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TIME LAGS ASSOCIATED WITH EFFECTS OF OCEANIC CONDITIONS ON SEABIRD BREEDING IN THE SALISH SEA REGION OF THE NORTHERN CALIFORNIA CURRENT SYSTEM

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ABSTRACT

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The effect of sea surface temperature (SST), as a proxy for more general oceanic conditions, on seabird reproduction includes a time lag. In this short communication, we use model-selection techniques to determine the time of year SST should be measured in the Salish Sea in order to best explain the variability in reproductive success the following breeding season at a Glaucous-winged Gull *Larus glaucescens* colony on Protection Island, Washington State, US. Average SST values computed from September and October before the breeding season were the best predictors of egg cannibalism and hatching success.

Key words: egg cannibalism, El Niño, Glaucous-winged Gull, hatching success, ocean warming, sea surface temperature

INTRODUCTION

Changes in sea surface temperature (SST), as an indicator of marine climate, can correlate with altered feeding behaviors and reproduction in seabirds (Murphy 1936; Ainley 1994; Ainley *et al.* 1994, 1995; Sydeman *et al.* 2015), including Glaucous-winged Gulls *Larus glaucescens* (Hipfner 2012, Hayward *et al.* 2014). SSTs have increased in many areas and, in particular, in the North American Pacific Northwest, where they have risen approximately 1 °C in the last few decades (Strom *et al.* 2004, Irvine & Crawford 2011). Increases in SST, especially in upwelling systems, can represent greater stratification of the water column, leading to a deeper thermocline and lower plankton levels, and often creating food deficits for marine birds (Barber & Chavez 1983, Schreiber & Schreiber 1984, McGowan *et al.* 1998, Stenseth *et al.* 2002). Decreases in SST, and associated lessened or shallower stratification, usually have the opposite result (e.g., Ainley *et al.* 1995, and references therein).

Glaucous-winged Gulls, which breed along the Pacific coast of the US and Canada from Oregon to Alaska, can be considered sentinels of certain environmental changes (Blight 2011, Kershner *et al.* 2011, Irvine & Crawford 2013). Hayward *et al*. (2014) demonstrated that increases in SST due to El Niño were associated with decreases in hatching success and increases in egg cannibalism among Glaucous-winged Gulls at Protection Island, Washington State's largest seabird colony in the Salish Sea. The Salish Sea, which consists of the marine waters of northwestern Washington State and southwestern British Columbia to the south and east of Vancouver Island, is influenced by factors in the adjacent Pacific Ocean. For example, changes in the strength of winds associated with coastal upwelling alter intrusions of deep coastal water into the Salish Sea; the intrusions, in turn, alter oxygen concentration, acidity, and temperature (Irvine & Crawford 2013).

For 2006–2011 data from the Protection Island gull colony, an increase of 0.1 °C in SST corresponded to a 10% decrease in the odds that an egg hatched and a 10% increase in the odds that an egg was cannibalized (Hayward *et al.* 2014). The measurement of SST chosen was the average of hourly SST measurements recorded by the nearby Port Townsend, Washington, buoy from 1 September to 31 May, which is generally the period between fledging in the previous breeding season and the beginning of egg laying in the current breeding season. A time lag was built into this measurement because the reproductive success of gulls, as capital breeders, depends on resource availability before egg production (Hodder & Graybill 1985, Boersma 1998, Blight 2011) and because the effects of a change in SST require time to propagate through the food web (Walther *et al.* 2002, Grémillet & Boulinier 2009). Such a time lag, however, may vary from days to decades (Boersma 1998), depending on the system. The appropriate time lag was unknown for waters around Protection Island, and the interval from 1 September to 31 May selected by Hayward *et al*. (2014) was their best estimate from information available at the time.

In this paper, we revisit the Protection Island study by systematically testing a variety of time intervals to determine which interval provides the best measurement of average SST as a predictor for hatching success and egg cannibalism.

METHODS

We used the data on hatching success and egg cannibalism from the Hayward *et al*. (2014) study, which were collected from May to July 2006–2011 at a large Glaucous-winged Gull breeding colony on Violet Point, Protection Island, located at the east end of the Strait of Juan de Fuca, Salish Sea (48°07′40″N, 122°55′3″W). We downloaded hourly SST data for 2005–2011 from the National

Oceanographic and Atmospheric Administration's (NOAA's) Port Townsend, Washington, buoy, located 12 km east of the breeding colony. We linearly interpolated the values of missing hourly SST entries based on preceding and subsequent values, and we averaged the resulting hourly entries for selected time intervals for each year. For each time interval for each year, <4.4% of the hourly data points were missing and had to be interpolated, leading to changes of <0.43% in the average SST calculations. This suggests that interpolation is not necessary if only a few hourly values are missing; however, in this paper we used interpolation for all missing values. The alternative time intervals created alternative measures of average SST that could be tested to determine the best predictor.

We used validated logistic regression models for egg cannibalism and hatching success obtained in Hayward *et al*. (2014; see p. 68 under "Model-Performance Analysis"). These models included the factors SST, nearest neighbor distance (NN), number of days before or after the mean laying date for the season (DAYS), total number of eggs laid in the nest (CSIZE), sample area of the colony (PLOT), and habitat type (HAB). Each model had the form

$$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \sum_{j=1}^{n} \beta_j x_j + \sum_{k=1}^{2} \beta_{n+1,k} D_k + \sum_{k=1}^{2}\sum_{j=1}^{n} \beta_{jk} x_j D_k \quad (1)$$

in which p is the probability of an egg being cannibalized (or, for the hatching success model, the probability that an egg hatches). For the cannibalism model, $n = 3$ with factors

$$\mathbf{x} = (SST, DAYS, CSIZE), D_1 = PLOT, D_2 = HAB \quad (2)$$

and for the hatching success model, $n = 4$ with factors

$$\mathbf{x} = (SST, NN, DAYS, CSIZE), D_1 = PLOT, D_2 = HAB. \quad (3)$$

See Hayward *et al*. (2014) for specific ecological details on the categorical variables PLOT and HAB.

Each alternative measure of SST gave rise to an alternative version of models (1) + (2) and (1) + (3). For each of these, we estimated parameters with the glmfit function in MATLAB on the same data set used in Hayward *et al*. (2014) and then used the Akaike Information Criterion (AIC) to rank them from best to worst (Burnham & Anderson 2010).

We followed the same model-selection procedure for both egg cannibalism and hatching success. We first compared the model using the original 1 September–31 May time interval (before the breeding season) for SST with the models using 1 September–31 December and 1 January–31 May (Table 1). The best of these intervals, 1 September–31 December, was further compared with its subintervals 1 September–31 October and 1 November–31 December. We also tested the interval 1 May–30 June during the breeding season and 1 July–31 August at the end of the previous breeding season, for a total of seven alternative time intervals (Table 1). Because each of the seven alternative cannibalism models (corresponding to the seven alternative measures of SST) had the same number of parameters, comparing their AIC values was equivalent to comparing their likelihood values; and the same was true for the seven alternative hatching success models. We used the AIC, however, in order to be consistent with the Hayward *et al*. (2014) study.

RESULTS AND DISCUSSION

Average SST values computed from September–October, before the breeding season, were the best predictors of egg cannibalism and hatching success; as well, the best three models for both cannibalism and hatching success were those that included the months of September and October in the calculation of SST (Table 1). The worst model was the one based on July–August, at the end of the previous breeding season. Interestingly, the next-worst model was based on November–December, before the breeding season. This suggests that early autumn SSTs before the breeding season are crucial to breeding success, and that winter and spring temperatures may not be as crucial.

Average SSTs associated with each time interval were quite similar (Fig. 1), but if they had been exact vertical translations of each other, they would have provided equally good AIC values in the model-selection process. Note that summer (July–August) and winter (November–December) SSTs show the least variability from year to year (Fig. 1, thin lines), so it is not surprising that they provide the worst models and explain the least amount of variability in the data. Time periods that include May show the most SST variability from year to year (Fig. 1, thick lines); they do not, however, provide the best models. Autumn SSTs (September–October and September–December; Fig. 1, intermediately thick lines) show an intermediate amount of variability and provide the two best models (Table 1). Why should year-to-year SST variation in early autumn matter?

During El Niño in upwelling systems, increased SSTs are associated with decreased plankton levels and fewer fish, creating food deficits for marine birds (Barber & Chavez 1983, Schreiber & Schreiber 1984, Ainley 1994, McGowan *et al.* 1998, Stenseth *et al.* 2002). Pacific herring *Clupea pallasii* and other fish are common food

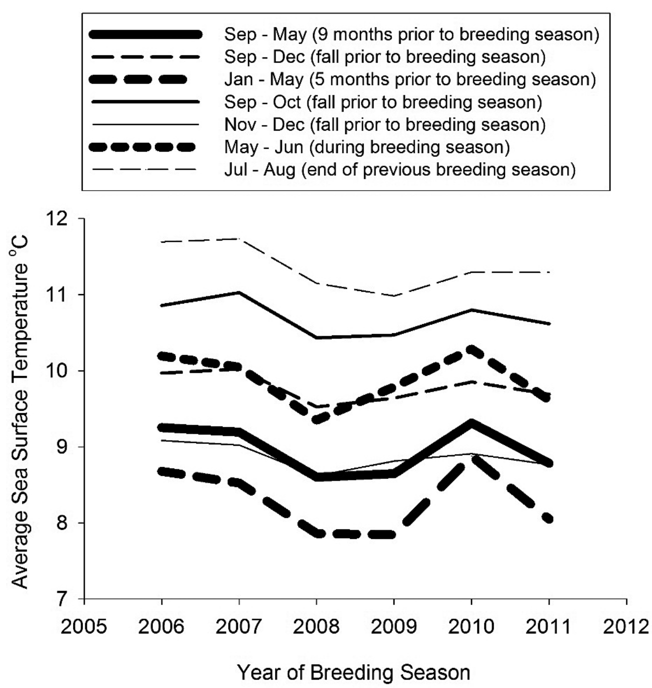

Fig. 1. Average sea surface temperatures for the seven alternative time intervals used as predictors for the Glaucous-winged Gull breeding seasons on Protection Island, 2006–2011.

items for Glaucous-winged Gulls (Trapp 1979, Irons *et al.* 1986). Decreased plankton abundance in early autumn could affect numbers of Pacific herring larvae in the spring. Indeed, in the North Atlantic Ocean, zooplankton abundance in October is the best predictor of the post-winter post-metamorphosis larvae of Atlantic herring *Clupea harengus* (Alvarez-Fernandez *et al*. 2015).

A recent study by Hipfner (2012) documented another relationship between high SST and reproduction in Glaucous-winged Gulls. At a colony at Triangle Island, British Columbia, 540 km northwest of Protection Island, mean egg volume for the lone egg of one-egg clutches and the two larger eggs of three-egg clutches increased slightly but significantly in response to higher mean April SST values. No relationship was found, however, between mean April SST and clutch size, despite the fact that yearly mean clutch size varied from 2.3 to 2.9. It would be interesting to determine whether the results would have been different if the dependent variables had been analyzed as a function of the mean September–October SST.

Discussion of three important caveats is in order. First, the methods in this paper are those of model selection, not model validation, and in that sense this is a descriptive rather than predictive study. However, we began with a model that was validated in Hayward *et al*. (2014). We combined the estimation and validation data from that study and used the validated model as a basis for generating a suite of alternative models with the same structure, to which we then applied model-selection techniques on the combined data set. Although we would normally attempt to validate the selected model, in this situation we had reason to expect the best model to be as predictive as the validated model from Hayward *et al*. (2014).

TABLE 1
Ranked logistic regression models of hatching success and egg cannibalism[a]

Cannibalism	**ΔQAICc**
1 Sep–31 Oct	0
1 Sep–31 Dec	5
1 Sep–31 May	8
1 May–30 Jun	10
1 Jan–31 May	12
1 Nov–31 Dec	17
1 Jul–31 Aug	25
Hatching	**ΔQAICc**
1 Sep–31 Oct	0
1 Sep–31 Dec	6
1 Sep–31 May	9
1 May–30 Jun	11
1 Jan–31 May	13
1 Nov–31 Dec	18
1 Jul–31 Aug	24

[a] QAICc is the second order quasi-likelihood Akaike Information Criterion (AIC; Burnham & Anderson 2010) used in the Hayward *et al*. (2014) study. All time periods are before the predicted breeding season except for 1 May–30 June, which is during the predicted breeding season.

Therefore, we have discussed prediction in this paper although, strictly speaking, we did not carry out a model validation.

Second, average SST can be determined over infinitely many time windows. We tried to test only those that might have biological significance; a more exhaustive accounting would generate biologically meaningless comparisons.

Third, the breeding season of 2016 was unusual and did not fit the pattern observed in the Hayward *et al*. (2014) study. SST was high, yet egg cannibalism was low in the Protection Island colony (Hayward *et al.*, unpubl. obs.). There appeared to be abundant young herring close to the surface, and Glaucous-winged Gulls seemed to have plenty of resources (Hayward *et al.*, unpubl. obs.), yet Rhinoceros Auklets *Cerorhinca monocerata,* also at the eastern end of the Strait of Juan de Fuca, were starving (Scott Pearson, pers. comm.). These unusual occurrences may be connected to the "Blob," a mass of warm water that gathered in the North Pacific in 2014 and 2015, and persisted into 2016, raising coastal SSTs to historically high levels, independent of the upwelling affected by El Niño–Southern Oscillation (Kintisch 2015, Moore *et al.* 2016, Peterson *et al.* 2016a,b). This unique event and others precipitated by atmospheric forcing have led to complex ecosystem responses (Norton & McLain 1994, Ainley *et al.* 1995, Peterson *et al*. 2016a,b).

In summary, the following are important for managers and seabird ecologists to consider:

- In the Salish Sea system, increased SST can be associated with food deficits for marine birds, along with changes in their feeding behavior and reproductive success. For data from 2006 to 2011, an increase of 0.1 °C in SST corresponded to a 10% decrease in the odds of hatching and a 10% increase in the odds an egg was cannibalized at a large Glaucous-winged Gull colony at Protection Island, Washington.
- When should a manager measure SST in order to predict its (time-lagged) effect on the upcoming breeding season? In this paper we illustrated a model-selection methodology for determining the best time interval over which to compute average SST. The result is expected to be species- and location-specific; the results in this paper are specific to the northern California Current region and, in particular, the Salish Sea.
- At the Protection Island gull colony, cannibalism and hatching success were best predicted by the average SST computed from September–October, before the late May–June egg-laying season. Early autumn SSTs before the breeding season appeared to be particularly crucial to breeding success.

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