# Prey switching and consumption by seabirds in the central California Current upwelling ecosystem: implications for forage fish management

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## ABSTRACT

Effective ecosystem-based fishery management involves assessment of foraging interactions among consumers, including upper level predators such as marine birds and humans. Of particular value is information on predator energetic and consumption demands and how they vary in response to the often volatile dynamics of forage populations, as well as the factors that affect forage availability and potential prey switching. We examined the prey requirements of common murre (*Uria aalge*), Brandt's cormorant (*Phalacrocorax penicillatus*), and rhinoceros auklet (*Cerorhinca monocerata*) in the central California Current over a 30-year period, 1986-2015. We developed a bioenergetics model that incorporates species-specific values for daily basic energy needs, diet composition, energy content of prey items and assimilation efficiency, and then projected results relative to stock size and levels of commercial take of several species. The most common forage species consumed were juvenile rockfish (*Sebastes* spp.), northern anchovy (*Engraulis mordax*), smelt (Osmeridae), and market squid (*Doryteuthis opalescens*). Total biomass of forage species consumed during the breeding season varied annually from 8,500 to >60,000 metric ton (*t*). Predator population size and diet composition had the greatest influence on overall prey consumption. The most numerous forage species consumed in a given year was related to abundance estimates of forage species derived from an independent ecosystem assessment survey within the central place foraging range of breeding avian predators. The energy density of dominant prey consumed annually affected predator energy expenditure during chick rearing and whether prey switching was required. Increased forage species take by predators, as revealed by seabirds, may be adding consumptive pressure to key forage fish populations, regardless of the potential additional impacts of commercial fisheries. Improving estimates of consumption by predators and fisheries will promote more effective management from an ecosystem perspective.

***Key words***: bioenergetics, Brandt's cormorant, California Current, common murre, ecosystem-based fishery management, forage fish, Gulf of the Farallones, northern anchovy, rhinoceros auklet, rockfish

# INTRODUCTION

Marine ecosystems are increasingly under pressure from climate change and direct human impacts such as fisheries and pollution (Halpern et al., 2008; Paleczny et al., 2015). Both climate change and human impacts alter the structure and dynamics of a given food web, with often dramatic consequences for many marine species, including commercially important fish stocks and dependent species (Frank et al., 2005; Mullon et al., 2005; Anderson et al., 2008; Baum and Worm, 2009; Estes et al., 2011). To address these concerns, fisheries managers are increasingly shifting beyond the estimation of sustainable yields of target species from the single population perspective (Pikitch et al., 2004; Hilborn and Ovando, 2014) toward an ecosystem-based perspective (e.g., Dayton, 1989, Hilborn, 2011). Effective ecosystem-based fisheries management (EBFM) should be centered on the assessment of interactions between fisheries and other top consumers, considering the needs of both. EBFM has arisen to ensure harvest of commercially valuable species, including forage species, in a way that does not seriously affect food web structure and dependent predators, such as fishes, marine mammals and seabirds (Holt and Talbot, 1978; Pikitch et al., 2004; Kaplan et al., 2013). EBFM is particularly important in highly variable ecosystems such as upwelling-driven eastern boundary currents, given the added elements of uncertainty (e.g., Glantz and Thompson, 1981; Checkley and Barth, 2009). However, amassing the necessary information, including dynamic ecosystem models, to implement EBFM requires heightened effort and time relative to single species approaches, and its employment has therefore been gradual (e.g., Collie et al., 2016, PFMC 2013, 2015).

Upper trophic level predators, which include seabirds, consume a significant portion of the biomass of the food web functional group known as micronekton (i.e., free-swimming organisms <200mm in length) (Brooke, 2004; Hunt et al., 2005; Roth et al., 2008). Some seabird populations have been found to consume 5-30% of micronekton biomass in coastal marine ecosystems (reviewed by Montevecchi, 1993) and seabird foraging can have measureable top-down impacts on food web dynamics (e.g., Toge et al., 2011; Sergio et al., 2014; Springer and van Vliet, 2014). As a result, seabirds and other mesopredators may compete directly with commercial fisheries for many of the same species (e.g., Bertrand et al., 2012). Indeed, owing to significant overlap in resource demands (Furness, 1990; Dayton et al., 2002; Jahncke et al., 2004), seabirds and commercial fisheries often consume similar quantities of prey (Brown and Nettleship, 1984; Brooke, 2004), often with broad overlap in the size and age classes taken (Tasker et al., 2000; Pichegru et al., 2012; Velarde et al., 2013; Shirley et al., 2017; Hilborn et al. 2017).

A well-known and important life history aspect of seabirds in dynamic ecosystems is their ability to switch among different forage species, upon the availability of the one currently favored becoming reduced or spatially altered compared to others (Ainley et al., 1990; Crawford et al., 1995; Velarde et al., 2013). During the breeding season, seabirds are central place foragers, commuting from colony to ocean, with foraging trip length and duration being dictated by reproductive needs (i.e., nest guarding, chick provisioning) and spatial aspects of prey availability. This foraging behavior constrains access to prey, highlighting the capacity to switch prey or foraging area and select the most energy dense forage species among those that are both abundant and within reach (Pichegru et al., 2012; Weller et al., 2014; Wells et al. 2017; Ainley et al. 2018). Seabird prey switching behavior may be impacted by either natural factors (e.g., forage fish availability as affected by oceanographic processes) or through competition with other mesopredators, including fisheries (Ainley et al., 2006; Pichegru et al., 2007; Gremillet et al., 2008; Ainley and Hyrenbach, 2010; Springer and van Vliet, 2014; Ainley et al., 2015b). In the California Current Ecosystem (hereafter California Current), commercial fisheries target important forage species such as market squid (*Doryteuthis opalescens*), northern anchovy (*Engraulis mordax*), and Pacific sardine (*Sardinops sagax*), as well as adult populations of rockfish (*Sebastes* spp.) and salmonids whose early life history stages are key forage for mesopredators. Consequently, these fisheries likely compete with seabirds at some level, as they effectively alter forage availability (similar to the Benguela and Peru current upwelling systems; Bertrand et al., 2012; Pichegru et al., 2012; Crawford et al., 2017; Shirley et al., 2017). Although many seabird species can compensate for some level of reduction in forage abundance by altering time budgets, such as through a reduction in “loafing time” (Piatt et al., 2007), central place foragers may experience reduced reproductive output (due to the inability to sufficiently provision or guard chicks) and reduced juvenile or adult survival (Ainley and

Boekelheide, 1990; Crawford et al., 2006; Field et al., 2010; Weller et al., 2014). Even when prey densities are not regionally reduced to critically low levels, central place foragers typically increase effort and energy expenditure searching for high quality prey aggregations if they are more patchily distributed or located farther from breeding areas than "normal" (Santora et al., 2011; Bertrand et al., 2012; Ford et al., 2004). Under unusual circumstances, some species may also change breeding location (Crawford et al., 2006; Ainley et al. 2018). Given the sensitivity of seabirds to forage availability, their demography, diet, and distribution, along with behavior and time-activity budgets, can become exceptional tools for monitoring marine environmental conditions and variability of prey populations (Cairns et al., 1987, 1988; Furness, 1990; Ainley et al., 1993; Montevecchi, 1993; Davoren and Montevecchi, 2003; Mills et al., 2007; Thayer et al., 2008) and for developing ecosystem-based fisheries management (Einoder, 2009; Ainley et al. 2018).

Combining diet composition and prey energetic value with bioenergetics models allows estimation of seabirds' daily energy needs, from which it is possible to derive the amount of prey required to meet those needs and identify thresholds that may lead to prey switching (Wiens and Scott, 1975; Furness, 1978; Wilson et al., 2004; Roth et al., 2008; Ridgway, 2010). However, to inform fisheries management, seabird population sizes, total consumption of key forage species, availability of those species, and energetic value of the overall diet also need to be considered. To draw inferences on when seabirds may have to switch prey, consumption time series should be compared with fishery-independent metrics of forage fish availability, fishery extraction patterns, and predator foraging effort to provide context on the demand by predators and fisheries alike.

Herein, we use a bioenergetics modelling approach to examine prey requirements of three fish-consuming, central place foraging seabirds nesting in the Gulf of the Farallones, located in the central California Current, during 1986-2015: common murre (*Uria aalge*), Brandt's cormorant (*Phalacrocorax penicillatus*), and rhinoceros auklet (*Cerorhinca monocerata*). The murre and cormorant are among the most abundant locally breeding species in the system (Carter et al., 1992; Ainley and Hyrenbach, 2010), and long-term datasets on breeding population sizes and the diet fed to chicks exist for all three species (e.g., Carter et al., 2001; Capitolo et al., 2014; Warzybok et al., 2015; Elliott et al., 2016; Carle et al., 2016). Together these species potentially account for a major percentage of total prey consumption among mesopredators, or at the least for seabirds, of this region (Briggs and Chu, 1987; Ainley et al., 2014; 2015a) and affect prevalence and survival of certain prey species, such as juvenile salmon (Wells et al., 2017). To inform ecosystem-based fisheries management, our primary objectives are to: (a) quantify temporal changes in seabird species population size and consumption of key forage species by combining energetic metrics from different breeding colonies; (b) relate seabird consumption patterns to spatial and abundance aspects of forage species availability derived from an ecosystem assessment trawl survey; and (c) compare seabird consumption to removals by commercial fisheries. Furthermore, to investigate seabird prey switching behavior, we assess how energetic demand, foraging trip duration (i.e. effort) and prey quality may combine to determine whether the most abundant of the study species, the common murre, feeds predominantly on juvenile rockfish or anchovy. Additionally, we explore whether this switch may impact their population dynamics, as apparently has been the case for the Brandt’s cormorant (Ainley et al., 2018).

## METHODS

### ***Study area***

This study was conducted in the Gulf of the Farallones off central California from Bodega Bay (38.31° N, 123.06° W) to Año Nuevo Island (37.11° N, 122.33° W) and out to the continental shelf break, including Farallon Ridge, and also included Monterey Bay waters (Fig. 1), during the summers of 1986-2015. This region contains important seabird breeding colonies offshore at the South and North Farallon islands (SFI and NFI) and along the mainland coast at Año Nuevo Island (ANI), Point Reyes, and several other rocks and headlands (Carter et al., 1992; 2001; Capitolo et al., 2014), as well as the foraging areas for these colonies. Field stations at SFI and ANI have enabled long-term study of population size, reproductive success, and diet of our three focal species: common murre, Brandt’s cormorant, and rhinoceros auklet. The murre and the cormorant often are intermixed at breeding colonies throughout the Study Area, except at ANI, where the murre does not breed. Brandt’s cormorant colonies are the most widely distributed in the study area, while the auklet breeds only at SFI and ANI. SFI and NFI, about 42 km west of San Francisco, CA, host the largest seabird colonies, together currently totaling more than 500,000 birds of 12 species (>80% of the regional population), with the three focal species contributing ~380,000 birds. The remaining breeding sites, including ANI, are smaller colonies situated within a kilometer of shore or on headlands, referred to as mainland colonies (e.g., Capitolo et al., 2014).

### ***Diet composition***

Diet composition on SFI and ANI was determined through observations of prey delivered to dependent offspring, collection of fresh prey from captured birds, or collection of regurgitated pellets and subsequent identification of prey based on hard parts. Data to assess diet composition were collected through a variety of species-specific methods. For common murres, which provision chicks by carrying single prey items lengthwise in their bills, data were only collected at SFI, where prey was visually identified by trained observers, using binoculars, during standardized daily feeding watches throughout the peak chick rearing period, late May to early July, 1986-2015 (Ainley and Boekelheide, 1990; Warzybok et al., 2015). During observations, all prey items were identified to the lowest possible taxon based on color, body shape, tail shape, and shape and position of fins (Miller and Lea, 1972; Follett and Ainley, 1975). When not possible to identify prey items to species level, species-group categories were used, i.e., juvenile rockfishes, northern anchovy/Pacific sardine, smelt (Osmeridae spp.), market squid, salmon (*Onchoronchys* spp.), flatfishes including sanddabs (Pleuronectidae spp. and Bothidae spp.), sandlance (*Ammodytes hexapterus*), lingcod (*Ophiodon elongatus*), sculpins (Cottidae spp.), Pacific saury (*Cololabis saira*), and “other” (including unidentified prey). In addition, we visually estimated the length of each prey item relative to the gape length of the adult (Ainley and Boekelheide, 1990; Cairns et al., 1990; Roth et al., 2008) and recorded these in increments of 0.1 gape lengths. The latter were converted to an estimate of standard length in millimeters (Ainley et al., 1990; 1996).

For rhinoceros auklets, fish were collected from birds captured in mist nets as they returned to feed chicks in the evening at both SFI and ANI. Diet sampling was conducted throughout the peak chick rearing period, from late June through early August. Auklet chick-diet data for SFI have been collected annually since 1987 and for ANI since 1993. Prey items were identified to individual species using various keys. All prey species were measured to determine standard length (fishes) or mantle length (squid) and weighed to the nearest 0.1 g (Thayer and Sydeman, 2007; Carle et al., 2015).

Brandt's cormorant diet was determined by collecting regurgitated pellets of indigestible material and identifying prey items based on otoliths and other hard parts (Ainley et al., 1981; Ainley and Boekelheide, 1990; Gagliardi et al., 2007; Elliott et al., 2016). Cormorants produce pellets daily (Jordán, 1959). We examined contents of each pellet under a dissecting microscope and identified species to the lowest taxonomic level possible (Harvey et al., 2000; Elliott et al., 2016). Pellets were collected at the end of the breeding season to reduce disturbance, and reflected adult and chick diet from May - September. Diet composition was summarized as the percent occurrence of each prey item (or group) observed each year. The diet data considered for SFI were those for 1994, 1999, and 2003-2015; ANI data were available for 2000-2015.

Prey mass was either measured directly (auklets) or estimated (murres, cormorants) based on mass-length regression equations derived from fish collected at SFI and ANI (Table 1) or from regressions developed from otolith size (see below). Fish mass (in grams) was determined by weighing the fresh sample on an electronic balance with an accuracy of 0.1 g. Fish standard length (in millimeters) was determined by measuring the specimen from the tip of the snout to the posterior edge of the hypural plate or the posterior end of the vertebral column (in fish lacking hypural plates). We then performed a linear regression analysis on log-log transformed data to determine the mass to length relationship, a method used commonly in fisheries research (Harvey et al. 2000; Love et al., 2002). For all prey species identified by hard parts, we derived an estimated mass for each prey item using previously published mass-length regression equations for whole prey items or derived these equations from otoliths extracted from collected fishes (e.g. Spear, 1993; Harvey et al., 2000; Elliott et al., 2016).

For the purposes of our models, and due to a lack of sufficient dietary information available for adults (but see Ainley et al. 1996, Carle et al. 2015), we assumed that diet proportions were equivalent for adults and chicks. Acknowledging those studies, we know that during the breeding season this is broadly true (Ainley et al. 2015a). For murres, Ainley et al. (1996) demonstrated that adult and chick diet largely overlap. However, adults may consume some prey that are not typically fed to chicks, such as small prey (e.g. krill) or fishes of a shape difficult for small chicks to swallow (e.g., deep-bodied surfperch (Embiotocidae spp.), butterfish (*Peprilus medius*), midshipman (*Porichthys notatus*) and large sanddabs (Ainley et al., 1996; Wilson et al., 2004)). We could not make a similar assumption that diet was invariant across seasons, because, while anchovy and juvenile rockfish (the two most common forage species) continue to be important components of the diet during the winter, other species may have increased importance in the diet (Ainley et al. 1996). Therefore, we have constrained our consumption models to the breeding season when the most comprehensive diet data are available, i.e. March-August (see below).

### ***Seabird population estimates***

For common murres, breeding population estimates were determined from annual aerial photographic surveys (Carter et al., 2001; Capitolo et al., 2014; U.S. Fish and Wildlife Service [USFWS] and U.C. Santa Cruz [UCSC] unpublished data). Colonies were photographed during the peak incubation period, typically early June, from a fixed-wing aircraft. All murres in attendance were counted using many images, with overlapping areas delineated to prevent double-counting. We then applied a year specific “k-correction factor” to the raw counts to adjust for mates not present at the time of the census as well as for the presence of non-breeding birds in the colony (Harris et al., 1983; Carter et al., 1992). Unfortunately, complete data from aerial surveys were not available for all years, especially for NFI and SFI after 2007. For SFI after 2007, population estimates for missing years were determined from repeated counts of representative index plots among several sub-colonies. The percent change in the seasonal mean index plot counts was then applied to complete aerial colony counts from previous years to estimate the overall population in that season (Warzybok et al., 2015). For NFI and mainland colonies, missing population data was estimated based on the mean relative contribution the uncounted area made to the regional population among years with complete data. During the time period considered, the SFI murre population contributed, on average, 50% (SD ± 3.6%) of the total Gulf population, while NFI contributed 27% (SD ± 2.4%) and mainland colonies 23% (SD ± 4.4%). Therefore, if NFI or mainland total counts were not available in a given year, we estimated the counts by applying these averaged contributions. Estimated counts were derived for one or more segments of the population (SFI, NFI or mainland colonies) for 10 of the 30 years (see Appendix II).

For Brandt's cormorants, populations were determined by counting the number of nests from aerial photographs or during ground-based surveys (SFI only for 2008-2015), and multiplying nest totals by two to account for both mates (Capitolo et al., 2014; USFWS, UCSC, Oikonos unpubl. data). It should be noted that population estimates from SFI ground-based counts are likely minimum values and may underestimate the total number of breeding birds when compared to aerial surveys (Capitolo et al. 2014). As with murres, aerial counts were not available for all colonies in all years and missing data were estimated by applying the mean contribution of the uncounted area to the overall population. During the time period considered, the SFI cormorant population averaged 73% (SD ± 4.6%) of the total regional population, while mainland colonies (including ANI) contributed 26% SD (± 4.5%) and NFI was a minor colony representing only 0.5% (SD ± 0.3%) of the regional population. Estimated counts were derived for NFI during 9 years (fewer than 100 birds per year) and for the mainland population during 2 years, but those years did not have diet data and were not used to estimate prey consumption (see Appendix II).

For rhinoceros auklets, the ANI population was determined by multiplying the total count of viable burrows on the island by the annual occupancy rate of monitored sample burrows, and adding that number to the number of known pairs in artificial nest boxes. On SFI, the auklet population was estimated by counting representative index plots in suitable habitat around the island. As on ANI, the occupancy rate was determined for burrows and crevices within these plots and for all natural and artificial nest sites monitored for reproductive success. The percent change in the seasonal mean index plot counts was then applied to the most recent complete colony burrow count to estimate overall population in that season (Warzybok and Bradley, 2009).

The non-breeding portions of the populations within the study area were determined from previously published modeling exercises (Nur and Sydeman, 1999a, b; Lee et al., 2008; Roth et al., 2008). The number of chicks produced was determined by multiplying the number of breeding pairs by the year-specific reproductive success determined from study plots on SFI and ANI, depending on species. Reproductive success was defined as the number of chicks fledged per breeding pair (Ainley and Boekelheide, 1990).

### ***Metabolic rate, assimilation efficiency and prey energy density***

Estimates of Daily Field Metabolic Rate for each species were obtained from the literature and is expressed as kilojoules of energy expended per day (kJ/d). For murres, metabolic rate was directly measured using respirometry (Cairns et al., 1987; Birt-Friesen et al., 1989), while for cormorants and auklets it was derived using allometric equations developed in accord with known relationships (Nagy et al., 1999; Ellis and Gabrielson, 2002). Assigned values were: murres 1530 kJ/d (Cairns et al., 1990; Roth et al., 2008), Brandt's cormorants 1883 kJ/d (Ancel et al., 2000) and rhinoceros auklets 1021 kJ/d (Ellis and Gabrielson, 2002). Energetic requirements vary with age, breeding status and season (Ellis and Gabrielsen, 2002), i.e., estimated energy intake for dependent chicks are 10-20% of adult energy requirements (Croll, 1990; Gabrielsen, 1996; Roth et al., 2008) and adults have an approximately 10% greater energy requirement when foraging for offspring due to the high energetic cost of flight (Brit-Friesen et al., 1989; Elliott et al., 2014; Collins et al., 2016). Therefore, populations were divided into three distinct segments based on these general energy requirements: 1) breeding adults during the breeding season, 2) non-breeding adults during the breeding season (90% of breeding energy requirement), and 3) dependent chicks (10%). For this study, the breeding season is defined as the period during which adults are tied to the colony for the purposes of territory acquisition, nest building, incubation, and chick rearing, and are consequently central place foragers. For the three species studied, this corresponds to the period of March through August, equal to 184 d for the consumption model (see Roth et al. 2008). Seasonal daily energy requirements were then assigned to each population segment and the prey required to meet these requirements was estimated on a daily basis.

Empirical estimates of assimilation efficiency (% of energy content of prey that is metabolized) were available in the literature for common murres (0.7839; Hilton et al., 2000); for Brandt's cormorants and rhinoceros auklets a consistent value of 0.8 was used (as per Ellis and Gabrielsen, 2002). Energy densities of prey (kJ/g) were determined from published sources (Table 1). Whenever possible, species-specific values were taken from the literature. Otherwise average values were of all prey for which the energy density was known (Roth et al., 2008; Spear, 1993).

***Bioenergetics model***

The seabird bioenergetics model was constructed separately for each species using year-specific parameters for diet composition and population size. Biomass consumed was calculated separately for each population segment (breeding adults, non-breeding adults during the breeding season, and chicks) and then summed to estimate total prey consumed by each species per year. Total annual biomass of prey consumed to meet daily energy requirement was determined by equation 1:

$$Biomass\ consumed\ (g) = \sum \frac{FMR \times Diet\ Composition}{E.D. \times A.E.} \times Days \times Population\ Size$$

where FMR is field metabolic rate (kJ/day) for individual seabird species; Diet Composition is the annual mean proportion by number of forage species in the diet, E.D. is the energy density value for each prey taxon (kJ/g), A.E. is assimilation efficiency, Population Size is annual population size (number of individuals) and Days is number of days in the breeding period. Biomass consumed was ultimately scaled up to metric tons (*t; also known as tonne*) where one *t* = $10^3$ kg. For Brandt's cormorants and rhinoceros auklets, we calculated separate models for Farallones and mainland colonies to reflect differences in diet composition at the two colonies. We assumed that dietary data from the South Farallon Islands (SFI) was representative of the North Farallon Islands (NFI) colony, while diet data from Año Nuevo Island (ANI) was representative of all mainland colonies (see Ainley et al., 2018). Dietary data for murres from mainland colonies were not available in most years. However, data available for

Devil's Slide Rock from 2006 and 2007 indicated that chick diet at that mainland colony was very similar to that of SFI murres and that foraging ranges overlapped (Eigner, 2009). Therefore, for murres, diet composition from SFI was assumed to be representative of the region throughout the study period and was used for all modeling in this study.

### ***Common murre feeding rate and foraging trip duration***

Feeding rate and foraging trip duration of common murres provisioning dependent chicks were examined as indicators of foraging effort. Feeding rate was calculated as the mean number of feedings per chick per day observed during all-day watches at study plots within the Farallon colony. Foraging trip duration was calculated as the elapsed time, in minutes, between feeding observations during standardized diet watches (see Diet Composition above). Each foraging trip was associated with the prey item delivered to the chicks upon return to the island. Average trip duration was then calculated annually for the two most common prey species consumed, northern anchovy and juvenile (primarily young-of-the-year)) rockfishes. Foraging trip data was not available for auklets or cormorants.

### ***Availability of forage species***

We compared seabird consumption estimates with independent data on prey availability derived from the NOAA-NMFS Rockfish Recruitment and Ecosystem Assessment Survey. Since 1983, the NMFS has conducted an annual vessel survey during late April to mid-June to assess ocean conditions and the abundance and distribution of micronekton off California. The survey samples a variety of forage species utilized by mid and upper trophic level predators, including pelagic juvenile rockfishes and groundfish species, adults and juvenile northern anchovy, juvenile market squid, and adult mesopelagic fishes (Ralston et al., 2015; Sakuma et al., 2016). The survey uses a modified mid-water Cobb trawl (target depth of 30 m, sampled at night) to enumerate forage species, as Catch-per-unit-effort (CPUE), throughout California waters. Herein we focus on the region extending from Bodega Bay through Monterey Bay (Fig. 1), which overlaps with the main seabird breeding and foraging areas and for which data are available during most of our study period (1990-2016).

### ***Analyses***

Combining the population estimates, diet, and a bioenergetics model framework, we conducted three complementary analyses to evaluate the temporal patterns of seabird prey consumption of the three focal seabird species, as well as the foraging behavior of common murres. First, we developed time series to assess the *per capita* and population level prey consumption patterns per species. *Per capita* prey consumption was defined as the total biomass consumed by an individual over the season as calculated from the bioenergetics equations, before scaling up to the population level. Examining *per capita* consumption allowed us to assess factors that influence the ability of individual birds to meet their energy demands, while controlling for the effect of population size on overall consumption. We examined each seabird species' prey consumption time series for trends using standard regression analyses, with population size, diet composition, and year as independent variables (for years in which complete colony count data were available; years with interpolated population estimates were excluded). We used Spearman's rank correlations to evaluate the relationship between *per capita* prey consumption (total biomass of prey required to meet individual energy needs) and the proportion of individual prey items (specifically juvenile rockfish or anchovy) as revealed in the seabird diet. This is not dependent on population size, but is strictly a function of energy requirements and diet composition, thus all years were included in these analyses.

Second, for common murre, to assess factors affecting prey switching, we examined the impact of prey type, juvenile rockfish vs anchovy, on feeding rates, foraging trip duration and mass of prey items fed to murre chicks at the South Farallon Islands. Between-year differences of these variables were evaluated using a one way ANOVA, and a *t*-test was used to test the hypothesis that trip duration increased when murres were foraging primarily on anchovies rather than rockfish (the two dominant prey types). In addition, we used regression analyses to examine the relationship between annual variation in energy gained by prey type and mean foraging trip duration to evaluate energetic drivers of prey switching.

Third, we used correlation analysis to compare time series of overall seabird species consumption (for years with complete colony count data), with CPUE of juvenile rockfish and sanddabs, market squid, euphausiids and anchovy (Santora et al., 2014; Sakuma et al., 2016). Due to seabird population increases over time, consumption time series displayed significant linear trends, and were detrended prior to comparing with standardized CPUE (lnCPUE+1) anomalies of forage species. Again, years with interpolated population estimates were excluded for these analyses.

## RESULTS

### ***Seabird populations***

The total breeding population for the three seabird species increased over the course of our study period, growing from ~110,000 to more than 475,000 birds, 1986 to 2015. This growth pattern since the early 2000s was driven largely by murres, whose population increased almost five fold. Likewise, the rhinoceros auklet population, though smaller overall, increased tenfold from 500 to >5,000 individuals since the 1980s. The Brandt's cormorant population, in contrast, has fluctuated between periods of rapid growth followed by population crashes. Notably, for this study, the population of Brandt's cormorants increased substantially during the early 2000s, growing from approximately 7,000 birds to a peak of more than 40,000 birds in 2007 before declining to a low point in 2009. Since then, the population has been slowly recovering (Appendix 2).

### ***Diet composition***

Seabirds fed on a variety of prey including commercially important fishes such as rockfish, northern anchovy, Pacific sardine, salmon, flatfishes and market squid. Northern anchovy (adults and juveniles) and juveniles rockfish were the dominant prey (by mass and number), although their relative importance varied considerably among years (Fig. 2). Juvenile rockfish were the primary prey fed to dependent chicks of the study species during the late 1980s but prevalence decreased during the early 1990s, becoming nearly absent by the end of the decade. There was a brief resurgence of juvenile rockfish in the diet between 2001 and 2004, and more recently (2009-2015) juvenile rockfish returned to being the most frequently consumed prey, consistent with a sharp increase noted in the abundance of juvenile rockfish in the midwater trawl survey (Sakuma et al. 2016). When rockfish were not a major dietary component, consumption of anchovy increased.

### *Total biomass consumed*

Total biomass of prey consumed by the three study species during the breeding season ranged from at least 8,200 (1992) to >60,000 *t* (by 2011; Fig. 2, 3, Appendix 1). Common murres were the dominant consumers, accounting for ~93% (SD ± 4%) of prey consumption in a given year, ranging from ~8,000 to 58,000 *t* (Fig. 4a). For murres, peak consumption included as much as 51,700 *t* juvenile rockfishes, 38,600 *t* anchovy, 10,800 *t* smelt, 11,900 *t* squid, and 3,800 *t* juvenile salmon. The other two seabird study species consumed relatively smaller though still significant amounts of these forage fish. Brandt's cormorants consumed 528 to 6,400 *t* per breeding season, including as much as 1,800 *t* juvenile rockfish, 3,900 *t* anchovy, and 3,100 *t* flatfish (Fig. 4b). Rhinoceros auklets consumed 45 to 485 *t* per breeding season, including as much as 370 *t* juvenile rockfish, 237 *t* anchovy, and 175 *t* Pacific saury (Fig. 4c).

For those years in which complete colony counts were available (i.e., no interpolated estimates), there was a significant increase over time in the total biomass consumed during the breeding season for all study species combined ($F_{(1,17)}$ = 192.25, $p < 0.001$, $R^2 = 0.9577$) as well as for each species individually (COMU: $F_{(1,17)}$ = 244.99, $p < 0.001$, $R^2 = 0.9665$; BRAC: $F_{(1,17)}$ = 9.57, $p = 0.002$, $R^2 = 0.5295$; RHAU: $F_{(1,26)}$ = 157.05, $p < 0.001$, $R^2 = 0.9236$, where subscripts represent the degrees of freedom based on the number of years used in the analysis) (Fig. 3a). Consumption during the El Niño years of 1986, 1992, 1998, and 2009-10 was lower than in other years due to a combination of a reduction in the number of breeding birds and lower hatching success, leading to fewer chicks requiring food (Fig. 2).

### *Drivers of prey consumption*

Seabird population size, particularly that of common murre, was the main driver of overall prey consumption and accounted for >95% of the variation observed in our bioenergetics model ($R^2 = 0.98$, $p < 0.001$). P*er capita* prey consumption ranged from 0.04 *t* (low year for auklets) to 0.11 *t* (high year for murres) during the breeding season in a given year (Fig.

3b). A significant linear relationship existed between the proportion of rockfish or anchovy in the diet and *per capita* consumption. On the basis of mass, a higher proportion of rockfish was associated with increased *per capita* prey consumption ($F_{(1,28}$ = 27.39; $p < 0.001$; $R^2 = 0.50$), whereas a higher proportion of anchovy was associated with lower *per capita* prey consumption ($F_{(1,28)}$ = 105.39; $p < 0.001$; $R^2 = 0.79$), likely due to the higher energy density of anchovies as prey. That is, murres were required to consume more to meet their energy demands when primarily consuming rockfish than when primarily consuming anchovy.

### *Common murre feeding rate and foraging trip duration*

The overall mean feeding rate for common murre provisioning fish to chicks was 2.97 ± 1.10 feedings (fish) per day, ranging 1.52 (1998) to 6.18 (2010). Both prey mass ($F_{(1,29)}$ = 33.60, $p < 0.001$) and feeding rate ($F_{(1,29)}$ = 9.38, $p < 0.001$) varied significantly among years and were highly correlated with the proportion of primary prey items in the diet. Feeding rate was positively correlated with the proportion of rockfish consumed ($\rho = 0.86$, $p < 0.001$, $N = 30$) and negatively correlated with the proportion of anchovy ($\rho = -0.86$, $p < 0.001$, $N = 30$). Similarly, mean foraging trip duration differed as a function of prey species ($t_{60} = 11.94$, $p < 0.001$) and averaged 92 min (range 43-150 min) when feeding on rockfish, compared to an average duration of 235 min (range 95- 346 min) when foraging for anchovy. Annual mean foraging trip duration varied significantly with the amount of energy gained from either anchovy or juvenile rockfish (Fig. 5). There was a significant positive relationship between energy gained from anchovy and trip duration ($F_{(1, 27)}$ = 75.01; $p < 0.001$; $R^2 = 0.74$) and a significant negative relationship between energy gained from juvenile rockfish and trip duration ($F_{(1, 27)}$ = 118.01; $p < 0.001$; $R^2 = 0.81$). There was no significant relationship between mean trip duration and breeding success ($F_{(1.28)}$ = 0.14; $p = 0.70$; $R^2 = 0.05$).

### *Seabird consumption and forage availability*

Relationships between seabird prey species consumption and forage indices derived from mid-water trawls yielded results verifying the general switch between modes of juvenile rockfish and northern anchovy availability off central California (Fig. 6). Consumption rates of forage species by common murres and rhinoceros auklets displayed several significant correlations with forage species abundance indices (Table 2). Murre and auklet consumption of juvenile rockfish was positively related to the abundance of mid-water trawl estimates of juvenile rockfish, young-of-the-year sanddabs, and market squid, and negatively related to anchovy abundance. By contrast, murre and auklet consumption of anchovy was positively related to anchovy abundance, and negatively related to juvenile rockfish, young-of-the-year sanddabs, and market squid (Table 2). Brandt's cormorant consumption of anchovy was negatively related to young-of-the-year sanddabs.

## DISCUSSION

Through application of a bio-energetics model using long-term observations of population size, diet and foraging effort, in conjunction with data on prey availability, we quantified how patterns of prey consumption for three seabird species have changed over several decades within the central California Current upwelling ecosystem. Previous studies estimated prey requirements for seabird species for a single year (Wiens and Scott, 1975; Roth et al., 2008) or for other regions (Cairns et al., 1990; Gabrielsen, 1996); and similar efforts have been made for other predators such as California sea lions (*Zalophus californianus*) and cetaceans for various time periods (Weise and Harvey, 2008; Barlow et al., 2008).

Our results clearly demonstrate that forage fish consumption by the target seabird species has greatly increased during the past few decades. Overall annual consumption of forage fish by just these three seabird species during the breeding season may now exceed 60,000 *t*, more than five times greater than during the mid-1980s. Population increases account for most of the increased consumption, particularly among common murres and Brandt's cormorants, as they recover from previous human impacts such as habitat degradation, mortality from fisheries bycatch, and oil spills (Carter et al., 2001; Ainley et al., 2018). Common murres, the most numerous breeding species in the area, accounted for >90% of the total biomass consumed. However, Brandt's cormorants also consumed large amounts of forage fish as their populations increased. While the rhinoceros auklet population is much smaller (~100x less numerous than murres) they still consumed a significant amount of forage fish biomass (>450 *t* annually).

The combined predation pressure on forage species by just the seabird component of mesopredators within this system is, thus, very high, and will continue to grow with further population recovery. We found, after statistically controlling for population increases, that consumption patterns were related to forage species abundance, as indicated by fishery surveys. Specifically, ocean climate variability inherent in upwelling ecosystems produces conditions favoring either juvenile rockfish or northern anchovy(Santora et al., 2014; Ralston et al., 2015; Wells et al., 2017), which in turn drives seabird consumption patterns. Although the three seabird species in this study represent the majority of breeding seabirds in the region, our analysis underestimates total seabird consumption by excluding breeding species such as Western Gull (*Larus occidentalis;* ~10,000 breeding pairs), Pelagic Cormorant (*Ph. pelagicus*; ~400 pairs) and Cassin's Auklet (*Ptychoramphus aleuticus*; ~35,000 pairs, e.g. Warzybok et al., 2015). Furthermore, our consumption estimates were limited to the breeding season (approximately half the year), due to inadequate diet information during other parts of the year and uncertainty involving numbers of birds overwintering in the region. However, resident seabirds must still meet their daily energy requirements during the non-breeding period. Likewise, our analysis did not include large summer-fall influxes of migratory species (e.g., sooty shearwaters (*Adrenna grisea;* tens of thousands of birds), or brown pelicans (*Pelecanus occidentalis;* many thousands; NOAA, 2003), which have major foraging demands (Briggs et al., 1983; Chu et al., 1984).

It is also important to note, that krill, while not observed in the breeding season diet data, is an important prey item for many adult seabirds and may contribute nontrivially to adult diets, with resultant implications for consumption of the focal species described in this study. Indeed, krill is a major component of common murre diet during early spring (Ainley et al., 1996) and may also be important for rhinoceros auklets in some regions (Davies et al., 2009), though not observed in local breeders (Carle et al., 2015). . Therefore, the consumption estimates presented herein should be considered a very conservative estimate of overall seabird consumption in this region. Annual consumption by seabirds is likely twice the estimates for breeding species and several times higher for the total avifauna.

### *Insights from seabird prey switching*

Either juvenile rockfishes or northern anchovy typically dominated the diet, their relative proportions varying considerably by year. In addition, many alternate forage species (i.e. smelt, squid, and juvenile salmon and flatfishes) at times contributed a significant proportion of the energy needed. Prey switching can have energetic consequences for central-place foraging seabirds (Davoren and Montevecchi, 2003; Langton et al., 2014,). In the case of murres, foraging trip duration was significantly longer and number of prey returned was lower when feeding on anchovy compared to when feeding primarily on juvenile rockfish, likely due to differences in the spatial distribution of these forage species in the Gulf of the Farallones (Santora et al., 2014; Wells et al., 2017). Anchovy tended to be concentrated closer to shore requiring murres at the Farallon Islands to travel a greater distance to find them when juvenile rockfish were not available (Santora et al., 2014, Wells et al., 2017).

For both cormorants and alcids, aerial flight is hugely expensive owing to their very high wing loading. Flight for these species is 5X more energetically costly than diving and 15X more costly than dwelling at the nest site (Elliott et al., 2014). Whereas Brandt’s cormorants responded to the decadal changes in juvenile rockfish vs. anchovy availability by exhibiting variable reproductive success and shifting their population more to the coast where prey access was more proximate and reliable (Ainley et al., 2018), murres did not. Murres showed little annual variation in reproductive success in most years, while simultaneously exhibiting a spectacular increase in their population throughout the study period (Warzybok et al., 2015; Appendix II). Murre population increase was probably, at least in part, a response to the appreciable increase during the 2000s in prevalence of energy-rich anchovy (reviewed in Ainley et al., 2018), which is also important to their diet after departing the island following the breeding season (Ainley et al., 1996). Murres are a very efficient central-place foraging seabird, given that they raise just one chick at a time, which is confined to the nest site for only three weeks. During that time the chick mostly develops its paddle-shaped wings (for diving) and develops thermoregulation. Then, long before it is capable of aerial flight, each follows its male parent to where forage is most available, remaining with the parent for the next several weeks (Ainley et al., 2002). During that period, chick and parent exhibit a similar diet (Ainley et al., 1996). The fact that the murre population did not decrease once the anchovy increase subsided (2009) and murres returned to feeding on smaller, less energy-dense juvenile rockfish, indicates that juvenile rockfish at times were available enough to allow short foraging trips (see below), with later movement to the coast where anchovy continued to be abundant (reviewed in Ainley et al., 2018).

For murres at the South Farallon Islands (SFI), foraging trips that returned juvenile rockfish to chicks averaged 92 min long, compared with 235 min for trips bringing anchovy. When feeding on rockfish, murres may forage within 5-10 km of SFI (Ainley et al., 1990; 1996), but for anchovy they likely foraged 80 km or more away (see also Wells et al., 2017). To understand better the murres' capabilities, we considered the size and energy density of juvenile rockfish (mean 74 mm SL, 4.85 kJ/g) vs anchovy (124 mm SL, 5.56 kJ/g), flight speed (Spear and Ainley, 1997) and other factors, as well as the 1530 kJ/d that murres needed to acquire (10% of that for chicks; Roth et al., 2008). Given the results of the bioenergetics model, adult murres would have to catch, on average, 106 juvenile rockfish/d or 26 anchovy/d to meet their energy needs. Assuming 20-30 dives per foraging trip (Elliott et al., 2014), such a catch is possible and, for chicks, would lead to ~10 rockfish feeds or ~3 anchovy feeds per day, which is consistent with observed feeds during years in which either rockfish or anchovy dominated the chick diet (Ainley et al., 1990; Point Blue unpublished data). Anchovies are approximately 15% more energetically valuable than rockfish per gram and approximately 70% larger on average, yielding approximately 4.5 times more energy per fish than juvenile rockfish. While the murres would seem to prefer the juvenile rockfish diet, since foraging closer to the colony reduces the energetic cost of flight and allows more time for nest and chick guarding, longer foraging trips can be energetically compensated by a diet richer in anchovy (Fig. 5). It appears that when the amount of energy derived from juvenile rockfish dips below 800 kJ/d, murres are forced to relax nesting site occupation/chick guarding and switch to the more energy-rich anchovy, despite higher foraging effort. Regardless of which prey species was most abundant, this prey switching strategy helps murres to cope with variability and allowed the population to increase steadily during the study period.

Brandt's cormorants, in contrast, exhibit a “boom or bust” strategy (Boekelheide et al., 1990; Wallace and Wallace, 1998) in which they attempt to raise as many as four chicks per nesting attempt, requiring much effort over a couple of months. One result was that fledging success varied dramatically depending on prey availability (Boekelheide et al., 1990). If forage fish are available nearby, chicks survive and fledge, but if cormorants have to travel farther to obtain adequate forage it often leads to reduction in brood size or breeding failure. Following the decline in rockfish abundance offshore and the increase in anchovies close to shore in the mid-2000s, the Brandt’s cormorant population shifted toward the coast (Capitolo et al., 2014, Ainley et al., 2018).

For rhinoceros auklets, the impact of prey switching is intermediate between the murre and cormorant. They nest in a deep cavity allowing both parents to forage simultaneously all day to acquire food for their single chick, rather than one parent having to remain with the nest, as with the cormorants and murres. However, each auklet parent typically provisions chicks only once in the evening, returning several fish per bill load (Bertram et al., 1991), limiting flexibility to compensate for poor prey availability. At-sea surveys (NOAA, 2003; McGowan et al., 2013) show that unlike murres and Brandt's cormorants, auklets at the Farallones tend to feed over the continental shelf break west of the islands. They are less able to adapt if juvenile rockfish are unavailable and anchovy is concentrated nearshore. In those years their diet is dominated by saury and other lower quality prey, resulting in lower productivity and lower fledging weights (Fig. 4c; see also Thayer and Sydeman, 2007). In contrast, rhinoceros auklets at mainland Año Nuevo Island preyed more consistently on anchovy, and demonstrate more consistently high reproductive success (Thayer and Sydeman, 2007).

### *Insights from the bioenergetics model*

Bioenergetics models, including ours, contain many assumptions that lead to uncertainty in model outcomes. Inaccurate estimates of population size (especially the non-breeding component) produces large errors in the output of the final model (Wanless et al., 1998; Roth et al., 2008; Ridgway, 2010). Also, seasonal or regional variation in prey energy density (Pedersen and Hilsop, 2001; Gatti et al., 2017) may impact the output if values are higher or lower than published values. Unfortunately, there is insufficient data to account for fine-scale variability in energy density for these prey species in our study. Thirdly, while the number of chicks and fledglings produced is normally estimated by multiplying the number of breeding pairs by the mean fledging success (fledglings/breeding pair), this fails to account for the consumption of food by chicks that do not reach fledging (Wanless et al., 1998; Fort et al., 2011) nor for, in the case of murres, consumption by chicks once departed from the breeding ledges. Fourth, diet composition during the breeding season is usually available from observations of chick provisioning, but, as noted, availability of diet information outside of the nesting season and for adults is sparse (Ainley et al., 1996; Carle et al., 2015). Finally, diet may vary considerably both spatially and temporally (Ainley et al., 1996; 2015a) and may differ among colonies, even within this relatively small region (Ainley et al., 2018). We did our best to account for this variability by using year-specific diet composition and including dietary data from both the offshore South Farallon Islands colony and the nearshore Año Nuevo Island colony whenever sufficient data were available. However, we acknowledge that seasonal and colony-dependent differences in seabird diets could not be fully accounted for and may have a significant impact on overall forage species consumption.

### ***Implications for Ecosystem-Based Fishery Management***

Our results demonstrate that even seabird species with relatively small populations consume a significant amount of forage fish to satisfy their energetic requirements, and do so by switching prey when necessary. In the interests of ecosystem-based fisheries management (EBFM), providing a diverse preyscape allows for predator prey switching, especially important for the highly variable California Current, regardless of fishing pressure. To support efforts to implement an ecosystem-based approach to fisheries management, the Pacific Fishery Management Council implemented a Fisheries Ecosystem Plan in 2013. Highlighted in that plan was the need to understand the trade-offs and buffers associated with maintaining the integrity of food web structure relative to achieving long-term benefits from the conservation and management of dependent and target species (PFMC, 2013). This in turn is dependent on an improved understanding of trophic energy flow and other ecological interactions, particularly with respect to removals by fisheries. For example, for the time period of the present study, California statewide fisheries removals of adult rockfish and northern anchovy were well below the estimated levels removed by seabirds, particularly in the later years (Fig. 7). However, as highlighted earlier, rockfish consumed by seabirds are almost exclusively young-of-the-year, and in this region are most likely to be shortbelly rockfish (*S. jordani*), an unfished species, while those targeted by fisheries are the adults of larger, longer-lived and slower growing species such as bocaccio, chilipepper, canary and widow rockfish (*S. paucispinis, S. goodei, S. pinniger* and *S. entomelas*). Due to both poor marketability and recognition of their role as forage, there is currently no fishery for shortbelly rockfish, which is the most abundant species in both fisheries independent surveys and seabird diets in this region. Consequently, competition between breeding seabirds and rockfish fisheries is likely to be modest (Field et al., 2010). However, reduced availability of juvenile rockfish leads to significantly higher take, and mortality of juvenile salmon by seabirds in this system (Wells et al., 2017), and reduced availability of juvenile rockfish during the 1980s, before closures were enacted, led to cormorants moving to inshore breeding sites (Ainley et al, 2018).

By contrast, both seabirds and fisheries exploit all age classes of northern anchovy, and thus both may have direct impacts on the availability of this resource and on each other (as well as the other predators in the ecosystem, e.g. salmon; Wells et al., 2017). The decline in northern anchovy landings in the early 1980s (Fig. 7) was a consequence of the northern anchovy fishery management plan, which sought to protect the role of northern anchovy as forage for dependent predators, and particularly for the brown pelican, which was critically endangered at the time (Anderson et al., 1982; Ainley et al., 2018). The plan called for the cessation of targeted landings for the reduction fishery, the primary fishery for northern anchovy at that point, when the stock biomass fell below 300,000 *t* (as it did within years of the plan’s implementation) (MacCall, 2009).

The current fishery for northern anchovy is not actively managed, as total catches are constrained to 25,000 *t* per year, with the fishery in most years at a fraction of that value; most landings, primarily for bait, are made in central, rather than southern California (Miller et al., 2017). Apparent anchovy declines in abundance during the late 2010s have been quantified based on the data streams that supported earlier stock assessments (MacCall et al., 2016) and other studies (Zwolinski et al., 2017), but such estimates have most recently produced total abundance values residing far below the estimated consumption of anchovy reported in our study. This leads both to questions regarding uncertainty in stock size estimation (e.g., the above mentioned studies acknowledge considerable challenges in the estimation of anchovy abundance in nearshore habitats), as well as confirmation that contemporary competition continues between seabirds and fisheries for this variable and high turnover resource. The recovery of salmon, sea lions and cetaceans, all being key predators of northern anchovy, has contributed to even greater complexity in the interactions among these ecosystem components (Ainley and Hybrenbach, 2010). It seems reasonable to assume that increased consumption by predators could be leading to changes in the abundance of key forage fish populations such as northern anchovy, regardless of the potential additional impacts of commercial fisheries (DeMaster et al., 2001). Indeed, fishery management practices established when predator populations were small a few decades ago are now being confronted by the growing needs of predators as their respective populations recover (e.g., Chasco et al., 2017). Maintaining and improving estimates of overall and spatial consumption of shared forage species among predators, including seabirds, will benefit the successful evaluation of interactions among protected species, fisheries removals, and the decisions made by fisheries and marine resource managers as progress is made toward effective ecosystem-based fisheries management.

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Table 1: Prey energy densities and relationship between mass ($M$) in grams and standard length (SL) or mantle length (ML) in millimeters for forage species consumed by seabirds in the Gulf of the Farallones region. Mass to length relationships are presented with their regression statistics and sample size. For most species, the mass to length relationship were calculated from prey items fed to chicks or regurgitated by adults at SFI and ANI. Published equations were used for flatfish, smelt (Spear, 1993), and sculpin (Lea et al., 1999) because of insufficient sample sizes in the diet dataset. Energy density values were collected from the literature: Spear, 1993 (rockfish, flatfish, smelt, squid); Dahudul and Horn, 2003 (anchovy, converted from 20.6 kJ/g dry mass); Harvey et al., 2000 (sardine); Roby et al. 2003 (salmon); Anthony et al., 2000 (lincod, saury); and Van Pelt et al., 1997 (sandlance).

| Species | Energy Density kJ/g wet $M$ | Mean standard length (mm) | Length Range (mm) | Mass/length relationship | $R^2$ | $F$ | $P$ | $N$ |
|---|---|---|---|---|---|---|---|---|
| Juvenile rockfish | 4.85 | 74 | 52 - 92 | $M = 1.449 \times 10^{-4}\ SL^{2.346}$ | 0.76 | 3637 | 0.00 | 1130 |
| Northern anchovy | 5.56 | 124 | 106 - 150 | $M = 3.273 \times 10^{-6}\ SL^{3.194}$ | 0.90 | 7028 | 0.00 | 742 |
| Sardine | 5.56 | 100 | 80 - 126 | $M = 3.24 \times 10^{-5}\ SL^{2.699}$ | 0.86 | 606 | 0.00 | 101 |
| Salmon (chinook) | 3.98 | 108 | 89 - 139 | $M = 1.535 \times 10^{-4}\ SL^{2.41}$ | 0.70 | 418 | 0.00 | 180 |
| Flatfish (pacific sandab) | 3.47 | 82 | 69 - 116 | $M = 1.2 \times 10^{-6}\ SL^{3.51}$ | n/a | n/a | n/a | n/a |
| Smelt (night smelt) | 4.33 | 90 | 77 - 116 | $M = 5.6 \times 10^{-5}\ SL^{2.54}$ | n/a | n/a | n/a | n/a |
| Squid | 4.14 | 77 | 59 - 109 | $M = 6.79 \times 10^{-4}\ ML^{2.203}$ | 0.78 | 396 | 0.00 | 116 |
| Lingcod | 3.98 | 84 | 77 - 101 | $M = 1.059 \times 10^{-4}\ SL^{2.320}$ | 0.70 | 366 | 0.00 | 159 |
| Pacific saury | 4.99 | 129 | 103 - 144 | $M = 8.016 \times 10^{-6}\ SL^{2.825}$ | 0.88 | 6960 | 0.00 | 935 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Sandlance | 4.95 | 118 | 98 - 154 | $M = 5.92 \times 10^{-6} SL^{2.868}$ | 0.80 | 125 | 0.00 | 33 |

Table 2: Correlation coefficients (Pearson) between time series of seabird consumption and forage species availability (ln(CPUE+1)) derived from the Rockfish Recruitment and Ecosystems Assessment Survey. Values in bold are significant at $p = 0.05$.

| | | **Forage species availability** | | | | |
|---|---|---|---|---|---|---|
| **Seabird consumption** | | **anchovy** | **juvenile rockfish** | **market squid** | **krill** | **juvenile sanddabs** |
| **Common Murre** | **juvenile rockfish** | **-0.5758** | **0.6390** | **0.5746** | 0.2296 | **0.5800** |
| | **anchovy** | **0.5946** | **-0.4907** | **-0.5243** | -0.1960 | **-0.4662** |
| | **total** | **-0.4391** | 0.2549 | 0.3391 | **0.4255** | 0.3700 |
| **Brandt's Cormorant** | **juvenile rockfish** | 0.2915 | -0.0005 | 0.1499 | -0.3203 | 0.1651 |
| | **anchovy** | -0.1331 | -0.1570 | -0.3668 | 0.1384 | **-0.4322** |
| | **total** | 0.2552 | -0.2402 | -0.1858 | 0.0777 | -0.0414 |
| **Rhinoceros auklet** | **juvenile rockfish** | -0.3762 | **0.5946** | **0.6011** | 0.2143 | **0.6576** |
| | **anchovy** | **0.5970** | -0.2564 | -0.2524 | -0.3448 | -0.2490 |
| | **total** | -0.2342 | 0.3589 | **0.4346** | 0.1028 | **0.4126** |

Figures:

Figure 1: Study area showing locations of seabird colonies and trawl stations in the Rockfish Recruitment and Ecosystem Assessment Survey. ANI – Año Nuevo Island, DSR — Devil's Slide Rock, LSR — Lobos/Seal Rock, DB — Drake's Bay rocks, PR — Point Reyes Headlands, SFI — South Farallon Islands, NFI — North Farallon Islands. Depth isobaths are 50, 100, 200, 500, 1000, and 2000 m.

Figure 2: Total forage fish consumption during the breeding season and annual prey composition for three abundant seabird species, which among seabirds are the most easily studied in terms of diet and foraging behavior: common murre, Brandt's cormorant, and rhinoceros auklet.

Figure 3: For three abundant seabird species breeding in the Gulf of the Farallones, 1986-2015: (a) total prey biomass consumed by year (all species combined) and (b) annual *per capita* prey biomass consumed for Brandt's cormorant (BRAC), common murre (COMU), and rhinoceros auklet (RHAU).

Figure 4: As a function of prey species, total prey biomass consumed by (a) common murre, (b) Brandt's cormorant, and (c) rhinoceros auklet in the Gulf of the Farallones, 1986-2015.

Figure 5: Relationship between foraging trip duration (min) and the average daily energy gained (kJ) from dominant prey species for common murres: (a) annual relative contribution of juvenile rockfish and anchovy to daily energy consumption (bars) with mean annual foraging trip duration (red line); (b) functional relationship between foraging trip duration and energy gained from juvenile rockfish (yellow circles) and anchovy (blue triangles). The data are fitted with a linear trend line to illustrate the relationship.

Figure 6: Standardized anomalies of forage species abundance (ln(CPUE+1) derived from the Rockfish Recruitment and Ecosystem Assessment Survey (1990-2016) in the study area (Fig. 1):

(a) juvenile rockfish, (b) market squid, (c) total euphausiids, (d) juvenile Pacific sanddabs, and (e) total northern anchovy

Figure 7: Commercial landings of adult rockfish and northern anchovy off California (bars) contrasted with seabird consumption within the Gulf of the Farallones (lines).

Appendix 1: Total biomass (metric tons) of prey species consumed during the breeding season (March – August) by three seabirds in the Gulf of the Farallones region, 1986-2015.

| YEAR | Brandt's Cormorant | Common Murre | Rhinoceros Auklet | Total |
|---|---|---|---|---|
| 1986 | - | 12,556 | - | 12,556 |
| 1987 | - | 11,894 | 46 | 11,940 |
| 1988 | - | 11,538 | 48 | 11,586 |
| 1989 | - | 10,955 | 54 | 11,009 |
| 1990 | - | 14,234 | 72 | 14,306 |
| 1991 | - | 9,185 | 91 | 9,276 |
| 1992 | - | 8,333 | 89 | 8,422 |
| 1993 | - | 14,636 | 127 | 14,763 |
| 1994 | 1,786[*] | 12,888 | 167 | 14,841 |
| 1995 | - | 14,688 | 168 | 14,857 |
| 1996 | - | 17,250 | 177 | 17,427 |
| 1997 | - | 19,241 | 216 | 19,457 |
| 1998 | - | 19,784 | 204 | 19,988 |
| 1999 | 1,286[*] | 22,787 | 236 | 24,309 |
| 2000 | 610[†] | 24,424 | 235 | 25,269 |
| 2001 | 605[†] | 26,554 | 265 | 27,424 |
| 2002 | 992[†] | 30,429 | 292 | 31,713 |
| 2003 | 3,500 | 29,085 | 321 | 32,906 |
| 2004 | 5,288 | 29,103 | 305 | 34,696 |
| 2005 | 3,740 | 30,913 | 284 | 34,937 |
| 2006 | 5,503 | 41,117 | 229 | 46,849 |
| 2007 | 6,749 | 46,452 | 246 | 53,447 |
| 2008 | 2,500 | 40,013 | 301 | 42,814 |
| 2009 | 528 | 45,635 | 332 | 46,495 |
| 2010 | 1,349 | 49,037 | 388 | 50,774 |
| 2011 | 2,356 | 57,605 | 401 | 60,362 |
| 2012 | 2,124 | 54,922 | 403 | 57,449 |
| 2013 | 3,049 | 57,551 | 487 | 61,087 |
| 2014 | 2,549 | 58,595 | 478 | 61,622 |
| 2015 | 2,492 | 58,651 | 397 | 61,540 |

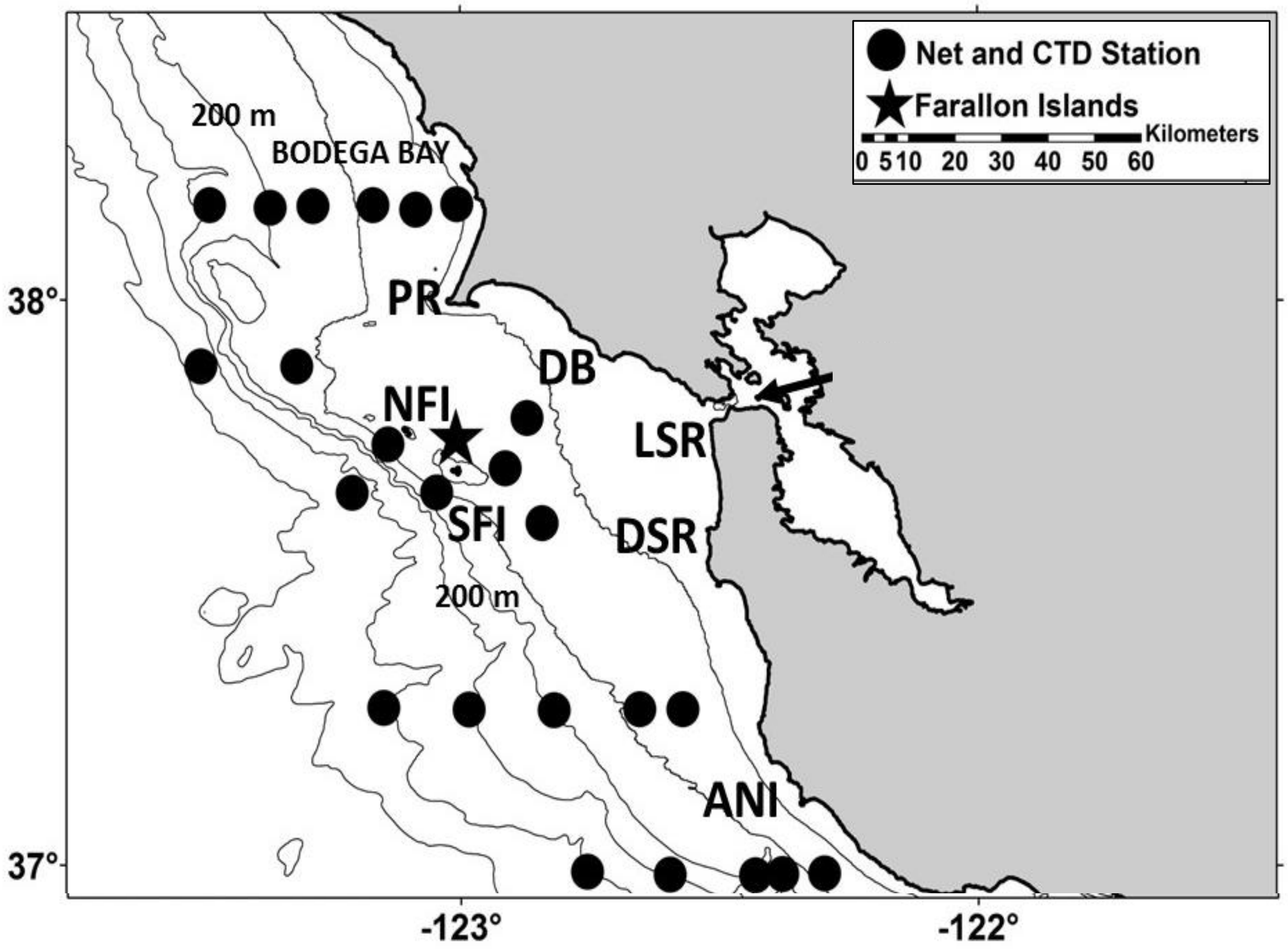
[*] Estimate for SFI only; [†] Estimate for Mainland colonies only

Appendix 2: Population estimates for common murre, Brandt's cormorant and rhinoceros auklet in the Gulf of the Farallones region, 1986-2015. Values underlined are derived estimates based on representative index plot counts, while values in *italics* are based on the mean relative contribution of the missing segment to the overall regional population (see text).

| | Common Murre | | | | Brandt's Cormorant | | | | | Rhinoceros Auklet | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Year | SFI | NFI | Mainland | Total | SFI | NFI | Mainland | ANI | Total | SFI | ANI | TOTAL |
| 1986 | 56,104 | 23,054 | 24,198 | 103,357 | 6,662 | 22 | 390 | 0 | 7,074 | . | . | 0 |
| 1987 | 39,195 | 26,213 | 27,101 | 92,508 | 8,074 | 148 | 1,014 | 0 | 9,236 | 500 | . | 500 |
| 1988 | 40,931 | 21,654 | 27,797 | 90,382 | 11,924 | 90 | 800 | 0 | 12,814 | 500 | . | 500 |
| 1989 | 38,028 | 25,436 | 24,448 | 87,912 | 15,220 | 146 | 1,540 | 4 | 16,910 | 516 | . | 516 |
| 1990 | 60,506 | 21,616 | 28,148 | 110,270 | 8,996 | 24 | 1,174 | 0 | 10,194 | 702 | . | 702 |
| 1991 | 35,000* | *18,780* | *16,496* | 70,276 | 12,309* | *67* | *2,367* | 0 | 14,743 | 888 | . | 888 |
| 1992 | 32,400* | *17,385* | *15,270* | 65,055 | 3,593* | *20* | *691* | 100 | 4,403 | 1,074 | . | 1,074 |
| 1993 | 54,977 | 30,759 | 36,188 | 121,924 | 9,438 | 44 | 1,872 | 650 | 12,004 | 1,260 | 112 | 1,372 |
| 1994 | 50,616 | 29,328 | 29,891 | 109,834 | 10,850 | 32 | 1,832 | 916 | 13,630 | 1,446 | 176 | 1,622 |
| 1995 | 55,492 | 31,699 | 36,282 | 123,472 | 10,402 | 4 | 1,870 | 902 | 13,178 | 1,632 | 190 | 1,822 |
| 1996 | 65,400* | *35,092* | 42,247 | 142,739 | 9,741* | *71* | 1,994 | 732 | 12,538 | 1,818 | 196 | 2,014 |
| 1997 | 77,564 | 44,492 | 38,951 | 161,007 | 10,324 | 100 | 1,832 | 1,322 | 13,578 | 2,004 | 220 | 2,224 |
| 1998 | 52,670* | *28,261* | *24,823* | 105,754 | 5,432 | 24 | 956 | 664 | 7,076 | 2,190 | 164 | 2,354 |
| 1999 | 92,284 | 51,494 | 43,383 | 187,161 | 7,848 | 54 | 1,906 | 1,210 | 11,018 | 2,376 | 188 | 2,564 |
| 2000 | 97,177 | 50,822 | 46,846 | 194,845 | 7,836 | 116 | 1,836 | 1,576 | 11,364 | 2,562 | 184 | 2,746 |
| 2001 | 100,343 | 57,539 | 47,982 | 205,864 | 9,492 | 116 | 2,076 | 1,360 | 13,044 | 2,748 | 212 | 2,960 |
| 2002 | 115,659 | 65,727 | 52,858 | 234,245 | 14,518 | 196 | 3,258 | 1,980 | 19,952 | 2,934 | 246 | 3,180 |
| 2003 | 115,079 | 64,955 | 48,088 | 228,122 | 13,602 | 196 | 3,158 | 1,938 | 18,894 | 3,120 | 284 | 3,404 |
| 2004 | 114,901 | 64,872 | 59,210 | 238,983 | 17,014 | 102 | 4,320 | 3,804 | 25,240 | 3,306 | 248 | 3,554 |
| 2005 | 129,485 | 67,196 | 55,702 | 252,383 | 14,874 | 40 | 3,892 | 3,426 | 22,232 | 3,315 | 210 | 3,525 |
| 2006 | 173,709 | 92,247 | 79,527 | 345,484 | 23,478 | 96 | 6,344 | 4,958 | 34,876 | 2,712 | 256 | 2,968 |
| 2007 | 210,962 | 95,430 | 90,866 | 397,258 | 27,120 | 62 | 9,004 | 5,256 | 41,442 | 2,969 | 216 | 3,185 |
| 2008 | 167,306 | *90,894* | *61,575* | 281,734 | 5,839* | *60* | 4,148 | 3,430 | 13,477 | 2,902 | 270 | 3,172 |
| 2009 | 167,348 | *90,917* | *80,811* | 339,076 | 1,506* | *20* | 696 | 692 | 2,914 | 3,192 | 248 | 3,440 |
| 2010 | 189,249 | *102,815* | 79,800 | 371,864 | 6,192* | *42* | 956 | 462 | 7,652 | 4,018 | 262 | 4,280 |
| 2011 | 226,161 | *122,868* | 76,549 | 425,578 | 5,931* | *72* | 2,842 | 2,926 | 11,771 | 4,029 | 236 | 4,265 |
| 2012 | 205,324 | *111,548* | 81,507 | 398,379 | 4,162* | *66* | 3,042 | 3,082 | 10,352 | 3,817 | 266 | 4,083 |
| 2013 | 232,006 | 114,281 | 88,655 | 434,942 | 8,943* | 24 | 3,786 | 4,012 | 16,765 | 4,877 | 264 | 5,141 |
| 2014 | 230,132 | *125,026* | 94,344 | 449,502 | 7,922* | *96* | 3,802 | 3,614 | 15,434 | 5,011 | 296 | 5,307 |
| 2015 | 233,219 | *140,000* | 85,190 | 458,409 | 6,602* | *78* | 3,766 | 3,294 | 13,740 | 4,498 | 330 | 4,828 |

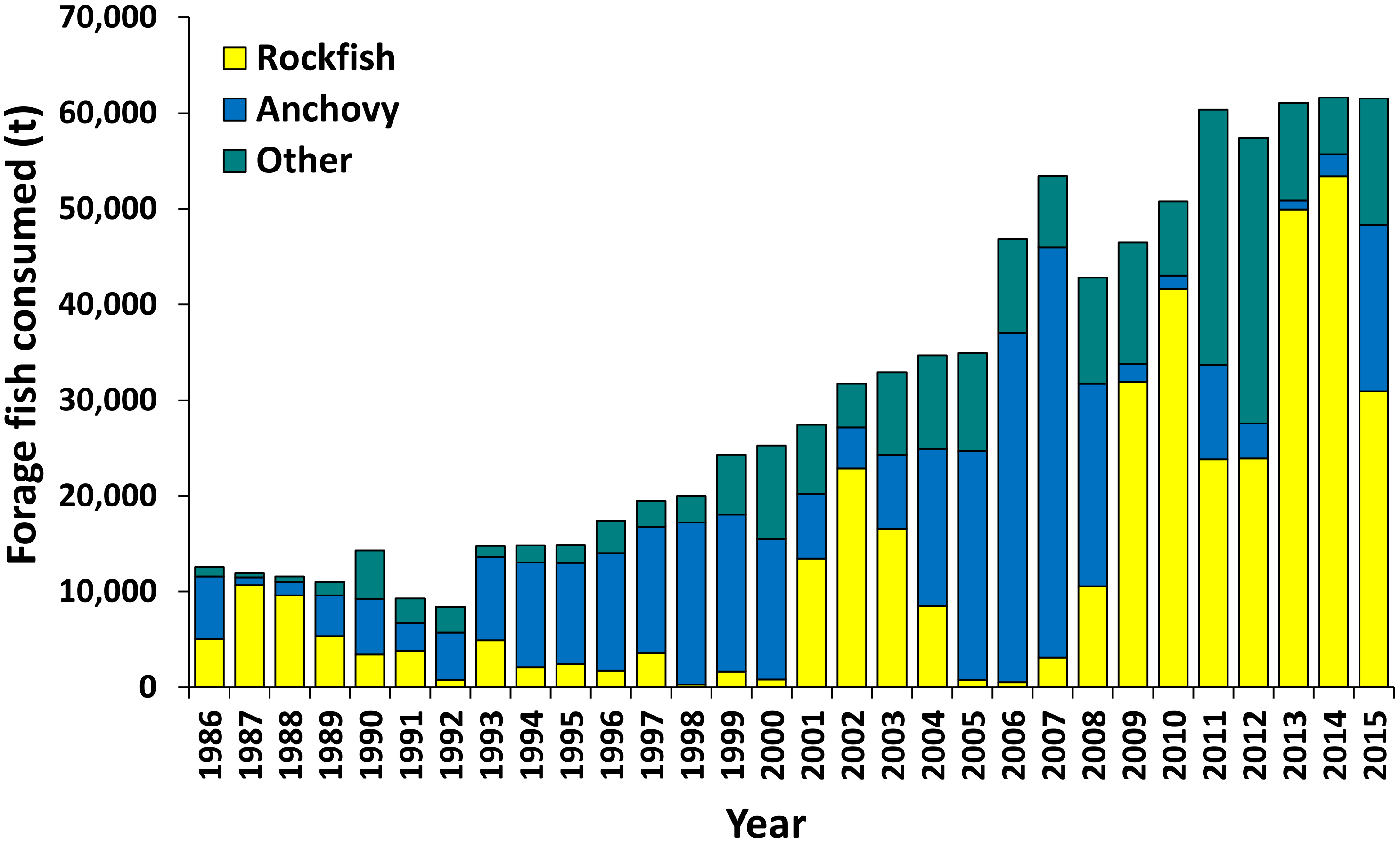
*Aerial survey data not available; SFI population from ground-based counts

# Figure 1

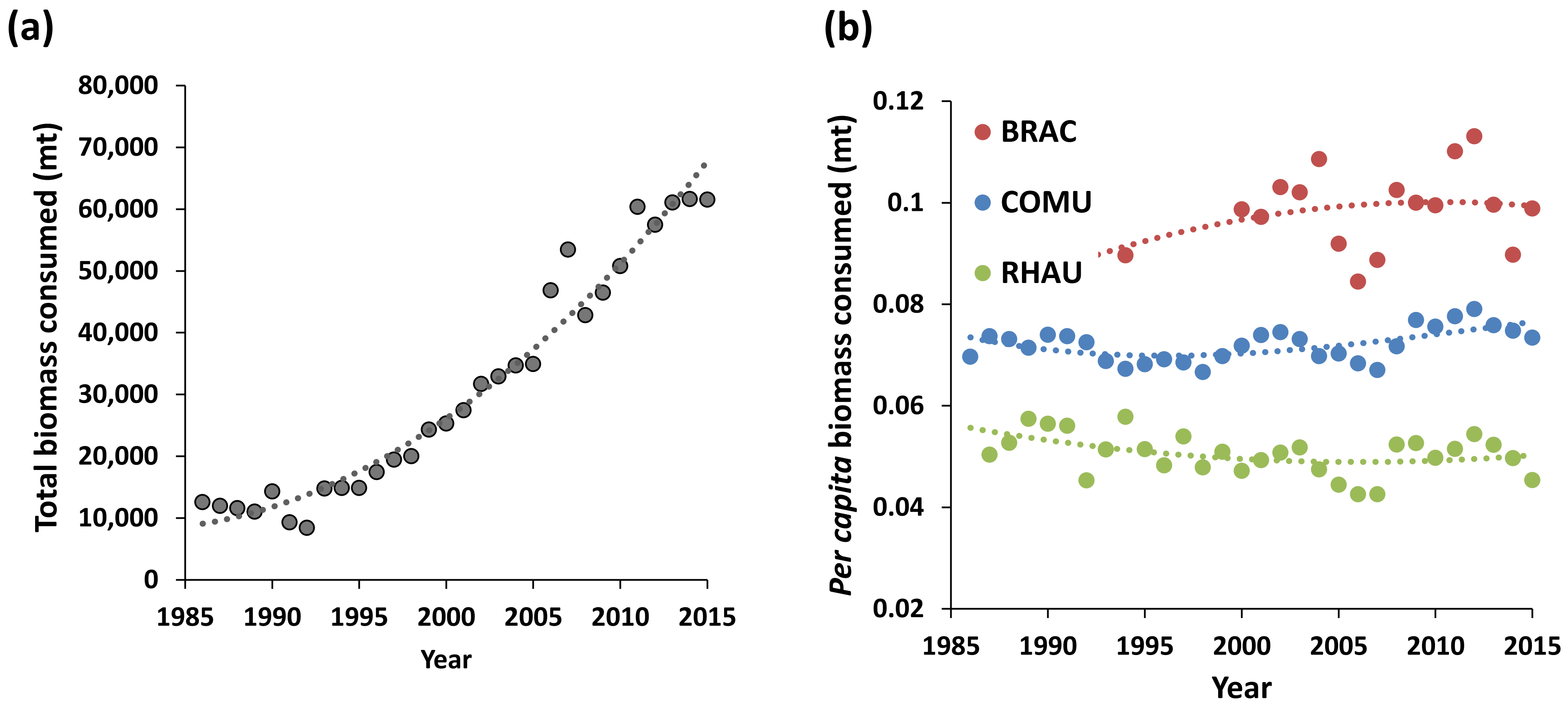


● Net and CTD Station
★ Farallon Islands
Kilometers
0 5 10 20 30 40 50 60
200 m
BODEGA BAY
PR
DB
NFI
LSR
SFI
DSR
200 m
ANI
38°
37°
-123°
-122°

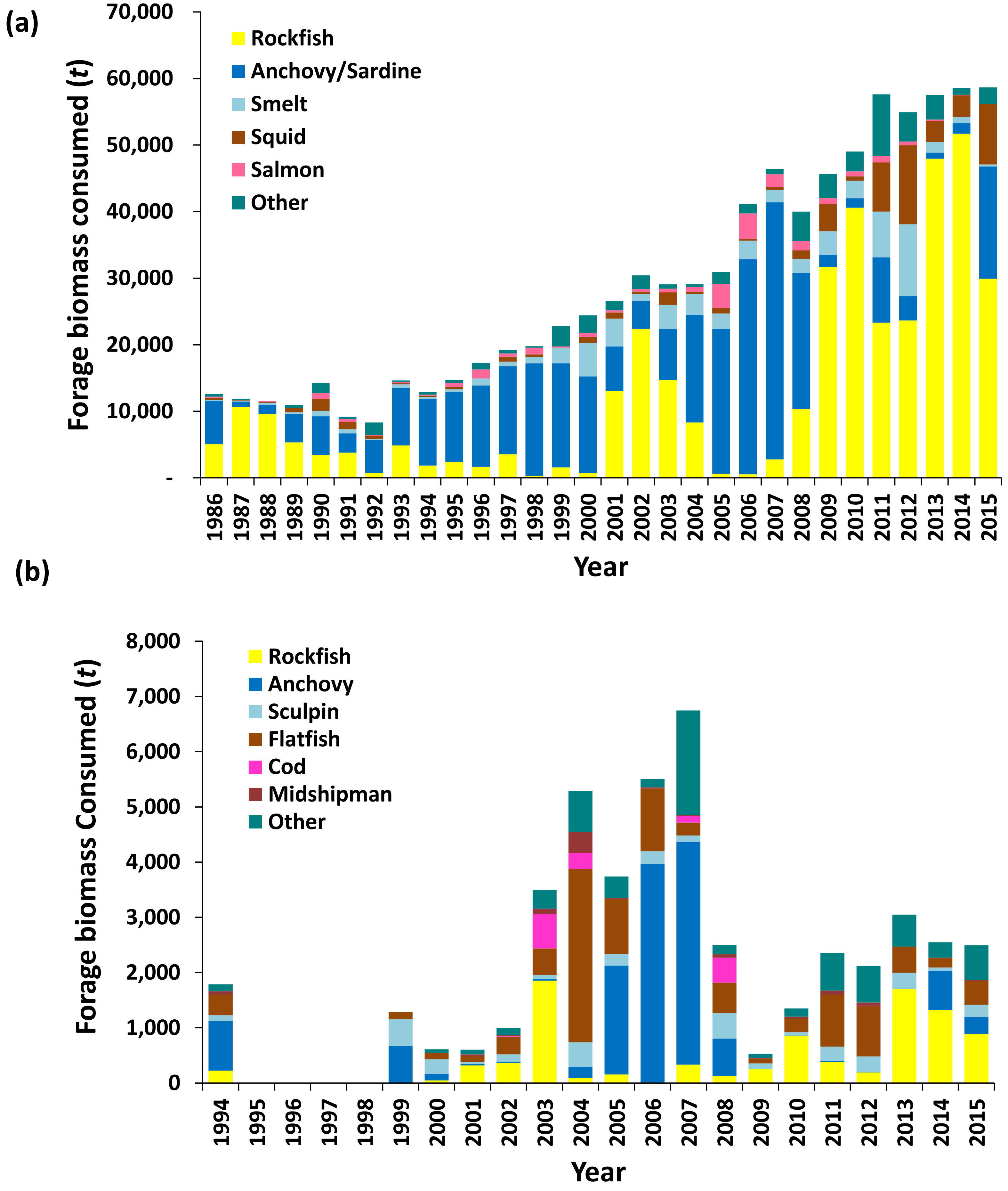
# Figure 2


70,000
60,000
50,000
40,000
30,000
20,000
10,000
0
Forage fish consumed (t)
Rockfish
Anchovy
Other
1986
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
Year

# Figure 3

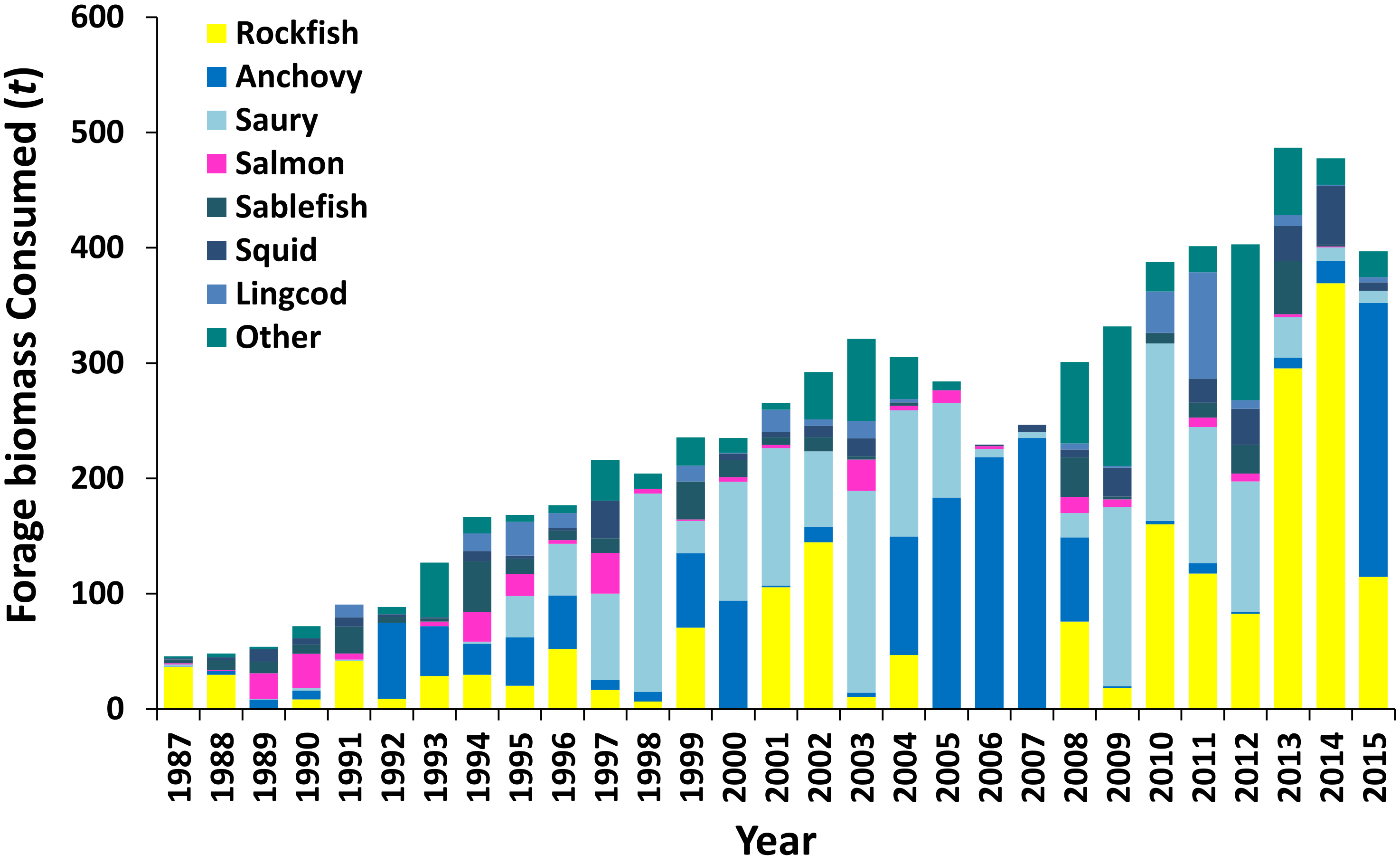

(a)
Total biomass consumed (mt)
80,000
70,000
60,000
50,000
40,000
30,000
20,000
10,000
0
1985
1990
1995
2000
2005
2010
2015
Year
(b)
Per capita biomass consumed (mt)
0.12
0.1
0.08
0.06
0.04
0.02
BRAC
COMU
RHAU
1985
1990
1995
2000
2005
2010
2015
Year

# Figure 4


(a)
Forage biomass consumed (t)
70,000
60,000
50,000
40,000
30,000
20,000
10,000
-
Rockfish
Anchovy/Sardine
Smelt
Squid
Salmon
Other
1986
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
Year
(b)
Forage biomass Consumed (t)
8,000
7,000
6,000
5,000
4,000
3,000
2,000
1,000
0
Rockfish
Anchovy
Sculpin
Flatfish
Cod
Midshipman
Other
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
Year

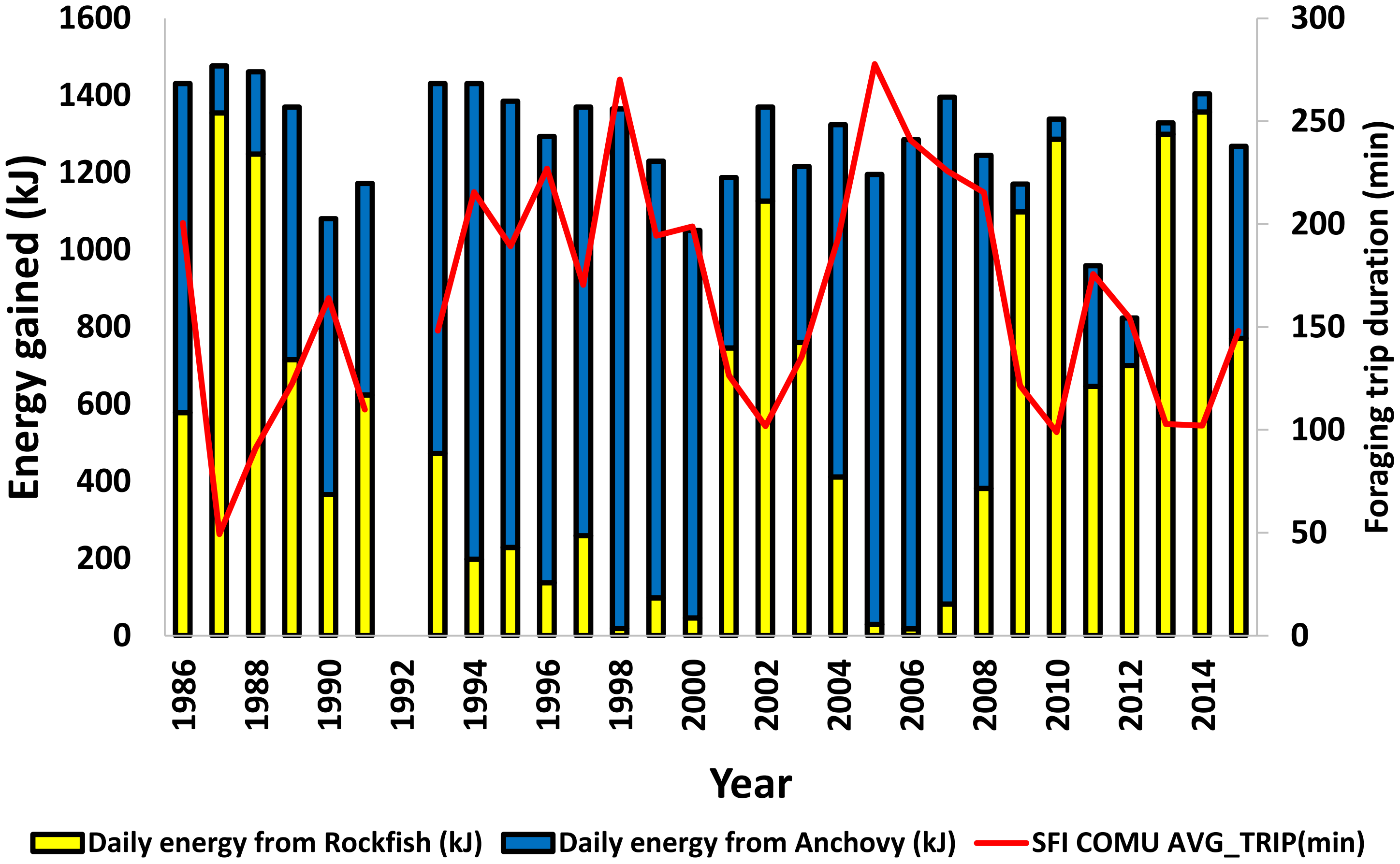
# Figure 4

(c)


Rockfish
Anchovy
Saury
Salmon
Sablefish
Squid
Lingcod
Other
Forage biomass Consumed (*t*)
0
100
200
300
400
500
600
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
Year

# Figure 5

(a)


1600
1400
1200
1000
800
600
400
200
0
Energy gained (kJ)
300
250
200
150
100
50
0
Foraging trip duration (min)
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
Year
Daily energy from Rockfish (kJ)
Daily energy from Anchovy (kJ)
SFI COMU AVG_TRIP(min)

(b)

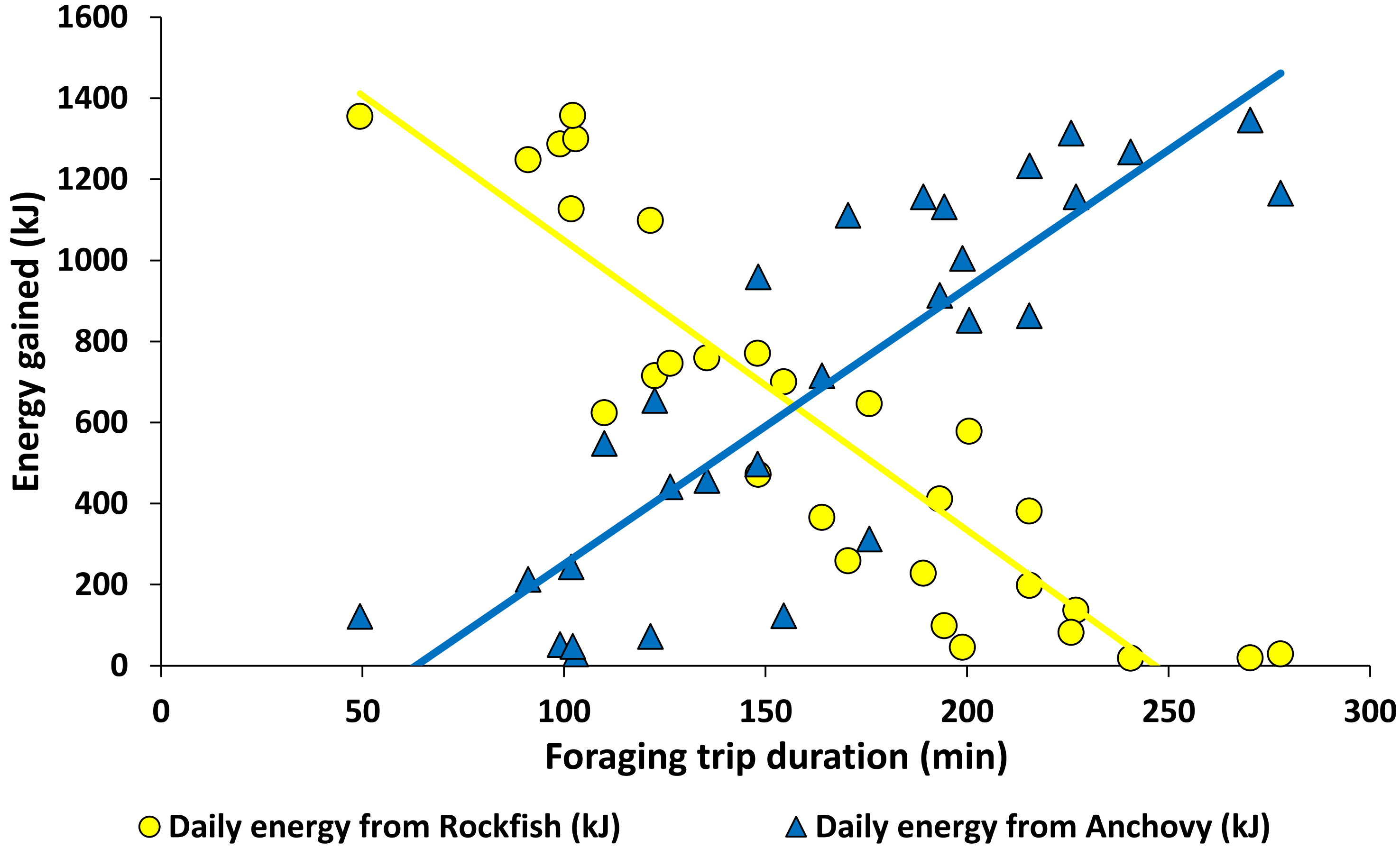
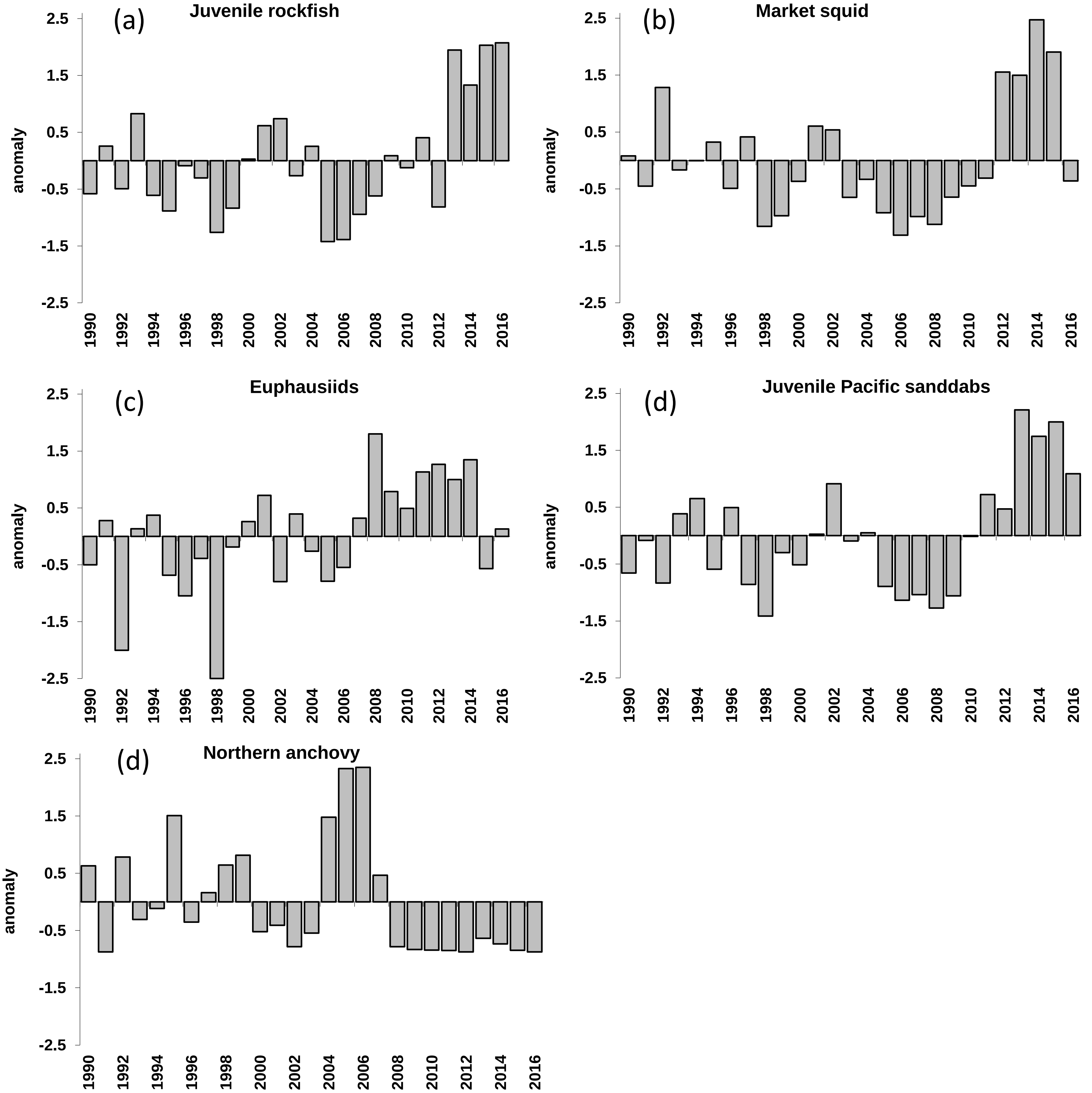
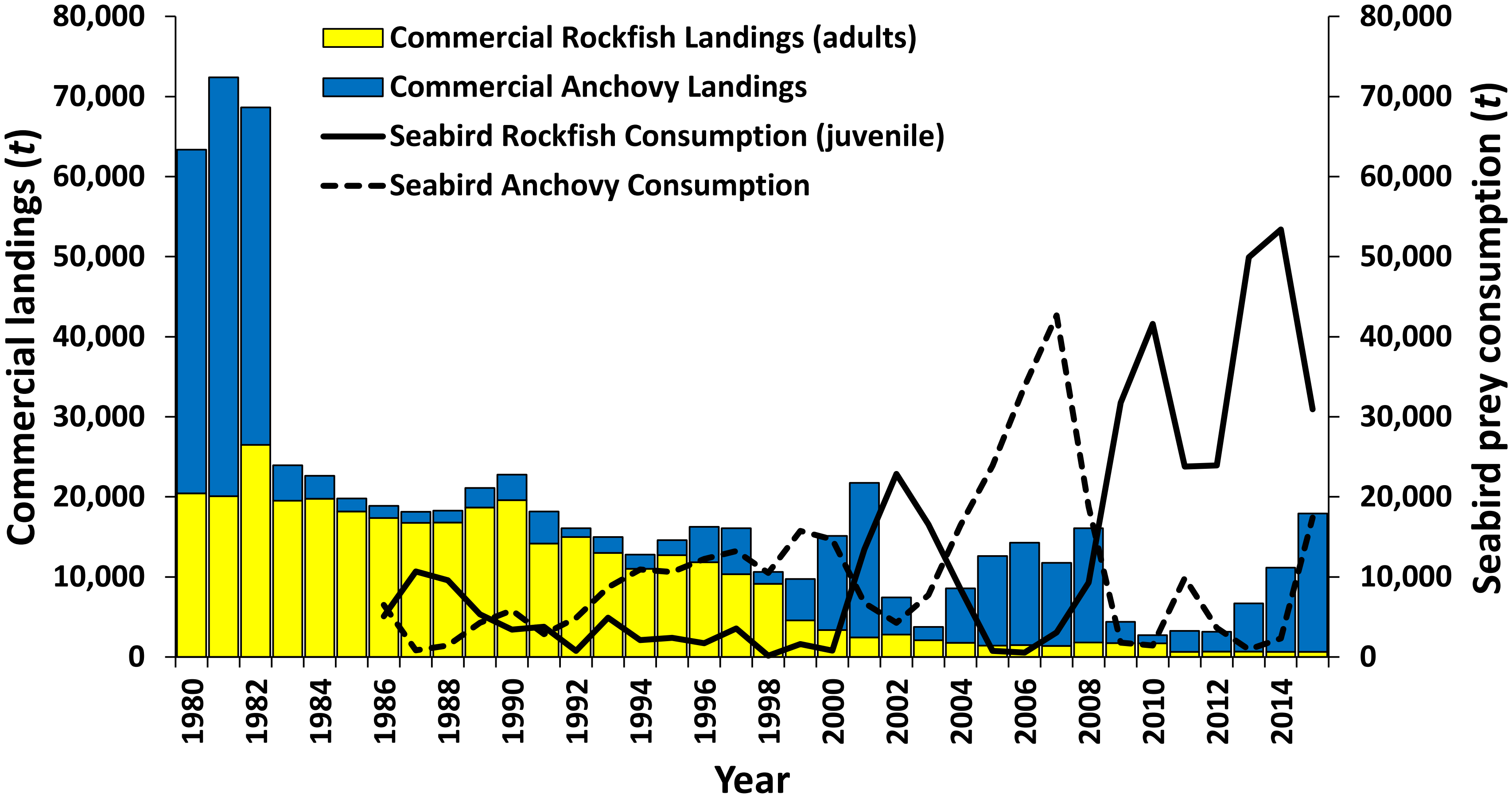

1600
1400
1200
1000
800
600
400
200
0
Energy gained (kJ)
0
50
100
150
200
250
300
Foraging trip duration (min)
Daily energy from Rockfish (kJ)
Daily energy from Anchovy (kJ)

Figure 6



(a)
Juvenile rockfish
(b)
Market squid
(c)
Euphausiids
(d)
Juvenile Pacific sanddabs
(d)
Northern anchovy
anomaly
2.5
1.5
0.5
-0.5
-1.5
-2.5
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016

# Figure 7



Commercial Rockfish Landings (adults)
Commercial Anchovy Landings
Seabird Rockfish Consumption (juvenile)
Seabird Anchovy Consumption
Commercial landings (t)
Seabird prey consumption (t)
80,000
70,000
60,000
50,000
40,000
30,000
20,000
10,000
0
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
Year