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Special Section:
Midlatitude Marine Heatwaves: Forcing and Impacts

Key Points:

- During the winter of 2014/2015, over 9,000 (>100 x normal) dead Cassin's Auklets were observed on beaches from California to British Columbia
- The die-off was ultimately caused by a reduction in zooplankton prey energy content as a result of the NE Pacific marine heatwave (MHW)
- The NE Pacific MHW likely inflated event magnitude by compressing cold-water habitat, and by proxy live birds, closer to shore than usual

Supporting Information:

- Supporting Information S1

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Massive Mortality of a Planktivorous Seabird in Response to a Marine Heatwave

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Abstract Climate change has exacerbated the occurrence of large-scale sea surface temperature anomalies, or marine heatwaves (MHWs)—extreme phenomena often associated with mass mortality events of marine organisms. Using a combination of citizen science and federal data sets, we investigated the causal mechanisms of the 2014/2015 die-off of Cassin's Auklets (*Ptychoramphus aleuticus*), a small zooplanktivorous seabird, during the NE Pacific MHW of 2013–2015. Carcass deposition followed an effective reduction in the energy content of mesozooplankton, coincident with the loss of cold-water foraging habitat caused by the intrusion of the NE Pacific MHW into the nearshore environment. Models examining interannual variability in effort-controlled carcass abundance (2001–2014) identified the biomass of lipid-poor zooplankton as the dominant predictor of increased carcass abundance. In 2014, Cassin's Auklets dispersing from colonies in British Columbia likely congregated into a nearshore band of cooler upwelled water and ultimately died from starvation following the shift in zooplankton composition associated with onshore transport of the NE Pacific MHW. For Cassin's Auklets, already in decline due to ocean warming, large-scale and persistent MHWs might represent a global population precipice.

Plain Language Summary During the winter of 2014/2015, thousands of Cassin's Auklets, a small seabird that breeds in the NE Pacific, were found dead on beaches from California to British Columbia, Canada. We show that wide-scale starvation was due to a change in food quality associated with warmer ocean temperatures preceding and during the die-off. This research highlights that more frequent and intense ocean warming events may have complex impacts on food webs with population consequences for marine predators, particularly seabirds such as Cassin's Auklets.

1. Introduction

Climate warming has been associated with an increase in extreme events, including several large-scale and persistent sea surface temperature (SST) anomalies, or marine heatwaves (MHW) (Bond et al., 2015; Chen et al., 2015; Hobday et al., 2016; Pearce & Feng, 2013; Scannell et al., 2016). The NE Pacific MHW became prominent in the Gulf of Alaska during the winter of 2013–2014 as a consequence of weak upper-ocean cooling (Bond et al., 2015; Di Lorenzo & Mantua, 2016). Positive SST anomalies persisted through 2014, becoming especially large by early 2015 along the west coast of North Americawith peak SST anomalies >3.5 °C above the 1981–2010 climatology (Bond et al., 2015). Collectively, this ranks the NE Pacific MHW as the largest on record (Di Lorenzo & Mantua, 2016). Documented ecological impacts include a northward shift in distribution of several marine species (Goddard et al., 2016), harmful algal blooms extending from California to Alaska

(McCabe et al., 2016), reduced ocean productivity (Whitney, 2015), and unusual mortality events of marine mammals (Di Lorenzo & Mantua, 2016).

From October 2014 through to March 2015, Cassin's Auklet (*Ptychoramphus aleuticus*) carcasses were observed in abnormally high numbers on beaches from central California through to British Columbia (BC) (Bond et al., 2015). Cassin's Auklets are small (mass: 150–200 g) zooplanktivorous seabirds that forage for copepods, euphausiids, and larval fish (Hipfner, 2009). Breeding in dense colonies from Mexico to Alaska, 60% of the global population (~3.3×10^6 breeding individuals) nest on the Scott Islands off the northwest tip of Vancouver Island, Canada, including the largest colony in the world (~1,095,000) on Triangle Island (50.86°N, 129.08°W) (Ainley et al., 2011). Postbreeding, the majority of birds from this population disperse south into the California Current Large Marine Ecosystem (Ainley et al., 2009). Cassin's Auklets have previously been identified as an indicator species of the effects of ocean warming on marine ecosystems (Wolf et al., 2009, 2010), and in recent decades breeding populations have declined due to changes in prey availability and phenology associated with climate variability (Lee et al., 2007; Morrison et al., 2011).

In this study we describe the extent, duration, and magnitude of carcass deposition during the 2014/2015 mass mortality event (MME) of Cassin's Auklets and test four nonexclusive hypotheses regarding the causal mechanism of this event: *Food quality/quantity*—higher abundance of energy-dense prey increases survival and/or higher abundance of low-energy prey increases mortality (Keister et al., 2011). *Habitat compression*—smaller areal extent of cold water on the continental shelf equates to foraging habitat compression, potentially increasing mortality due to intraspecific competition. *Storminess*—storm exposure leads to increased physiological stress and/or decreased foraging ability, elevating mortality (Fort et al., 2009). *Colony production*—higher production of hatch-year birds absolutely increases carcass numbers via postbreeding juvenile mortality (Ydenberg, 1989). Separately, we also hypothesize that altered spatial distribution, specifically nearshore aggregation of birds, may have exaggerated mortality-event magnitude through an increase in proportional carcass deposition. Our results suggest that large-scale shifts in shelf ecosystem composition associated with the NE Pacific MHW provoked both behavioral and nutritional responses in these birds that ultimately resulted in mass mortality.

2. Methods

2.1. Beached Bird Surveys

We used beached bird survey data collected by participants in three citizen science programs: COASST (39.19–48.34°N), BeachWatch (37.11–38.96°N), and BeachCOMBERS (35.32–37.19°N). All programs employed effort-standardized (beach length) monthly or more frequent surveys. Each carcass encountered was marked to avoid double counting and identified to species by morphology, morphometric measurements, and plumage characteristics.

The extent and duration of the mortality event were determined by calculating the month-averaged encounter rate (ER—birds per kilometer of beach surveyed) of Cassin's Auklet carcasses for all surveys performed between September 2014 and March 2015 within 1° latitudinal bands ($N = 14$, 34.4°N to 48.4°N) of coastline. Expected carcass ER (month-specific baseline or "climatology") was calculated by applying the same procedure to each prior year of data (2001–2013, except southern Oregon: 2004–2013 and northern California: 2006–2013), and then averaging across years.

2.2. Temperature Anomalies

Given that Cassin's Auklets forage predominantly in cold water (Wolf et al., 2010), we obtained daily SST anomaly (SSTa—anomalies relative to the 1971–2000 climatological mean; Reynolds et al., 2007) maps from the National Oceanic and Atmospheric Administration OI V2 high-resolution data repository (latitude: 36–60°N, longitude: coast to 147°W, resolution: 0.25°) to examine the spatial distribution of cold-water habitat. To identify the temporal availability of cold-water habitat, we calculated the proportional ocean area from the coast to 100 km offshore with SSTa within 1 °C bands from −4 °C to 4 °C for each day from May 2014 to May 2015. This was performed for the coastline from Cape Blanco (42.837°N, 124.566°W) to Cape Flattery (48.382°N, 124.732°W), the range of coastline within which ~85% of carcass-fall was recorded.

2.3. Zooplankton Composition

Monthly time series of mesozooplankton composition were used to proxy the quality and availability of prey in the northern California Current Large Marine Ecosystem: copepod biomass anomalies measured at Newport

(44.625°N, 124.125°W; Hooff & Peterson, 2006), and the mean size of adult Euphausiids (*Euphausia pacifica* and *Thysanoessa spinifera*) measured at Trinidad Head (41.125°N, 124.125°W; Bjorkstedt & Peterson, 2015). Copepod samples were processed to measure the biomass of northern and southern assemblage copepods, here expressed as the anomaly relative to the month-specific average (Hooff & Peterson, 2006; Keister et al., 2011). The northern copepod assemblage consists of cold-water species that are larger and richer in lipids, and therefore represent higher quality prey than copepods comprising the southern assemblage (Peterson et al., 2014).

2.4. At-Sea Spatial Distribution

To examine the spatial distribution of Cassin's Auklets in 2014, we used at-sea survey data of seabird density in October–December (the observed MME time window) collected by the National Oceanic and Atmospheric Administration. Strip-transect-based seabird surveys were performed off the coast of California to Washington in 2001, 2005, 2008, and 2014 (Figure S1) (for more details see Ballance, 2007). Generalized additive models (counts modeled according to a negative binomial distribution; Wood, 2011) were fitted to these data to estimate the density of Cassin's Auklets as a nonlinear function of distance from shore. Due to temporal constraints, this analysis excluded sampling north of 39.4°N, which in 2014 was conducted from August to September (Figure S1). Models included an offset for transect area to account for differential survey effort, and a fixed term of year to account for differences in overall density among years. Alternate models were trialed to test whether fitted relationships were the same or different among years, and then ranked according to small-sample-size corrected Akaike information criterion (AICc).

2.5. Mechanistic Models

To explore the factors that may influence Cassin's Auklet mortality and/or carcass deposition, we created annual indices (2001–2014) of the winter (November to February; ~95% of Cassin's Auklet deposition in 2014/2015) abundance of Cassin's Auklet carcasses, standardized for survey effort. Annual indices were calculated as the average across beach-specific ER (November to February surveys for beaches from 42 to 48.4°N) for each year. To test our hypotheses, we created annual indices representative of each forcing factor.

Annual indices of food quantity and quality were created from 4 month (the time window of our response variable) averages of southern and northern copepod biomass anomalies (section 2.3). As food supply effects precede mortality, alternate indices were calculated for four temporal lags: three months' prior (e.g., August–November), two months' (September–December), one month (October–January), and no lag (November–February).

Annual habitat compression indices were calculated as the average proportional area from the coast to 200 km offshore where SSTa >1 °C (from daily SSTa maps; section 2.2). Alternate indices were created by averaging across different spatiotemporal windows corresponding to the approximate distribution of Cassin's Auklets breeding in BC during three life-history stages: (1) *breeding* (March–June) birds foraging close to colonies (48 to 52 °N), (2) *postbreeding* (August–October) southward dispersal (42–52°N), and (3) *overwintering* (November–February) birds foraging at lower latitudes (42–48°N).

Storm indices were calculated from significant wave height (H_{sig}) recorded at three National Data Buoy Center stations (46041: 47.353°N, 124.731°W; 46029: 46.159°N, 124.514°W; and 46050: 44.656°N, 124.526°W) for the months of November to February. Three indices were created: (1) average H_{sig}, (2) proportion of time that $H_{\text{sig}} \geq 4$ m, and (3) number of "storm events," where an event was defined as $H_{\text{sig}} \geq 4$m for $\geq$6 consecutive hours. Station-specific indices were calculated and then averaged to create a regional measure.

Because direct measures of overall colony output were not available, colony production was proxied by the 25 day chick-mass anomaly on Triangle Island, BC. Chick mass at 25 days provides a good measure of the conditions during the provisioning period (Hedd et al., 2002), and therefore proxies overall colony production (Hipfner et al., 2010).

We used generalized linear models on log-transformed annual ER to identify which factors best described relative Cassin's Auklet carcass abundance. Because we calculated multiple indices for each forcing factor (e.g., alternate copepod lags), we trialed predictors within forcing factor groups against each other. Northern and southern copepod biomass indices were allowed in the same model as these represent two different hypotheses: the influence of high-quality food (northern copepods) versus the influence of poor-quality food (southern copepods). Candidate predictor sets (n = 36) were generated by selecting a single

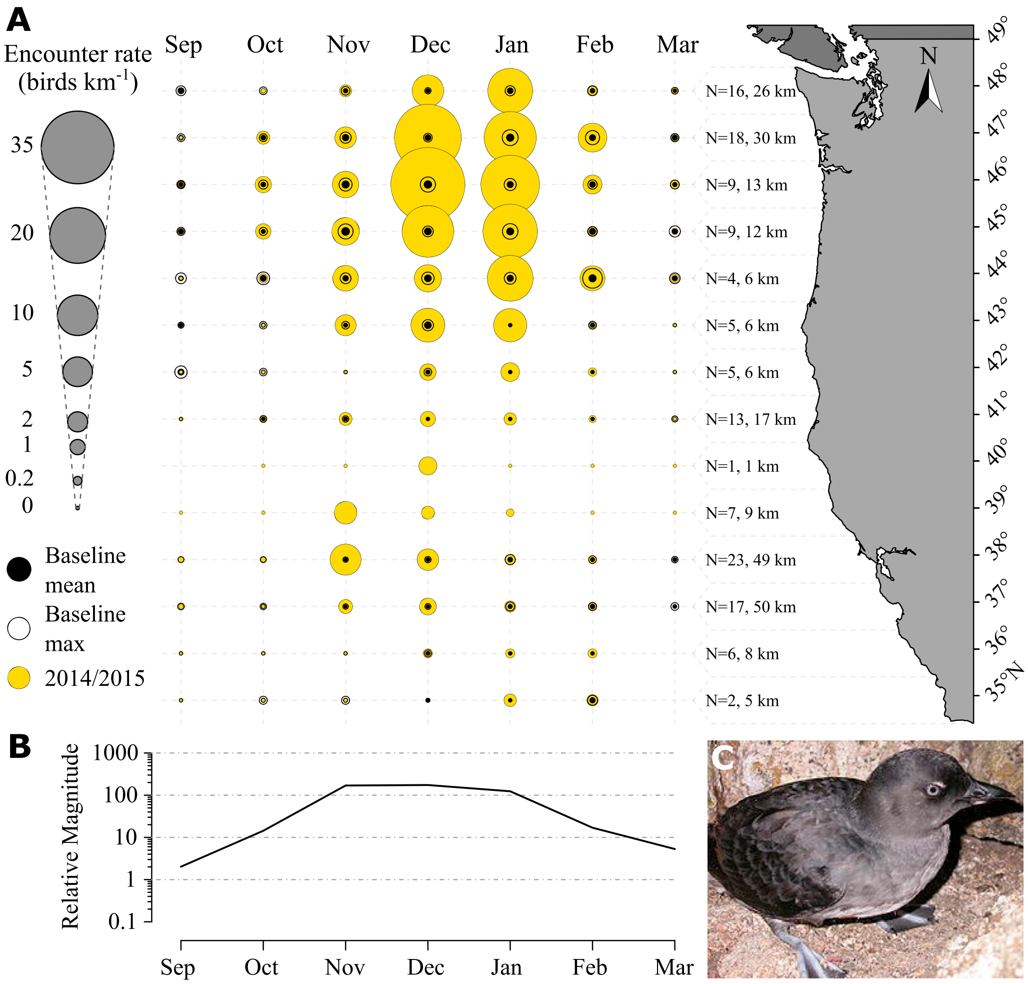

Figure 1. (a) Carcass encounter rate (ER; carcasses km^{-1}) averaged into month by 1° latitudinal bands, with years prior to 2014 (6–13 years, location dependent) defined as baseline. Survey coverage in 2014/2015 is indicated by median (across months) number of beaches (N) and cumulative beach-length (km) surveyed. (b) Mean magnitude of 2014/2015 observations (2014/15 ER divided by baseline ER) across latitudinal bands. (c) Cassin's Auklet, courtesy of Duncan Wright.

index for each forcing factor, and for each set, all possible combinations of predictors and two-way interactions were fitted. The best predictor set was defined as the one with the lowest Akaike weight, $w = e^{-\Delta_{\text{AICc}}/2}$, summed across the top-20 models, as well as containing the model with the overall lowest AICc. This procedure was carried out with data from all years, and also with 2014 excluded to examine whether relationships persisted upon the removal of this influential data point. Model Akaike weight and coefficient of determination, R^2, are presented as measures of model confidence and explanatory power, respectively. Predictor importance was represented as the summed Akaike weight of models in which that predictor appeared ($\sum w$), with model-averaged regression coefficients $\overline{\beta} = \sum_i w_i \widehat{\beta}_i / \sum_i w_i$ ($\widehat{\beta}_i$ = model-specific coefficient estimate) included to represent relationship strength and direction. All analyses were performed in R version 3.4.0 (R Core Team, 2017), and a more detailed discussion of all methods can be found in the supporting information (Barth et al., 2007; Pinheiro et al., 2017; Pyle, 2009; Rose, 1981; Schwing et al., 2006; Spear et al., 1992; Speich & Manuwal, 1974; Tasker et al., 1984).

3. Results

3.1. Event Description

Starting in October 2014, Cassin's Auklet carcasses were observed at higher than average numbers from central California through northern Washington, in two distinct spatial clusters. In central California, carcass ER

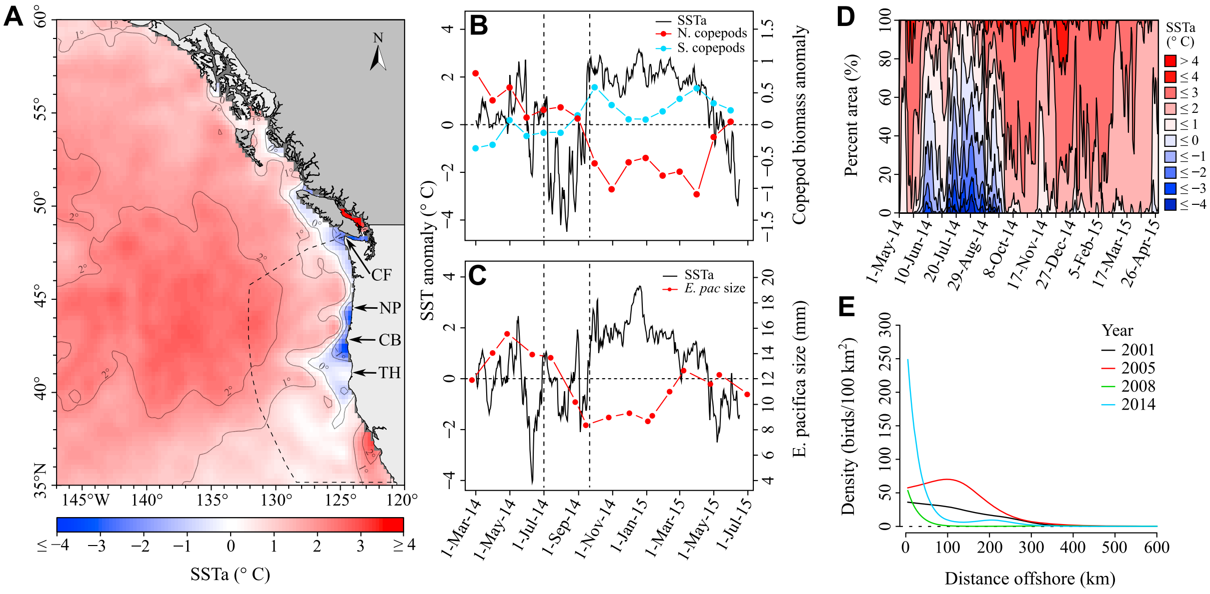

Figure 2. (a) Spatial distribution of sea surface temperature anomaly (SSTa) averaged from July through to the end of September. The dashed polygon shows the area surveyed during NOAA seabird surveys. CF: Cape Flattery, NP: Newport, CB: Cape Blanco, TH: Trinidad Head. Time series of SSTa and measures of prey availability: (b) Copepod biomass anomalies ($\log_{10}$ scale) measured at Newport and (c) *Euphausia pacifica* mean size measured at Trinidad Head. (d) Proportional temperature anomaly extent by area (≤100 km offshore, Cape Flattery, to Cape Blanco) through time. (e) Fitted densities (generalized additive model) of Cassin's Auklets as a function of distance from shore based on NOAA at-sea surveys performed in October–December of 2001, 2005, 2008, and 2014.

peaked in November with a spatial maximum (per 1° band) of 5.6 birds km^{-1} at the Gulf of the Farallones (1,000 × baseline rate), with anomalously high rates through to January (Figure 1). Central California carcasses were dominated by hatch-year birds (76%; Table S1). Given the timing and proximity to the Farallon Islands breeding colonies, it is likely that this event was primarily fledglings from California populations.

Carcass counts in Oregon and Washington began to increase in October. In mid-December, thousands of carcasses were deposited over a short period of time throughout this region, with ER peaking at >20 birds km^{-1} for the areas adjacent to the Columbia River (200–400 × baseline; Figure 1). Carcasses were observed in high numbers throughout Oregon and Washington through January (ER > 10 birds km^{-1}, 100–200 × baseline), with ER decreasing to <5 × baseline rates by March (Figure 1). December carcasses collected in BC were dominated by adults (70%), with relatively fewer hatch-year birds (13%; Table S1). Given the magnitude, spatiotemporal profile, and age composition, it is likely that this event was predominantly birds dispersing southward from breeding colonies in BC. By April 2015, 9,148 carcasses had been recorded across 407 km of surveyed beaches, with deposition in Oregon and Washington accounting for 86% of the total (Table S2).

3.2. Temperature Anomalies and Zooplankton Composition

Despite the predominance of anomalously warm surface water throughout the northeast Pacific in 2014, the nearshore environment was anomalously cool from mid-May to mid-September (Figures 2a–2d). Averaged over the July–September period, 80% of this cold-water band (SSTa ≤ 0 °C) was <100 km offshore (Figure 2a). After the fall transition in mid-September, nearshore surface waters from Vancouver Island to northern California became anomalously warm indicating the introgression of the NE Pacific MHW (Figures 2b–2d and S3). By contrast, in central California (38.00°N to 36.28°N), the cold-water refuge was less prominent and persisted only until mid-July (Figure S4).

Prior to the fall transition, waters off Newport featured higher than normal biomass of northern assemblage copepods (Figure 2b). Favorable prey conditions were also evidenced by higher than normal chick weights on Triangle Island (Figure S5). After the transition, biomass of southern copepods increased dramatically off of Newport, concurrent with a decrease in biomass of northern assemblage copepods (Figure 2b) and reductions in the average size of adult euphausiids (Figures 2c and S6) recorded off Trinidad Head (see also McClatchie et al., 2016). These observations suggest that the introgression of the NE Pacific MHW water mass

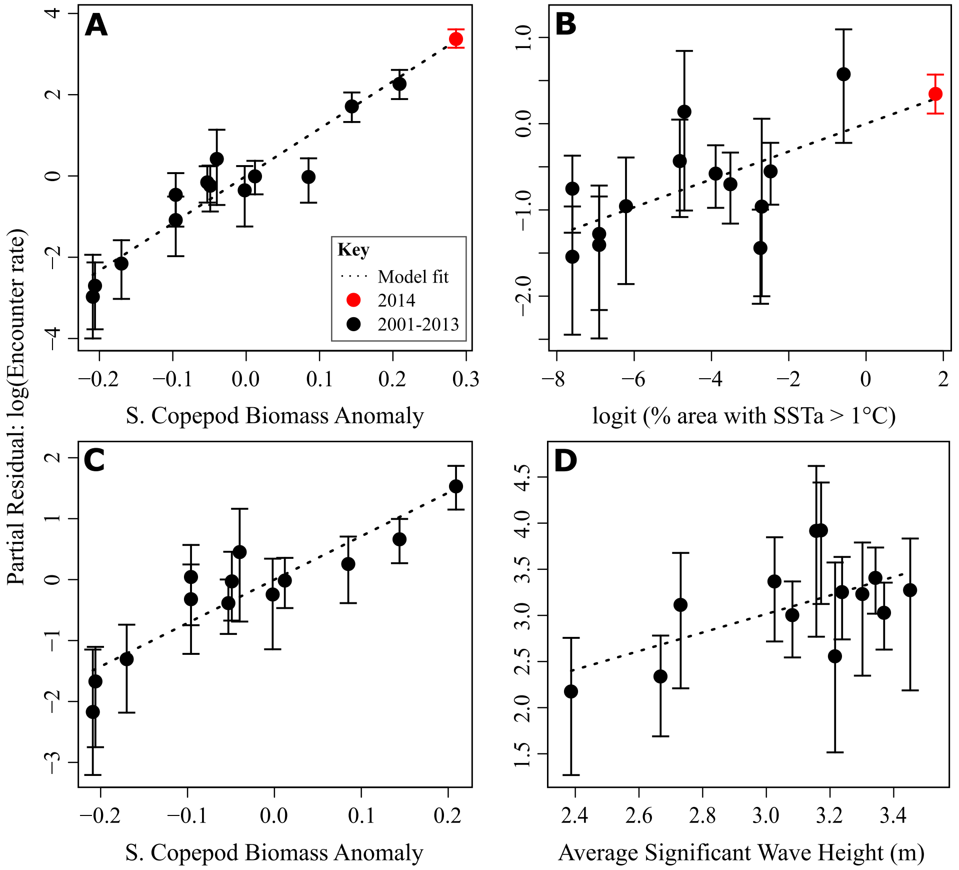

Figure 3. Annual average encounter rate (± 95% CI; November–February) plotted against bio-physical predictors contained within the best model (based on AICc) of an ensemble of generalized linear models, (a and b) with and (c and d) without 2014. (a and c) Average southern copepod biomass anomaly measured along the Newport Line (44.6°N) and lagged two months (i.e., September–December). (b) Habitat compression index: the logit-transformed proportion of ocean area with SSTa >1 °C averaged over November–February within the nearshore wintering area of Cassin's Auklets dispersing from British Columbia (42–48°N, ≤200 km from shore). (d) Storminess: mean significant wave height from November–February.

effectively reduced the energy content of mesozooplankton in the nearshore environment, prey conditions which then persisted over several months (Figures 2b and 2c).

3.3. At-Sea Spatial Distribution

The year-specific model of Cassin's Auklet density resulted in a lower AICc (AICc = 2979.6) than the static distribution model (AICc = 3038.3), indicating variable distributions among years. The best model indicated that more birds were adjacent to shore in 2014 (October to December) than any other surveyed year, with ~85% of birds (by density) within 100 km (Figure 2e). Given at-sea survey coverage in 2014 (Figure S1), it is unknown whether this pattern prevailed north of 39.4°N.

3.4. Mechanistic Models of Increased Carcass Abundance

The best models of effort-standardized carcass abundance (ER) included copepod indices lagged by two months, habitat compression during winter, and average significant wave height (Table S3). The best model for annual ER included positive relationships with habitat compression indices and southern copepod biomass anomaly (Figures 3a and 3b) as well as the interaction between these factors ($w_{\mathrm{AICc}} = 0.65$, $R^2 = 0.93$; Table 1). Northern copepod biomass anomaly, significant wave height, and colony production were not strong predictors, as indicated by low Akaike weights (Table 1). Excluding 2014, habitat compression dropped from the best model, likely because this variable predominated only in 2014. However, southern copepod biomass anomaly was retained as a strong positive predictor of ER (Figure 3c and Table S4). The best model also included average significant wave height as a positive term ($w_{\mathrm{AICc}} = 0.27$, $R^2 = 0.80$; Table S4) indicating that storms play a role in regulating Cassin's Auklet mortality and/or carcass deposition.

Table 1

Regression Coefficients, Model, and Parameter Statistics for the Top-10 Generalized Linear Models, Based on AICc, Fitted to Annual Cassin's Auklet Carcass Encounter Rates (2001–2014)

Model rank	Regression coefficients, $\hat{\beta}$										Model statistics			
	(intercept)	Colony.25d	Hs.ave	N.cope.l2	SSTa1. Winter	S.cope.l2	Hs.ave.:SSTa1. Winter	Hs.ave:S. cope.l2	N.cope.l2:S. cope.l2	SSTa1.Winter:S. cope.l2	AICc	Δ_{AICc}	w	R^2
1	−2.0				0.16	11.6				1.34	33.8	0.0	0.65	0.93
2	−2.0			1.01	0.19	12.7				1.47	37.0	3.2	0.14	0.94
3	−2.0	−0.01			0.16	11.9				1.45	38.4	4.6	0.06	0.93
4	−3.2		0.37		0.15	12.1				1.38	39.3	5.5	0.04	0.93
5	−2.7			0.04		8.9			−14.8		40.3	6.5	0.03	0.89
6	−4.9		0.77			49.6		−12.7			40.8	7.0	0.02	0.88
7	−1.5				0.20	8.6					42.6	8.8	0.01	0.83
8	−5.4		0.87	−0.38		9.0			−15.9		43.4	9.6	0.01	0.90
9	5.6		−2.51		1.66	8.1	−0.52				43.5	9.7	0.01	0.90
10	−2.3					11.0					43.7	9.9	0.00	0.77
Parameter statistics														
$\sum w$		0.08	0.09	0.19	0.93	1.00	0.01	0.03	0.04	0.91				
$\bar{\beta}$		−0.00	0.03	0.22	0.16	12.60	−0.00	−0.31	−0.62	1.24				

Note. Model statistics include AICc, $\Delta_{\text{AICc}} = \text{AICc} - \min(\text{AICc})$, model Akaike weight, *w*, and R^2. Parameter statistics include summed Akaike weight of all models featuring that parameter ($\sum w$), and model-averaged regression coefficients ($\bar{\beta} = \sum_i w_i \hat{\beta}_i / \sum_i w_i$).

4. Discussion

Our results suggest that the Cassin's Auklet MME of 2014/2015 occurred as a consequence of changes in prey abundance and quality during the NE Pacific MHW. Furthermore, coastward compression of cold-water habitat likely exaggerated the perceived magnitude of the MME by driving birds closer to shore, increasing the probability of carcass beaching,

4.1. Mortality Event Mechanism

Of the four hypotheses we examined, we found evidence for effects of food quality, habitat compression, and storminess on annual measures of carcass abundance. Northern copepod biomass anomaly, our proxy for positive prey conditions, was not a strong predictor of beaching rates. By contrast, the southern copepod biomass anomaly accounted for 70–77% of interannual variance in carcass ER (Tables 1 and S4), suggesting that this index proxies a decrease in Cassin's Auklet prey quality and/or availability. Lower energy content and/or smaller prey may have served as "junk food" (Österblom et al., 2008; Rosen & Trites, 2000; Wanless et al., 2005), which for small-bodied pursuit divers, such as Cassin's Auklets, may be particularly detrimental given their energetically expensive mode of feeding (Romano et al., 2006).

The change in zooplankton composition preceded the peak in mortality in 2014/2015 (mid-December off the coast of Washington and Oregon) by two months, suggesting additional mechanisms responsible for increased mortality. The interactive effects of diminished food supply and storms have been implicated in previous seabird MMEs (Harris & Wanless, 1996; Ryan et al., 1989), and our models excluding 2014 support that storms regulate Cassin's Auklet mortality. The ability to meet increased energetic demands brought on by winter conditions and/or survive extended periods of diminished foraging success during storm events (Camphuysen et al., 1999; Schreiber, 2001) point to early winter (November–December) as a survival bottleneck for marine birds (Fort et al., 2009). Our 2014 data are consistent with this scenario as the onset of carcass deposition coincided with stronger winds in late October (Figure S8). Furthermore, the mid-December peak in carcass deposition followed four consecutive days (8–11 December) of north to north-northwest bearing winds in excess of 35 km hr^{-1} (Figure S9). Storms of this magnitude or greater are a common feature of winters in the NE Pacific (Table S6), but only precipitated mass mortality in 2014. This suggests that although diminished food quality associated with the NE Pacific MHW was the ultimate cause of mortality, storms were the proximal factor leading to both mortality and deposition.

At its peak, relative carcass abundance was more than 100 times baseline (Figure 1b), implying that increased mortality alone could not have accounted for the observed rate of carcass deposition. The likelihood of carcass deposition is dependent on the proximity to shore of moribund birds, and on-shore flow (Wiese, 2003). We believe that the largest single factor influencing beached carcass abundance during the Cassin's Auklet MME was altered spatial distribution of live birds. Cassin's Auklets forage predominantly in cold surface waters (Wolf et al., 2010), a habitat that was constricted to a narrow nearshore band during the postbreeding season of 2014 (Figure 2a). We posit that auklets dispersing south from colonies in BC crowded into the nearshore environment. When this cold-water refuge collapsed in mid-September (Figures 2b–2d), birds were left with no suitable foraging habitat (Figures 2d and S3), and likely did not disperse out of the nearshore, significantly increasing the likelihood of carcass deposition following mortality-inducing conditions (Wiese, 2003). This dynamic highlights the need for careful assessment of seabird MMEs, as changes in distribution may be equally as important as increased mortality in explaining elevated counts of beached seabirds.

Exclusion of colony production as an explanatory variable suggests that strong reproductive success does not necessarily translate to increased carcass abundance even given absolutely higher juvenile mortality (Ydenberg, 1989). To the south of our modeling region (e.g., central California), carcass deposition primarily consisted of hatch-year birds (Table S1). The earlier reduction in cold-water habitat/prey quality in central California (Figure S4) may have resulted in the earlier peak in carcass deposition and disproportionately affected fledglings relative to the northern events where fewer fledglings were recorded (Table S1).

4.2. Global Warming, Extremes, and Ecological Impacts

Although many studies have focused on the long-term ecological implications of climate change (Bellard et al., 2012; Garcia et al., 2014), our understanding of extreme temperature events and their impact on ecosystems is less well understood (Wernberg et al., 2012). Several MHWs of unprecedented scale have been observed in recent history (Hobday et al., 2016), including events in the Northern Mediterranean (2003; Garrabou et al., 2009), offshore of Western Australia (2011; Pearce & Feng, 2013; Wernberg et al., 2013), and in the NW Atlantic (2012; Scannell et al., 2016). In each case, there were significant and abrupt changes to the marine ecosystem, from benthic primary producers to top predators (Di Lorenzo & Mantua, 2016; Garrabou et al., 2009; Marba & Duarte, 2010). Our study adds marine birds to this list and provides a mechanistic explanation of increased mortality. Finally, this study highlights the importance of rigorous, broad-scale citizen science data in documenting these ecosystem responses, as these data are otherwise unobtainable across these temporal and spatial scales (Theobald et al., 2015).

As the world's oceans continue to warm it is likely that large-scale temperature anomalies will increase in frequency, magnitude, and duration (Di Lorenzo & Mantua, 2016; Hobday et al., 2016; Scannell et al., 2016), raising the likelihood of more frequent MMEs (e.g., Fey et al., 2015) and correspondingly rapid changes to marine ecosystem structure and functionality (Wernberg et al., 2013). Breeding populations of Cassin's Auklets have declined significantly in recent decades (Lee et al., 2007; Morrison et al., 2011), with studies implicating lower reproductive success and lower survival during warm water years (Bertram et al., 2005; Wolf et al., 2009, 2010). Furthermore, burrow occupancy rates on Triangle Island (a proxy for breeding population size; Rodway & Lemon, 2011) declined by 15% between 2014 (78.4%) and 2015 (65.5%; Table S7), indicative of a population-level effect of this MME and that population viability may be seriously impacted should the incidence and intensity of warming events increase. Thus for Cassin's Auklets, MHWs of the scale of the NE Pacific event may well represent a global population precipice.

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