Vol. 579: 111–127, 2017
https://doi.org/10.3354/meps12253

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 14

Mass mortality of marine birds in the Northeast Pacific caused by *Akashiwo sanguinea*

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ABSTRACT: Harmful algal blooms (HABs) are dense concentrations of phytoplankton that can have deleterious effects on marine life. We documented two of the largest marine bird mortality events ever definitively ascribed to a single HAB, the cause of which was death resulting from plumage fouling by surfactant-like proteins produced by the dinoflagellate *Akashiwo sanguinea*. The two mortality events were observed along the coast of Washington State in September and October 2009, collectively representing an estimated deposition of 10 500 carcasses, of which the majority were surf scoters, white-winged scoters and common murres. Each mortality event was coincident in space and time with observed bloom landfall, with each event preceded by a similar chain of environmental conditions. Prior to each event, the presence of *A. sanguinea* and upwelling-favourable conditions likely led to bloom proliferation. In both cases, this period was followed by conditions that transported the senescent bloom into the nearshore environment, whereupon subsequent wave action lysed *A. sanguinea* cells, creating foam that contained surfactant-like compounds. This sequence of conditions, exacerbated by the presence of aggregations of marine birds in wing moult, appear to be the necessary requirements for marine bird mortality of this scale due to foam-induced plumage fouling. This mechanism of HAB-induced mortality may become more prevalent in the California Current System given the apparent increasing occurrence of HABs and the broad environmental tolerances exhibited by *A. sanguinea*.

KEY WORDS: Harmful algal bloom · Dinoflagellates · Scoters · Common murres · Beached birds · Citizen science

INTRODUCTION

Harmful algal blooms (HABs) are a global problem (Anderson et al. 2012) with bloom events increasing in frequency and extent in coastal regions worldwide (Anderson et al. 2008, Heisler et al. 2008, Hallegraeff 2010). The causative algae are functionally grouped according to their negative effects on humans and wildlife, and mostly cause harm through the production of toxins (Glibert et al. 2005), that are often concentrated and sequestered by shellfish, other invertebrates (Bargu et al. 2002, Durbin et al. 2002, Wekell et al. 2004) and forage fish (Lefebvre et al. 2002, Busse et al. 2006). When toxic prey are ingested, these compounds can produce respiratory, gastrointestinal, motor and/or neurological effects (Landsberg 2002, Landsberg et al. 2005), occasionally resulting in unusual or anomalous mortality events among marine

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wildlife (Scholin et al. 2000, Shumway et al. 2003, Landsberg et al. 2009, Bargu et al. 2010, Miller et al. 2010).

Mortality events due to HABs have been recorded for many bird groups, including cormorants (Coulson et al. 1968, O'Shea et al. 1991, Fritz et al. 1992), terns (Nisbet 1983), waterfowl (Sasner et al. 1974, Forrester et al. 1977), alcids (Peery et al. 2006, Shearn-Bochsler et al. 2014), shearwaters (Bargu et al. 2012, Ayala et al. 2013) and pelicans (Work et al. 1993). While many of these events have been relatively small in magnitude (hundreds of fatalities recorded), several events have affected over a thousand birds, occasionally decimating small bird colonies (Coulson et al. 1968, Sasner et al. 1974, Sierra Beltrán et al. 1997). In 2007, a new HAB etiology was recognized during a marine bird mass mortality event (MME; Fey et al. 2015) in Monterey Bay, California (Jessup et al. 2009). Results from that event linked the presence of 'red tide' concentrations of the dinoflagellate *Akashiwo sanguinea* (=*Gymnodinium splendens*, *G. nelsonii*, *G. sanguineum*) to the production of powerful surfactant-like proteins that coated bird plumage and collapsed feathers, with a resultant loss of waterproofing and thermal insulation of over 700 birds. Blooms of *A. sanguinea* have been recorded globally in coastal areas (Trainer et al. 2010), including in the eastern Pacific (Cloern et al. 2005). Furthermore, this species has been identified as one of several species responsible for an increase in red-tide events in Central California and San Francisco Bay over recent years (Kudela et al. 2008). In August 2009, a large-scale *A. sanguinea* bloom formed in the Northeast Pacific off the coast of Washington and Oregon (White et al. 2014) during a period of relaxed upwelling and elevated seawater temperatures, conditions typical of dinoflagellate blooms (Cloern et al. 2005). Unusually, this bloom persisted for several months, lasting into November (White et al. 2014). During this period, dead and moribund marine birds washed ashore in highly elevated numbers at 2 locations along the Washington coastline, concurrent with the observation of foam production and deposition on coastal beaches (Phillips et al. 2011).

In this paper, we quantified this mortality, estimating total carcass deposition during these events, which cumulatively represent one of the largest death tolls of marine birds ever definitively ascribed to a single HAB. To understand the cause of these mortality events, and why it affected so many individuals, we examined the environmental conditions leading to foam production, the spatio-temporal patterns of bloom landfall and the natural history of the marine birds affected. Recent reports have identified that the occurrence and magnitude of avian MMEs is increasing globally due to biotoxicity and multiple stressors, including shifting climate (Fey et al. 2015). Therefore, understanding the environmental and biological conditions conducive to HABs and within which HABs can cause MMEs is crucial to both local (e.g. setting state-level hunting limits) and regional (e.g. redefining transboundary population status) conservation and resource management (Zingone & Enevoldsen 2000).

MATERIALS AND METHODS

Data collection

Data on the location, number and species identification of beach-cast carcasses of marine birds were collected by the Coastal Observation and Seabird Survey Team (COASST; a citizen science program at the University of Washington), supplemented by reports from personnel from the Quinault, Quileute, Hoh, and Makah Nations, the Olympic National Park, the Olympic Coast National Marine Sanctuary,

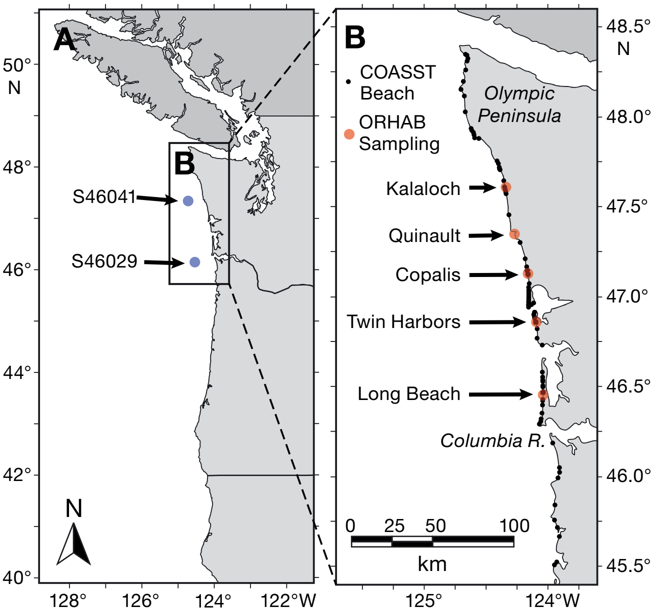

Fig. 1. (A) Study region within the northwest USA, with (B) map inset indicating the affected region within the Pacific Northwest, and the region for which deposition estimates were calculated. Blue dots: location of NOAA's National Data Buoy Center (NDBC) environmental monitoring buoys; black dots: Coastal Observation and Seabird Survey Team (COASST) survey beaches; red dots associated with place names: Olympic Region Harmful Algal Bloom (ORHAB) sampling locations

and the Washington Department of Fish and Wildlife. Data collected by COASST from the same geographic location in non-HAB years were used to provide a baseline. In COASST, trained participants conduct standardized surveys of specific sites approximately monthly, recording all new and previously found (identified by unique tags) carcasses within a prescribed length of beach. On-site identifications are made with the help of a field guide (Hass & Parrish 2013), and all identifications are subsequently verified by experts.

We focused our analysis on Washington outer coast beaches (Fig. 1) from August through November 2009, and on 5 groups of marine birds that comprised the majority of reported live and dead strandings (Phillips et al. 2011): (1) scoters (white-winged scoter *Melanitta deglandi*, surf scoter *M. perspicillata* and unidentified scoters *Melanitta* spp.), (2) common murres *Uria aalge*, (3) loons (Pacific loon *Gavia pacifica*, common loon *G. immer*, red-throated loon *G. stellata* and unidentified loons *Gavia* spp.), (4) large grebes (western grebe *Aechmophorus occidentalis*, Clark's grebe *A. clarkii* and unidentified grebes *Aechmophorus* spp.) and (5) cormorants (Brandt's cormorant *Phalacrocorax penicillatus*, pelagic cormorant *P. pelagicus* and unidentified cormorants *Phalacrocorax* spp.).

Quantifying magnitude versus baseline

Count data were used to calculate encounter rate (carcasses km^{-1}). Mortality event and baseline (2001 to 2014, excluding 2009) carcass encounter rates were compared by calculating bootstrap mean and 95 % confidence interval estimates for various spatiotemporal scales, and species groupings (see Section 1 of the Supplement at www.int-res.com/articles/suppl/m579p111_supp.pdf for detailed description of the bootstrapping procedure). To examine the spatiotemporal distribution of carcass deposition, survey-specific encounter rates for the combined counts of the 5 species groups (scoters, murres, grebes, loons and cormorants) were binned by location (six 50 km latitudinal bands from 45.75 to 48.5° N) and month (July to December).

Deposition modelling

To quantify total carcass deposition, we constructed a model describing daily deposition rates of newly found carcasses of the target species for surveys carried out between 1 August 2009 and 30 November 2009, and from 45.64° N (~ 50 km south of the Columbia River mouth) north to 48.34° N (the NW tip of the Olympic Peninsula). This incorporated 73 surveyed beaches and 387 surveys (Fig. 1). Daily carcass deposition rate was modelled assuming that the number of new carcasses on beach, *b*, on day, *d*, varied according to:

$$N_{b,d} = SN_{b,d-1} + A_{b,d} \qquad (1)$$

where S is the probability that an individual carcass remains from $d-1$ to d (i.e. persistence) and $A_{b,d}$ is the number of birds newly deposited on beach b on day d. Initial examination of the data revealed 2 peaks in carcass encounter rate relative to baseline. Therefore we modelled the beach- and day-specific rate of carcass deposition, $A_{b,d}$, as the summation of 2 events overlaid onto a baseline representing usual carcass deposition:

$$A_{b,d} = \lambda_1 f_1(d)\tilde{A}_1(b) + \lambda_2 f_2(d)\tilde{A}_2(b) + B(b,d) \qquad (2)$$

where λ_i determines the magnitude of event i; $f_i(d)$ and $\tilde{A}_i(b)$ determine the temporal and spatial profile of each event, respectively; and $B(b,d)$ is the spatiotemporal pattern of baseline carcass deposition. The temporal functions, $f_{1-2}(d)$, determine the relative number of birds deposited on day d, modelled as a double logistic function in time:

$$f_i(d) = [(1 + \mathrm{e}^{-(d-\overline{d_{is}})/\beta_{is}})(1 + \mathrm{e}^{-(\overline{d_{ie}}-d)/\beta_{ie}})]^{-1} \qquad (3)$$

where $\overline{d_i}$ determines the timing of the start and end of each event, i, and β_i controls the rate of increase/decrease in deposition with respect to time. Subscripts s and e indicate parameters that control the rising rate/time and falling rate/time of the function, respectively.

The value of $\tilde{A}_i(b)$ is the value of $R_i(l)$: the rate at which birds were deposited at location, l, along the coast for each event, evaluated at the mid-point of the survey beach, m_b, multiplied by beach length, L_b:

$$\tilde{A}_i(b) = R_i(m_b)\,L_b \qquad (4)$$

The rate, $R_i(l)$, was similarly modelled as a double logistic function in space:

$$R_i(l) = [(1 + \mathrm{e}^{-(l-\overline{e_{is}})/\gamma_{is}})(1 + \mathrm{e}^{-(\overline{e_{ie}}-l)/\gamma_{ie}})]^{-1} \qquad (5)$$

where $\overline{e_i}$ determines the location and spatial extent of the events, and γ_i controls the rate of increase/decrease in deposition with respect to location alongshore.

The baseline function, $B(b,d)$, was defined as 3 separate components:

$$B_1(b,d) = L_b\lambda_3 f_3(\mathrm{d})[(1 + \mathrm{e}^{-(m_b-\overline{e_{3s}})/\gamma_{3s}})]^{-1} \qquad (6a)$$

$$B_2(b,d) = L_b\lambda_4[(1 + \mathrm{e}^{-(\overline{d_{4e}}-d)/\beta_{4e}})]^{-1}[(1 + \mathrm{e}^{-(\overline{e_{4e}}-m_b)/\gamma_{4e}})]^{-1} \tag{6b}$$

$$B_3(b,d) = L_b\mu_0 \tag{6c}$$

The first component (Eq. 6a) models a persistent signal (see Fig. S1 in Section 2 of the Supplement) of higher encounter rate on beaches at the northwestern tip of the Olympic Peninsula. This was modelled as a double logistic function ($f_3(d)$) in time, but as a logistic function in space, as the northern boundary of this signal corresponds to the northern boundary of our data collection. The second component (Eq. 6b) models elevated deposition as a consequence of post-breeding mortality, predominantly common murres diffusing north from colonies in Oregon (Fig. S1). Only the northern edge of this signal was captured, therefore the signal was modelled as a logistic function in space and time. The third component (Eq. 6c) models a constant rate of carcass deposition (μ_0) to account for deposition not encompassed by the other model components.

Model parameters were estimated from the beach-specific time series of the number of newly identified carcasses, $C_{b,d}$, which was assumed to be distributed according to the negative binomial distribution, with dispersion parameter, ν_C:

$$C_{b,d} \sim NB(\hat{C}_{b,d}, \nu_C) \tag{7}$$

where $\hat{C}_{b,d}$ is the expected number of carcasses identified for the first time on beach b on day d, given as:

$$\hat{C}_{b,d} = \begin{cases} 0 & d = 1 \\ \phi\left[\hat{C}_{b,d'}(1-\phi)S^{(d-d')} + \sum_{d''=d'+1}^{d} A_{b,d''}S^{(d-d'')}\right] & d \neq 1 \end{cases} \tag{8}$$

The number of carcasses on beach b available to be identified for the first time on day d is therefore the number of carcasses which were available to be identified during the previous survey on beach b (on day d') but were not, less the proportion of carcasses removed from the beach (e.g. via scavenging, resuspension), plus the number of birds which were deposited on beach b since the previous survey and not yet removed. The expected count of new carcasses is then the number available to be counted multiplied by the detection rate, ϕ.

We estimated daily persistence rate, $S = 0.935$ (95% confidence interval, CI: 0.914–0.951), and detection rate, $\phi = 0.773$ (95% CI: 0.741–0.802), from a daily survey study on selected beaches in southern Washington from 2007 to 2009. During this study, beaches were surveyed up to 10 consecutive days per month, and the unique identity of re-found birds was recorded on all surveys. These data were reduced to individual capture histories (e.g. 1, 0, 1, 1, 0, 0) and analysed using Program MARK (White & Burnham 1999) to determine S and ϕ. To control for seasonal variation in persistence rate, we only analysed capture histories collected during the months of September and October, the months in which the MMEs were observed in 2009. The mean estimates of S and ϕ were included in the full deposition rate model (Eq. 8) as constants.

To inform the modelling of baseline mortality, we used previous years' data to identify priors for the spatio-temporal parameters of $B(b,d)$, (i.e. $\overline{e_{3s}}$, $\overline{e_{4e}}$, $\overline{d_{4e}}$, γ_{3s}, γ_{4e}, β_{4e}). Using data from 2003 to 2008, we fitted the corresponding carcass count data with deposition rate modelled as $B(b,d)$ (i.e. Eq. 8 with $A_{b,d} = B(b,d)$). The resulting posterior parameter estimates were used to define prior distributions of these parameters in the full deposition rate model (see Section 3 of the Supplement for more information). For all other parameters, flat priors were defined, with the exception of those controlling the start time/locations of each event (space: $\overline{e_{1s}}$, $\overline{e_{2s}}$; time: $\overline{d_{1s}}$, $\overline{d_{2s}}$) that were bounded so that label-switching (i.e. a set of parameters switching from modelling one event to another) did not occur (see Table S1 in the Supplement). Model parameters (both for the 2009-specific model and the baseline-only model) were estimated in OpenBUGS (Lunn et al. 2000) using 5 Markov chain Monte Carlo (MCMC) chains, each starting at a randomly generated set of values, with a burn-in period of 50 000 iterations or until convergence was reached (determined by Brooks-Gelman-Rubin diagnostics; Brooks & Gelman 1998). Upon convergence, a further 50 000 iterations were performed to estimate model parameters see Section 3 of the Supplement. Model checks were performed based on comparisons of observed and simulated counts (see Section 4 of the Supplement).

The total number of birds deposited was determined in post-processing based on deposition rate model parameters. Total deposition, D, is given by the sum over $A_{b,d}$, evaluated across the entire shoreline, broken into segments denoted by h:

$$D = \sum_h \sum_d A_{h,d} I_h \tag{9}$$

where I_h is the proportion of each shoreline segment where bird carcasses could be deposited (i.e. excluding river mouths, inlets and coastal cliffs). To control for differences in coastline complexity, shoreline segments were interpolated to a minimum length of 1 km. For each segment, the proportion of beach substrate, I_h, was calculated by summing the end-to-end distances of beach substrate relative to the combined length of beach and non-beach substrate in ArcMap v.10.4.1 (ESRI 2016). Shoreline segments were evaluated from 45.64° N, 123.94° W to 48.34° N, 124.69° W, representing a summed distance of 338 km. A distribution of total deposition estimates was obtained by sampling model parameters from converged model MCMC chains (n = 10 000; or 2000 chain^{-1}), and calculating D according to Eq. (9) for each mortality event, minus baseline carcass deposition. This was subsequently processed to provide a mean and 95% credible interval of total carcass deposition.

To identify the bird species composition of each event, the deposition model results were processed to identify the spatio-temporal extent, which was then used to assign survey- and species-specific counts to individual events. This was converted to the relative proportion of each species in each event, which was then multiplied by the estimated deposition for each event to identify species-specific estimates of carcass deposition. All post-processing of model parameters was performed in R v.3.3.2 (R Core Team 2016).

Environmental conditions and bloom landfall

Jessup et al. (2009) alluded to the conditions necessary for a marine bird mortality event caused by *Akashiwo sanguinea*: (1) the presence of *A. sanguinea* in a physiological state conducive to the release of chemical compounds characteristic of mycosporine-like amino acids, (2) transport of the cells into the nearshore surf-zone, (3) wave action to lyse the cells and churn cell contents/proteins into foam, and (4) spatio-temporal co-occurrence of foam and birds. Based on these requirements, we examined the time series of available environmental data in addition to shoreside observations of *A. sanguinea* abundance to identify the environmental precursors observed in 2009, and then tested for the presence of these conditions in other (e.g. baseline) years.

Hourly wind speed/direction and significant wave height data were obtained from buoys situated at the Columbia River Bar (Stn 46029: 47.1324° N, 124.518° W) and Cape Elizabeth (Stn 46041: 47.350° N, 124.704° W) (NOAA/NDBC: www.ndbc.noaa.gov/). Hourly wind speed and direction data were used to calculate alongshore wind stress, τ_y, as:

$$\tau_y = \rho_a C_d |W| V \tag{10}$$

where ρ_a is the density of air (1.225 kg m^{-3}), C_d is a dimensionless drag coefficient (taken to be 1.2×10^{-3}), $|W|$ is wind speed and V is the northerly component of wind velocity (Nelson 1976). Alongshore wind stress is proportional to average cross-shore transport over the surface layers via Ekman dynamics (Bakun 1975), and will be used here as a proxy for onshore–offshore transport; northward wind stress is a proxy for shoreward transport and downwelling and southward wind stress is a proxy for seaward transport and upwelling. Hourly significant wave height and τ_y values were then day-averaged. Hourly significant wave height was used as a proxy for the chance of cell lysis given the precursor conditions of off/onshore transport corresponding to bloom-favourable conditions followed by bloom-senescent conditions.

Observations of bloom landfall were collected by the Olympic Region Harmful Algal Bloom (ORHAB) Partnership program (Trainer & Suddleson 2005). Seawater samples were collected on a weekly basis from the surf zone at 5 accessible beaches on the outer coast of Washington State (Fig. 1). Whole water and net tows were collected for algal species identification and enumeration following standard protocols (Trainer & Suddleson 2005). Phytoplankton were enumerated from the coastal sampling sites using light microscopy. *A. sanguinea* is a naked flagellate that does not preserve well; therefore, whole water counts were performed on live samples that had been chilled (4°C) to slow cell movement. A 0.1 ml subsample was loaded into a Palmer-Maloney counting cell and individual algal cells were counted at 100× magnification.

Cell counts, day-averaged significant wave height and transport indices were plotted and aligned to identify the timing and location of bloom landfall, and the conditions that preceded and coincided with bloom landfall and seabird mortality events. Based on the observed conditions prior to the marine bird mortality events in 2009, we determined thresholds of τ_y to proxy upwelling and onshore transport favourable conditions, and significant wave height to model hydrodynamic disturbance. These thresholds were compared to the recorded environmental conditions from 1998 to 2015 in the August to November time period, which coincides with the timing of the seabird MMEs and more frequent dinoflagellate blooms (Jester et al. 2009, Du et al. 2011).

Moult model

To explore the relationship between moulting and deposition, we used our baseline (i.e. not 2009) data to model the proportion of carcasses in moult as a function of time. These models were then used to statistically compare the proportion of moulting carcasses found in 2009 to what would be expected given usual (baseline) mortality processes. Moult state was assessed for all adult birds (assessed from culmen measurement: murres; feather wear: all species) where carcass condition permitted an examination of moult based on available morphometric information (wing chord measurement) and photographic evidence. Because there were insufficient numbers of loons, grebes and cormorants in the baseline dataset, these analyses were confined to scoters and common murres.

Observed moult state, $M(d)$ (moult = 1; not-moult = 0), was modelled as a Bernoulli random variable, with probability $p(d)$, modelled as a double-logistic function corresponding to proportional moult as a function of time, d:

$$p(d) = \lambda\left[\left(1+\mathrm{e}^{-\left(d-\overline{d_1}\right)/\beta_1}\right)\left(1+\mathrm{e}^{-\left(\overline{d_2}-d\right)/\beta_2}\right)\right]^{-1} \tag{11}$$

$$M(d) \sim B(p(d)) \tag{12}$$

where $\overline{d_1}$ and $\overline{d_2}$ control moult timing, β_1 and β_2 control the rate of increase and decrease, respectively, and λ controls the peak proportion of moulting individuals. The model described in Eqs. (11) & (12) was fitted to the moult data using OpenBUGS (Lunn et al. 2000) as described for the deposition rate model. Using the fitted models, we generated distributions of expected values for the proportion of birds in moult based on the timing and number of birds observed. The observed proportion of moulting birds was then compared to those distributions to examine whether the moulting birds were statistically more prevalent than expected. This was performed separately for each event and species group (common murres and scoters). See Section 5 of the Supplement for a detailed description of model priors and test statistics.

RESULTS

Observations and comparison with baseline

The first reports of unusual numbers of marine birds on the beach came from hikers and rangers in the

Table 1. Carcass counts, bootstrapped average carcass encounter rates (ER; carcasses km^{-1}), and relative magnitude of the northern (10-Sep-2009 to 10-Oct-2009, 47.46 to 47.95° N) and southern (19-Oct-2009 to 9-Nov-2009, 46.26 to 46.66° N) events by taxonomic group. Encounter rates include the mass mortality event (MME) and baseline, with the latter calculated for the same space–time bounds across 2001 to 2014, excluding 2009. Numbers in brackets: 95 % confidence intervals (CI). **Bold** indicates no overlap between baseline and 2009 MME 95 % CIs. COMU: common murre; WWSC: white-winged scoter; SUSC: surf scoter; UkSC: scoter (unknown species); WEGR: western grebe; UkGR: grebe (unknown species, but one of Western or Clark's grebe); PALO: Pacific loon; RTLO: red-throated loon; COLO: common loon; UkLO: loon (unknown species); BRCO: Brandt's cormorant; PECO: pelagic cormorant; UkCO: cormorant (unknown species)

Species	Northern event (73 surveys, 16 beaches, 22.0 km)				Southern event (27 surveys, 14 beaches, 17.8 km)			
	Count	ER 2009	Baseline	Magn.	Count	ER 2009	Baseline	Magn.
COMU	60	0.58 (0.31–0.86)	0.61 (0.22–1.47)	0.9	234	5.4 (3.4–7.8)	0.31 (0.09–0.52)	**17.4**
Scoters								
WWSC	174	12.0 (7.8–17.1)	0.09 (0.01–0.25)	**138.3**	2	0.16 (0.04–0.31)	0.05 (0–0.12)	3.0
SUSC	599				5			
UkSC	548				0			
Grebes								
WEGR	1	0.01 (0–0.04)	0	/	48	1.50 (0.78–2.32)	0.16 (0.06–0.28)	**9.4**
UkGR	0				18			
Loons								
PALO	1	0.05 (0.01–0.09)	0	/	10	1.04 (0.37–1.82)	0.02 (0–0.07)	**49.5**
RTLO	3				25			
COLO	0				4			
UkLO	2				6			
Cormorants								
BRCO	0	0.23 (0.11–0.49)	0	/	1	0.10 (0.02–0.19)	0.01 (0–0.05)	6.9
PECO	22				4			
UkCO	1				0			
Total	1411	12.9 (8.5–18.1)	1.0 (0.5–1.9)	**13.0**	357	8.2 (5.5–11.8)	0.6 (0.3–0.8)	**15.0**

Olympic National Park around 10 September 2009. Within 15 d, COASST participants and others had counted over 1000 carcasses, 94 % of which were scoters, predominantly surf scoters (Table 1). This first occurrence of marine bird mortality was restricted in space along the approximately 50 km stretch of coastline from La Push (47.91° N, 124.64° W) south to the mouth of the Queets River (47.51° N, 124.36° W) (Fig. 2). Within this affected area over the 30 d period from 10 September to 10 October, carcass encounter rates were significantly elevated for scoters (~140× baseline). In addition, carcasses of several species of coastal diving seabirds (loons, grebes and cormorants) were observed on beaches where they had not been observed prior to, or subsequent to, 2009, including relatively high numbers (n = 22) of pelagic cormorants (Table 1). However, other species present in the affected area were not visibly impacted. Most notably, common murres were only observed at baseline levels (Table 1). Elsewhere along the Washington and northern Oregon coastline, carcass encounter rates were at or near baseline levels during September (Fig. 2). However, several scattered observations from Raft River (47.46° N, 124.34° W) south to Pacific Beach (47.20° N, 124.20° W) of high carcass encounter rates were indicative of the possible southern extent of the September event (Fig. 2).

Approximately 1 mo later (19 or 20 October 2009), marine bird carcasses were again observed in elevated numbers, this time along the Long Beach Peninsula in southern Washington (Fig. 2). From 19 October through to 9 November, a total of 357 carcasses were counted, with carcass encounter rates significantly elevated for all species groups, but primarily affecting murres (68 % of carcasses), grebes (19 %) and loons (9 %) (Table 1). Carcasses of scoters and cormorants were much less abundant, constituting only 4 % of the carcass count (Table 1). Unlike the September event, which occurred in a remote area, the October event occurred along a populated strip of sandy beaches, from approximately North Surfside (46.55° N, 125.06° W) south to the mouth of the Columbia River (Fig. 2). Efforts to rescue impaired birds at this time were immediate, and a total of 770 birds were collected and taken to rehabilitation centres. Elsewhere along the Washington and northern Oregon outer coast, carcass encounter rates were within the baseline range in October, with the excep-

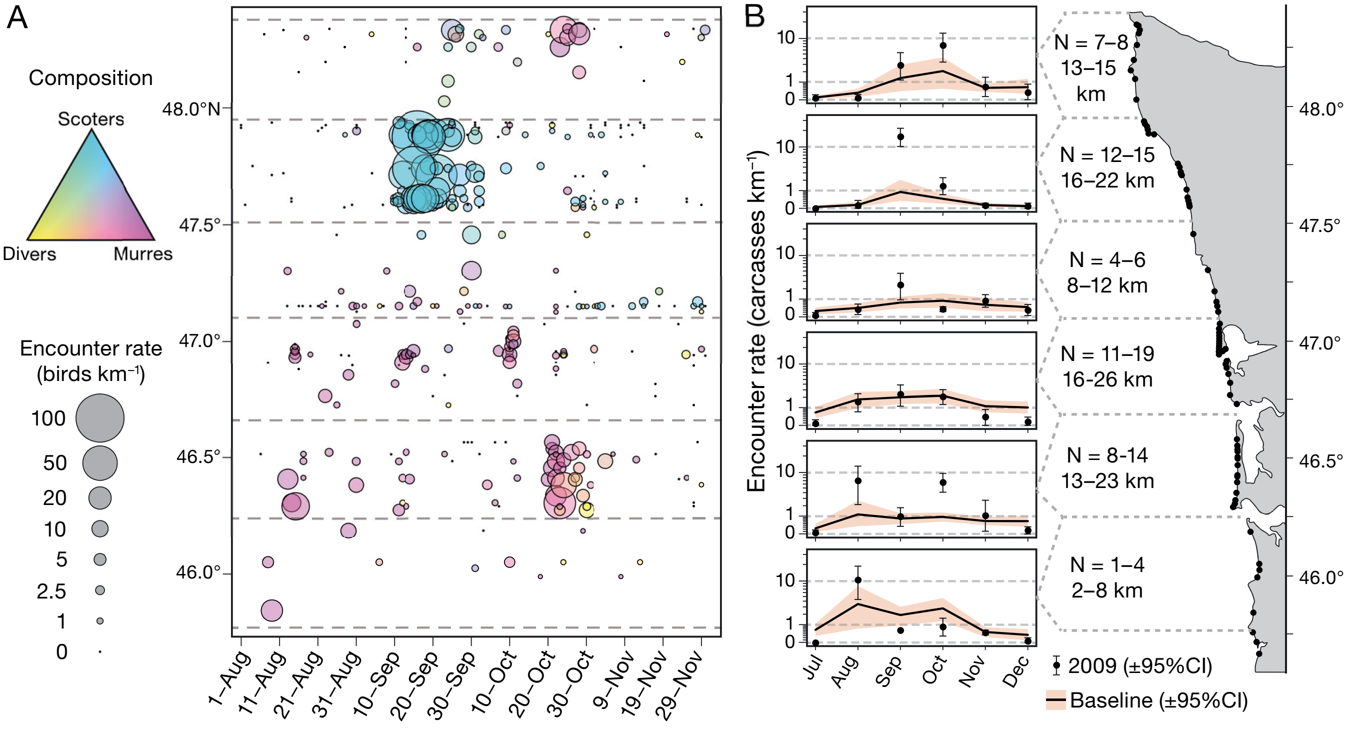

Fig. 2. (A) Observed carcass encounter rates (carcasses km^{-1}) plotted as a function of date and survey latitude, with observations scaled according to recorded encounter rate, and colour coded by species composition. Divers refers to combined counts of loons, grebes and cormorants. (B) Average carcass encounter rates (log scale, ±95 % CI) in 2009 compared to baseline encounter rates by month within 50 km latitudinal bands for outer-coast Washington and northern Oregon beaches. The monthly range in the number of beaches surveyed in 2009 (N) and cumulative survey coverage (km), from July to December are presented for each latitudinal band

tion of a small cluster of high encounter rate surveys (consisting of predominantly common murres) observed at the northwestern tip of the Olympic Peninsula in late October (Fig. 2). This signal had been observed in previous years (see Fig. S1 in Section 2 of the Supplement, and although elevated, was not significantly above baseline (Fig. 2). By November, carcass encounter rates were at baseline levels across all locations and affected species groups.

Carcass deposition

Daily deposition rate was modelled as 2 independent events in space and time representing the northern (predominantly scoter) and southern (predominantly murre) events (Fig. 3). We estimated total deposition for the northern event at 8460 (95% credible interval: 6250–11700), of which ~ 7560 were estimated to be scoters (Table 2). This event peaked in mid-September near La Push, Washington at 34.6 carcasses km^{-1} d^{-1}; thereafter, deposition rates declined to <10× baseline deposition rate by 27 September (Table 2). The southern event was shorter in duration, less extensive and smaller in magnitude than the northern event. Restricted to the Long Beach peninsula (Fig. 3), this event peaked on 20 October at only 3.9 carcasses km^{-1} d^{-1}, generating an estimated 1292 carcasses (95% CI: 714–2404), mostly common murres (Table 2). Adding the 770 birds recovered live and sent to rehabilitation facilities would increase this figure to 2062. However, assuming these birds beached in a similar pattern over space and time as the carcasses recovered during COASST surveys—that is we extrapolate counts of birds taken to rehabilitation centers according to the multiplication factor between observed carcass counts and estimated deposition for this event (multiplier = 3.62, derived from a deposition estimate of 1292 and 357 observed carcasses) would instead add 2780 birds (3.62 times 770), approximately tripling our deposition estimate to ~4000 for this event. Thus, across the 2 events, our best estimate of total deposition is 10500, when simply adding birds taken to rehabilitation centers, or 12500, when counts of birds taken to rehabilitation centers are corrected for the difference between observed counts and estimated deposition.

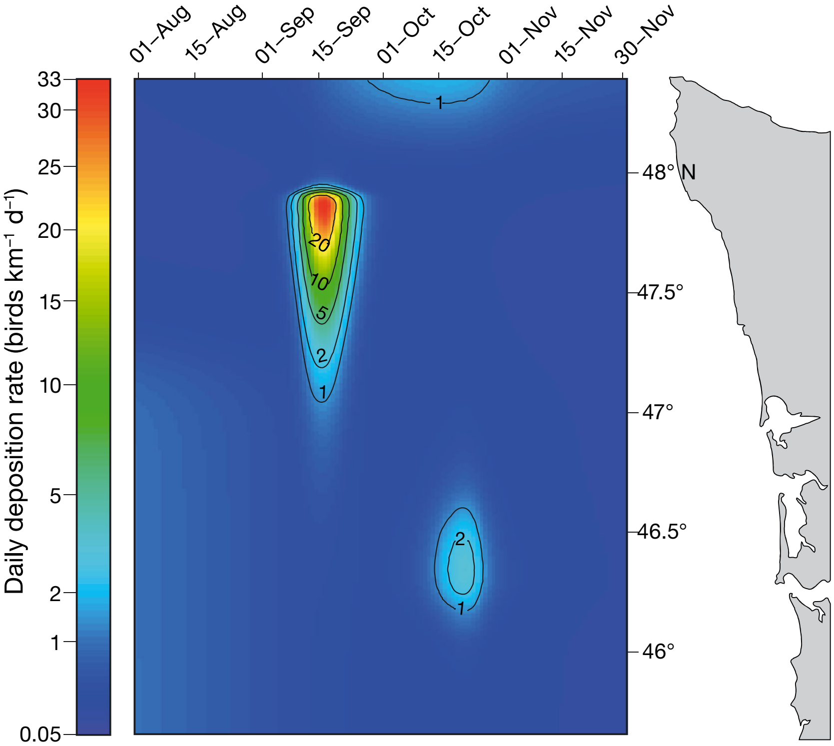

Fig. 3. Heatmap showing the mean estimated daily deposition rate (carcasses km^{-1} d^{-1}) from August through November for the Washington and northern Oregon outer coastline. Plotted values are the mean across 10000 model predictions, with each prediction parameterized by values drawn at random from the Markov chain Monte Carlo (MCMC) set of converged deposition model parameter estimates

Moult timing and tests of 2009 moult proportions

The baseline moult profile for scoters displayed a peak in August/early September, with proportional moult increase from essentially zero in early June, and falling back again to zero by February (Fig. 4). For common murres, the baseline moult profile had a slightly later peak (mid-September/early October) with proportional moult increasing from essentially zero in early July, also falling back to zero by February (Fig. 4). Relative to this baseline model, there were significantly more moulting scoters recovered in the 2009 *Akashiwo sanguinea* northern event (67.6%; n = 441, $p < 1 \times 10^{-6}$), and marginally more common murres in moult (53%; n = 55, p = 0.02). Scoters were only nominally present in the southern event (n = 7, and moult state could only be determined for 5 individuals) precluding statistical comparisons; however, common murres were significantly more

Table 2. Results of the deposition model including central tendency and range in timing, location, deposition rate and taxonomic group-specific estimates of total deposition, of the northern and southern events of the mass mortality event (MME). Event bounds were set at latitudinal and date limits where deposition rate exceeded 0.5 carcasses km^{-1} d^{-1}, or 10 times baseline. Timing, location and daily deposition values include the estimated mean and 95% credible intervals in brackets

	Event	
	Northern	Southern
Timing		
Start	7 Sep (3–10 Sep)	13 Oct (5–19 Oct)
Peak	16 Sep (13–18 Sep)	20 Oct (13–25 Oct)
End	27 Sep (22 Sep–1 Oct)	27 Oct (24 Oct–3 Nov)
Location (° N)		
Southern extent	46.94 (46.72–47.23)	46.15 (45.89–46.26)
Peak	47.88 (47.82–47.89)	46.35 (46.14–46.60)
Northern extent	47.95 (47.92–48.03)	46.70 (46.58–46.95)
Daily deposition		
Peak rate (carcasses km^{-1} d^{-1})	34.6 (17.2–67.2)	3.9 (1.1–11.9)
Summed deposition	8460 (6250–11700)	1292 (714–2404)
% Species composition (n/n$_{tot}$)		
Common murre	7.9 (119/1500)	65.5 (234/357)
White-winged scoter	11.9 (179/1500)	0.6 (2/357)
Surf scoter	40.8 (612/1500)	1.4 (5/357)
Unknown scoter	36.6 (549/1500)	0
Common loon	0	1.1 (4/357)
Pacific loon	0.2 (3/1500)	2.8 (10/357)
Red-throated loon	0.3 (4/1500)	7.0 (25/357)
Unknown loon	0.1 (2/1500)	1.7 (6/357)
Western grebe	0.1 (1/1500)	13.4 (48/357)
Unknown grebe	0.1 (1/1500)	5.0 (18/357)
Pelagic cormorant	1.7 (25/1500)	1.1 (4/357)
Brandt's cormorant	0.1 (1/1500)	0.3 (1/357)
Unknown cormorant	0.3 (4/1500)	0
Estimated group-specific deposition		
Murres	671	847
Scoters	7558	25
Loons	51	163
Grebes	11	239
Cormorants	169	18

likely to be in moult relative to the baseline model (55%; n = 137, p = 2 × 10^{-3}).

Environmental conditions and observations of *A. sanguinea* concentration

The marine bird mortality events were concurrent with episodes of *A. sanguinea* bloom landfall (Fig. 5A,B). ORHAB sampling at northern stations (Kalaloch and Quinault) during the initial phase of the northern event (10 to 15 September) *A. sanguinea* cell concentrations ranged from 6.2 × 10^5 to 15.5 × 10^5 cells l^{-1}. Prior to and during the initial phase of the southern event (12 to 15 October), cell concentrations were highest at southern locations, including Long Beach (6.3 × 10^5 cells $^{-1}$) and Twin Harbors (1.5 × 10^5 cells l^{-1}). However, high *A. sanguinea* concentrations were recorded in locations/times with no corresponding marine bird mortality (e.g. 4 October: Twin Harbors; Fig. 5B), indicating that bloom landfall alone was not a sufficient precondition for marine bird mortality.

To explore the environmental conditions necessary to induce an MME, we constructed proxies of nutrients (upwelling or offshore transport), bloom senescence and concurrent landfall (downwelling or onshore transport) and foam creation (storm events punctuated by large and sustained waves), and compared these time series to the known timing of bloom landfall and marine bird mortality. Prior to each mortality event, surface transport conditions switched from an approximate 20 d period of predominantly offshore transport and upwelling-favourable conditions to a 4 d period of consistent onshore transport and downwelling-favourable conditions (Fig. 5D). Downwelling conditions persisted during the mortality events, and were punctuated by peaks in significant wave height (6 September: H_s = 2.91; 14 October: H_s = 3.76) indicative of storm conditions (Fig. 5C). By contrast, the early October bloom landfall at Twin Harbors occurred after much smaller transport reversal within a long period of upwelling, and no storm activity (Fig. 5B–D).

These lines of evidence support the following set and order of criteria for marine bird mortality: (1) an extended period of upwelling-favourable conditions promoting bloom proliferation, (2) a shorter period of onshore transport and downwelling-favourable conditions that moves the bloom into the surf zone and may also result in a cessation of nutrient input leading to senescence, (3) somewhat elevated wave heights allowing foam formation from lysis of senescing *A. sanguinea* cells without overly dissipating the senescent bloom, and (4) the spatial and temporal co-occurrence of foam formation with marine bird aggregations.

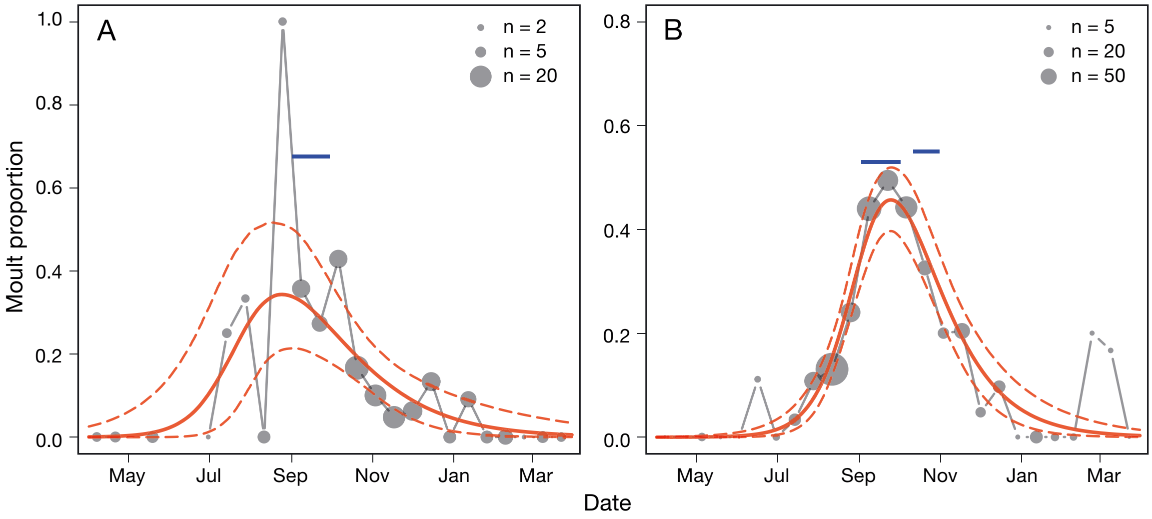

Fig. 4. Species-specific moult profiles derived from the baseline dataset: (A) scoters and (B) common murres. Grey circles: observed data averaged into 14 d time windows (for visualization purposes), with the number of individuals contributing toward that proportion illustrated by dot size. Red lines: fitted moult profiles (mean ± 95% CI). Horizontal blue bars: the observed proportion of scoters and murres, respectively, in moult during the northern (September) and southern (October) events. Scoters were omitted from the southern event due to a paucity (n = 5) of carcasses observed

Thresholds for criteria 1 to 3 were determined based on the conditions observed prior to each MME (Fig. 5) and applied to data from 1998 to 2015 in order to examine how frequently these conditions co-occurred in other years (Table 3). Individually, these thresholds were met on between 1 and 46 days in the August to November time period, and 2009 was not particularly anomalous relative to other years (Table 3). However, specifying that these conditions occur in sequence — upwelling followed by transport followed by waves — narrows the number and extent of events. We allowed a 7 d gap between the upwelling and onshore-transport criteria (the observed gap for the northern and southern events was 1 to 4 d), and a 2 d gap between transport and wave action criteria (in 2009 these criteria were met coincidentally) to account for offshore and onshore bloom persistence, respectively (alternate criteria allowances were tested, but resulted in similar conclusions; see Section 6 of the Supplement). The combined, sequential criteria were met in 6 of the 18 years examined (Table 3), suggesting that had *A. sanguinea* been a dominant component of the coastal phytoplankton community, landfall of foam would have been possible. Autumn 2009 was unique in that 2 distinct events met these combined criteria, with the September event occurring much earlier in the season than in any of the other years examined, whereas the October event occurred slightly later than when these criteria are typically met in other years (Table 3).

DISCUSSION

The extended 2009 *Akashiwo sanguinea* bloom off the coast of Washington State resulted in the observed death of ~1800 marine birds, impairment of an additional 770 (Phillips et al. 2011), and a best estimate of carcass/moribund bird deposition of ~10 500 to 12 500 individuals, making the cumulative death toll of these mortality events the largest ever definitely ascribed to a single HAB. Total mortality, including birds that died but were not deposited onshore, was certainly higher due to a combination of scavenging and sinking of carcasses at sea prior to deposition (Wiese 2003).

The majority of reported HAB-related seabird MMEs have resulted from toxin-producing algal blooms (Shumway et al. 2003), primarily those that produce saxitoxins (*Alexandrium* sp. and *Gymnodinium* sp.; Landsberg et al. 2008), domoic acid (*Pseudo-nitzschia* sp.; Work et al. 1993) and brevetoxins (*Karenia* sp.; O'Shea et al. 1991). However, large die-offs have been rare. Per event, documented mortality has been relatively low in magnitude, ranging from <10 individuals (Shearn-Bochsler et al. 2014) up to several thousand individuals in only a few cases (McKernan & Scheffer 1942, Sasner et al. 1974). The 2007 MME in Monterey Bay, also a consequence of an *A. sanguinea* bloom, only resulted in ~200 carcass recoveries and ~500 live impaired birds, and species-specific encounter rates that were 2 to 24

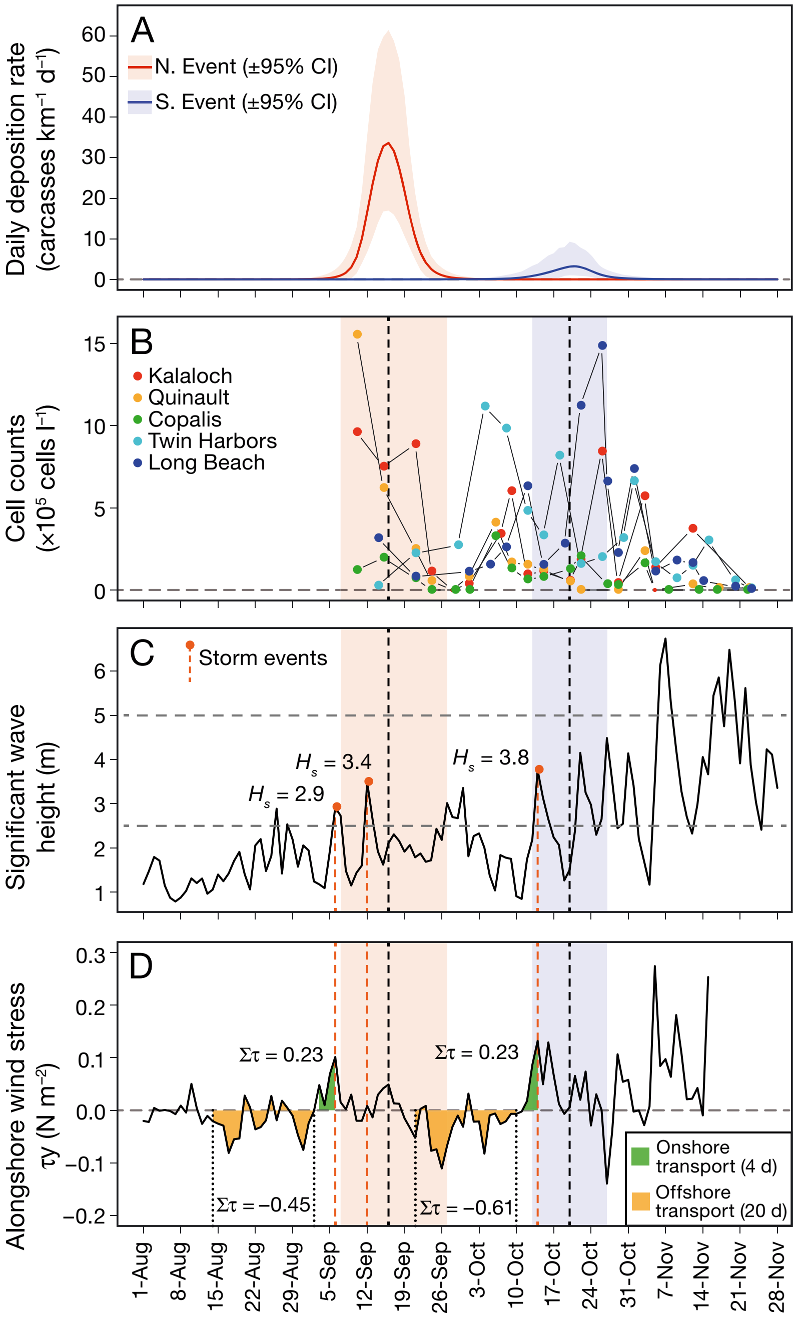

Fig. 5. (A) Time series of fitted daily deposition rates (±95% credible interval) at the peak spatial location for northern and southern events of the marine bird mass mortality event (MME). (B) Time series of *Akashiwo sanguinea* cell counts measured by the Olympic Region Harmful Algal Bloom (ORHAB) partnership at 5 locations along the Olympic Peninsula coastline. (C) Time series of day-averaged significant wave height H_s measured off the Washington outer coastline. Horizontal dashed lines represent significant wave height limits of 2.5 and 5 m, and storm events preceding MME events are highlighted with red dots and vertical red dashed lines. (D) Time series of day-averaged alongshore wind stress (τ_y) as a proxy of onshore/offshore transport calculated from wind speed/direction measured off the Washington outer coastline. Periods of onshore (downwelling) and offshore (upwelling) transport are shaded. Vertical shading: temporal limits of the northern (red) and southern (blue) MME events; dashed black lines: peak time of each event

times the long-term baseline (Jessup et al. 2009) as opposed to the ~140 times baseline rate for scoters encountered along the Washington coastline during 2009. Scoters represented 79% of the estimated deposition, with an estimated ~5800 surf scoters alone washing ashore. Comparatively, this was approximately 2 times the average annual harvest of surf scoters (2717, ranging from 400 to 6487; Olson 2016) by waterfowl hunting along the Pacific flyway, with upper confidence bound deposition estimates 3 times the annual harvest. Although surf scoter breeding populations, recorded from breeding grounds in Alaska, declined over the 1993 to 2012 period (Bowman et al. 2015), the observed mortality in September/October 2009 represents only 1 to 2% of the surf scoter population that winters on the Pacific Coast (~400 000; Anderson et al. 2015), suggesting that the MME caused by *A. sanguinea* in 2009 likely did not have a population effect.

Although the 2009 seabird mortality events were unlikely to have had long-term population effects on those species affected, they do highlight the potential catastrophic effects that HABs may have on smaller and/or local species populations (Coulson et al. 1968, Sasner et al. 1974, Sierra-Beltrán et al. 1997). In comparison, blooms of *Alexandrium* sp. have caused 2 large marine bird MMEs (McKernan & Scheffer 1942, Sasner et al. 1974), one of which occurred along the northern coast of Washington State. During that bloom, an estimated ~2000 birds, primarily gulls (Laridae), scoters, murres and loons were killed (McKernan & Scheffer 1942). Peak encounter rates were ~62.5 birds km^{-1} (McKernan & Scheffer 1942), or roughly half of the maximum encounter rate during the 2009 *A. sanguinea* MME of 120 birds km^{-1} (191 birds over 1.6 km). Larger marine bird MMEs have been associated with red tide and/or paralytic shellfish poisoning events; however, definitive causality has been lacking.

Table 3. Incidence of sequential environmental conditions identified as requirements for an *Akashiwo sanguinea* foam event along the outer coast of Washington State, evaluated from 1 August to 30 November, from 1998 to 2015. Criterion 1: upwelling conditions necessary for nutrient transport from depth; Criterion 2: downwelling inducing bloom senescence via depleted nutrients and simultaneous onshore transport of the bloom; Criterion 3: foam formation via wave action. Combined criteria allow up to a 7 d gap between Criteria 1 and 2, and up to a 2 d gap between Criteria 2 and 3, respectively. N and Dates represent the number of contiguous events and the date range where all 3 criteria were met in sequence, respectively

Year	Individual criteria (no. days)			Combined criteria (no. days)			N	Dates
	Upwelling: $C_1(d)$	Transport: $C_2(d)$	Waves: $C_3(d)$	$C_1(d')$ & $C_2(d)$	$C_2(d')$ & $C_3(d)$	C_1 & C_2 & C_3		
	$\sum_{d-19}^{d}\tau_y \le -0.4$	$\sum_{d-3}^{d}\tau_y \ge 0.2$	$5 \ge H_s(d) \ge 2.5$	$d-7 \le d' \le d$	$d-2 \le d' \le d$			
1998	42	26	32	0	19	0	0	
1999	35	28	36	2	28	3	1	7–9 Oct
2000	28	12	32	0	11	0	0	
2001	16	14	38	0	8	0	0	
2002	53	16	20	0	13	0	0	
2003	28	19	29	2	17	4	1	8–11 Oct
2004	1	7	40	0	13	0	0	
2005	32	18	44	0	22	0	0	
2006	57	24	37	0	21	0	0	
2007	35	26	41	4	27	6	1	30 Sep to 5 Oct
2008	16	14	40	0	18	0	0	
2009	20	19	29	7	13	5	2	6–7 Sep, 14–16 Oct
2010	28	26	44	0	23	0	0	
2011	41	19	38	1	16	3	1	24–26 Sep
2012	38	32	30	5	21	5	1	14–18 Oct
2013	33	8	22	2	6	0	0	
2014	30	34	37	0	29	0	0	
2015	18	14	35	0	19	0	0	

Shumway et al. (2003) posited that the massive die-off of an estimated ~15 000 alcids and other seabirds in the Irish Sea in 1969 (Furphy et al. 1971) and the estimated mortality of 13 000 black-legged kittiwakes *Rissa tridactyla* in northeast England (Coulson & Strowger 1999) may have been the result of HABs, although no evidence for (or against) phytoplankton as the causative agent was collected in either case.

In fact, the majority of confirmed and suspected HAB-induced seabird MMEs have not been well documented, and both cumulative deposition and total mortality may be much higher than reported (Shumway et al. 2003). In part, this is due to a lack of spatio-temporally comprehensive monitoring data, either at the event scale or with regard to baseline conditions. Use of standardized, rigorous citizen science monitoring efforts, including COASST and similar beachcast bird programs, can simultaneously provide needed data at a fraction of the cost of traditional science, while increasing science agency and environmental awareness of the non-scientist public (Burgess et al. 2016). Furthermore, if rigorously collected beachcast bird monitoring data were globally available, the methods applied here to estimate total carcass deposition could allow for direct comparisons of total deposition/mortality among MMEs. This would allow for better assessments of the likely relative impacts on species populations of MMEs, as the resulting estimates are not effort-dependent and allow carcass deposition to be integrated over the spatial and temporal extent of events.

Managing the effects of HABs on marine birds requires an understanding of the environmental and biotic conditions necessary for bloom proliferation, so that blooms, and the subsequent harmful impacts, can be forecasted. *A. sanguinea* is a cosmopolitan species (Trainer et al. 2010), previously associated with shellfish/fish die-offs and red tide events in coastal regions of Japan (Fukuyo et al. 1990), Australia and New Zealand (Hallegraeff 1992) and from the Atlantic and Pacific North American coasts (Robinson & Brown 1983, Bockstahler & Coats 1993, Voltolina 1993). This study, in combination with White et al. (2014), reveals the precise set, and perhaps more importantly, order of conditions necessary to produce an MME of this magnitude. The 2009 *A. sanguinea* bloom was unusual in that it occurred during a period of relaxed upwelling and warm temperatures, followed by a resumption of upwelling (Du et al. 2011, White et al. 2014), conditions which likely maintained and promoted further bloom proliferation. Lab cultures of *A. sanguinea* have been reported to tolerate a wide range of temperatures (10 to 30°C) and salinities (5 to 40) (Matsubara et al. 2007, Boyd et al. 2013). Both broad environmental tolerances and the capacity to form resting cysts (Robinson & Brown 1983, Voltolina 1993) may enable *A. sanguinea* to persist for extended periods of time.

While *A. sanguinea* was present in significant concentrations along coastal Washington from approximately mid-August to November (White et al. 2014), the MME was confined to 2 restricted time windows in September and October, respectively (Figs. 2 & 3) suggesting that the bloom alone, pre-senescence, was not harmful. Following Jessup et al. (2009), we explored the 2009 data for specific environmental and natural history conditions which, when present in sequence, create ideal conditions for a MME of coastal seabirds: the presence of a senescent *A. sanguinea* bloom; onshore transport; enhanced wave action to lyse cells; co-occurrence of the foam and birds; and birds in moult (e.g. Figs. 4 & 5). While we have no data on the ecophysiological condition of the extant blooms, the proxy time series for upwelling/downwelling (i.e. Fig. 5D) suggests biological drawdown of nutrients during the first half of September with nutrient enhancement from upwelling (as indicated by offshore transport conditions) during late September to early October (White et al. 2014). We note that during most of early October, cells were present (White et al. 2014; Fig. 5B) and birds were present, but excessive bird mortalities were not reported. This mismatch was characterized by conditions suggestive of weak upwelling (Fig. 5D) and a lack of storm events, conditions not conducive to foam production. However, it is also clear from the water sampling data that at least portions of the bloom did reach the shore during this period (Fig. 5B) and that the bloom was also present along the coastline of Oregon (Du et al. 2011), but did not result in elevated rates of carcass deposition there. Although the Washington coastline is not considered a retentive system, the wide shelf, the relatively weak upwelling winds and the frequent presence of the plume from the Columbia River along the coast north of the river mouth during storms (Hickey & Banas 2008) likely result in this region retaining particles, including HABs, for longer periods than, by comparison, the Oregon coast (Siedlecki et al. 2015). Thus, high concentrations of mycosporine-like amino acid compounds released from senescing cells during storm events may have been trapped as foam along the Washington shoreline. By contrast, because the Oregon coastline is relatively less retentive (Siedlecki et al. 2015), neither foam nor unusually high carcass deposition were observed along northern Oregon beaches despite the presence of the *A. sanguinea* bloom. Retentive systems, including Monterey Bay (Ryan et al. 2008), may be particularly prone to this specific etiology of HAB impact.

Our results also indicate that moulting birds were disproportionately affected. Moult may make individuals more susceptible in several ways: inability to escape, increased susceptibility to fouling and increased energy demand when fouled. Flight-feather moult in these species is synchronous (Bridge 2006), rendering the birds flightless for 45 to 50 d (Markones et al. 2010, Dickson et al. 2012). During this period, birds are particularly susceptible to locally deleterious events, such as oil spills or algal blooms (Savard et al. 2007). Pre-moult birds may also have been more susceptible to the surfactants produced by the *A. sanguinea* bloom, due to reduced waterproofing and insulation as a consequence of disrupted pore structure and other damage typical of pre-moult worn or damaged feathers (Stephenson 1997). The timing and species composition of the MMEs largely coincided with the timing of moult apparent in our baseline dataset (Fig. 4). Dickson et al. (2012) reported moult timing of surf and white-winged scoters to occur from late-June through late-September, overlapping the mid-September northern event — which overwhelmingly consisted of scoters, almost 70% of which were moulting their flight feathers. The southern event, which occurred in mid-October, involved a greater proportion of murres, grebes and loons, and relatively fewer scoters (Table 3). By mid-October the majority of scoters should have completed moulting (Dickson et al. 2012), whereas some proportion of murres (Thompson et al. 1998), loons (Barr et al. 2000) and grebes (up to 25%; Henny et al. 1990) were likely still in an impaired state at this time due to flight-feather moult. Taken in combination, the environmental conditions necessary for foam production (e.g. Fig. 5), and the temporal overlap of moulting marine birds (e.g. Fig. 4) has occurred in approximately one-third of the last 2 decades, both before and after the 2009 *A. sanguinea* bloom (Table 3). However, only in 2009 were these conditions met multiple times, starting in early September. This timing suggests that while common murres and other diving piscivores prevalent along the outer coast of Washington may be at some degree of risk annually, only in 2009 were scoters significantly at risk, as the moult timing of this species is earlier, peaking in September (Fig. 4).

Several studies have found that HABs are becoming more frequent, both globally (Hallegraeff 1993, Anderson et al. 2012) and along the Pacific Coast of the US (Lewitus et al. 2012). Future projections indicate a likely expansion of the spatio-temporal window for HAB development (Glibert et al. 2014), with causes variously attributed to anthropogenic sources of nutrient input (Smayda 1989, Hallegraeff 1993, Anderson et al. 2008, Heisler et al. 2008), as well as to changing climatic and oceanographic conditions, including shifts in sea surface temperature, upwelling intensity and storm-associated forcing (Bejarano et al. 2008, Moore et al. 2009, McCabe et al. 2016). Along the Iberian Peninsula, large dinoflagellate blooms — previously absent for ~10 yr — are now recurring, as are seasonal diatom/dinoflagellate oscillations comparable to those in the California system (Kudela et al. 2005, Trainer et al. 2010). The Humboldt Current System has also experienced blooms of both harmful diatom and dinoflagellate species in regions where HABs have not historically been recorded (cf. Kudela et al. 2010, Trainer et al. 2010). Within the central and southern California Current System (CCS), relative abundances of diatoms and dinoflagellates common to Monterey Bay shifted to a flagellate-dominated assemblage in 2004, prior to the 2007 *A. sanguinea* bloom (Jessup et al. 2009), part of a more general shift observed in the southern CCS (Venrick 2012). The unusual bloom of *A. sanguinea* in San Francisco Bay in 2004 was linked to anomalously warm conditions (Cloern et al. 2005). There is also evidence that eastern boundary current systems generally are undergoing fundamental ecological shifts and becoming more productive (Kahru et al. 2009). These conditions may lead to an increased frequency of both dinoflagellate and diatom HABs (e.g. McCabe et al. 2016), consequently increasing the potential for more frequent marine bird MMEs, particularly given the simultaneous increase in decadal wave height trends in the Pacific Northwest (Allan & Komar 2006).

Marine bird mortality events as a likely or actual result of surfactant-producing algal blooms have rarely been reported. Suspected cases include a bloom of *Coscinodiscus concinnus* in the Southern German Bight in 1996 that resulted in the largest mass stranding of red-throated loons ever recorded in Europe (~100s recorded dead; Camphuysen 1997). Other examples of plumage fouling and loss of waterproofing by an unknown green-yellow substance, similar to fouling by *A. sanguinea* foam, include 700 Cape gannets *Morus capensis* affected on Ichaboe Island, Namibia (du Toit & Bartlett 2001) and incapacitation of ~100 swift terns *Sterna bergii* on Robben Island, South Africa (Parsons et al. 2006). Furthermore, the Robben Island observations co-occurred with heavy wave action and observations of meter-thick foam coming ashore (Parsons et al. 2006). However, the etiology of foam-based marine bird mortality events was not identified until the *A. sanguinea* bloom in Monterey Bay in 2007 (Jessup et al. 2009). Given the physiological flexibility of *A. sanguinea* (Ryan et al. 2009, Kudela et al. 2010) the rapid response of this species to favourable environmental conditions (Cloern et al. 2005) and the increase in coastal warming and climate variability, including marine heatwave events (Hobday et al. 2016, Scannell et al. 2016, McCabe et al. 2016, McKibben et al. 2017), we speculate that the frequency of foam-induced bird mortality events may continue to increase in the CCS and perhaps elsewhere.

Acknowledgements. COASST acknowledges the many hundreds of participants who have collected beachcast bird data, as well as J. Dolliver and C. Wright for their efforts coordinating the response in 2009 and H. Burgess for discussion and comments on an earlier version of the manuscript. These analyses were supported by NSF EHR/DRL awards 1114734 and 1322820, and Washington Department of Fish and Wildlife award 13-1435, to J.K.P. B.H. and R.K. were supported by the Center for Sponsored Coastal Ocean Research of the National Ocean and Atmospheric Administration (NOAA) by the ECOHAB PNWTOX program (Contribution #892, NA09NOS4780180) and by the National Science Foundation (NSF) (PNWTOX Study, OCE–0942675). V.L.T. and B.H. were supported by the MERHAB Pacific Northwest Studies program (Contribution #208, NA16N054780189). A.O. was supported by a surcharge to Washington State recreational shellfish licenses that provides funding to the University of Washington for monitoring by the Olympic Region Harmful Algal Bloom program (House Bill 1620). The findings and conclusions are those of the authors and do not necessarily reflect those of NSF, NOAA or the Department of Commerce.

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Submitted: April 5, 2017; Accepted: July 7, 2017
Proofs received from author(s): August 21, 2017