BLACK OYSTERCATCHER *HAEMATOPUS BACHMANI* PRODUCTIVITY IN CALIFORNIA AND OREGON AND THE EFFECTS OF NEST SITE AND ENVIRONMENTAL COVARIATES

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ABSTRACT

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Black Oystercatcher *Haematopus bachmani* is a species of conservation concern due to its small global population, reliance on somewhat restricted intertidal habitat, and vulnerability to climate change impacts. Concern for this species, along with a lack of demographic information from the southern portion of its range, gave rise to a community science project to monitor pair productivity, nest characteristics, and nest disturbance from 2012 through 2022 across three study regions in Oregon and California. A clear spatial gradient existed in productivity, with relatively low values in the southern region (0.37 fledged young per pair per year, 95% confidence interval [CI] = 0.32–0.43; Southern California) compared to central (0.46, 0.41–0.51; Northern California and southern Oregon) and northern (0.60, 0.47–0.77; northern Oregon) regions. While productivity varied systematically across space, there was no general trend over time. Pair productivity was slightly higher at mainland nests than island nests when nest position above high tide was low, but it was highest at island nests when nest position was high. Productivity was negatively related to observed human disturbance but not consistently related to non-human disturbance or food availability, represented by estimates of mussel bed cover and depth near nests. We discuss our results in light of known and anticipated impacts of ocean and climate change on intertidal habitats of the coastal northeast Pacific region. We provide management recommendations and suggest avenues of new research to help in the conservation of this vulnerable species.

Key words: *Haematopu*s, productivity, disturbance, ocean climate, oystercatcher, prey

INTRODUCTION

The Black Oystercatcher *Haematopus bachmani* (hereafter, BLOY) is a long-lived marine shorebird that lives along the Pacific coast from the Aleutian Islands to Baja California Sur (Tessler *et al.* 2014). Throughout its range, the species feeds on intertidal primary consumers, particularly mussels and limpets (Tessler *et al.* 2014, Carney *et al.* 2023). The species is a key structuring agent for intertidal communities (Wootton 1993, Lindberg *et al.* 1998).

The global population of BLOY has been estimated to be 12 000–17 000 individuals (Tessler *et al.* 2014, Weinstein *et al.* 2014). Major factors thought to limit the species' abundance are the narrow (linear), discontinuous habitat in which it nests and forages, nest disturbance by predators and humans, and wave action (Tessler *et al.* 2014). The species is of international, national, and local conservation concern given the relatively small global population, anthropogenic increases in potential nest predators, reliance on increasingly disturbed intertidal habitat, and vulnerability to climate impacts such as rising sea level (Oregon Department of Fish and Wildlife 2016, Tessler *et al.* 2007, Senner *et al.* 2016).

Informed management of vulnerable species relies on demographic information such as pair productivity and age-specific survival rates (Morris & Doak 2002, Meehan *et al.* 2018, Maillet *et al.* 2023). By 'pair productivity' we mean the number of chicks fledged per year per breeding pair. To date, most demographic data for BLOY comes from research conducted in the northern part of its range, from Washington through Alaska (Tessler *et al.* 2014). Yet, a substantial portion of its population occurs in Oregon (600 individuals; Liebezeit *et al.* 2020) and California (6000 individuals; Weinstein *et al.* 2014).

Without demographic information in the southern portion of the species' range, it is not possible to know how that segment contributes to the overall population. A recent literature review and modeling study suggested that, given the known adult and juvenile survival rates, an average productivity rate of ~0.50 fledged young per pair per year is necessary to maintain a stable population. Productivity of ~0.65 or greater is likely a good sign for persistence of a local population, but productivity < 0.35 is likely a sign of a declining population and potential local extirpation (Meehan *et al.* 2018).

Concern for BLOY and the lack of demographic information for southern populations motivated a public/private community science project to monitor BLOY productivity, nest-site characteristics, and nest disturbance in Oregon and California (Fig. 1). The project was conducted from 2012 through 2022 and involved over 150 trained volunteers and professional biologists monitoring BLOY in three study regions. Our analysis objectives were to (1) explore spatial and temporal variation in BLOY productivity among the three regions over the 11 y of the study, and (2) evaluate the influence

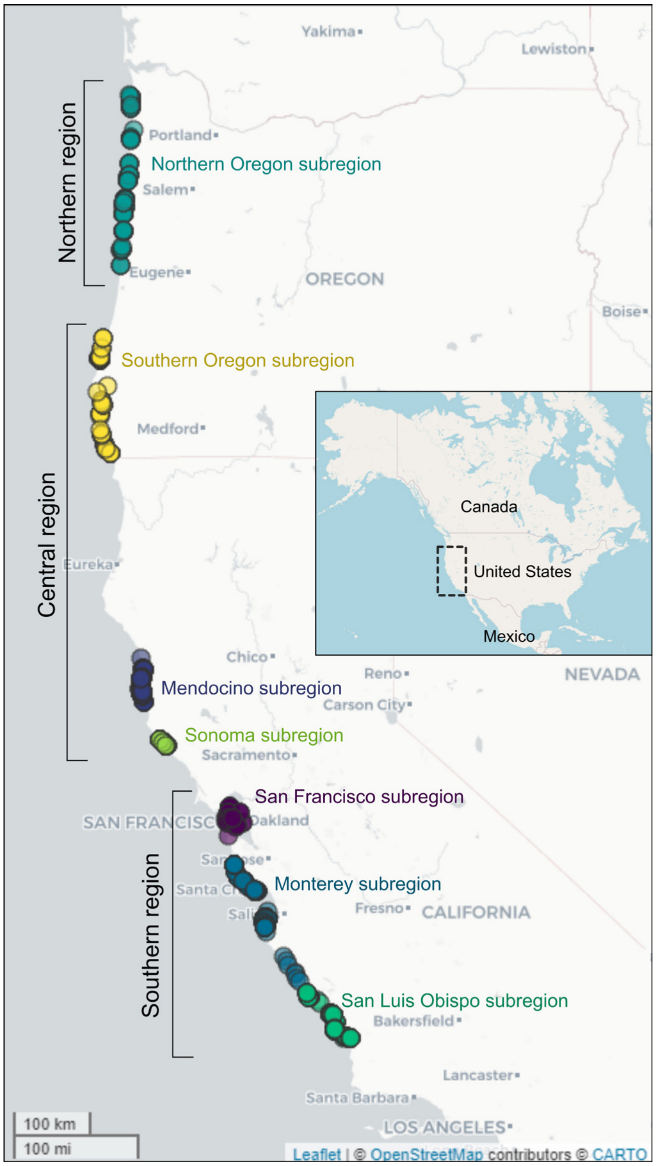

Fig. 1. Biogeographically defined regions and administrative subregions used in this study of breeding Black Oystercatcher *Haematopus bachmani* (BLOY), 2012 through 2022, in California and Oregon, USA. Subregions were selected for ease of project management and coordination of observers.

of potential covariates of productivity, including nest location, nest disturbance, and food availability. We discuss our results in light of known and anticipated impacts of ocean and climate change on intertidal habitats of the northeast Pacific. We provide management recommendations and suggest avenues of new research to help in the conservation of this vulnerable species.

METHODS

Study area

BLOY monitoring was conducted in California (southernmost latitude 35.1487°N) from 2012 through 2021 and Oregon (northernmost latitude 45.9308°N) from 2015 through 2022 (Fig. 1). This study area comprises ~10% of the BLOY global range, though it excluded southern California south of Point Conception (34°N) and Baja Mexico, where it is likely that < 200 individuals occur (Palacios *et al*. 2009). Boundaries of the study region (Point Reyes, California and Coos Bay, Oregon) were modified according to the oceanography literature, based on similarities between intertidal communities and sea surface temperatures, as well as known biogeographical and oceanographic discontinuities (Blanchette *et al*. 2008, Fenberg *et al*. 2014; P. Raimondi & M. Miner pers. comm. 2023). While our main interest was to describe spatial variation in BLOY productivity with respect to ecological factors, we also summarized data across seven administrative subregions (Fig. 1). Subregion summaries are provided in the Appendix (Table A1, available on the website) both to inform local management and to illustrate finer-scaled spatiotemporal variation in productivity.

Field methods

Subregion coordinators—primarily professional biologists—recruited, trained, and organized teams of observers each season. After training, observers searched on foot looking for nests wherever viable nesting habitat was accessible. Subsequent selection of nests for longer-term monitoring was non-random and contingent upon permission, travel time, and nest visibility.

Nesting surveys were conducted using binoculars or spotting scopes, usually from land but occasionally from boats. Observers remained at sufficient distances from nests to avoid disturbance. Nests were monitored at least once per week for a minimum of 30 min, and data collection included number of eggs and number and approximate age of chicks. If a nest failed, defined as total loss of eggs or chicks, an observer would continue to survey the site in subsequent weeks to confirm nest failure and check for re-nesting attempts. In instances where a nest was not discovered until after hatching, chicks were monitored weekly until they either fledged or failed to fledge. Chicks were considered fledged if flying was observed or if the chicks were documented 36–40 d after their estimated hatch date.

In addition to the status of eggs and chicks, nest site characteristics and disturbance events were recorded. Nest site characteristics included visual estimates of nest height in meters above the average high tide, and classification of nests into island or mainland nests based on dry access at low tide. Disturbance observations included the type of disturbance and included human disturbance (such as humans, pets, or drones coming close enough to the nest to visually alarm birds; see Appendix, Table A2) and non-human disturbance (such as gulls, ravens, or falcons coming close enough to the nest to visually alarm birds; see Appendix, Table A2). Note that disturbance by non-breeding BLOY was not included in the non-human disturbance category. A third proxy for disturbance was if the nest was accessible to dry foot traffic from a public access point (such as a parking area, beach, trailhead, or picnic area), with the average (± 1 standard deviation [SD]) distance from the public access point being 160 ± 197 m.

Data analysis

Pair productivity was defined as the number of chicks fledged each breeding season per documented nesting pair. In the denominator, this definition of productivity does not include non-breeding floaters, pairs that chose not breed in a given year, or pairs whose nest may have failed very early in the breeding season before initial detection. BLOY were typically not color-banded, and thus we had no idea whether there was turnover in pair composition from one year to the next, should, for instance, one member of a pair disappear to be replaced by a new mate. Thus, in a sense, our 'pair productivity' is 'site productivity.' We found that once a nest was located during the initial survey, a nest was present in the same vicinity for the duration of annual monitoring. For these monitored nests, we collected various data for each nest locality in each year, within each region, and we developed statistical models to explain the factors behind the degree of nesting success achieved.

At the end of each season, subregion coordinators compiled data and worked with the authors to conduct quality control. BLOY typically lay up to three eggs, so productivity for each nest took integer values from 0 through 3 fledged chicks. Data were discarded if there was any uncertainty over nest fate or location. Before 2018, data were entered by observers onto paper data forms, whereas after 2018 data were entered via a digital data form (ESRI 2011). The digital data entry process ensured higher quality covariate data during the latter half of the study period. For example, nest locations could be entered by observers via a mapping interface. Also, the digital form forced observers to explicitly state when disturbance was or was not detected, allowing us to identify situations having no data and zero disturbance events. We analyzed productivity from the entire 11-y period, but because of the change in data-input methods, most data for the covariate analysis comes from 2018 forward.

The first stage of data analysis explored spatial and temporal variation in productivity using all productivity measurements collected during the 11-y study period. For this analysis, productivity was modeled using a generalized linear model (GLM) with a fixed categorical effect of the three study regions, a continuous loglinear effect of year, and an interaction between region and year. The interaction between region and year was added to determine if different regions experienced different temporal trends. The data were modeled as count data with a negative binomial distribution to account for abundant zeros (all nests by a breeding pair failed in a given year). The full GLM was fit using the "glmmTMB" package (Brooks *et al*. 2017) in R (R Core Team 2022). The contributions of region, year, and their interaction to the model were evaluated using Akaike's Information Criteria (AIC), which is often used to rank models according to their balance between predictive ability and parsimony (Burnham & Anderson 2002). AIC was calculated for each subset of the full GLM (including the intercept-only model), and then differences in AIC values between each subset model and the lowest-AIC model (ΔAIC) were calculated. The ΔAIC were then used to rank models (model with lowest AIC was ranked highest), compute model weights, and compute variable weights (Burnham & Anderson 2002).

The second stage of data analysis explored variation in productivity in relation to six potential covariates, using a subset of measurements for which we had sufficient observer inputs. For this analysis, pair productivity was modeled using a generalized linear mixed model (GLMM) with a random effect for the three oceanographic regions, a continuous loglinear effect of nest height above average high tide, binary fixed-effects for island versus mainland nesting, observation of human disturbance, observation of non-human disturbance, public shoreline access, an interaction between nest height and island nesting covariates, and a continuous loglinear effect of modeled mussel bed cover and depth (Pacific Blue Mussels *Mytillus trossulus* and California Mussels *M. californicus*). The interaction between nest height above sea level and island nesting covariates was added to the model because of several anecdotal observations of nest loss due to washout of island nests by waves.

The mussel cover and depth index (hereafter "mussel index") was included in the model as a proxy for BLOY food availability, because mussels are directly measurable and are an important food source for BLOY (Miner *et al*. 2021). We calculated the mussel index using intertidal mussel plot and mussel size data from 37 locations spanning the BLOY study area for years 2011–2021 (Multi-Agency Rocky Intertidal Network *et al.* 2022). The mean annual mussel index per site was calculated as the mean of mussel percent cover × mussel bed depth × mussel size per sampling plot (typically five mussel plots per site). The resulting indices were then rescaled to range from 0 to 1. We used these 37 sites × 11 y values to create an annual kriged surface for the mussel index with a resolution of 25 km^2. Spatiotemporal kriging was conducted using the R-INLA (Rue *et al*. 2009) package for R statistical computing software following Krainski *et al*. (2019). Annual mussel indices were extracted for BLOY sites per year using the kriged surfaces. Given the similarity in the kriged surfaces across years and the lack of mussel data from 2022, we used the 2021 surface to estimate the mussel index for 2022.

As above, we estimated the full GLMM using the "glmmTMB" package in R (R Core Team 2022). We evaluated the contribution of the six covariates and the single interaction using AIC, where each subset model (including a null model with global and regional intercepts) was estimated, AIC was calculated, and ΔAIC values were used to rank models, compute model weights, and compute variable weights (Burnham & Anderson 2002). Before covariate analyses, binary variables were coded as -0.5 and 0.5, and continuous variables were centered on the mean and scaled by the standard deviation to produce comparable coefficients. Collinearity was not a major concern for this analysis as there was low correlation among the six covariates (mean $R^2 = 0.047$, max $R^2 = 0.270$).

RESULTS

A total of 160 trained observers collected 1709 measurements of pair productivity across California and Oregon from 2012 through 2022. Additionally, complementary data on six covariates were collected for a subset of 397 productivity measurements. Regarding effort, over the study period, the mean number of observer visits per monitored nest (± 1 SD) was 13.36 ± 7.00 visits and mean total hours of observer visitation per monitored nest was 10.20 ± 10.49 h. The mean number of nest attempts observed per pair and year was 1.34 ± 0.50 (range 1–3). Regarding covariates, visual estimates of nest height averaged 8.36 ± 7.64 m above high tide. Sixty-seven percent of nests were on islands. One or more human-related disturbances were reported for 31% of nest attempts, and one or more non-human-related disturbances were reported for 42% of nest attempts. Most observations of human disturbance involved people walking too close to nests, followed by pets and drones (by too close, this means oystercatchers indicated annoyance through behaviors such as calling or leaving the nest). Most observations of non-human disturbance involved Western Gulls *Larus occidentalis*, followed by Common Ravens *Corvus corax*, and Peregrine Falcons *Falco peregrinus* (Appendix, Table A2).

For GAMs using all 1709 productivity estimates (stage-one analysis), the model with a study region effect (1st-ranked, model weight = 0.67) was highly preferred over other models. In the highest-ranked model, productivity showed a clear latitudinal gradient (Fig. 2) and was lowest in the southern region (0.37 fledged young per pair per year, 95% confidence interval [CI] = 0.32–0.43, *n* = 677 nests monitored), intermediate in the central region (0.46, 0.41–0.51, 873), and highest in the northern region (0.60, 0.47–0.77, 873). While the highest-ranked model included no systematic temporal trend, productivity in each subregion appeared highly variable across years, with intermittent years of mass failure in southern California (Appendix, Table A2). Other models with much lesser weights were those including an additional year effect (2nd-ranked, ΔAIC = 1.93, model weight = 0.25), a year × region interaction (3rd-ranked, ΔAIC = 4.85, model weight = 0.06), and an intercept-only model (4th-ranked, ΔAIC = 7.50, model weight = 0.02).

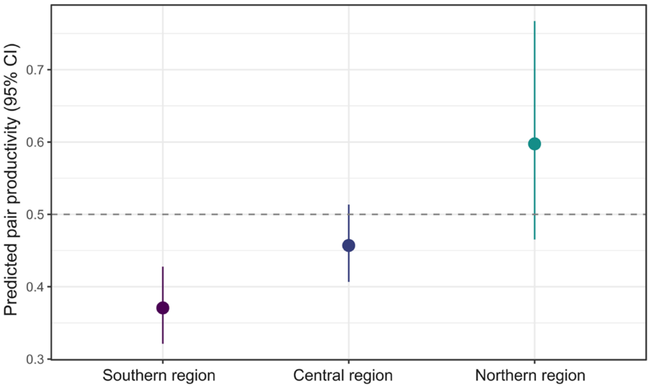

Fig. 2. Mean (± 95% confidence interval [CI]) Black Oystercatcher *Haematopus bachmani* (BLOY) productivity (chicks fledged per pair per year), 2012–2022, for each biogeographically defined region (Fig. 1).

For covariate GAMMs using 397 productivity estimates (stage-two analysis; Table 1), the highest-ranked model indicated an overall positive effect of nest height (standardized coefficient = 0.30) and an overall negative effect of human disturbance (-0.32) on productivity (Fig. 3). There was a negative effect of nesting on islands when nest height was low (-0.75); however, the strong interaction (0.30) indicated that nesting on islands, high above sea level and with little human disturbance, yielded the highest productivity by far (Fig. 3). While the best model (model weight = 0.21, Table 1) was not clearly preferred over several lower-ranked models (0.08–0.17, Table 1), the effect strengths and directions demonstrated in the best model were consistent across competing models (Table 1). In contrast, effects of non-human disturbance, mussel index, and beach access were infrequently included and were much smaller in magnitude (Table 3).

DISCUSSION

Regional and subregional productivity comparisons and population stability

We conducted the first comprehensive study of BLOY nest productivity and the effects of covariates on nesting success across a latitudinal gradient in their core distribution in California and Oregon. There was a striking latitudinal gradient in productivity, with the mean in the southern region (0.37) significantly lower than that in the central and northern regions (0.46 and 0.60, respectively). In contrast to this latitudinal pattern in productivity, there was no trend in productivity over time.

Mean productivity in the southern region fell below the reported ~0.50 productivity threshold needed to sustain a stable population for the species (Meehan *et al.* 2018). Low productivity, and more frequent incidents of mass nesting failures in the southern region than in other regions, could highlight a threat to the viability of

TABLE 1
Model selection results showing rank and standardized coefficients of candidate models predicting Black Oystercatcher *Haematopus bachmani* (BLOY) pair productivity, along with parameter importance weights, 2012–2022

Model rank	ΔAIC	Model weight	Nest height	Island nest	Human disturbance	Height × Island	Non-human disturbance	Mussel index	Public access point
1	0.00	0.21	0.30	-0.75	-0.32	0.30			
2	0.42	0.17	0.30	-0.83		0.29			
3	1.48	0.10	0.27	-0.40	-0.31				
4	1.51	0.10	0.21		-0.37				
5	1.69	0.09	0.26	-0.49					
6	1.75	0.09	0.31	-0.74	-0.30	0.29	-0.10		
7	1.78	0.09	0.31	-0.79	-0.33	0.29		-0.04	
8	1.83	0.08	0.31	-0.81		0.28	-0.15		
9	1.98	0.08	0.30	-0.74	-0.33	0.30			0.03
…									
49	9.31	0.00							
Importance weights			**0.99**	**0.79**	**0.55**	**0.50**	**0.32**	**0.30**	**0.27**

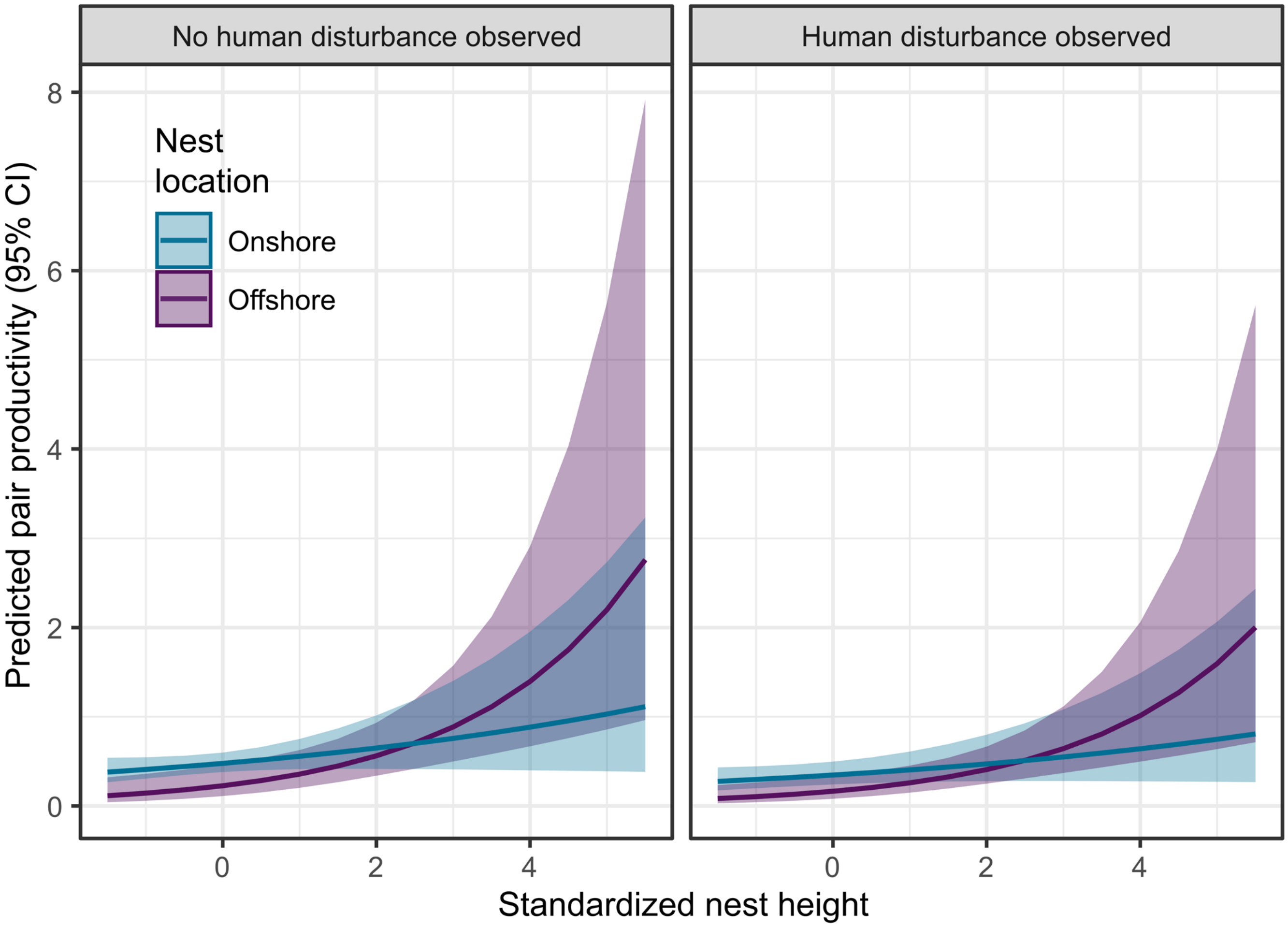

Fig. 3. The effects of Black Oystercatcher *Haematopus bachmani* (BLOY) nest location, height above high tide, and exposure to human disturbance on productivity (chicks fledged per pair per year), 2012–2022.

the species in the southern extent of its range. The central and northern regions had higher productivity, as well as some of the greatest densities of individual and nesting birds documented in the species' global range (Weinstein *et al*. 2014). Therefore, those regions could serve as a source population for the southern region. Productivity in the central and northern regions were comparable to productivity values determined in 14 other studies from Alaska, British Columbia, Washington (median 0.45, mean 0.54, range 0.25–0.95; Meehan *et al*. 2018), and Oregon (mean 0.74 in 2007 and 0.61 in 2008; E. Elliott-Smith unpubl. data). Furthermore, regional productivity across most of the species' range, spanning 25 degrees of latitude, from southern Alaska through central California, met or exceeded the reported ~0.50 threshold for population sustainability (Meehan *et al*. 2018).

Though there were no overall trends in productivity over time during the study period, there were high levels of interannual variability, including years of mass failure in most subregions, especially within the southern region. Explanations for high reproductive variability where it has been observed in other areas of the species' range include competitive exclusion (see below), depredation, human and non-human disturbance causing increased vulnerability in nests and chicks, and loss of eggs and chicks to physical impacts such as high swells and major storms (Andres 1998, Morse *et al*. 2006, Poe *et al*. 2009, Tessler *et al*. 2014). It is unclear from our results which factors drove latitudinal differences in productivity or caused subregions to experience occasional mass nesting failures. However, based on observations from our study, competitive exclusion or interference from other wildlife species sometimes negatively affected BLOY nesting in the southern region. For example, Brown Pelicans *Pelicanus occidentalis* and California Sea Lions *Zalophus californianus*, both of which have experienced rapid population increases in the southern region in recent years (Laake *et al*. 2018, McHuron *et al*. 2018), impeded BLOY nest attempts in San Luis Obispo County and at Año Nuevo Island (Santa Cruz County), both in the southern region (Warheit *et al*. 1984, Carle *et al*. 2020, Isaacs 2020). Some localized nest failures were also linked to Common Raven and Peregrine Falcon depredation, species whose populations have also increased in the study area in recent years (Wilson *et al*. 2000, Marzluff & Neatherlin 2006, Lau *et al*. 2021).

Relationships of productivity with environmental covariates, and the role of climate change

Our model results indicate a positive relationship between BLOY productivity and nest height, as well as a positive relationship with height of nests, particularly when nests were on islands. In fact, BLOY were most productive when nests were located on islands at relatively higher nest heights

(Fig. 3). Conversely, nesting on islands had a strong negative relationship with BLOY productivity overall. Though we did not evaluate the mechanism driving the link between covariates and BLOY productivity, the negative relationship with island nesting and the positive relationship with nest height suggest the possibility that wave action and/or high tides could drive failure of nests at lower elevations, especially on islands exposed to greater wave action. Other explanations are that nests with lower height could be exposed to more negative interactions with other wildlife (e.g., sea lions), or they could be subject to more human disturbance. The presence of observed human disturbance was also a significant negative factor in nest success. From a management perspective, these results underscore the importance of protecting higher elevation nest sites, both physically and from human disturbance. Given that sea level in central California is predicted to rise by 0.48–3.04 m by 2100 (50% probabilities with different models and scenarios; Griggs *et al*. 2017), the importance of protected suitable nesting habitat at higher elevations will only increase in the 21st century.

Our mussel index covariate was not significantly related to individual pair productivity. However, mussel index values increased from south to north, similar to BLOY regional productivity, suggesting that food availability could play a part in the lower productivity in the southern region. It is possible that our mussel index did not have a significant relationship with BLOY productivity because it failed to capture prey availability at a relevant spatial or temporal scale for BLOY productivity. For example, BLOY that choose to breed may be effective at selecting sites with ample nearby prey, and our relatively coarse-scale mussel index did not capture those local prey conditions. Supporting this idea, Hipfner & Elner (2013) found that the propensity of BLOY to nest was reduced with increasing sea surface temperature (SST), but productivity was not affected in pairs that chose to nest.

BLOY are considered climate-endangered due to their total reliance on the narrow band of rocky intertidal habitat, their low population size, and their low breeding pair density, the latter of which is thought to be approximately 0.07 pairs/km on the outer Pacific coast (Andres & Falxa 2020), approximately 0.4 pairs/km on the outer coast in California (Weinstein *et al*. 2014), and as high as 3.72 pairs/km on protected inner coast islands (Hipfner *et al*. 2012). Some researchers hypothesize that even short term climate-related shifts in intertidal invertebrates could impact BLOY populations by decreasing the propensity to nest (Hipfner & Elner 2013) and increasing parental effort to find scarcer prey of suboptimal size and/or energy density (Hollenbeck *et al*. 2014, Robinson *et al*. 2019). Warmer SST reduces growth, metabolism, and body mass of intertidal invertebrates (Hipfner & Elner 2013, Martel *et al*. 2022), and community-level climate-driven changes are already occurring in the BLOY's range. Observed climate-driven changes to intertidal BLOY habitat include decreased resilience of intertidal communities (Sanford *et al*. 2019, Menge *et al*. 2022); increased intertidal temperatures and decline of mussel cover in the Southern California Bight (Miner *et al*. 2021); and catastrophic cascades of mass mortality of kelp, sea stars, and abalone in response to prolonged marine heatwaves (Rogers-Bennett & Catton 2019). We agree with others that future research should address how climate-driven changes in nearshore ecosystems will affect food resources and predator communities with respect to BLOY populations (Robinson *et al*. 2019). We suggest BLOY be added as a metric within multivariate ongoing assessments of community-level change in the intertidal zone.

In sum, the knowledge gained from the present study of the productivity of BLOY and influence of covariates provides a baseline for management of the species in the southern portion of its range, against which the anthropogenic and natural changes of the future may be assessed. We recommend the continuation of stewardship and educational activities, as well as prioritization of the protection of suitable BLOY nesting habitat on islands and in areas with potential for higher-elevation nest sites near mussel beds.

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Daniel Orr and Joe Liebezeit contributed equally to the project and share second co-authorship.

AUTHOR CONTRIBUTIONS

A. Weinstein: conceptualization, funding acquisition, investigation, methodology, administration, validation, writing (original draft), writing (reviewing and editing). J. Liebezeit: data curation, funding acquisition, investigation, methodology, administration, validation, writing (reviewing and editing). D. Orr: conceptualization, data curation, formal analysis, methodology, validation, visualization, writing (reviewing and editing). T. Meehan: formal analysis, methodology, visualization, writing (reviewing and editing). R. Carle: conceptualization, investigation, methodology, writing (reviewing and editing).

DATA AVAILABILITY

Data from this project, including nest locations and productivity results, are stored at the Multiagency Rocky Intertidal Network located at https://pacificrockyintertidal.org. The platform describes program findings, provides data access, and has graphics capabilities that allow exploration of spatial and temporal patterns for over 300 invertebrate species, physical attributes of sites (e.g., geology, rugosity, tidal exposure), and a suite of community metrics (e.g., measures of species diversity, stability, and vulnerability). Housing the BLOY data on this platform provides perpetual access to the data for researchers and the public.

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