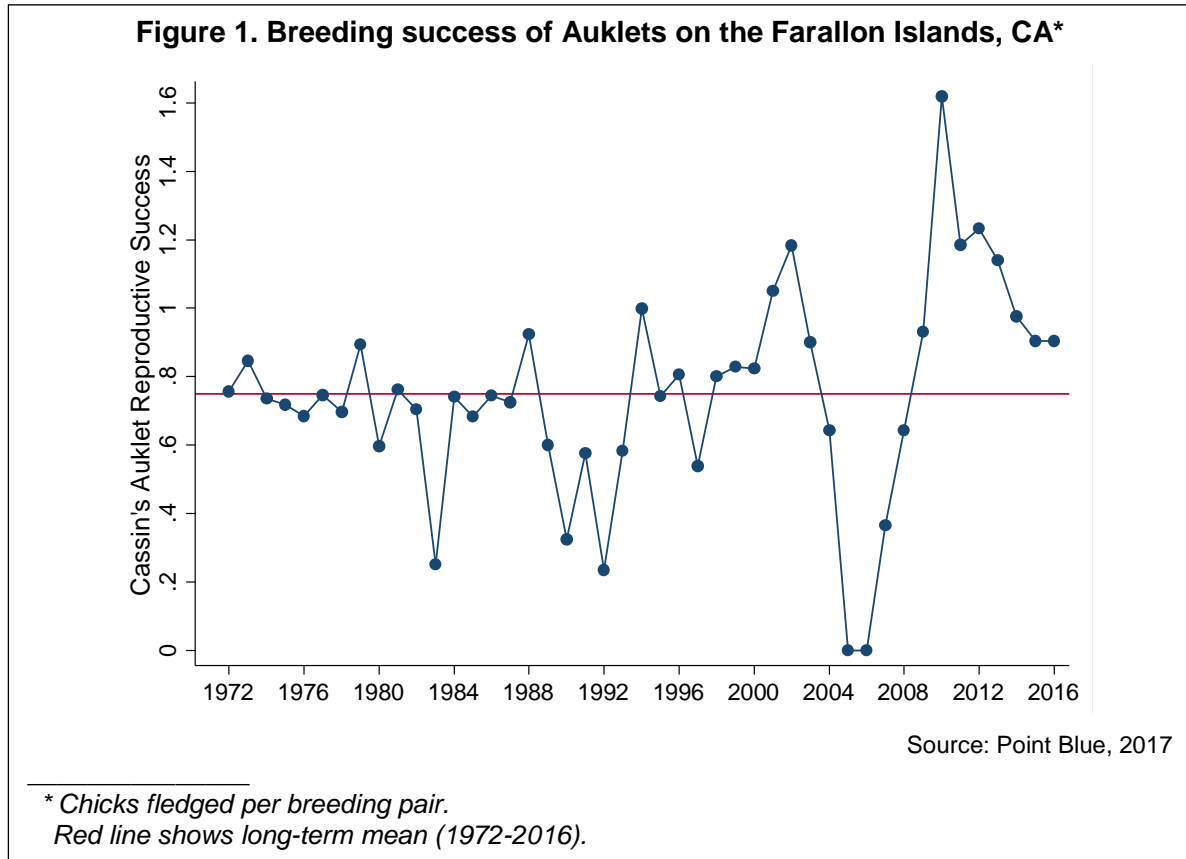


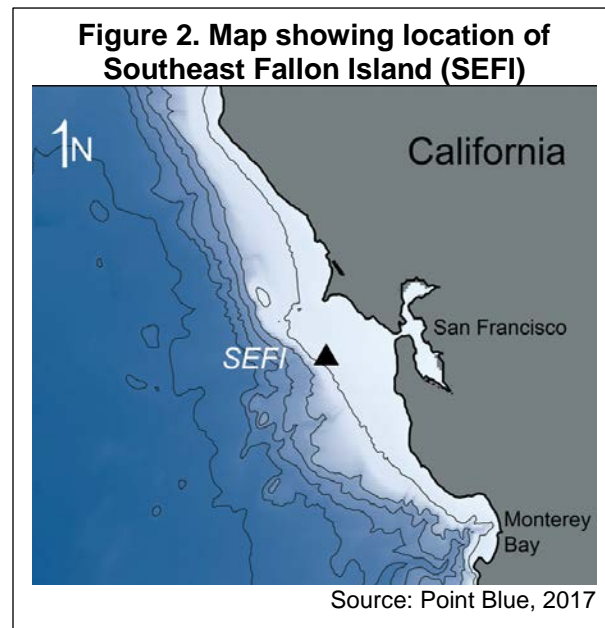
CASSIN'S AUKLET BREEDING SUCCESS

Over a 45-year period, the reproductive success of the Cassin's auklet has exhibited increasing variability (extremely low and extremely high reproductive success) with time, while showing an overall increase in reproductive success over the past 25 years.



What does the indicator show?

Figure 1 shows the variable year-to-year reproductive success of Cassin's auklets over the period 1972-2016 in study sites on Southeast Farallon Island (see map, Figure 2). Reproductive success, measured as the mean number of offspring produced per year per breeding pair declined slightly until about 1992 but since then has exhibited a significantly increasing trend. In the last 15 years, reproductive success has averaged 0.842 chicks produced ("fledged") per pair, above the previous 15-year average of 0.704 (see Table 1); the 45-year mean value is 0.75 chicks per pair.



Notable is the increase in year-to-year variability: reproductive success during the last 15 years was three times more variable than during the first 15 years (see Table 1). The two years with the lowest values and the five with the highest also occurred during the last 15 years.

Table 1. Annual variability in Cassin's Auklet breeding success, divided into three 15-year intervals

| Time period | Reproductive success, Mean (Standard deviation) | Proportion of double-brooding | Rate of abandonment |
|-------------|---|-------------------------------|---------------------|
| 1972-1986 | 0.704 (0.143) | 0.137 | 0.215 |
| 1987-2001 | 0.704 (0.230) | 0.234 | 0.251 |
| 2002-2016 | 0.842 (0.451) | 0.334 | 0.239 |



The Cassin's auklet (*Ptychoramphus aleuticus*) is a small, diving seabird. Its breeding range extends from the Aleutian Islands, Alaska to islands off the middle Baja California peninsula. Its center of distribution is located off British Columbia, on Triangle Island (Rodway, 1991). Important colonies in California occur on Southeast Farallon Island (part of the Farallon Islands National Wildlife Refuge, located 30 miles west of San Francisco) and on the Channel Islands off southern California.

Cassin's auklets lay one egg per breeding attempt, and are the only species in the Alcidae family which show regular behavior of "double-brooding," that is, rearing a second chick after successfully fledging their first chick (Johns et al., 2017). Double-brooding allows productivity of the population to exceed 1.0 chick per pair in exceptionally good years. There have only been six years when mean reproductive success for the population exceeded this threshold, all since 2000. The rate of double-brooding varies among years, and as shown in Table 1, has increased over time ($P = 0.043$).

Double-brooding and the rate of abandonment of eggs during incubation are two components that account for much, but not all, of the annual variation in reproductive success. While double-brooding has increased over time, the abandonment rate has shown no such trend (Table 1). Two recent years (2005 and 2006) were unusual in that reproductive success was zero and the abandonment rate was also extremely high (100 percent and 86 percent, respectively). Neither of these years were El Niño years, but they were years in which krill were absent from the diet fed to chicks (see below). In the other 43 years, the relationship between abandonment and reproductive success was more variable. Some years with low reproductive success also had high abandonment (67 percent in 1983 and 65 percent in 1992); in 1990 reproductive success was low but abandonment was also low (17.5 percent compared to the 45-year mean of 24 percent).



Why is this indicator important?

Seabirds such as the Cassin's auklet respond to changes in prey availability and prey quality, which in turn are influenced by climate (Lee et al., 2007; Wolf et al., 2009). Hence, seabirds can be, and have been, used as reliable indicators of food web changes in marine ecosystems (Piatt et al., 2007). Seabirds are among the most conspicuous of all marine organisms and changes in their populations or vital rates may reflect changes in their prey base, such as krill, that are more difficult to study (Ainley et al., 1995; Piatt et al., 2007; Manugian et al., 2015).

Studies of seabirds suggest that ocean warming and other forms of marine climate change are affecting the coastal food web, particularly krill. Krill is a major food resource not only for seabirds, but also for salmon, other fish, and marine mammals, including whales (Dransfield et al., 2014, Sydeman et al. 2014). Ocean warming may reduce the efficacy of upwelling — the upward movement of deep, cold, nutrient-rich waters to the surface, where plankton growth occurs (Snyder et al., 2003; Manugian et al., 2015). Reduced upwelling decreases nutrient availability and photosynthesis by phytoplankton, ultimately leading to a reduction in krill and other zooplankton. Hence, upwelling is key for many seabirds in the California Current.

Measurements of auklet reproductive success provide a strong signal of changes in ocean conditions — as reflected in prey availability — in the ecosystem over the period of time when the birds are reproductively active each year (March through August). Recent years of record-high auklet productivity on the Farallones have been associated with large local increases in krill, as documented below. In addition, seabird reproductive success has been shown to correlate with salmon abundance (Roth et al., 2007), suggesting that the reduction of krill abundance may be affecting salmon as well. Thus, the auklet reproductive success indicator reflects bio-physical processes occurring in the marine ecosystem. The recent increase in both overall reproductive success and annual variability of this indicator provide insights into temporal patterns of variation in the local marine ecosystem.

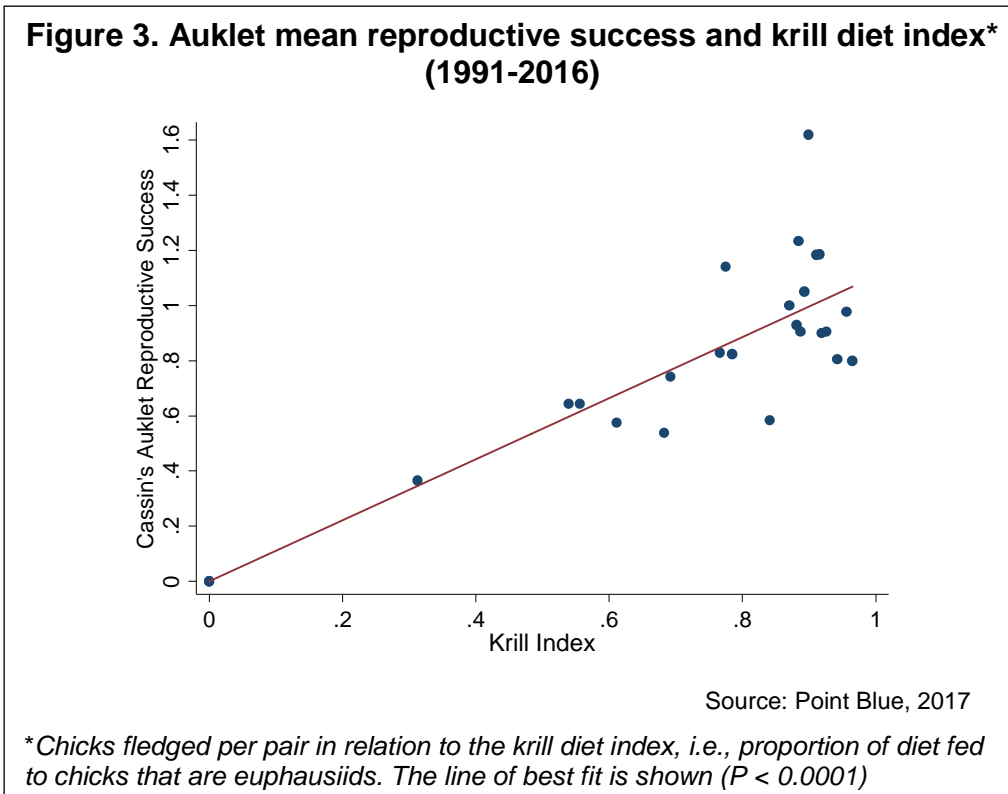
What factors influence this indicator?

Cassin's auklet breeding success on Southeast Farallon Island is most closely associated with variation in the availability of their prey, particularly krill. Krill are the main prey consumed by auklet chicks on Southeast Farallon Island, accounting for about 80 percent of their diet in typical years (Abraham and Sydeman, 2004). Auklets feed primarily on two krill species — *Euphausia pacifica* and *Thysanoessa spinifera* — as well as mysids and some larval fishes (sanddabs, rockfish, etc.). Years characterized by low krill biomass in the auklet's foraging grounds in the Gulf of the Farallones (e.g., 2005 and 2006) were associated with low reproductive success (Sydeman et al., 2006; Jahncke et al., 2008; Manugian et al., 2015). Conversely, during years when krill was abundant in the region (e.g., 2010 and 2011), auklets exhibited high productivity, more specifically high rates of double-brooding, as described below.

Auklet reproductive success is strongly related to measures of krill abundance and/or availability. There was a strong, linear relationship between the "krill diet index" for



Cassin’s auklets and their reproductive success (see Figure 3 below). The krill diet index is the proportion of prey fed to Cassin’s auklet chicks that consists of the two krill species listed above. The median value of the krill diet index was 87 percent (n = 25 years). However, in years when the krill diet index was less than 75 percent, reproductive success was in every case (n = 8 years) below the mean (and median) value for the entire time series. The krill index in 2005 and 2006 was zero. Conversely, high krill index values are associated with moderate to high reproductive success, though, even then, auklets exhibit considerable variability in outcome.



In addition, measures of krill abundance or biomass (to 30 meters deep, estimated by acoustic surveys conducted by Point Blue’s ACCESS Project) (Manugian et al., 2015) were more closely related to reproductive success than the krill diet index alone. In particular, the frequency of double-brooding is more closely related to krill biomass than the krill diet index. These results make clear that krill abundance and/or availability determines both high values of reproductive success (when double-brooding is common) and low values.

The influence of seasonal, wind-driven upwelling processes off the California coast on the productivity of the marine food web is well established (Garcia-Reyes et al., 2015). Upwelling brings deep, nutrient-rich waters to the surface. These nutrients are vital to the growth of plankton, which form the base of the marine food chain. Upwelling is driven by oceanographic conditions, especially wind patterns, which in turn reflect large-scale climate signals associated with the tropical Pacific Ocean – El Niño-Southern Oscillation (ENSO) (WRCC, 1998) — as well as with the North Pacific (Pacific Decadal



Oscillation and the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al. 2008)). ENSO is a cyclic interaction between the atmosphere and ocean in the tropical Pacific that has manifold effects, including the periodic variation between below-normal and above-normal sea surface temperatures. NPGO is part of a large-scale pattern of climate variability in the North Pacific that affects sea surface height and sea surface temperature; it also influences the strength of ocean circulation in the North Pacific Gyre, which includes waters transported into the California Current Ecosystem.

Cassin's auklet reproductive success, in turn, has been associated with these underlying patterns of climate variability (Abraham and Sydeman, 2004; Sydeman et al., 2006; Jahncke et al., 2008; Wells et al., 2008). During two of the strongest El Niño periods in the last four decades (1982-83 and 1991-1992), there was a substantial decrease in auklet breeding success. In contrast, recent years have shown auklet reproductive success to be less linked to ENSO signals and more strongly associated with the NPGO (Di Lorenzo et al. 2008, Schmidt et al., 2014). Changes in both the characteristics of the El Niño Southern Oscillation (such as a shift in the center of the warm water anomaly from the eastern Pacific to central Pacific) and a shift to greater positive values of the NPGO (which is associated with the earlier onset of upwelling favorable conditions) are likely playing a role in the shift in the auklet response (Schmidt et al., 2014). It is hypothesized that local changes in upwelling winds in the California Current are more consistent with changes in the NPGO index than indices of ENSO.

Technical Considerations

Reproductive success of Cassin's Auklets is measured by monitoring breeding birds in 44 nest boxes on Southeast Farallon Island (Abraham and Sydeman, 2004; Lee et al., 2007). Greater than 90 percent of the boxes are occupied by breeding birds each year, although fewer pairs attempt reproduction in years of poor food availability. Each nest box is checked every 5 days for nesting activity. Parent birds are uniquely banded for future identification. The date of egg-laying, number of eggs laid and hatched, and the number of chicks raised to independence by each breeding pair is counted. For this indicator, the overall annual reproductive success is assessed as the average number of offspring fledged per breeding pair per year. "Double brooding" rate, as discussed here, is defined as the proportion of birds that initiate a second reproductive effort (i.e., lay an egg) after fledging a chick successfully in their first attempt. "Abandonment rate" is defined as the proportion of breeding pairs which permanently left eggs unattended during incubation, leading to egg failure.

Strengths and Limitations of the Data

Cassin's Auklets and other breeding seabirds have been monitored on the Farallon Islands using standardized methods since 1972 (Boekelheide et al., 1990; Johns et al., 2017). During the 45-year period, great care was taken to keep the methodology as comparable as possible. Field biologists are intensively trained by professional biologists from Point Blue Conservation Science. Thus, methodology has remained highly consistent over the past 45 years.



Seabirds have demonstrated that they are excellent indicators of ecological conditions (Parsons et al., 2008). One strength of the indicator is the ability to correlate reproductive success directly with a key determinant of this ecological variable, the availability and/or abundance of two key prey species. The time series reflecting krill in the chick diet is now 25 years. The time series based on direct measures of krill biomass in the areas near the breeding colony is now 13 years. The longer time series has provided a better understanding of determinants of krill abundance (Manugian et al., 2015).

Their ability to initiate a second clutch after a successful first breeding make Cassin's auklets particularly valuable as an ecosystem indicator among seabirds. Their flexible reproductive strategy allows for tracking both positive deviations (when double-brooding is more common) and negative deviations (when mortality of eggs and/or chicks is high). Thus, the range of outcomes for Cassin's auklets is greater than that of species that lay only one clutch of a single egg.

A limitation of the indicator is that identifying a climate change signal due to anthropogenic influences is difficult to discern, compared to the effect of natural climate variability (e.g., impacts of the El Niño Southern Oscillation). In this regard, the increased variability of the indicator in recent years is a finding of note; it improves the understanding of what may be underlying both the especially low and especially high values of auklet reproductive success.

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