Annual prey consumption of a dominant seabird, the common murre, in the California Current system

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Information compiled from the literature on population size, diet composition, field metabolic rate, prey energy densities, and assimilation efficiency is used to estimate annual prey consumption by common murres (*Uria aalge*), between Cape Blanco, OR, and Point Conception, CA, USA. The population consumed an estimated 172 313 t of prey based on population estimates and diet data from the mid- to the late 1980s, including 50 125 t consumed by breeding adults, 36 940 t by non-breeding birds during the breeding season, 85 098 t by all birds during the wintering period, and 150 t by dependent chicks before their leaving the breeding colonies. The population in the mid-2000s consumed 225 235 t of prey based on population estimates from 2004, including 65 516 t consumed by breeding adults, 48 283 t by non-breeding birds during the breeding season, 111 226 t by all birds during the wintering period, and 210 t by chicks at breeding colonies. Monte Carlo simulations indicated that the coefficients of variation around our overall prey consumption estimates were $\pm 14.4\%$ for the 1980s and $\pm 13.2\%$ for the 2000s.

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Introduction

Seabirds are top predators in marine ecosystems, with substantial energetic needs and, as such, they consume a significant proportion of available resources (Brooke, 2004; Hunt *et al.*, 2005). Estimates of local fish consumption by seabird species or communities range from 5% to 64% of pelagic production (reviewed in Montevecchi, 1993). In addition, commercial fisheries (Jahncke *et al.*, 2004) and other top predators (large fish and marine mammals; Furness, 1990) often utilize the same prey resources. For instance, some researchers have estimated that seabirds and commercial fisheries harvest similar quantities of prey (Brown and Nettleship, 1984; Brooke, 2004), and others have found overlap in the size classes harvested by seabirds and humans (Schaffner, 1986; Bunce, 2001). As a result of this overlapping resource use, commercial fisheries may compete directly with seabirds for their prey. Indeed, the commercial harvest of forage fish has been linked to seabird population declines in some areas (Burger and Cooper, 1984; Tasker *et al.*, 2000; Jahncke *et al.*, 2004). Conversely, fisheries may, in some instances, enhance prey populations by removing large, predatory fish from the system that would otherwise compete with seabirds for prey (Hatch and Sanger, 1992; Tasker *et al.*, 2000). Additionally, prey consumption by marine mammals and predatory fish can be significant and may equal or exceed that of both seabirds and humans (Brown and Nettleship, 1984). Understanding the prey requirements of top predators is, therefore, important for understanding the dynamics of predator and prey populations and for managing living marine resources from an ecosystem perspective (May *et al.*, 1979).

The common murre (*Uria aalge*) is one of the most abundant seabird species in the California Current system (CCS), a large marine ecosystem in the northeast Pacific Ocean, throughout the year (Briggs *et al.*, 1987; Ford *et al.*, 2004). Adult murres consistently attend breeding colonies during the March–August breeding season (Boekelheide *et al.*, 1990; Manuwal *et al.*, 2001), and concentrate in the surrounding waters during that time (Oedekoven *et al.*, 2001; Yen *et al.*, 2004). Females lay a single egg in April or May that is incubated by both adults during the subsequent 32-d incubation period. Chicks begin hatching in May or June and are fed by both adults until they leave the colony at ~24 days old (June or July). Males care for the chicks at sea for an additional 2–3 months after they leave the colony, whereas females remain at the colony for several more weeks (Gaston and Jones, 1998; Ainley *et al.*, 2002). All birds leave breeding colonies by late August and spend several months at sea while they moult, dispersing along the coast (Wiens and Scott, 1975; Briggs *et al.*, 1987). Murres then spend most of the winter at sea, with sporadic colony attendance from October to February (Boekelheide *et al.*, 1990; Sydeman, 1993). Non-breeding murres (subadults) begin attending breeding colonies at 2 or 3 years of age, following the general pattern described above, but with less consistent attendance patterns. Murres typically forage in waters

overlying continental shelf and shelf break habitats in all seasons (Oedekoven *et al.*, 2001; Yen *et al.*, 2004), and can dive to depths of up to 180 m (Piatt and Nettleship, 1985), giving them access to a wide variety of prey species. In Oregon and California waters, the primary prey species include juvenile rockfish (*Sebastes* spp.), market squid (*Loligo opalescens*), northern anchovy (*Engraulis mordax*), Pacific hake (*Merluccius productus*), shiner surfperch (*Cymatogaster aggregata*), and midshipman (*Porichthys notatus*; Baltz and Morejohn, 1977; Croll, 1990a; Scott, 1990; Ainley *et al.*, 1996; Sydeman *et al.*, 1997b, 2001; Miller and Sydeman, 2004).

Bioenergetics models have been used to estimate the prey consumption of seabirds in many marine ecosystems based on estimates of daily energetic demand, efficiency of energy assimilation from prey, and energy density of prey (Wiens and Scott, 1975; Furness, 1978). Previous models constructed for common murres in other areas have concluded that adult murres require 200–500 g of prey daily (Brown and Nettleship, 1984; Cairns *et al.*, 1990; Gabrielsen, 1996). Based on these requirements, estimates of total prey consumption during the breeding season range from 3000 to 28 000 t per colony, depending on abundance. Wiens and Scott (1975) developed the first comprehensive bioenergetics model for four species of seabird along the Oregon coast. They estimated that prey consumption by the murre population remained relatively constant throughout the year and that murres consume ∼11% of the total pelagic fish biomass in the neritic zone. Briggs and Chu (1987) developed a similar model for all seabird species along the California coast, and estimated that seabirds take up to 193 000 t of prey annually, and that murres and sooty shearwaters (*Puffinus griseus*) are the dominant consumers.

Murre abundance has changed considerably since those estimates were made. In particular, the murre population in central California has increased steadily over the past several decades as it recovers slowly from dramatic population declines attributed to egg collecting, gillnet mortality, and oil spills, although it remains well below historical levels and of conservation concern (Takekawa *et al.*, 1990; Manuwal *et al.*, 2001). In addition, there have been several empirical studies that have provided additional information on murre energy requirements that were not available when the previous estimates were made. Here, therefore, the annual prey consumption by the entire murre population on a regional scale is estimated to understand better the birds' needs as predators, and to provide insight into predator–prey population dynamics. Specifically, existing data are used to (i) develop a bioenergetics model for murres between Cape Blanco, OR, and Point Conception, CA, USA, using population and diet data from the mid- to late 1980s, (ii) compare the 1980s estimate with projected prey consumption in the mid-2000s based on recent population counts, (iii) compare prey consumption for all subsets of the population, including breeding birds, non-breeding birds, wintering birds, and chicks at breeding colonies, and (iv) compare prey consumption estimates by prey species to determine which ones are most heavily utilized by murres. Ultimately, the aim is to have this information included in fishery–ecosystem plans for the region (e.g. CDFG, 2005a).

Methods and parameter estimates

The focus area is between Cape Blanco, OR, and Point Conception, CA, an area selected because it is oceanographically and biologically distinct from the areas to the north and the south, facilitating an estimate of regional prey consumption for colonies that are likely influenced by similar oceanographic processes. The region is very productive and characterized by stronger coastal upwelling, lower sea surface temperature, higher salinity, higher nutrient levels, and higher phytoplankton biomass in spring and summer than the area to the north of Cape Blanco (US GLOBEC, 1992; Huyer *et al.*, 2005). The area south of Point Conception is also characterized by less intense upwelling and relatively low productivity (US GLOBEC, 1992). In addition, several Subarctic zooplankton species reach their southern limit at Cape Blanco, and many epipelagic fish species reach their northern spawning limit at Point Conception (US GLOBEC, 1992).

Murre diet is assumed to be similar throughout the study area based on these biogeographic boundaries. The year was divided into two periods, the March–August breeding season and the September–February wintering period, based on the general patterns of murre breeding phenology described above. Three groups of birds are addressed: breeding birds during the breeding season, non-breeding birds during the breeding season, and wintering birds during the wintering period. For simplicity, adults and chicks are referred to throughout the paper. However, the non-breeding and wintering categories include both subadult (1–5 years old) and adult (6+ years old) birds. The wintering category also includes juveniles (chicks produced earlier in the year or "age 0" birds). The term "chicks" is used specifically to refer to dependent chicks at breeding colonies. The most recent and applicable information on field metabolic rate (FMR), diet composition, energy densities of prey, and assimilation efficiency available is included in the model. Colony counts from 1988 and 1989 were used as the basis for the population estimate, because the counts and the diet information (1985–1988) were obtained during roughly the same period. Prey consumption for the mid-2000s was estimated based on the most recent complete colony counts (2004). Chicks were not included in the bioenergetics model; chick prey consumption was instead estimated from direct observations of chick feedings. Details on the data used for each parameter are provided below.

Field metabolic rate

An average value of 1789 kJ d^{-1} measured during the breeding season in Newfoundland, Canada (Cairns *et al.*, 1990), was used as the basis for the model. This value was then adjusted to account for possible differences in FMRs between the two study areas. Ellis and Gabrielsen (2002) examined a variety of correlates to basal and FMRs and found that latitude and adult body weight had the greatest influence on the resulting values. Latitude in their equations is a proxy for regional differences in environmental factors. Sea surface temperature is likely the most important of these factors. Croll (1990b) found that thick-billed murres (*Uria lomvia*) expend a large portion (63%) of their daily energy budget sitting on the water surface or diving. Croll and McLaren (1993) then found that water temperatures <15°C are below the thermo-neutral zone for common murres and likely pose a significant energetic challenge to the birds. Based on this information, the estimate was adjusted to account for differences in sea surface temperature and adult body weight of murres between Newfoundland and California.

The adjustment for differences in sea surface temperature was made by calculating the portion of daily energy expenditure affected by that factor, based on the finding of Croll (1990b) that thick-billed murres expend 63% of their daily energy budget on or in the water (FMR$_{Water}$ = FMR$_{Newfoundland}$ × 0.63).

The metabolic rate (MR) for birds in each region was then estimated using the equation $MR = 17.39 - 0.60 \times$ water temperature (Croll and McLaren, 1993), where water temperature $= 11.97°C$ in California and $5.67°C$ in Newfoundland. These water temperatures reflect the average sea surface temperatures during the breeding seasons from 1995 to 2004. The measurements were obtained from Southeast Farallon Island, CA (SEFI; 37°42′N 123°00′W) and Hydrographic Station 27 off St John's, Newfoundland (47°32′N 52°35′W). Finally, the ratio between the two MRs was calculated, multiplied by the portion of the daily energy budget affected by water temperature $[(MR_{California}:MR_{Newfoundland}) \times FMR_{Water}]$, and added to the portion of the daily energy budget spent out of the water, to obtain an adjusted FMR of 1485 kJ d^{-1}.

An additional adjustment for differences in average adult body weight between the two populations was made by estimating basal MR (BMR) separately for each population using the equation $BMR = 3.201 \times weight^{0.719}$ (Ellis and Gabrielsen, 2002), where weight $= 980$ g in California and 940 g in Newfoundland. The ratio between the two values was then multiplied by the adjusted FMR described above $[(BMR_{California}:BMR_{Newfoundland}) \times FMR_{Adjusted}]$ to obtain an average FMR of 1530 kJ d^{-1} for breeding murres in Oregon and California. Weights from freshly caught, rather than post-absorptive, birds were used in the BMR equations, so the values may have been overestimated. However, this should not affect the ratio between the two values used for the adjustment. The energy requirements of breeding birds were assumed to be 10% higher than those of non-breeding and wintering birds, largely because of the high energy cost of flying between the colony and foraging areas during chick provisioning (Ricklefs, 1983; Gales and Green, 1990). A FMR of 1392 kJ d^{-1} was therefore assigned to models of non-breeding and wintering populations. Finally, the energy requirements of non-breeding and wintering birds were assumed to be equal owing to the similar foraging requirements and a relatively mild climate throughout the year (i.e. thermoregulatory requirements should not vary much seasonally).

Adult diet composition

Estimates of adult diet composition were based on Ainley *et al.* (1996). Those authors summarized diet composition (proportion weight) for the pre-breeding (March–April), breeding (April–August), and non-breeding (September–February) seasons in coastal, mid-shelf, and outer shelf habitats from 1985 to 1988. Weighted averages were calculated for the breeding season as defined (March–August), based on the number of months in the Ainley *et al.* (1996) pre-breeding and breeding seasons (Table 1), but values reported as <1% in the original source were considered to be zero. Weighted averages across the habitat types of Ainley *et al.* (1996; coastal, mid-shelf, and outer shelf) for the breeding and wintering periods were calculated based on the densities of murres in each habitat type.

Density estimates were drawn from data contained within the marine mammal and seabird computer database analysis system: Washington, Oregon, California 1975–1997, Version 2.1 (MMS CDAS; ECI, 2001). The database contains seabird distribution and abundance data summarized as densities for each 5′-latitude by 5′ longitude block, based on low aerial and ship transects that covered the entire study area. The data were collected between the coast and 60 nautical miles offshore from 1989 to 1990 in Oregon, and between the coast and 100 nautical miles offshore from 1980 to 1983 in central and northern California. In addition,

Table 1. Adult common murre diet composition data (% by weight) based on Ainley *et al.* (1996).

Prey species	Breeding season[a] March–August	Wintering period[a] September–February
Euphausia pacifica	0.20	0
Thysanoessa spinifera	1.05	0.43
Market squid	8.01	40.59
Octopus	0.32	0
Northern anchovy	17.06	10.33
Shiner surfperch	4.18	15.00
Kelp surfperch	1.54	0
Pacific hake	39.68	0
Lingcod	3.30	0
Pacific sanddab	5.74	0
Midshipman	0	13.10
Spotted cusk-eel	0.16	1.77
Pacific herring	5.79	4.09
Night smelt	0.40	2.33
Rockfish	10.92	11.01
Jacksmelt	1.29	0
Pacific butterfish	0	0.68
Unidentified	0.08	0.22

Columns do not add to 100% because values <1 in the original source were treated as zero.
[a]Original values averaged across seasons and habitat types.

more focused studies in central and northern California coastal waters in 1985 and from 1994 to 1997 are included. ArcView 3.2 (ESRI, 1998) was used to determine the depths of the midpoint of each $5′ \times 5′$ block that fell within the study area of Ainley *et al.* (1996), and each block was categorized according to the depth categories (coastal 0–40 m; mid-shelf 41–70 m; outer shelf 71–120 m) used by Ainley *et al.* to derive averaged murre densities for each category. The densities used to weight prey composition data were 32.19 birds km^{-2} in coastal, 26.40 birds km^{-2} in mid-shelf, and 8.08 birds km^{-2} in outer shelf habitats during the breeding season, and 47.57 birds km^{-2} in coastal, 61.85 birds km^{-2} in mid-shelf, and 30.08 birds km^{-2} in outer shelf habitats during the wintering period.

Chick diet composition

Prey deliveries to dependent offspring were observed at a large colony on SEFI to determine chick diet composition. Specifically, daily observations were made in rotating 2-h blocks from 07:00 to 19:00 for 30–35 d during the peak chick-rearing period in each season. In addition, observations were made during 2–4 "all-day" periods (06:00–20:00) to determine the total number of feedings each site received in a single day for later calculation of provisioning rates. These observations were summarized for 1986–1988 (119–136 breeding pairs; 309 observation hours), representing the earlier period, and for 2000–2004 (105–185 breeding pairs; 476 observation hours), representing the later period.

During these observations, all prey items were identified to the lowest possible taxon, based on external morphological characteristics such as colour, body shape, tail shape, and shape and position of fins (Miller and Lea, 1972; Sydeman *et al.*, 2001; Miller and Sydeman, 2004). Prey were grouped into the categories: juvenile

rockfish, northern anchovy/Pacific sardine (*Sardinops sagax*), smelt (Osmeridae), market squid, salmon (*Onchorhynchus* spp.), flatfish (Pleuronectidae and Bothidae), sandlance (*Ammodytes hexapterus*), lingcod (Hexagrammidae), sculpins (Cottidae), Pacific saury (*Cololabis saira*), and other (including unidentified prey). In addition, the length of each prey item relative to the gape length of the adult was estimated visually. However, it was sometimes impossible to see the entire fish during these observations because a portion of the fish was held in the gullet of the adult. To assess whether this led to underestimation of prey sizes, the visual estimates were compared with measured lengths of rhinoceros auklet (*Cerorhinca monocerata*) prey collected at SEFI during the same period. The two species generally prey on similar age and size classes (Gaston and Dechesne, 1996; Ainley et al., 2002), and direct comparisons of prey selection have shown no difference in size classes taken during the non-breeding season (Lance and Thompson, 2005). The sizes of anchovy and salmon, the two largest species in murre diet, were consistently underestimated by an average of 22% and 13%, respectively, so the visual estimates were adjusted for those species. Visual estimates for all other prey species that could be compared were within a few percentage points above or below the measured values and were not underestimated consistently. Finally, the length estimates were converted to weight using length–weight regression equations derived from the auklet prey (PRBO, unpublished data). Sample sizes used to generate the regression equations were: 742 northern anchovy, 101 Pacific sardine, 1130 juvenile rockfish, 180 salmon, 116 market squid, 935 Pacific saury, and 159 lingcod.

Prey energy density

Energy densities for prey species from the literature were utilized when available (Table 2), but some substitutions for prey species without published values of energy density had to be used. A value for "euphausiids" (Davis et al., 1998) was used for both *Euphausia pacifica* and *Thysanoessa spinifera*, a value for market squid (Spear, 1993) for octopus (*Octopus rufescens*), a value for "surfperch" (Roby et al., 2003) for both kelp (*Brachyistius frenatus*) and shiner surfperch, and a value for topsmelt (*Atherinops affinis*; Dahdul and Horn, 2003) for jacksmelt (*Atherinopsis californiensis*). Estimates for Pacific hake and Pacific butterfish (*Peprilus simmillimus*) were calculated from published values of percentage lipid and protein of Pacific hake (protein 15.7%, lipid 1.44%) and Atlantic butterfish (*Peprilus triacanthus*; protein 16.55%, lipid 1.60%) fillets (C. Harvey, NOAA, pers. comm.). Protein values were multiplied by their calorific equivalent of $17 \, \text{kJ g}^{-1}$, and lipid values were multiplied by $38 \, \text{kJ g}^{-1}$. A value for short-bellied rockfish (*Sebastes jordani*; Spear, 1993) was used for all rockfish species, and an average, weighted by diet composition, for all prey items to estimate the energy density of the unknown prey taken during the breeding and wintering periods.

Assimilation efficiency

An average assimilation efficiency of 78.39% was used, based on data from Hilton et al. (2000) for common murres fed diets of lesser sandeel (*Ammodytes marinus*) and whiting (*Merlangius merlangus*). These prey items were the only two prey types in the Hilton et al. (2000) study and had similar energy densities ($4.63 \, \text{kJ g}^{-1}$ for sandeel and $4.41 \, \text{kJ g}^{-1}$ for whiting) to the prey types consumed by murres in California.

Adult and chick abundance

Breeding season (March–August). Abundance data are based on aerial photographic counts of 25 colonies in southern Oregon in 1988 (Naughton et al., in press) and 23 colonies in California in 1989 (Carter et al., 1992; Table 3). A correction factor was applied to the raw counts to account for non-breeding birds in the colony and mates away from the colony at the time the photographs were taken (Sydeman et al., 1997a). Correction factors were calculated from study plots on SEFI according to the equation: Correction factor = (2 × breeding sites)/adult count. An average value of 1.68 for 1980, 1981, 1985, and 1986 was used, following Carter et al. (1992). Current prey consumption was estimated based on the most recent complete census available for California (2004; G. McChesney, USFWS, pers. comm.). The most recent complete census available for southern Oregon is from 1988, but data from ten sample colonies counted in both 1988 and 2004 indicate an 11% decline in the murre population since that census (D. Pitkin, USFWS, pers. comm.). Consequently, the raw count was decreased by this percentage to derive a population estimate for southern Oregon in 2004. A correction factor of 1.50 was applied to these counts, based on more recent data (2000–2004) from SEFI (PRBO, unpublished).

A Leslie projection matrix approach was used to estimate the number of non-breeding birds in the study area (Table 3). Specifically, the proportion of the population that were non-breeders was estimated, based on two stable age structures for the SEFI population. The two scenarios were based on different estimates of age-specific survival, to allow for uncertainty in that parameter (Appendix). The results of the first scenario indicated that the population consists of 58.8% breeding and 41.2% non-breeding birds. The results of the second scenario indicated that breeding birds comprise 51.5% of the total population, and non-breeding birds 48.5%. The proportions from the two scenarios were averaged, and it was assumed that the population consisted of 55.1% breeding birds and 44.9% non-breeding birds for both periods.

The average number of chicks hatched (0.89 chicks hatched pair^{-1} from 1985 to 1989; 0.86 chicks hatched pair^{-1} from 2000 to 2004) from four study plots on SEFI was used to estimate the number of chicks at breeding colonies. The study plots are located around the island and cover all major habitat types. Each plot contained between 30 and 185 breeding pairs. Daily nest checks were conducted at all sites from 16 April until the last chick fledged (approximately early August), to determine whether an egg was laid, if a chick hatched, and if it fledged, at each site. Mean hatching success was taken to be the number of chicks hatched divided by the number of eggs produced. Sample sizes for determining hatching success were 736 breeding sites for the 1980s estimate (120 in 1985, 119 in 1986, 153 in 1987, 163 in 1988, and 181 in 1989) and 1752 breeding sites for the 2000s estimate (276 in 2000s, 327 in 2001, 369 in 2002, 372 in 2003, and 408 in 2004). The overall estimate of hatching success was multiplied by the number of breeding pairs in the study area, to calculate the number of chicks hatched in the region (Table 3). The number of chicks in each successive age class (e.g. 1, 2, and 3 d) between hatching and fledging was based on the proportion of chicks surviving to each age in SEFI plots. It was assumed that the offspring population joined the wintering population once they left breeding colonies at ~24 days old, and were counted during the winter surveys described below.

Table 2. Published energy densities for common murre diet items.

Prey species	Energy density (kJ g^{-1} wet weight)	Source
Euphausia pacifica	**3.11**	Davis *et al.* (1998)
Thysanoessa spinifera	**3.11**	Davis *et al.* (1998)
Market squid	4.14	Spear (1993)
Octopus	4.14	Spear (1993)
Northern anchovy	5.56	Dahdul and Horn (2003)
Shiner surfperch	**4.16**	Roby *et al.* (2003)
Kelp surfperch	**4.16**	Roby *et al.* (2003)
Pacific hake	**3.2**	C. Harvey, NOAA, pers. comm.
Lingcod	3.98	Anthony *et al.* (2000)
Pacific sanddab	3.47	Spear (1993)
Plainfin midshipman	5.23	Spear (1993)
Spotted cusk-eel	3.39	Spear (1993)
Pacific herring	5.78	Roby *et al.* (2003)
Night smelt	4.33	Spear (1993)
Rockfish	4.85	Spear (1993)
Jacksmelt	**4.44**	Dahdul and Horn (2003)
Pacific butterfish	**3.4**	C. Harvey, NOAA, pers. comm.
Unidentified (breeding season)	**4.04**	–
Unidentified (wintering period)	**4.56**	–

Diet composition is based on Ainley *et al.* (1996). Emboldened values indicate substitutions that are explained in text.

Winter (September–February). Abundance during the wintering period was estimated using data from the MMS CDAS (ECI, 2001) database described above (see section on Adult diet composition above). Murre distribution data for the breeding and wintering periods for the entire study area were imported into ArcView 3.2 (ESRI, 1998), then densities were averaged across all blocks to estimate the overall density for the region. Abundance was

Table 3. Population estimates for common murres from Cape Blanco, OR, to Point Conception, CA.

Parameter	Season	Number of birds		Source
		1988/1989	2004	
Adult population estimates				
Breeding population	March–August	547 030	715 000	a
Non-breeding population	March–August	443 090	579 150	b
Wintering population	September–February	1 188 150	1 552 970	c
Chick population estimate				
Number of chicks at breeding colonies	March–August	243 430	307 450	d

[a]Raw counts obtained from Carter *et al.* (1992) and G. McChesney (USFWS) for California, and from Naughton *et al.* (in press) for Oregon. Counts were adjusted using a correction factor of 1.68 for 1988/1989 (Carter *et al.*, 1992) and 1.50 for 2004 (PRBO, unpublished data).
[b]Breeding population × 0.81 (PRBO, unpublished data).
[c]Total breeding season population × 1.2 (ECI, 2001).
[d][Total breeding population/2] × 0.89 for 1988/1989 and Total breeding population/2] × 0.86 for 2004 (PRBO, unpublished data).

estimated by multiplying the overall density by the total area sampled for the breeding and wintering periods, and the ratio between wintering period and breeding season abundance was taken as 1.2, which multiplied by the breeding season estimate yielded final winter population estimates for both periods (Table 3).

The model and model error

The biomass of each prey species consumed by the adult population was calculated from

$$\text{Biomass consumed (g)} = \sum_i \frac{\text{DC}_i}{\text{ED}_i} \times \frac{\text{FMR}}{\text{AE}} \times \text{PS} \times D,$$

where DC_i is the diet composition (proportion by weight), ED_i the energy density for each prey species (kJ g^{-1}), FMR the field metabolic rate (kJ d^{-1}), AE the assimilation efficiency, PS the population size (number of birds), and D the number of days (184 during the breeding season, 181 during the wintering period). These calculations were made separately for breeding birds, non-breeding birds, and wintering birds for each period.

Chick prey consumption was estimated based on direct observations of chick feedings using the equation

$$\text{Biomass consumed (g)} = \sum_i \sum_j \text{PR}_i \times \text{PM}_i \times \text{CD}_i \times \text{DC}_j$$

where PR_i is the mean provisioning rate (number of fish fed to chicks per day) for each chick age class, PM_i the mean prey weight (g fish^{-1}) for each chick age class, CD_i the number of "chick days" for each chick age class, based on the total number of chicks in the study area and the proportion that survived to a given age, and DC_j the chick diet composition (proportion by weight). The resulting values for all subsets of the population

were converted to tonnes, then summed to obtain the total biomass consumed by murres in the study area during one annual cycle. Results are rounded to the nearest 10 t, except for prey-specific estimates that are rounded to the nearest tonne for chicks.

Model error

Monte Carlo simulations were used to calculate standard errors for population-level energy requirements (varying FMR and population size), population-level prey consumption given specified energy requirements (varying energy density and assimilation efficiency), and the overall model (all errors combined) for the breeding and wintering periods in each period. In all, 1000 simulations were run for each of the above categories, and each parameter varied based on the parameter-specific standard error estimates described below. When parameters were calculated from multiple values, each value was allowed to vary independently of the others. The samples came from uniform distributions to allow for all possible values within the range of each parameter. The error for the chick prey consumption model was not estimated. However, chick prey consumption was <0.1% of the total estimate, so it was assumed that the error associated with this parameter was insignificant overall.

The average FMR reported by Cairns *et al.* (1990) was used in the model and its associated standard error in the simulations (Table 4). The standard error of the equations used to make the sea surface temperature and adult body weight adjustments to the original FMR value were estimated based on the standard errors of the regression coefficients. The effect of the assumption that there is a 10% cost of breeding was addressed by allowing the ratio to vary between 0% (no cost) and 20% (higher cost). An average energy density, weighted by diet composition, was calculated for each season and again the associated standard errors of the estimates used in the simulations. The average assimilation efficiency was used in the model and the associated standard error in the simulations, based on Hilton *et al.* (2000). It was not possible to estimate the error associated with diet composition because there are no comparable data from another 4-year period or another colony.

The error associated with the breeding bird counts in the earlier period was estimated by fitting a cubic curve to the relationship between breeding population size on SEFI and year, using data from 1984 to 1995. A predicted value for 1989 and the standard error of the prediction were calculated based on that relationship, then the ratio of the standard error of the prediction to the prediction was used as the error estimate in the simulations (Table 4). The same procedure for estimating the error associated with the 2004 counts was followed, using data from 1995 to 2004 for the regression and calculating a predicted value for 2004. The standard error of the average correction factors applied to the raw counts was estimated, and the effect of variation in non-breeding population size assessed by allowing the value to vary between the minimum estimate from Scenario 1 in the Leslie matrix analysis (41.2% of the population are non-breeders) and the maximum estimate from Scenario 2 (48.5% of the population are non-breeders). The ratio of wintering period:breeding season abundance was used to estimate wintering numbers in the model, and allowed to vary based on its associated standard error.

Results

Prey consumption

Wintering birds required an estimated 396 g d^{-1}, non-breeding birds some 453 g d^{-1}, and breeding birds 498 g d^{-1}. The murre population in our study area therefore consumed 172 313 t of prey annually based on diet and population data from the mid- to the late 1980s (Table 5). This estimate included 50 125 t for breeding birds, 36 940 t for non-breeding birds during the breeding season, 85 098 t for all birds during the wintering period, and 150 t for chicks at breeding colonies (Tables 5 and 6). Market squid and Pacific hake each constituted >20% of adult annual consumption at 44 203 and 42 425 t, respectively (Table 5). Other species making up at least 10% of adult annual consumption included northern anchovy (17 622 t) and shiner surfperch (17 267 t). Chick diet was dominated by anchovy/sardine (53%) and rockfish species (44%; Table 6).

The estimates were projected into the mid-2000s using population data from 2004 (Table 5). These estimates indicated that breeding birds consumed 65 516 t, non-breeding birds 48 283 t during the breeding season, wintering birds 111 226 t, and chicks at breeding colonies 210 t, for a total of 225 235 t annually (Tables 5 and 6). Based on the earlier diet data, adults consumed 57 776 t of market squid, 55 452 t of Pacific hake, 23 033 t of northern anchovy, and 22 570 t of shiner surfperch. Based on recent diet information, chick diet continued to be dominated by anchovy/sardine (63%) and rockfish (21%), although the proportions indicated that anchovy/sardine became even more dominant in the later period (Table 6).

Model error

The coefficients of variation (CVs) associated with population-level energy requirements were estimated as 11.15% for the breeding season, 16.98% for the wintering period, and 13.17% annually for the 1980s. The corresponding estimates for the 2000s were 10.53% for the breeding season, 16.55% for the wintering period, and 12.64% annually. When energy requirements were held constant, the CVs for the population-level prey consumption estimates were 2.45% for the breeding season, 4.01% for the wintering period, and 2.38% annually for both estimates (the parameters included in this part of the model were the same for both periods). The CVs associated with the overall prey consumption estimates (all errors combined) were 11.44% for the breeding season, 18.45% for the wintering period, and 14.38% annually for the 1980s estimate, and 10.82% for the breeding season, 17.70% for the wintering period, and 13.15% annually for the 2000s.

Discussion

Daily prey consumption

Murres require seemingly ∼396−498 g d^{-1} of food, depending on the season. The breeding season estimate (498 g d^{-1}) is somewhat higher than those from other studies. Gabrielsen (1996) estimated that common murres consume 440 g d^{-1} during chick-rearing, and Croll (1990b) estimated that thick-billed murres consume 286 g d^{-1} during the same period. These differences may be attributable to differences in the FMRs, energy densities of prey, or assimilation efficiencies included in the models. The FMR used in the current model was lower than those used by Gabrielsen (1996) and Croll (1990b), so it does not appear to be contributing to the higher estimate. However, there are differences in the average estimates of metabolizable energy (prey energy

Table 4. Parameter values and standard errors used in Monte Carlo simulations.

Parameter *Component*	1988/1989		2004	
	Parameter value	**Standard error**	**Parameter value**	**Standard error**
Breeding population size	547 028	n/a	714 995	n/a
Raw count	*325 612*	*± 25 333*	*476 663*	*± 23 833*
Correction factor	*1.68*	*± 0.04*	*1.50*	*± 0.02*
Non-breeding population size	443 093	n/a	579 146	n/a
Non-breeding population:breeding population ratio	*0.81*	*± 0.12*	*0.81*	*± 0.12*
Wintering population size	1 188 145	n/a	1 552 969	n/a
Wintering period:breeding season ratio	*1.2*	*± 0.24*	*1.2*	*± 0.24*
Breeding FMR	1 530	n/a	1 530	n/a
FMR estimate	*1 789*	*± 132.50*	*1 789*	*± 132.50*
Sea surface temperature and weight adjustment	*0.86*	*± 0.08*	*0.86*	*± 0.07*
Non-breeding FMR	1 392	n/a	1 392	n/a
Reduction from breeding rate	*0.91*	*± 0.08*	*0.91*	*± 0.08*
Assimilation efficiency	0.7839	*± 0.0041*	0.7839	*± 0.0041*
Average prey energy density (breeding season)	4.04	*± 0.25*	4.04	*± 0.25*
Average prey energy density (wintering period)	4.56	*± 0.21*	4.56	*± 0.21*

Components of each parameter and associated standard errors are shown in italics; n/a, not applicable.

density × assimilation efficiency) among the three studies [5.0 kJ g^{-1} in the Gabrielsen (1996) model, 4.52 kJ g^{-1} in the Croll (1990b) model, and 3.25 kJ g^{-1} in the current model] that likely contribute to the differences, largely in terms of differences in prey energy densities. Murres in the other studies fed primarily on a few fish species with relatively high energy densities, whereas in central California they fed on a wider variety of prey with a greater range of energy densities and likely consumed more prey per day to meet their energy requirements.

Seasonal and annual comparisons

The present estimate of prey consumption per day was lower for wintering birds (∼396 g d^{-1}) than for non-breeding birds (∼453 g d^{-1}) during the breeding season, despite the assumption that energy requirements and assimilation efficiencies were the same. The switch in diet from hake (3.20 kJ g^{-1}) during the breeding season to the more energy-dense squid (4.14 kJ g^{-1}) during the winter may be partly responsible for this result. Other fish species with relatively high energy densities (e.g. shiner surfperch,

Table 5. Biomass (t) of each prey type consumed by adult common murres from Cape Blanco, OR, to Point Conception, CA.

Prey species	Breeding adults		Non-breeding adults		Wintering adults		Total	
	1988/1989	**2004**	**1988/1989**	**2004**	**1988/1989**	**2004**	**1988/1989**	**2004**
Euphausia pacifica	128	167	94	123	0	0	222	290
Thysanoessa spinifera	667	872	492	643	532	695	1 691	2 210
Market squid	3 811	4 981	2 808	3 671	37 584	49 124	44 203	57 776
Octopus	153	200	113	148	0	0	266	348
Northern anchovy	6 044	7 900	4 454	5 822	7 124	9 311	17 622	23 033
Shiner surfperch	1 981	2 590	1 460	1 909	13 826	18 071	17 267	22 570
Kelp surfperch	727	950	536	700	0	0	1 263	1 650
Pacific hake	24 425	31 925	18 000	23 527	0	0	42 425	55 452
Lingcod	1 633	2 135	1 204	1 573	0	0	2 837	3 708
Pacific sanddab	3 257	4 257	2 400	3 137	0	0	5 657	7 394
Plainfin midshipman	0	0	0	0	9 599	12 546	9 599	12 546
Spotted cusk-eel	94	122	69	90	2 005	2 621	2 168	2 833
Pacific herring	1 975	2 581	1 455	1 902	2 714	3 547	6 144	8 030
Night smelt	183	239	135	176	2 063	2 696	2 381	3 111
Rockfish	4 437	5 799	3 270	4 274	8 701	11 373	16 408	21 446
Jacksmelt	571	747	421	550	0	0	992	1 297
Pacific butterfish	0	0	0	0	769	1 005	769	1 005
Unidentified	39	51	29	38	181	237	249	326
Total	50 125	65 516	36 940	48 283	85 098	111 226	172 163	225 025

Table 6. Biomass (t) of each prey type consumed by common murre chicks from Cape Blanco, OR, to Point Conception, CA.

Prey species	Biomass (t)	
	1988/1989	**2004**
Rockfish	66	44
Northern anchovy/Pacific sardine	79	134
Smelt spp.	2	15
Squid spp.	2	7
Pacific butterfish	0	3
Flatfish spp.	0	1
Salmon spp.	2	4
Pacific saury	0	<1
Pacific sandlance	0	1
Lingcod	0	<1
Unidentified / Other	0	4
Total[a]	150	210

[a]Totals rounded to the nearest 10 t.

anchovy, midshipman, rockfish, and herring) also contributed a greater proportion of the diet during the wintering period, contributing to the lower prey consumption then. Ainley *et al.* (1996) discussed these seasonal differences in diet and noted that the differences were primarily attributable to seasonal differences in foraging habitats occupied by murres. There are also seasonal differences in prey availability across the region that may contribute to seasonal changes in diet and, hence, prey consumption. For example, hake spawn south of Point Conception in winter and move north into murre foraging areas in spring and summer (Bailey *et al.*, 1982; Dorn, 1995). Conversely, squid spawn in Monterey Bay during summer and autumn (CDFG, 2005a), and may be most available to murres later in the year, when young-of-the-year squid have dispersed more widely and have grown to the size taken by murres. Morejohn *et al.* (1978) documented a decrease in the mean size of squid in the diets of seabirds, marine mammals, and fish in Monterey Bay from March to July, suggesting that squid of the appropriate size are not as available later in that period. Weise and Harvey (2005) found a similar seasonal shift in the relative importance of hake and squid in California sea lion (*Zalophus californianus*) diets in central California. Another possibility is that squid are relied on more heavily when other prey species become less available. The regional murre population is here estimated to have consumed ~172 313 t of prey annually in the mid- to late 1980s, and ~225 235 t of prey annually in the mid-2000s. Our estimates are similar to the estimate made by Wiens and Scott (1975) for Oregon on a per-bird basis (~82 000 vs. ~88 000 g bird^{-1} year^{-1}).

Adult vs. chick prey consumption

Chick requirements were minimal compared with those of adults. Chicks were fed a maximum of 45 g of food d^{-1} (~9% of breeding adult requirements) at peak growth according to the 1980s data, and a maximum of 49 g of food d^{-1} (~10% of breeding adult requirements) at peak growth according to the 2000s data. Other models for alcids have estimated that chick requirements constitute 16–20% of adult requirements at that stage of life (Croll, 1990b; Konarzewski *et al.*, 1993; Gabrielsen, 1996). The difference may be the result of differences in chick feeding

frequency and prey weight at the different colonies. For instance, Croll (1990b) collected data on thick-billed murre chicks and calculated a higher feeding frequency and higher average prey weight, which could be responsible for the differences between the two studies. Also, the current chick estimate is based on direct observations that do not necessarily provide a measure of energy requirements. Chicks in the study area may or may not be getting enough prey to meet their energy requirements, and may be fledging at lower weights than in other areas in any given period. Possibly too, the total chick requirements are being underestimated by restricting the observations to the time the chicks are at the colony and assuming that they have the same energy requirements as wintering adults after they leave the colony. Chick growth rates peak after colony departure (Ainley *et al.*, 2002), so they may have greater energy requirements than wintering adults during this period.

Caveats

The results of the Monte Carlo simulations indicate that the variation around the overall prey consumption estimate was ±14.4% for the mid- to late 1980s and ±13.2% for the mid-2000s, because of error in the model parameters. In addition, there are assumptions inherent in the present model whose impact had to be minimized, where possible. The parameters used in the bioenergetics model included FMR, prey energy density, assimilation efficiency, population size, and diet composition, for many of which no measurements were available in the study area. For instance, an average FMR from Newfoundland was used as the basis for the model, although energy requirements may differ between Newfoundland and California. The estimate was adjusted, however, to account for the factors that appear to contribute most to regional differences in FMR (sea surface temperature and adult body weight; Croll, 1990b; Croll and McLaren, 1993; Ellis and Gabrielsen, 2002). It was also assumed that breeding birds have greater energy requirements than non-breeding birds, so a range of values was used in the simulations. Notwithstanding, there may be more or less of a difference between breeding and non-breeding birds than the current calculations assume. Energy densities of prey vary with species, region, fish size, and reproductive condition (Anthony *et al.*, 2000); the energy densities of prey used here may not apply to the prey being consumed by murres in the study area, and they may change throughout the year. Assimilation efficiency may vary with species and prey type (Castro *et al.*, 1989; Hilton *et al.*, 2000); a value determined for common murres (the same species) fed prey with similar energy densities to those used here was employed to minimize the error associated with this parameter.

There are also some assumptions inherent in the breeding, non-breeding, and wintering population estimates. Although correction factors were applied to colony counts in the study area to estimate breeding population size, they assume that there is no spatial variation in the proportion of breeding birds in the colony, and hence overestimate the number of breeding birds in areas where there are large numbers of roosting (non-breeding) birds. In addition, the correction factors were applied to all colonies in the study area, although there may be geographic variation in attendance patterns. Leslie matrices were used to estimate the number of non-breeding birds present during the breeding season; the estimate depends on the estimates of survival, fecundity, age at first breeding, and breeding propensity used in the matrices. To allow for uncertainty in the age structure of the population, two population estimates were calculated, and the average

of the two was used in the model. Wintering population estimates were calculated from a ratio of winter to summer bird density based on at-sea data collected between 1980 and 1997, applied to both the 1988/1989 and 2004 population estimates. The ratio between wintering and breeding season numbers may have changed since those surveys were conducted and may not apply to the more recent estimate. Also, there were no data available to adjust the at-sea counts during the breeding season for the number of birds attending the colony at the time of the at-sea censuses, so the wintering population size may have been overestimated. Finally, estimates of hatching success and chick prey consumption were applied to the entire study area based on data collected on SEFI, although there may be geographic variation in both parameters.

Diet composition was based on an average from a 4-year study conducted in the Gulf of the Farallones between 1985 and 1988. Unfortunately, it was not possible quantitatively to assess the effect of spatial or temporal variation in this parameter because of an absence of comparable information from another area or 4-year period. However, the proportions of prey species in the diet showed substantial variation among years (Ainley *et al.*, 1996) that would result in annual variation in estimates of prey consumption. For instance, rockfish constituted a larger proportion of the diet in 1985 and 1986 than in the other 2 years, squid were more important in 1988 than in the other years, and anchovy comprised a greater proportion of the diet in 1986 and 1987 than in the other years. In addition, murre diet composition may have shown longer term changes since the Ainley *et al.* (1996) study was completed, and the current murre population may be consuming prey in different proportions than the projections suggest. Available information on chick diet shows that the proportion of juvenile rockfish in the diet was high in the 1980s, decreased through the 1990s, and increased slightly in the early 2000s, apparently in response to changes in rockfish abundance in the environment (Sydeman *et al.*, 2001; Miller and Sydeman, 2004; Mills *et al.*, 2007). The proportion of anchovy in the chick diet increased as the proportion of rockfish decreased in the 1990s. Similar long-term changes in the importance of these species have likely occurred in adult diet composition. Unfortunately, no data exist to assess changes in other prey items important for adults (e.g. hake, squid) that are not represented in the chick diet. More recent information on adult diet is clearly needed to understand better their prey requirements, the impact murres currently have on prey populations, and how that impact varies over time.

Ecosystem considerations

The estimates suggest that murres require a substantial amount of prey per year. Importantly, this estimate represents only a portion of total prey consumption for predators in the study area. Baltz and Morejohn (1977) found that anchovy, squid, rockfish, and flatfish were common in the diets of most seabirds wintering in Monterey Bay. Morejohn *et al.* (1978) looked at the diets of seabirds and other top predators in Monterey Bay and found substantial overlap in what seabirds, marine mammals, and predatory fish consumed. The combined harvest of these top predators is likely substantial; Briggs and Chu (1987) estimated that marine mammal prey consumption is 3–11 times that of seabird prey consumption in California. Commercial fisheries also affect some of these prey populations. The squid fishery is currently the largest in California (CDFG, 2005a), peak catches exceeding

100 000 t in some years (Zeidberg *et al.*, 2006). Commercial fisheries also take anchovy, hake, and rockfish to a lesser extent (CDFG, 2005b). A greater understanding of the combined requirements of these top predators is needed to manage the ocean resources more effectively. It is also important to recognize that the prey densities necessary to support consumption by top predators require prey abundances that are many times that of prey consumption alone (Furness, 2007). For instance, murre populations in the Barents Sea crashed after the capelin stock dropped from 6 million to 500 000 t; the lower value was seven times that of estimated murre consumption (Mehlum and Gabrielsen, 1995; Furness, 2007). A greater understanding of what are the threshold values, along with more information on prey population sizes, would be beneficial. Inclusion of this information in fishery management plans would likely contribute to the sustainable harvest of commercially important species. Certainly, understanding the interactions between seabirds, commercial fisheries, and other top predators, and assessing the impact of the combined harvest on prey populations, is important to a multispecies, ecosystem-based approach to management of marine resources that would yield healthy populations of both predators and prey.

Acknowledgements

References

Ainley, D. G., Nettleship, D. N., Carter, H. R., and Storey, A. E. 2002. Common murre (*Uria aalge*). *In* The Birds of North America. No. 666. Ed. by A. Poole, and F. Gill. Academy of Natural Sciences, Philadelphia and American Ornithologists' Union, Washington, DC.

Ainley, D. G., Spear, L. B., Allen, S. G., and Ribic, C. A. 1996. Temporal and spatial patterns in the diet of the common murre in California waters. Condor, 98: 691–705.

Anthony, J. A., Roby, D. D., and Turco, K. R. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. Journal of Experimental Marine Biology and Ecology, 248: 53–78.

Bailey, K. M., Francis, R. C., and Stevens, P. R. 1982. The life history and fishery of Pacific whiting, *Merluccius productus*. CalCOFI Report, 23: 81–98.

Baltz, D. M., and Morejohn, G. V. 1977. Food habits and niche overlap of seabirds wintering on Monterey Bay, California. Auk, 94: 526–543.

Boekelheide, R. J., Ainley, D. G., Morrell, S. H., Huber, H. R., and Lewis, T. J. 1990. Common murre. *In* Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-System Community, pp. 245–275. Ed. by D. G.

Ainley, and R. J. Boekelheide. Stanford University Press, Stanford. 450 pp.

Briggs, K. T., and Chu, E. W. 1987. Trophic relationships and food requirements of California seabirds: updating models of trophic impact. *In* Seabirds: Feeding Ecology and Role in Marine Ecosystems, pp. 279–304. Ed. by J. P. Croxall. Cambridge University Press, Cambridge. 408 pp.

Briggs, K. T., Tyler, W. M. B., Lewis, D. B., and Carlson, D. R. 1987. Bird communities at sea off California: 1975 to 1983. Studies in Avian Biology, 11: 1–74.

Brooke, M. de L. 2004. The food consumption of the world's seabirds. Proceedings of the Royal Society of London Series B (Supplement), 271: S246–S248.

Brown, R. G. B., and Nettleship, D. N. 1984. Capelin and seabirds in the Northwest Atlantic. *In* Marine Birds: their Feeding Ecology and Commercial Fisheries Relationships, pp. 184–194. Ed. by D. N. Nettleship, G. A. Sanger, and P. F. Springer. Canadian Wildlife Service, Ottawa. 220 pp.

Bunce, A. 2001. Prey consumption of Australasian gannets (*Morus serrator*) breeding in Port Phillip Bay, southeast Australia, and potential overlap with commercial fisheries. ICES Journal of Marine Science, 58: 904–915.

Burger, A. E., and Cooper, J. 1984. The effects of fisheries on seabirds in South Africa and Namibia. *In* Marine Birds: their Feeding Ecology and Commercial Fisheries Relationships, pp. 150–160. Ed. by D. N. Nettleship, G. A. Sanger, and P. F. Springer. Canadian Wildlife Service, Ottawa. 220 pp.

Cairns, D. K., Montevecchi, W. A., Birt-Friesen, V. L., and Macko, S. A. 1990. Energy expenditures, activity budgets, and prey harvest of breeding common murres. Studies in Avian Biology, 14: 84–92.

Carter, H. R., McChesney, G. J., Jaques, D. L., Strong, C. S., Parker, M. W., Takekawa, J. E., Jory, D. L., et al. 1992. Breeding populations of seabirds in California, 1989–1991. United States Fish and Wildlife Service, Dixon, California, and Newark, California Report.

Castro, G., Stoyan, N., and Myers, J. P. 1989. Assimilation efficiency in birds: a function of taxon or food type? Comparative Biochemistry and Physiology, 92A: 271–278.

CDFG. 2005a. Final Market Squid Fishery Management Plan. California Department of Fish and Game, Sacramento, CA. http://www.dfg.ca.gov/mrd/msfmp/index.html (last accessed 31 July 2007).

CDFG. 2005b. Final California Commercial Landings for 2004. California Department of Fish and Game, Sacramento, CA. http://www.dfg.ca.gov/mrd/landings04.html (last accessed 31 July 2007).

Croll, D. A. 1990a. Physical and biological determinants of the abundance, distribution, and diet of the common murre in Monterey Bay, California. Studies in Avian Biology, 14: 139–148.

Croll, D. A. 1990b. Diving and energetics of the thick-billed murre, *Uria lomvia*. PhD thesis, University of California, San Diego.

Croll, D. A., and McLaren, E. 1993. Diving metabolism and thermoregulation in common and thick-billed murres. Journal of Comparative Physiology B, 163: 160–166.

Dahdul, W. M., and Horn, M. H. 2003. Energy allocation and postnatal growth in captive elegant tern (*Sterna elegans*) chicks: responses to high- versus low-energy diets. Auk, 120: 1069–1081.

Davis, N. D., Myers, K. W., and Ishida, Y. 1998. Caloric value of high-seas salmon prey organisms and simulated salmon ocean growth and prey consumption. North Pacific Anadromous Fish Commission Bulletin, 1: 146–162.

Dorn, M. W. 1995. The effects of age composition and oceanographic conditions on the annual migration of Pacific whiting, *Merluccius productus*. CalCOFI Report, 36: 97–105.

ECI. 2001. Marine mammal and seabird computer database analysis system: Washington, Oregon, California 1975–1997, Version 2.1. Ecological Consulting, Inc., Portland, Oregon.

Ellis, H. I., and Gabrielsen, G. W. 2002. Energetics of free-ranging seabirds. *In* Biology of Marine Birds, pp. 359–407. Ed. by E. A. Schreiber, and J. Burger. CRC Press, Boca Raton. 722 pp.

ESRI. 1998. ArcView GIS, Version 3.1. Environmental Systems Research Institute, Inc., Redlands, CA.

Ford, R. G., Ainley, D. G., Casey, J. L., Keiper, C. A., Spear, L. B., and Ballance, L. T. 2004. The biogeographic patterns of seabirds in the central portion of the California Current. Marine Ornithology, 32: 77–96.

Furness, R. W. 1978. Energy requirements of seabird communities: a bioenergetics model. Journal of Animal Ecology, 47: 39–53.

Furness, R. W. 1990. A preliminary assessment of the quantities of Shetland sandeels taken by seabirds, seals, predatory fish and the industrial fishery in 1982–83. Ibis, 132: 205–217.

Furness, R. W. 2007. Responses of seabirds to depletion of food fish stocks. Journal of Ornithology, 148: S247–S252.

Gabrielsen, G. W. 1996. Energy expenditure of breeding common murres. *In* Studies of High-Latitude Seabirds. 4. Trophic Relationships and Energetics of Endotherms in Cold Ocean Systems, pp. 49–58. Ed. by W. A. Montevecchi. Canadian Wildlife Service Occasional Paper, 91.

Gales, R., and Green, B. 1990. The annual energetics cycle of little Penguins (*Eudyptula minor*). Ecology, 71: 2297–2312.

Gaston, A. J., and Dechesne, S. B. C. 1996. Rhinoceros auklet (*Cerorhinca monocerata*). *In* The Birds of North America. No. 212. Ed. by A. Poole, and F. Gill. Academy of Natural Sciences, Philadelphia and American Ornithologists' Union, Washington, DC.

Gaston, A. J., and Jones, I. L. 1998. The Auks. Oxford University Press, Oxford. 349 pp.

Hatch, S. A., and Sanger, G. E. 1992. Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. Marine Ecology Progress Series, 80: 114.

Hilton, G. M., Furness, R. W., and Houston, D. C. 2000. A comparative study of digestion in North Atlantic seabirds. Journal of Avian Biology, 31: 36–46.

Hunt, G. L., Drew, G. S., Jahncke, J., and Piatt, J. F. 2005. Prey consumption and energy transfer by marine birds in the Gulf of Alaska. Deep-Sea Research II, 52: 781–797.

Huyer, A., Fleischbein, J. H., Keister, J., Kosro, P. M., Perlin, N., Smith, R. L., and Wheeler, P. A. 2005. Two coastal upwelling domains in the northern California Current system. Journal of Marine Research, 63: 901–929.

Jahncke, J., Checkley, D. M., and Hunt, G. L. 2004. Trends in carbon flux to seabirds in the Peruvian upwelling system: effects of wind and fisheries on population regulation. Fisheries Oceanography, 13: 208–223.

Konarzewski, M., Taylor, J. R. E., and Gabrielsen, G. W. 1993. Chick energy requirements and adult energy expenditures of dovekies (*Alle alle*). Auk, 110: 343–353.

Lance, M. M., and Thompson, C. W. 2005. Overlap in diets and foraging of common murres (*Uria aalge*) and rhinoceros auklets (*Cerorhinca monocerata*) after the breeding season. Auk, 122: 887–901.

Manuwal, D. A., Carter, H. R., Zimmerman, T. S., and Orthmeyer, D. L. 2001. Biology and Conservation of the Common Murre in California, Oregon, Washington, and British Columbia. 1. Natural History and Population Trends. United States Geological Survey, Biological Resources Division, Information and Technology Report USGS/BRD/ITR-2000-0012, Washington, DC.

May, R. M., Beddington, J. R., Clark, C. W., Holt, S. J., and Laws, R. M. 1979. Management of multispecies fisheries. Science, 205: 267–277.

Mehlum, F., and Gabrielsen, G. W. 1995. Energy expenditure and food consumption by seabird populations in the Barents Sea region. *In* Ecology of Fjords and Coastal Waters, pp. 457–470. Ed. by H. R.

Skjoldal, C. Hopkins, K. E. Erikstad, and H. P. Leinaas. Elsevier, Amsterdam. 623 pp.

Miller, A. K., and Sydeman, W. J. 2004. Rockfish responses to low-frequency ocean climate change as revealed by the diet of a marine bird over multiple time scales. Marine Ecology Progress Series, 281: 207–216.

Miller, D. J., and Lea, R. N. 1972. Guide to the Coastal Marine Fishes of California. California Department of Fish and Game Fish Bulletin, 157.

Mills, K. L., Laidig, T., Ralston, S., and Sydeman, W. J. 2007. Diets of top predators indicate pelagic juvenile rockfish (*Sebastes* spp.) abundance in the California Current system. Fisheries Oceanography, 16: 273–283.

Montevecchi, W. A. 1993. Birds as indicators of change in marine prey stocks. *In* Birds as Monitors of Environmental Change, pp. 217–266. Ed. by R. W. Furness, and J. J. D. Greenwood. Chapman and Hall, London. 356 pp.

Morejohn, G. V., Harvey, J. T., and Krasnow, L. T. 1978. The importance of *Loligo opalescens* in the food web of marine vertebrates in Monterey Bay, California. Fish and Game Fish Bulletin, 169: 67–98.

Naughton, M. B., Pitkin, D. S., Lowe, R. W., So, K. J., and Strong, C. S. Oregon Seabird Colony Catalog. United States Department of Interior, Fish and Wildlife Service, Region 1, Biological Technical Publication FWS/BTP-R1009-2007, Washington, DC, in press.

Oedekoven, C. S., Ainley, D. G., and Spear, L. B. 2001. Variable responses of seabirds to change in marine climate: California Current, 1985–1994. Marine Ecology Progress Series, 212: 265–281.

Piatt, J. F., and Nettleship, D. N. 1985. Diving depths of four alcids. Auk, 102: 293–297.

Ricklefs, R. E. 1983. Some considerations on the reproductive energetics of pelagic seabirds. Studies in Avian Biology, 8: 84–94.

Roby, D. D., Lyons, D. E., Craig, D. P., Collis, K., and Visser, G. H. 2003. Quantifying the effect of predators on endangered species using a bioenergetics approach: Caspian terns and juvenile salmonids in the Columbia River estuary. Canadian Journal of Zoology, 81: 250–265.

Schaffner, F. C. 1986. Trends in elegant tern and northern anchovy populations in California. Condor, 88: 347–354.

Scott, J. M. 1990. Offshore distributional patterns, feeding habits, and adult-chick interactions of the common murre in Oregon. Studies in Avian Biology, 14: 103–108.

Spear, L. B. 1993. Dynamics and effect of western gulls feeding in a colony of guillemots and Brandt's cormorants. Journal of Animal Ecology, 62: 399–414.

Sydeman, W. J. 1993. Survivorship of common murres on Southeast Farallon Island, California. Ornis Scandinavica, 24: 135–141.

Sydeman, W. J., Carter, H. R., Takekawa, J. E., and Nur, N. 1997a. Common murre *Uria aalge* population trends at the South Farallon Islands, California, 1985–1995. PRBO Conservation Science, Petaluma, California, the United States Geological Survey, Dixon, California, and the United States Fish and Wildlife Service, Newark, California Report.

Sydeman, W. J., Hester, M. M., Thayer, J. A., Gress, F., Martin, P., and Buffa, J. 2001. Climate change, reproductive performance, and diet composition of marine birds in the southern California Current system. Progress in Oceanography, 49: 309–329.

Sydeman, W. J., Hobson, K. A., Pyle, P., and McLaren, E. B. 1997b. Trophic relationships among seabirds in central California: combined stable isotope and conventional dietary approach. Condor, 99: 327–336.

Takekawa, J. E., Carter, H. R., and Harvey, T. E. 1990. Decline of the common murre in central California, 1980–1986. Studies in Avian Biology, 14: 149–163.

Tasker, M. L., Camphuysen, C. J., Cooper, J., Garthe, S., Montevecchi, W. A., and Blaber, S. J. M. 2000. The impacts of fishing on marine birds. ICES Journal of Marine Science, 57: 531–547.

US GLOBEC. 1992. Report on climate change and the California Current ecosystem. Eastern Boundary Current Program, United States Global Ocean Ecosystems Dynamics, Davis, CA, Report 7.

Weise, M. J., and Harvey, J. T. 2005. California sea lion (*Zalophus californianus*) impacts on salmonids near Año Nuevo Island, California. Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California Report.

Wiens, J. A., and Scott, J. M. 1975. Model estimation of energy flow in Oregon coastal seabird populations. Condor, 77: 439–452.

Yen, P. P. W., Sydeman, W. J., and Hyrenbach, K. D. 2004. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. Journal of Marine Systems, 50: 79–99.

Zeidberg, L. D., Hamner, W. M., Nezlin, N. P., and Henry, A. 2006. The fishery for California market squid (*Loligo opalescens*) (Cephalopoda: Myopsida), from 1981 through 2003. Fishery Bulletin US, 104: 46–59.

Appendix

Parameter	Age	Value	
		Scenario 1	Scenario 2
Age-specific survival	0–1	0.44	0.55
	1–2	0.8	0.8
	2–3	0.87	0.87
	3–4	0.933	0.92
	4+	0.933	0.92
Age-specific reproductive success[a]	1–5	0	0
	6	0.564	0.564
	7	0.736	0.736
	8+	0.764	0.764
Age at first breeding	–	6.5	6.5
Breeding propensity	–	0.928	0.928

[a]Models assume that 50% of 6-year-old birds and 100% of 7-year-old birds are mature enough to breed.