Chapter 5
Climate and Food: “Bottom-Up” Control of Seabird Population Parameters and Population Dynamics
CHAPTER 5. CLIMATE AND FOOD: “BOTTOM-UP” CONTROL OF SEABIRD POPULATION PARAMETERS AND POPULATION DYNAMICS

“Bottom-up” control of seabird populations includes those factors that influence the prey that are consumed by seabirds, namely zooplankton, squid, and fish. Climate, which alters the ocean characteristics responsible for cascading effects up the food chain, is the principal mechanism for bottom-up control of seabird population parameters and dynamics.

In this chapter we begin by exploring climate variability in the CCS, including a description of large-scale oceanographic and atmospheric processes, operating at short and long timescales, which affect ocean habitats of seabirds and how seabirds respond to marine climate variability.

After this discussion of climate, we describe the consequences of food limitation on seabirds, and the usefulness of seabird prey consumption models for determining the amount of prey required to sustain seabird populations, which can, in turn, be valuable for fisheries management and seabird conservation.

Seabirds are important predators in marine ecosystems, consuming large proportions of the biomass in the CCS. Briggs and Chu (1) estimated that off California alone, 1.8 million (midsummer) to 7.0 million (fall) seabirds are present, and consume on average 44,000 tonnes of plankton and 149,000 tonnes of fish and squid each year (4-7% of production).

The results of prey consumption models are highly valuable for practical conservation and management of both predator and prey species. Prey consumption models can be useful in a variety of manners, including: (1) incorporation of models into fisheries management plans to establish ecologically sensitive fishery quotas (a true multi-species approach), which incorporate local or regional prey consumption of predator species; (2) as baseline data in the event of development and management of future fisheries; (3) to strengthen arguments against opening certain fisheries that may deplete the prey base needed to sustain certain predator populations; and (4) to enhance available information and provide more “realistic” information for estimating natural mortality of fish populations to incorporate in stock assessments.

From a seabird management perspective, prey consumption models may be used to: (1) examine the impacts of fisheries on seabird populations, for example the evaluation of the effects of fishing down the food web; (2) assess potential impacts and competition between seabirds and fisheries, such as targeting the same fish, which may lead to seabird bycatch and reduction of the availability of seabird prey; and (3) to characterize the effects of both interannual and interdecadal variability and trends in ocean climate in the CCS, and how this variability may affect both seabird and prey populations in terms of food web dynamics and ecosystem productivity.
5.1 CLIMATE VARIABILITY ON MULTIPLE TIMESCALES

Naturally occurring climate cycles in the world’s oceans and atmosphere strongly influence the CCS and central North Pacific Ocean (NPO) ecosystems, and therefore the ocean habitats that seabirds depend on for their survival. Within the CCS ecosystem, seabirds respond to El Niño (the periodic, every 4-7 years, warming of the ocean), La Niña (ocean cooling associated with the El Niño-Southern Oscillation cycle), and lower-frequency ocean warming and cooling due to polarity reversals of the Pacific Decadal Oscillation (PDO).

Large-Scale Ocean/Climate Processes: El Niño, La Niña, the Southern Oscillation, and Currents

El Niño and La Niña are linked via changes in global pressure systems of the tropical Pacific Ocean. In the early 1970s, it was recognized that these events were part of an ocean-wide fluctuation in the atmosphere, called the “Southern Oscillation.”

In this oscillation, the usual pressure gradient from a region of high pressure in the western tropical Pacific Ocean to a region of low pressure in the Australia-Asian Pacific becomes higher or lower than average. Lower than average pressure gradients favor El Niño, whereas the higher than average situation promotes La Niña.

Typically, the pressure differences are measured as the difference in barometric pressure of Tahiti versus Darwin, Australia. This pressure difference is referred to as the Southern Oscillation Index (SOI), and has been used to study and predict El Niño/La Niña events. The connection of El Niño with the Southern Oscillation has led to the acronyms ENSO and LNSO, a convenient means to encapsulate this phenomenon. Figure 5.1d shows the SOI between 1987 and 2002.

La Niña is the inverse of El Niño and has occurred almost as frequently as El Niño over the past 3 decades. During La Niña, sea level in the eastern North Pacific Ocean decreases, thermocline depths become shallow resulting in a less stratified ocean, and ocean mixing of nutrients becomes more efficient. Upwelling results in mixing of cold, nutrient-rich water in the euphotic zone with positive effects on food web development.

Other changes that may be related to, or independent of, the ENSO cycle include a strengthening/weakening of the major currents, such as the California and North and South Equatorial currents. The latitudinal and longitudinal transport of nutrients and organisms by currents across ocean basins and within and between water masses may strongly influence the productivity of the ocean habitats of seabirds, but further research is required to understand the interactions of varying large-scale physical oceanographic processes with food web dynamics.

The Pacific Decadal Oscillation (PDO)

In the North Pacific Ocean, one of the “low frequency” marine climate shifts has been referred to as the Pacific Decadal Oscillation (PDO) (2-5). According to Mantua et al. (5), the PDO is “an El Niño-like phenomenon operating on timescales of decades.” In particular, a mid-1970s intensification of the Aleutian Low Pressure System (ALPS) has been related to long-term ocean warming in the CCS.

Under these barometric conditions, southwesterly winds and subtropical storms increase along much of the West Coast of North America. As a result, there is an increase in the transport of warm, equatorial water from the south through a strengthening of the California undercurrent and a weakening of the south-flowing, subarctic California Current.

Similar to El Niño effects, intensification of the ALPS causes thermocline deepening, increased ocean stratification, and a cessation of effectual upwelling (6-8). In short, intensification of the ALPS leads to warming of the North Pacific Ocean. Polarity reversals of the PDO occurred in 1900-1901, 1925-1926, 1949-1950, 1976-1977, and possibly 1998-1999, suggesting a 50-60 year periodicity to this cycle of climate variability (half cycles representing “cold” periods and “warm” periods last 20-30 years). Studies on effects of PDO on marine birds are few, but have documented some similar ecological effects as El Niño/La Nina in the Pacific Ocean.
5.2 SEABIRD RESPONSE TO CLIMATE VARIABILITY

Long-term population studies have clearly demonstrated the deleterious effects that El Niño can have on breeding seabirds, some of which are the reduction of breeding probabilities, reproductive performance, and survival.

Conversely, many of the same long-term studies have demonstrated the equally important and positive effects of La Niña events. Strong La Niña years may result in exceptional production of cohorts which sustain seabird populations for decades. Studies of the Pacific Decadal Oscillation (PDO) and similar low-frequency climate variations (e.g., intensification of the Aleutian Low Pressure System) are few, but have documented some similar effects to El Niño in the California Current.

Ocean Climate and Seabird Prey

Diet composition of Farallon alcid nestlings is related to various indices of ocean climate variability in the CCS: sea-surface temperature (SST, collected on the Farallones), the upwelling index (UI, average of values at 36°N and 39°N), the Pacific Decadal Oscillation (PDO), and the Southern Oscillation Index (SOI).

For each species, we examine the potential effects of these ocean climate indices on the proportion (by mass for Cassin’s and Rhinoceros Auklets, by number for Common Murre and Pigeon Guillemot) of primary prey species or groups in the diet (methods described in section 5.6).

Seasonal ocean climate indices showed substantial variability through time (Fig. 5.1). Generally, for the total range of years in which we present data (1987-2002), the Gulf of the Farallones was characterized by relatively cool conditions until 1992, when conditions became warmer (higher SST especially in winter, negative SOI, positive PDO). Following the ENSO year of 1998, cooler conditions prevailed for the remaining years.

Figure 5.1 - Annual seasonal (winter and spring) mean values of (A) Farallon sea-surface temperature (SST), (B) the Upwelling Index (UI), (C) the Pacific Decadal Oscillation (PDO), and (D) the Southern Oscillation Index (SOI). We used seasonal mean values (winter = January-March, spring = April-June) of each climate index.
The results of the correlations between diet composition and ocean climate indices are presented in Table 5.1. These results indicate that the proportion of euphausiids in the diet of Cassin’s Auklet nestlings was negatively correlated with the spring PDO: when the value of PDO is low in spring (cool conditions), there is a greater proportion of euphausiids in the diet.

Interestingly, the correlations between the proportion of euphausiids in the diet and winter PDO and SOI values show the opposite results, suggesting that when winter conditions are relatively warm, there is a greater proportion of euphausiids in the diet. For Rhinoceros Auklets, both northern anchovy and sablefish were correlated significantly with the spring SOI: the proportion of anchovy increased with increasing spring SOI values (cool conditions) and sablefish increased with decreasing spring SOI values (warm conditions). For Pigeon Guillemots, an increased proportion of Sculpin spp. was correlated significantly with increasing spring SST, decreasing spring and winter UI, and low winter SOI values (warm conditions).

In contrast to the trends observed for anchovy in Rhinoceros Auklet diet, the proportion of anchovy in Common Murre diet is greater when winter SST and the spring PDO are high (warm conditions).

**Table 5.1** – Results of Spearman-rank correlations (rs-values) for each primary prey species/group consumed by alcid nestlings versus mean winter (January-March) and spring (April-June) values of sea-surface temperature (SST), the upwelling index (UI; average of values at 36°N and 39°N), the Pacific Decadal Oscillation (PDO), and the Southern Oscillation Index (SOI). Sample sizes for tests are in parentheses. Significant values (p ≤ 0.05) are shaded in light grey and significant values (p ≤ 0.10) are shaded in dark grey.

<table>
<thead>
<tr>
<th>SEABIRD, PREY</th>
<th>Winter SST</th>
<th>Spring SST</th>
<th>Winter UI</th>
<th>Spring UI</th>
<th>Winter PDO</th>
<th>Spring PDO</th>
<th>Winter SOI</th>
<th>Spring SOI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cassin’s Auklet</td>
<td>-0.10</td>
<td>-0.27</td>
<td>0.02</td>
<td>0.33</td>
<td>0.22</td>
<td>-0.62</td>
<td>-0.28</td>
<td>0.12</td>
</tr>
<tr>
<td>Euphausiids (n=9)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Rhinoceros Auklet</td>
<td>-0.11</td>
<td>-0.09</td>
<td>-0.14</td>
<td>-0.19</td>
<td>-0.37</td>
<td>0.05</td>
<td>0.22</td>
<td>0.46</td>
</tr>
<tr>
<td>N. Anchovy (n=16)</td>
<td>0.07</td>
<td>0.14</td>
<td>-0.06</td>
<td>-0.04</td>
<td>-0.06</td>
<td>0.05</td>
<td>-0.19</td>
<td>-0.44</td>
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<tr>
<td>Sablefish (n=16)</td>
<td>-0.01</td>
<td>-0.02</td>
<td>0.08</td>
<td>0.21</td>
<td>0.24</td>
<td>0.01</td>
<td>-0.36</td>
<td></td>
</tr>
<tr>
<td>Rhinoceros Auklet</td>
<td>-0.12</td>
<td>-0.07</td>
<td>0.09</td>
<td>-0.16</td>
<td>-0.24</td>
<td>0.13</td>
<td>-0.11</td>
<td>-0.23</td>
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<tr>
<td>Rockfish (n=16)</td>
<td>-0.05</td>
<td>-0.19</td>
<td>0.11</td>
<td>0.37</td>
<td>0.15</td>
<td>-0.12</td>
<td>0.25</td>
<td>0.12</td>
</tr>
<tr>
<td>Rhinoceros Auklet</td>
<td>-0.04</td>
<td>-0.06</td>
<td>0.22</td>
<td>0.21</td>
<td>0.41</td>
<td>0.17</td>
<td>-0.07</td>
<td>-0.22</td>
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<tr>
<td>Pacific Saury (n=16)</td>
<td>0.77</td>
<td>0.48</td>
<td>-0.82</td>
<td>-0.56</td>
<td>0.10</td>
<td>0.15</td>
<td>-0.71</td>
<td>-0.35</td>
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<tr>
<td>Pigeon Guilemot</td>
<td>-0.52</td>
<td>0.26</td>
<td>-0.42</td>
<td>-0.32</td>
<td>0.04</td>
<td>0.54</td>
<td>-0.22</td>
<td>-0.16</td>
</tr>
<tr>
<td>Rockfish (n=11)</td>
<td>-0.28</td>
<td>0.03</td>
<td>0.29</td>
<td>0.03</td>
<td>0.01</td>
<td>0.01</td>
<td>-0.01</td>
<td>-0.24</td>
</tr>
<tr>
<td>Common Murre</td>
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<td>N. Anchovy (n=16)</td>
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<td>Common Murre</td>
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<tr>
<td>Rockfish (n=16)</td>
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These results demonstrate that certain prey species/groups may be sensitive to perturbations in ocean climate conditions in the CCS, especially during warm-water or ENSO events.

If these prey species typically comprise a substantial portion of either adult or nestling diet, a reduction in abundance of these species may ultimately result in (1) a delay in the timing of breeding or cessation of reproductive efforts, (2) reduced rates of nestling growth and development, (3) reduced reproductive success, and (4) reduced adult survival.

Indeed, reductions in Farallon seabird productivity, breeding propensity, and survival probability are all associated with negative SOI values (warm-water episodes; PRBO unpublished data), further illustrating the effects of ocean climate variability on seabird population processes.

**Life History and Reproductive Consequences of the ENSO Cycle**

Declines and increases in the zooplankton, squid, and fish populations that compose the food webs of most seabirds in the Pacific Ocean can be linked directly to a variety of physical oceanographic changes, which occur during ENSO/LNSO events.

These changes include a rise in sea level, a deepening of the thermocline, and a cessation of effeuctual ocean mixing. Under these conditions, while upwelling may or may not remain a dominant physical force, deepening of the thermocline results in mixing of warm, nutrient-poor water that has little positive effects on food web development.

As a consequence of poor nutrient input, there are changes in characteristics of phytoplankton and zooplankton communities. For example, larger diatoms are often replaced by smaller dinoflagellates, which, in turn, support smaller zooplankton. Eventually, poor nutrient levels cascade up the food web, with effects on seabird time and energy budgets.


The El Niño of 1982-1983 dramatically focused attention on the effects of large-scale changes in circulation patterns of the tropical Pacific Ocean on biological communities worldwide.

In particular, oceanic and atmospheric effects from this event penetrated higher latitudes along the West Coast of North America, raising sea surface temperatures and causing mass mortality of many temperate region fish, marine birds, and mammal species. Seabird responses have varied by species in relation to the intensity and timing of each El Niño.

El Niño has been linked to the population dynamics of seabirds in the Central Pacific Ocean, and Eastern North Pacific Ocean (PRBO unpublished data) suggesting an important natural mechanism for understanding seabird population regulation. Life history and demographic parameters affected include the timing of egg-laying, proportion of adults breeding, offspring developmental patterns, reproductive performance, adult, subadult, and juvenile mortality rates, foraging habits, and diet.

Boekelheide conducted a 13-year study of the Farallon Islands seabird community, and demonstrated several effects associated with El Niño, such as substantial delays in the timing of breeding and breeding effort (numbers attempting to reproduce) for many species (alciids and cormorants). More recently, Sydeman studied the oceanographic relationships of timing of egg-laying in Common Murres, and demonstrated later breeding in years of warmer ocean temperatures associated with a series of El Niño events while controlling for confounding variables. However, the mechanism to later timing of breeding is not well understood.

Whether the reduction in prey associated with El Niño limits the condition of birds, thereby preventing earlier egg-laying, or whether birds delay reproduction to match the chick-rearing period with later blooms in prey species is an important question open for future research.

Seabirds in California often experience reproductive failure during the severe ENSO events. Ainley et al. and Sydeman et al. in extending earlier observations of the Farallon Island seabird community, showed that the response of various seabird species to El Niño and other warm-water anomalies depends on life history characteristics.
Species that foraged in nearshore habitats and those with more aggressive reproductive strategies (i.e., laying > 1 egg per clutch) often showed the greatest variability and decline in reproductive response. In studying reproductive performance (young fledged pair\(^{-1}\) year\(^{-1}\)) of the Farallon seabird community, Brandt’s (\textit{Phalacrocorax penicillatus}) and Pelagic (\textit{P. pelagicus}) cormorants and Pigeon Guillemots (\textit{Cepphus columba}) were the species apparently most sensitive to interannual climate variability, i.e., El Niño/La Niña events associated with the ENSO cycle. These species also were exceptionally successful during La Niña years.

In Oregon, Hodder and Graybill (20) demonstrated reductions in reproductive success for cormorants and Common Murres (\textit{Uria aalge}) and an increase in mortality for adults in Oregon during the 1982-1983 El Niño. Bayer et al. (21), who studied deposition rates of adult and juvenile murres on beaches in Oregon, reported larger than normal numbers of dead hatching-year birds on beaches in 1982, but not 1983.

In Washington, Wilson (22) showed that colony attendance of murres during the 1983 El Niño was 87% lower than in the previous year. Starvation appears to be the likely cause of elevated mortality, but direct relationships between prey availability and seabird reproductive success in relation to ENSO events have been infrequently developed. This remains an important area for future climate-seabird interaction research.

The El Niño of 1997-1998 was predicted well in advance of its arrival; hence, a number of investigations were designed specifically to investigate effects of this event. Sydeman et al. (pers. communication) assessed these effects on 12 geographically and temporally extensive time-series databases of 3 marine bird species from southern California through the Bering Sea, and found strong indications of reduced ecosystem productivity and effects on marine birds throughout the CCS and into the southern Gulf of Alaska (to ~56° N). The results showed ocean warming affected ecosystem productivity and seabirds in southern California in 1997, while populations in northern California were affected more in 1998. Notably, in central California in 1998, there was less of an effect of El Niño conditions on the planktivorous Cassin’s Auklet (\textit{Cepphus columba}) and omnivorous Common Murre, than the obligate piscivore, Rhinoceros Auklet (\textit{Cerorhinca monocerata}) (23). This result led Sydeman and colleagues to propose that cessation of El Niño relatively early (in May) 1998, followed by moderate upwelling, allowed the planktivorous auklet and murre to take advantage of late season zooplankton blooms.

In northern California, Common Murres attended the Castle Rock colony throughout the 1998 breeding season, but experienced nearly complete reproductive failure, and Tufted Puffin numbers were the lowest on record (D. Jaques and C. Strong, pers. communication).

In southern British Columbia, the mean frequency of occupied detections for Marbled Murrelets, a possible measure of near-nest flight behaviors, was negatively correlated with nearshore ocean temperatures over a 7-year period including the 1998 El Niño when temperatures were the warmest (A. Burger, pers. communication). Also in British Columbia, the reproductive effort of breeding Cassin’s Auklet on Triangle and Frederick Islands was significantly reduced and timing of breeding was delayed for those that tried (D. Bertram et al., pers. communication). Interestingly, nestling growth and breeding success were also reduced on Triangle Island (50° N), but not on Frederick Island (54° N). Breeding of Ancient Murrelets on Limestone Island began relatively early, but was spread over a much longer period than usual. In addition, 50% of the monitored burrows were deserted during incubation, far more than had been observed in any previous year (T. Gaston, pers. communication).

**Effects of the 2003 El Niño Event on Seabirds Breeding on the Farallon Islands**

Generally, the 2003 El Niño event showed all the classic signs of an El Niño for the seabirds on the Farallon Islands, but with much reduced effects. El Niño conditions during the winter of 2002/2003 resulted in reduced productivity for the seabirds during the spring/summer breeding season. The effects on individual species, however, were varied.

Brandt’s Cormorant and Rhinoceros Auklet productivity was down from the 2002 season and well below the long-term mean for these species. Pigeon Guillemot and Common Murre productivity was also down from 2002, but still at or above their long-term mean reproductive success. However, Pelagic Cormorant and Cassin’s Auklet productivity, although down from 2002, was still very high. The observed decline in Cassin’s Auklet productivity is driven solely by a reduction in the number of second broods attempted and successfully fledged, although productivity among first broods was higher than in the 2002 breeding season.
In addition to generally lower productivity, 2003 was characterized by delayed breeding relative to the previous two seasons, moderately lower growth rates among chicks, a high rate of nest abandonment among Brandt’s Cormorants, and a reduction in the proportion of rockfish in chick diet (although still close to 50% of the diet for murres and guillemots). The rate of chick provisioning was also lower for murres and guillemots.

Finally, large numbers of emaciated sea lions were observed around the island during 2003, probably due to a lack of sufficient food available during the winter and spring months. These individuals then had a direct impact on seabirds by crawling into the colonies, causing disturbance to nesting seabirds, scavenging the carcasses of dead birds, and in one case, actively preying upon murre chicks.

By all accounts the first El Niño of the current “cold-water regime” was much more moderate in its effects than previous events, possibly because of the very high productivity (and presumably excellent feeding conditions) of most species in the past 4 years. Productivity, while reduced, was much higher in 2003 than in 1998, 1992, or 1983 (Table 5.2), particularly among those species thought to be most sensitive to oceanographic changes, such as Pelagic Cormorants, Pigeon Guillemots, and Brandt’s Cormorants.

The exceptionally high productivity among Pelagic Cormorants is most unusual for an El Niño event, as is the fact that Brandt’s Cormorants had low productivity while Pelagics did well. Cassin’s Auklets, though largely unsuccessful, still attempted second broods, which did not occur in previous events. The mean seasonal SST for 2003 (12.07°C), though higher than the past few years, was considerably lower than in previous El Niño years.

Table 5.2 – Comparison of seabird productivity on the Farallon Islands during the last six “El Niño” events. (COMU = Common Murre, BRCO = Brandt’s Cormorant, PECO = Pelagic Cormorant, PIGU = Pigeon Guillemot, CAAU = Cassin’s Auklet, RHAU = Rhinoceros Auklet, WEGU = Western Gull).

<table>
<thead>
<tr>
<th>YEAR</th>
<th>COMU</th>
<th>BRCO</th>
<th>PECO</th>
<th>PIGU</th>
<th>CAAU</th>
<th>RHAU</th>
<th>WEGU</th>
</tr>
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<tr>
<td>1978*</td>
<td>0.67</td>
<td>0</td>
<td>0</td>
<td>0.2</td>
<td>0.7</td>
<td>na</td>
<td>1.04</td>
</tr>
<tr>
<td>1983</td>
<td>0.04</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.24</td>
<td>na</td>
<td>0.63</td>
</tr>
<tr>
<td>1986</td>
<td>0.73</td>
<td>1.33</td>
<td>0.1</td>
<td>0.02</td>
<td>0.74</td>
<td>0.55</td>
<td>1.28</td>
</tr>
<tr>
<td>1992</td>
<td>0.08</td>
<td>0</td>
<td>0</td>
<td>0.31</td>
<td>0.25</td>
<td>0.73</td>
<td>0.51</td>
</tr>
<tr>
<td>1998</td>
<td>0.39</td>
<td>0.42</td>
<td>0.06</td>
<td>0.05</td>
<td>0.79</td>
<td>0.13</td>
<td>0.52</td>
</tr>
<tr>
<td>2003</td>
<td>0.72</td>
<td>1.01</td>
<td>2.21</td>
<td>0.92</td>
<td>0.9</td>
<td>0.43</td>
<td>0.81</td>
</tr>
<tr>
<td>Mean Prod.**</td>
<td>0.75</td>
<td>1.45</td>
<td>0.92</td>
<td>0.83</td>
<td>0.72</td>
<td>0.56</td>
<td>1.09</td>
</tr>
</tbody>
</table>

* 1978 was a warm water year, but not a tropical El Niño.

** Mean productivity represents the 32-year average productivity for each species.
Survival of Adults and Population Consequences of ENSO

El Niño has been linked to the population dynamics of seabirds in the central North Pacific Ocean (15), suggesting an important natural mechanism for understanding seabird population regulation.

In the CCS, evidence of population-level consequences of ENSO events depends on the species under investigation. In Washington, Wilson (22) showed that colony attendance of murres during the 1983 El Niño was 87% lower than abundance in the previous year, but suggested anthropogenic factors were responsible for continuing low numbers of murres attending colonies after 1983. Sydeman (24) found no change in the survival of adult, color-banded murres on the Farallon Islands in relation to the weak 1986 ENSO event.

However, Hodder and Graybill (20) documented an increase in mortality for murres and cormorants in Oregon during the 1983 event, and in relation to the 1997-1998 El Niño, deposition rates of murres (numbers/mile/week) on beaches on the outer coast of Washington were higher in 1997 than in both 1996 and 1998 (T. Good and C. Thompson, unpublished data).

For other species, mortality of breeding age adults is clearly elevated during El Niño. For example, Boekelheide and Ainley (25) and Nur and Sydeman (26) demonstrated considerable declines in survival and recruitment of Brandt’s Cormorants during warm-water anomalies in the CCS. Massey et al. (27) showed a decline in the return rates of older, rather than younger, breeding Least Terns in southern California.

Thus, while El Niño has been shown to have considerable effects on the demographic processes of seabirds, long-term population-level consequences are less convincing. In the only modeling exercise published to date on this issue, MacCall (28) investigated the effects of repeated El Niño events and chronic reproductive failures on CCS seabirds; indeed in this case, population declines were inevitable.

Seabird Responses to La Niña Events


Seabird Responses to the Pacific Decadal Oscillation

Natural cycles that occur on timescales of decades or centuries, such as the PDO, add to the difficulty in interpreting the effects of ENSO/LNSO on seabird communities, species, and populations (29).

Biological communities have responded to PDO-related low frequency ocean warming in the Pacific Ocean. For example, zooplankton biomass in the Southern California Bight has declined significantly over the past 40 years (30, 31), and compositional changes in rocky-intertidal communities in central California have been documented (32). However, there has been little study on the direct effects of variability in the PDO on seabird populations in the Pacific. The results of Sydeman et al. (19), the only published work to date to explicitly examine patterns of response in seabirds to changes to the PDO, were equivocal. While some Farallon Island and Channel Island species showed long-term declines in productivity, others did not, and there was no obvious “step-wise” change in reproductive performance after the 1976-1977 PDO shift. Instead, Sydeman et al. suggested that a “regime shift” occurred in 1989-1990, which explained a reduction in the use of juvenile rockfish and declines in seabird productivity starting in the late 1980s (Figure 5.2).

The concept of a regime shift in 1989-1990 has now been strongly supported by many publications (33), but this ecosystem change, unlike shifts in 1976-1977 and earlier, was most pronounced in the biological time series rather than temperature and other environmental measurements. The concept of “regime shifts” and consequences for fish populations have been long discussed (reviewed by Chavez et al. 2003).
Chapter 5. Climate and Food: “Bottom-Up” Control of Seabird Population Parameters and Population Dynamics

In British Columbia, there have been considerable inter-decadal changes in the timing of breeding for 4 species of alcid breeding at Triangle Island (16). Chick growth of both Tufted Puffins and Rhinoceros Auklets has declined since the mid-1970s, and Tufted Puffins experienced reproductive failure from 1994-1998 (J. Ryder and D. Bertram, unpublished data).

Concurrently, there has been an overall decline in the proportion of sandlance in the nestling diet of both species. However, in the absence of sandlance, auklets switched to alternative prey, whereas puffins did not; for this species, breeding failure thus coincided with the timing of substantial decline of sandlance from nestling diet (D. Bertram et al. unpublished data).

At sea, changes in seabird communities and populations in the CCS may be related to variability in the PDO, although results are unclear. Veit et al. (34), in studying the seabird community off southern California, reported that overall seabird abundance decreased by 40% between 1987-1994, mostly due to the 90% decline in the dominant cold-water species, the Sooty Shearwater (Puffinus griseus).

Hyrenbach and Veit (35) have extended these observations, and remarked that since 1994, total seabird abundance and Sooty Shearwater numbers have remained consistently lower than during 1987-1994, suggesting that long-term changes to the ecosystem persist. In central California, Ainley et al. (85) and Oedekoven et al. (36) demonstrated interannual and long-term avifaunal changes, and declines in many cold-water, locally breeding species, including Common Murres and Cassin’s Auklets.

The most parsimonious explanation for changes in seabirds at sea in southern and north-central California in the late 1980s is probably a response to ecosystem change at that time (~1989-1990), rather than a lagged response to the 1976-1977 regime shift. Wahl and Tweit (37) studied decadal trends in seabird populations off the coast of Washington, and demonstrated a decline in cold-water species and a concomitant increase in warm-water species over the past 3 decades.

Finally, in recent reports on the state of the California Current developed as part of the California Cooperative Oceanic Fisheries Investigation (38-40), combined colony and at-sea datasets have been used to investigate seabird response to a purported shift in the PDO in 1998-1999. Colony data from the Farallon Islands clearly demonstrates an increase in productivity for 6 species of seabirds after 1998. Moreover, Schwing et al. (40) demonstrate not only an increase in mean reproductive performance after 1998, but also a decrease in variance.

In contrast, the overall abundance of seabirds at sea in southern California has not changed simultaneously; numbers remain low when compared with the seabird communities of the late 1980s. However, in both 1999 and 2001, cold-water, subarctic species comprised a greater proportion of the avifauna.

Future surveys will reveal if this represents a consistent long-term change in seabird community composition or an intermittent change associated with cold-water intrusions during these years.
5.3 CONSEQUENCES OF GLOBAL WARMING

Despite controversies regarding the causes of climate change, the earth is getting warmer. Recent climate models from the U.K. Hadley Centre (41) combined with models of past climate indicate that mean global surface air temperatures have already increased 1ºC in the past century. Under the models’ mid-range estimates, temperatures are expected to increase by 3ºC within the next 100 years if “greenhouse gases” such as carbon dioxide and methane continue to grow at present rates. Rising global temperatures can affect marine life, including seabirds, in many ways, both directly and indirectly.

Because of their high status in the food web, seabird species are likely to be some of the most sensitive to human-induced climate change (42). Reductions in marine productivity associated with higher ocean temperatures directly impact seabird foraging, causing serious negative consequences for seabird reproduction and survival. In the California Current, both high frequency (El Niño) and low frequency (PDO) warm-water events have negative effects on seabird breeding. Seabirds breed later, lay fewer eggs, and fledge fewer chicks during El Niño events (19, 43).

Reduced prey availability causes changes in marine distribution as birds have to search wider areas to feed (44). As well, extreme El Niño warm-water events are associated with dramatically increased adult mortality due to starvation (19, 43). If global warming affects the frequency and duration of both high and low frequency warm-water anomalies in the California Current, there could be dramatic impacts on seabird populations.

Global warming may also have direct affects on marine bird populations. Sea level rise, increased precipitation, and increased storm activity – all predicted outcomes of increased warming, could destroy nests or eliminate breeding habitat altogether (45). Species that rely on low elevation islands (i.e. terns) for breeding would be greatly affected by these sorts of impacts.

5.4 FOOD AS A FACTOR LIMITING POPULATION GROWTH

The factors influencing the population dynamics of seabird colonies are of extreme interest to biologists and marine resource managers. Various natural mechanisms for regulating population dynamics have been proposed, ranging from predation to habitat availability to competition for resources such as nest sites and food. Studies have shown that among these, seabird populations track fluctuations in food availability more closely than other ecological factors (46) and that food is often an important factor regulating the growth or recovery of populations (47, 48).

Food resources are highly variable both spatially and temporally, and many factors may limit the amount of food available to seabirds in any given year. Among these are natural variability in oceanographic conditions (such as El Niño), which can negatively affect prey resources (19, 50, 51); competition with fisheries (51, 52); and density dependent intraspecific competition (47, 53).

Density dependent regulation of populations is predicated on the idea that there is an upper limit (the carrying capacity) of a population that is the maximum number of individuals that the most limited resource of an area can support (54). So as the population increases, more food is required, until the population size reaches a balance with the amount of food available. Studies have suggested that as seabird colonies increase in size, there is an increase in intraspecific competition and a reduction in the amount of food available close to the colony, thereby limiting the further growth of that colony (47, 55).

Food availability (or lack thereof) can limit population growth through two important mechanisms. The first is through limiting reproductive output of a colony during the breeding season. Food availability is closely linked to seabird reproductive success (56, 57) so that when food resources are limited, a seabird’s ability to successfully raise young is hampered, and productivity declines (19, 22, 58), resulting in slower or even negative population growth.

Food availability can also affect seabird populations during the non-breeding season through reduced adult survival (20, 26) as well as the decreased survival and recruitment of immature birds (56). For example, reductions in food availability during El Niño events in the 1980s resulted in large-scale adult mortality of murres and cormorants in the CCS (20, 59).
In order to determine if population growth will be limited by food availability, researchers will need to acquire: 1) accurate estimations of seabird populations both on colony and at sea; 2) energetic requirements of CCS seabird populations (see section 5.2); 3) information on the abundance and distribution of prey resources around breeding colonies and winter foraging areas; 4) foraging range of CCS marine birds; and 5) information on competition for resources with other species (fish and marine mammals) and fisheries.

5.5 PREY DEPLETION IN FISHERIES

Fishing activities can have both direct (see Chapter 6) and indirect effects on seabirds. Even though indirect effects are known to occur (and there are many studies that attempt to demonstrate that prey depletion in fisheries has a detrimental effect on seabirds) it is very difficult to provide a direct link between cause and effect (60). Even when it is documented that seabirds are affected by a reduction in prey, it is difficult to prove that this reduction is a direct result of fisheries (61, 62).

Prey depletion refers to the decrease in seabird prey as a result of fishery activity. In some ecosystems it has been estimated that seabirds consume between 20 to 30% of the annual pelagic production of fish (63, 64), which can place them in direct competition with fisheries.

Seabirds can be affected by a direct depletion of their food by fisheries, when seabirds and fisheries target the same species and age classes. Similarly, if fisheries target adults of the fish population, forage for seabirds may be affected if the spawning population is significantly reduced. The seabird species that are most vulnerable to these types of indirect effects are those that have a restricted foraging range or that are specialized in a certain feeding method or prey (63).

In the CCS, there are currently 22 fisheries that target the same species that seabirds consume (Table 5.3), and therefore may be a potential source of conflict by reducing seabird prey biomass. As stated above, it is difficult to provide evidence for detrimental effects on seabirds as a result of prey depletion from these fisheries. However, seabird prey consumption models can provide a starting point for examining potential overlap between seabird prey requirements and fisheries catch (see section 5.6). This type of information is extremely valuable for setting fisheries management limits.

In certain cases, a positive effect of fisheries on seabirds may occur when the fishery targets predatory fish, which may in turn decrease predation pressure on smaller fish. This can result in an increase in seabird forage, such as the case for seabirds in the North Sea (65).
However, in certain cases, the removal of large predatory fish may also cause a decrease in the availability of prey to seabirds. In certain habitats such as in the tropics, some predatory fish (such as tuna) are essential for driving smaller seabird prey to the surface, where non-diving or shallow-diving seabirds can access them (66, 67). Therefore, by removing these predatory fish, seabird access to smaller fish may decrease, resulting in more limited feeding opportunities. Whether the effect of predatory fish removal is positive or negative for seabirds, it has been recently estimated that 90% of large predators have been removed from global oceans, which will undoubtedly cause ecosystem-level repercussions yet to be determined (68).

Fisheries managers need to consider all possible conflicts and overlaps between seabird forage fish and fisheries that target the same fish. It is also important to understand natural prey fluctuations, which undoubtedly affects both seabirds and fishery catches.

When environmental perturbations such as an El Niño are coupled with poor fisheries management, dire situations can occur, such as the 1971-72 Peruvian anchovy collapse, which is thought to have been a result of a strong El Niño event coupled with over-fishing (69).

Seabird researchers need to be aware of these possible indirect conflicts with fisheries and provide assistance and information to fisheries managers, if deemed necessary. It is also of extreme importance for seabird researchers and fisheries managers alike to stay informed of potential emerging fisheries.
Table 5.3 – Fisheries that operate in the CCS and have the potential of reducing prey for seabirds.

<table>
<thead>
<tr>
<th>FISHERY</th>
<th>TARGET SPECIES</th>
</tr>
</thead>
<tbody>
<tr>
<td>WA Puget Sound Region salmon drift gillnet</td>
<td>salmon</td>
</tr>
<tr>
<td>CA squid purse seine</td>
<td>squid, loligo</td>
</tr>
<tr>
<td>WA/OR gillnet</td>
<td>herring, smelt, shad, sturgeon, bottom fish, mullet, perch, rockfish</td>
</tr>
<tr>
<td>WA/OR lower Columbia River salmon drift gillnet</td>
<td>salmon</td>
</tr>
<tr>
<td>CA anchovy, mackerel, tuna</td>
<td>anchovy, mackerel, tuna</td>
</tr>
<tr>
<td>CA herring purse seine</td>
<td>herring (roe and fresh herring)</td>
</tr>
<tr>
<td>CA sardine purse seine</td>
<td>sardine</td>
</tr>
<tr>
<td>CA/OR/WA salmon troll</td>
<td>salmon</td>
</tr>
<tr>
<td>WA groundfish, bottomfish jig</td>
<td>groundfish and bottomfish</td>
</tr>
<tr>
<td>CA/OR/WA sablefish pot</td>
<td>sablefish</td>
</tr>
<tr>
<td>WA Grays Harbor salmon drift gillnet</td>
<td>salmon</td>
</tr>
<tr>
<td>WA salmon purse seine</td>
<td>salmon</td>
</tr>
<tr>
<td>WA salmon reef net</td>
<td>salmon</td>
</tr>
<tr>
<td>WA Willapa Bay salmon drift gillnet</td>
<td>salmon</td>
</tr>
<tr>
<td>WA/OR herring, smelt, squid purse seine or lampara</td>
<td>herring, smelt, squid</td>
</tr>
<tr>
<td>WA/OR North Pacific halibut longline/set line</td>
<td>halibut</td>
</tr>
<tr>
<td>WA/OR smelt, herring dip net</td>
<td>smelt, herring</td>
</tr>
<tr>
<td>CA/OR/WA groundfish trawl</td>
<td>hake, flatfish, sablefish, lingcod, rockfish</td>
</tr>
<tr>
<td>CA/OR/WA groundfish, bottomfish longline/set line</td>
<td>groundfish, bottomfish</td>
</tr>
<tr>
<td>WA (all species) beach seine or drag seine</td>
<td>various species</td>
</tr>
<tr>
<td>WA groundfish, bottomfish jig</td>
<td>groundfish and bottomfish</td>
</tr>
<tr>
<td>Baja California sardine/anchovy</td>
<td>sardine/anchovy</td>
</tr>
</tbody>
</table>
5.6 SEABIRD PREY CONSUMPTION MODELS

The main goal of the prey consumption models we present here is to estimate the minimum amount of biomass of individual prey species or group of species consumed by dependent alcid nestlings (Common Murre, Pigeon Guillemot, Rhinoceros Auklet, and Cassin's Auklet) on Southeast Farallon Island (SEFI), California.

We chose to construct prey consumption models rather than bioenergetics models, as there is little physiological data available regarding the energy requirements of these seabird species at this location.

Species-Specific Models:

1. Cassin's Auklet

Cassin's Auklet responds to interannual variability in ocean climate by alternating diet between *Thysanoessa spinifera* and *Euphausia pacifica*, although both are consumed in all years (19, 87). Euphausiid crustaceans comprised between 60% and 85% (by mass) of nestling auklet diet annually (Fig. 5.3). In fact, although *E. pacifica* is substantially more abundant (>100 times) than *T. spinifera* in the region (70), the two species comprise relatively equal proportions of auklet diet. Additionally, two subtropical euphausiid species, *Nyctiphanes simplex* and *Nematocelis difficilis*, are consumed occasionally by Farallon auklets during ocean warming events such as El Niño (19, 71, 72). In years when the overall abundance of euphausiids is relatively low in the diet, auklets supplement nestling diet primarily with amphipods, decapods, copepods, mysids (Class Crustacea), and larval fish.

![Figure 5.3](image)

*Figure 5.3 – Proportion diet composition (by mass) of Cassin's Auklet nestlings on SEFI, 1994-2002. “Other” includes Nematodes, Cirripedia, Molluscs, Isopods, larval Pisces and unidentified organic matter.*

The biomass of prey consumed by Cassin’s Auklet nestlings varied interannually (Fig. 5.4), ranging from 3.0 metric tons in 1998 to 15.6 metric tons in 1994. Prey consumption was relatively low during the 1997/1988 ENSO event, reflecting poor reproductive success in 1997 (55%, the lowest in this series), a reduced breeding population estimate and reduced parental food delivery amounts in 1998 (both the lowest in this series). The annual estimate of nestling food mass delivered per chick per day (assuming a constant annual rate of parental food delivery; Fig. 5.5) was also lowest during the 1998 ENSO year.
Figure 5.4 – Cassin’s Auklet nestling prey consumption in metric tons, 1994-2002.

Figure 5.5 – Mass (g) of food delivered per Cassin’s Auklet nestling per day.
2. Rhinoceros Auklet

Although the diet of Rhinoceros Auklet nestlings is more diverse than for Cassin’s Auklet, our results show that there are between one and three primary prey species or groups utilized in each year, and that these vary on an interannual basis (Fig. 5.6).

Salmon spp., Northern Anchovy, Sablefish, Rockfish spp., and Pacific Saury together comprised the major diet items, in varying proportions in all years, ranging from 70-98% of diet composition by mass. Northern Anchovy was one of the two most consistently present species in the diet, appearing in all years in varying amounts (0.5-62%), except in 2001. Anchovy were present in low amounts (less than 4%) in 1987, 1991, 1997, and 1998. This variability corresponds to the ENSO events in 1986 and 1997/1998 and possibly with a climatic regime shift in 1989/1990.

Sablefish were present in varying amounts (2-47%) in all years except 1998 and in low amounts (less than 6%) in 1990, 1993, 1996, and 2000-2002.

Pacific Saury comprised 17% of diet by mass in 1987, then disappeared or was present in low amounts (less than 5%) until 1995, when it reappeared in the diet in relatively large amounts (9-92%) for the remainder of the time series.

The proportion of Salmon spp. (mostly unidentified salmon spp. and King Salmon) in the diet (when present) ranged from 2% in 1988 to 42% in 1990. Salmon was absent or in low amounts (less than 6%) in 1988, 1992, and 1998-2002.

The proportion of Rockfish [various species, including Shortbelly (S. jordani), Widow (S. entomelas), Yellowtail (S. flavidus), Blue (S. mystinus), Square spot (S. hopkinsi), Striped tail (S. saxicola), Black (S. melanops), Halfbanded (S. semicinctus), Bank (S. rufus), Boccacio (S. paucispinis), Speckled (S. ovalis), and Dark-blotched Rockfish (S. pinniger)] in the diet (when present) ranged from 0.5% in 1990 to 39% in 2002. Rockfish were absent or in low amounts (less than 9%) in 1989, 1990, 1992, and 1994-2000.

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Figure 5.6 – Proportion diet composition (by mass) of Rhinoceros Auklet nestlings on SEFI, 1987-2002. “Other” category includes: Slender Barracudina, Mackerel, Sardine/Herring unidentified, Stickleback, Plainfin Midshipman, Smelt, Pacific Hake, Butterfish, Sculpin spp., Greenling spp., Lamprey, and Lanternfishes.
The biomass of prey consumed by Rhinoceros Auklet nestlings varied interannually (Fig. 5.7), ranging from 0.52 metric tons in 1988 to 0.036 metric tons in 1998. Prey consumption was relatively low during the 1998 ENSO event, reflecting poor reproductive success (13%, the lowest in this series) and reduced parental food delivery amounts. The annual estimates of nestling food mass delivered per chick per day were also lowest during the 1992 and 1998 ENSO years (Fig. 5.8).

Figure 5.7 – Rhinoceros Auklet nestling prey consumption (in metric tons), 1987-2002.

Figure 5.8 – Mass (g) of food delivered per Rhinoceros Auklet nestling per day.
3. Common Murre

Our results suggest that there are between one and two primary prey species or groups delivered to Common Murre nestlings in each year, and that these vary on an interannual basis (Fig. 5.9).

Northern Anchovy, Anchovy/Sardine, and Rockfish spp. together comprised the major diet items, in varying proportions in all years, ranging from 62-95% of diet composition by number. Northern Anchovy was present in all years in varying amounts, ranging from 1% in 2002 to 81% in 1994. Anchovy were present in low amounts (less than 8%) in 1987, 2001, and 2002. Anchovy/Sardine was present in 1995 and 1997-2002 in varying amounts, ranging from 2% in 1997 to 43% in 1998. Rockfish were present in all years except 1998. When present, rockfish varied from 87% in 1978 to 3% in 2000. Rockfish were absent or in low amounts (less than 9%) in 1992, 1996-1998, 1999, and 2000. The proportion of unknown prey items in the diet was relatively low in all years, ranging from 0.3% in 1994 to 12% in 1999.

Figure 5.9 – Proportion diet composition (by number) of Common Murre nestlings on SEFI, 1987 – 2002.

The biomass of known prey items (prey included in model, but not representing all diet items) consumed by Common Murre nestlings varied interannually (Fig. 5.10), ranging from 1.02 metric tons in 1992 to 25.0 metric tons in 2002. The proportion of prey items in the diet (by number) included in the model varied from 70% in 2000 to 97% in 1987. Prey consumption was relatively low during the 1992 and 1998 ENSO events (8% in 1992 and 39% in 1998, the lowest in this series), reflecting poor reproductive success in 1992 and reduced parental food delivery amounts. However, the annual estimate of nestling food mass delivered per chick per day was high during the 1992 ENSO year (second highest in this series, Fig. 5.11).
Figure 5.10 – Common Murre nestling prey consumption (in metric tons), 1987-2002.

Figure 5.11 – Number of prey items and estimated mass (g) of food delivered per Common Murre nestling per day.
4. Pigeon Guillemot

Sculpin spp. and Rockfish spp. together comprised the majority of known diet items delivered to nestlings, in varying proportions in all years, ranging from 24-83% of diet composition by number (Fig. 5.12). Rockfish were present in all years in varying amounts, ranging from 56% in 1993 to 0.5% in 2000. Sculpin were also present in all years in varying amounts, ranging from 41% in 1995 to 19% in 1999.

![Figure 5.12](image_url)  
Figure 5.12 – Proportion diet composition (by number) of Pigeon Guillemot nestlings on SEFI, 1991-2002. “Other” includes Flatfish spp., Cuskeel, Gunnel/Prickleback, Kelpfish, Greenling, Shrimp, Crab, Red Brotula, Worm (polychaete), Blenny, Señorita, Octopus, Squid Sandlance, Anchovy, Anchovy/Sardine, Butterfish, Sablefish, and Pacific Saury.

The biomass of known prey items (prey included in model, but not representing all diet items) consumed by Pigeon Guillemot nestlings varied interannually (Fig. 5.13), ranging from 0.72 metric tons in 1995 to 0.032 metric tons in 1999. However, the proportion of prey items in the diet (by number) included in the model was relatively low, and varied from 83% in 1993 to 24% in 2000. Prey consumption was relatively low (less than 0.17 metric tons) for all years except 1991, 1995, 2001, and 2002, when it was greater than 0.4 metric tons. The annual estimate of nestling food mass delivered per nest site per day was high during the 1992 ENSO year (second highest in this series, Fig. 5.14).
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Figure 5.13 – Pigeon Guillemot nestling prey consumption (in metric tons), 1991-2002.

Figure 5.14 – Number of prey items and estimated mass (g) of food delivered per Pigeon Guillemot nest site per day.
Conclusions – Prey Consumption Models

Changes in annual diet composition (and thus prey consumption) of SEFI alcids are coincident (for some species) with interannual changes in local or basin-wide ocean climate conditions.

For example, the proportion of Rockfish spp. in the diet showed substantial interannual variability, ranging from 0-39% in Rhinoceros Auklet diet (Fig. 5.6) and 0-87% in Common Murre diet (Fig. 5.9). During the ENSO year of 1992 rockfish were present in very low amounts in the diet of both species and were totally absent in the ENSO year of 1998. Rockfish abundance in Pigeon Guillemot diet, however, did not display these trends (Fig. 5.12). This result must be taken with caution, however, as the proportion of known prey items in guillemot diet was consistently low (less than 61% by number for each year with the exception of 83% in 1992, but where there were only 34 prey items observed in that year).

In contrast, the primary prey utilized (euphausiids) by planktivorous Cassin’s Auklet nestlings shows relatively little interannual variability, ranging from 60-85% of the diet (Fig. 5.3), and remained relatively high during the 1997-98 ENSO event. Our results also suggest that the rockfish abundance in the diet varied, to some degree, with regime shifts in the North Pacific ocean in 1989-1990 and 1998-1999. The abundance of rockfish in Rhinoceros Auklet and Common Murre diet was relatively high prior to the 1989-90 regime shift, followed by a reduction throughout most of the 1990s. In 2001/2002, rockfish began to appear in the diet of both species in relatively high numbers, suggesting a slow recovery of this long-lived species, possibly in response to the 1998-99 regime shift to cooler conditions.

The models presented suggest substantial interannual and inter-decadal variability in diet composition and prey consumption, and also indicate that these trends are likely reflective of variability in ocean climate conditions (and possibly prey availability) in the CCS.

Seabirds are useful sampling devices of the marine environment and several investigators have reported that aspects of their biology, including diet characteristics, likely reflect relative prey availability (57, 73-75) as well as characterization of ocean climate conditions (16, 76) (Abraham and Sydeman in press). This is considered in greater detail in chapter 8.

The models we present are good examples of estimation of prey consumption at a local scale. Development of prey consumption models for seabirds throughout the entire CCS would be extremely valuable for ecosystem-level predator and prey species management and for assessing effects of climate variability and change.

In order to make better predictions regarding the effects of ocean climate and prey variability on seabird populations throughout the CCS, it is necessary to obtain detailed seabird diet data from all significant seabird breeding colonies in the eco-region. To expand these analyses to include the entire CCS, cooperation between researchers is essential.
5.7 Intra-annual Variations in Diet Composition

The diet composition and prey consumption models outlined above describe variations in the diet of marine birds both over years (interannual) and over decades (inter-decadal).

Diet can also vary at smaller temporal scales, such as within a year (intra-annual). Smaller timescales allow a glimpse of more subtle patterns of prey consumption that might be missed when examining the big picture. These short-term changes in prey resources can be important to the reproductive success and survival of seabirds, may increase our understanding of the life cycles and population dynamics of their prey species, and can contribute to our understanding of long-term trends in prey resources.

The diet of many seabird species changes between winter and the breeding season due to annual cycles of prey abundance. In many species this includes a change in the trophic level of their prey, meaning that they are eating “higher up on the food chain” during part of the year. For example, Common Murres in central California feed primarily on small fish during the spring and summer, while in the winter they also depend on krill (71, 72).

The prey of marine birds also changes within seasons. During the breeding season, when adults are often bringing prey items into the colonies for their chicks on a daily basis, these changes can be tracked closely. Seasonal changes in the prey fed to chicks have been shown for many seabird species in the CCS from British Columbia to the Gulf of Mexico (77, 78).

On Triangle Island in Southern BC, Cassin’s Auklets switched from copepods to fishes during the course of the season in several years. In other years, however, fishes were not an important part of the diet at any time during the chick-rearing period (79). When rockfish are present in the diets of Rhinoceros Auklets on Ano Nuevo Island, in central California, they are typically only an important prey item early in the season (PRBO, unpublished data).

Changes are also seen in other areas of the North Pacific such as the Sea of Japan and the Gulf of Alaska (80, 81). In some cases, these seasonal diet changes may represent the appearance or disappearance of higher quality prey thereby altering the total caloric or nutrient intake of chicks (80, 82).

On the Farallon Islands, Common Murres primarily feed their chicks small forage fish. As shown in Fig. 5.10, the most common prey items that murres feed their chicks are juvenile rockfish, anchovies, and sardines, though the relative importance of these prey groups varies between years and decades. Common Murre diet tracks changes in rockfish populations very closely, as shown by the correlation between the percentage of rockfish taken by murres and the abundance of rockfish estimated by the National Marine Fisheries Service. This within-season relationship is therefore of particular interest as a proxy for rockfish population changes.

When we look at within-season changes in nestling diet, we can characterize the short-term changes in rockfish population dynamics. There are several important questions related to this pattern: Does the proportion of rockfish increase, decrease, or remain steady during the season? And do these within-season patterns differ between years?

Results indicate that the proportion of rockfish in the diet often decreased during a season, sometimes by as much as 50%. These decreases suggest that rockfish become more difficult to catch (i.e. scarcer) later in the summer, possibly because at this time of year juvenile rockfish reach the age or size when they shift to benthic (ocean floor) habitats instead of schooling within the water column. In some years, however, there was no within-season change in rockfish found in chick diet. The timing between the rockfish and murre breeding seasons may be more “matched” in these years, or the population of rockfish may have been larger, with more individuals available even late in the season.

Patterns of rockfish use by murres tend to remain the same for several consecutive years, which may suggest that the changes in patterns may be related to climate regime changes that affect rockfish populations. During our 30-year study period we found that seasonal rockfish use was steady during the 1970s (Fig. 5.15a), decreased within each season in the 1980s (Fig. 5.15b) and early 1990s, and was again steady in the late 1990s – though by this time total quantities of rockfish were very low to begin with (Figure 5.15c).
The decreasing seasonal patterns in the 1980s and early 1990s show several periods of multi-year declines that led to the near absence of rockfish in the late 1990s (Fig. 5.16). In annual diet summaries a major decrease in rockfish consumption was shown after the 1989 and late 1990s regime changes, but surprisingly no diet changes were evident before 1989 despite a major regime shift in 1976-77.

The seasonal patterns show that changes to rockfish populations were in fact starting in the 1980s, well before the changes became apparent in the annual diet summaries. The affects were subtle and slow, probably due to the long lifespan of rockfish. By looking at these intra-annual patterns over long time periods, we get a clearer picture of what is happening with rockfish over decades in response to climate regime changes.

Intra-annual changes in prey availability may be important to seabirds that depend on particular prey species during breeding when energy needs are high, or during the winter when food sources may be particularly scarce. Decreases in food availability, or even switching to lower quality prey, can significantly reduce the energy seabirds are getting from their food, or force them to expend more energy finding food. These energy losses can negatively impact chick development and reproductive success (83, 84), and may also impact juvenile and adult survival.
Short-term patterns in prey use can also help give clues about the life cycles of some prey species. Studying fish and plankton populations directly is both difficult and expensive so the population dynamics of many of these species are poorly understood. Decreases in certain prey items can indicate movement of these species either horizontally, out of the foraging range of birds, or vertically, to depths the birds cannot reach. These seasonal changes in prey may also be indicators of the peaks in prey populations.

When seasonal patterns are compared across years, we can learn about changes in prey population over time. As seen in the example of rockfish in the diet of Common Murres on the Farallon Islands, seasonal diet patterns can help us understand the long-term (interannual and inter-decadal) patterns in the diet.

The results from the observations of murre diet presented in this section provided a time series and a level of detail that is unlikely to be found in any direct fish population monitoring program. The importance of short-term patterns in interpreting the effects of long-term patterns highlights the value of considering multiple timescales when looking at the biological effects of climate change, as well as the value of using marine birds as indicators of local ecosystems.

**Research and Monitoring Recommendations**

1. Investigate prey consumption by seabirds (at short and long timescales) in the CCS to assess seabird prey requirements, seabird-based prey mortality, potential conflicts with current or future fisheries, and the consequences of removal of predatory fish to ecosystem structure and functioning.

2. Continued monitoring of the effects of climate change on diet shifts and population dynamics.

3. Evaluate erosion rates for burrow nesters based on weather.

4. Develop programs that enable regional comparisons of diet.

5. Establish standardized methodologies for use in monitoring diet and prey consumption, including defining which reproductive, diet, and climate parameters are essential to monitor.

**Conservation and Management Recommendations**

1. Integrate seabird prey requirements into fishery management plans.

2. Investigate seabird prey requirements prior to opening new fisheries.
CHAPTER 5 LITERATURE CITED


Chapter 5. Literature Cited


