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Using ocean gliders to characterize baleen whale habitat in the Northwest Atlantic

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ABSTRACT: Characterizing baleen whale habitat is challenging because of the difficulty in obtaining sufficient spatially and temporally concurrent *in situ* observations of whales and oceanographic conditions. We collected a multi-year series of concurrent whale detections and high-resolution oceanographic measurements from Slocum ocean gliders to evaluate baleen whale habitat associations. The study area was Roseway Basin, a relatively small (30 × 60 km), shallow (<180 m) basin located ~40 km seaward of SW Nova Scotia, Canada. Data were collected from 13 fall (August–November) glider surveys of the basin over an 8 yr period (2014–2021). Gliders collected profiles of salinity and temperature as well as audio to detect and classify whale sounds. Acoustic analysis revealed spatial, diel, and within-season patterns in whale detections. Whale occurrence and a suite of oceanographic variables were computed in 20 km grid cells in each month and year of the study (n = 267). Descriptive and statistical (logistic regression) analyses were used to explore associations between the occurrence of each species and depth, topographic relief, water column stratification, current speed, and bottom mixed layer thickness and density. Results suggested strong, positive associations for fin, sei, and right whale occurrence and depth. They also showed that right whale occurrence in August–September was associated with a well-stratified water column overlying a thick, dense bottom mixed layer, consistent with conditions known to have a role in aggregating their copepod prey. Although exploratory, our results demonstrate the utility of profiling gliders for making inferences about baleen whale habitats.

KEY WORDS: Baleen whale · Slocum glider · Autonomous platform · Oceanography · Habitat

1. INTRODUCTION

Baleen whales filter feed on dense, ephemeral patches of low trophic level prey (Goldbogen et al. 2017). Their survival depends on reliably finding and effectively exploiting these aggregations, the dynamics of which are governed by a variety of cryptic biophysical processes (Durham & Stocker 2012). Characterizing the associations between baleen whales and their ocean environment can reveal insights into their ecology, improve our understanding of the physical proxies of prey availability, and ultimately inform whale risk mitigation (Baumgartner et al. 2017). The latter is particularly salient given the conservation status of many large baleen whale populations, coupled with intensifying risks from human activities and climate change.

Quantifying these ecological associations is challenging because of the difficulty in obtaining sufficient spatially and temporally concurrent observa-

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tions of the whales and oceanographic conditions. Typical correlative habitat models rely on environmental covariates that are collected at different time or space scales, are often restricted to the ocean surface, and may or may not be representative of the oceanographic processes responsible for prey aggregation (Redfern et al. 2006). A common example is the combination of remotely sensed dynamic variables (e.g. sea surface temperature) with results from visual surveys. This is often because it is resource-intensive to conduct fine-scale habitat sampling over sufficiently large time and space scales required to develop rigorous statistical relationships. While these approaches can sometimes generate relatively accurate predictions, they are typically unable to resolve many of the processes that whales, and their prey, may be responding to underwater because processes in the water column can quickly decouple from surface processes with increasing depth (Palacios et al. 2013).

Autonomous platforms have great potential for addressing this knowledge gap, as they are becoming more commonly used in oceanographic research and can often be configured to monitor both whale occurrence and underwater oceanographic habitat persistently over large temporal and/or spatial scales. Profiling ocean gliders (hereafter 'gliders') are especially desirable autonomous platforms for this application, as they are acoustically quiet and collect high-resolution observations throughout the water column. Passive acoustic monitoring (PAM) from gliders has been used to monitor a wide range of marine mammal species (Baumgartner et al. 2014, Kusel et al. 2017, Verfuss et al. 2019, Cauchy et al. 2020, Fregosi et al. 2020, Buchan et al. 2022). Several systems are capable of transmitting survey data in near real-time (within ~24 h) while the glider is still at sea (Klinck et al. 2012, Baumgartner et al. 2013, 2020, Kowarski et al. 2020), facilitating the use of these platforms for dynamic planning of research and management activities (e.g. Indeck et al 2025). One such system, the digital acoustic monitoring instrument (DMON)/low-frequency detection and classification system (LFDCS), is commonly deployed on Slocum gliders (Teledyne Webb Research; Baumgartner et al. 2013, 2020) and moored buoys (Baumgartner et al. 2019) to monitor baleen whales, especially the endangered North Atlantic right whale *Eubalaena glacialis* (hereafter 'right whale'). Since 2014, the DMON/LFDCS has been deployed on over 90 glider missions around North and South America, amassing nearly 5000 d at sea and over 600 d with right whale detections (https://robots4whales.whoi.edu). Effort has been concentrated on the continental shelf along the east coast of the USA and Atlantic Canada within the right whale migration range. These detections are relayed to managers in both the USA and Canada, where they are used to inform risk mitigation measures (Johnson et al. 2021).

To date, near real-time monitoring of right whales has been the primary motivation for many of these deployments. While achieving this goal, gliders are also monitoring for the presence of other baleen whale species as well as collecting large quantities of hydrographic observations. These oceanographic data can provide useful ecological context for whale detections (Aniceto et al. 2020, Burnham et al. 2021). The primary objective of this work is to conduct an exploratory analysis to evaluate the feasibility of using the concurrently collected environmental and whale occurrence data from glider deployments to evaluate how baleen whale species associate with and partition oceanographic habitat.

2. MATERIALS AND METHODS

2.1. Study area

The study area was Roseway Basin, a relatively small (30 × 60 km), shallow (<180 m) basin on the Scotian Shelf located ~40 km seaward of SW Nova Scotia, Canada (Fig. 1). Variation in the hydrography is dominated by seasonal solar heating and cooling as well as inputs from the Nova Scotia Current (NSC) and Warm Slope Water (WSW) intrusions. The NSC, a buoyancy-driven coastal current, delivers relatively cool, fresh water from the Gulf of St. Lawrence predominately to the upper layer (30–50 m) of the water column. Intrusions of WSW contribute to relatively warm, saline water below 100 m (Dever et al. 2016). Studies of right whale occurrence (Brown et al. 2007, Durette-Morin et al. 2019), habitat (Baumgartner et al. 2003, Davies et al. 2012, 2013, 2014, 2015a,b), and vessel strike risk (Vanderlaan et al. 2008, Vanderlaan & Taggart 2009, van der Hoop et al. 2012) have informed the implementation of an 'Area To Be Avoided' (ATBA) by the International Maritime Organization in the basin (Brown et al. 2009). In 2017, shortly after the start of a significant right whale mortality event in the southern Gulf of St. Lawrence (Daoust et al. 2018), the ATBA region was designated as a right whale critical habitat area (DFO 2017). Both right whale occurrence and right whale prey concentrations have declined in the Gulf of Maine and Scotian Shelf regions starting around 2010, correlated with increased water temperatures throughout the water column (Davies et al. 2019, Record et al. 2019, Sorochan et al. 2019, Meyer-

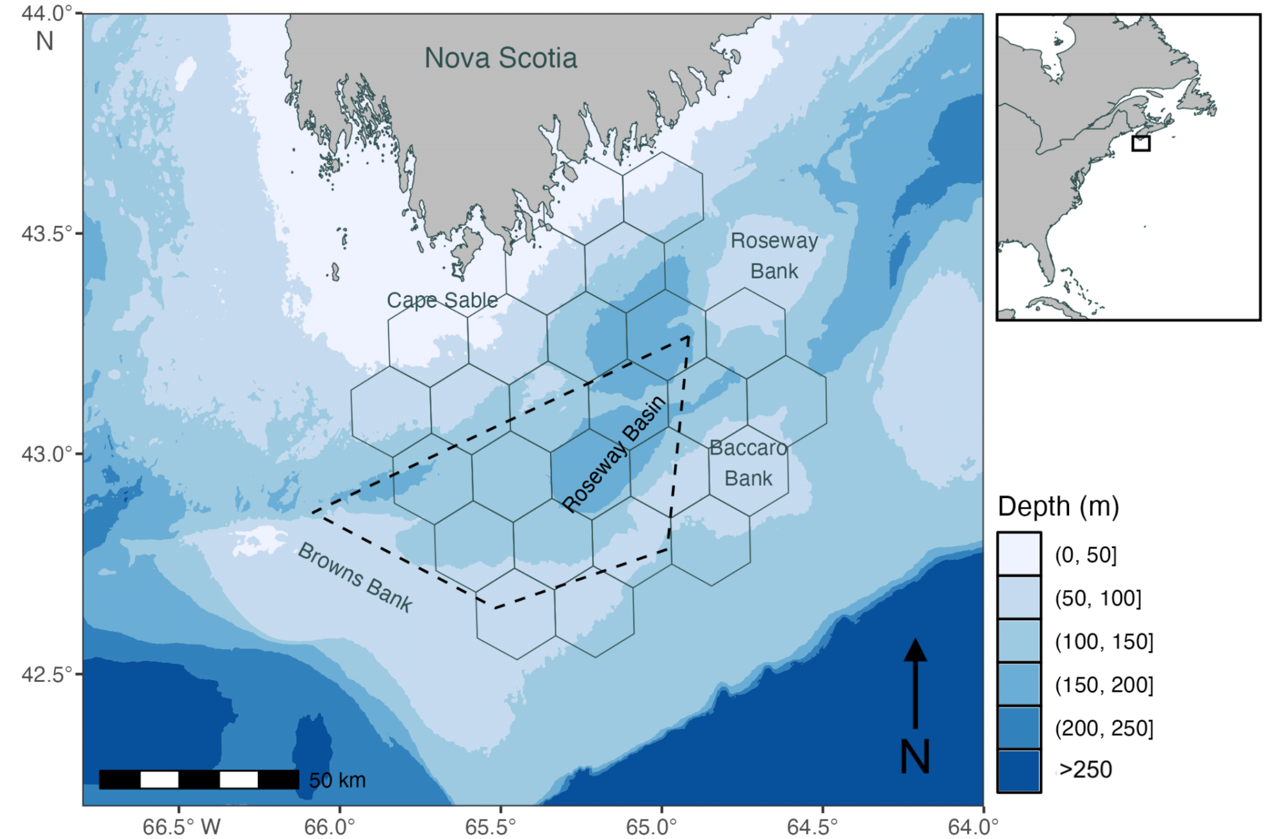

Fig. 1. The Roseway Basin study site off Nova Scotia, Canada. Color indicates depth contours (in m) derived from the GEBCO bathymetric data set (GEBCO Bathymetric Compilation Group 2024); dashed line: the Roseway Basin Area To Be Avoided; solid black lines: grid of 20 km diameter hexagons (n = 20) used in the habitat analysis

Gutbrod et al. 2021, 2023). Fin whales *Balaenoptera physalus* (COSEWIC [Committee on the Status of Endangered Wildlife in Canada] status: special concern), humpback whales *Megaptera novaeangliea* (COSEWIC status: not at risk), sei whales *Balaenoptera borealis* (COSEWIC status: endangered), and blue whales *Balaenoptera musculus* (COSEWIC status: endangered) have also been sighted and acoustically detected in Roseway Basin (Davis et al. 2020, Johnson et al. 2021), although their habitat associations have not been studied in detail.

2.2. Data collection

Data were collected from 13 Slocum glider surveys of Roseway Basin in the fall (August through November) over an 8 yr period (2014–2021; Fig. 2, Table 1). Our survey area encompassed a roughly 100 × 100 km region (42.7–43.6° N and 65.8–64.6° W) approximately centered on the ATBA. Slocum gliders are small (1.75 m long), battery-powered, buoyancy-driven autonomous vehicles that profile the water column at slow vertical (0.1–0.2 m s^{-1}) and horizontal (20–30 km d^{-1}) velocities for missions lasting weeks to months in duration. They surface at regular intervals (typically 2–6 h) to determine their position, transmit data, and receive new mission commands via satellite. The specific configuration of each glider varied by mission, but at a minimum, all gliders were equipped with a calibrated conductivity–temperature–depth (CTD) sensor to measure temperature and salinity profiles and a PAM system to detect and classify baleen whale vocalizations. The CTD sensors used were either an unpumped CTD from Neil Brown Ocean Sensors or an unpumped SBE41 or pumped Glider Payload CTD (GPCTD) from Seabird Scientific. All were calibrated, regularly maintained, and sampled at 1 Hz to ensure comparable results and a vertical resolution of approximately 0.5 m. The gliders were programmed to conduct cross-basin transits of the region approximately perpendicular to the axis of the SE basin margin, but strong currents, particularly the semi-diurnal tidal currents, introduced considerable tortuosity in the tracklines. Logistical constraints (resources, weather, etc.) caused interannual variability in platform availability and survey coverage. A CTD malfunction rendered the environmental data on the 2017 hydrographic survey unusable, so this deployment was not included in the habitat analyses, but the DMON/LFDCS data from that deployment were usable and included in the whale detection analysis.

2.3. Data processing

2.3.1. Whale detection data

Each glider was equipped with a PAM system comprised of the low-power digital acoustic monitoring instrument (DMON; Johnson & Hurst 2007) and an onboard detection algorithm (low-frequency detection and classification system; LFDCS; Baumgartner & Mussoline 2011). The DMON recorded audio at 2 kHz continuously with a sensitivity of −203 dB re 1 V μPa^{-1}, gain of 33.2 dB, zero-to-peak voltage of 1.5V, and flat frequency response between approximately 10 and 1000 Hz. The LFDCS algorithm running on board the DMON facilitated near real-time baleen whale detection and classification (Baumgartner et al. 2013). In brief, the LFDCS produces spectrograms of the audio data, accounts for spurious broadband noise and continuous tonal noise, and then uses a contour-following algorithm to create pitch tracks of tonal sounds from the spectrogram. Each pitch track is classified by comparing attributes of the pitch track to a library of call types using quadratic discriminate

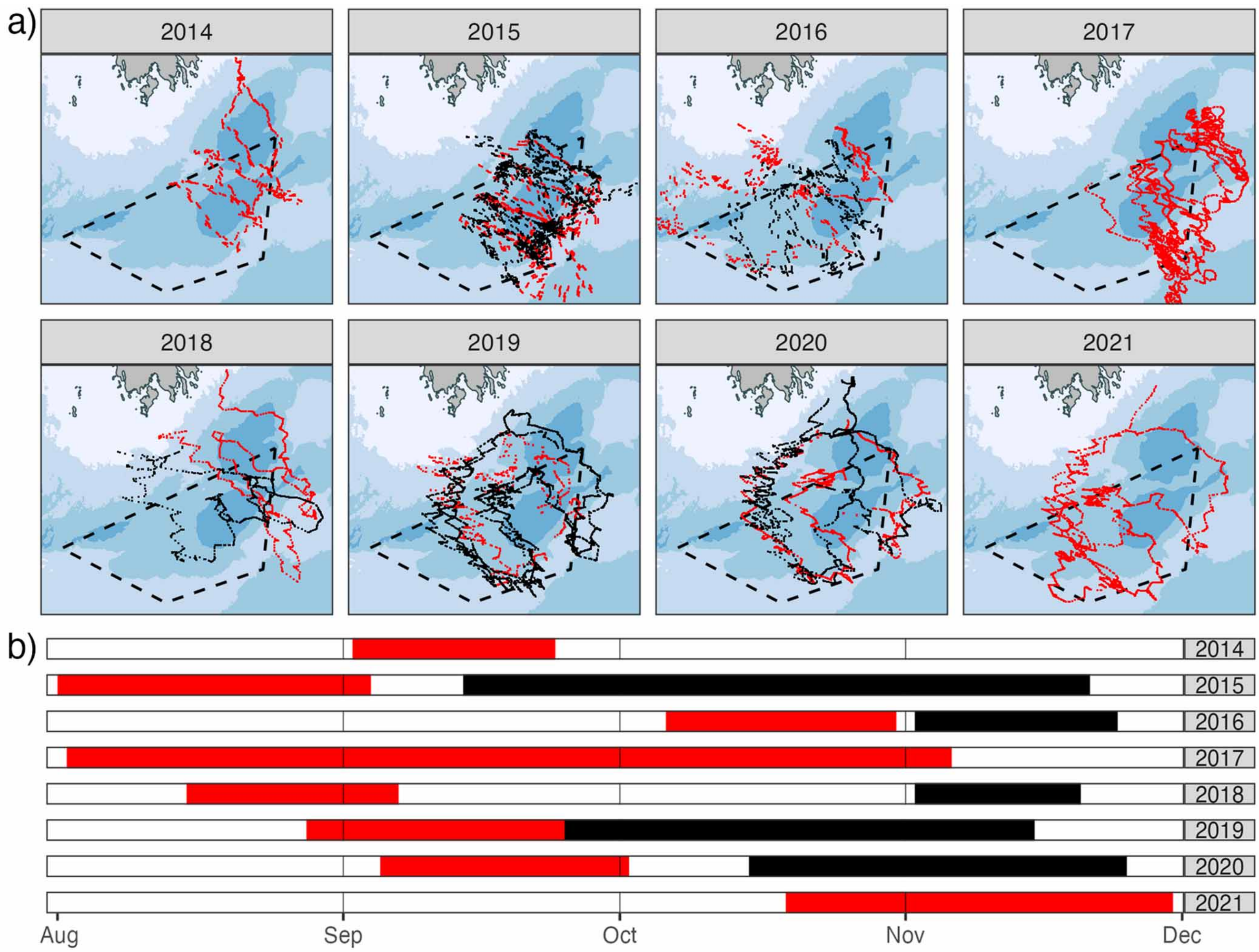

Fig. 2. (a) Spatial and (b) temporal distributions of effort from Slocum glider surveys (n = 13) of Roseway Basin from 2014 through 2021. Colors distinguish the first (red) and second (black) surveys in a given year. Points in (a) show average glider position within a ~15 min acoustic analysis (tally) period. Bathymetric scale is consistent with that of Fig. 1. Environmental data were not available for the 2017 mission, so were not included in the habitat analysis

Table 1. Summary of Slocum glider missions (n = 13) in Roseway Basin from 2014 through 2021. 'Days' indicates the number of days in which both whale detection and environmental data were collected. 'Dist.', 'Profiles', and 'Tally' provide the total along-track survey distance (km), total number of glider profiles, and the total number of tally periods analyzed for whale detections, respectively. The species columns show the number of days in which each species was detected

	Glider	Year	Start	End	Days	Dist.	Profiles	Tally	Fin	Humpback	Right	Sei
1	we10	2014	02 Sep	24 Sep	23	658	1011	1408	15	3	6	11
2	we04	2015	28 Jul	04 Sep	39	1371	1516	2470	34	1	15	6
3	dal556	2015	14 Sep	30 Nov	78	2193	2777	2902	68	16	14	23
4	dal556	2016	06 Oct	31 Oct	26	981	1194	1126	16	5	5	15
5	otn200	2016	02 Nov	24 Nov	23	768	255	915	21	8	8	13
6[a]	otn200	2017	02 Aug	06 Nov	97	1945	0	5486	77	1	5	10
7	otn200	2018	15 Aug	07 Sep	24	467	1044	707	2	0	0	0
8	otn200	2018	01 Nov	20 Nov	20	495	769	719	16	0	0	4
9	bond	2019	28 Aug	25 Sep	29	759	673	1172	2	4	0	0
10	scotia	2019	25 Sep	15 Nov	52	1460	1388	2995	43	20	1	21
11	fundy	2020	05 Sep	02 Oct	28	668	1010	1799	22	5	11	2
12	fundy	2020	15 Oct	25 Nov	40	1111	1025	1868	29	16	4	16
13	qala1	2021	19 Oct	08 Dec	51	1398	1527	2983	44	4	2	12
Total					530	14274	14189	26550	389	83	71	133

[a]Environmental data not available for this mission

function analysis. When the glider surfaces, a maximum of 8 kB h^{-1} of the pitch track and classification data are transmitted to a land station via Iridium satellite, where they are divided into ~15 min analysis (tally) periods that are manually reviewed by a trained analyst following a documented protocol (Wilder et al. 2023) for the acoustic presence of several species, including right, fin, sei, and humpback whales. Over daily time scales, the system has a false detection rate of 0% for all 4 species, and a missed detection rate of 17–24% (Baumgartner et al. 2020). See Baumgartner & Mussoline (2011) for more information on the LFDCS and Baumgartner et al. (2013, 2020) for system performance from Slocum gliders.

This analysis protocol was used to determine the acoustic occurrence of 4 baleen whale species (fin, humpback, right, and sei whales) in near real-time for all glider deployments in this study. For each species, tally periods marked as 'detected' or 'not detected' were given a numeric score of 1 or 0, respectively. Tally periods marked 'possibly detected' were considered not detected and given a score of 0. The number of tally periods, cumulative duration of tally periods, number of tally periods with detections of each species, proportion of detected tally periods of each species, and species occurrence scores (0: absent; 1: present) were computed for each survey day and within each 20 km grid cell for the habitat analysis (see below).

2.3.2. Oceanographic data

Glider science and engineering data from each deployment were extracted from the raw binary format and merged using a common timestamp. Spurious (i.e. non-physical) values for time, position, temperature, salinity, and pressure were removed. Profiles were isolated based on a dive or climb state variable recorded by the glider. Ascending profiles were used in the analysis because the CTD was not configured to record descending profiles for several deployments. Profiles with fewer than 30 points, a maximum depth of less than 10 m, a minimum depth of greater than 15 m, depth intervals exceeding 5 m, or those that traversed less than 75% of the full water column were excluded from subsequent analyses. Temperature and salinity profiles were decimated into 1 m depth bins and smoothed using a centered 9-point moving average. The potential density anomaly (kg m^{-3} − 1000; hereafter 'density') was computed for each smoothed profile. The profiles were then visually reviewed to confirm successful profile isolation and quality control. Unless otherwise noted, all oceanographic quantities were computed using the 'oce' package (Kelley & Richards 2024) in R version 4.4.2 (R Core Team 2024).

2.3.3. Habitat data

A goal of this work was to explore the feasibility of using glider-derived environmental data and acoustic detections to make inferences about whale habitat use and associations. These data are collected over very different scales: a glider profile is usually collected within a few hundred meters (horizontally), while baleen whale calls in a continental shelf environment are commonly detected at scales of kilometers to tens of kilometers (e.g. Stafford et al. 2007, Johnson et al. 2022). Thus, the first step towards characterizing whale–habitat associations was to define an appropriate spatial and temporal scale over which to compare the environmental and detection data. We imposed a regular hexagonal grid over the study area and aggregated whale detection and habitat data within each cell. A cell diameter of 20 km was selected based on average detection ranges of right whales (Johnson et al. 2022). It also balanced statistical constraints, where preliminary analysis suggested models constructed using smaller cell sizes showed signs of residual autocorrelation for all species, while the use of larger cell sizes reduced sample size, spatial resolution, and statistical power. In an effort to reduce potential bias arising from uneven sampling, we only included cells in the analysis that had been surveyed in at least 1 yr in both the early (August–September) and late (October–November) months of the study (n = 20).

Several habitat variables were computed within each grid cell (Table 2). The average water depth (*depth*) and standard deviation of the water depth (*depth_sd*), an index of topographic relief, were calculated within each grid cell using GEBCO digital bathymetry at 30 arc-second resolution (accessed from https://download.gebco.net/). Both water depth and topographic relief were included as environmental variables given their many established links to baleen whale distribution (Redfern et al. 2006). Dynamic variables were computed for each profile, and the median value for all profiles within a given month and year was assigned to each cell. Surface stratification strength (*surf_strat*) was defined as the difference in average density between the 5–10 and 45–50 m depth strata. Stratification strength was included for its potential role in zooplankton aggregation and previous associations with right whales (Woodley & Gaskin 1996, Baumgartner & Mate 2005). It is also highly correlated with sea surface temperature, which has been commonly related to the distribution of many cetacean species (Redfern et al. 2006), as well as sea surface temperature gradient, which Baumgartner et al. (2003) linked with right whale spatial distribution in the region. The bottom mixed layer thickness (*bml_thickness*) was defined as the height from the maximum profile depth to a density change of -0.05 kg m^{-3}, and the bottom mixed layer density (*bml_density*) was the average density within this depth stratum. We included bottom mixed layer thickness based on a previously documented positive association with right whale presence in Roseway Basin, where a thicker bottom mixed layer makes dense patches of the copepod *Calanus finmarchicus* aggregated just above the bottom mixed layer occur at shallower depths that can be more easily exploited by right whales (Baumgartner et al. 2003). Results of H. D. Johnson et al. (unpubl. data) suggest that a similar mechanism occurs in the southern Gulf of St. Lawrence. The density of the bottom mixed layer was included to resolve hydrographic variability from flushing events or intrusions. Using CTD and echosounder data from one of the Slocum glider surveys presented here (Survey 3; Table 1), Ruckdeschel et al. (2020) observed a significant freshwater flushing event in the deep basin in October 2015 that was associated with a significant reduction in zooplankton backscatter. The depth-integrated horizontal current velocity (*current_v*) was computed for each glider segment (interval between surfacings) on board the glider during the mission based on the offset between the measured glider position and the glider position predicted using dead reckoning (see Appendix of Dever et al. 2016). It was considered as an environmental variable owing to previous associations between tidal current magnitude and the concentration of zooplankton along the SE margins of the basin (Davies et al. 2013) and because of its apparent spatial variability as evidenced by the increasing tortuosity of glider tracks towards the western edge of the study area (Fig. 2).

Table 2. Description of environmental variables used in the habitat analysis

Variable	Units	Definition
depth	m	Median seafloor depth within a grid cell (from GEBCO)
depth_sd	m	The standard deviation of seafloor depth within a grid cell (from GEBCO)
surf_strat	kg m^{-3}	The difference in average density between the 5–10 m and 45–50 m depth strata
bml_thickness	m	Height from the maximum profile depth to a density change of -0.05 kg m^{-3}
bml_density	kg m^{-3}	Average density within the bottom mixed layer
current_v	m s^{-1}	Magnitude of the depth-integrated horizontal current

2.4. Statistical analyses

2.4.1. Diel variation in detection rates

Diel patterns of detection rates of each species were investigated based on previously described linkages with foraging behavior (Baumgartner & Fratantoni 2008). The 'sunAngle()' function from the 'oce' package was used to determine the solar altitude (in degrees above the horizon) at the time and position of each tally period from the full data set. These fields were then used to sort detections into 4 light regimes: dawn ($-12° < \text{altitude} < 0°$), day ($\text{altitude} > 0°$), dusk ($-12° < \text{altitude} < 0°$), and night ($\text{altitude} < -12°$). The detection rate (number of tally periods with detections / total tally periods) was computed within each light regime on every day for which there were detections. To facilitate comparison among days, the detection rates for each light regime and day were adjusted by subtracting the daily average detection rate (Stafford et al. 2005). The results were not normally distributed, so Kruskal-Wallis (KW) tests followed by Dunn's multiple comparisons tests (with Bonferroni adjustment) were used to compare detection rates among light regimes for each species. These tests were implemented using the 'dunn.test()' function in the 'dunn.test' R package (Dinno 2017).

2.4.2. Habitat associations

The association between whale presence and each environmental variable was assessed using logistic regression. Whale occurrence was expressed as 1 if whale acoustic presence was manually validated in at least one tally period within a grid cell unit and 0 if tally periods were reviewed and no presence was detected. The general form of the logistic regression is as follows:

$$\text{logit}(\pi) = \beta_0 + \sum_{i=1}^{p} \beta_i V_i \tag{1}$$

where the logit of the probability of species occurrence, π, is modelled as a linear function of the predictor variables, V_i, and β_0 is the intercept, β_i are the model coefficients, and p is the number of predictor variables. There were a number of practical considerations that were also weighed during model construction. The first was the issue of overfitting, wherein an overly complex model (i.e. one that contains too many parameters) artificially conforms to the underlying data and produces inaccurate results that are not repeatable. As a general rule, at least 10 observations of both presence and absence are necessary for each model term to avoid overfitting. Right and humpback whales were rarely detected (61 and 54 survey units, respectively, where a survey unit is a detection in a grid cell in a given month), which restricted model design for these species to a maximum of 5 or 6 terms. A second consideration was the potential for correlation among independent variables, as multicollinearity can also generate unreliable model estimates (Hosmer et al. 2013).

With these considerations in mind, several sets of models were constructed to evaluate the effect of a single variable on whale occurrence while attempting to control for other sources of variability. The simplest model set contained a single independent variable and a term, *effort*, containing the number of tally periods per grid cell to correct for variation in acoustic monitoring effort. It was structured as follows:

$$\text{logit}(\pi) = \beta_0 + \beta_1(\textit{effort}) + \beta_2(V) \tag{2}$$

The variable *depth* was associated with whale occurrence, and several of the environmental variables were correlated with *depth* (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m764p189_supp.pdf), which can confound the results. To account for the influence of depth, a second set of models including *depth* was constructed as follows:

$$\text{logit}(\pi) = \beta_0 + \beta_1(\textit{effort}) + \beta_2(V) + \beta_3(\textit{depth}) \tag{3}$$

Temporal variation in whale occurrence can also confound model results. To account for the influence of time on detection rates, a categorical variable was added to represent each month. These are included in the model as 3 dummy variables (*Sep*, *Oct*, *Nov*), each taking a value of 0 or 1 to represent a given month (e.g. August is represented as: *Sep*: 0; *Oct*: 0; *Nov*: 0). The model took the following form:

$$\text{logit}(\pi) = \beta_0 + \beta_1(\textit{effort}) + \beta_2(V) + \beta_3(\textit{Sep}) + \beta_4(\textit{Oct}) + \beta_5(\textit{Nov}) \tag{4}$$

which was expanded as follows with the addition of a term for *depth*:

$$\text{logit}(\pi) = \beta_0 + \beta_1(\textit{effort}) + \beta_2(V) + \beta_3(\textit{Sep}) + \beta_4(\textit{Oct}) + \beta_5(\textit{Nov}) + \beta_6(\textit{depth}) \tag{5}$$

The previous 2 models have 6 and 7 terms, respectively, which begin to raise concerns of overfitting, particularly for the rarely detected species (right whales and humpbacks). To reduce the number of model terms while still resolving some of the temporal variability, we developed another set of models where the month terms were replaced with a single categorical variable, *late*, representing each half of the study period (*late*: 0 for August–September; *late*: 1 for October–November). These terms allow comparison between the first and second half of the study period, which was motivated by the noticeable change in detection rates of some species between the early and late periods. A set of models were formed with this new term:

$$\text{logit}(\pi) = \beta_0 + \beta_1(\mathit{effort}) + \beta_2(V) + \beta_3(\mathit{late}) \quad (6)$$

which were further expanded to include *depth* as follows:

$$\text{logit}(\pi) = \beta_0 + \beta_1(\mathit{effort}) + \beta_2(V) + \beta_3(\mathit{late}) + \beta_4(\mathit{depth}) \quad (7)$$

All the terms in the previous formulations are additive, such that the effect of each model term is evaluated independently of the others. A set of models with an interaction term was developed to assess whether or not a habitat association changed between the first and second half of the study period:

$$\text{logit}(\pi) = \beta_0 + \beta_1(\mathit{effort}) + \beta_2(V) + \beta_3(\mathit{late}) + \beta_4(V \times \mathit{late}) \quad (8)$$

where the categorical variable for time, *late*, was expressed as an interaction with the variable of interest, *V*. This set was expanded once again with a *depth* term as follows:

$$\text{logit}(\pi) = \beta_0 + \beta_1(\mathit{effort}) + \beta_2(V) + \beta_3(\mathit{late}) + \beta_4(V \times \mathit{late}) + \beta_5(\mathit{depth}) \quad (9)$$

The values of environmental variables in each cell were expressed as monthly anomalies (i.e. the value in each cell was subtracted from the average value of all cells in that month across all years) prior to model fitting. This helped to account for inter-annual variability in the environmental variables and aided in model fitting and coefficient interpretability, although the analysis was repeated without calculating anomalies and the same models emerged as significant. Models including *depth* terms (Eqs. 3, 5, 7, and 9) produced similar results when fit with the results of a principal components analysis of the variable of interest and *depth*, suggesting their results are robust to multicollinearity. All models only consider temporal trends within the August–November period. We made no attempt to explicitly quantify or account for interannual variability due to the heterogeneity in annual sampling effort and relatively short time series. We make the implicit assumption that pooling environmental data by month across years is appropriate, which may be justified because the region has been under a consistent climatic regime from 2010 through present day (i.e. no known regime shifts occurred during our sampling years; Sorochan et al. 2019, Meyer-Gutbrod et al. 2021, 2023). The results thus reflect whale–habitat associations within the time and space of our observations using the best representation of environmental conditions in Roseway Basin as our observations allow.

These models were implemented using the 'glm()' function in the 'stats' package in R. Model assumptions (independence of residuals, linearity of predictor variables, absence of multicollinearity, and lack of strong outliers) were assessed graphically, supplemented with computation of the variance inflation factor (using the 'vif()' function in the 'car' R package; Fox & Weisberg 2019) to check for multicollinearity and Box-Pierce tests (using the 'Box.test()' function in the 'stats' R package [R Core Team 2024]) to identify autocorrelation in the residuals at lag 1. Preliminary analyses suggested a potentially quadratic relationship between whale occurrence and *current_v*, so *current_v* was included in all models as a second-order polynomial (i.e. expressed as $\mathit{current\_v} + \mathit{current\_v}^2$). These analyses also revealed significant autocorrelation in the residuals of models with fin whales. We successfully mitigated autocorrelation via subsampling, using only every third data point for fin whale models. This reduced sample size (number of absences: 31) substantially increased the risk of overfitting for models with more than 3 terms (i.e. model sets 2–8). The significance of each model was evaluated using drop-in-deviance (likelihood ratio) tests between the full model and a reduced version lacking the variable of interest (i.e. the term $\beta(V)$). The significance of individual model terms was assessed using Wald's tests.

Unless indicated specifically above, all analyses were conducted in R (R Core Team 2024) using various utility functions from 'tidyverse' (Wickham et al. 2019), 'lubridate' (Grolemund & Wickham 2011), and 'sf' (Pebesma 2018), while visualizations were implemented using 'ggplot2' (Wickham 2016), 'ggspatial' (Dunnington 2021), and 'patchwork' (Pedersen 2020) packages.

3. RESULTS

3.1. Whale detections

The 13 glider surveys amassed 530 d at sea, travelled over 14 000 km, and collected over 14 000 full depth profiles. They also transmitted 26 550 tally periods containing 242 d of pitch track data. Near real-time analysis of these pitch track data verified detections of fin, humpback, right, and sei whales on 389, 83, 71, and 133 days, respectively (Table 1).

3.1.1. Fin whales

On average, fin whales were detected on nearly every calendar day from August to December and were consistently present in >20% of tally periods per day after mid-October (Fig. 3). In some years, it was not uncommon for fin whales to be detected nearly continuously (>90% daily detection rate) over multiple days (Fig. S2). Detections were spatially concentrated in the central and southern portions of the study area in August, then shifted eastward and intensified for the remainder of the period. Fin whale detections were consistently absent from the northwest coastal portion of the study area and were less commonly observed along the western and southern margins of the study area later in the period (Fig. 4). A KW rank sum test provided inconclusive evidence of variation in detection rates of fin whales among light regimes (KW = 7, p = 0.06; Fig. 5).

3.1.2. Humpback whales

Humpback whales were only detected during 2 tally periods in late August and sporadically in September. Daily detection rates increased and became more consistent in mid-October but remained relatively low (<10%; Fig. 3, Fig. S3). The spatial extent of detections also increased substantially in October and November relative to the earlier months, with most detections occurring within the ATBA (Fig. 4). Humpback detection rates varied by light regime

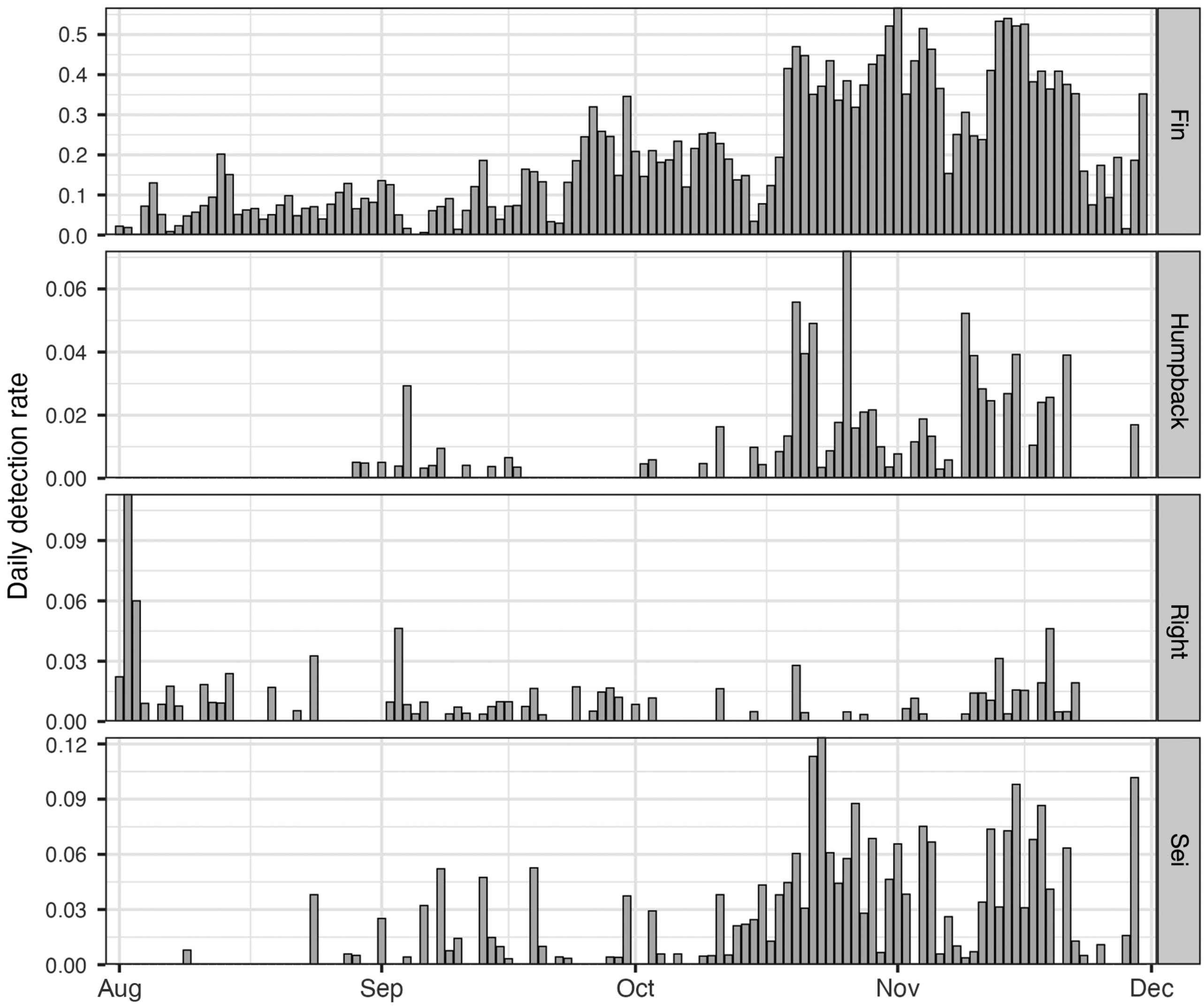

Fig. 3. Time series of daily detection rates of each species (rows) pooled across all years, computed as the number of tally periods with detections divided by the total number of tally periods for each calendar date

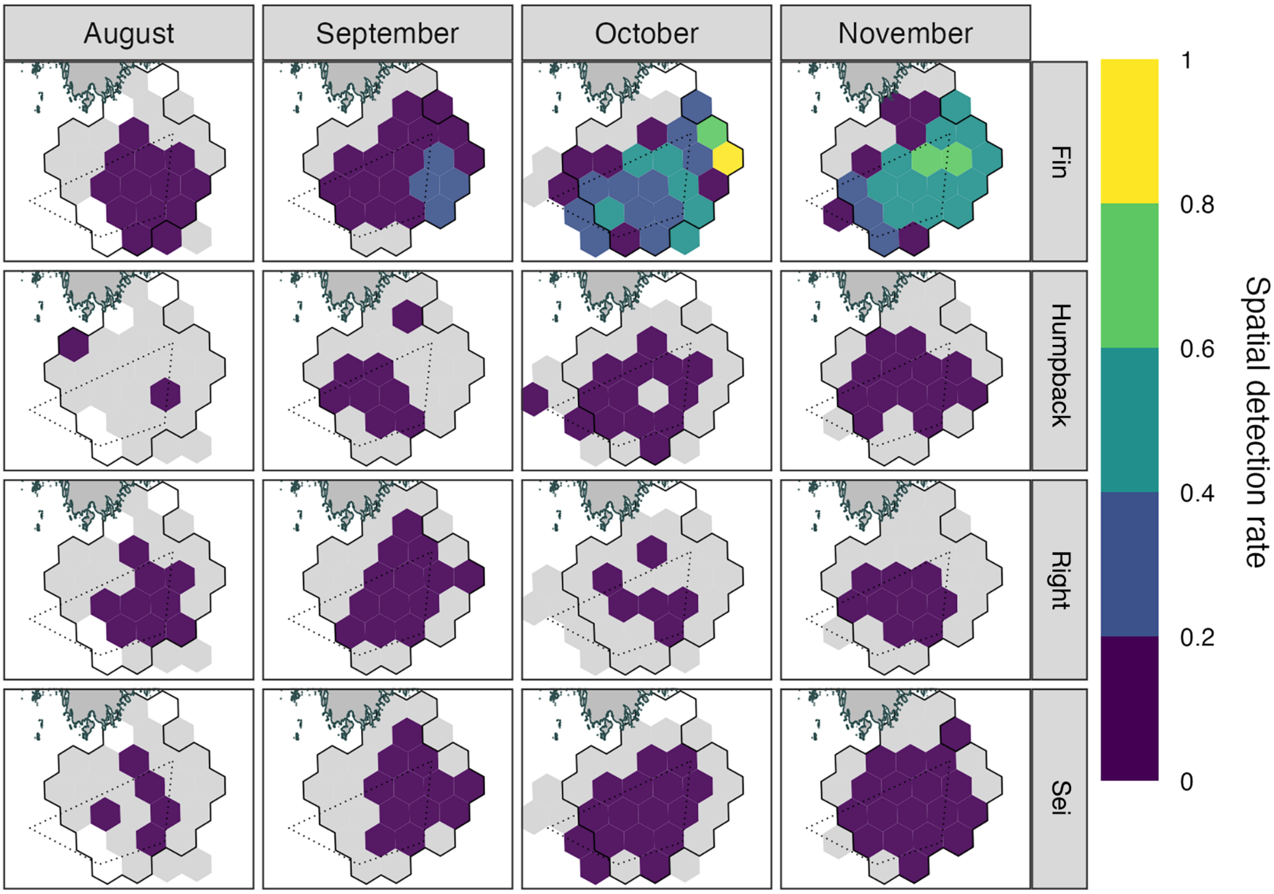

Fig. 4. Spatial detection rates (computed as the number of detected tally periods divided by the total number of tally periods per species, grid cell, and month across years) of each species (rows) and survey month (columns) in 20 km (diameter) hexagonal grid cells. Hexagonal cells outlined in black are used for the habitat analysis. Dashed polygon: the Roseway Basin Area To Be Avoided; grey cells: areas with survey effort but no detections

(KW = 60.5, $p < 0.001$), with significantly higher rates at night relative to dawn, day, or dusk (Dunn's multiple comparison test, $p < 0.001$; Fig. 5).

3.1.3. Right whales

Daily detection rates of right whales were highest (~10%) in August (Fig. 3), driven primarily by a single 2015 deployment (Fig. S4). Right whales were detected sporadically throughout the season, with the lowest occurrence in October. The minimum and maximum monthly spatial extent of detections occurred in October and September, respectively. Although the spatial extent of detections varied from month to month, occurrence was most consistent along the SE margin of the deep basin (eastern margin of the ATBA; Fig. 4). There appears to be substantial interannual variability, although this is difficult to characterize given temporal and spatial variation in survey effort (Fig. 2). Right whale detection rates varied by light regime (KW = 23, $p < 0.001$). Detection rates during dawn hours were significantly lower than those during day or night. Detection rates at dusk were variable but significantly higher than those during the day (Dunn's multiple comparison test, $p < 0.001$; Fig. 5).

3.1.4. Sei whales

Sei whales were infrequently detected in August (only 4 d in 2015; Fig. S5). Daily detection rates tended to increase from September through November (Fig. 3). Similar to fin whales, the distribution of sei whale detections encompassed the entire study area except for the NW margin along the coast (Fig. 4). Sei whale detections varied by light regime

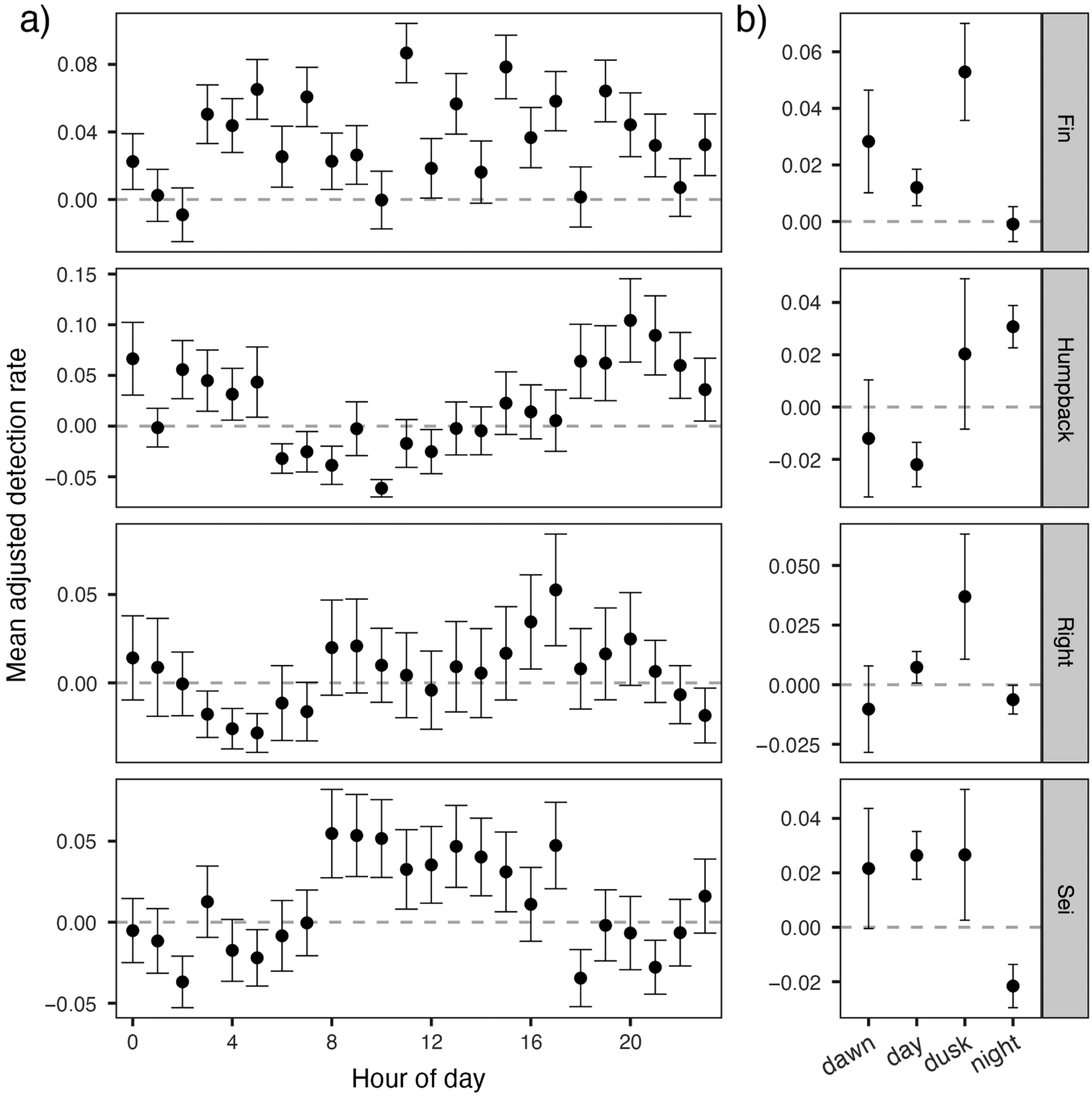

Fig. 5. Mean (±SE) adjusted detection rate (proportion of detected tally periods per hour) for each species (rows) by (a) hour of day (local time) or (b) light regime from all glider surveys

(KW = 40, $p < 0.001$) and were highest during day, low at night, and variable during dawn and dusk (Fig. 5).

3.2. Habitat associations

3.2.1. Whale occurrence in survey units

Across all years, survey effort was conducted in 30 grid cells in August, 70 in September, 70 in October, and 97 in November (total of 267 grid cells). These surveys transmitted 4478 h (187 d) of pitch track data divided into 19 578 tally periods, all of which were analyzed in near real-time. This amounted to a mean (±SD) of 73 ± 68 tally periods and 16.7 ± 15.8 h of pitch tracks per cell (total: 267). The gliders collected 12 863 profiles over the same period, with an average of 48 ± 46 profiles per cell. Spatial and temporal patterns in whale occurrence (presence—absence) in grid cells followed similar patterns to detection rate

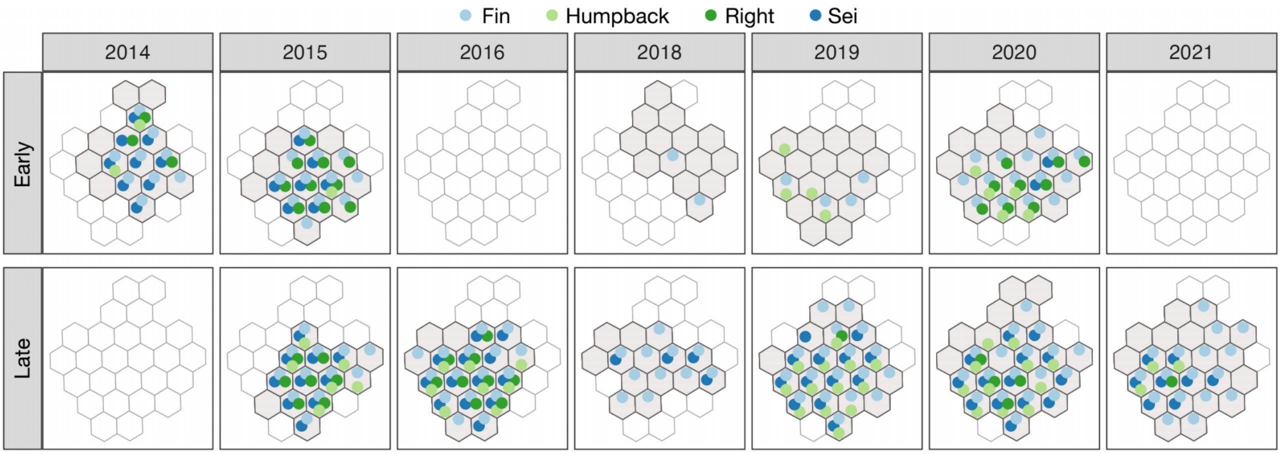

Fig. 6. Distribution of glider survey effort and whale occurrence in each time period (in rows, where 'Early' refers to August–September and 'Late' refers to October–November) and year (2014–2021; columns) in 20 km (diameter) hexagonal grid cells in Roseway Basin. Colored points: acoustic presence of a given whale species within a grid cell. Cells with survey effort (grey) were included in the habitat analysis; cells without effort (white) were not. Spatial extent of these grid cells within the study area is shown in Fig. 1

(Figs. 4 & 6). Fin whales were detected in 68.5% of cells (183 out of 267), humpbacks in 22.8% (61 out of 267), right whales in 20.2% (54 out of 267), and sei whales in 36.7% (98 out of 267). There appeared to be interannual variability in the occurrence of some species, but this was difficult to assess given the heterogeneity in survey effort.

3.2.2. Environmental data

The median *depth* and *depth_sd* of each grid cell were 114.7 m (interquartile range, IQR: 96.6–132.8) and 16.4 m (IQR: 11.8–21.1), respectively, with *depth* ranging from 36 to 160 m and *depth_sd* from 2 to 28 m. The distributions of *depth* and *depth_sd* were similar across months, suggesting consistent sampling with respect to bathymetry. The median stratification strength was 1.4 (IQR: 1–1.9) kg m^{-3} and decreased from August to November at an approximate rate of −0.4 kg m^{-3} mo^{-1}. The median bottom mixed layer thickness was 18.8 m (IQR: 10.9–26.8) over the full study period and was about 6 m thicker in the first half of the period (August–September; median: 21.8 m) than in the second (October–November; median: 15.9 m). The median density of the bottom mixed layer was 25.9 kg m^{-3} (IQR: 25.6–26.2), with skewed distributions in October and November driven primarily by a freshwater flushing event in 2015 (described in Ruckdeschel et al. 2020). The depth-integrated current ranged from 0.01 to 0.48 m s^{-1} with a median of 0.23 (IQR: 0.16–0.29).

3.2.3. Descriptive analysis

Graphical comparisons of the distribution of environmental variables in grid cells where whales were acoustically detected to the distribution of all observations in a given time period revealed possible associations that could inform and corroborate statistical modelling. Few observations of any species occurred in cells with shallow (<100 m) depths (Fig. 7). Right whales were present in cells with higher surface stratification in each time period, despite the seasonal decrease in stratification. Right whale occurrence was apparently associated with a thin bottom mixed layer in the early period (August–September) and a thick bottom mixed layer in the late period (October–November). The bottom mixed layer density in cells with right and sei whale detections was heavier than average in the early period, but lighter in cells with right whale detections in the late period. Occurrence did not appear to be influenced by current speed (Fig. 7).

3.2.4. Logistic regression analysis

Logistic regression analysis provided evidence of associations among environmental variables and the occurrence of fin, right, and sei whales (Tables 3 & 4, Fig. 8). Similarity of drop-in-deviance test results among models fit using 1 and 2 mo time intervals suggested that the coarser time resolution successfully accounted for the major sources of temporal variabil-

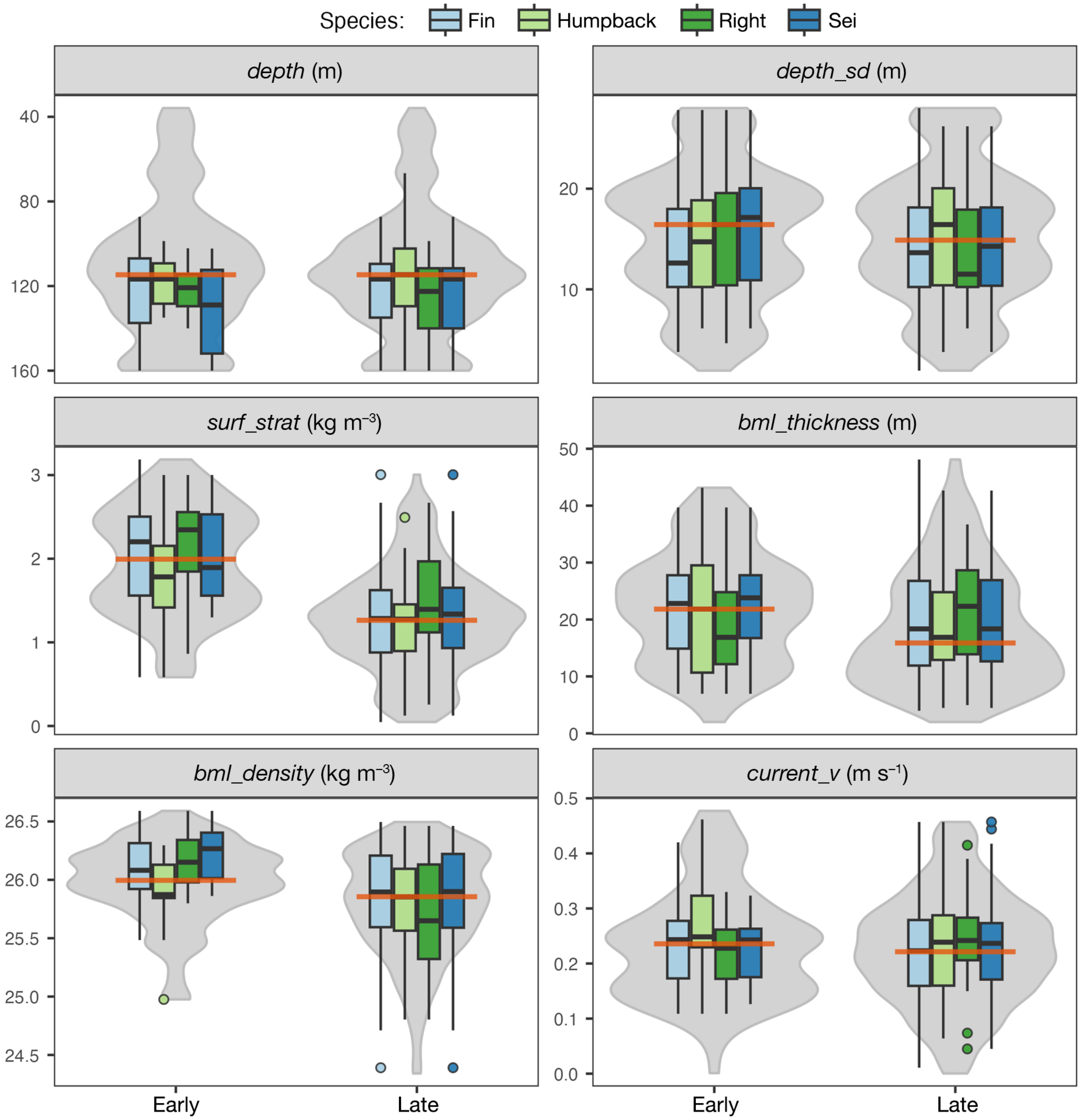

Fig. 7. Distribution of environmental variables from grid cells in which a given whale species was detected (colored boxplots) compared to the median (red bar) and distribution (grey violin plots) of values from all grid cells in each time period (where 'Early' is August–September and 'Late' is October–September). Boxplots show the median, upper and lower quantiles; upper and lower whiskers extend no further than 1.5 times the interquartile range to the largest and smallest values, respectively; points outside that range: individually plotted outliers. The violin plots show a mirrored kernel density estimate, or essentially a smoothed histogram, of the distribution of all cells in each period. Definitions of each environmental variable are available in Table 2

ity. For sei whale models, the addition of a *depth* covariate removed the significance of *bml_thickness*, *bml_density*, and *current_v*, suggesting that the significance of each of these terms was driven by their correlation with *depth* (Table 3). The significant model in set 8 showing an influence of *bml_density* on humpback occurrence is disproportionately influenced by a single detection in very light waters in August, and as such should be treated with suspicion. The occurrence of fin, right, and sei whales was posi-

Table 3. Results (p-values) of drop-in-deviance tests of 8 sets of logistic regression models. Model sets 1–8 were constructed with Eqs. (2) to (9) in the text and evaluated against models of the same form but lacking the variable of interest. The number of cells with whale presence and absence are given in N_1 and N_0, respectively. Significance (*) was evaluated at $\alpha = 0.05$. Dashes indicate inapplicable statistical tests that were not conducted because the variable of interest was included as a covariate in the full model. Underlined values indicate models that likely suffer from overfitting. Additional information for significant models is provided in Table 4

Species	N_0	N_1	Variable	Set 1	Set 2	Set 3	Set 4	Set 5	Set 6	Set 7	Set 8
Fin	28	61	*depth*	0.001*	–	< 0.001*	–	< 0.001*	–	< 0.001*	–
	28	61	*depth_sd*	<0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*
	28	61	*surf_strat*	0.8	0.24	0.6	0.14	0.97	0.32	0.93	0.6
	30	59	*bml_thickness*	0.013*	0.28	0.007*	0.1	0.012*	0.16	0.002*	0.019*
	31	58	*bml_density*	0.001*	0.07	< 0.001*	0.025*	< 0.001*	0.028*	0.004*	0.031*
	26	62	*current_v*	0.49	0.28	0.32	0.22	0.35	0.19	0.26	0.07
Humpback	206	61	*depth*	0.64	–	0.6	–	0.59	–	0.44	–
	206	61	*depth_sd*	0.68	0.57	0.73	0.61	0.69	0.58	0.81	0.75
	206	61	*surf_strat*	0.14	0.12	0.12	0.11	0.11	0.1	0.28	0.26
	205	61	*bml_thickness*	0.34	0.39	0.3	0.36	0.32	0.38	0.57	0.65
	205	61	*bml_density*	0.45	0.26	0.54	0.34	0.51	0.31	0.1	0.048*
	203	60	*current_v*	0.38	0.31	0.39	0.31	0.41	0.32	0.43	0.39
Right	213	54	*depth*	0.014*	–	0.015*	–	0.015*	–	0.044*	–
	213	54	*depth_sd*	0.17	0.49	0.16	0.44	0.17	0.48	0.31	0.62
	213	54	*surf_strat*	<0.001*	0.001*	<0.001*	0.001*	<0.001*	0.002*	0.004*	0.007*
	212	54	*bml_thickness*	0.59	0.8	0.6	0.8	0.6	0.81	0.03*	0.036*
	212	54	*bml_density*	0.9	0.16	0.96	0.12	0.93	0.14	0.015*	0.029*
	209	54	*current_v*	0.08	0.11	0.08	0.1	0.07	0.09	0.09	0.09
Sei	169	98	*depth*	<0.001*	–	<0.001*	–	<0.001*	–	<0.001*	–
	169	98	*depth_sd*	0.15	0.58	0.1	0.5	0.1	0.5	0.14	0.31
	169	98	*surf_strat*	0.69	0.99	0.7	0.87	0.71	0.89	0.93	0.98
	168	98	*bml_thickness*	0.028*	0.3	0.018*	0.26	0.019*	0.27	0.06	0.53
	168	98	*bml_density*	0.024*	0.77	0.015*	0.69	0.018*	0.73	0.007*	0.25
	166	97	*current_v*	0.06	0.05	0.047*	0.05	0.05	0.06	0.1	0.08

tively associated with depth such that the probability of occurrence increased in deeper-than-average depths (Tables 3 & 4, Fig. 8). Model sets 2–8 for fin whales, which explored associations with depth and time, showed evidence of overfitting due to limited sample size and should be interpreted with caution. The effect of depth was indistinguishable between the first and second half of the study period for right whales, but significantly stronger in the second half of the study period for sei whales. Right whale occurrence was consistently associated with stronger-than-average surface stratification in both the first and second half of the study period. In contrast, their relationship to bottom mixed layer thickness and density appeared to change between the first and second half of the survey period. Occurrence in the first half of the study period was associated with a thinner, denser bottom mixed layer, and a thicker, lighter bottom mixed layer in the second half of the study period. There is evidence that the association with *bml_density*, but not *bml_thickness*, was driven by the late-season flushing event in 2015 (Table S1). There was limited evidence that *depth_sd* or *current_v* was associated with whale occurrence, although drop-in-deviance test p-values in model sets 1–6 hinted at a potentially weak relationship to sei whale occurrence (Table 3).

4. DISCUSSION

4.1. Right whales

While a sharp decline in sighting rates in the last decade is suggestive of a change in the importance of Roseway Basin to right whales, our results indicate that at least in some years, right whales may be sporadically present in the basin throughout the study period (August through November). This corroborates and extends recent analyses by Durette-Morin et al. (2022) and Davis et al. (2017), as well as earlier results from Mellinger et al. (2007), suggesting right whale presence in the basin extends into early winter. The occurrence of right whales in late fall and early

Table 4. Parameters of significant models identified from drop-in-deviance tests (see Table 3); error is the standard error of the estimate of a given coefficient. Model sets 1, 5, and 8 were fit using Eqs. (2), (6), and (9), respectively. The p-value shows results of the Wald's test of each coefficient, with significance (*) evaluated at $\alpha = 0.05$

Species	Set	Variable	Coefficient	Estimate	Error	p
Fin	1	*depth*	(Intercept)	−0.34	0.47	0.48
			depth	0.03	0.01	0.003*
			effort	0.03	0.01	0.009*
Right	5	*depth*	(Intercept)	−2.15	0.35	<0.001*
			depth	0.02	0.01	0.02*
			effort	0.01	0	<0.001*
			late	−0.4	0.34	0.24
Right	5	*surf_strat*	(Intercept)	−2.23	0.35	<0.001*
			surf_strat	1.08	0.34	0.001*
			effort	0.01	0	<0.001*
			late	−0.43	0.34	0.21
Right	8	*bml_thickness*	(Intercept)	−2.21	0.36	<0.001*
			bml_thickness	−0.06	0.03	0.042*
			late	−0.41	0.35	0.24
			effort	0.01	0	<0.001*
			depth	0.02	0.01	0.023*
			bml_thickness:late	0.09	0.04	0.012*
Right	8	*bml_density*	(Intercept)	−2.27	0.38	<0.001*
			bml_density	1.41	1.16	0.23
			late	−0.24	0.37	0.53
			effort	0.01	0	<0.001*
			depth	0.02	0.01	0.044*
			bml_density:late	−2.47	1.18	0.037*
Sei	5	*depth*	(Intercept)	−3.47	0.48	<0.001*
			depth	0.02	0.01	<0.001*
			effort	0.02	0	<0.001*
			late	2.33	0.41	<0.001*

winter and their detection in near real-time are especially notable from a conservation perspective given the challenges (e.g. weather, visibility) of conducting regular visual surveys at that time of year, compounded with the risk of entanglement and vessel strike in the region (Vanderlaan et al. 2008, van der Hoop et al. 2012). It further demonstrates the utility of an autonomous platform for conducting persistent surveys in adverse conditions.

Right whales were most consistently detected along the SE margin of Roseway Basin. This agrees with findings from Davies et al. (2014) that suggest the combined influence of slope water intrusions, tidal advection, and bathymetric constraints function to concentrate *Calanus* spp. along this margin of the basin. It also aligns with the highest sighting probability derived from vessel-based surveys of the region (Davies et al. 2014). These findings suggest that glider-based PAM is capable of resolving spatial associations at scales of approximately the same order of magnitude of the expected maximum detection range (~30 km; Johnson et al. 2022).

Diel patterns in right whale detections have been studied previously. The increased detection of right whale calls in twilight hours reported here is consistent with findings from Wilkinson Basin (Mussoline et al. 2012) and for periods of the year with high vocal activity in Massachusetts Bay (Morano et al. 2012). In the central Gulf of Maine, Bort et al. (2015) documented a bimodal diel pattern of upcalls with peaks at both dawn and dusk. Mellinger et al. (2007) reported no diel pattern at a site located in our study area (on the SE margin of Roseway Basin), and an increase in calling during daylight hours at a site in Emerald Basin (approximately 150 km eastward of Roseway). Their analysis omitted crepuscular periods (dawn and dusk) and compared between light and dark hours. We also found no statistically significant difference between light and dark hours (Fig. 5).

The biological significance of diel patterns in vocal behavior is unknown for right whales. There is evidence that changes in calling rates are linked to behavioral states, where calling is higher during socializing and lower during foraging (Parks et al. 2011). In other baleen whale species, diel patterns have been associated with diel changes in prey availability (e.g. Baumgartner & Fratantoni 2008). The apparent spatial and temporal variation in diel patterns observed across these different studies is perhaps indicative of specific behaviors. An improved understanding of the mechanisms behind diel periodicity may permit the use of broadscale PAM networks to elucidate behavior and inform more effective management.

Comparison of the right whale detections with local hydrography from the glider provided evidence of time-varying associations among right whale occurrence and the bottom mixed layer, where the odds of right whale presence early in the study period increased with a shallow, dense bottom mixed layer. The association with a dense bottom mixed layer early in the study period is expected based on work from Davies et al. (2014) showing evidence of a strong positive correlation between the water mass density and *Calanus* spp. energy density in the deep basin. Our findings conflict with those of Baumgartner et al. (2003) for Roseway and the Bay of Fundy,

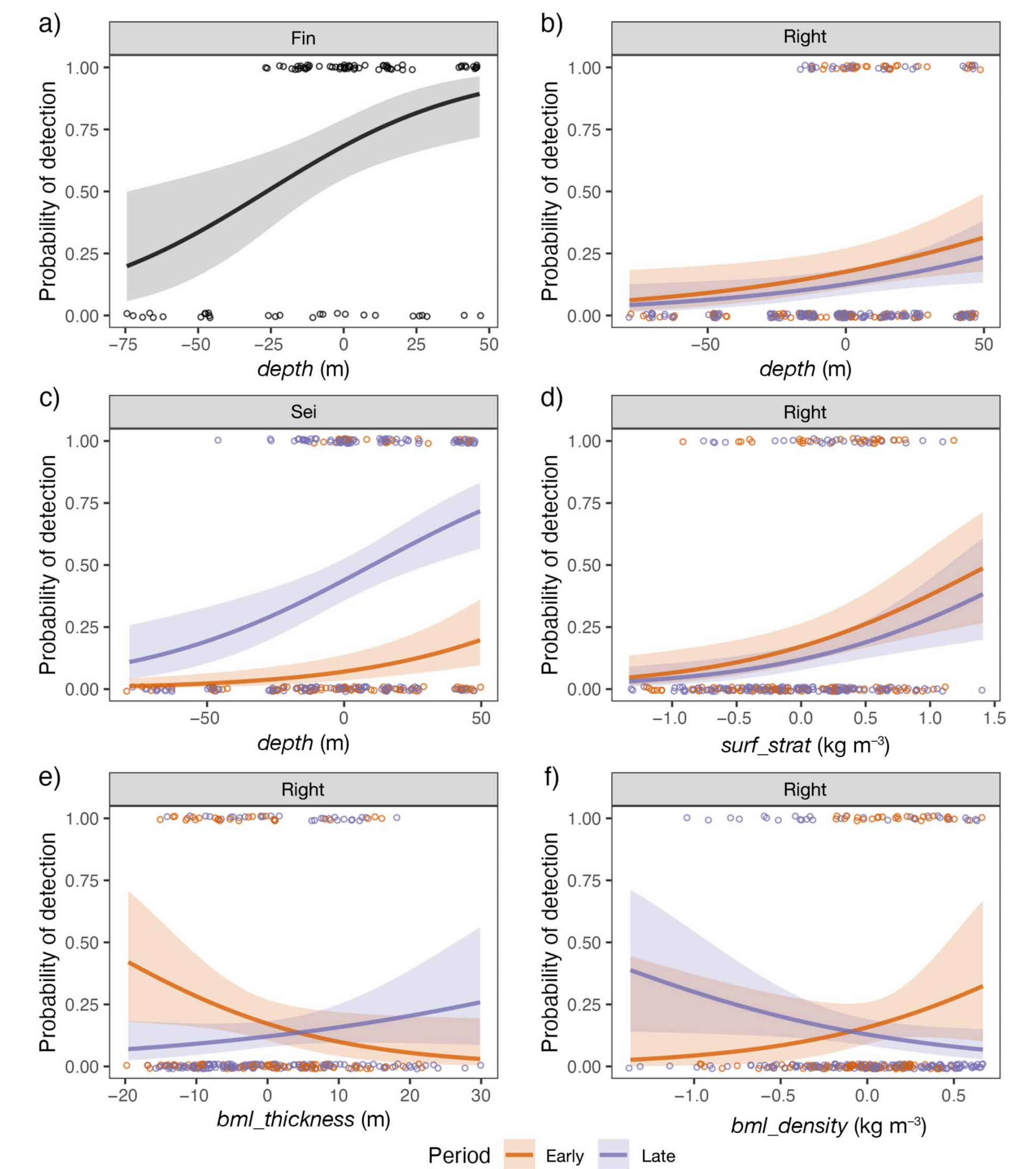

Fig. 8. Selected results of the logistic regression analysis of whale–habitat associations over the full study period (all months; black) or in the first half (Early; August–September; orange) versus second half (Late; October–November; blue) of the study period. (a) Relationship between depth and probability of fin whale detection over the full study period (corresponds to model set 1, fit with Eq. 2). (b,c) Additive effects of survey time (early or late) and depth on the probability of right and sei whale detection, respectively. (d) Additive influence of time and surface stratification on right whale detection. Models in (b–d) were from set 5 (fit with Eq. 6). (e,f) Interactive effects of time and (e) bottom mixed layer thickness or (f) bottom mixed layer depth on right whale detections (models correspond to set 8, fit with Eq. 9). Solid lines: model fit; shaded region: 95% confidence limits; jittered points: raw data used to construct the regressions. Values of environmental variables are expressed as anomalies from the monthly average across all years. Definitions of each environmental variable are available in Table 2. Model comparison results and parameters are available in Tables 3 & 4, respectively

as well as those from H. D. Johnson et al. (unpubl. data) for the Gulf of St. Lawrence, in which there was evidence of a positive association between whale occurrence and bottom mixed layer thickness (i.e. whale presence was more likely when the bottom mixed layer was thick). A potentially confounding factor is that the inflection depth of the glider (~8 m above the sea floor) prevented us from sampling as close to the sea floor as is typically achieved with CTD casts, so bottom mixed layer thicknesses measured with a glider and a CTD cast may not be directly comparable. A possible explanation for the discrepancy is that the zooplankton layer can be either concentrated just above the bottom mixed layer, as suggested by Baumgartner et al. (2003), or within it, as suggested by Davies et al. (2014). If above it, a thicker bottom mixed layer would place the zooplankton layer closer to the surface where it can be more easily accessed by a foraging right whale. If within it, a thicker bottom mixed layer would dilute the zooplankton concentration (i.e. the copepods would be mixed over a greater depth span) and reduce foraging efficiency. Although the dynamics of patch formation are not well understood, the position of *Calanus* is likely a function of their physiological state (e.g. active or in diapause), the density of the surrounding seawater (and associated impact on copepod buoyancy), and local hydrodynamic forcing (Baumgartner & Tarrant 2017).

Previous studies of right whale habitat in Roseway have been restricted to the summer months. This study is the first to demonstrate changes in the strength of these associations late into the fall. The change over time may reflect a shift in the factors affecting right whale distribution and/or right whale calling behavior. It is difficult to assess the cause of this trend as the fall is an especially dynamic period, but the temporal shift in right whale habitat associations was notably absent in the habitat associations of other species. It is also possible that the reason for the change is driven primarily by behavioral factors, such as a transition from foraging into travelling states, but this is speculation based loosely on observed seasonality in right whale distribution patterns (Brown et al. 2007).

We also observed strong evidence that right whale presence was associated with a positive anomaly in stratification strength, and that this relationship persisted over time as the water column destabilized. Baumgartner et al. (2003) tested for and did not find evidence of a similar relationship to stratification strength in Roseway, but Baumgartner & Mate (2005) observed that right whales equipped with satellite tags tended to visit areas characterized by high surface stratification. Right whales are known to feed on surface and near-surface layers of copepods in other habitats, such as Cape Cod Bay (Mayo & Marx 1990). Within Roseway, perhaps right whales are associated with times and places of relatively high stratification and reduced vertical mixing because these conditions are more likely to result in the formation of dense aggregations of copepods. Although speculative, the differences in habitat associations observed here and in the early 2000s suggest that right whales are using this habitat differently than they have in the past, which may be the result of a substantial decline in the availability of late-stage *C. finmarchicus* across the region (Record et al. 2019, Sorochan et al. 2019).

4.2. Fin whales

Fin whale calling was extraordinarily prolific and detections were nearly constant within the deep basin, especially later in the study period. The signal we used to detect fin whale presence, repeated sequences of the 20 Hz pulse, is considered song and suspected to be produced solely by males as part of a reproductive display (Croll et al. 2002). It is highly seasonal, and some evidence suggests it is not produced in association with feeding behavior (Romagosa et al. 2021). It also has the potential to propagate long distances, perhaps up to 100 km (Stafford et al. 2007), which is approximately the scale of our study area. The abundance of song on every deployment in this data set suggests that Roseway Basin plays a potentially important role in fin whale reproduction. This is reinforced by findings from Davis et al. (2020) that show fin whale detections on the Scotian Shelf are low in June and July, increase in August, and are consistent from September through December. Although beyond the scope of this study, a detailed analysis of the song structure, namely the inter-pulse interval, could identify the population of the singer(s), which could prove useful for population assessment and management (Delarue et al. 2009).

The same factors that likely make fin whale song an effective reproductive display impose significant barriers to using song to infer habitat associations, particularly over small spatial scales. Although modelling efforts were compromised by high autocorrelation and the rarity of absences, some interesting patterns emerged from our analyses. The first is the near-complete absence of fin whale detections in the coastal shallows in the NW of the study area. This absence is most pronounced in November, when areas without detections were only separated by ~50 km from areas where detections were nearly constant. The most likely explanation is that fin whales avoid shallow areas. It is also likely that the shoaling bathymetry increases transmission loss of fin whale calls, effectively restricting detections to deeper water (Jensen et al. 2011). Perhaps both factors are at play, as fin whales seeking to advertise their reproductive status over a large range would likely avoid, or at least avoid vocalizing within, areas characterized by reduced propagation range. Future efforts could focus on the 40 Hz fin whale call, which has been linked to prey biomass and as such may be more appropriate for habitat analyses (Romagosa et al. 2021).

4.3. Sei whales

The spatial and temporal patterns of sei whale detections were similar to those of fin whales. This includes the seasonal increase in detection rate and the nearly complete absence of detections in the NW portion of the study area near the coast. Compared with fin whales, however, sei whale calling was much less prolific, and, although the spatial extent of the region with detections in October and November was comparable to that of fin whales, the detection rates were much lower.

The downsweep call used to identify sei whales has been linked to both foraging and song behavior. Baumgartner & Fratantoni (2008) documented diel patterns in call rate in close association with the diel vertical migration of zooplankton prey. The authors suggested that vocalizations were reduced at night while whales were foraging on zooplankton near the surface and increased during the day when the migrating layer was deep and whales engaged in social behaviors. Tremblay et al. (2019) observed these downsweeps produced in association with other calls in a structure consistent with that of song. Our analysis did not distinguish between potential song or non-song, but our observation of the same diel pattern as described by Baumgartner & Fratantoni (2008) provides circumstantial evidence that sei whales were engaged in foraging behavior.

The intermediate detection rates and reduced autocorrelation also facilitated more detailed habitat analyses than were possible with fin whales. The reduced detection and autocorrelation may have resulted from smaller detection ranges of sei whales (10–15 km; Baumgartner & Fratantoni 2008) compared to fin whales (50–100 km; Stafford et al. 2007). The results provided evidence of a positive association with depth that strengthened in the second half of the study period. This was consistent using time resolutions of 1 or 2 mo. The cause of this trend is difficult to determine but could be ecological (e.g. the transition to a different foraging strategy) as sei whales are perhaps the most general predators of the baleen whales considered here, capable of foraging on copepods, krill, and schooling fish. The shift could also be behavioral, particularly given the evidence that the same call type can be produced in association with foraging (Baumgartner & Fratantoni 2008) as well as in patterned bouts consistent with song (Tremblay et al. 2019). An additional confounding factor in these analyses — and perhaps a reason for the similarity between sei and fin whale associations with depth — is that their low-frequency, high-amplitude vocalizations likely propagate over even greater ranges in deep areas (Jensen et al. 2011).

4.4. Humpback whales

Humpback occurrence was determined based on the presence of song. The sparse detections in September followed by the increase in October coincides exactly with the timing of the transition from the production of song fragments to full song described by Kowarski et al. (2021). They attribute the timing of song onset to changes in photoperiod. The time series suggests coincident increases in sei and fin detection rates. Although speculative, the apparent synchronization of this increase could be due in part to photoperiod. It could also be a result of interannual variation in detections and/or effort, or a host of additional unresolved factors.

Similar to Kowarski et al. (2018), humpback detections occurred predominately during evening and night hours. The reasons for the diel pattern are unknown. Given the relatively low numbers of humpback whale detections, as well as the potentially confounding effects of using song as a detection cue, it is perhaps not surprising that the habitat analysis did not reveal any robust associations between humpbacks and their environment. Furthermore, our model was designed to target hydrographic processes known to aggregate right whale prey. These are likely less effective prey proxies for piscivorous humpbacks, as the distribution and abundance of the schooling fish they prey upon may be decoupled from or less influenced by these physical properties and dynamics (Hazen et al. 2009).

4.5. Challenges and caveats

Though the use of gliders for PAM is well-established (Baumgartner & Fratantoni 2008, Klinck et al. 2012, Baumgartner et al. 2020), the use of these platforms to make habitat inferences is in its relative infancy. We therefore consider our habitat analyses as exploratory and sought to conduct them in such a way as to overcome several of the challenges inherent to this data set. The first potential issue is the use of acoustic detections as a measure of whale presence without accounting for call availability (the probability a whale will produce a call) or detectability (the probability that a produced call will be detected). Call production by baleen whales is highly variable and behaviorally mediated, and the reasons for calling are poorly understood (e.g. Parks et al. 2011). While some calling behaviors may relate directly to foraging or habitat quality, others are likely produced in an unrelated context, serving to, for example, advertise reproductive status or maintain long-range group cohesion during migration (Payne & Webb 1971, Clark & Ellison 2004). There is evidence that several species vocalize less frequently while foraging (Baumgartner & Fratantoni 2008, Parks et al. 2011). That said, baleen whales are mobile predators with high energy demands whose distribution must at some point be correlated with that of their prey (Palacios et al. 2013).

Variability in detection poses another challenge for interpreting whale presence. The detection range varies by source (species), environment, noise level, glider depth, and analysis protocol (Helble et al. 2013, Marques et al. 2013, Fregosi et al. 2022, Johnson et al. 2022). Furthermore, for baleen whales, the area being monitored is almost certainly an order of magnitude larger than the area over which environmental data are being collected, leading to a time–space mismatch between occurrence and environmental data. This issue would likely be mitigated considerably for other species with smaller detection ranges, such as odontocetes. Accounting for this mismatch of scales is not trivial. We pursued a variety of other different definitions of survey units (e.g. trackline segments, time-averaged glider position) before selecting a monthly gridding approach as the most suitable for retaining as much data and resolution as possible while addressing the temporal and spatial correlation structure and the significant heterogeneity of survey effort. Future studies could explore optimizing grid sizing for each species based on the autocorrelation structure and/or estimated detection range. An alternative approach would be to apply an amplitude threshold to species detections, such that only loud calls presumably originating at close ranges from the glider would be considered in the analysis. This was not feasible in our exploratory analysis, given that we determined acoustic occurrence by evaluating multiple calls over the course of a 15 min tally period rather than on a call-by-call basis. A further limitation of this approach is that the occurrence of some species, especially humpback and right whales, was relatively rare. Rejecting additional calls under an amplitude threshold would likely further reduce sample size and statistical power. A more nuanced alternative to a threshold approach could be to include amplitude as a model covariate. All of the archived audio for these deployments is available, so such analyses could be conducted in the future. Another suggestion for future studies would be to plan surveys that cover a much larger spatial scale than the detection scale(s) of the animals of interest, as this could help mitigate some of the issues with autocorrelation.

Our overall goal was to evaluate the ecological importance of specific physical processes to baleen whales rather than develop a predictive model of whale occurrence. This is an important distinction that informed our choice of statistical approach. We chose to avoid stepwise variable selection from a large, multivariate model, as the ecological influence of several simultaneously selected variables can become difficult to explain, and the resulting p-values are potentially compromised by the selection process (Palacios et al. 2013). Similarly, we avoided the use of 'black box' modelling approaches, which produce a result with little to no information about the internal process, in favor of the ecologically interpretable results of the logistic regression (Redfern et al. 2006). We conducted preliminary analyses using generalized additive models to avoid making any assumptions about the functional form of the relationship among the predictor and response variables. We found this approach was limited by its inability to readily resolve interactions among predictor variables. The results of our analysis demonstrate the importance of resolving these interactive effects. This makes ecological sense, as baleen whale foraging and the dynamics that aggregate their prey are almost certainly mediated by the complex interaction of multiple factors (e.g. Hazen et al. 2009). The next step in our modelling procedure would be to increase the number of predictor variables to represent additional processes, especially those of relevance for rorqual foraging, and to use those results to inform the careful construction of multivariate models to address specific hypotheses about whale–habitat associations.

Although we made efforts to thoroughly evaluate and address all the underlying assumptions of the logistic regression analysis, the significance levels of our tests should be interpreted with caution. Repeated hypothesis testing raises the multiple comparisons problem, wherein the likelihood of erroneous results increases with the number of tests conducted. This can be controlled by using a single, multivariate model, which would be a logical next step for this analysis (Hosmer et al. 2013). Another mitigation measure is to increase the significance level proportionally to the number of models run, referred to as a Bonferroni adjustment. In our case, the Bonferroni-adjusted significance level for a given species and model set would be 0.008 (0.05 / 6 models). At this level, observed associations between right whales and *depth*, *bml_density*, and *bml_thickness* would no longer be significant. We opted to use the uncorrected p-values to avoid missing weak but ecologically relevant relationships but suggest that precautionary treatment of these values is warranted. That said, the relationships that emerged from the statistical analyses were also evident in the raw data (Fig. 7), instilling confidence in both the statistical approach and results.

4.6. Conclusions

We gathered a large data set of passive acoustic and hydrographic data using autonomous vehicles and conducted an analysis of baleen whale occurrence and potential habitat associations in Roseway Basin. Our results provide insights into the spatial and temporal distribution of the acoustic occurrence of each species within the habitat and corroborate previously documented diel vocalization patterns. Although it was challenging to account for the mismatch of observational scales and behaviorally mediated acoustic behavior, our results identified right whale habitat associations that align with those that have been established previously. The high-resolution, fine-scale, vertical sampling of the Slocum glider provided insights into whale associations with subsurface features that would not have been possible using traditional remote-sensed data, nor feasible using shipboard methods. These platforms have great potential for helping to move the study of cetacean habitat associations beyond correlative analyses by elucidating the underlying biophysical mechanisms that influence species distribution.

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