



## RESEARCH ARTICLE

# Episodes of high recruitment buffer against climate-driven mass mortality events in a North Pacific seabird population

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## Abstract

1. Longitudinal studies of marked animals provide an opportunity to assess the relative contributions of survival and reproductive output to population dynamics and change.
2. Cassin's auklets are a long-lived seabird that maximizes annual reproductive effort in resource-rich years through a behaviour called double brooding, the initiation of a second breeding attempt following the success of the first during the same season. Our objective was to explore whether double brooding influenced population change by contributing a greater number of future recruits.
3. We fit temporal symmetry models to 32 years of mark-recapture data of Cassin's auklets to infer the mechanisms underlying the observed variability in per capita recruitment rates.
4. We found that periodic peaks in recruitment were explained by an increase in available nest sites, the proportion of the population double brooding 4 years prior, and spring upwelling conditions. Estimates of population change suggests a relatively stable population throughout the time series, attributable to a 'floating' demographic class of sexually mature individuals excluded from breeding by competition which quickly fill vacant sites following periods of low adult survival.
5. Our results highlight the importance of recruitment in maintaining the population of a long-lived seabird periodically impacted by adverse environmental conditions.

## KEYWORDS

auklets, demography, double brooding, life history, marine heatwave, mark-recapture, recruitment, seabirds

## 1 | INTRODUCTION

Understanding the biotic and abiotic factors controlling a population's vital rates is critical for successful conservation and management. Even in systems where parameters such as survival, breeding propensity, reproductive success and recruitment can be easily estimated, it is often difficult to discern which of these factors contributes most to population change, or how these factors may interact. Long-term mark-recapture studies of individuals from wild

populations provide an opportunity to evaluate the interplay between the impacts of vital rates and the environment on overall population dynamics (Clutton-Brock & Sheldon, 2010). Some of the most complete long-term datasets of marked animals have been collected from colonial seabirds, which often exhibit high natal philopatry, site and mate fidelity, and can be easy to capture, handle and mark.

In long-lived vertebrate species, adult survival is a conserved trait that is generally high and consistent across years (Caswell, 1989; Stearns, 1992), leaving juvenile survival and reproductive rates as

the main driver of population dynamics for species with longer generation times (Gaillard et al., 1998). Indeed, results from long-term demographic studies of seabirds show high adult survival across a range of taxa (Sæther & Bakke, 2000), specifically including Larids (Coulson & Thomas, 1985; Sandvik et al., 2005), penguins (Gownaris & Boersma, 2019), albatrosses (Weimerskirch, 2018) and auks (Sandvik et al., 2005). The annual rate of new individuals entering the breeding population (hereafter simply 'recruitment'), a delayed outcome of fecundity during previous breeding season(s) and juvenile survival, is expected to be more variable in seabirds compared to short-lived taxa (Fay et al., 2015; Szostek & Becker, 2015), as natural selection favours a conservative approach with respect to higher residual reproductive value for long-lived species (Erikstad et al., 1998). While adult survival is typically high for most seabirds, infrequent but strong perturbations can lead to rapid and substantial mortality of breeding adults (Frederiksen et al., 2008; Piatt et al., 2020). Following such events, compensatory recruitment resulting from greater fecundity during earlier periods of favourable environmental conditions may be one possible buffer against episodes of reduced adult survival. While many studies have focused on the contribution of adult survival to population growth and stability, few have quantified the relative importance of, and factors that lead to, increased recruitment rates following major mortality events.

Double brooding, defined as a second breeding attempt following the success of the first in a single breeding season, is a strategy used by some bird populations to maximize reproductive output (Hoffmann et al., 2015; Husby et al., 2009; Johns et al., 2017; Moore & Morris, 2005; Nagy & Holmes, 2005). The proportion of double brooding in a population is highly variable across years and among individuals, and often only attempted in years with favourable environmental conditions or by females assumed to be of higher 'individual quality' (Cornell & Williams, 2016; Johannesen et al., 2003; Johns et al., 2017, 2018). In this case, individual quality is defined as variation in intrinsic reproductive ability among individuals (Wilson & Nussey, 2009), where higher quality is expressed through a positive correlation between reproductive effort and longevity. Given the potential for double brooding to support increased offspring production and its association with higher quality females, double brooding individuals in the population may play a key role in population dynamics. No individuals may double brood in poor years when prey resources are limited, whereas a large percentage may double brood in favourable years when prey are readily available, leading to a population structure with large (and small) year classes and periodic demographic bulges. When the population is already large and suitable nest sites are all or mostly occupied, young mature individuals that have yet to breed may not have a place to recruit, and instead may either emigrate or enter a so-called 'floating' class of non-breeding but reproductively capable individuals (Brown, 1969; Manuwal, 1974a), a common feature that has been well studied in territorial species such as prairie voles (Solomon & Jacquot, 2002; Voigt & Streich, 2003) and many bird species from a wide range of taxonomic groups (Newton, 1992).

A long-running demographic study of Cassin's auklets (*Ptychoramphus aleuticus*) on Southeast Farallon Island (Farallones, SEFI), off the California Coast in Western North America, presents an opportunity to investigate the role of double brooding in population dynamics. Cassin's auklets feed primarily on zooplankton, especially krill, and respond predictably to shifts in bottom-up forces that shape primary and secondary production in the California Current System (Wolf et al., 2009). Cassin's auklets exhibit a slow-paced reproductive strategy, with a single egg per clutch and a potential life span of up to 22 years (Johns et al., 2018), although the earliest age at first reproduction is year 2 (Pyle, 2001). Relaying (a second breeding attempt made by the same pair following a failed first attempt) is a common feature in Cassin's auklet populations range-wide, while double brooding only occurs in populations in California and Baja California, Mexico. (Adams et al., 2014; Carle et al., 2020; Johns et al., 2017; Wolf et al., 2009). Double brooding is most common in Cassin's auklets on SEFI when spring upwelling is strong and the onset of reproduction is early (Manuwal, 1979), particularly among middle to older aged females (8–15+ years; Johns et al., 2017). A small subset of auklets in the SEFI population have repeated double brooding multiple times throughout their lives and still lived into old age (Johns et al., 2018), providing the basis for assuming these individuals are of higher quality.

For North Pacific seabird populations like Cassin's auklets, occasional mass mortality of breeding adults in response to periodic warm water El Niño events is common, but a wide variety of other ocean and atmospheric weather phenomena can also result in mass die offs (Jones et al., 2018; Piatt et al., 2020). In these situations, individuals in the floating demographic class may be extremely important in carrying the population through periods of poor environmental conditions. There have been four major mortality events for the SEFI Cassin's auklet population since data collection began in the early 1970s, all correlated with declines in prey availability that resulted from large-scale climate fluctuations such as El Niño Southern Oscillation (Lee et al., 2007; Wolf et al., 2010), marine heatwaves (Jones et al., 2018) and local delays in the development of seasonal spring upwelling conditions due to anomalous meridional flow that interrupts the normal zonal flow along the central California Coast (Sydeman et al., 2006). Breeding propensity and success, as well as average lay date, have also been linked to ocean climate indices, with higher nest site occupancy, earlier breeding attempts and higher fledging success recorded when spring conditions are more favourable (Lee et al., 2007). The strong relationship between these reproductive parameters and environmental variability mean recruitment rates of Cassin's auklets are also likely explained by marine conditions.

Removal experiments conducted on Cassin's auklets at SEFI in the early 1970s showed rapid colonization of open sites when established breeders were manually evicted, and the occasional immediate appearance of a new egg suggested that some individuals were already paired with a mate and immediately prepared to breed if a site became available (Manuwal, 1974a), leading him to speculate a substantial floating population of non-breeding adults

existed. Recent work on the Farallon population has shown that double brooding results in large year classes and demographic bulges (Johns et al., 2018), likely resulting in the large floating population observed by Manuwal. Here, we examine the importance of this floating class, combined with a maturation period that typically ranges from 3 to 6 years (Lee et al., 2007), for maintaining the population of active breeding birds in a large seabird colony. Our first objective was to test whether observed patterns in annual recruitment could be explained by the contributions of high rates of double brooding in previous years, relaxed competition for nesting sites, environmental conditions leading up to the breeding season, or some combination of these factors. The second objective was to gauge the contributions of adult survival and annual recruitment to annual population change. To do so, we fit temporal symmetry models (Pradel, 1996) to a 32-year mark-recapture dataset of Cassin's auklets from SEFI to simultaneously estimate apparent survival, breeding propensity, recruitment rates and derived estimates of realized population change. Model selection was used to test whether hypothesized explanatory behavioural and environmental covariates explained annual variation in recruitment, providing a means of inferring the mechanisms underlying the observed variability.

## 2 | MATERIALS AND METHODS

Continuous monitoring of breeding Cassin's auklets has occurred on SEFI (37°42'N, 123°00'W) since the establishment of a field station in 1968, when a collection of 44 wooden nest boxes were installed in areas that contained suitable breeding habitat for burrow nesting auklets. These boxes remained in their original locations and were replaced or repaired when needed throughout the duration of the project. Beginning in 1972 and continuing until 2019, each box was checked in early March to note the presence of an active breeding pair. Once an egg was confirmed, both adults were handled for identification and banded with a stainless-steel leg band if a new individual was encountered. Each box was revisited every 5 days throughout the breeding season (March–September) to document the outcome of a breeding attempt (success or failure), and the possible initiation and outcome of a second brood. Permission to handle auklets and conduct field work on the Farallon Islands National Wildlife Refuge was granted through a Cooperative Agreement #F19AC00242 with the US Fish and Wildlife Service and banding and geolocator deployments were conducted under the Federal bird banding permit #09316.

Individual recapture histories were constructed based on annual encounters of new or previously banded breeding birds within the sample of nest boxes. Pradel temporal symmetry models, an extension of Cormack–Jolly–Seber models that can estimate 'entry' of individuals into a population (Pradel, 1996), were fit with MARK (White & Burnham, 1999) using the package R<sub>MARK</sub> (Laake, 2013) in R (R Core Team, 2018). With this approach, capture histories are read in forward time to estimate annual apparent survival ( $\phi$ ) and

detection probabilities ( $p$ ) both bound by 0 and 1 with a logit link, and in reverse time to estimate the seniority parameter ( $\gamma$ ) with a log link which can be used to derive annual per capita recruitment rate ( $f$ ). Apparent survival is defined as the probability an individual alive and breeding in a nest box at time  $t$  was alive at time  $t + 1$ , and detection as the probability an individual was encountered in a nest box at time  $t$  given it was alive at time  $t$  and previously banded. The seniority parameter is defined as the probability an individual alive and breeding at time  $t$  was also alive and breeding at time  $t - 1$ . Per capita rate of recruitment, defined as the proportion of new previously undetected individuals in the population at time  $t$  given all of the previously detected individuals present at time  $t - 1$ , is derived in R<sub>Mark</sub> with the following expression (see Cooch & White, 2019),

$$f_t = \phi_t \left( \frac{1 - \gamma_{t+1}}{\gamma_{t+1}} \right). \quad (1)$$

Realized annual population growth rate ( $\lambda_t$ ) was calculated as the sum of  $\phi_t$  (exiting population through emigration and death) and  $f_t$  (entering the population through immigration and recruitment), with standard errors computed using the delta method (Powell, 2007). Given limited movements away from the breeding colony during the winter months (Johns, Warzybok, et al., 2020), and relative isolation of the Farallon Islands from the next nearest major colony in the Channel Islands at approximately 500km distance, there is little evidence for substantial contributions or losses of auklets from emigration or immigration. The realized population growth rate from Pradel models is an estimate of the actual change in population size between successive sampling events and does not require the assumption of a stable age structure at equilibrium like many studies based only on changes in abundance. These more realistic estimates of population change were possible because the sampling design met the stringent assumptions of Pradel models (Franklin, 2000); namely fixed sampling locations throughout the duration of the study period, equal probability of being detected across all boxes, and no losses on capture. Parameters  $\phi$  and  $p$  were also modelled as functions of the linear and nonlinear effects of continuous environmental covariates Southern Oscillation Index, SST and upwelling strength, that have been demonstrated to be important in previous mark-recapture analyses that used a smaller portion of this dataset (Lee et al., 2007; Wolf et al., 2010); however, no meaningful covariates were found (Supporting Information Table S2). Given this,  $\phi$  and  $p$  were modelled as fully time dependent using a categorical year term with meaningful biological and environmental covariate effects applied only on the recruitment ( $f$ ) parameter (Franklin, 2000). Results from a previous analysis using a larger sample of nest boxes showed that, on average, auklets from this population only use one to two sites and maintain a single mate over their reproductive life spans (Johns et al., 2018). High site and mate fidelity in Cassin's auklets indicates any biases for parameters estimates introduced from individuals using multiple boxes are likely small or negligible. High nest box fidelity of established breeding pairs also allows us to assume that estimates of recapture probabilities are analogous to the propensity of pairs to initiate a breeding attempt in each season.

Two classes of covariates were hypothesized to explain patterns in annual variation recruitment rates: intrinsic population effects (double brooding rates and population density), and extrinsic oceanographic and climatic effects (Supporting Information Table S1). Because Pradel models estimate per capita rates of recruitment from year  $t$  to  $t$ , covariates influence the rate of recruitment the following year. Annual double brooding rates ( $DB$ ), defined as the proportion of breeding pairs that attempted a second brood following a successful first brood, were hypothesized to increase future recruitment mainly through an increased number of fledglings and a connection between double brooding and higher quality parents (Johns et al., 2017, 2018). Average age of new recruits from banding and recapture data for the SEFI population has been estimated at 3.6 ( $SD \pm 1.54$ ) years (Lee et al., 2012), so double brooding would have a delayed effect on recruitment rates and was modelled as the proportion of the population that double brooded 3 ( $DB_{t-3}$ ) and 4 ( $DB_{t-4}$ ) years prior. Annual occupancy rate ( $Occ$ ) was included as a measure of population density to test for negative density-dependent effects on recruitment, defined as the proportion of boxes containing a breeding pair given total nest boxes available in each year.

Environmental covariates were included as indirect measures of density-dependent and -independent factors, with the hypothesis that increased primary production in the California Current System would increase reproductive propensity of breeding age adults and intensify competition for nest sites, reducing the odds of recruitment due to a shortage of available breeding habitat. Decreased primary production in the California Current System, however, might also result in lower recruitment rates, as poor foraging conditions would lead to lowered breeding propensity in mature adults and potential new recruits alike. Local environmental variables of interest that can influence primary production in the California Current System included mean pre-breeding (February–April) sea surface temperature ( $SST$ ) from daily measurements at SEFI, and the mean spring Biologically Effective Upwelling Transport Index ( $BEUTI$ , henceforth ‘*upwell*’) for the coastal region of latitude 38°N as a measure of coastal vertical nitrate flux relevant to biological processes (Jacox et al., 2018). Broad scale ocean covariates known to influence primary production that were considered included mean spring El Niño Southern Oscillation Index ( $ENSO$ ), North Pacific Gyre Oscillation index ( $NPGO$ ) and Southern Oscillation Index ( $SOI$ ). Starting in the mid-1990s,  $NPGO$  replaced  $ENSO$  as the dominant driver of reproductive success for Cassin's auklets on SEFI (Schmidt et al., 2014). This shift was explained by earlier spring transitions into favourable upwelling conditions generally associated with positive  $NPGO$  (Chenillat et al., 2012), which resulted in improved foraging conditions for Cassin's auklets. To reduce the number of candidate models, given  $SOI$  represents the primary signal for  $ENSO$  conditions, and the potential shifting influences of  $ENSO$  and  $NPGO$  to Cassin's auklets during our time series, we selected spring  $SOI$  as the representative basin-scale phenomenon for this analysis.

A total of 53 competing models were fit and compared with Akaike's information criterion corrected for sample size (Burnham & Anderson, 2002;  $AIC_c$ ). The model set included all possible

combinations of the environmental covariates, double brooding lagged at 3 or 4 years ( $DB$ ), and occupancy rates ( $Occ$ ). In addition to the main effects, biologically relevant interactions between  $DB$  and  $Occ$ ,  $DB$  and the environmental covariates, and  $Occ$  and the environmental covariates were tested based on the following predictions: (a) a higher proportion of double brooding in years prior would have a greater positive effect on recruitment rates when occupancy (competition) was lower compared to higher, (b) a higher proportion of double brooding in years prior would have a greater positive effect on recruitment if spring conditions were good compared to poor and (c) higher occupancy rates would have a greater negative effect on recruitment when spring conditions were good compared to poor. Due to limitations with the available years for upwelling strength as defined by  $BEUTI$ , the analysis was limited to recapture histories from 1988 to 2019 (32 years of a 48-year dataset). Probability of apparent survival from 2019 to 2020 and recapture for 1988, and per capita recruitment from 1988 to 1989 were inestimable due to parameter identifiability.

Estimating the variation inflation factor ( $\hat{c}$ ) of the fully saturated model is the preferred diagnostic tool for quantifying the amount of overdispersion (extra binomial variation) in recapture data. Goodness-of-fit tests for temporal symmetry models have not been fully developed, so we assessed model assumptions and estimated  $\hat{c}$  for the fully time-dependent Cormack–Jolly–Seber ( $\phi$  and  $p$  only) model. The overall test for equal probability of recapture and survival (Test 1) in the R package  $R2UCARE$  (Gimenez et al., 2017) was performed on the capture histories to look for evidence of lack of fit. A significant result for Test 1 was followed up by tests for trap dependence (Test 2; null hypothesis is an equal chance of future recapture between individuals that are missed or captured during the current sampling event) and trap effects on survival (Test 3; null hypothesis is an equal chance of future recapture between newly or previously marked individuals) to explain the source(s) of lack of fit. Finally,  $\hat{c}$  was estimated by dividing  $\chi^2$  by the degrees of freedom from the results of Test 1 (the overall test for the time-dependent CJS model). If  $\hat{c}$  was larger than 1 (where 1 = perfect fit), a sensitivity analysis on the model selection results was performed by incrementally adjusting  $\hat{c}$  until it was just over the amount estimated for the general CJS model to be conservative, and observing if and how the rank of models within the candidate set changed following Cooch and White (2020). Little to no change in the  $AIC_c$  weights of top models would indicate little or no effect of lack of fit on the conclusions drawn from the model selection and ranking process. The fraction on inter-annual variation ( $R^2_{Dev}$ ) in recruitment rates explained by each covariate and interaction in the top model was estimated following Skalski (1996) and Grosbois et al. (2008) with the equation,

$$R^2_{Dev} = \frac{Dev(f_{null}) - Dev(f_{cov})}{Dev(f_{null}) - Dev(f_t)}, \quad (2)$$

where  $Dev(f_{null})$  = deviance from the null model with constant recruitment,  $Dev(f_t)$  = deviance from the time-varying model with categorical year recruitment and  $Dev(f_{cov})$  = deviance from the

model with each focal covariate from the top model. Parameters  $\phi$  and  $p$  were modelled with fully time-dependent structures for this procedure.

Derived estimates of realized population growth rate ( $\lambda$ ) using the Pradel recruitment model were compared to  $\lambda$  using annual estimates of the entire SEFI breeding population, to gauge potential biases in estimates of  $\lambda$  using a small sample of followed nest boxes. Twelve 10 m  $\times$  10 m fixed index plots were established in similar habitat to the nest boxes in 1991 to track changes in mean burrow density (den) over time (Johns, Spears, et al., 2020; Johns, Warzybok, et al., 2020). A complete census of presumed active burrows on SEFI conducted in 1989 resulted in an estimated breeding population (pop) of 29,880 birds (Carter et al., 1992). With the assumption that the population did not change substantially between 1989 and 1991, annual population estimates were calculated with the following equation:

$$\text{pop}_{t(\text{pre } 2009)} = \text{pop}_{1989} \times \left( \frac{\text{den}_t}{\text{den}_{1991}} \right). \quad (3)$$

A second island-wide burrow census was conducted in 2009, yielding a new baseline estimate of 14,512 breeding birds. This value was used to generate population estimates between 2010 and 2019.

$$\text{pop}_{t(\text{post } 2009)} = \text{pop}_{2009} \times \left( \frac{\text{den}_t}{\text{den}_{2009}} \right). \quad (4)$$

### 3 | RESULTS

Annual recaptures from 1988 to 2019 resulted in 942 unique individuals that bred in the sample of 44 nest boxes. The mean annual proportion of new individuals encountered during the study period rarely dropped below 0.32, a baseline number of new recruits similar to previous estimates in this population (Lee et al., 2007; Manuwal, 1974a). Peaks in the proportion of newly encountered birds occurred in 1993, 1998–99, 2006–07 and 2015 (Figure 1). These periods of high recruitment aligned with low occupancy the year prior except for 2015, and roughly followed patterns of higher rates of double brooding 3–5 years prior (Figure 1). A prolonged period of relatively high nest box occupancy was observed between 2008 and 2019, and during that time the colony experienced generally low recruitment rates.

The overall fit test of the time-dependent CJS model showed evidence of a lack of fit (Test 1:  $\chi^2_{103} = 183.81$ ,  $p < 0.001$ ). The test for trap dependence was significant (Test 2ct:  $\chi^2_{27} = 99.37$ ,  $p < 0.001$ ) with a negative signed square root indicating individuals encountered at time  $t - 1$  were more likely to be recaptured at time  $t$ . The test for a transient effect was also significant (Test 3sr:  $\chi^2_{29} = 51.08$ ,  $p < 0.01$ ), with a positive signed square root test providing evidence that newly marked individuals were more likely to never be observed again. Individuals in this study are observed at their nest sites rather than trapped in the traditional sense (e.g. by using a mist net), so positive tests for transience and trap

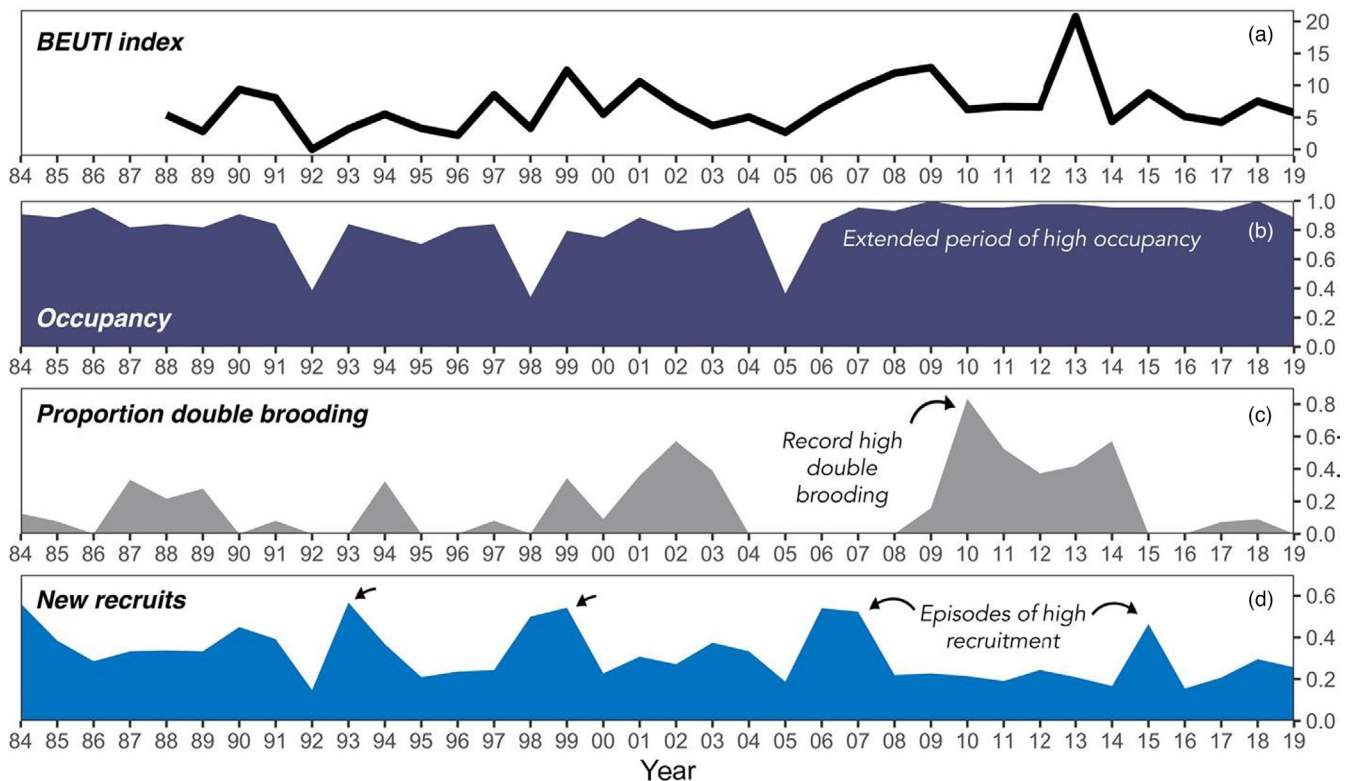


FIGURE 1 Annual upwelling index at the Farallones (a), proportion of boxes that contained a breeding pair (b), proportion of pairs that attempted a double brood (c), and proportion of individuals in the breeding population in their first recorded breeding attempt (new recruits; d). Note that the x-axes begin in 1984 to show the 3- and 4-year lags in double brooding

dependence were likely not an actual behavioural response from 'trapping'.

Nest box occupancy, double-brooding history and upwelling were all important predictors of recruitment, occurring in the two best supported models with  $\Delta AIC_c$  scores <2 from the candidate set tested (Table 1). Recruitment rates from year  $t - 1$  to  $t$  were most parsimoniously modelled as a linear function of occupancy ( $Occ$ ), double brooding 4 years prior ( $DB_{t-4}$ ) and spring upwelling ( $upwell$ ), with an interaction between  $DB_{t-4}$  and  $upwell$ . There was only a 0.77 difference in  $\Delta AIC_c$  for the model containing the linear effects of  $Occ$ ,  $DB_{t-3}$  and  $upwell$  without the interaction. Using estimates of  $R^2_{Dev}$  from Equation (2), the interaction between  $upwell$  and  $DB_{t-4}$  and the main effects of  $Occ$  both explained 48% of the inter-annual variation in recruitment rates. The main effects of  $upwell$  and  $DB_{t-4}$  explained 34% and 1% of the variation respectively, showing that much of the variation explained by these two variables occurred with the interaction (Supporting Information Figure S1).

Incrementally adjusting AIC selection results up to slightly over the estimate of 1.78 for  $\hat{c}$  (Test  $1 \chi^2/df$ ) did not dramatically change the ranking of the models (Supporting Information Table S3). The interaction between  $upwell$  and  $DB_{t-4}$  became less important when model selection was adjusted for a  $\hat{c}$  of 1.4 or higher but remained competitive up to a  $\hat{c}$  of 2.2 (well above our estimate for  $\hat{c}$  of 1.78). All other variables remained the same up to a  $\hat{c}$  of 2.2. These findings indicate a similar fit between  $DB$  lagged at 3 and 4 years; however, the model fit was slightly improved when using a 4-year lag and including the interaction with  $upwell$ . Following model selection, parameter estimates from the top model were used for inference.

There were three major peaks in estimated per capita rates of new recruits per individual [standard error] throughout the time series: 0.80 [0.11] in 1993, 0.78 [0.12] in 1999 and 0.85 [0.13] in 2006,

**TABLE 1** Ranking of the top 7 best fitting candidate models with lowest  $\Delta AIC_c$  values, including results of models with single covariates and the time-only year model for comparison. Top model had an  $AIC_c$  of 8138.05. Number of parameters ( $K$ ),  $AIC_c$  weights ( $w_i$ ), inter-annual deviance explained by covariates in each model ( $R^2$ ) are also given. Apparent survival and recapture probabilities were modelled with time-dependent structures  $\phi(\sim\text{year})$  and  $p(\sim\text{year})$  respectively

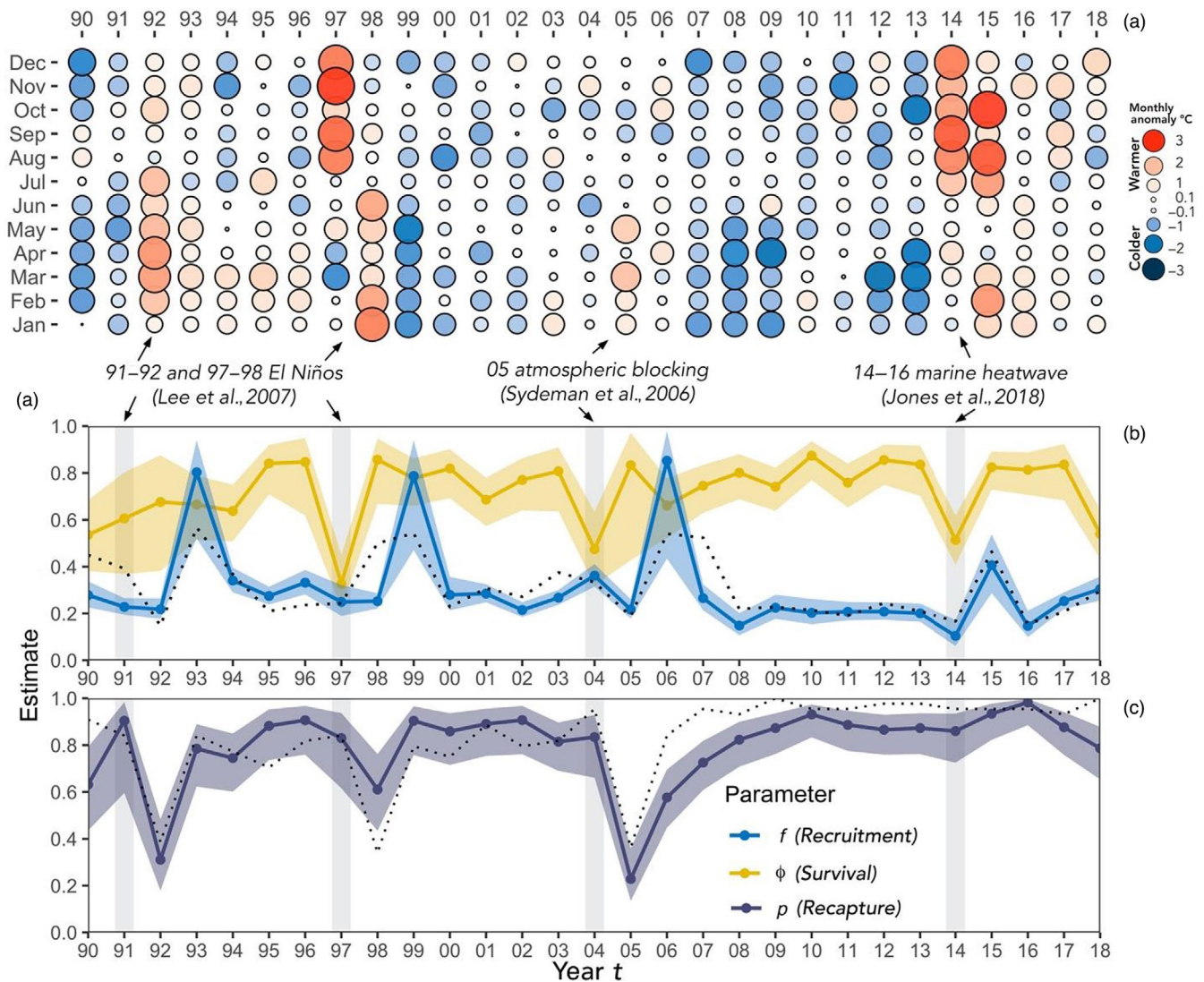
Model	$K$	$\Delta AIC_c$	$w_i$	$R^2$
$f(\sim Occ_t + DB_{t-4} * upwell_t)$	66	0	0.30	0.68
$f(\sim Occ_t + DB_{t-3} + upwell_t)$	65	0.77	0.21	0.65
$f(\sim Occ_t + DB_{t-3} * upwell_t)$	66	2.35	0.09	0.65
$f(\sim Occ_t * DB_{t-3} + upwell_t)$	66	2.74	0.08	0.65
$f(\sim Occ_t * upwell_t + DB_{t-3})$	66	2.88	0.07	0.65
$f(\sim Occ_t + DB_{t-3})$	64	4.70	0.03	0.57
$f(\sim Occ_t + upwell_t)$	64	6.86	0	0.55
$f(\sim Occ_t)$	63	10.42	0	0.48
$f(\sim upwell_t)$	63	22.81	0	0.33
$f(\sim year)$	91	26.69	0	NA
$f(\sim DB_{t-4})$	63	51.61	0	0

along with a smaller peak of 0.4 [0.07] in 2015 (Figure 2). Parameter estimates (log scale with [standard error]) suggest these peaks in recruitment were partially explained by the contribution of a higher proportion of double brooding 4 years prior ( $DB_{t-4}$ ; 2.32 [0.71]) and spring upwelling conditions ( $upwell$ ; 0.01 [0.02]). The inclusion of an interaction between previous double brooding rates and spring upwelling ( $DB_{t-4}$ ;  $upwell$ ; -0.34 [0.12]) shows the effect of lagged double brooding on recruitment was most pronounced when spring conditions were poor (Figure 3). Occupancy rate had a negative effect on recruitment ( $Occ$ ; -1.58 [0.37]), indicating high nest box use limited the possible number of new recruits. Annual estimates of apparent survival remained high at approximately 0.8 throughout the time series except when dropping to 0.32 [0.06] in 1996–97, 0.47 [0.08] in 2003–04, and 0.51 [0.05] in 2013–14 (Figure 2). Estimated recapture probabilities also remained consistently high at ~0.8 (Figure 2), except for notable dips in 1992 (0.31 [0.08]), 1998 (0.61 [0.09]), 2005 (0.23 [0.06]) and 2006 (0.58 [0.06]). The three major peaks in recruitment occurred the year after estimated dips in recapture probability (which can be interpreted as reductions in breeding propensity) in 1992, 1998 and 2005, which in turn had followed spikes in apparent mortality in the early 1990s and the winters of 1997 and 2004 (Figure 2). This pattern of reduced survival, reduced occupancy and increased recruitment did not hold during the latter part of the time series; decreased survival in 2014 did not result in a reduction in breeding propensity the following year. Instead, recruitment rates spiked following this event.

There was general agreement between realized  $\lambda$  estimated from the top model for recruitment and estimates obtained by comparing empirical changes in burrow densities across index plots over time (empirical trend generally within confidence intervals around model fit; Figure 4), suggesting a good fit with the Pradel recruitment model used. The population growth rate fell below 1 (declining) following the mortality events of 1997 and 2004, reverted to well above 1 (increasing) the year after these events, but on average this parameter from mark-recapture estimates was consistently near 1 (stable) throughout the time series with a geometric mean  $\lambda$  of 1.02. The model-derived  $\lambda$  tracked the empirical index plot estimates very closely until 2005 (correlation coefficient = 0.67), at which point several mismatches occurred, particularly in 2006–07 (Figure 4). A major reduction in the odds of birds surviving the 2014–15 winter was apparently mitigated by a large increase in new recruits in 2015, which resulted in the breeding population remaining unchanged.

## 4 | DISCUSSION

The Southeast Farallon Island Cassin's auklet population has been maintained at a steady state over much of the past three decades. Although this relative stability can mostly be attributed to high adult survival, occasional climate-related spikes in adult mortality were always followed by rapid increases in recruitment, buffering the population against poor environmental conditions. Such episodes of increased recruitment corresponded with a large proportion of the



**FIGURE 2** Monthly mean sea surface temperature anomalies (month  $i$  year  $t$  – mean month  $i$  across all years) from Southeast Farallon Island (a). Estimated annual per capita recruitment rate (from year  $t - 1$  to  $t$ ) with 95% CI (panel b, blue line and shading) from the best most supported Pradel recruitment model  $f \sim Occ + DB_{t-4} * upwell$ . Annual apparent survival (from year  $t$  to  $t + 1$ ; panel b, yellow) and recapture (for year  $t$ ; panel c, purple) probabilities were estimated from time-dependent structures  $\phi(\sim year)$  and  $p(\sim year)$  respectively. For comparison to model predictions, the dotted line in panel (b) is the proportion of new recruits in followed nest boxes, and the dotted line in panel (c) is the proportion of occupied boxes in the study from empirical data. Grey vertical lines in panels (b) and (c) highlight extreme adult mortality events during El Niño conditions and warm water anomalies. Panels a–c have been clipped to only show years where all parameters were estimable

population attempting double brooding 4 years prior and a relaxation of competition for available breeding habitat, which tended to follow periods of high adult mortality. The effect of greater previous population-level double brooding attempts was most pronounced when spring upwelling was less than average leading up to the observed spike in recruitment. Low breeding propensity as measured by nest box occupancy was not a necessary condition to increased recruitment rates (as observed in 2015), so long as double brooding rates 4 years prior were high enough and environmental conditions were poor. Although the dataset used for this study represents 32 years of mark-recapture information, the conclusions drawn from this analysis rely on changes in parameters coincident to four

major perturbation events, which may limit the strength of our ability to confirm the mechanisms proposed here.

With sampling and modelling caveats in mind, several possible mechanisms might explain the relationship between periodic increases in recruitment and population-level double brooding rates. The connection with double brooding and individual quality shown in this population (Johns et al., 2018), and for other bird species (Cornell & Williams, 2016), may provide some insights. Offspring of parents that double brood may have a greater chance of recruiting than those from lower quality parents either through inherited traits or by improved parental care. In some years only 20%–40% of double brooding attempts were successful (Johns et al., 2017), likely due

to a sudden decrease in upwelling during late summer months that reduced local productivity after a second brood had been initiated. Thus, at the population level, higher rates of double brooding do not always result in a substantial increase in fledglings produced in each season. It is also possible that because double brooding is more likely to occur in years with favourable oceanic conditions, the behaviour serves as a metric for improved environmental quality during an individual's hatch year not captured by any physical metric classically used to define the state of the California Current. Chicks hatched during years when double brooding is high would benefit from better foraging conditions during early development compared to those hatched during average to poor years when resources would be scarcer. These individuals would receive better parental provisioning

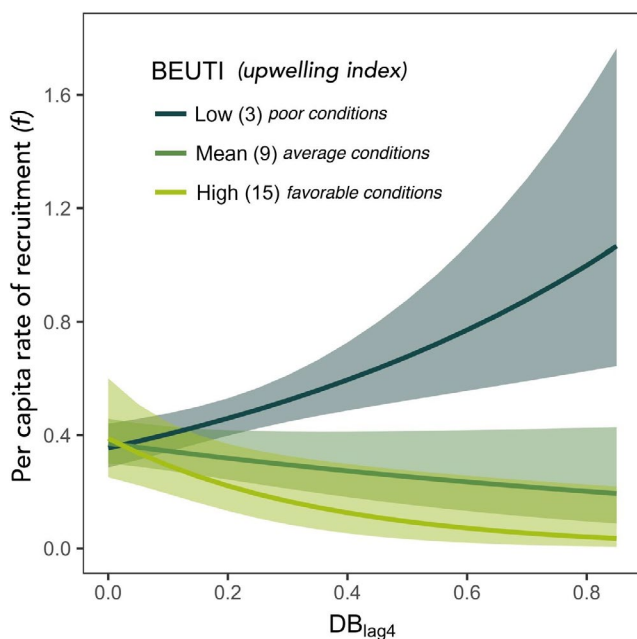


FIGURE 3 Estimated recruitment rate ( $f$ ) with 95% CI (shaded ribbons) for the interaction between proportion of pairs that double brood 4 years prior ( $DB_{t-4}$ ) and three discrete levels of biologically relevant upwelling (low, mean and high). Annual proportion of occupied nest boxes ( $Occ$ ) was held constant at 0.6

and be more likely to survive the juvenile period, increasing their odds of recruiting into the breeding population once matured.

The number of occupied boxes was retained in all the top models, and established breeders almost certainly outcompete potential new recruits for available nesting habitat. Similar findings have been reported for other bird colonies, where nesting density and high competition for available sites controls annual recruitment (Crespin et al., 2006; Lawson et al., 2017). Aside from simply occupying a site, territorial behaviour of Cassin's auklets in the form of acoustic displays and rushes up to 1 m from burrow entrances provides a mechanism for further limiting burrow density on the Farallones (Manuwal, 1974a), as this would deter prospecting individuals from digging new burrows in close proximity to established burrow entrances. Defensive behaviour of burrows is likely responsible for the apparent trap dependence and a transient effect in the recapture data. Since birds are not 'trapped' in the traditional mark-recapture sense in this study and are instead sampled from a fixed set on nest boxes, high site fidelity means that established breeders were more likely to be recaptured, and newly marked individuals would have been excluded from recruiting into monitored boxes.

The interaction between spring upwelling conditions as measured by the  $BEUTI$  and lagged double brooding rates indicates another dimension to the negative density-dependent effect on recruitment. Since occupancy rates and site retention were generally high throughout the observed time series, the population-level benefit of double brooding was only realized when sub-optimal upwelling conditions leading up to the breeding season occurred. It is possible that more experienced adults decided not to breed in response to poor environmental conditions, opening breeding sites previously occupied by established pairs. Inexperienced first-time breeders would likely be unsuccessful but would benefit by controlling a breeding site until conditions improved.

The quick response of new recruits following years of low occupancy supports the hypothesis that a sizable floating demographic class of reproductively capable adults that do not breed is a large and persistent feature of this population. In our demographically explicit analysis, although the breeding population has fluctuated between roughly 10,000 to 30,000 individuals (Johns, Spears, et al., 2020; Johns, Warzybok, et al., 2020), an estimated geometric mean  $\lambda$  of

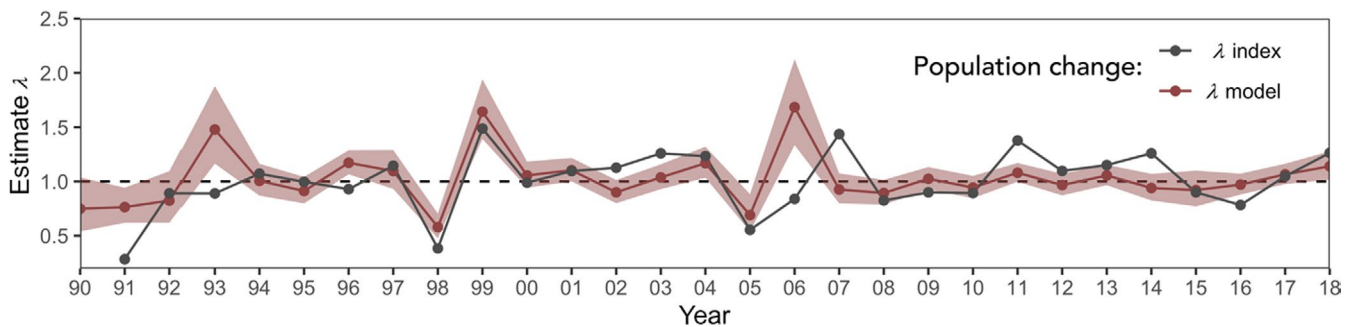


FIGURE 4 Annual estimates of realized  $\lambda$  derived from the Pradel recruitment model  $\phi(\sim\text{year}) p(\sim\text{year}) f(\sim Occ + DB_{t-4} * \text{upwell})$  in red, with the shaded band showing the 95% CI. Empirical estimates of  $\lambda$  derived from changes in mean burrow density of fixed index plots are shown in dark grey



1.02 over the last three decades indicates the active breeding population has almost certainly remained effectively stable. This stability can be attributed to the contribution of new recruits from a surplus of breeding-capable individuals in the super-population that accumulate when oceanographic conditions are favourable. Individuals from this floating class then quickly replace breeders lost following a year of poor adult survival and/or decreased breeding propensity of established pairs. Evidence of long-term stability in the size of this population calls into question an initial early estimate of more than 100,000 breeding individuals made in 1970 (Manuwal, 1974b). This large initial population estimate relative to current population size now appears likely to have been caused by sampling error or differences in sampling design, although we cannot exclude the possibility that a large, undetected change in the local ecological controls on this population may have occurred, such as increased predation from western gulls, competition with other burrow nesting species, or habitat loss from invasive vegetation.

No single environmental covariate (of those tested) explained the variability in survival or occupancy better than a year-dependent term, given AIC selection results and assessment of inter-annual variation explained by covariates tested (see Supporting Information Table S2). Changes in the timing and duration of local sea surface temperature anomalies around the Farallones, driven by various climatic sources, nonetheless tell a compelling story (Figure 2). In the last three decades there were four major events that significantly reduced adult survival of auklets on the Farallones, two of which were directly linked to El Niño conditions that resulted in warming of local waters in the spring of 1992, winter of 1997 and spring of 1998 (Lee et al., 2007). An observed reduction in adult survival leading up to 2005 coincided with an unusual atmospheric blocking event that caused a delay in spring upwelling, which has been proposed to explain low occupancy rates and the only complete reproductive failure for Cassin's auklets on the Farallones in our long-term record (Sydeman et al., 2006). A slight reduction in adult survival estimated in 2014 coincides with an unprecedented die-off of Cassin's auklets recorded by beach surveys in Northern California, Oregon and Washington (Jones et al., 2018). This mass mortality event was attributed to a pervasive marine heat wave that started in the winter of 2014 (Bond et al., 2015) and lingered in the eastern North Pacific into the summer of 2016. Unlike years following the El Niño of 1997 or the local anomaly of 2005, the recapture data and occupancy rates remained high after the low adult survival estimate in 2014. The period of cooler than average SST between 2007 and 2013 (Figure 2), indicative of favourable foraging conditions, likely resulted in high rates of successful double brooding attempts that increased the pool of potential future breeders. The new breeders were available to replace individuals that either did not breed during or did not survive the marine heat wave. In addition, given double brooding is a behavioural marker of higher individual quality, this prolonged period of higher double brooding rates would indicate a possible substantial cohort of high-quality individuals that were able to survive and successfully defend breeding sites even during suboptimal conditions of the marine heatwave.

## 5 | CONCLUSIONS

This work highlights the value of long-term demographic studies, which are necessary for revealing population-level response to episodic climate anomalies that occur on decadal time-scales. It is evident that periodic major perturbation events can result in negative impacts to individuals through increased mortality and to populations through the loss of established breeders, but we show that increased reproductive effort by a subset of individuals and subsequent future recruitment rates can help to protect a population against such events (Gaillard & Yoccoz, 2003). For Cassin's auklets on the Farallones, double brooding appears to be one such strategy that enables this population to recover from years where adult survival is low. Earlier studies on kittiwakes (Porter & Coulson, 1987) and flamingos (Pradel et al., 1997), for example, suggest large pools of potential new recruits ready to move in following substantial mortality to breeding adults, which allows the population to remain relatively stable. Our study shows that periods of increased double brooding might allow a substantial floater cohort to accumulate that can respond immediately to a relaxation of competition for available breeding habitat following periods high adult mortality or reduced propensity of established breeders to continue breeding. In the absence of high-resolution mark-recapture data and careful demographically explicit analysis, such populations may appear resilient and stable, and many other seabird populations with similar life histories may be similarly demographically buffered. An increase in the frequency or severity of warm water events, as is expected under climate change, could exhaust the pool of floaters at a faster rate than can be replenished. Under such a scenario, the demographic buffering from the floating classes may break down in this and similar seabird populations.

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## CONFLICT OF INTEREST

None to report.

## AUTHORS' CONTRIBUTIONS

M.E.J., P.D., M.L. and G.A.B. designed research objectives and methods; M.E.J. and P.W. carried out data collection and field logistics, M.E.J. analysed the data and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Recapture histories and environmental covariates used to conduct all statistical analysis are available online at <https://doi.org/10.5061/dryad.9kd51c5j9> (Johns et al., 2021). Please email corresponding author or contact a representative at Point Blue Conservation Science for future collaborations with updated data.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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