model should be further updated or refined to ensure more accurate predictions. The temporal period of data inputs were similar, arising largely from surveys conducted in the Gulf during spring and summer months. However, skate diet and consumption data were restricted to the western Gulf of Alaska, requiring extrapolations for Gulfwide estimates. Anecdotal evidence suggests that Tanner crab abundance, and therefore consumption, may be greater in the study site than more eastward regions of the Gulf. In addition, 1) hard-bodied prey such as crabs transit slower through skates than soft-bodied prey (e.g., polychaetes, fishes) (Nelson and Ross 2005), and 2) skates do not crush crab shells but rather digest them whole and dissolve them with enzyme (Chitinases) (Holmgren and Nilsson 1999). Based on these factors, Tanner crab consumption probably has been overestimated in the updated food web model. In addition, only the skate inputs were changed between the original and modified model; therefore, skate biomass, diet composition, and consumption data from 2006–2007 were compared to similar data for other species/groups from the early 1990s. Updating the model with newer inputs for all functional groups would be a beneficial exercise to evaluate temporal changes and to improve model accuracy. There is feedback loop in the model, by which increased predation on a prey species without a biomass estimate results in increased standing biomass of that prey species (e.g., Tanner crab). Perhaps because of this behavior, and because only skate inputs were updated, a large amount of biomass in the new modeled system was lost as detritus. Incorporating biomass estimates for prey species with high biomass flows that are also monitored in annual ADFG trawl surveys (e.g., Tanner crabs, pandalid shrimps) may help to resolve this issue.

Consumptive removals of skates also may be substantially underestimated in the model. A recent laboratory study on the clearnose skate (*Leucoraja eglanteria*) reported gastric evacuation rates that are up to five times greater than those used in this study and in food web models of the Northeast U.S. continental shelf and the Gulf of Alaska (S. Gaichas, NMFS-Northeast Fisheries Science Center, pers. comm.). The clearnose skate is similar in size to the Bering skate, the smallest species in the Gulf of Alaska assemblage, and individuals were maintained at temperatures (15º C, 20º C) that were much greater than those associated with skates in the Gulf of Alaska (Chapter 1). Gastric evacuation rates of captive clearnose skate are probably greater than those in the Gulf; however, any increase in gastric evacuation rate would result in greater consumption estimates for Alaskan skate species. The predatory impact skates and their importance to biomass flows in the Gulf may therefore be even greater than predicted by the updated Gulf of Alaska food web model.

3.4.2. *West Coast Skates*

U.S. West Coast skate occurrence was most strongly determined by depth. Depth zonation was clearly apparent in the assemblage, but common depths and depth ranges of species overlapped considerably. For example, big, California, and starry skates were the only species with common depth ranges confined to shelf waters but all skates ranged onto the inner shelf. Big skate, especially, commonly occur on in subtidal waters (Chapter 1; Love 2011). Because the WCGBTS was restricted to depths $\geq$ 55 m, the observed and predicted distributions in this study probably were artificially truncated at depths shallower than their actual occurrence. This sampling bias is expected to have a greater effect on shallower-occurring skates (big, California, starry). Although their distribution extends to the inner shelf, longnose and sandpaper skates mainly are found on the outer shelf and upper slope off the U.S. West Coast. In these regions, they are among the most abundant fishes by biomass (Tolimieri and Levin 2006). Skates within these shallower and deeper occurring groups exhibited similar common ranges.

Juveniles of hardnosed skates typically are reported as more shallow-dwelling than adults (Ebert et al. 2008) but results from this study were mixed. Life stages of big and California skates had comparable common ranges and juveniles of all hardnose species ranged into deeper waters than adults. Depth of maximum occurrence, however, was substantially greater for big, California, and longnose skate adults, and the common range of longnose adults was reported > 60 m deeper than that of juveniles.

Depth range extensions were documented, and the episodic occurrence of anomalously deep individuals was observed for the shallower-dwelling species. Maximum depth was extended for longnose skate (from 1,069 m to 1,227 m), sandpaper skate (1,050 m to 1,162 m), and starry skate (from 732 m to 982 m) (Love et al. 2005). Maximum observed depths of big (459 m) and California skate (792 m) did not approach previously reported maximums (800 m and 1600 m, respectively) (Love et al. 2005). The depth ranges of longnose and sandpaper skate were expansive, and additional records at similar depths validate new maximums for these species. Maximum depths of the shallower-occurring species, however, either represent stray occurrence or spurious records. For example, no starry skates were collected within ~400 m of the new depth record, and few big or California skates were reported at depths near the reported maximums. Anomalously deep depths have been typically reported for skates (Love et al. 2005), and may be a result of misidentification. This is almost certainly the case for California skate and big skate, as depth records from these species are derived from faunal surveys at anomalously deep, generalized depths. It also is possible that skates in the water column are captured upon gear retrieval and misassigned to bottom depths. Pelagic swimming may be common for adults of large skates (e.g., big skate), but is not typically reported in relatively small species (e.g., starry skate, California skate) (Wearmouth and Sims 2009; Frisk 2010). Pelagic swimming also typically occurs at night, whereas trawl surveys are conducted during daylight hours. The reported maximum depths for starry, big, and California skates may indeed be accurate, but video observations, telemetry studies, or documented captures at depth are needed for verification.

Skates exhibited broad temperature tolerances with overlapping common ranges along the U.S. West Coast. Big skate can tolerate waters ranging from 2.5–19º C (Love 2011).

However, the West Coast populations was limited to waters > 5.0º C, and therefore occupied a more restricted temperature range than other skates. This finding reinforces the idea that big skate is a shallow water species (Chapter 1), and its inshore population (to < 1 m) is not adequately covered by the WCGBTS (depths ≥ 55 m). Since there is growing concern about the population status of big skates along the west coast (Kelly Ames, NMFS-Northwest Fisheries Science Center, pers. comm.), any stock assessment developed for this species should address this "deep water" survey bias. Common temperature ranges were consistent between juvenile and adult big and California skate, but warmer for juvenile longnose skate. Temperature of maximum occurrence was warmer for juveniles than adults of these species, in association with relatively shallower depths. This type of ontogenetic depth segregation is commonly reported for hardnosed skates (Ebert et al. 2008). The lowest observed temperature records were associated with longnose and sandpaper skates, which is indicative of the deeper depth ranges of these species as compared to big, starry, and California skates. The common temperature range of the California skate was the most restrictive and the warmest among species. Temperature is considered to be a major driving force in determining the structure and dynamics of skate assemblages (Frisk et al. 2010, Chapter 1), but in isolation, temperature did not serve to distinguish occurrence among West Coast skates.

Latitude was an important predictor of occurrence for West Coast skates, and geographic ranges of occurrence varied among species. The two largest species, the big (to 2.44 cm LT) and longnose skates (to 1.89 cm TL), range from the Bering Sea to the Gulf of California, whereas the other species (≤ 76 cm TL) have more restricted ranges (Love et al. 2005; Love et al. 2011). Most skates seem to remain in within a limited home range (10kms of kilometers), but some larger specimens undergo extensive migrations (to 2,340 km) (King and McFarlane 2008;

Wearmouth and Sims 2009). It is possible that the larger species, like big and longnose skates, are more mobile and capable of maintaining an interbreeding population over an expansive region. Batoids with extensive geographic ranges are often actually composed of species complexes, however, as has been evidenced in the eastern North Pacific by *Gymnura marmorata*/*crebripunctata* and *Bathyraja interrupta*/*kincaidii* (Ebert 2003; Smith and Bizzarro 2009). Furthermore, maximum sizes and sizes at maturity are substantially greater in individuals from the Gulf of Alaska than those off the West Coast (Ebert et al. 2008). Population genetics of big and longnose skate could therefore yield interesting results. Along the West Coast, relatively few adult big and longnose skate were collected. This lack of large specimens may be a true aspect of regional population demographics, or it could reflect a greater ability of large skates to avoid sampling gear or a lack of inshore survey coverage (for big skate). California skate had restricted geographic ranges with both life stages mainly occurring off central California. Very few records of California skate were reported north of California during 2003–2013 and, specimens collected off the Northwest Coast should be retained to verify identification. The greatest concentration of sandpaper skate was located north of 40º N. This species was described from a specimen collected at Friday Harbor, WA, and it is know to commonly occur off the Pacific Northwest (Ebert 2003). Starry skate was found as far north as Oregon, which represents the general extent of its range (Love et al. 2005).

Most skates were preferentially associated with specific habitat types that helped to further characterize their occurrence patterns and began to establish distinctions between species and life stages. It is apparent that the historic belief that skates are restricted to soft bottom habitats (e.g., Compagno 1990) is invalid. West Coast skates preferentially occupied a variety of habitat types, including mixed and hard bottom habitats. Juvenile big and California skates were strongly associated with soft substrate types, whereas adults of these species preferred mixed habitat types. Sandpaper skate and longnose skate juveniles were found mainly on combinations of mixed and soft sediments, whereas adult longnose skates also were associated with soft-hard sediment types. Longnose skate adults and starry skates were the only species that preferentially occupied habitats with hard-bottom components. Species-specific habitat associations are consistent with those reported from submersible observations and anecdotal evidence (Chapter 1, Love 2011), but differences between life stages have not previously been reported in these species. Clear differences in skate ecology with size are becoming apparent; as larger skates exhibit diet and habitat shifts that functionally distinguish them from smaller individuals. The importance of habitat in predicting skate occurrence also is likely underestimated. Depth and latitude data are collected during survey operations and accurately represent seafloor conditions associated with tows. Because only tow midpoints and lengths were available, however, a generalized buffer had to be used to characterize habitat, resulting in relatively less accurate data. In addition, the habitat map used for this study was compiled from an amalgam of data sources collected at different scales and levels of detail (NMFS 2013). As more accurate substrate data are available, habitat associations of skates may be further refined.

The results of this study substantially modified and improved EFH characterization for three federally managed skate species and two other skates that commonly occur along the West Coast. Skate distribution and abundance information in the HUD was incomplete as originally compiled and has not been updated since its original creation (NMFS 2005), resulting in a database that did not accurately portray EFH for West Coast skates. An example of the mismatch between original and updated data inputs was evidenced by the disparate habitat suitability probability (HSP) profiles that were created for the California skate (Chapter 1). The absolute, common, and maximum ranges that were determined from this study are directly applicable to current inputs for the HUD and will be used to update information each species/life stage. Since the HUD is used in the development of fishery management strategies (NMFS 2005), these updates can serve as a basis for the improved management for West Coast skates. Skates have broad ranges, but each species and life stage has a characteristic core distribution and abundance pattern that serves to denote EFH. When distribution and abundance patterns are considered on a large scale (entire West Coast), considerable spatial overlap is evident among species. However, on a regional scale, species exhibit marked spatial segregation (Chapter 1). The results of this study can be used to broadly establish regions of high occurrence that can be further considered on a more localized basis for the potential establishment of no take zones for skates. Spatial management of skates may have promise, since species tend to remain somewhat localized (King and McFarlane 2010; Frisk 2010) and exhibit characteristic environmental (e.g., depth, latitude, temperature, habitat) preferences.

ZIP model predictions generally were consistent with observed counts but were greatly influenced by anomalous depth and latitude records, and tows with abnormally high occurrences. This situation was especially apparent in the adult California skate model, which substantially overpredicted occurrence in the northern part of the study range because of the high leverage of a few anomalous northern records. Trawl catches of some species/life stages, such as juvenile big skate and juvenile longnose skate, contained a few extremely high counts. In these instances, ZIP models routinely overpredicted median and total count and underpredicted maximum count. Only GAM, Poisson, and ZIP models were compared in this study. These models were appropriate for the less expansive central California data sets that were analyzed in Chapter 1, and were therefore also considered to be applicable to the larger, WCGBTS data set. However, zero-inflated negative binomial (ZINB) models. ZINB models typically provide better fits than ZIP models for overdispersed data, such as that of most skate species and life stages off the U.S. West Coast, and may facilitate more accurate predictions (Ridout et al. 2001). ZINB models should be constructed and compared with the ZIP models used in this study before predictive results of skate distribution and abundance patterns are published or applied for management purposes.

Reliable predictive models may serve to assist fishery managers in determining if a particular area may be suitable habitat for a skate species of life stage. NMFS developed HSP models to characterize EFH for commercially important groundfishes (see Chapter 1 for description of HSP models). Depth, latitude, and habitat information were incorporated into these models, as they were in the ZIP models used in this study, but habitat data was given twice the weight as depth or latitude. HSP models also are deterministic, in that the output values are fully determined by the estimated input parameter values without error. Given the low relative importance of habitat in predicting skate occurrence, HSP models may not accurately reflect distribution and abundance patterns for skates. However, ZIP and HSP models may be used in tandem to provide alternative predictions of EFH that can be compared and evaluated. For instance, the updated HSP map for transitional/adult California skate exhibited the same distribution and abundance pattern as that of juvenile California skate from this study and was useful to resolve errors in the adult ZIP model map.

3.4.3. *Conclusions*

Skates are important predators in the Gulf of Alaska ecosystem. Highly dissimilar skate (big, longnose, softnosed species) diet compositions between the original and updated Gulf of Alaska food web models drove substantial differences in biomass flows between models. Skates, formerly considered to exert negligible predation pressure on Tanner crab, were estimated to cause more Tanner crab mortality than any other predatory group in the updated model. These and other relevant findings, such as refined consumption:biomass estimates for managed species/groups and substantial increases in consumption of juvenile halibut, may have bearing on the development of EBFM strategies for groundfishes and commercially important decapods in the Gulf of Alaska (e.g., Zador 2014).

Skates have distinctive distribution and abundance patterns that can be used to determine EFH for West Coast species. The establishment of observed and predicted overall, common, and maximum ranges among environmental variables (depth, latitude, habitat, temperature) for U.S. West Coast skates has improved our understanding of skate ecology and substantially modified EFH characterizations. Although skates have broad environmental tolerances, they exhibit specific, core preferences that serve to characterize EFH and each species. Some species with limited common ranges and low relative abundance, such as the California skate, may benefit from improved spatial management strategies developed from these findings.

3.5. LITERATURE CITED

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3.6 TABLES

Table 3.1. Diet composition (Mean %W) of the big skate, *Beringraja binoculata*, as calculated from non-empty stomach samples collected during 2006 and 2007 in Kamishak Bay (*n* = 30, 56) and Shelikof Strait (*n* = 49, 32), and during 2007 off the east side of Kodiak Island (*n* = 75) and the Alaska Peninsula (*n* = 30). Median values > 0.0 and 1st (Q1) and 3rd quartiles (Q3) are provided where indicated by superscripts. * = contributed < 0.05% to diet composition. Spatio-temporal grouping with sufficient sample size is indicated in bold.

Higher Taxon	Lower Taxon	2006 Kamishak	**2007 Kamishak**	2006 Shelikof	2007 Shelikof	2007 Kodiak	2007 Peninsula
Mollusca	Bivalvia and Gastropoda	*		0.5		0.2	0.1
	Cephalopoda		*		*		
	Octopoda	*		0.1	1.4	*	1.0
Crustacea	Caridea	1.1	2.0	1.7	0.1	0.3	0.4
	Crangonidae	11.7^{A}	6.6	3.4	8.0^{E}	0.8	2.4
	Argis spp.	*	1.0	2.6	0.3	2.7	14.2^{H}
	Hippolytidae			*		0.1	
	Eualus spp.			*	0.2		
	Pandalidae	0.4	0.1	2.3	5.5	0.1	0.3
	Anomura	0.3		1.3	0.2	0.1	
	Paguroidea	1.3	3.3	6.6	4.9	0.2	0.2
	Brachyura	3.2	3.0	6.9	3.4	0.3	10.6
	Chionoecetes bairdi	59.3^{B}	73.4^{C}	55.0^{D}	66.7^{F}	79.9^{G}	51.3^{I}
Actinopterygii	Acinopterygii	4.7	2.3	10.7	6.3	4.2	6.3
	Clupeiformes					1.4	1.0
	Osmeriformes	6.6	0.1			0.1	
	Gadiformes		0.6	0.9			
	Stichaeidae	2.9	1.4	0.6		2.6	1.1
	Scorpaeniformes	1.3	0.3			0.1	
	Pleuronectiformes	7.2	5.9	7.5	3.1	6.9	11.1

A) Median = 1.1, Q1 = 0.0, Q3 = 13.1; B) Median = 66.2, Q1 = 24.4, Q3 = 96.6; C) Median = 89.3, Q1 = 70.6, Q3 = 99.6, D) Median = 67.9, Q1 = 0.0, Q3 = 92.6; E) Median = 0.2, Q1 = 0.0, Q3 = 3.5; F) Median = 74.8, Q1 = 50.6, Q3 = 91.5; G) Median = 97.7, Q1 = 70.7; Q3 = 100.0; H) Median = 1.7, Q1 = 0.0, Q3 = 12.6; I) Median = 65.6, Q1 = 0.0, Q3 = 86.2.

Table 3.2. Diet composition (Mean %W) of the big skate, *Beringraja binoculata*, as calculated from non-empty stomach samples collected from individuals measuring 50−99 cm (*n* = 92), 100−149 cm (*n* = 155), and 150−199 cm (*n* = 38) in total length during 2006 and 2007 throughout the west-central Gulf of Alaska. Median values > 0.0 and 1st (Q1) and 3rd quartiles (Q3) are provided where indicated by superscripts. * = contributed < 0.05% to diet composition.

Higher Taxon	Lower Taxon	50−99 cm	100−149 cm	150−199 cm
Mollusca	Bivalvia and Gastropoda	0.2	0.1	0.2
	Cephalopoda		0.3	
	Octopoda			0.9
Crustacea	Caridea	0.8	0.4	*
	Crangonidae	9.3	0.7	1.4
	Argis spp.	5.8	1.4	1.3
	Hippolytidae	0.1		
	Eualus spp.	0.1		
	Pandalidae	1.7	1.1	0.2
	Anomura	0.8	0.1	
	Paguroidea	3.2	2.6	0.9
	Brachyura	4.9	3.5	2.1
	Chionoecetes bairdi	65.6^{A}	74.8^{B}	51.5^{C}
Actinopterygii	Acinopterygii	4.2	6.3	5.1
	Clupeiformes		0.7	3.3
	Osmeriformes		1.4	
	Gadiformes			2.1
	Stichaeidae	1.6	1.4	1.5
	Ammodytidae			2.6
	Scorpaeniformes	0.4	0.1	0.2
	Pleuronectiformes	1.5	5.1	26.8

A) Median = 80.0, Q1 = 44.1, Q3 = 95.0; B) Median = 91.0, Q1 = 65.2, Q3 = 99.6; C) Median = 60.9, Q1 = 0.0, Q3 = 98.2.

Table 3.3. Diet composition (Mean %W) of the longnose skate, *Raja rhina*, as calculated from non-empty stomach samples collected during 2006 and 2007 off the east side of Kodiak Island (*n* = 37, 126) and in Shelikof Strait (*n* = 56, 102), and for individuals measuring < 50 cm (*n* = 66), 50−99 cm (*n* = 133), and 100−149 cm (*n* = 142) in total length from throughout the west-central Gulf of Alaska. Median values > 0.0 and 1st (Q1) and 3rd quartiles (Q3) are provided where indicated by superscripts. * = contributed < 0.05% to diet composition.

Higher Taxon	Lower Taxon	2006 Kodiak	2007 Kodiak	2006 Shelikof	2007 Shelikof	< 50 cm	50-99 cm	100-149 cm
Polychaeta	Polychaeta			*		*		
Mollusca	Bivalvia and Gastropoda	0.1	0.1		*		0.1	*
	Cephalopoda	*						
	Teuthida				*			*
	Gonatidae	1.5		1.3	*		0.5	0.4
	Berryteuthis magister				0.5		0.3	*
Crustacea	Amphipoda		0.8			1.5		
	Mysida	0.1	0.5	1.1	3.2	2.6	1.5	0.5
	Euphausiacea		0.1	0.1	1.9	1.0	1.0	0.2
	Penaeoidea, Sergestoidea, and Caridea			0.8	1.9	0.6	1.5	*
	Caridea	0.5		2.5	1.4	1.1	0.9	0.7
	Crangonidae	4.2	*	6.0	1.1	4.7	1.1	1.0
	Argis spp.	2.1	0.7	5.9	3.2	1.3	4.9	2.0
	Crangon spp.	9.0	21.5^{A}	17.2	25.1^{B}	45.5^{C}	24.3^{D}	3.3
	Neocrangon communis	7.1	1.4	7.2	2.8	7.8	4.0	0.7
	Hippolytidae			0.4	0.1		0.3	
	Eualus spp.	0.8	5.4	1.7	0.8	9.3	1.8	0.2
	Pandalidae	5.7	0.6	9.7	10.0	2.3	5.4	8.1
	Pandalopsis spp.	2.2	0.1	3.0	0.3		0.6	1.5
	Pandalus spp.	9.1	20.2	25.2	19.5	19.2	17.8	21.4
	Anomura			0.2	0.3			0.3
	Paguroidea	0.1					*	
	Brachyura		*	0.2	0.1		0.1	0.1
	Majoidea				*			
	Chionoecetes bairdi	29.4	31.5	6.5	11.0	2.9	20.2	28.7
Actinopterygii	Acinopterygii	15.4	5.5	5.4	6.1	0.1	5.9	10.9
	Clupeiformes	2.7						0.7
	Osmeriformes	2.7		0.5	0.3		0.4	1.5
	Mallotus villosus				0.2			0.1
	Gadiformes				0.1			*
	Theragra chalcogramma	1.2	0.5	1.8	1.9		0.5	2.9
	Stichaeidae			0.1				*
	Zoarcidae	6.2	5.0		0.7		4.4	3.1
	Ammodytidae		0.3	0.2	0.1		0.4	*
	Scorpaeniformes				2.8		0.8	2.0
	Pleuronectiformes		5.7	3.2	4.7		1.3	9.2

A) Median = 1.1, Q1 = 0.0, Q3 = 25.9; B) Median = 7.7, Q1 = 0.0, Q3 = 45.2; C) Median = 37.7, Q1 = 1.1, Q3 = 86.4; D) Median = 8.5, Q1 = 0.0, Q3 = 41.4.

Table 3.4. Diet composition (Mean %W) of the Aleutian skate, *Bathyraja aleutica*, as calculated from non-empty stomach samples collected during 2006 and 2007 in Shelikof Strait (n = 39, 59) and off the Alaska Peninsula (n = 31, 33), during 2006 off the east side of Kodiak Island (n = 36), and during 2006 and 2007 for individuals measuring 50−99 cm (n = 37) and 100−149 cm (n = 171) in total length from throughout the west-central Gulf of Alaska. Median values > 0.0 and 1st (Q1) and 3rd quartiles (Q3) are provided where indicated by superscripts. * = contributed < 0.05% to diet composition. Length class with sufficient sample size is indicated in bold.

Higher Taxon	Lower Taxon	2006 Shelikof	2007 Shelikof	2006 Peninsula	2007 Peninsula	2007 Kodiak	50−99 cm	**100−149 cm**
Polychaeta	Polychaeta	0.1	0.2		*	*	*	0.1
Mollusca	Bivalvia and Gastropoda				*	*	*	0.1
	Cephalopoda		0.5	0.1		0.1	0.8	*
	Teuthida		*					*
	Gonatidae		6.0				0.2	2.1
	Berryteuthis magister		4.2					1.5
	Octopoda		1.7			*		0.6
Crustacea	Amphipoda		0.2		*	0.3	0.3	0.1
	Isopoda	0.2	0.6	*	0.2	0.2	0.8	0.2
	Mysida		*			0.1	*	*
	Euphausiacea					*	*	
	Thysanoessa spp.		9.5^{D}	*	0.4	0.4	12.6	0.7
	Penaeoidea, Sergestoidea, and Caridea		*		*	0.3	0.1	0.1
	Caridea					*	*	
	Crangonidae	*	0.2	0.1				*
	Argis spp.			2.4	5.1	0.1	1.0	1.2
	Crangon spp.	0.1					0.2	*
	Neocrangon communis	2.2^{A}	3.6	0.5	1.6	3.9	9.6^{J}	1.0
	Hippolytidae	*	*	0.1	0.2	0.3		0.1
	Eualus spp.	0.1	5.1	0.4	0.3	1.0	6.7^{K}	0.7
	Pandalidae	0.3	2.8	0.7		0.3	0.8	1.3
	Pandalopsis spp.	0.5	3.9	0.5	0.2	5.2	0.8	1.7
	Pandalus spp.	63.6^{B}	28.1^{E}	24.8^{F}	39.7^{H}		26.6^{L}	32.6^{M}
	Pasiphaeidae		2.0				1.3	0.4
	Anomura					2.4		
	Paguroidea	0.1	0.3				0.2	0.6
	Brachyura	1.0	1.3		*		0.7	0.6
	Majoidea					2.0		0.4
	Chionoecetes bairdi	22.2^{C}	14.9	39.3^{G}	25.8	39.0^{I}	22.4	27.5^{N}
Actinopterygii	Acinopterygii	3.1	6.9	0.3	0.6	6.9	2.4	4.6
	Clupeiformes		0.4					0.1
	Osmeriformes	*	0.3		0.7		0.1	0.2
	Mallotus villosus		2.2	17.9	3.0		5.4	3.8
	Gadiformes	2.2	0.1	2.1			1.4	0.6
	Theragra chalcogramma	4.1	3.3	4.2	9.5	3.9	1.4	5.3
	Cryptacanthodes aleutensis		0.3			6.7	0.9	2.4
	Stichaeidae			6.0	4.9	6.3	1.6	3.1
	Zoarcidae				1.6	17.7		4.1
	Ammodytidae		0.9		0.4	2.8	0.2	0.9
	Scorpaeniformes		0.5	0.6	0.9		0.8	0.2
	Pleuronectiformes	*			4.8	0.1	0.4	1.0

A) Median = 0.2, Q1 = 0.0, Q3 = 2.2; B) Median = 76.2, Q1 = 44.4, Q3 = 93.4; C) Median = 4.4, Q1 = 0.0, Q3 = 42.6; D) Median = 12.2, Q1 = 0.0, Q3 = 53.0; E) Median = 0.2; Q1 = 0.0, Q3 = 8.0; F) Median = 7.5, Q1 = 0.0, Q3 = 35.6, G) Median = 13.0, Q1 = 0.0, Q3 = 76.3; H) Median = 34.7; Q1 = 0.0, Q3 = 81.7; I) Median = 43.2, Q1 = 3.1, Q3 = 69.7; J) Median = 1.9, Q1 = 0.0, Q3 = 6.9; K) Median = 0.2, Q1 = 0.0, Q3 = 2.9; L) Median = 12.0, Q1 = 0.0, Q3 = 45.3; M) Median = 17.8, Q1 = 0.0, Q3 = 61.5; N) Median = 6.10, Q1 = 0.0, Q3 = 53.1.

Table 3.5. Diet composition (Mean %W) of the Bering skate, *Bathyraja interrupta*, as calculated from non-empty stomach samples collected during 2006 and 2007 off the east side of Kodiak Island (*n* = 41, 74) and in Shelikof Strait (*n* = 65, 65), and during 2006 and 2007 for individuals measuring 50−99 cm (*n* = 49) and 100−149 cm (*n* = 239) in total length from throughout the west-central Gulf of Alaska. Median values > 0.0 and 1st (Q1) and 3rd quartiles (Q3) are provided where indicated by superscripts. * = contributed < 0.05% to diet composition.

Higher Taxon	Lower Taxon	2006 Kodiak	2007 Kodiak	2006 Shelikof	2007 Shelikof	< 50 cm	50−99 cm
Polychaeta	Polychaeta	2.3	2.1	2.8	3.1	4.1	2.2
Mollusca	Cephalopoda	0.1	*	0.1		0.2	*
	Teuthida	0.1		2.0	4.9	*	1.9
Crustacea	Amphipoda	5.6	3.5	0.4	0.4	6.6[I]	2.0
	Isopoda	3.3	11.5	1.5	0.9	3.1	4.2
	Mysida	2.0	1.6	5.0	3.8	10.8[J]	1.0
	Euphausiacea	0.4	2.3	0.4	42.2[G]	15.1	9.3
	Penaeoidea, Sergestoidea, and Caridea	1.3	*	5.0[C]	0.1	1.6	1.4
	Crangonidae	6.9	1.1	2.2	4.9	3.5	1.6
	Argis spp.		0.1	3.0	2.0		3.0
	Crangon spp.		5.3	18.7[D]	9.3	14.9	7.9
	Hippolytidae	*	0.3	1.3	0.4	0.5	0.4
	Eualus spp.	3.0	1.8	12.3[E]	3.7	9.1[K]	4.3
	Pandalidae	11.8	14.6	20.3[F]	9.3[H]	10.5	15.1[L]
	Paguroidea	13.2	5.3	2.9	3.5	4.2	5.2
	Brachyura	4.0		2.2	0.5	1.1	1.2
	Majoidea		0.5	0.4	0.1		0.3
	Chionoecetes bairdi	26.4[A]	46.0[B]	12.3	6.9	9.0	27.8[M]
Actinopterygii	Acinopterygii	2.9	0.1	2.2	1.7	2.3	1.3
	Clupeiformes			0.1			0.2
	Mallotus villosus	10.2	1.6	1.2	0.2	1.9	5.6
	Gadiformes		0.1	0.5	0.6	0.1	0.5
	Theragra chalcogramma	3.6		2.6			1.4
	Cryptacanthodes aleutensis	1.3	2.1	*		1.3	0.6
	Ammodytidae		*		1.1		0.3
	Scorpaeniformes	0.5		*	0.4		0.2
	Pleuronectiformes	1.3	*	0.7	0.1	*	0.9

A) Median = 14.8, Q1 = 0.0, Q3 = 39.0; B) Median = 44.5, Q1 = 0.0, Q3 = 92.0; C) Median = 0.3, Q1 = 0.0, Q3 = 2.7; D) Median = 2.0, Q1 = 0.0, Q3 = 38.5; E) Median = 2.0, Q1 = 0.3, Q3 = 19.7; F) Median = 7.4, Q1 = 1.4, Q3 = 30.0; G) Median = 37.5, Q1 = 10.4, Q3 = 72.8; H) Median = 0.5, Q1 = 0.0, Q3 = 15.0; I) Median = 0.4, Q1 = 0.0, Q3 = 7.2; J) Median = 0.1, Q1 = 0.0, Q3 = 3.9; K) Median = 0.3, Q1 = 0.0, Q3 = 15.8; L) Median = 1.5, Q1 = 0.0, Q3 = 18.6; M), Median = 6.7, Q1 = 0.0, Q3 = 52.6.

Table 3.6. Diet composition (Mean %W) of the Alaska skate, *Bathyraja parmifera*, as calculated from non-empty stomach samples collected during 2007 off the east side of Kodiak Island ($n = 27$), and during 2006 and 2007 for individuals measuring 50−99 cm (total length, $n = 32$) from throughout the west-central Gulf of Alaska. Median values > 0.0 and 1st (Q1) and 3rd quartiles (Q3) are provided where indicated by superscripts.* = contributed < 0.05% to diet composition. Neither groups had sufficient sample size.

Higher Taxon	Lower Taxon	2007 Kodiak	55−99 cm TL
Polychaeta	Polychaeta		*
Crustacea	Amphipoda	0.5	0.1
	Isopoda	3.7	
	Mysida	0.1	0.1
	Euphausiacea	3.7	7.6
	Argis spp.	0.1	1.8
	Crangon spp.	13.7	2.6
	Hippolytidae	0.1	*
	Eualus spp.		0.1
	Pandalidae	0.1	7.3
	Paguroidea	7.2	7.0
	Brachyura		0.1
	Majoidea	0.3	0.2
	Chionoecetes bairdi	53.6^{A}	52.7^{B}
Actionpterygii	Actionpterygii	5.2	8.4
	Theragra chalcogramma	2.3	7.7
	Zoarcidae	0.2	0.2
	Pleuronectiformes	9.2	4.3

A) Median = 86.1, Q1 = 0.0, Q3 = 100.00; B) Median = 79.0, Q1 = 0.0, Q3 = 97.3.

Table 3.7. Depth, latitude, temperature, and habitat parameters of big, longnose, and California skate juvenile and adult life stages collected off the U.S. West Coast during NMFS WCGBTS operations conducted from 2003−2013. Observed and predicted values from ZIP (Depth, Latitude, Habitat) and GAM (Temperature) model outputs are provided in association with overall (min−max), common (Q1−Q3), and maximum (< 10% of maximum value) counts. No habitat information was available from the WCGBTS. Observed habitat preference was calculated using G-Tests, with habitat type corresponding to trawl locations extracted from a substrate map that recently was created for the study site (NMFS 2013).

		Big (Juvenile)	**Big (Adult)**	**Longnose (Juvenile)**	**Longnose (Adult)**	**California (Juvenile)**	**California (Adult)**
Depth (m)	Overall	56−459	59−250	57−1227	65−787	57−792	58−738
	Pred. Overall	56−340	58−639	56−1088	125−509	57−302	56−428
	Common	79−123	82−130	123−404	186−418	78−108	75−103
	Pred. Common	91−159	129−348	117−494	214−369	88−165	89−149
	Max	63	150	281, 135	159, 178, 414	76	125
	Pred. Max	83, 107	248, 340	248	270, 340	58, 64, 81	87, 97
Latitude (degrees N)	Overall	32.9−48.3	33.9−48.4	32.3−48.5	32.8−48.5	32.6−45.6	32.6−48.0
	Pred. Overall	32.9−48.4	35.0−48.5	32.0−48.5	32.3−48.5	32.6−40.8	32.7−48.5
	Common	40.5−45.0	38.5−44.7	37.0−45.2	42.8−46.8	34.2−38.2	35.6−38.5
	Pred. Common	38.5−45.9	39.1−45.1	35.5−45.0	40.6−45.7	34.4−39.0	38.2−46.3
	Max	37.7, 43.0	37.8	35.1, 40.0	48.3, 47.8, 43.7	35.4	40.1
	Pred. Max	44.2	39.7, 48.1	39.7	48.2, 48.1	37.1, 37.5, 37.0	48.2, 48.3
Habitat (type)	G-Test	Soft	Mixed	MS	MS, SM, SH	Soft	Mixed
	Pred.	Soft	NA	MS	NS	NS	NA
Temperature (degrees C)	Overall	5.0−12.7	5.9−12.4	3.0−12.7	4.0−12.7	4.2−12.7	4.2−12.7
	Pred. Overall	6.0−10.1	4.1−9.9	2.6−10.1	4.7−9.5	7.3−10.1	5.2−10.1
	Common	6.2−10.2	6.2−10.4	5.3−10.0	5.2−7.9	8.0−11.6	8.0−11.4
	Pred. Common	7.2−9.0	5.9−9.1	5.1−9.0	6.0−7.6	8.5−9.7	7.1−9.8
	Max	10.3	9.3	8.8, 7.9	6.3, 6.9, 5.8	10.1	8.9
	Pred. Max	8.0, 7.0	7.7, 6.0	7.7	6.4, 6.0	9.5, 9.5, 9.3	7.6, 7.5

Table 3.8. Depth, latitude, habitat, and temperature parameters of sandpaper skate and starry skate juvenile and adult life stages collected off the U.S. West Coast during NMFS WCGBTS operations conducted from 2003−2013. Observed and (for sandpaper skates) predicted values from ZIP (Depth, Latitude, Habitat) and GAM (Temperature) model outputs are provided in association with overall (min−max), common (Q1−Q3), and maximum (< 10% of maximum value) counts. No habitat information was available from the WCGBTS. Observed habitat preference was calculated using G-Tests, with habitat type corresponding to trawl locations extracted from a substrate map that recently was created for the study site (NMFS 2013). *Too few occurences were available to evaluate habitat associations with predominantly hard and mixed substrate types; juvenile (*n* = 141) and adult (*n* = 27) life stages were combined for habitat analysis because of low sample sizes.

		Sandpaper	**Starry (Juvenile)**	**Starry (Adult)**
Depth (m)	Overall	60−1162	63−982	61−190
	Pred. Overall	56−803	-	-
	Common	160−400	83−140	77−115
	Pred. Common	115−428	-	-
	Max	246, 309	112	61
	Pred. Max	340	-	-
Latitude (degrees N)	Overall	32.3−48.5	32.3−48.4	32.8−44.3
	Pred. Overall	32.0−48.5	-	-
	Common	38.9−45.9	34.1−40.1	34.3−43.3
	Pred. Common	35.6−45.1	-	-
	Max	41.0, 42.6	38.0	43.1
	Pred. Max	48.1	-	-
Habitat (type)	G-Test	SM, MS	SM, SH*	SM, SH*
	Pred.	MS, SM	-	-
Temperature (degrees C)	Overall	3.2−12.7	4.3−11.5	6.8−10.5
	Pred. Overall	3.4−10.1	-	-
	Common	5.3−9.1	6.2−11.1	8.0−10.3
	Pred. Common	5.5−9.0	-	-
	Max	6.9	9.3	8.1
	Pred. Max	6.0	-	-

3.7 FIGURES

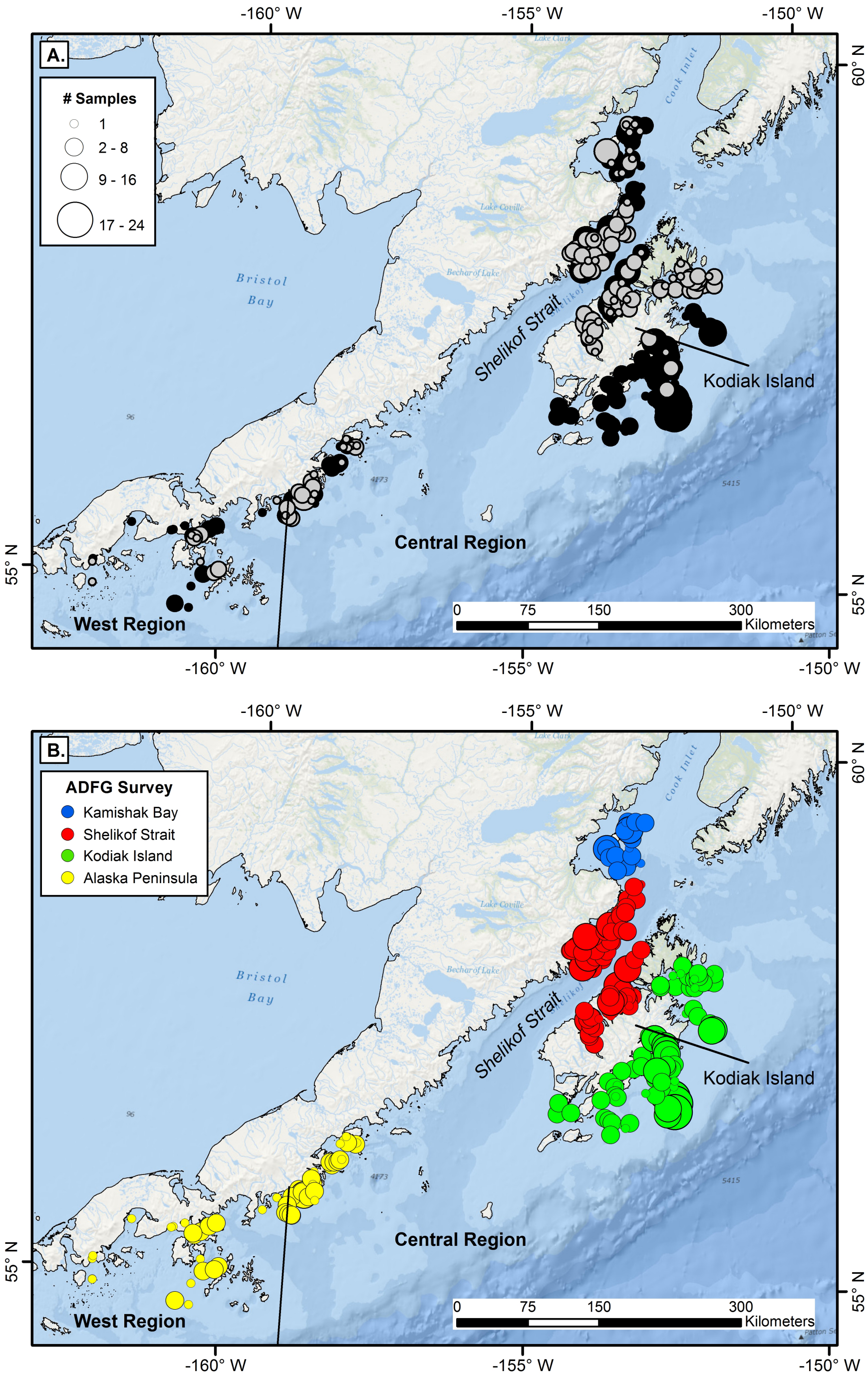


Figure 3.1. Number of (non-empty) stomach samples collected from the five most abundant skate species among trawl sets conducted on the continental shelf and upper continental slope of the west-central Gulf of Alaska between years (A; 2006 = grey, 2007 = black) and among Alaska Department of Fish and Game (ADFG) regions (B). National Marine Fisheries Service management region boundaries (West, Central) are depicted.

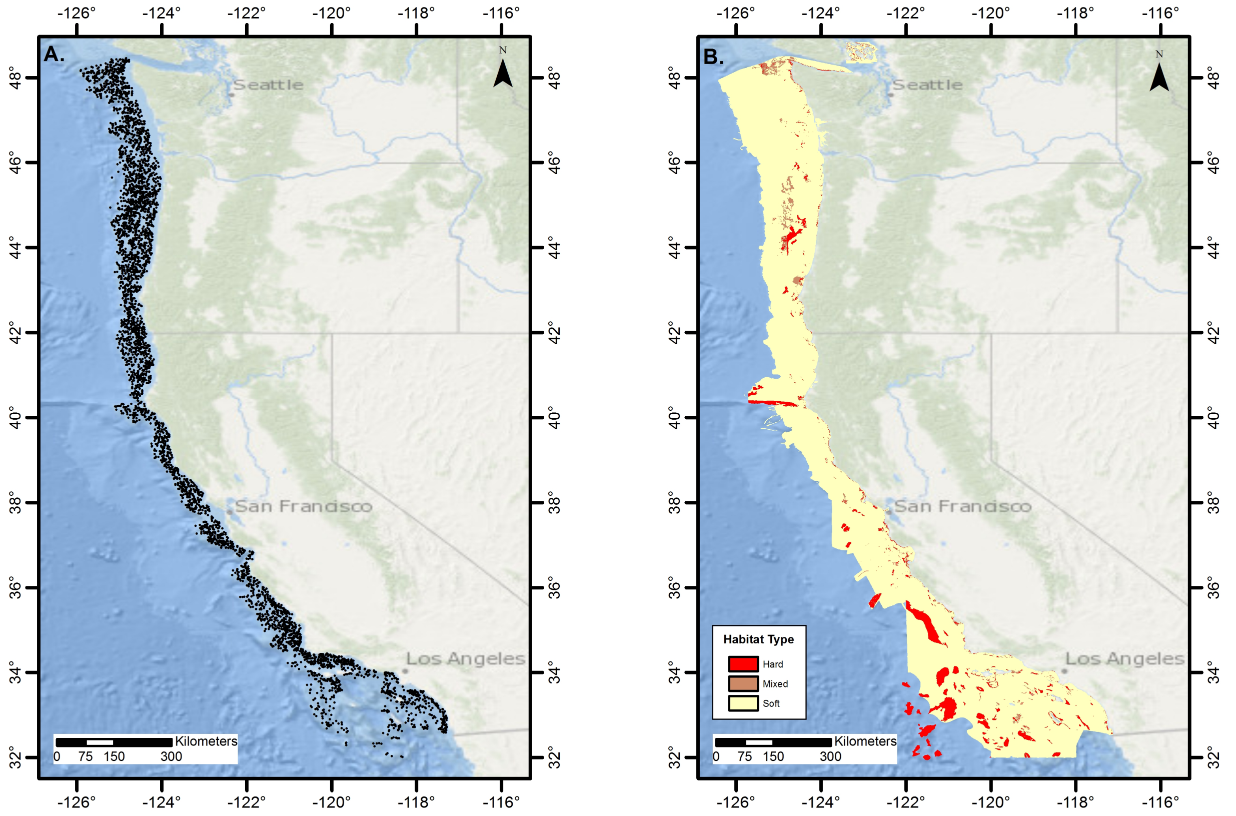
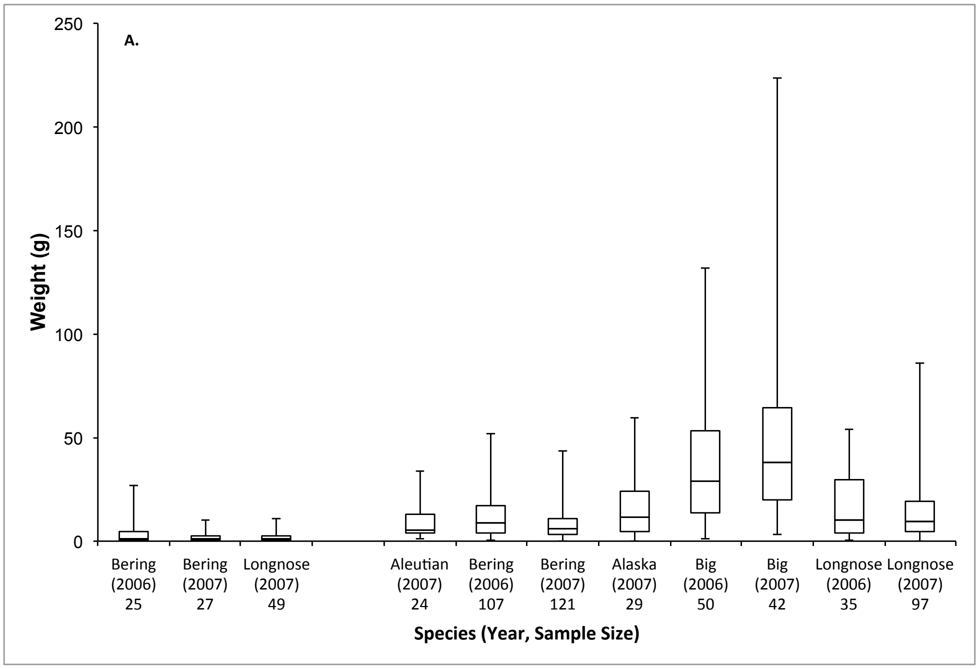


Figure 3.2. (A) Locations of fishing operations conducted during 2003–2013 National Marine Fisheries Service (NMFS) West Coast Groundfish Bottom Trawl Surveys, and (B) benthic habitat map produced during NMFS' recent 5-year review of Essential Fish Habitat for West Coast groundfishes (NMFS 2013).



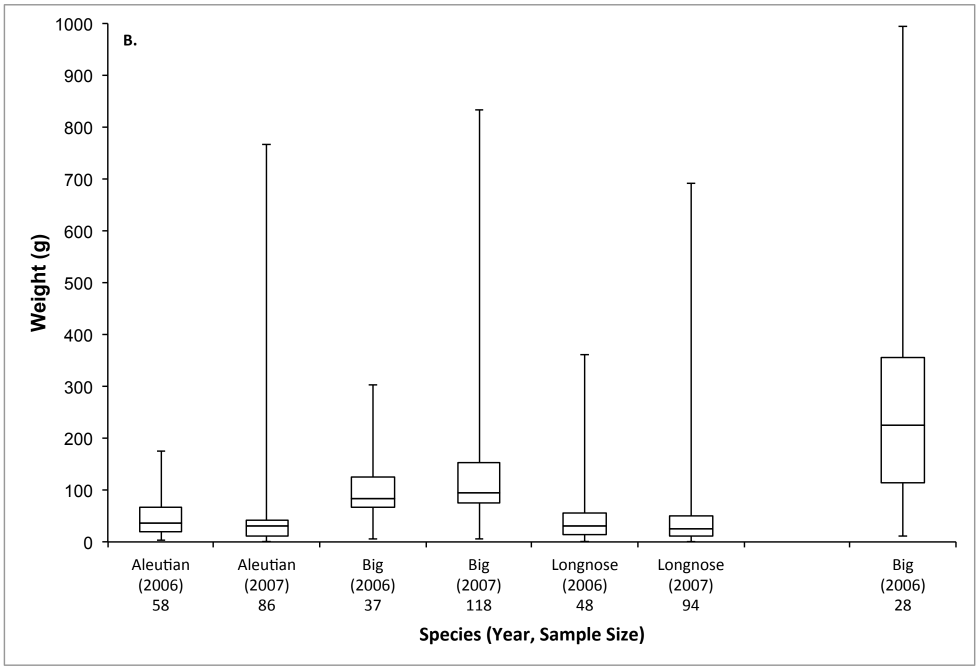


Figure. 3.3. Per capita daily consumption estimates (weight/individual/day) for small (A; < 50 cm total length, TL), medium (A; 50–99 cm TL), large (B; 100–149 cm TL), and extra-large (B; 150–199 cm TL) skates collected in the National Marine Fisheries Service Central Region of the Gulf of Alaska during 2006 and 2007. Box and whisker plots depict median values, first and third quartiles, and minimum and maximum values. Smaller groups are depicted on the left side of the x-axis of each plot.

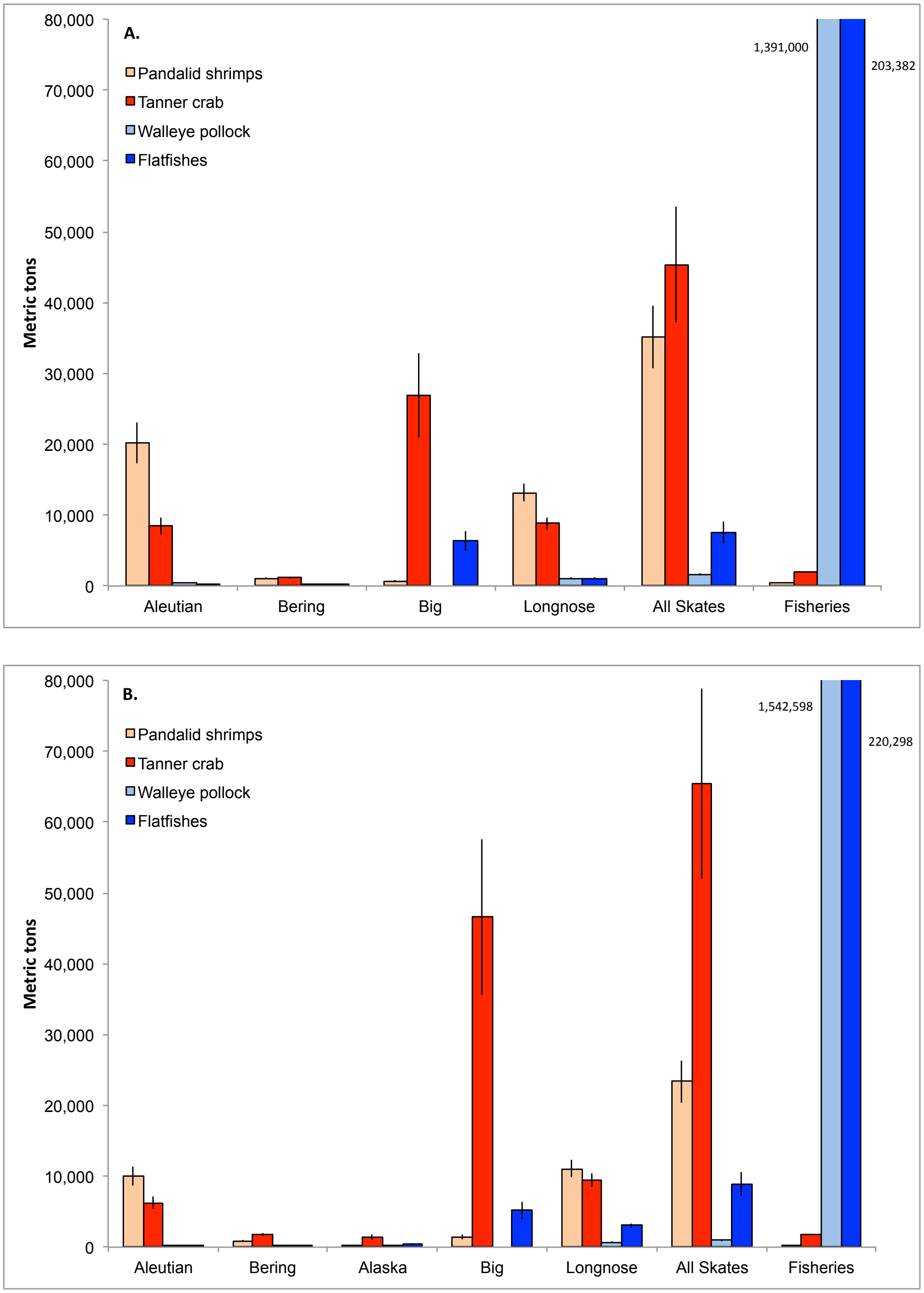


Figure 3.4. Estimated annual consumptive removals of commercially important taxa by skate species in the National Marine Fisheries Service (NMFS) Central Region of the Gulf of Alaska during May–September of 2006 (A) and 2007 (B), and by commercially fisheries throughout Alaskan waters (NMFS landings data). The estimated amount of taxon-specific removals (with SD) are provided for skates, and total landings are provided for commercial fisheries.

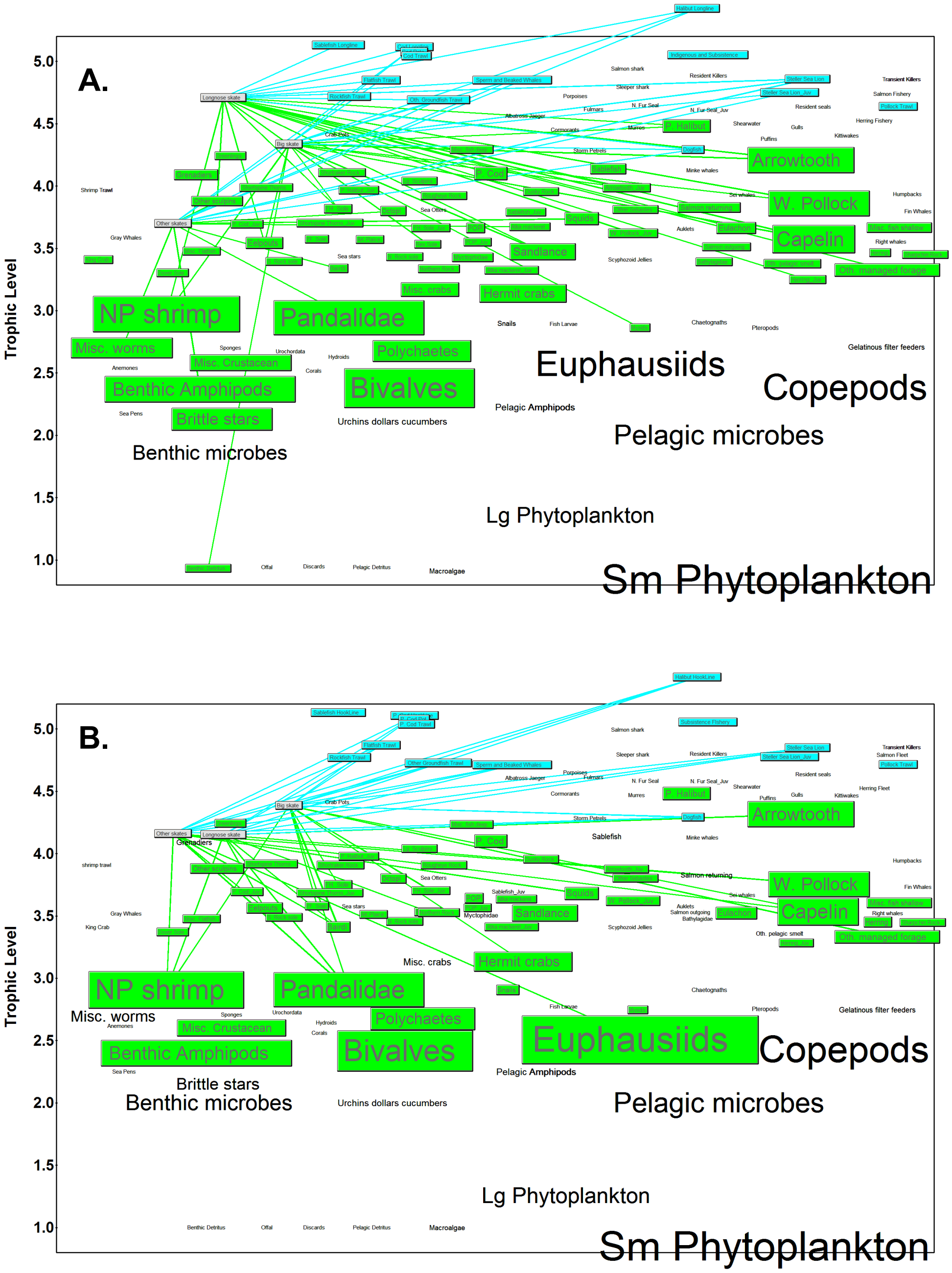


Figure 3.5. Original Gulf of Alaska food web model output (A) and output of updated model (B), incorporating diet composition and annual consumption:biomass (Q/B) estimates from this study. Lines indicated linkages between skate prey (green) and skate predators (blue, including fisheries). Font size indicates the relative amount of biomass in the system.

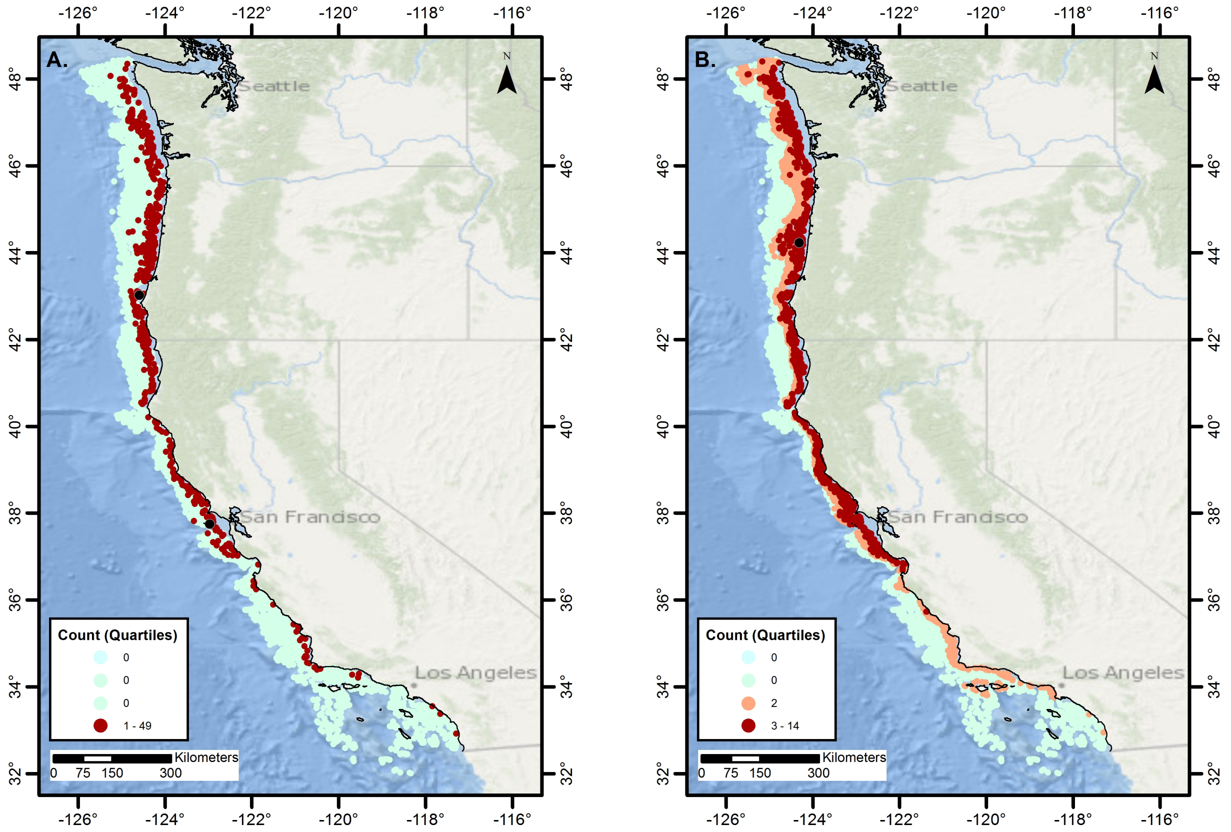


Figure 3.6. Actual (A) and predicted (B) count of juvenile big skate (*Beringraja binoculata*) collected during NMFS WCGBTS operations. Data are given in quartiles, with individual numbers representing upper quartile boundaries. Maximum counts (threshold = within 10% of maximum counts) are indicated with black circles.

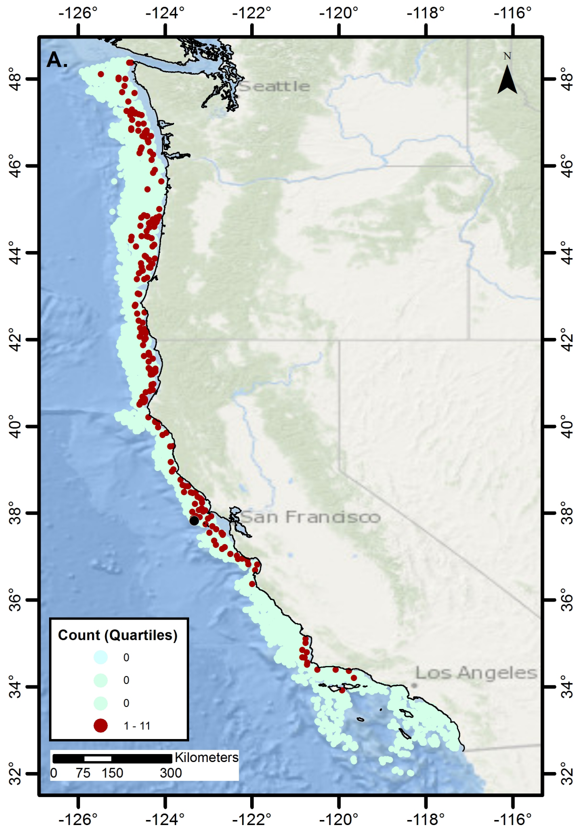


Figure 3.7. Actual (A) and predicted (B) count of adult big skate (*Beringraja binoculata*) collected during NMFS WCGBTS operations. Data are given in quartiles, with individual numbers representing upper quartile boundaries. Maximum counts (threshold = within 10% of maximum counts) are indicated with black circles.

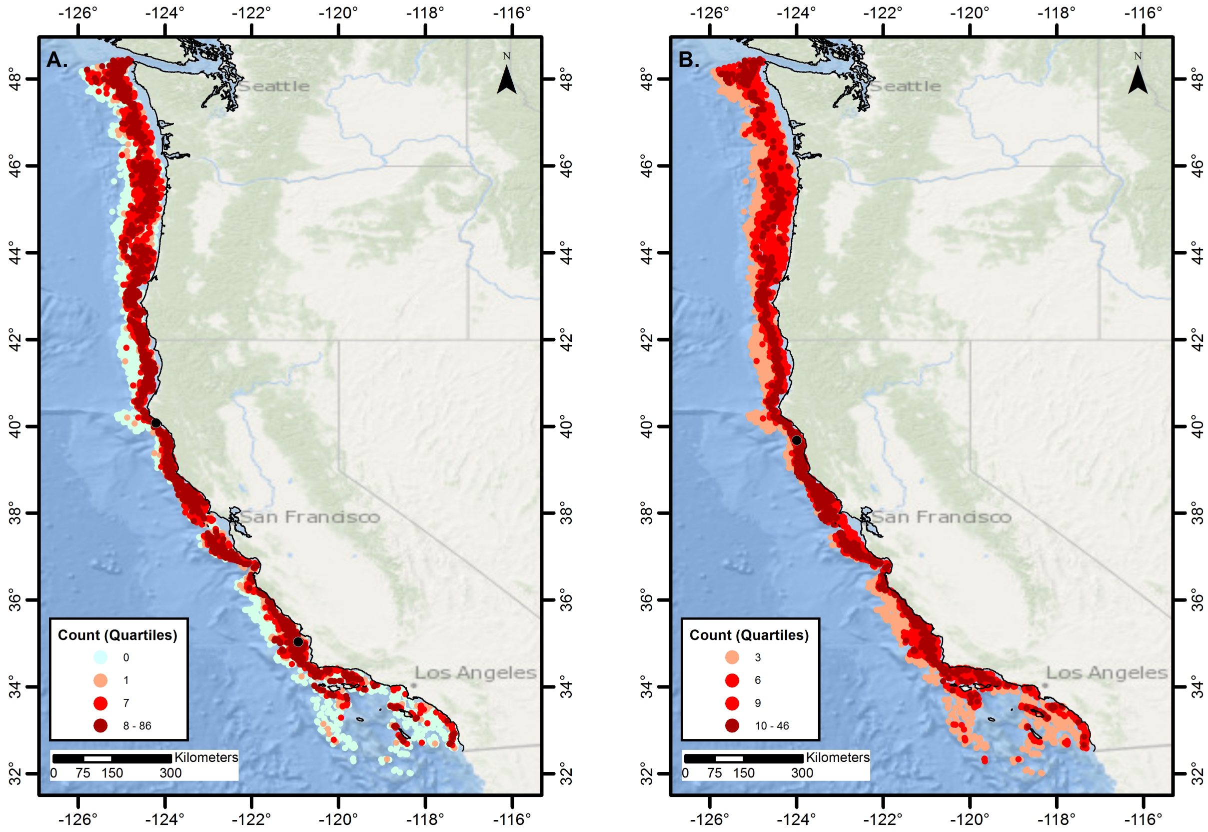


Figure 3.8. Actual (A) and predicted (B) count of juvenile longnose skate (*Raja rhina*) collected during NMFS WCGBTS operations. Data are given in quartiles, with individual numbers representing upper quartile boundaries. Maximum counts (threshold = within 10% of maximum counts) are indicated with black circles.

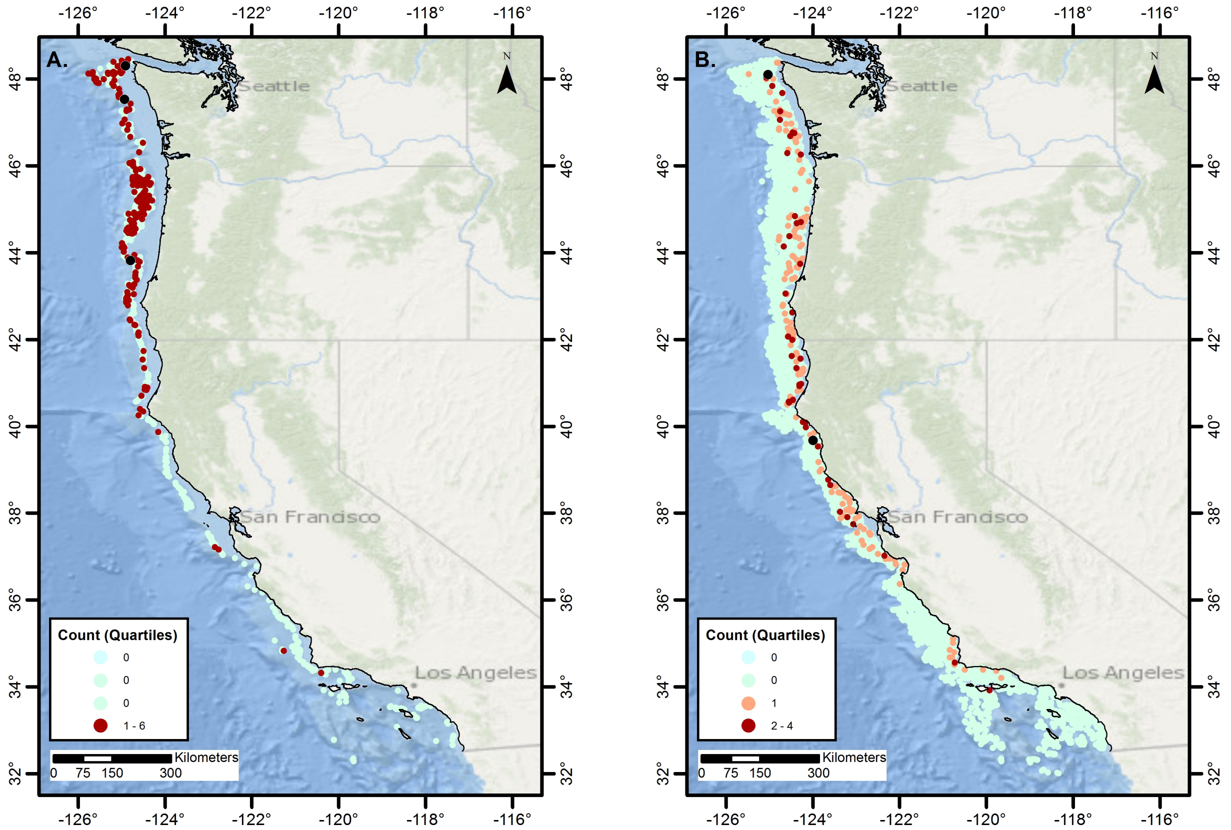


Figure 3.9. Actual (A) and predicted (B) count of adult longnose skate (*Raja rhina*) collected during NMFS WCGBTS operations. Data are given in quartiles, with individual numbers representing upper quartile boundaries. Maximum counts (threshold = within 10% of maximum counts) are indicated with black circles.

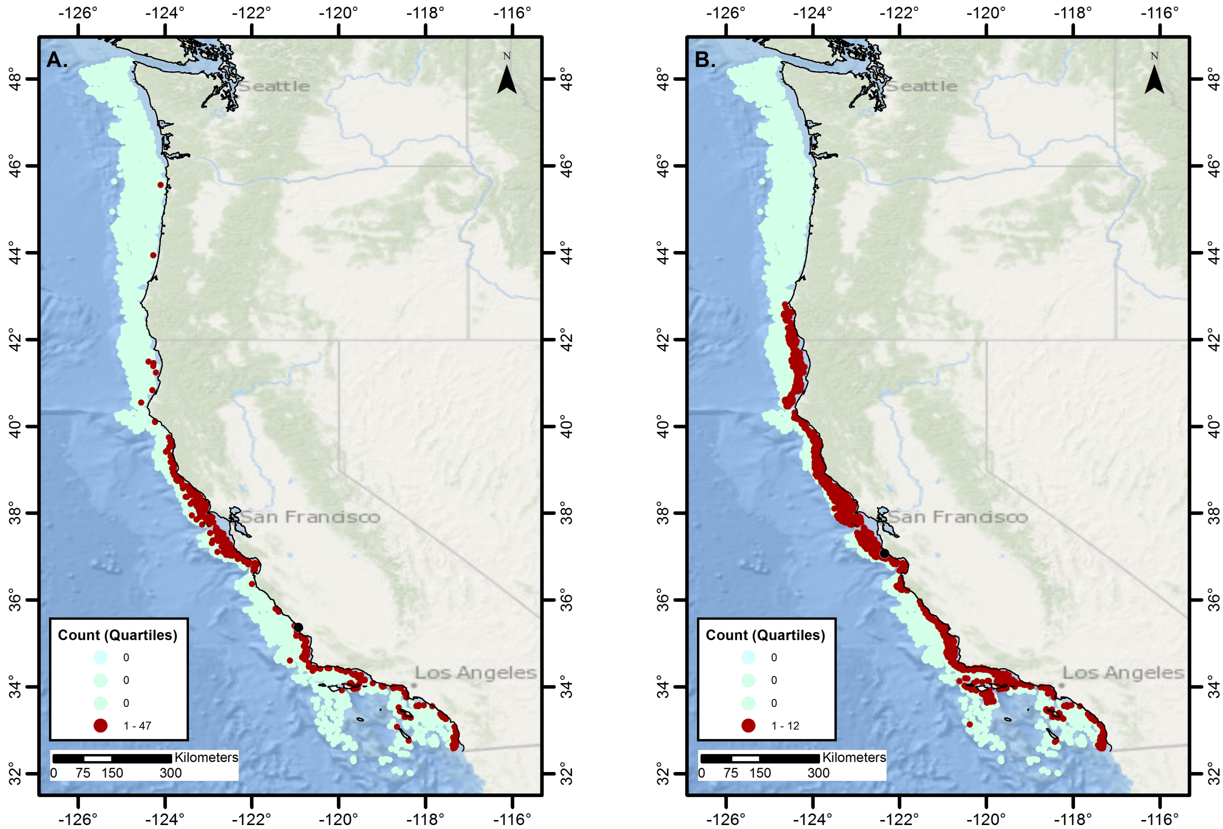


Figure 3.10. Actual (A) and predicted (B) count of juvenile California skates (*Raja inornata*) collected during NMFS WCGBTS operations. Data are given in quartiles, with individual numbers representing upper quartile boundaries. Maximum counts (threshold = within 10% of maximum counts) are indicated with black circles.

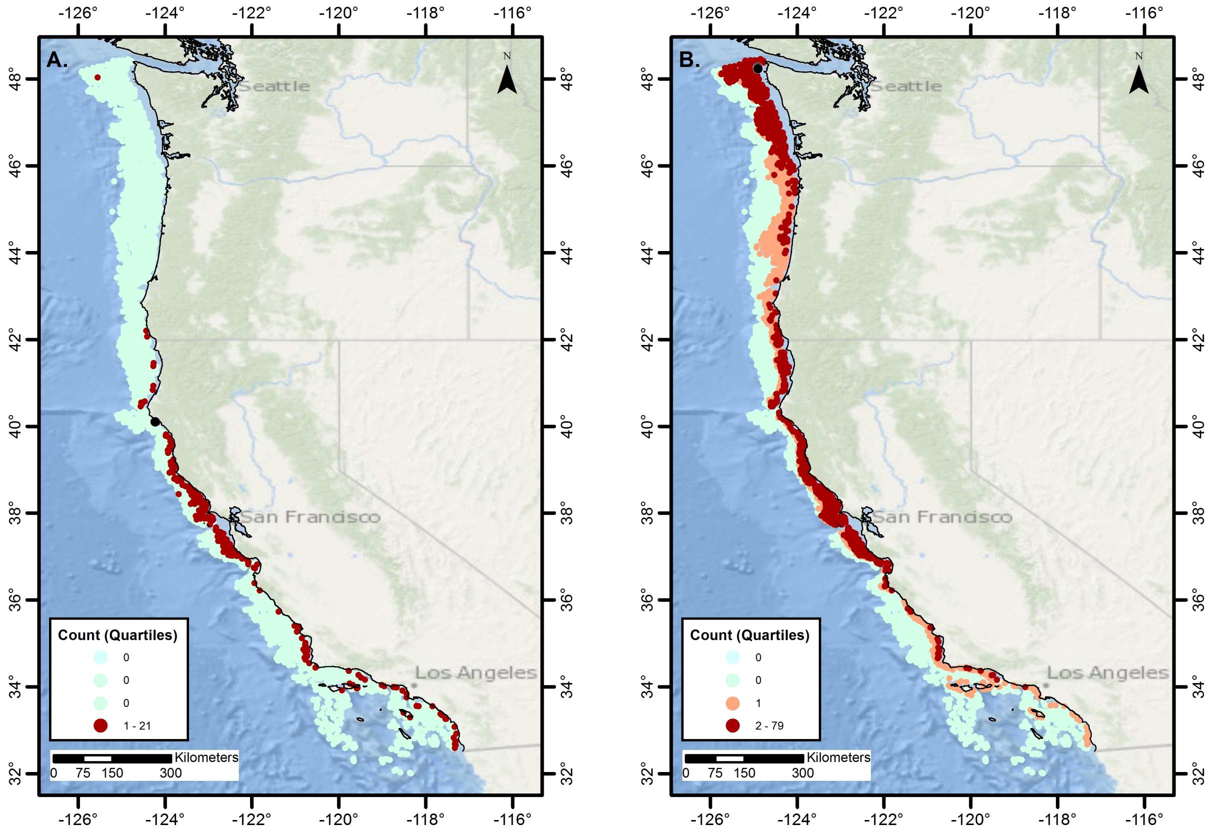


Figure 3.11. Actual (A) and predicted (B) count of adult California skates (*Raja inornata*) collected during NMFS WCGBTS operations. Data are given in quartiles, with individual numbers representing upper quartile boundaries. Maximum counts (threshold = within 10% of maximum counts) are indicated with black circles.

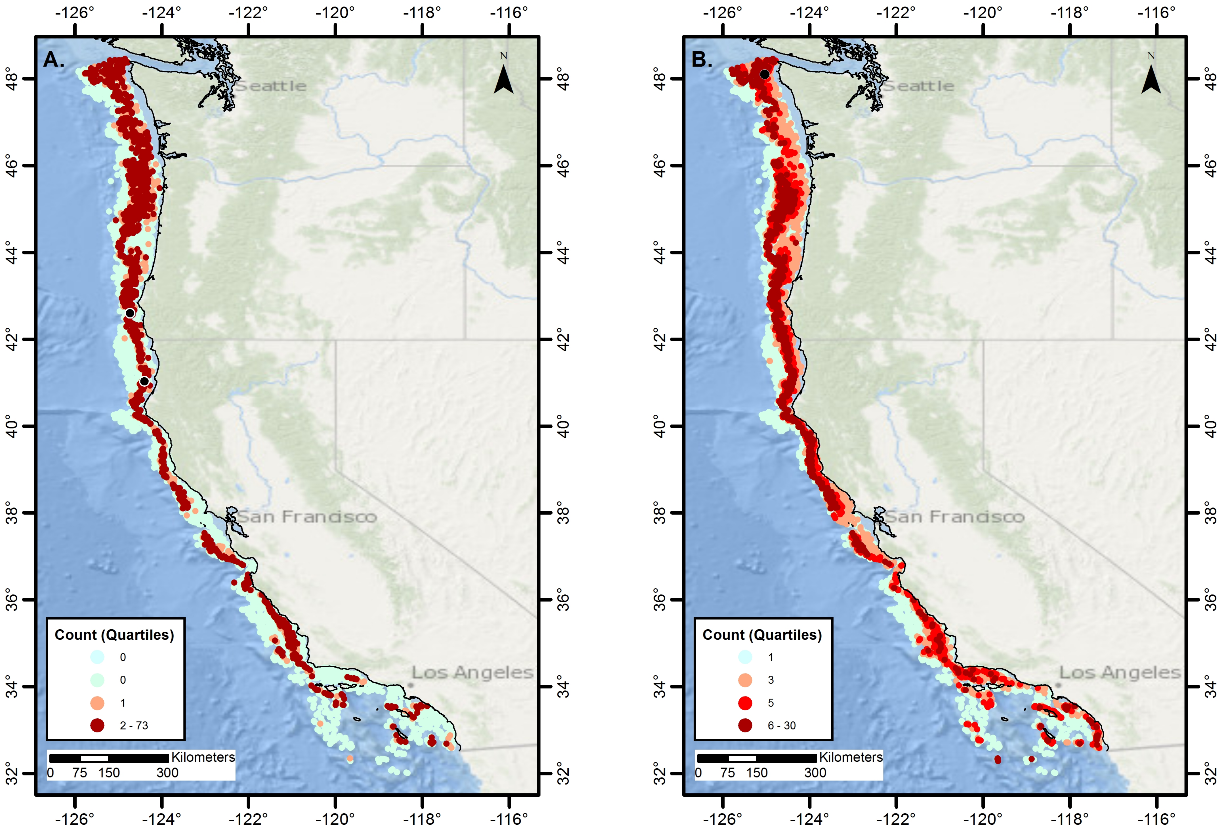


Figure 3.12. Actual (A) and predicted (B) count of combined juvenile and adult sandpaper skates (*Bathyraja kincaidii*) collected during NMFS WCGBTS operations. Data are given in quartiles, with individual numbers representing upper quartile boundaries. Maximum counts (threshold = within 10% of maximum counts) are indicated with black circles.

Conclusions

Space appears to be more important than food in structuring eastern North Pacific (ENP) skate assemblages, based on the combined results of Chapters 1 and 2. Spatial segregation among sympatric skate species and their life stages was demonstrated off central California and in the western Gulf of Alaska. In contrast, ENP skate assemblages displayed a high degree of trophic redundancy, with the timing and location of collection trawls explaining the great majority of dietary variation. Resource competition often is relaxed in open, unstructured marine environments (e.g., soft-bottom, offshore regions such as those generally occupied by skates, flatfishes, and cods) as compared to closed, structured systems (e.g., mangrove swamps, such as those occupied by early life stages of many coral reef fishes, or reef systems, such as those occupied by moray eels, groupers, and rockfishes). It may be that a traditional, Hutchinsonian view of niche differentiation, where competition for limiting resources shapes community structure, is not directly applicable to skates or other generalist predators that occupy open, unstructured environments (e.g. Pacific cod). The Unified Neutral Theory of Biodiversity, as hypothesized by Hubbell, provides an alternative hypothesis for observed patterns of biodiversity. By this theory, differences between members of an ecologically community of trophically similar species are irrelevant to their evolutionary success. Instead, each species follows a random walk, and biodiversity arises by chance. Extant skate diversity may have arisen from a strict adherence to either hypothesis, of from a combination of their main tenants (i.e., Niche-Neutrality, after Vergnon). Skates could provide an interesting test of these biodiversity hypotheses. Further research in different regions is needed to determine if the findings of this study are generally applicable to all skate assemblages, and to better understand why there are so many skate species.

Determining fine-scale spatial and temporal habitat use is an important next step in understanding skate ecology and the possible mechanisms driving the co-occurrence of speciose skate assemblages. Where data are available, adult female and male skates, which often are spatially segregated, have been shown to make coordinated seasonal migrations for spawning purposes. In addition, the timing of these migrations typically differs among sympatric species. Sequential nursery use of inshore regions has been demonstrated within ray and shark assemblages. A similar mechanism may be evident in the deeper waters that are typically occupied by skates. Recent studies of skates have documented daily vertical migrations in some species, probably to feed in pelagic waters nocturnally, where they have a predatory advantage of enhanced electro and chemical reception. This use of specific regions for feeding and reproduction may provide another source of spatial separation among skate species that is currently overlooked or not well understood from fishery survey data. Furthermore, skates have electrical organs in their tails that enable them to recognize conspecifics and facilitate a variety of behaviors, including mate recognition, aggregating behaviors, and territoriality. This communicative ability also could drive spatial differentiation among sympatric skates. Directed, ontogenetic telemetry studies are necessary to better understand movement patterns and habitat use in skates. Coupled, experimental laboratory studies could be used to assess the importance of behavior in coordinating short- and long-term movement patterns.

Spatio-temporal patterns of prey availability largely dictated trophic relationships of ENP skates. In both study regions, the timing and location of collection hauls was the primary factor in explaining diet composition within an assemblage. Species-level differences and length-based differences also were highly significant, but explained a relatively minor portion of the observed dietary variability, especially in the western Gulf of Alaska. Skates are extreme generalists that eat locally abundant crustaceans and fishes within their common environmental (e.g., depth, temperature) ranges. Even within a species or life stage, skate diet is highly variable among individuals. Additionally, skates may have different ecological roles in different systems. For instance, although big and longnose skates reached larger sizes in the western Gulf of Alaska, they were more piscivorous off central California. Anecdotal evidence suggests that skates form multi-species aggregations feed on punctuated, high-density prey pulses (e.g., rockfish recruitment, euphausiid entrainment). Conversely, in times of relative prey scarcity, individual species may retreat to core regions (i.e., those with optimal environmental conditions) and feed on the available crustaceans and fishes.

Diet composition studies of skates now are rather common, but the methods employed and the opportunistic, generalist nature of skate feeding have obscured a true understanding of skate trophic ecology. Most studies include only a small, arbitrary number of variables (e.g., length, depth) for dietary comparisons. The location and timing of collection hauls rarely are included in skate diet composition studies, but were of paramount importance in explaining variability in the diet composition of ENP skates. Although tested variables often are significant sources of dietary variability, they may be biologically meaningless if other, untested factors have greater explanatory power. For instance, maturity was a highly significant factor for the California skate assemblage, but only explained 0.4% of dietary variability. Sex-based differences sometimes are reported, but these differences typically are a result of variability in size (female skates generally grow larger than males) or habitat use. Diet composition studies on skates represent a static, often subjective condition for a group of trophically redundant predators with highly dynamic diets and require a considerable investment of time and money. They should therefore should discontinued until they can be informed through an improved understanding of skate spatial associations.

Once fine-scale spatial associations of skates are better understood, more informative diet composition studies can be conducted. Knowledge of daily movements to foraging grounds and seasonal use of nursery grounds could be utilized to focus sampling efforts on skate species/life stages in specific habitats. This practice would probably help to untangle some of the dietary variability that arises by considering each sample region of similar use and importance to skates. Underwater acoustic arrays and coordinated benthic sampling could be employed to distinguish foraging habitats of individual species and overall skate assemblages. In addition, some aspects of skate trophic ecology that were determined in this study have broad support in the literature and can help shape future research. Skates can be used to monitor changes in local prey abundance and to document the occurrence of small, difficult to capture prey fauna. In this capacity, range extensions of crustaceans and fishes have been determined from skate stomachs. Small skates (< ~50 cm total length, TL) consume a diet of mainly amphipods, polychaetes, small crustaceans. As they grow (~50-99 cm TL), they incorporate more decapods and some fishes, with the proportion of fishes:decapods increasing in larger individuals (~100-149 cm TL), and fishes often dominate the diet of the largest skates (> 150 cm TL). Skates are gape-limited predators. In this study, the weight, but not number of Tanner crabs increased with TL in big skates. Prey size is therefore also an important consideration that should be included in future diet studies. Because TL is an important source of dietary variability in skates, skates of different sizes should not be lumped together when investigating trophic relationships.

The spatial associations determined for skate species/life stages off the U.S. West Coast can be applied to improve regional skate management. Depth was the most important factor in explaining the distribution and abundance patterns of West Coast skates, followed by latitude. However, the current habitat suitability probability model, used by the National Marine Fisheries Service to determine essential fish habitat (EFH) for managed species, considers habitat to be twice as important as either of these factors. Regression models, such as those used in this study, are a better choice for the purpose of modeling distribution and abundance patterns. They can be used to determine regions of differential importance within overall skate distributions and to predict the occurrence of skates in unsampled areas. Spatial closures could then be developed for skates to reduce fishing pressure on important migration corridors and nursery or foraging habitats. In this study, EFH of each West Coast study species was clarified and updated. The California skate provided the greatest example of a mismatch between the original and updated EFH designations. The prime habitat of this species was reduced by 95% based on the results of this study. Instead of having a widespread distribution, the California skate is essentially a northern California endemic with a limited amount of prime habitat that occurs in an area of historically intense fishing pressure. Since no stock assessment has been conducted on this species and none is planned, establishing a no take zone in the region of prime habitat could be an effective management option to safeguard the California skate stock.

Estimating diet composition and consumption of skates in the Gulf of Alaska was a necessary first step to improving regional food web models and ultimately advancing an ecosystem approach to fisheries management. Diets of big and Alaska skates consisted primarily of Tanner crab, pandalid shrimps were the main prey of the Aleutian skate, and longnose and Bering skates ate a mixture of pandalid, crangonid, and hippolytid shrimps. During 2006 and 2007, consumptive removals of Tanner crab and pandalid shrimps by skates in the Gulf of Alaska exceeded commercial landings of these decapods throughout Alaskan waters. However, because hard-bodied crustacean prey are retained longer in skate stomachs than other prey types (e.g., fishes, polychaetes), consumption estimates for pandalid shrimps and especially Tanner crab may be substantially overestimated. Updating diet compositions and annual consumption to biomass ratios of skates in the Gulf of Alaska food web model substantially altered trophic interactions and system dynamics. In the original model, skate consumption of Tanner crab was trivial. In the new model, however, skates (especially big skate) were the most important predatory group of Tanner crab. These findings indicate that original diet composition inputs, mainly taken from distant regions, are not appropriate for generalist predators such as skates. For samples collected in the Gulf of Alaska, dietary differences between modeled time periods probably also reflect differences in relative prey abundance resulting from a regime shift (from groundfish dominated to decapod dominated).

The results of this study have advanced our understanding of skate ecology and serve as a precursor for improved management of skates in the ENP, and the development of research plans to address remaining knowledge gaps. Long-term areas of differential aggregation were documented among sympatric species, but skates overlapped considerably in distribution on smaller spatial scales and shorter time frames. Where they overlapped in distribution, skates typically ate similar prey spectrums. Research should therefore focus on documenting spatial associations on shorter time scales and finer spatial resolutions, and then applying this improved understanding to construct more informative trophic studies. Skates are garnering increased scientific and management attention in each study region as their ecological importance and vulnerability to fishing pressure are better documented. Research on ENP skates provided important baseline information that is consistent with current ecosystem approaches to management off the U.S. West Coast (i.e., spatial management) and in Alaska (i.e., food web modeling). Future management considerations include using regression models to estimate ideal locations for the establishment of no take zones for skates off the U.S. West Coast, and updating the Gulf of Alaska food web model for all incorporated species.

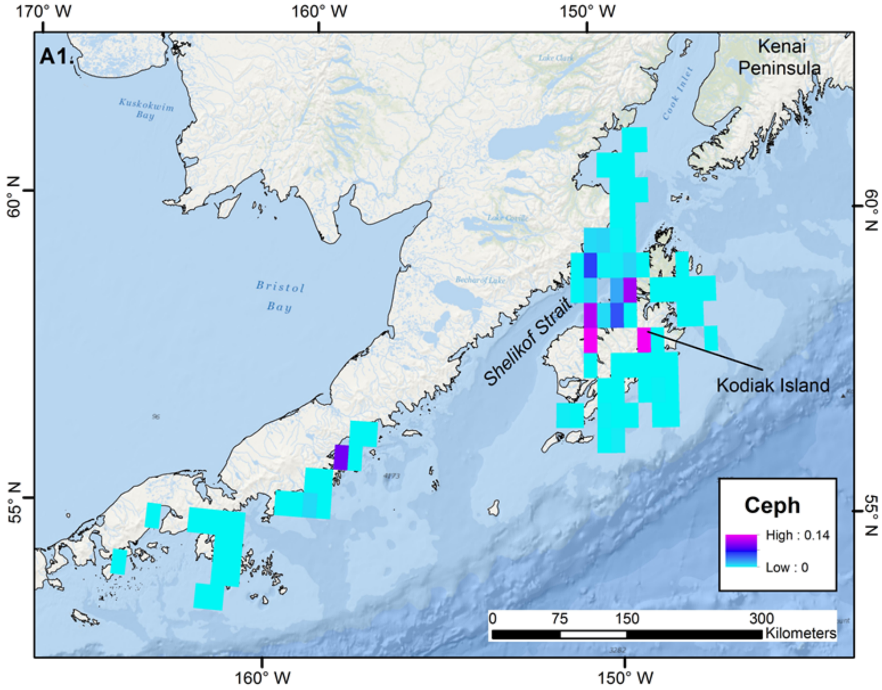
APPENDIX 1: PERMANOVA Assessment Criteria

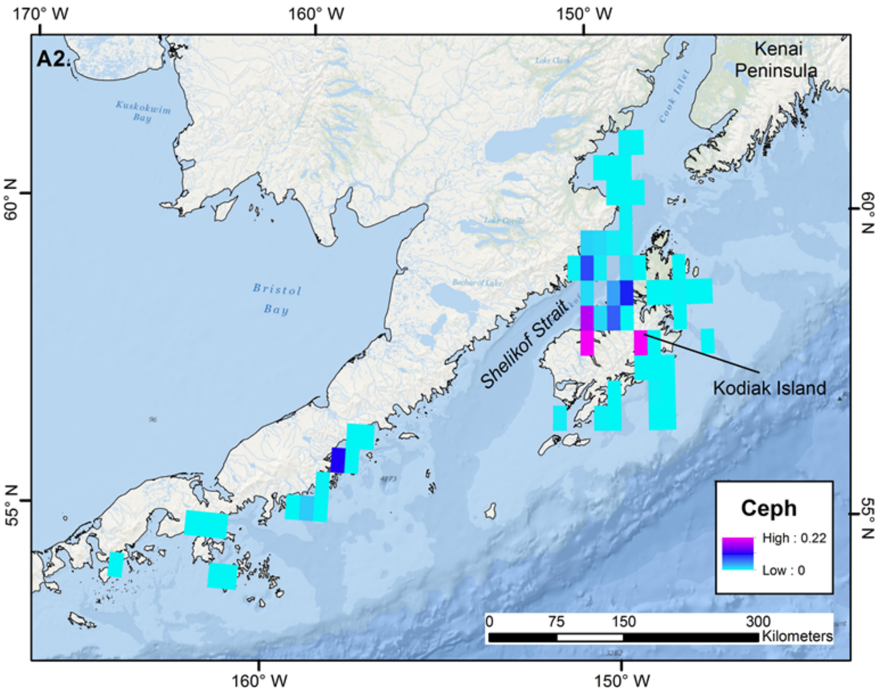
Assessment criteria for determination of the %W threshold used for inclusion of prey categories in PERMANOVA models calculated for each skate assemblage. Considerations included: sample size (*n*), number of prey categories, and the amount of variability explained by the model for four different threshold values (i.e., "cut off' values").

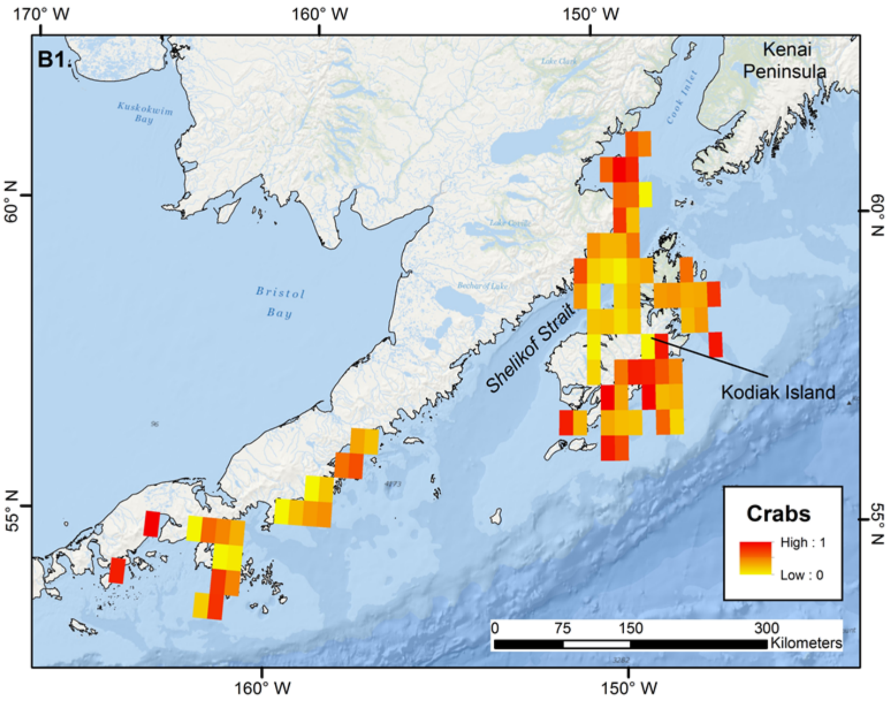
Region	Consideration	None	1%	2%	4%
CA	Sample Size	1254	1253	1253	1253
	Prey Categories	46	34	28	24
	Variability Explained	0.382	0.346	0.390	0.375
AK	Sample Size	1170	1170	1165	1163
	Prey Categories	58	43	38	28
	Variability Explained	0.726	0.775	0.756	0.731

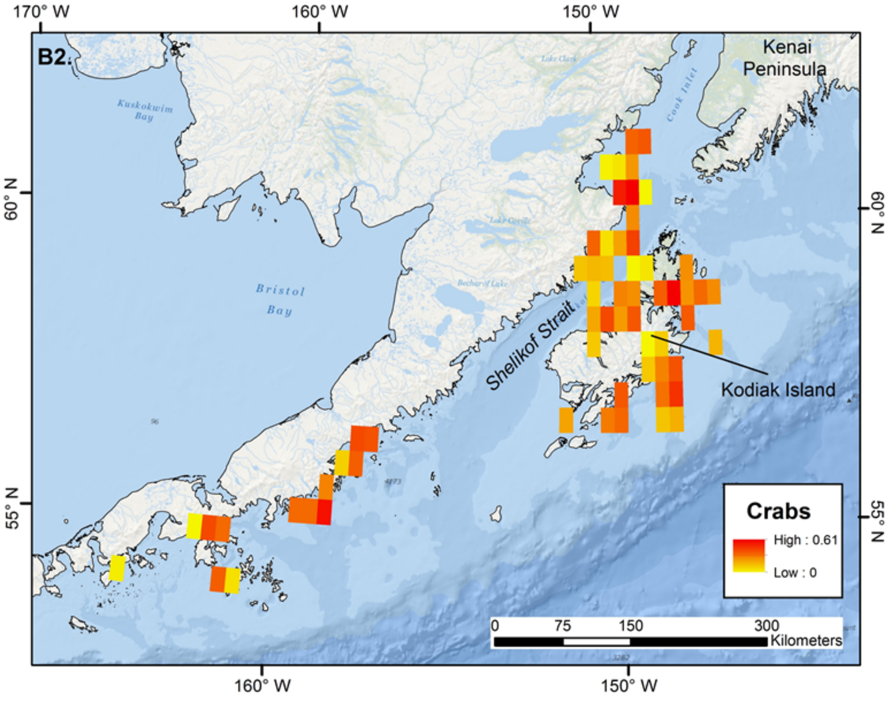
APPENDIX 2: Spatial Distribution of Prey Taxa for Alaskan Skates

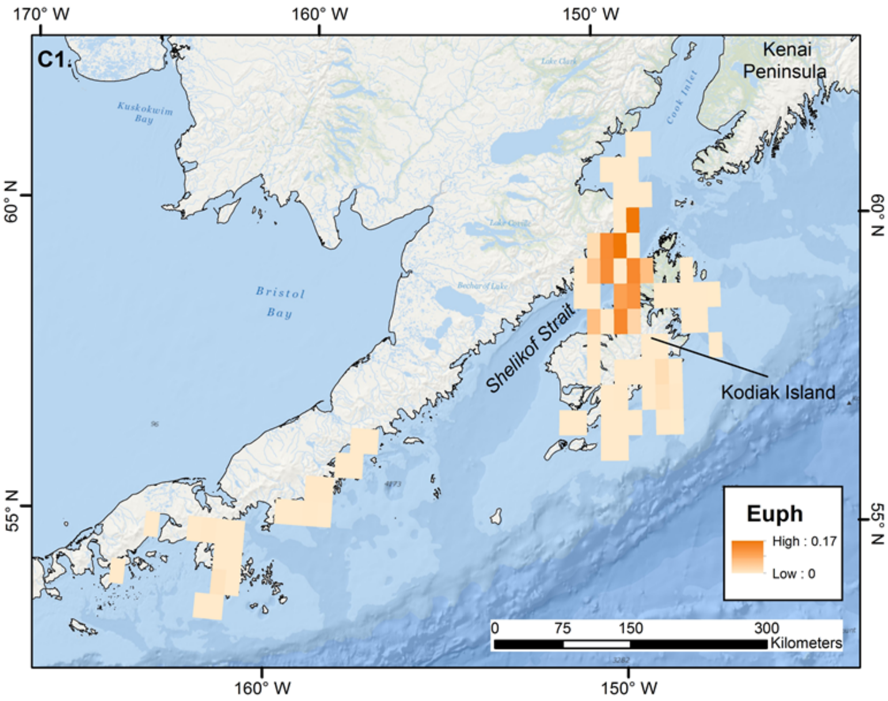
Spatial distribution of prey taxa in the diets of the western Gulf of Alaska skate assemblage. Data were gridded to 0.25º and grouped among the five dominant prey taxa (A = Cephalopods, B = Crabs, C = Euphausiids, D = Fishes, E = Shrimps). Maps display the mean (1) and SD (2) of the dietary proportion of each taxa among all the stomach samples collected per grid cell.

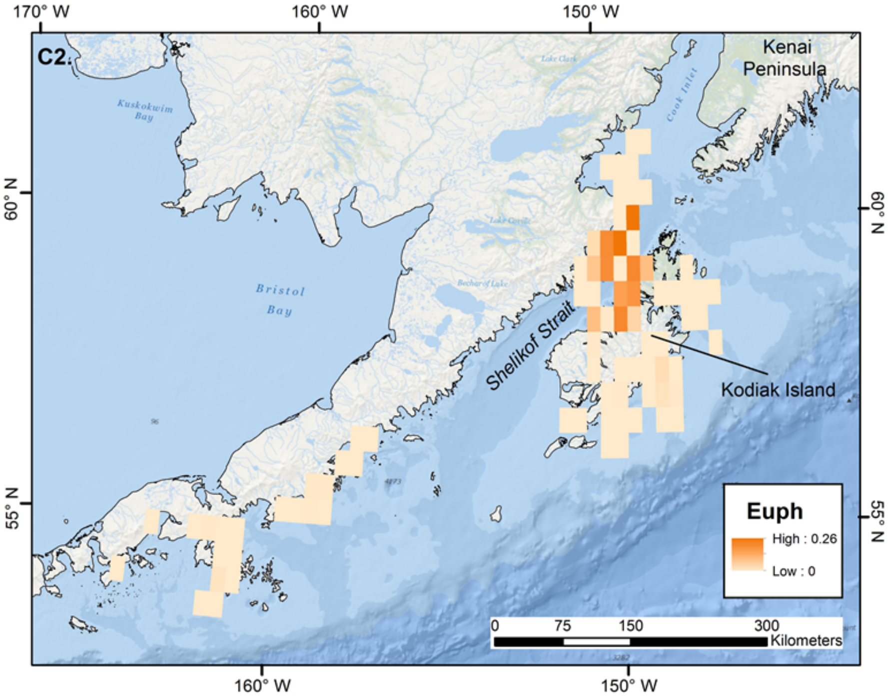


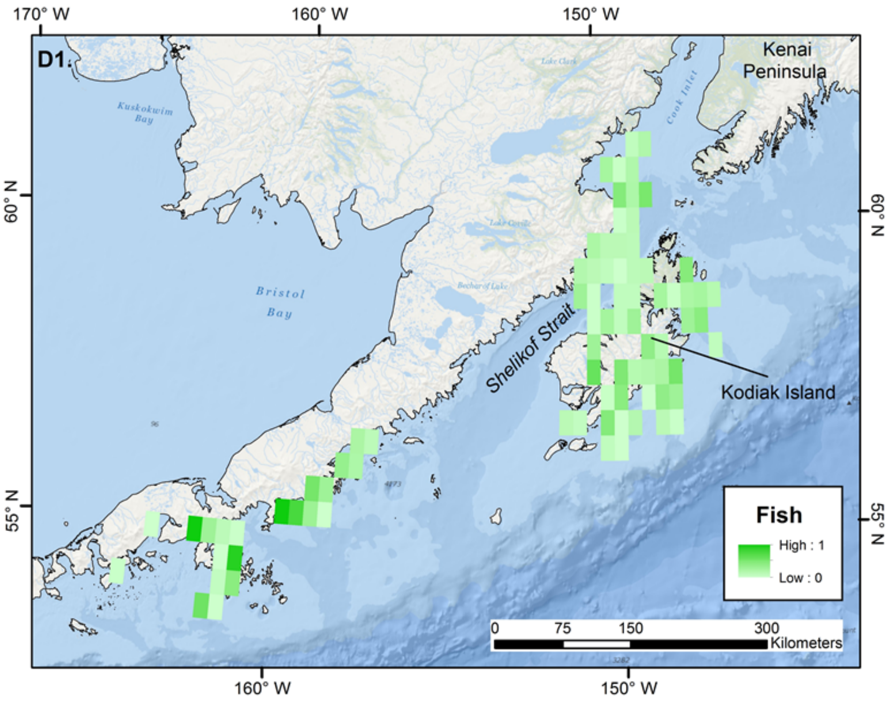

A2.
170° W
160° W
150° W
60° N
55° N
Kenai Peninsula
Cook Inlet
Kuskokwim Bay
Bristol Bay
Shelikof Strait
Kodiak Island
Ceph
High : 0.22
Low : 0
0
75
150
300
Kilometers

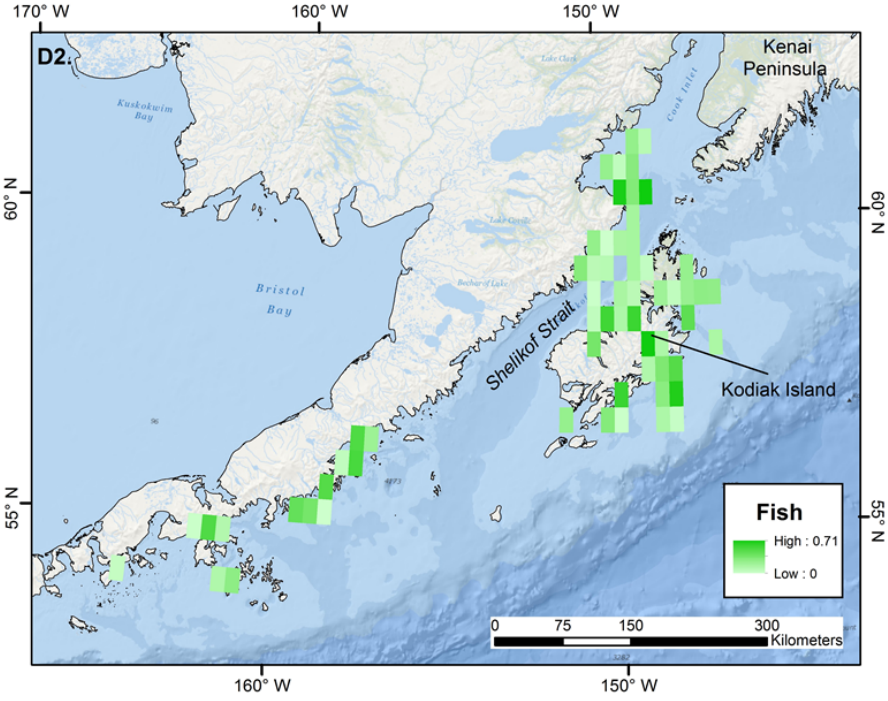

B1.
170° W
160° W
150° W
60° N
55° N
Kenai Peninsula
Cook Inlet
Lake Clark
Kuskokwim Bay
Lake Iliamna
Bristol Bay
Becharof Lake
Shelikof Strait
Kodiak Island
Crabs
High : 1
Low : 0
0
75
150
300
Kilometers

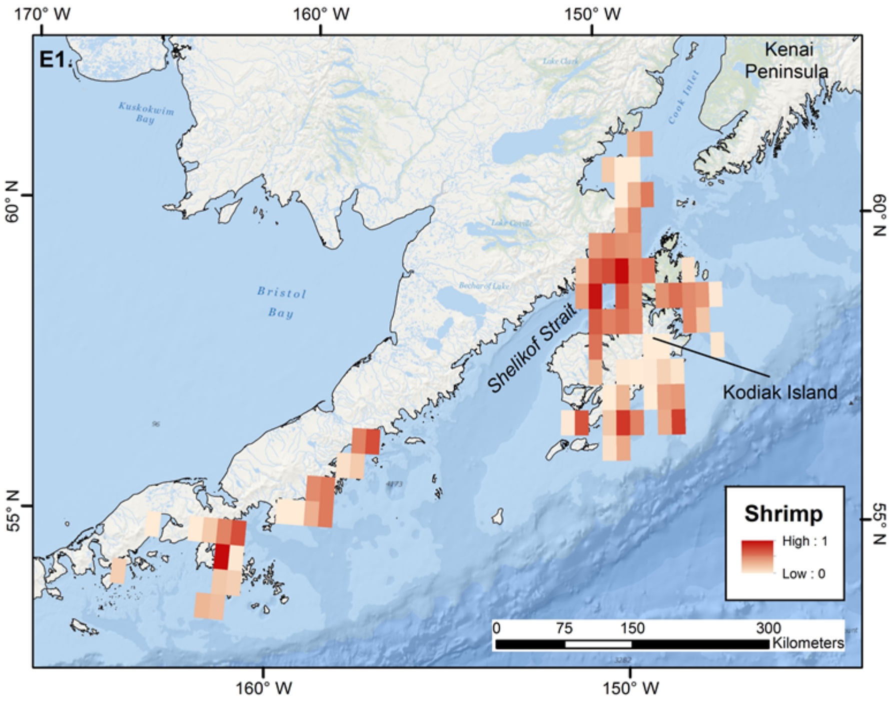

B2.
170° W
160° W
150° W
60° N
55° N
Kenai Peninsula
Cook Inlet
Lake Clark
Kuskokwim Bay
Lake Iliamna
Bristol Bay
Becharof Lake
Shelikof Strait
Kodiak Island
Crabs
High : 0.61
Low : 0
0
75
150
300
Kilometers

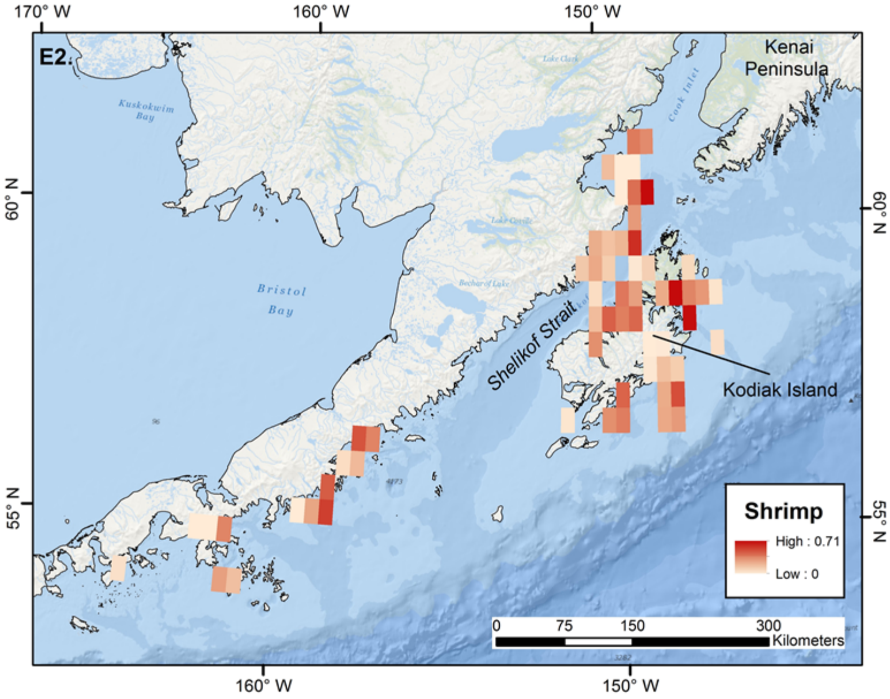

170° W
160° W
150° W
C1.
Kenai Peninsula
Kuskokwim Bay
Cook Inlet
Bristol Bay
Shelikof Strait
Kodiak Island
60° N
55° N
Euph
High : 0.17
Low : 0
0
75
150
300
Kilometers
160° W
150° W


170° W
160° W
150° W
C2.
Kenai Peninsula
Kuskokwim Bay
Cook Inlet
Bristol Bay
Shelikof Strait
Kodiak Island
60° N
55° N
Euph
High : 0.26
Low : 0
0
75
150
300
Kilometers
160° W
150° W


D1.
170° W
160° W
150° W
60° N
55° N
Kenai Peninsula
Kuskokwim Bay
Bristol Bay
Cook Inlet
Shelikof Strait
Kodiak Island
Fish
High : 1
Low : 0
0
75
150
300
Kilometers

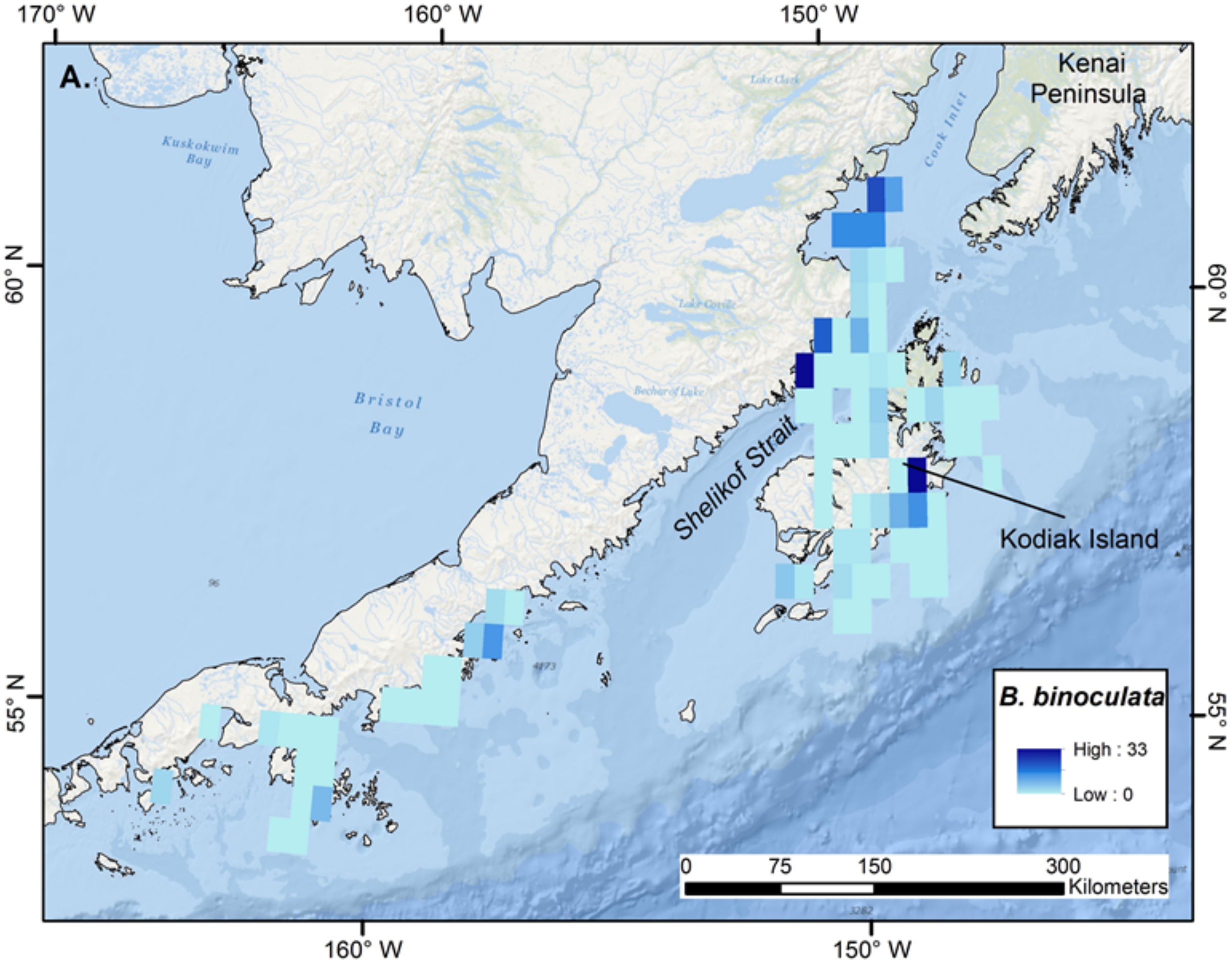

D2.
170° W
160° W
150° W
60° N
55° N
Kenai Peninsula
Kuskokwim Bay
Bristol Bay
Cook Inlet
Shelikof Strait
Kodiak Island
Fish
High : 0.71
Low : 0
0
75
150
300
Kilometers

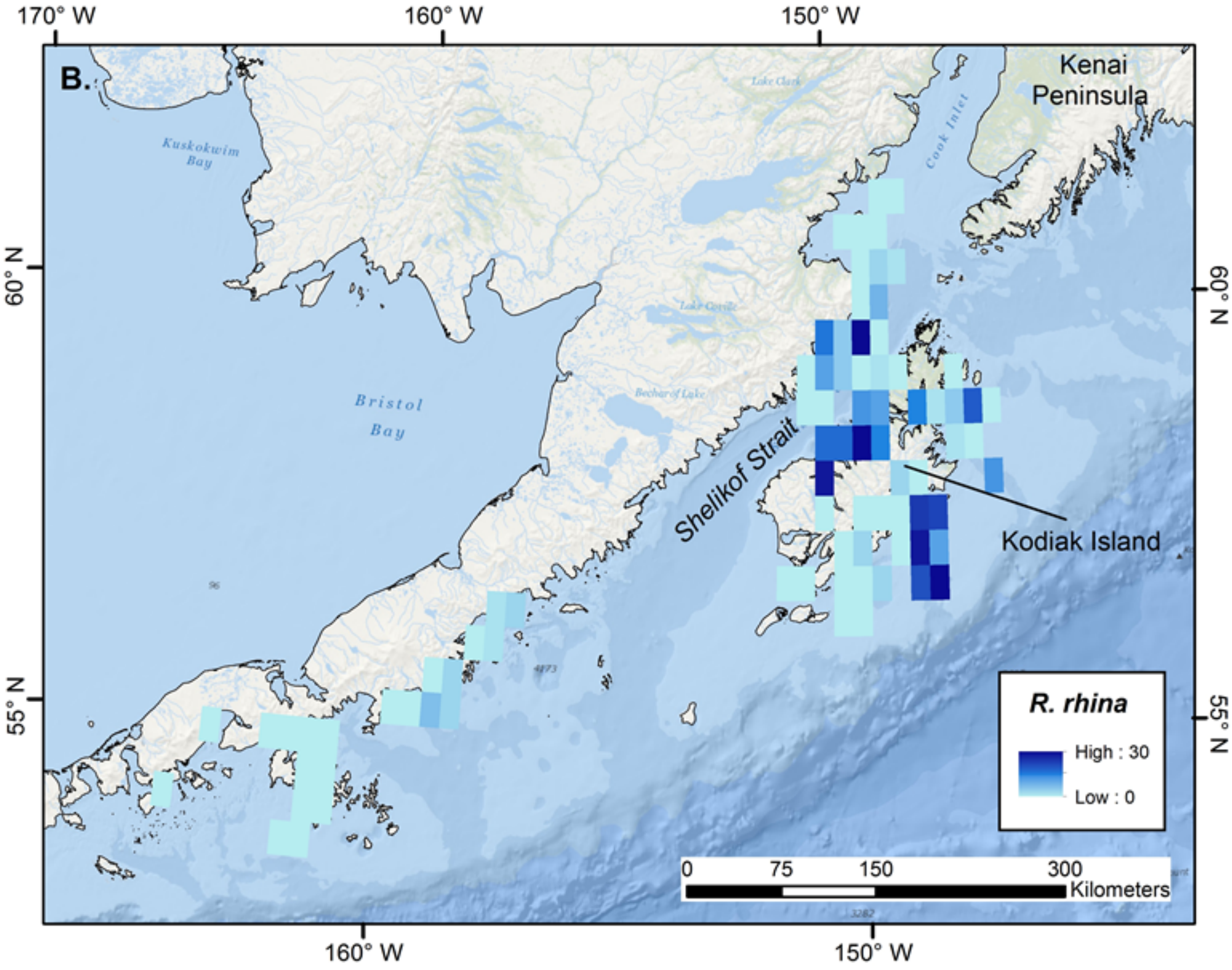

E1.
170° W
160° W
150° W
60° N
55° N
Kenai
Peninsula
Kuskokwim
Bay
Cook Inlet
Bristol
Bay
Shelikof Strait
Kodiak Island
Shrimp
High : 1
Low : 0
0
75
150
300
Kilometers

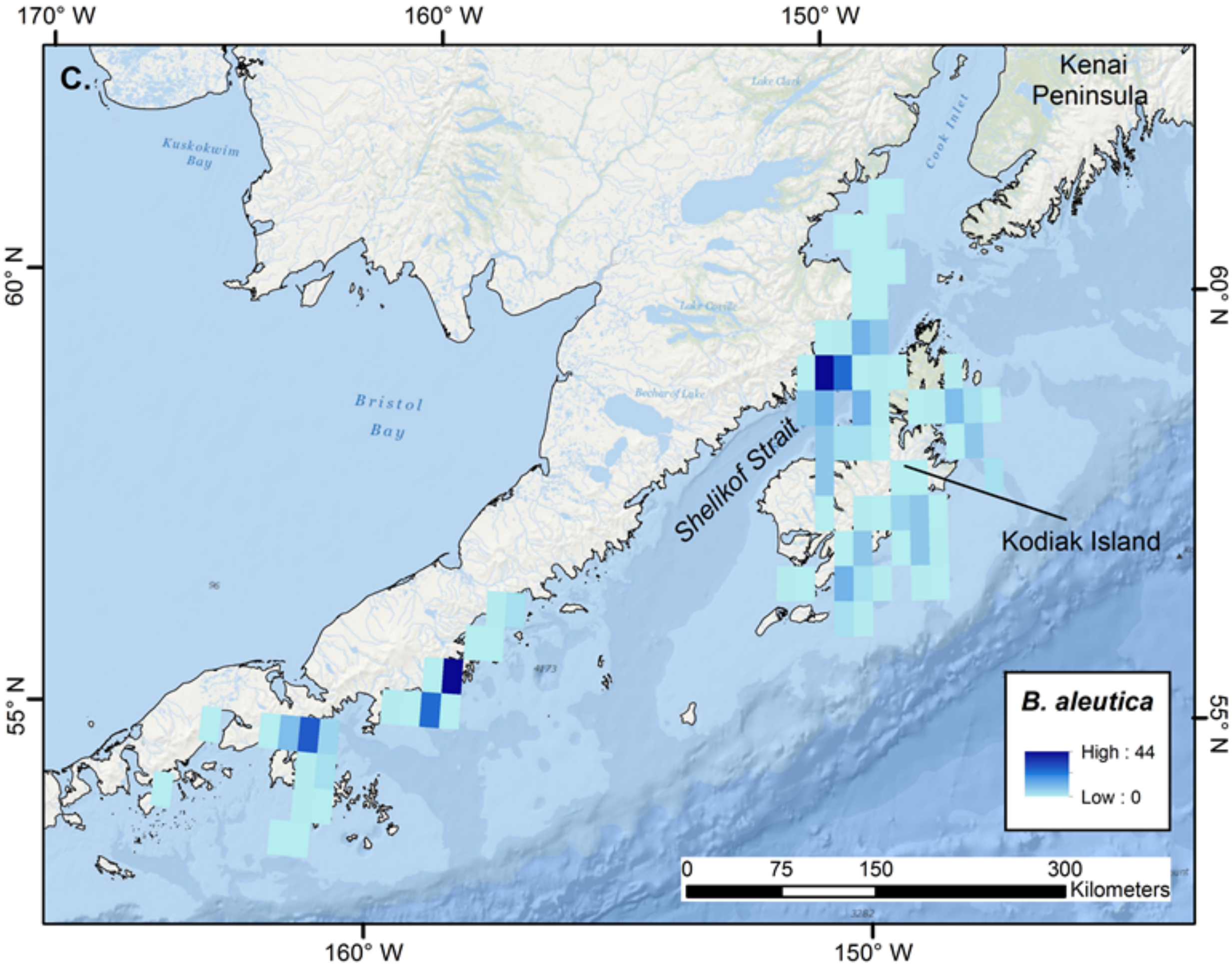

E2.
170° W
160° W
150° W
60° N
55° N
Kenai
Peninsula
Kuskokwim
Bay
Cook Inlet
Bristol
Bay
Shelikof Strait
Kodiak Island
Shrimp
High : 0.71
Low : 0
0
75
150
300
Kilometers

APPENDIX 3: Spatial Distribution of Alaskan Skates

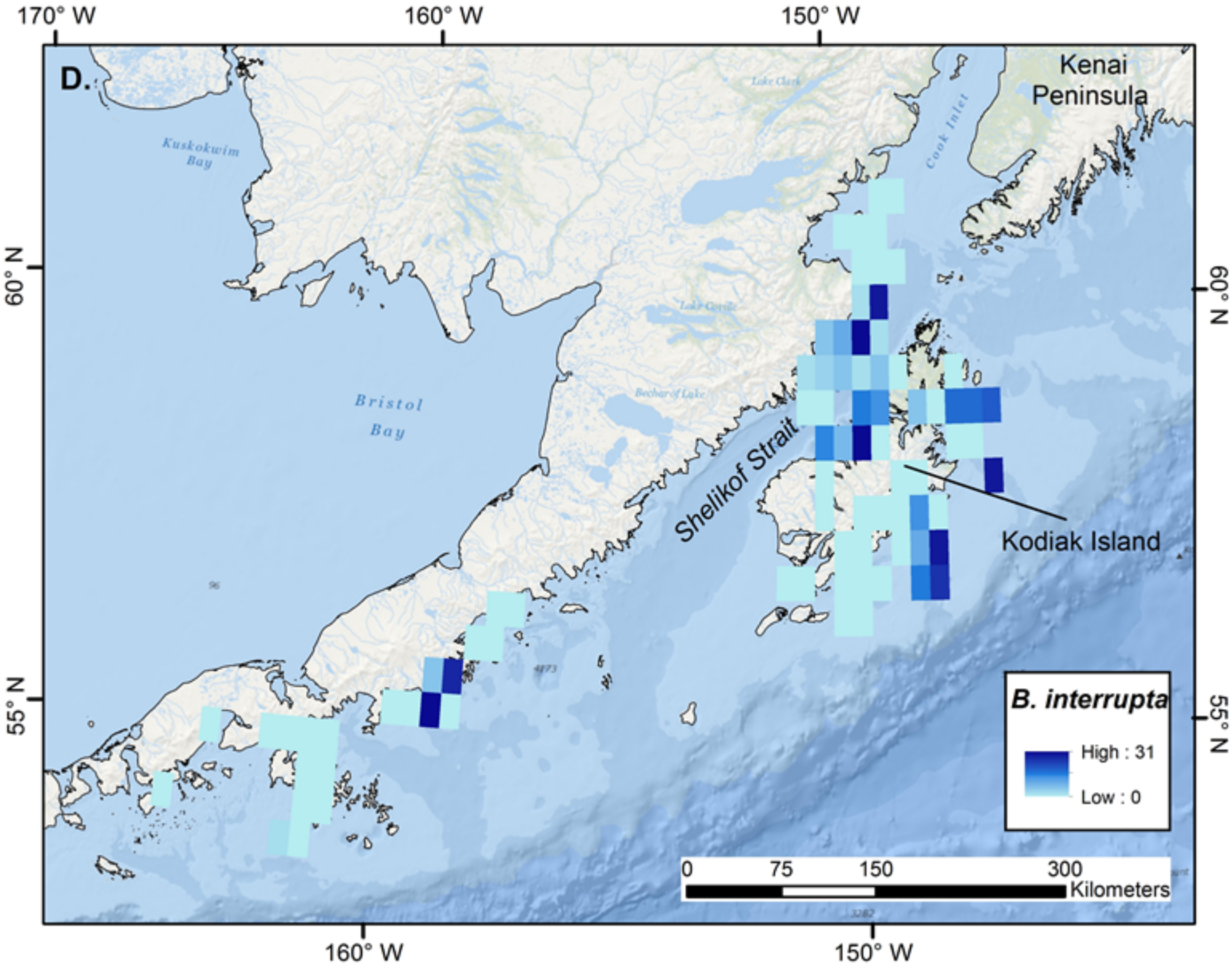
Spatial distribution of species that comprise the western Gulf of Alaska skate assemblage. Data were gridded to 0.25° and grouped among the five study species (A = *Beringraja binoculata*, B = *Raja rhina*, C = *Bathyraja aleutica*, D = *Bathyraja interrupta*, E = *Bathyraja parmifera*). Maps display the total number of stomach samples of each species per grid cell.




170° W
160° W
150° W
B.
Kuskokwim Bay
Bristol Bay
Lake Clark
Lake Iliamna
Becharof Lake
Cook Inlet
Kenai Peninsula
Shelikof Strait
Kodiak Island
60° N
55° N
R. rhina
High : 30
Low : 0
0
75
150
300
Kilometers
160° W
150° W



C.
170° W
160° W
150° W
60° N
55° N
Kenai Peninsula
Cook Inlet
Kuskokwim Bay
Lake Clark
Lake Iliamna
Becharof Lake
Bristol Bay
Shelikof Strait
Kodiak Island
B. aleutica
High : 44
Low : 0
0
75
150
300
Kilometers


D.
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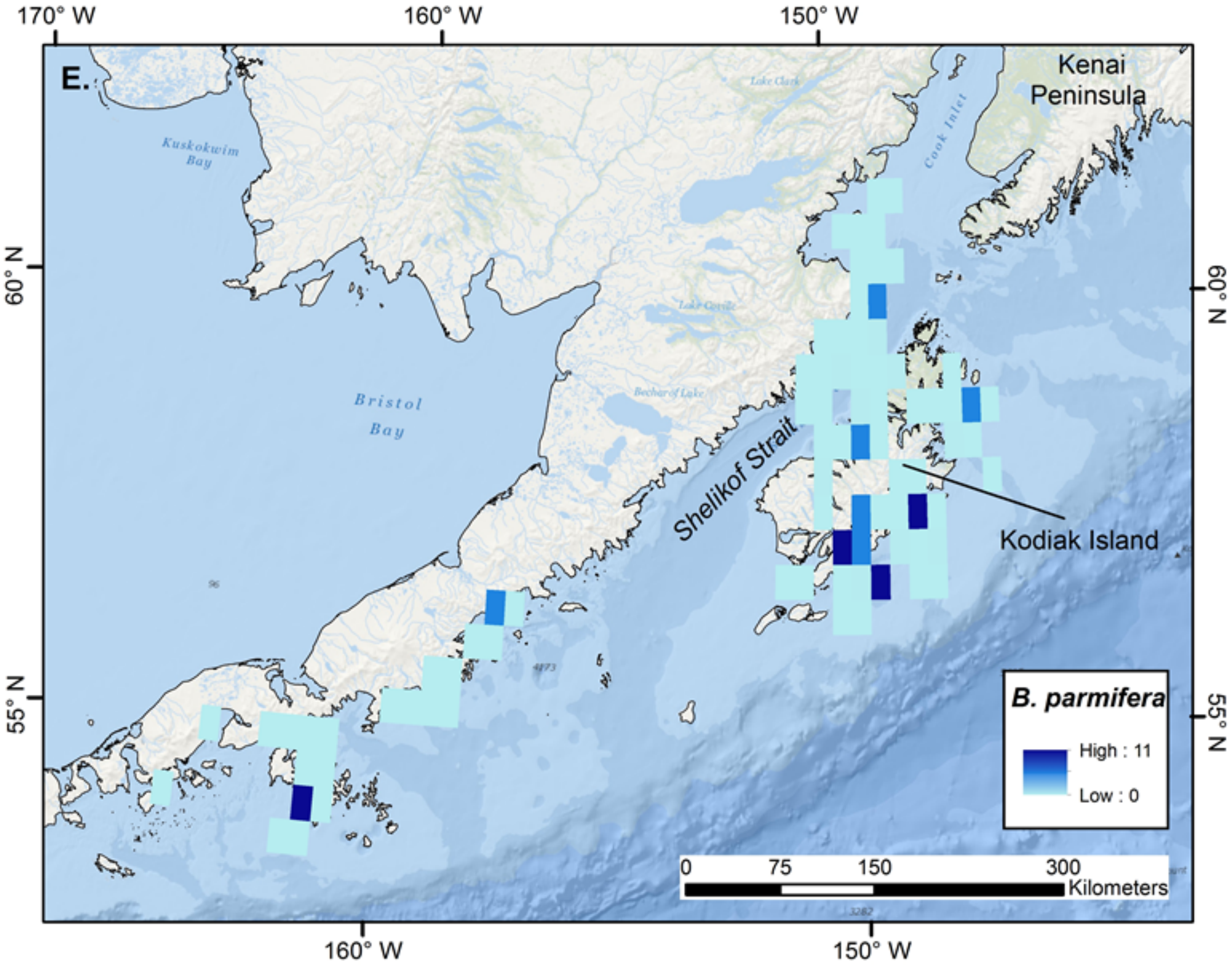
160° W
150° W
60° N
55° N
Kuskokwim Bay
Bristol Bay
Lake Clark
Lake Iliamna
Becharof Lake
Cook Inlet
Kenai Peninsula
Shelikof Strait
Kodiak Island
B. interrupta
High : 31
Low : 0
0
75
150
300
Kilometers


E.
170° W
160° W
150° W
60° N
55° N
Kenai Peninsula
Cook Inlet
Lake Clark
Kuskokwim Bay
Bristol Bay
Becharof Lake
Shelikof Strait
Kodiak Island
B. parmifera
High : 11
Low : 0
0
75
150
300
Kilometers

VITA

Joseph J. Bizzarro was born in Belleville, NJ on 1/24/1970 to Joseph B. and Bernadette M. Bizzarro. He relocated to the West Coast after college, and grew up to become a marine biologist.