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Will climate change affect the survival of tropical and subtropical species? Predictions based on Bulwer's petrel populations in the NE Atlantic Ocean

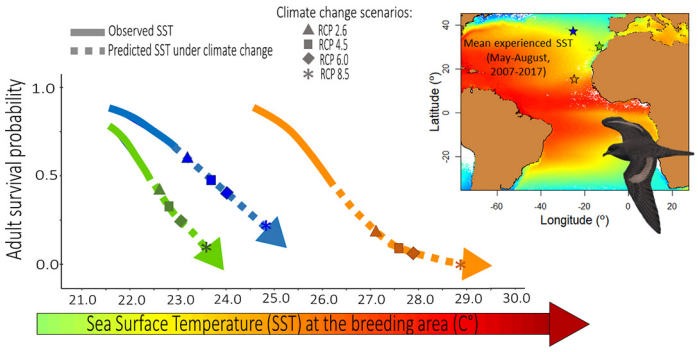
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HIGHLIGHTS

- The rise in sea surface temperature results in a decrease of Bulwer's petrel survival.
- Climate change impacts will particularly affect the survival of tropical populations.
- Multi-population approaches are needed due to the uneven climate change impacts.

GRAPHICAL ABSTRACT



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ABSTRACT

Climate change has repeatedly been shown to impact the demography and survival of marine top predators. However, most evidence comes from single populations of widely distributed species, limited mainly to polar and subpolar environments. Here, we aimed to evaluate the influence of environmental conditions on the survival of a tropical and migratory seabird over the course of its annual cycle. We used capture-mark-recapture data from three populations of Bulwer's petrel (*Bulweria bulwerii*) spread across the NE Atlantic Ocean, from the Azores, Canary, and Cabo Verde Islands (including temperate to tropical zones). We also inferred how the survival of this seabird might be affected under different climatic scenarios, defined by the Intergovernmental Panel on Climate Change. Among the environmental variables whose effect we evaluated (North Atlantic Oscillation index, Southern Oscillation Index, Sea Surface Temperature [SST] and wind speed), SST estimated for the breeding area and season was the variable with the greatest influence on adult survival. Negative effects of SST increase emerged across the three populations, most likely through indirect trophic web interactions. Unfortunately, our study also shows that the survival of Bulwer's petrel will be profoundly affected by the different scenarios of climate change, even with the most optimistic trajectory involving the lowest greenhouse gas emission. Furthermore, for the first time, our study predicts stronger impacts of climate change on tropical populations than on subtropical and temperate ones. This result highlights the devastating effect that climate change may also have on tropical areas, and the importance of considering multi-population approaches when evaluating its impacts which may differ across species distributions.

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1. Introduction

Climate change continues to have profound and varied consequences for marine ecosystems. Since the end of the 20th century, the rate of ocean warming has more than doubled; marine heatwaves have increased in frequency, intensity, and duration; stronger thermoclines result in losses of oxygen in the upper parts of the ocean column; and even the chemical composition of most water masses has changed through surface acidification (IPCC, 2019).

These changes produce shifts in the abundance, phenology, and distribution of marine organisms, often propagated by a cascading effect from primary producers to top predators (Doney et al., 2012). In this situation, seabirds are good indicators of global changes (Hazen et al., 2019). Certain species or populations may benefit from the new conditions (e.g., reduced predation or competition) whereas for others the consequences can be detrimental, with reduced survival and reproduction rates among other impacts (Doney et al., 2012). Environmental conditions, inferred using Sea Surface Temperature (SST), wind intensity and other integrative climate proxies (e.g., North Atlantic Oscillation [NAO] index and Southern Oscillation Index [SOI]), affect the survival and demography of many marine top predators, mostly due to indirect trophic effects (Frederiksen et al., 2008; Guéry et al., 2017; Jenouvrier et al., 2003; Trathan et al., 2007). For instance, in the Southern Ocean, climate change has been shown to be the driver of changes in distribution, breeding phenology, adult survival, and growth rate of several seabird populations due to increases in SST and changes in ice extent (Barbraud et al., 2012, 2011; Croxall et al., 2002; Jenouvrier et al., 2018).

To secure optimal climatic and trophic conditions and to reduce year-round environmental heterogeneity, wild fauna inhabiting ecosystems with high-seasonality from mid to high latitudes often migrate (Dingle, 1996). However, they still face slightly different environmental conditions in their breeding and non-breeding areas (Newton, 2010). In the case of species with strong breeding site fidelity, individuals are forced to confront the environmental conditions in their breeding areas (Coulson, 2016). Nervertheless, during the non-breeding season they may exhibit more flexibility in choosing their environmental conditions, either by performing facultative migrations or by changing their non-breeding areas (Newton, 2010). Thus, although several studies have shown strong seabird fidelity to wintering areas (Léandri-Breton et al., 2021; Merkel et al., 2021) it may be important to consider the different year-round environmental conditions experienced by individuals (e.g., during both the breeding and non-breeding seasons) in assessing effects of climate on demography.

Several demographic studies have evaluated the effects of climate change on migratory wildlife inhabiting the high seas. However, most studies (Barbraud et al., 2011; Hawkes et al., 2007) did not predict the effects of changing conditions of future scenarios (Jenouvrier, 2013; Jenouvrier et al., 2009), and have focused mainly on polar and subpolar environments (Barbraud et al., 2012; Trathan et al., 2007). Only a handful of studies have focused on tropical areas (e.g., Precheur et al., 2016). Therefore, there is a clear gap in our knowledge of the past, current and future impacts of climate change on tropical and subtropical seas, despite the evidence suggesting that it is these areas, and consequently the animals inhabiting them, that will be exposed to the earliest occurrence of historically unprecedented climates (Mora et al., 2013). Furthermore, to properly understand the potential effects of climate change on a given species, it is important to consider the widest possible range of distribution through multi-population studies (Frederiksen et al., 2005).

Migratory seabirds are ideal organisms for monitoring the impact of climate change in the marine ecosystem. They are at or near the top of marine food webs and the variation in their demographic parameters and/or their diet may reflect changes occurring at lower levels (Lescroël et al., 2016); many are relatively easy to monitor (Hazen et al., 2019); and their wide-ranging distributions and the differences and distance between their breeding and non-breeding areas allow comparisons between dissimilar biogeographic areas and regions (Ramos and González-Solís, 2012).

Here, we evaluated the effect of environmental conditions on the demography of a partially migratory and pantropical oceanic seabird, the Bulwer's petrel (*Bulweria bulwerii*), by monitoring three populations spread across a tropical-temperate gradient in the NE Atlantic Ocean. We first assessed whether the survival probability of adult Bulwer's petrels varied according to colony, time (year), and sex. Second, we evaluated the effects of several environmental proxies, namely SST, wind, NAO, and SOI, estimated for the breeding and non-breeding seasons, on the survival probability of this seabird. SST has been recognized as an important factor driving the year-round distribution of this species (Ramos et al., 2015). Accordingly, we hypothesized that this parameter would have an important influence on its survival probability and, as reported for many other seabirds (Jenouvrier et al., 2003; Precheur et al., 2016; Ramos et al., 2012), we expected to find a negative relationship between SST and survival. Because Bulwer's petrels show strong breeding site fidelity (Mougin, 1996; 90 % of nest fidelity rate between 2002 and 2004 on Vila islet, Azores; Bried and Bourgeois, 2005) but can hypothetically be more flexible in choosing non-breeding areas in response to environmental conditions, we anticipated a higher impact of SST during the breeding than during the non-breeding season. Finally, we also predicted variation in survival in each Bulwer's petrel population under different climate change scenarios, as defined by the projections of the Intergovernmental Panel on Climate Change (IPCC, 2014). Due to our expectations of a negative SST-survival relationship, we also foresaw a decline in survival probabilities of the three populations under the aforementioned climate change scenarios, especially in the ones with high GreenHouse Gas (GHG) emissions for which more extreme environmental conditions are expected.

2. Materials and methods

2.1. Species and study populations

Bulwer's petrel is a ca. 95-g burrow/cavity-nesting procellariiform whose maximum recorded longevity is 23 years (Blumstein and Møller, 2008). In the Atlantic Ocean, it breeds on small islets and islands throughout all the Macaronesian archipelagos (Brooke, 2004). Bulwer's petrel is usually considered as a pantropical species, although some populations in the Atlantic Ocean may be better described as subtropical (e.g., in the Canary Islands) or even at the edge of the subtropical/temperate zones (e.g., in the Azores archipelago). Almost half of the individuals from the Azores and the Canary Islands migrate to the South Atlantic, while the remaining individuals from these archipelagos and all birds from Cabo Verde spend the non-breeding season in the Central Atlantic. This migration pattern, known as “leapfrog migration”, is believed to result from differences in habitat preferences of northern and southern populations (Ramos et al., 2015).

Fieldwork was carried out in three different populations from Macaronesia (Fig. 1), from north to south: Vila Islet (hereafter Vila, Azores archipelago; 36°55′ N, 25°10′ W; ca. 50 breeding pairs; Monteiro et al., 1999; J. Bried unpublished data), Montaña Clara Islet (hereafter M. Clara, Canary Islands; 29°18′ N, 13°32′ W; ca. 100 breeding pairs; Cruz-Flores et al., 2019), and Cima Islet (hereafter Cima, Cabo Verde archipelago; 14°58′ N, 24°38′ W; ca. 450 breeding pairs; T. Militão & J. González-Solís unpublished data; Table A1 in Appendix A).

2.2. Capture-Mark-Recapture (CMR) sampling strategy

Birds were captured in their burrows at each colony, during incubation and/or chick-rearing period. Each individual was ringed with a single stainless-steel ring at its first capture, and every subsequent recapture was recorded. The dataset considered 2058 encounters from the three study colonies: Vila (n = 261 adults, data from 2007 to 2012 and 2016), M. Clara (n = 415, 2010–2018) and Cima (n = 418, 2010–2018). Forty-six males and

45 females on Vila (17.6 and 17.2 % of the total number of adults from Vila respectively), 46 males and 24 females on M. Clara (11.1 and 5.8 % respectively), and 14 males and 13 females on Cima (3.3 and 3.1 % respectively) were molecularly sexed following Fridolfsson and Ellegren (1999). Sex was unknown for the remaining individuals. Differences in sex ratios of sexed individuals are due to differences in sampling strategies and fieldwork schedules on the three islets. On Vila, we carried out two fieldwork seasons per year: the one during incubation and the other during chick-rearing period, which allowed us to capture both pair members in most cases. On M. Clara, until 2014, we visited the colony at the beginning of the incubation period, when we found mainly males (sexed molecularly). Bewteen 2015 and 2018 we visited M. Clara during incubation and chick-rearing period, but we did not sex more individuals. On Cima, fieldwork was carried out mainly during pre-laying and chick-rearing periods (when both pair members were present). M-array summaries by colony and sex are shown in Table B1 in Appendix B.

2.3. Tracking data

Since Bulwer's petrels face different environmental conditions in their breeding and non-breeding areas (a situation that may ultimately have different effects on their survival), we determined the areas used during the two seasons by fitting breeding adults with small Global Location Sensing loggers (GLS hereafter; $n = 14$ for Vila, 94 for M. Clara and 19 for Cima; more information in Table C1 in Appendix C), leg-mounted with PVC rings over several years. The GLS models we used were Mk13, Mk14, and Mk18 from the British Antarctic Survey (BAS; Cambridge, UK), Mk4083 from BioTrack (Wareham, UK) and Intigeo-C65 from Migrate Technology (Cambridge, UK). GLS weighed from 1 to 2 g, which represents 0.8 % to 2.4 % of the body mass of a Bulwer's petrel (range: 83–132 g; authors' unpublished data). GLS data were processed as explained in Appendix C. We defined some phenological dates to determine the breeding and non-breeding seasons for each population. The non-breeding season was defined as the period between the date of departure from and the date of arrival in the breeding area (see Appendix C for details). Generally, the non-breeding season of Vila and M. Clara individuals lasts from September to April, and for Cima individuals from August to January. The breeding season of each colony was defined as the remaining months (Fig. 1).

For each colony and for the breeding and non-breeding seasons separately, we calculated the 50 % Kernel Density Estimates (KDE), as a proxy for the core-use area of Bulwer's petrel distribution during these seasons (Fig. 1), and the 75 % KDE as a proxy for the broad-use area, based on the individuals tracked at each colony. To do so, we used the `kernelUD` function in `adehabitatHR` package (Calenge, 2011) from the R software

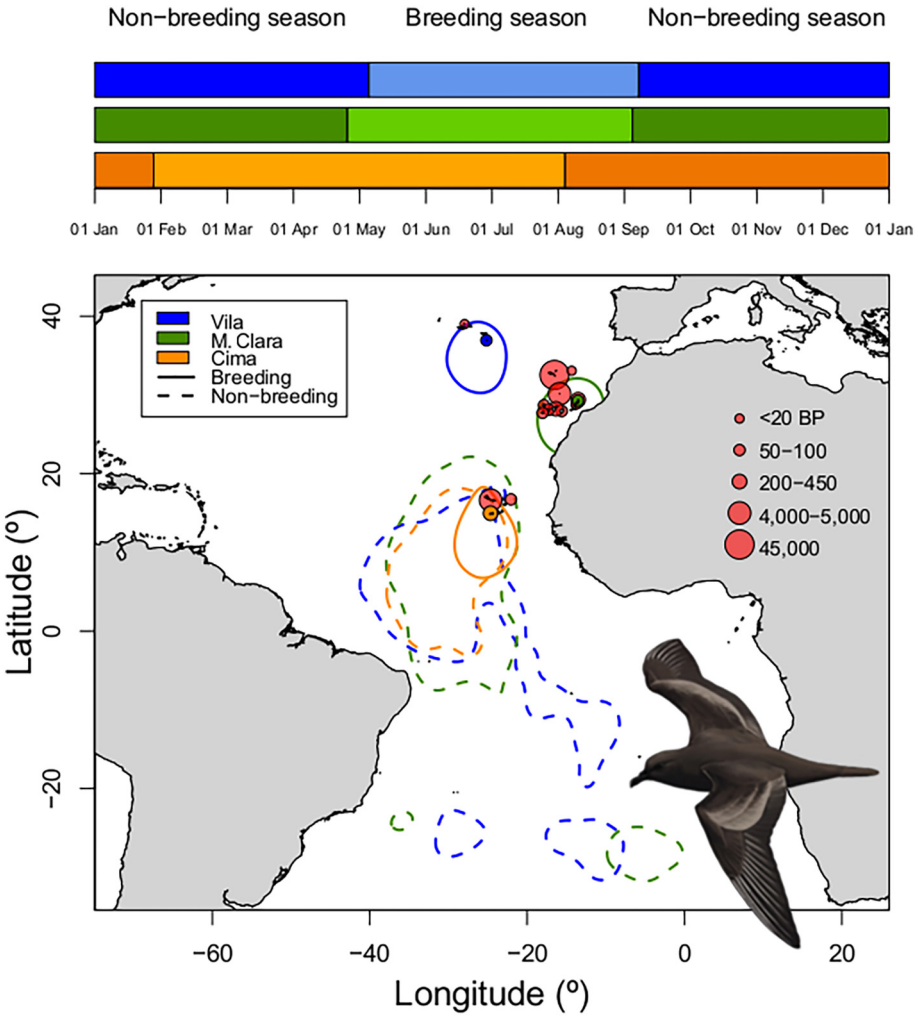


Fig. 1. Bulwer's petrel populations in the NE Atlantic Ocean are represented with circles whose area is proportional to the number of breeding pairs (determined using data from the literature specified in Table A1 in Appendix A). Contours of the 50 % kernel utilization distribution (core-use area) during the breeding (continuous lines) and non-breeding seasons (dashed lines) are shown based on global location sensing logger data. Horizontal bars at the top show the phenology and duration of the breeding (light colors) and the non-breeding season (dark colors). Data for Vila, M. Clara and Cima islets are represented in blue, green and orange, respectively; and the rest of Bulwer's petrel populations in red. Drawing by courtesy of Sergi Torné.

(R Core Team, 2019) and a smoothing parameter (*h*) value of 1.82, which corresponds to the longitudinal GLS error in degrees following Lascelles et al. (2016).

2.4. Environmental data

We evaluated the influence of environmental conditions on survival for each Bulwer's petrel population using four variables commonly related to seabirds' survival: (a) NAO (https://climatedataguide.ucar.edu/sites/default/files/nao_pc_monthly.txt), (b) SOI (www.esrl.noaa.gov/psd/data/correlation/soi.data), (c) SST (www.oceancolor.gsfc.nasa.gov/cgi/l3; monthly Aqua MODIS Sea Surface Temperature (11 μ daytime) product in °C, with a 9-km resolution), and (d) wind speed (marine.copernicus.eu/; Global Ocean Wind L4 Reprocessed Monthly Mean Observations product in m/s).

Monthly estimates of NAO and SOI were averaged for the breeding and non-breeding seasons (months described above for each colony; Fig. D1 in Appendix D) and year. Mean SST and maximum wind speed estimates were calculated for each colony and season for the values that fell within the 50 % and 75 % KDE (Fig. D2 in Appendix D). To do so, we removed areas <200 m deep, given that Bulwer's petrels tend to avoid the continental shelf (Cruz-Flores et al., 2019) and, in the case of SST, we used an equal-area projection before calculating the average for the whole 50 % or 75 % KDE area. To evaluate whether these variables could have a delayed effect from basal trophic organisms to top predators, we also considered a lagged effect of one year, except for wind speed, since we only expected a direct effect of wind speed on Bulwer's petrel survival through an increase in energy demands or a decrease in foraging efficiency due to turbidity, as observed in the European shag (*Phalacrocorax aristotelis;* Frederiksen et al., 2008). In the case of SST, we also considered a lagged effect between seasons; thus, we combined the breeding distribution of the individuals (50 % or 75 % KDE) with SST values from the non-breeding season, and the non-breeding distributions with SST values from the breeding season (Fig. D1 in Appendix D). All spatial analyses were carried out using the `Terra` package (Hijmans, 2021).

2.5. CMR models and statistical analyses

We first evaluated whether the general model for single-state data with only time-dependent parameters (Cormack-Jolly-Seber [CJS] model) might be an acceptable starting point for our dataset. To do so, we carried out standard Goodness-Of-Fit (GOF) tests by group (males, females, unknown sex) using U-CARE 2.3.4 software (Choquet et al., 2009a).

Second, we carried out multievent models with uncertainty in sex assignment to determine whether survival probabilities varied by colony, time (here, year) and sex, and if these probabilities were influenced by the environment. We assumed that individuals that had not been sexed comprised 50 % of males and 50 % of females (i.e., we fixed the sex ratio to 0.5 as explained in Appendix E). We further assumed that, at any time, an individual was in one of the following three states: alive male, alive female or dead. Regarding the detection process, we considered the alternative events of being or not being detected with some recapture probability (*p*, probability that an individual alive and present at the breeding colony at Year *t* is captured during Year *t*; see Appendix E). We modeled recapture probabilities as depending on sex, colony and time, or a combination of these. We always included time and colony, in order to fixed at zero the recapture probabilities in the years and colonies where there had been no visits. Once we selected the best structure for recapture probability (Model 1: *p*(sex + colony*time), see Group 1 In Table 1), we modeled survival (Φ, probability that an individual alive at Year *t* survives until Year *t* + *1*) as either constant, conditional on colony, time or sex, or a combination of these, and keeping the best estructure for recapture probabilities. Also, when modeling survival, we considered as covariates the environmental variables mentioned above during both the breeding (suffix $_{br}$) and non-breeding seasons (suffix $_{n\text{-}br}$; Fig. D1 in Appendix D). To do so, we kept the best structure found when modeling survival probabilities without environmental variables (Model 4: Φ(sex), see Group 2.1 in Table 1), and we always included colony as a factor since each colony withstands different environmental conditions. In the case of global indexes (NAO and SOI), we modeled survival using both common and different slopes among colonies (additive and interaction effects, noted "+" and "*" in Table 1, respectively), whereas for SST and wind speed we only considered colony-specific slopes (interaction effect), because these two spatial covariates were spatially scaled according to colony-specific tracking data (Fig. D2 in Appendix D). As SST values differed notably between colonies, we standardized SST of a year *i* and a colony *e* as follows:

$$Stardardized\ SST_{i,e} = \frac{SST_{i,e} - mean\ SST_e}{SD\ SST_e}$$

Additive and interactive sex effects were considered when modeling survival and recapture parameters. Finally, we calculated the average survival probability over the survey years (geometric mean) for each colony and sex. The average survival probabilities obtained were in turn averaged (arithmetic mean) to provide a single value for the species.

CMR models were run using E-SURGE 2.2.3 (Choquet et al., 2009b), and model selection was based on Akaike Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson, 2002). The model with the lowest AICc has the best compromise between bias and variance (Burnham et al., 2011). In addition, Akaike weights were calculated as an index of the relative plausibility of each model (Wagenmarkers and Farrell, 2004). Finally, to evaluate the relevance of environmental covariates from the best model, we calculated (1) the proportion of deviance (Dev) explained by this covariate following Grosbois et al. (2008) as:

$$R^2_{Dev} = \frac{Dev(Mcst) - Dev(Mco)}{Dev(Mcst) - Dev(Mt)}$$

where *Mcst*, *Mco* and *Mt* are models with constant, covariate and temporal effect (constant and temporal models are shown in Table 1, Group 1 and Group 2.1), and (2) its statistical significance using an analysis of deviance test (ANODEV, Grosbois et al., 2008) as:

$$Ftest = \frac{\frac{Dev(Mcst) - Dev(Mco)}{np(Mcst) - np(Mco)}}{\frac{Dev(Mco) - Dev(Mt)}{np(Mco) - np(Mt)}}$$

with *[np(Mcst) – np(Mco)]* and *[np(Mco) - np(Mt)]* degrees of freedom, where *np* represents the number of parameters.

2.6. Climate change scenarios and effects

Since the best model took into account the SST of the breeding season at the core-use area (50 % KDE; see Results), for each Representative Concentration Pathway (a stringent mitigation scenario RCP 2.6, two intermediate scenarios RCP 4.5 and RCP 6.0, and a scenario with very high GHG emissions RCP 8.5; IPCC, 2014), we downloaded the predicted monthly mean surface temperature with one-degree resolution for the period 2090–2100 and with "ensemble average" of model runs (the mean state of the climate among all model runs; https://gisclimatechange.ucar.edu/gis-climatedata).

For each month and scenario, we calculated a spatial mean between all their values from 2090 to 2100. For each colony and scenario, we calculated a mean with the months belonging to the breeding season, selected the 50 % KDE of the tracked birds from this colony, and removed areas <200 m deep. Finally, we calculated a mean with all the values of the raster using an equal-area projection (Hijmans, 2021).

We inferred the survival for the SST values expected under the various climate change scenarios mentioned above using the regression functions obtained from the best supported model (Model 34 in Table 1). To calculate 95 % CI values, we calculated a set of survival probabilities using the equation: $logit\Phi = intercept + slope * SST$, where pair of intercepts and slopes for each sex and colony were generated randomly 10,000 times from a

Table 1
Modeling recapture (p) and survival (Φ) probabilities, for Bulwer's petrel at three colonies (Vila, M. Clara and Cima) situated along a latitudinal gradient in the NE Atlantic Ocean, depending on sex, colony, and time (year), with and without temporal environmental variables. In recapture probabilities, we set years without data for each colony. Within each group of models (delimited with a horizontal line), we provide Akaike Information Criterion values corrected for small sample sizes (AICc) in ascending order. For Group 2 (modeling survival probabilities), we used as structure of recapture probabilities the structure from the best model obtained in Group 1 (Model 1). Models weights were calculated for those models sharing the same best structure for recapture probabilities (p(sex + colony*time)). R^2_{Dev} and ANODEV were calculated using as constant (Mcst) and temporal (Mt) models those without environmental variables (Group 1 and 2.1), and whose numbers are specified in the Table. The best-supported model is highlighted in bold.

										ANODEV	
		np	Dev	AICc	ΔAICc	Weight	Mcst	Mt	R^2_{Dev}	F	p-value
1. Modeling recapture probabilities (p):											
1 Φ(sex + colony*time)	p(sex + colony*time)	47	3347.0	3443.2	26.9	0.00	–	–	–	–	–
2 Φ(sex + colony*time)	p(colony*time)	46	3355.8	3450.0	33.6	–	–	–	–	–	–
3 Φ(sex + colony*time)	p(sex*colony*time)	65	3321.7	3456.0	39.7	–	–	–	–	–	–
2. Modeling survival probabilities (Φ):											
2.1. Without environmental variables:											
4 Φ(sex)	p(sex + colony*time)	25	3376.6	3427.3	11.0	0.00	–	–	–	–	–
5 Φ(c)	p(sex + colony*time)	24	3380.1	3428.7	12.4	0.00	–	–	–	–	–
6 Φ(sex + colony)	p(sex + colony*time)	27	3374.6	3429.4	13.0	0.00	–	–	–	–	–
7 Φ(colony)	p(sex + colony*time)	26	3378.0	3430.7	14.4	0.00	–	–	–	–	–
8 Φ(sex*colony)	p(sex + colony*time)	29	3372.8	3431.6	15.3	0.00	–	–	–	–	–
9 Φ(sex + colony + time)	p(sex + colony*time)	37	3357.7	3433.1	16.8	0.00	–	–	–	–	–
10 Φ(time)	p(sex + colony*time)	34	3366.4	3435.6	19.3	0.00	–	–	–	–	–
11 Φ(sex*time)	p(sex + colony*time)	45	3348.8	3440.9	24.6	0.00	–	–	–	–	–
12 Φ(colony*time)	p(sex + colony*time)	45	3350.0	3442.1	25.8	0.00	–	–	–	–	–
13 Φ(sex*colony*time)	p(sex + colony*time)	65	3325.8	3460.1	43.8	0.00	–	–	–	–	–
2.2. With environmental variables:											
2.2.1. North Atlantic Oscillation (NAO)											
14 Φ(sex + colony*NAO_{br})	p(sex + colony*time)	30	3365.8	3426.7	10.4	0.00	6	1	0.32	2.8	0.070
15 Φ(sex + colony + NAO_{br})	p(sex + colony*time)	28	3372.3	3429.1	12.8	0.00	6	9	0.14	1.4	0.264
16 Φ(sex + colony*$NAO_{n\text{-}br}$)	p(sex + colony*time)	30	3368.4	3429.3	13.0	0.00	6	1	0.22	1.7	0.195
17 Φ(sex + colony + NAO_{nbr})	p(sex + colony*time)	28	3374.4	3431.2	14.9	0.00	6	9	0.01	0.1	0.737
18 Φ(sex + colony + NAO_{br1})	p(sex + colony*time)	28	3374.6	3431.4	15.0	0.00	6	9	0.00	0.0	0.866
19 Φ(sex + colony + $NAO_{n\text{-}br1}$)	p(sex + colony*time)	28	3374.6	3431.4	15.1	0.00	6	9	0.00	0.0	1.000
20 Φ(sex + colony*$NAO_{n\text{-}br1}$)	p(sex + colony*time)	30	3371.8	3432.8	16.4	0.00	6	1	0.10	0.7	0.581
21 Φ(sex + colony*NAO_{br1})	p(sex + colony*time)	30	3373.7	3434.6	18.3	0.00	6	1	0.03	0.2	0.895
2.2.2. South Oscillation Index (SOI)											
22 Φ(sex + colony + $SOI_{n\text{-}br}$)	p(sex + colony*time)	28	3373.4	3430.2	13.9	0.00	6	9	0.07	0.7	0.424
23 Φ(sex + colony*$SOI_{n\text{-}br}$)	p(sex + colony*time)	30	3370.0	3430.9	14.6	0.00	6	1	0.17	1.2	0.338
24 Φ(sex + colony + SOI_{br1})	p(sex + colony*time)	28	3374.3	3431.1	14.8	0.00	6	9	0.02	0.2	0.665
25 Φ(sex + colony + $SOI_{n\text{-}br1}$)	p(sex + colony*time)	28	3374.5	3431.3	15.0	0.00	6	9	0.01	0.1	0.759
26 Φ(sex + colony + SOI_{br})	p(sex + colony*time)	28	3374.5	3431.3	15.0	0.00	6	9	0.01	0.1	0.759
27 Φ(sex + colony*$SOI_{n\text{-}br1}$)	p(sex + colony*time)	30	3372.2	3433.1	16.8	0.00	6	1	0.09	0.6	0.623
28 Φ(sex + colony*SOI_{br1})	p(sex + colony*time)	30	3372.9	3433.8	17.5	0.00	6	1	0.06	0.4	0.755
29 Φ(sex + colony*SOI_{br})	p(sex + colony*time)	30	3373.5	3434.4	18.1	0.00	6	1	0.04	0.3	0.825
2.2.3. Wind speed											
30 Φ(sex + colony*$Wind_{br}$ $K50_{br}$)	p(sex + colony*time)	30	3364.1	3425.0	8.7	0.01	6	1	0.38	3.7	0.031
31 Φ(sex + colony*$Wind_{br}$ $K75_{br}$)	p(sex + colony*time)	30	3365.9	3426.8	10.5	0.00	6	1	0.32	2.8	0.070
32 Φ(sex + colony*$Wind_{n\text{-}br}$ $K50_{n\text{-}br}$)	p(sex + colony*time)	30	3366.3	3427.2	10.9	0.00	6	1	0.30	2.6	0.084
33 Φ(sex + colony*$Wind_{n\text{-}br}$ $K75_{n\text{-}br}$)	p(sex + colony*time)	30	3370.6	3431.6	15.2	0.00	6	1	0.14	1.0	0.415
2.2.4. Sea Surface Temperature (SST)											
34 **Φ(sex + colony*SST_{br} $K50_{br}$)**	**p(sex + colony*time)**	**30**	**3355.4**	**3416.3**	**0.0**	0.57	**6**	**1**	0.70	**13.7**	**0.000**
35 Φ(sex + colony*SST_{br1} $K50_{n\text{-}br}$)	p(sex + colony*time)	30	3357.2	3418.1	1.8	0.24	6	1	0.63	10.3	0.000
36 Φ(sex + colony*SST_{br} $K75_{br}$)	p(sex + colony*time)	30	3359.5	3420.5	4.1	0.07	6	1	0.55	7.2	0.002
37 Φ(sex + colony*SST_{br1} $K75_{br}$)	p(sex + colony*time)	30	3360.8	3421.8	5.4	0.04	6	1	0.50	6.0	0.005
38 Φ(sex + colony*SST_{br1} $K50_{br}$)	p(sex + colony*time)	30	3361.3	3422.3	5.9	0.03	6	1	0.48	5.5	0.007
39 Φ(sex + colony*SST_{br1} $K75_{n\text{-}br}$)	p(sex + colony*time)	30	3365.4	3426.3	10.0	0.00	6	1	0.33	3.0	0.058
40 Φ(sex + colony*SST_{br} $K50_{n\text{-}br}$)	p(sex + colony*time)	30	3365.4	3426.3	10.0	0.00	6	1	0.33	3.0	0.058
41 Φ(sex + colony*SST_{br} $K75_{n\text{-}br}$)	p(sex + colony*time)	30	3366.0	3426.9	10.6	0.00	6	1	0.31	2.7	0.076
42 Φ(sex + colony*$SST_{n\text{-}br1}$ $K50_{n\text{-}br}$)	p(sex + colony*time)	30	3366.3	3427.2	10.9	0.00	6	1	0.30	2.6	0.084
43 Φ(sex + colony*$SST_{n\text{-}br}$ $K50_{n\text{-}br}$)	p(sex + colony*time)	30	3366.7	3427.6	11.3	0.00	6	1	0.29	2.4	0.102
44 Φ(sex + colony*$SST_{n\text{-}br1}$ $K50_{br}$)	p(sex + colony*time)	30	3366.7	3427.6	11.3	0.00	6	1	0.29	2.4	0.102
45 Φ(sex + colony*$SST_{n\text{-}br}$ $K50_{br}$)	p(sex + colony*time)	30	3367.5	3428.4	12.1	0.00	6	1	0.26	2.1	0.136
46 Φ(sex + colony*$SST_{n\text{-}br}$ $K75_{n\text{-}br}$)	p(sex + colony*time)	30	3367.6	3428.5	12.2	0.00	6	1	0.26	2.1	0.136
47 Φ(sex + colony*$SST_{n\text{-}br}$ $K75_{br}$)	p(sex + colony*time)	30	3367.7	3428.7	12.3	0.00	6	1	0.25	2.0	0.150
48 Φ(sex + colony*$SST_{n\text{-}br1}$ $K75_{br}$)	p(sex + colony*time)	30	3369.2	3430.1	13.8	0.00	6	1	0.20	1.5	0.248
49 Φ(sex + colony*$SST_{n\text{-}br1}$ $K75_{n\text{-}br}$)	p(sex + colony*time)	30	3369.2	3430.1	13.8	0.00	6	1	0.20	1.5	0.248

Variable effects were tested for the breeding (suffix $_{br}$) or non-breeding season (suffix $_{n\text{-}br}$), and without or with a time lag of one year (suffix $_1$). For wind speed and SST, we specified if the data belong to the 50 % or 75 % kernel density estimates during the breeding ($K50_{br}$ or $K75_{br}$) or non-breeding season ($K50_{n\text{-}br}$ or $K75_{n\text{-}br}$). Additive (+) or interaction (*) effects were considered. 'np' is the number of estimated parameters; 'Dev' deviance; 'AICc' represents the Akaike Information Criterion values for small samples sizes; 'ΔAICc' is the difference between a specific model and the model with the lowest AICc value (in bold). Weight is the probability that a model is the expected best model based on AICc. R^2_{Dev} is the proportion of the temporal variability explained by the covariates, and the ANODEV test is their statistical significance; both were calculated with the constant (Mcst) and temporal (Mt) models shown in Group 1 and 2.1; see Grosbois et al. (2008) for test details.

multivariate normal distribution using the intercepts and slopes for each sex and colony obtained from the best model (Model 34 in Table 1) as means, and their covariance-variance matrix. Finally, we calculated the 95 % CI values from the set of survival probabilities obtained for each SST value.

3. Results

3.1. GOF test results

The overall GOF test for the CJS model was not significant, and was therefore an acceptable point of reference for further models (Table E1 in Appendix E).

3.2. Best-supported model

In the best-supported model, recapture and survival probabilities varied among colonies and years; and were higher for males than for females (Model 34 in Table 1, model weight 0.57; Figs. E1 and E2 in Appendix E). Survival geometric means ± SD for males and females, respectively, were 0.81 ± 0.03 and 0.75 ± 0.03 on Vila (n = 9 years, from 2008 to 2016), 0.77 ± 0.03 and 0.69 ± 0.05 on M. Clara (n = 8 years, from 2011 to 2018), and 0.82 ± 0.04 and 0.73 ± 0.03 on Cima (n = 8 years, from 2011 to 2018). Survival probability at the species level was estimated at 0.76 ± 0.02.

Survival probabilities at Year $t + 1$ were negatively correlated with SST experienced during the previous breeding seasons at Year t in the core-use area (i.e., SST_{br} $K50_{br}$). An increase in SST values in a given breeding area and season (at Year t) was reflected in a decrease in survival probability in the subsequent breeding season (at Year $t + 1$; Table 2 and Fig. 2). This influence of SST on the survival probabilities of Bulwer's petrel was highly relevant since this variable explained 70 % of the data temporal variability and was statistically significant (Table 1). Furthermore, the influence of SST on survival varied slightly among colonies: for the same increase in SST, the decrease in survival probability was lowest for Vila and highest for M. Clara (Table 2 and Fig. 2).

A similar model, but considering the 75 % KDE (instead of 50 % KDE) for SST caluculations, also explained an elevated percentage of temporal variability (Model 36, SST_{br} $K75_{br}$, R^2_{Dev} = 0.55). In addition to them, other models accounting for the SST experienced during the breeding season with a lag effect of one year (SST at Year t-1 affects survival until Year $t + 1$) both at the breeding (Model 37, SST_{br1} $K75_{br}$, R^2_{Dev} = 0.50; and Model 38, SST_{br1} $K50_{br}$, R^2_{Dev} = 0.48) and non-breeding areas (Model 35, SST_{br1} $K50_{n\text{-}br}$, R^2_{Dev} = 0.63) also explained an elevated percentage of data temporal variability. Finally, a model considering wind speed during the breeding season at the breeding area (Model 30, $Wind_{br}$ $K50_{br}$) explained 38 % of the total temporal variability of the data (R^2_{Dev} = 0.38).

3.3. Climate change effects

If the effect of SST on survival remains the same under higher temperatures, we will expect a dramatic reduction in survival probabilities of all colonies under the different scenarios as GHG emissions increase. Survival probabilities of Bulwer's petrel on Vila will be above 0.5 both under the RCP 2.6 climate change scenario (the stringent mitigation scenario) and under the RCP 4.5 for males (one of the intermediate scenarios), and will be below 0.5 for females under the RCP 4.5 scenario and for both sexes under the RCP 6.0 and RCP 8.5 scenarios (one of the intermediate scenarios and the scenario with the highest GHG emissions respectively; Table 3 and Fig. 2 in dashed lines). In the case of M. Clara, survival probabilities will remain above 0.3 (but below 0.5) under the RCP 2.6 scenario for both sexes and under the RCP 4.5 scenario for males, and will be equal to or below 0.3 for females under the RCP 4.5 scenario and for both sexes under the RCP 6.0 and RCP 8.5 scenarios, being below 0.1 for females under the RCP 8.5 scenario. In the case of Cima, survival probabilities will be very low (below 0.23) irrespective of the scenario: below 0.1 for females under the RCP 4.5 scenario and for both sexes under the RCP 6.0 and RCP 8.5 scenarios.

Table 2
Regression functions for Bulwer's petrel survival for each colony and sex and depending on SST (in °C). These functions were obtained from the best model (Model 34: Φ(sex + colony*SST_{br} K_{br}) p(sex + colony*time), in Table 1).

Colony	Sex	Regression function
Vila	Males	logitΦ = 24.3–1.0 * SST
	Females	logitΦ = 23.9–1.0 * SST
M. Clara	Males	logitΦ = 38.3–1.7 * SST
	Females	logitΦ = 37.9–1.7 * SST
Cima	Males	logitΦ = 38.3–1.5 * SST
	Females	logitΦ = 37.9–1.5 * SST

4. Discussion

To our knowledge, this is the first study to evaluate the demographic responses to climate change of several populations of a marine top predator breeding at tropical and subtropical latitudes. This approach has allowed us to identify interpopulation dissimilarities in the effect of the environment, i.e. SST, on survival. The study highlights the importance of evaluating the demography of a given species through its entire latitudinal distribution when assessing climate change impacts.

4.1. Bulwer's petrel survival in the NE Atlantic Ocean

The survival probabilities of Bulwer's petrel given in this study are much lower than those expected for a long-lived species (Weimerskirch, 2002), which could involve long-term viability issues (Sanz-Aguilar et al., 2009). At the colony level, Vila and Cima, with higher survival probabilities than M. Clara, would be at a lower risk than M. Clara. These differences in survival rates may be attributed to differences in predator abundance among the three colonies. On Vila, Bulwer's petrel may suffer predation by the long-eared owl (*Asio otus*), which resides on Santa Maria Island (BirdLife International, 2018), and has been observed on Vila solitarily (authors' personal observations). On Cima, the barn owl (*Tyto alba*) preys on Bulwer's petrels (Garcia del Rey, 2016; authors' personal observation). On M. Clara, the main predator of Bulwer's petrel is probably Eleonora's falcon (*Falco eleonorae*; Cruz-Flores et al., 2019) which breeds at high densities on this Islet (López-Darias and Rumeu, 2010), and whose large-scale predation of Bulwer's petrel individuals may be responsible for the low survival rates of this seabird there compared to Vila and Cima, where nocturnal raptors are present but in lower numbers. Finally, in addition to the survival surveillence, some of the adults were also tracked with GLS for complementary migratory assesements. Although such devices may affect the fitness and survival of some avian predators (Costantini and Møller, 2013), a previous study on Bulwer's petrel showed no effect of logger deployment on subsequent adult survival (Ramos et al., 2015). Therefore, we are confident that our estimates of adult survival in Bulwer's petrel are accurate and unbiased by this secondary sampling.

4.2. Effect on survival of the SST at the breeding area

As expected, the most influential environmental variable on the survival of Bulwer's petrel was SST, at the breeding area and during the breeding season. In the closely related Audubon's shearwater (*Puffinus lherminieri*), a tropical and neritic species, others found a positive effect on survival of SST during the non-breeding season, most likely due to the relationship between the rise in SST and a higher discharge from the nearby rivers, which increases primary productivity and prey availability (Precheur et al., 2016). The difference in the exploitation of marine areas between Audubon's shearwater and Bulwer's petrel, the latter being strictly oceanic (Cruz-Flores et al., 2019), might explain why we did not find the same relationship (Table 2 and Fig. 2). Actually, this negative relationship between SST

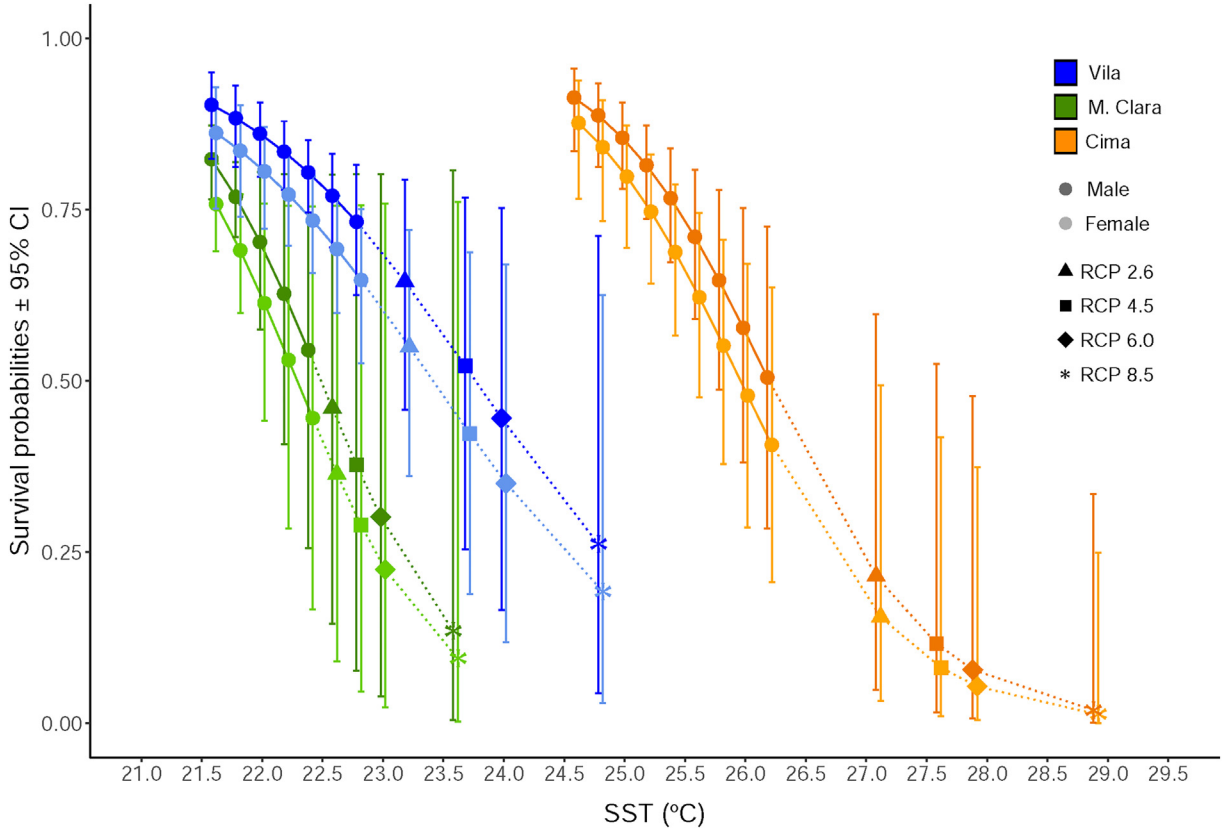


Fig. 2. Relationships between survival probabilities (± 95 % CI) and the Sea Surface Temperature (SST, °C) at the breeding areas for the Bulwer's petrels from Vila, M. Clara and Cima islets in blue, green and orange, respectively. Survival probabilities were inferred from the regression functions obtained from the best supported model (Table 2) for those SST values between the minimum and maximum values of the set of mean experienced SST during the breeding season and introduced in the best model as a covariate (Model 34 in Table 1, continuous lines). We inferred the survival for the SST values expected under different climate change scenarios (dashed lines and different symbols per scenario). To estimate 95 % CI values, we first calculated a set of survival probabilities using the equation $logit\Phi = intercept + slope * SST$, where pairs of intercepts and slopes for each sex and colony were generated randomly 10,000 times from a multivariate normal distribution using the intercepts and slopes for each sex and colony obtained from the best model (Model 34 in Table 1) as means, and their covariance-variance matrix. Finally, we calculated the 95 % CI values from the set of survival probabilities obtained for each SST value. Males and females are represented in dark and light colors, respectively.

Table 3
Survival probabilities (± SD) expected under each Representative Concentration Pathway (RCP) scenario per colony and sex, and mean SST value (± SD) expected at each colony. For comparison purposes, we added for each colony the experienced SST (for those years with CMR data and introduced into the model as a covariate) ± SD, and range.

Colony	Mean experienced SST ± SD (°C)	RCP scenarios	Mean expected SST ± SD (°C)	Sex	Survival ± SD
Vila	22.3 ± 0.5 (21.5–22.8)	RCP 2.6	23.2 ± 0.5	Males	0.65 ± 0.09
				Females	0.55 ± 0.09
		RCP 4.5	23.7 ± 0.5	Males	0.52 ± 0.13
				Females	0.42 ± 0.13
		RCP 6.0	24.0 ± 0.5	Males	0.45 ± 0.16
				Females	0.35 ± 0.15
		RCP 8.5	24.8 ± 0.5	Males	0.26 ± 0.18
				Females	0.19 ± 0.16
M. Clara	21.7 ± 0.3 (21.4–22.4)	RCP 2.6	22.6 ± 0.4	Males	0.46 ± 0.16
				Females	0.36 ± 0.16
		RCP 4.5	22.8 ± 0.4	Males	0.38 ± 0.18
				Females	0.29 ± 0.18
		RCP 6.0	23.0 ± 0.4	Males	0.30 ± 0.20
				Females	0.22 ± 0.18
		RCP 8.5	23.6 ± 0.5	Males	0.13 ± 0.21
				Females	0.09 ± 0.19
Cima	25.1 ± 0.6 (24.4–26.2)	RCP 2.6	27.1 ± 1.2	Males	0.22 ± 0.14
				Females	0.16 ± 0.12
		RCP 4.5	27.6 ± 1.2	Males	0.12 ± 0.13
				Females	0.08 ± 0.11
		RCP 6.0	27.9 ± 1.2	Males	0.08 ± 0.12
				Females	0.05 ± 0.10
		RCP 8.5	28.9 ± 1.3	Males	0.02 ± 0.10
				Females	0.01 ± 0.07

and survival found in Bulwer's petrel was reported for another seabird by Ramos et al. (2012), who found an indirect and delayed negative effect of SST through interactions within the food web. Similarly, our result is likely to be explained by prey availability during the breeding season, and is unlikely to reflect a direct effect of temperature per se on Bulwer's petrel survival. SST has been identified as the variable contributing the most to shaping the composition of the myctophid community in open waters (Olivar et al., 2016), a key prey taxon in the diet of Bulwer's petrel (Cruz-Flores et al., 2019; Neves et al., 2011; Waap et al., 2017) and whose distribution can vary depending on environmental conditions (Milligan and Sutton, 2020). Several studies have reported changes in fish community composition, abundance and distribution due to changes in sea temperature (Genner et al., 2004; Parker and Dixon, 1998; Perry et al., 2005), which can ultimately affect seabirds' fish intake (Thayer and Sydeman, 2007). Thus, although our study did not measure prey availability, we may expect that the cause of the decline in Bulwer's petrel survival when SST increases is due to a direct and negative effect on the availability of the seabirds' prey. However, the temporal variability explained by different models considering lag effects in SST during the breeding season, suggested that the SST effect can also be transmitted from the base of the local trophic chain up to Bulwer's petrels, as found by Ramos et al. (2012) in another seabird predator.

In contrast, the effect of SST in non-breeding areas was less relevant than the effect of the variable in the breeding areas. Since breeding individuals must behave as central place foragers, they are exposed to the environmental conditions around the colony. Procellariiform species show a strong breeding site fidelity, even under unfavorable conditions (Igual et al., 2007); thus, the breeding colonies of the Bulwer's petrels may remain unchanged once they are chosen, even when environmental conditions worsen. However, during the non-breeding season, when petrels are not attached to any specific breeding duty (i.e., incubating an egg or rearing a chick) and site, they may be more prone to change their foraging areas during the non-breeding period in response to unfavorable environmental conditions, or to change their diet (Phillips et al., 2017). In fact, during the non-breeding period, approximately half of the Bulwer's petrels from the Azores and the Canary Islands migrates to the South Atlantic, and the other half remains in the Central Atlantic with individuals from Cabo Verde (Ramos et al., 2015). Ramos et al. (2015) concluded that this particular migration pattern (known as "partial leapfrog migration") mirrors differences in habitat preference between northern and southern Bulwer's petrel populations, and differences in prey availability between the Central and South Atlantic. Although there is some evidence that individuals repeat the selection of their main non-breeding areas (i.e., they visit either the Central or the South Atlantic year after year), Cruz-Flores et al. (2019) found some differences on a smaller scale (e.g., individuals going further south in a given year, or spending more time in a stop-over area). Therefore, the interindividual differences in non-breeding areas, in comparison with the much more restricted area used by all individuals during the breeding season (see Fig. 1), may indeed dilute the effect of SST on survival during the non-breeding season.

Differential effect of SST on survival among breeding populations (less pronounced on Vila and more pronounced on M. Clara), may result from differences in population densities when interacting with specific environmental conditions (Portier et al., 1998). For example, a dramatic decline in survival of blue petrels (*Halobaena caerulea*) was observed at high population densities only when environmental conditions deteriorated (Barbraud and Weimerskirch, 2003). In line with these results, the increasement in SST affected Bulwer's petrels survival less severely in the Azores, where the small population size suggests a weak intraspecific competition for food resources. However, the Canary Islands and the Cabo Verde archipelago hold much larger populations than the Azores (Table A1 in Appendix A and Fig. 1). In addition, the Canary Islands are located very close to the Madeira and Salvages archipelagos, which hold the largest populations of Bulwer's petrel in Macaronesia (Table A1 in Appendix A). This may result in the strongest intraspecific competition in this area compared to any other location. Although interspecific competition for nesting places may occur in the Azores with Cory's shearwaters (*Calonectris borealis*; Bried and Bourgeois, 2005; Ramos et al., 1997), Bulwer's petrel does not compete actively for food resources with other seabird species due to its very specific oceanic behaviour (Cruz-Flores et al., 2019). Thus, we do not think interspecific competition for food resources could play a role in the differential effect of SST on survival between breeding populations.

Finally, other environmental variables apart from SST can affect Bulwer's petrel survival, such as wind speed. The effect of wind on seabirds demography was already reported, for instance, on the breeding performance of wandering albatrosses (*Diomedea exulans;* Weimerskirch et al., 2012), as well as on the survival of European shags during the non-breeding season (Frederiksen et al., 2008), both through a reduction in their foraging efficiency. However, in our case, although wind speed (during the breeding season at the breeding area) explains 38 % of the temporal variability of Bulwer's petrel survival, its effect is not as relevant as that of SST.

4.3. Bulwer's petrel under different climate change scenarios

Under the predictions of future climate change, Bulwer's petrel may experience a notable decrease in survival throughout its Atlantic distribution, especially for the tropical populations under less moderate scenarios of climate change. However, these results have to be interpreted with caution since the functional relationships found between survival and SST were extrapolated outside the observed historical range of SST values. In fact, these decreases in survival due to climate change could be mitigated if the species is able to overcome future challenges. To cope with reduction in prey availability due to an increase in SST, Bulwer's petrels might eventually switch their diet to new prey, or travel further and spend more energy when foraging, as it has been reported in little auks (*Alle alle*; Grémillet et al., 2012). Bulwer's petrels might also adjust their breeding phenology to match the period of highest prey abundance or shift their distribution to higher latitudes where environmental conditions are more suitable, as has been reported in many other species, including Procellariiformes (Chen et al., 2011). The latter phenomenon is possible during the non-breeding distribution, as reported for Balearic shearwaters (*Puffinus mauretanicus*) in the NE Atlantic (Luczak et al., 2011), but it is unlikely for the breeding distribution due to the high philopatry and extreme fidelity of adult Procellariiformes to their breeding colonies (Brooke, 2004; Coulson, 2016). Furthermore, in the case of the Atlantic, available breeding sites for Bulwer's petrels are very limited to a few oceanic archipelagos, and in the event that Bulwer's petrel could establish new populations, the redistribution of the species could lead to new biotic interactions (Poloczanska et al., 2016). Finally, this petrel might also compensate for decreases in survival through changes in other life-history traits, such as reproduction, as has been reported in other seabird species (Nevoux et al., 2010).

5. Conclusions

The pessimistic future scenario we have set out for Bulwer's petrel may apply to other oceanic species with similar requirements and distributions. This study highlights the potentially devastating impact of climate change also on tropical to temperate top predators, an issue that it is often overlooked. It also stresses the importance of considering multi-population approaches when evaluating climate impacts of this kind.

CRediT authorship contribution statement

MCF led the fieldwork in the Canary Islands, conceived the study, contributed to the design of the methods, analyzed the data and wrote first drafts of the publication; RP designed the methods; JB and VN led fieldwork and acquired scientific permits and funding in the Azores; TM led fieldwork in Cabo Verde; JGS conceived the study, acquired scientific permits and funding in the Canary Islands and in Cabo Verde; and RR conceived the

study and contributed to the design of the methods. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data accessibility

CMR data (including colony and sex codes) are accessible through the repository of the University of Barcelona: https://doi.org/10.34810/data220. Geolocation data are available at the Seabird Tracking Database (http://www.seabirdtracking.org/).

Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.157352.

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