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Influences of environmental and individual-level covariates on movement behaviour in American lobster *Homarus americanus*

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ABSTRACT: Movements reflect important activities and life history events for animals, and therefore understanding what influences movement in organisms is increasingly important as climate change alters environmental conditions at unprecedented rates. This has relevance for predicting the effects of climate change on fitness and interpreting stock status of species such as American lobster *Homarus americanus*, whose catchability is behaviourally mediated. We analysed movement tracks from tagged lobsters in a natural environment over short (10 d, n = 37) and long timescales (up to 7 mo, n = 16), applying hidden Markov models to investigate the influence of individual-level and environmental covariates on movement patterns. We classified movement tracks to identify behavioural states through time and compared the distribution of states across habitats to understand how movement may relate to bottom composition. In the short-term analysis, we found evidence for 3 behavioural states: Sheltered, Exploratory, and Transit. In the long-term analysis, we found evidence of Sheltered and Exploratory states, but the Transit state was absent. Movement parameters varied across temperature, with higher velocities and more tortuous movements at higher temperatures. Our results demonstrate that lobsters spend most of their time Sheltered, with state probabilities being altered by diel period, time since release, sex, carapace length, temperature, and tide trend. Further, mobile states were typically observed in areas of low algal cover. Our results underscore the importance of environmental and individual-level factors in understanding lobster movement and suggest that such factors could obscure population depletion if not accounted for in a warming environment.

KEY WORDS: Hidden Markov models · Telemetry · Habitat · Temperature · Diel cycle · Tagging effects

1. INTRODUCTION

Understanding responses of animals to their environment is the basis on which we predict, manage, and mitigate impacts to populations from potential stressors (Hussey et al. 2015). While laboratory-based studies allow us to test interactions between animals and a variety of biotic and abiotic variables in a controlled setting, field-based movement studies are needed to reveal important insights into behavioural and physiological responses across environmental gradients, habitat associations, species interactions (Florko et al. 2021), and key ecological processes (Bianchi et al. 2023). Further, understanding animal movement patterns has relevance in an applied context to identify biases in survey methodologies

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(Geraldi et al. 2009), assess the effectiveness of proposed conservation initiatives (Bowlby et al. 2007), predict population responses to changing environments (McMahan et al. 2013, Hussey et al. 2015, Florko et al. 2021), and inform fisheries management (Lees et al. 2018). Climate-driven changes are impacting marine systems, and movement models offer a valuable approach to understanding the conditions that influence species-specific behaviours at fine spatial and temporal scales. By incorporating these dependencies into stock assessments, movement models can enhance adaptive management-based decision-making in the face of changing environmental conditions.

Demands for informed management are particularly stringent for valuable fisheries, as their importance creates pressure to maximize yields without compromising the long-term sustainability of the stocks. The American lobster *Homarus americanus* is one of the most commercially valuable species, worth more than 3 billion Canadian dollars (~2.2 billion USD) annually to the Canadian economy (Fisheries and Oceans Canada 2022). These trap fisheries are a key economic driver of many coastal communities along the northeastern USA and Atlantic Canada. In the centre of the species' distribution, the role of lobster in both the economy and ecosystem has changed substantially over the past 25 yr, as many of the historically important fisheries such as Atlantic cod and herring have collapsed due to climate change and high fishing pressures (Pershing et al. 2015, Trochta et al. 2020). The dramatic increase in lobster biomass over a similar time scale has been attributed to improved climate conditions, release from predators, and implementation of conservation measures (Le Bris et al. 2018). In contrast, at the southern extent of the species' range, climate change, and in particular, warming waters, have contributed to the collapse of lobster fisheries (Wahle et al. 2015, Lebris et al. 2018, Reardon et al. 2018). Pathways of effects of warming water on lobsters include elevated activity rates (McLeese & Wilder 1958), more time outside of refuge habitats while foraging to meet increased energetic demands (Wang et al. 2016), and increased exposure to disease (e.g. shell disease; Groner et al. 2018). These factors can impact long-term population persistence (Harrington 2019).

Compared to many invertebrates that are chronically understudied (Hussey et al. 2015, Florko et al. 2021), the habitat use (Geraldi et al. 2009, Morse et al. 2018, Carloni et al. 2021), home range size (Scopel et al. 2009, Watson et al. 2009, McMahan et al. 2013, Morse & Rochette 2016, Morse et al. 2018), and long-range movements of lobsters are relatively well documented (Pezzack & Duggan 1986, Florko et al. 2021). Despite this, few of these studies were conducted in natural environments (but see Bowlby et al. 2007, Morrison 2014, Morse et al. 2018, Lees et al. 2020) over long time periods or examined fine-scale movements. Fine-scale movements in particular are important, as they are fundamental to understanding the behavioural ecology of lobsters, their use of habitats, energy allocation (Hussey et al. 2015), and the biases they impose upon assessment methods through changes in catchability. The efficiency of capturing lobsters during assessment surveys or by fisheries may be influenced by a number of factors including temperature (Jury & Watson 2013), wind speed and direction (Drinkwater et al. 2006), and gear configuration. As such, there is a need for a deeper understanding of the factors affecting the fine-scale movement behaviour of lobsters.

As benthic marine animals are difficult to observe directly, researchers often infer movement behaviour using a variety of techniques that include mark—recapture and telemetry (Hussey et al. 2015, Florko et al. 2021). The drawback of using mark—recapture or simple telemetry receiver detections is that they only provide coarse positional data and leave the researcher to infer behaviour over considerable temporal periods between relocations. Positioning-telemetry studies provide greatly enhanced temporal resolution on movements of animals, but researchers are often left to interpret the resulting animal tracks 'by eye' to infer behaviour, making it challenging to quantify the characteristics of behavioural states and when they are employed by study animals. Recent advances in analytical methods such as hidden Markov models (HMMs; Whoriskey et al. 2017, 2022, McClintock & Michelot 2018), combined with precise positioning telemetry systems, are now allowing researchers to infer hidden behavioural states of marine animals more objectively from movement characteristics (e.g. speed and directional persistence of movement) and link these behaviours to environmental conditions and stressors, or interactions with marine infrastructure (e.g. wind turbines; Bacheler et al. 2019, Cote et al. 2020, van der Knaap et al. 2022, Elings et al. 2023, Hewitt et al. 2023).

In this study, we applied HMMs to tagged American lobsters to understand their fine-scale movement behaviour in a natural environment over short and long timescales, with detection periods up to 7 mo for some individuals. Specifically, we (1) defined 3 behavioural states exhibited by lobsters, (2) evaluated how the movement parameters of these states are modified by temperature, and (3) assessed the tendency of lobsters to be in these states based on explanatory variables such as bottom temperature, sex, diel period, carapace length, tide trend, and tagging effects. Our results are presented in the context of previous work and highlight the potential utility of integrating these quantitative movement and behavioural state estimates into applied conservation and management actions.

2. MATERIALS AND METHODS

2.1. Study area

Our study was conducted in the nearshore waters off Point Aconi, Nova Scotia, Canada (Fig. 1), at a location of potential interaction between lobsters and the Maritime Link Subsea High Voltage DC cables (Cote et al. 2019). The lobster movement data presented in this study were collected as part of the pre-installation phase to which post-installation data will be compared in the future. Since no post-installation data were available at the time of publication, this study focuses on the natural movement ecology of lobsters.

2.2. Telemetry array design and deployment

A high-resolution VEMCO Positioning System array, consisting of 16 independent receiver moorings, was deployed in the study area (Fig. 1) from autumn through spring over 2 consecutive years (2014–2016). Array design was informed *a priori* through *in situ* range tests to define optimal receiver spacing.

Acoustic receiver moorings were deployed in a standard Ocean Tracking Network configuration, using a combination of 69 kHz VEMCO VR2w (n = 9) and VR2AR (n = 7) receiver models (InnovaSea). Floatation consisted of a single syntactic foam float (40.6 cm diameter, 17.2 kg buoyancy; DeepWater Buoyancy), and all receivers were positioned approximately 3 m above the seabed. For moorings using VR2AR model receivers, which featured integrated acoustic release and sync tags, the floatation was tethered 1 m above the receiver. For VR2w model receivers, the receiver was positioned at the terminal end of the assembly, with the receiver oriented vertically and attached within a mounting cup to enable clean lines of sound transmission. Acoustic releases (875-TD, Teledyne Benthos) were used on VR2w receivers positioned on rope risers extending 1 m above the approximately 80 kg steel mooring weight. Fixed delay, time-synchronizing transmitters (sync tags), internal to VR2AR model receivers and separate external transmitters (V16-5H) for VR2w model receivers, were programmed to transmit at high power (160 dB) at fixed intervals of 600 s to permit calculation of precise receiver positions on the seabed. A single V13-1H reference (or sentinel) transmitter

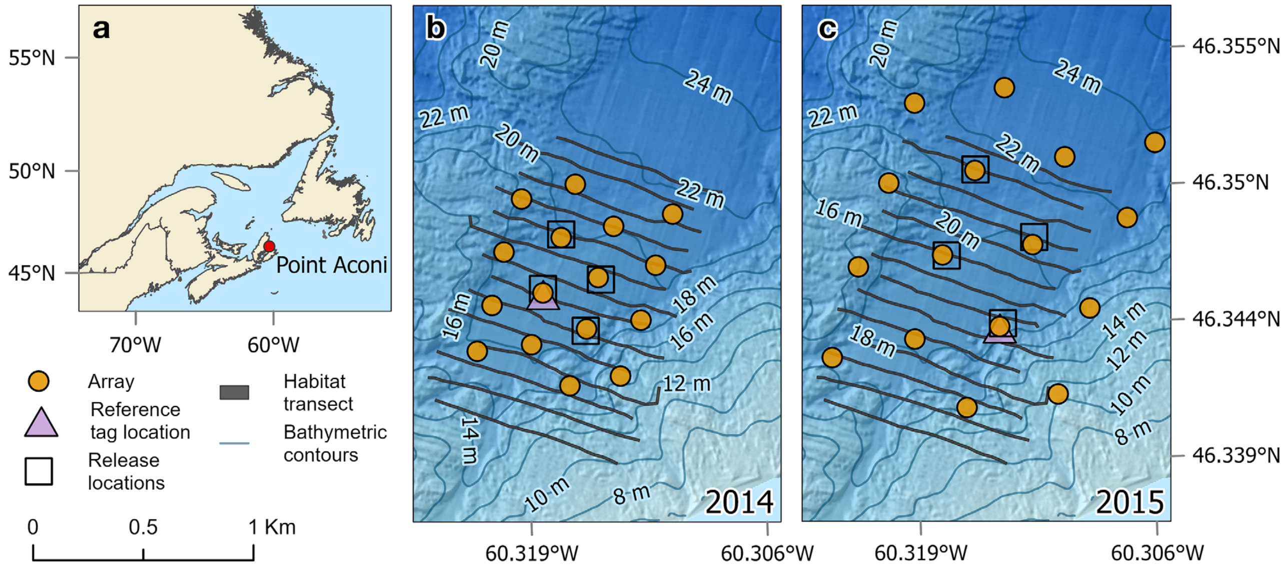

Fig. 1. (a) Location of the Point Aconi study area off Cape Breton, Nova Scotia, Canada, and the telemetry array orientation within the study area for (b) 2014 and (c) 2015 field seasons. Bathymetric contours (2 m) are shown for reference along with habitat transects, lobster release locations (4 per year), and reference tag locations. While the array maintained a 4 × 4 receiver configuration across years, spacing between receivers was extended in 2015. Habitat transects were conducted in 2014 and hence only reach the 2014 study area limits

was attached to the rope riser of a central mooring assembly 0.5 m above bottom, to approximate a tagged lobster, and served to evaluate detection efficiency throughout the study duration.

The array was deployed on 21 October 2014, prior to the release of tagged animals, and remained until 15 January 2015, when it was downloaded and removed to prevent data loss during the peak winter ice period. The array was redeployed on 23 February 2015 and subsequently removed on 14 May 2015 to avoid conflicts (e.g. entanglement in traps) with the commercial lobster fishery. In the first season (2014), receiver moorings were deployed at approximately 250 m spacing (in 0.65 km^2), with deployment depth ranging between 14 and 21 m (Fig. 1). Following the first year of data collection, the manufacturer advised that detection range was better than determined from range testing trials and suggested that the array spacing could be extended to 400 m during the 2015 deployment without significantly compromising data integrity (Fig. 1). Consequently, the array was redeployed after cessation of commercial fishing (13 September 2015) with the new configuration, where it remained through 16 May 2016. Due to logistical and weather delays associated with winter redeployment in the first year of the study, the array was left in the water for the entire winter in the second year of the study.

2.3. Animal capture, holding, and tagging

Local commercial harvesters were chartered to set baited traps overnight within the study area to catch American lobsters. Upon capture, lobsters were removed from the traps and inspected for physical damage or signs of decreased health and vitality and were banded and crated prior to being transferred to another chartered vessel for tagging. Lobster catches comprised primarily males in both 2014 and 2015; however, enough females were captured in 2015 so that the tags were almost spread evenly across both sexes (Table 1). Lobsters were tagged with VEMCO V13-1H (diameter: 13 mm; length: 36 mm, mass in water: 6.0 g, 69 kHz, estimated tag life: 653 d, transmission frequency: 60–180 s; Innovasea). Transmitter attachment methods were modified from those outlined by Bowlby et al. (2007), Morrison (2014), and Zisserson & Cameron (2016). Individual lobsters were measured (carapace length) and sexed. The area of transmitter attachment on the dorsal surface of the carapace was lightly abraded using a rotary tool with a flap-wheel sanding disc to improve tag adhesion. A vinyl tubing, spaghetti-style tag (Floy Tag) was attached through a cap built into the transmitter and positioned around the carapace between the first and second walking legs. A small volume of 3M® 5200 marine adhesive was then placed on the carapace area prepared with the rotary tool and the cap pressed into the adhesive. Once the acoustic tag was mounted in the adhesive, the spaghetti tag was tightened, the aluminum sleeve was crimped to secure it in place, and excess tubing was trimmed. Thin wire pipe cleaners were used to secure the posterior portion of the acoustic tag to further ensure tag position and adhesive contact throughout curing. These pipe cleaners were used as they corrode quickly and would fall off the animals soon after the adhesive cured.

Tagged lobsters were released in 4 equal-sized groups within each quadrant of the array (Fig. 1). These locations were selected to safeguard against any bias due to directional currents, and to avoid signal collisions associated with having too many animals in one location.

2.4. Data preparation

Acoustic positioning systems are designed to track fine-scale underwater movements of marine animals, but positions triangulated using these systems are often subject to some degree of measurement error. The fixed-position reference tag located within the array revealed that measurement error in the array during the study period was low (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m729p151_supp.pdf). Comparing the sync and reference tag observations to their respective centroid (grouped by transmitter) showed that 90% of observations were within 7.8 m of the centroid while 50% of observations were within 1.9 m. Similar to Cote et al. (2019), we managed these position outliers using a one-behaviour first-difference correlated random walk state-space model. This analysis attempts to reveal the underly-

Table 1. Summary of tagged American lobsters for 2014 and 2015

Total tagged	Male	Female	Transmitter	Date tagged	Date released
40	32	8	V13-1H	25 October 2014	26 October 2014
40	21	19	V13-1H	6 October 2015	6 October 2015

ing movement process while accounting for the measurement errors. Details of this approach are provided in Text S1.

HMMs were fitted using the 'momentuHMM' package in R (McClintock & Michelot 2018) to classify the lobster telemetry data into behavioural states and explore the effect of measured covariates on the transition probabilities between identified states. Behavioural states were inferred from 2 data streams: step lengths (straight-line distance between locations of a fixed temporal interval; Fig. S2) and turn angles (the angle measured between $t-1$, t_0 and $t+1$). One requirement of HMMs is that observations are spaced regularly through time (McClintock 2017). As a result, prior to HMM fitting, a continuous-time correlated random walk (CTCRW) model (Johnson et al. 2008) was fitted to regularize the time interval of the locations. The median time interval in the data prior to regularization was approximately 3 min, but due to the large number of observations and the time required to fit these models, we compared the results of HMMs fitted to a subset of the data with locations interpolated at both 3 and 15 min time intervals. Overall, movement speeds and turn angles showed similar patterns across inferred states, and therefore tracks were regularized to 15 min in order to balance computational efficiency with temporal resolution.

There were several temporal gaps in the location data exceeding the maximum expected detection interval (3 min) and the interpolation interval. These detection gaps could have occurred when lobsters moved beyond the array. Alternatively, periods of signal loss could have occurred when lobsters sheltered in structurally complex habitats such as boulders or vegetation (Karnofsky et al. 1989a). We identified segments when animals were likely sheltering in place by flagging detections separated by >1 h with ≤50 m of displacement. In instances when consecutive detections were separated by >1 h and >50 m of displacement, we assumed they represented periods when the animal had left the array and re-entered later. The latter were removed from the data before fitting the CTCRW, whereas the former were retained and assigned a Sheltered behavioural state (using the 'knownState' parameter in the 'fitHMM' function). Positions were interpolated at 15 min intervals for segments with more than 100 observations (sufficient data to avoid HMM convergence issues) using the 'crawlWrap' (McClintock & Michelot 2018) function, resulting in 74 segments across 39 individuals (Table S1).

It was apparent that the number of individuals within the array decreased over time. As random effects are not easily incorporated into HMMs to account for variation between individuals (but see McClintock 2021), we chose to divide the data into short- and long-term data sets. This prevented the few individuals with a high number of observations from having a disproportionately high influence on the model results. All observations recorded in the first 10 d post release across all individuals with an adequate number of observations (N = 37) were included in a short-term data set. Individuals (N = 16) with 1000 or more observations were included in the long-term data set. Further, observations from the first 10 d of the study were excluded from the long-term data set. This allowed us to exclude possible tagging effects from the long-term data set and modelling. We further restricted the long-term analysis to observations recorded when bottom temperature was <15.5°C, as the remaining data points were recorded from 1 individual at 16°C and had a disproportionate influence on movement parameter estimates at higher temperatures.

2.5. State assignment

American lobster movement has been described in the literature predominately in terms of 3 distinct behavioural states; Sheltered, Exploratory/Foraging, and Dispersal/Transit behaviours (Karnofsky et al. 1989a, Watson et al. 1999). We therefore fitted and compared 2- and 3-state models for the short- and long-term data sets. Bearing in mind that step length divided by the standardized time interval is equal to movement speed, we expected that the Transit state would represent long step lengths (i.e. higher movement speeds) and less tortuous movements, and the Exploratory state would capture intermediate step lengths and turn angles. The Sheltered state represented an absence of movement; however; because of slight positioning error, stationary transmitters can appear to be moving within a confined area. Consequently, we expected that Sheltered states would be manifested with short step lengths (i.e. slower movement speeds) and highly tortuous movements. HMMs require a distribution to model each input data stream. We assumed that the step length data followed a gamma distribution and that the turn angles followed a wrapped Cauchy distribution (Fig. S3). We made this selection by comparing (using Akaike's information criterion [AIC] values, evaluation of pseudo-residual plots) HMM model fits associated with other distributions commonly used to model step length (Weibull) and turn angles (von Mises).

2.6. Model fitting

For both data sets, we initially fitted 2- and 3-state HMMs without covariates (null model) to determine which models best fit the data. To estimate reasonable starting values for the state-dependent model parameters (step length mean and standard deviation, turn angle concentration parameter), we fit each model (2- and 3-state models for each data set) 50 times, iterating over a range of starting values for each state-dependent parameter. The best model was selected as the model with the global largest likelihood (i.e. smallest negative log-likelihood). For the short-term data set, a 3-state model was favoured with a lower AIC value. For the long-term data set, however, despite the 3-state model having a lower AIC value, the state characteristics were not biologically interpretable (step lengths with a mean near 0 m and high turn angle concentration parameters of 0.99 were classified into the third state), and therefore we chose to move forward modelling these data using a 2-state model (see Table S2 for model comparison).

To explore possible effects of covariates on the probability of lobster being in a behavioural state, we modelled state transition probabilities for both data sets as a function of the following covariates: time since release (with values greater than 24 h set to 24 h; only applicable to the short-term data set), bottom temperature (taken from 1 central reference tag within the array), hour of day (modelled using a cosinor model with a period of 24 h), diel period (day/night calculated from daily sunset/sunrise data), tide height (Government of Canada 2023), tide trend (Δ tide height [m] / 15 min), carapace length, and sex. To remove redundant covariates prior to model selection, we fitted models with each variable separately and selected the covariate (hour of day vs. diel period, tide height vs. tide trend) for inclusion in subsequent model selection with the lowest AIC value. In the short-term model, tide height was selected with a lower AIC over tide trend, but in the long-term model, the opposite was true. For both time periods, diel period was selected over hour of day. For each data set, we then performed forward model selection using AIC values to determine the best model (threshold for model selection: $\Delta\text{AIC} \geqslant 2$; Burnham & Anderson 2002) using the refined list of covariates.

Considering the large range of temperatures (−1.7 to 13.8°C) measured in the long-term data set and the previously documented influence of temperature on lobster movement rates (McLeese & Wilder 1958), we chose to compare the conventional HMM with covariate effects on state transition probabilities to a generalized HMM (as in Carter et al. 2020), with temperature effects on the state-dependent movement parameters (step length and turn angle concentration) and state transition probabilities. Forward model selection was used to determine the best generalized HMM, and this was compared to the best conventional HMM model. The best overall model for the long-term data set was selected as the model with the lowest AIC score.

Following model selection, the Viterbi algorithm (Zucchini & MacDonald 2009) was used to assign the most likely behavioural state to each location using the best HMM for each data set. Using the 'plotStationary' function, stationary state probabilities were calculated at a fixed set of covariate values. The default covariate values for this function are the means of numerical covariates appearing in the model or the first level of factor variables. Since lobsters tend to be sheltered during the day, and male lobsters tend to be more active than females, we used a diel period of 'night' and sex of 'male' for the plots, as there was greater scope for change across values of the other covariates. Similarly, we used the mean temperature from the first 10 d of the long-term study (10.6°C) as the temperature covariate value, since the mean temperature over the entire long-term data set was low (3.7°C), and lobsters tend to stay sheltered at these temperatures. These stationary state probabilities represent the long-term probability of lobsters being in a state given the covariate values (Michelot et al. 2016).

To better understand patterns of behaviour across habitats within the study area, an algal cover layer was created using video transect data collected in August 2015 at 30 m intervals along transect lines spaced 100 m apart (covering the extent of the 2014 study area). In the absence of reliable substrate data beneath algal canopies, algal cover was used as a proxy for substrate, where high algal cover is assumed to be indicative of hard (i.e. rock, cobble) substrate, and lower values of algal cover indicate mixed substrate/soft sediment (as in Henderson & Hakai Institute 2018). The algal cover layer was produced from the transect data using the Euclidean allocation tool (maximum distance set to 100 m) in ArcGIS Pro (v. 2.8.8; ESRI 2021). Behaviour-classified movement tracks were plotted in relation to algal cover, and the proportion of observations attributed to each behavioural state was plotted by algal cover (where data overlapped spatially). As algal cover was only surveyed once, we cannot determine how this coverage may vary seasonally or across years, but it does still serve as a proxy of substrate, which is likely less dynamic. To better characterize the behavioural states in lobsters, the average time spent in each state was calculated for both the short- and long-term data sets from the behaviour-classified observations. Finally, to shed light on potential patterns in behaviour sequences, for the long-term study period, we calculated the proportion of transitions in the classified data from each behaviour to the next. All statistical analyses were conducted in R v. 4.3.1 (R Core Team 2016).

3. RESULTS

3.1. Short-term model

Over the 2 yr study, a total of 37 individuals (16 released in 2014, 21 released in 2015) were tracked in the first 10 d after release, with track durations by individual ranging from 11 h to 9.9 d. AIC model selection revealed that a 3-state HMM (with states defined as Sheltered, Exploratory, and Transit behaviours) best fit this data set, with covariate effects of diel period, time since release, sex, carapace length, and bottom temperature included in the transition probability between states (see Fig. S3a for model evaluation plots). Sheltered behaviour was characterized by the shortest step lengths (2.43 m) and undirected movements (concentration parameter 0.29). Transit behaviour showed the longest step lengths (36.96 m) and the most directed turn angles (concentration parameter of 0.81), while Exploratory behaviour was characterized by intermediate step lengths (13.48 m) and angle concentrations (0.74; see Table 2a for all parameter estimates). The model classified approximately 5% of the observations as Transit, 10% as Exploratory, and 25% as Sheltered behaviour (Fig. S4a). The remaining 60% of interpolated observations were assigned to a 'known' Sheltered state. Despite the lack of signal detection during these 'known' Sheltered periods, the track segmentation rules used (see Section 2.4) suggest that individuals moved little during these times.

State probabilities differed across the range of covariates measured. Lobsters showed a higher probability of being Sheltered during the day compared to night when there was an increased probability of lobster being in both mobile states (Fig. 2a). Immediately following their release, the probability of lobster being in the Transit state was highest, but this decreased sharply in the first 24 h as the probability of sheltering increased (Fig. 2b). The probability of lobster being in an Exploratory state remained fairly constant through the study period as time since release increased. There was a higher probability for females to be in the Sheltered state compared to males, where the probability of both mobile states was slightly higher than in females (Fig. 2c). There was a decreased probability of sheltering as temperature increased (Fig. 2d), and the same pattern was found as carapace length increased (Fig. 2e). In contrast, the probability of lobster being in an Exploratory state increased with increasing temperature and carapace length while the probability of being in a Transit state remained consistently low across measured values.

Habitat was not included as a covariate in the HMMs due to the limited coverage compared to the observation data. Despite this, the behavioural state-classified tracks showed a strong association between behavioural states and algal cover across the study area (Fig. 3). Notably, Transit behaviour was most

Table 2. Behavioural state parameters for (a) short- and (b) long-term American lobster telemetry data sets. For the long-term data set where temperature was included as a covariate on movement parameters, values were extracted for the temperature range limits. Step parameters are measured at 15 min intervals. Movement rates (m h^{-1}) are shown in parentheses

Behavioural state	Step parameters (m)				Angle parameters	
	Mean		SD		Concentration	
(a)						
Sheltered	2.43 (9.7)		2.05		0.29	
Exploratory	13.48 (53.9)		6.47		0.74	
Transit	36.96 (147.8)		14.92		0.81	
	−1.71°C	13.83°C	−1.71°C	13.83°C	−1.71°C	13.83°C
(b)						
Sheltered	2.02 (8.1)	2.48 (9.9)	2.15	1.68	0.67	0.06
Exploratory	6.23 (24.9)	12.32 (49.3)	3.77	7.84	0.83	0.23

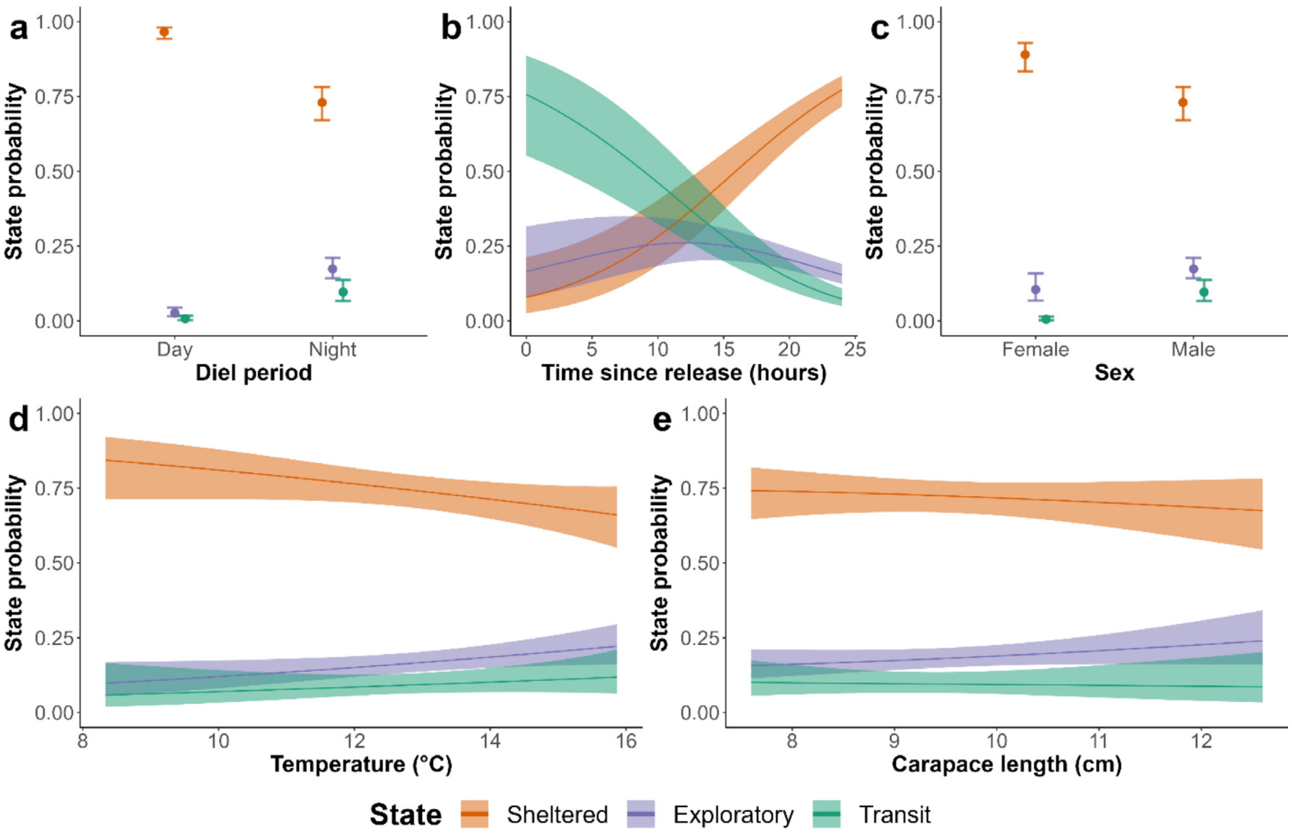

Fig. 2. Stationary state probabilities for the short-term American lobster data set with 3 behavioural states (Sheltered, Exploratory, Transit). Unless otherwise indicated, stationary state probabilities were calculated using covariate values of night (diel period), 22.5 h (time since release), Male (sex), 13.4°C (temperature), and 9 cm (carapace length). Lines show model estimates across these covariate values, and shading shows 95% confidence intervals

often seen in areas of low algal cover and rarely in areas of high algal cover (Fig. S5a). Exploratory behaviour was observed across all levels of algal coverage, and while sheltering behaviour made up the majority of observations across all habitats, the highest proportion of 'known' state (Sheltered — no detection) observations coincided with areas of high algal cover (Fig. 3).

In the first 10 d after release, sheltering episodes lasted an average of 19.4 h (range: 0.25–222 h). From a Sheltered state, lobsters transitioned predominantly (93% of the time) to an Exploratory state and transitioned much less frequently (7% of the time) to a Transit state (Fig. 4; Fig. S6). When in an Exploratory state, episodes averaged 1.9 h (range: 0.25–11.5 h) in duration before transitioning to another behavioural state. From an Exploratory state, lobsters transitioned to a Transit state 29% of the time and to a Sheltered state 71% of the time. Lobsters spent an average of 2.6 h (range: 0.5–9.3 h) in Transit, at which point they had an 80% chance of transitioning back to an Exploratory state and a 20% chance of sheltering.

3.2. Long-term model

In total, 16 individuals (8 released in 2014; 8 released in 2015) were included in the long-term model, with the total track durations (total of multiple segments) by individual ranging from 3.4 to 208.6 d over the study period (i.e. not including the first 10 d of observations that were included in the short-term model). Overall, the best-fit model was a 2-state HMM with a covariate effect of temperature on movement parameter estimates and covariate effects of sex, temperature, diel period, and carapace length on state transition probabilities (see Fig. S3b for model evaluation plots). As with the short-term model, the state with the shortest step length (mean 2.17 m) and less directed movement (concentration parameter 0.37) was assigned as the Sheltered state. The second state had a mean step length of 7.9 m and an intermediate turn angle concentration parameter (0.65). This state was assigned as Exploratory, given that the turn angle was less directed and step length was shorter than the Transit state identified in the short-term data set.

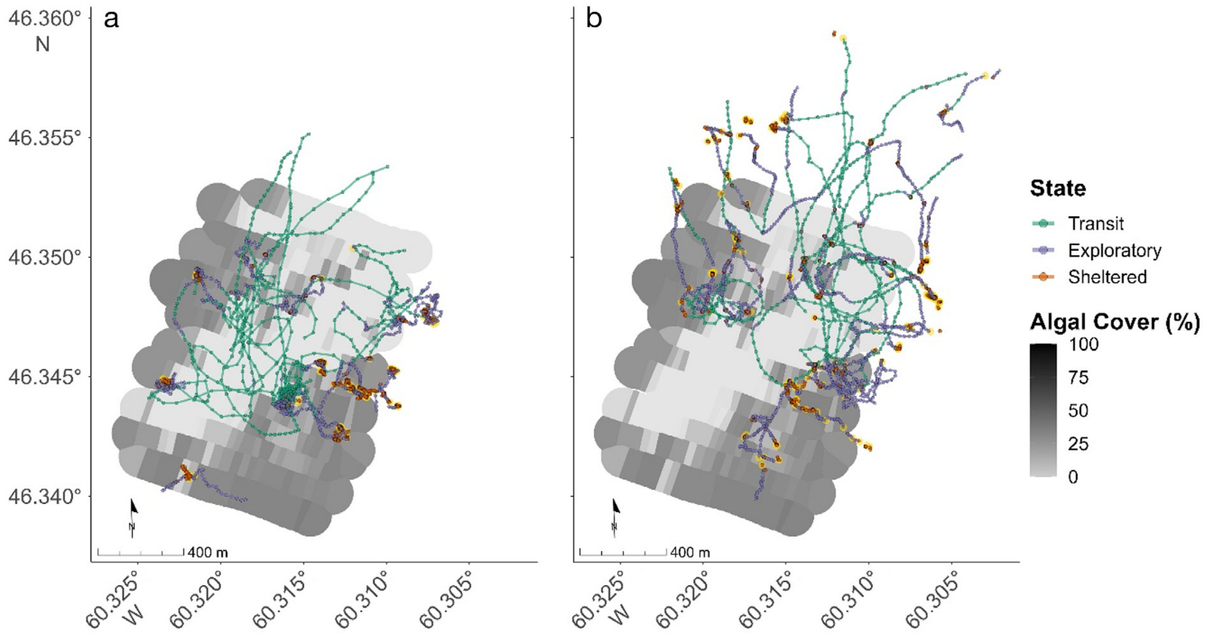

Fig. 3. Associations of inferred behavioural state (Transit, Exploratory, Sheltered) with algal cover classes for American lobsters for the short-term data set in (a) 2014 and (b) 2015. Yellow points show areas where lobsters were inferred to be in a Sheltered state (i.e. 'known' states based on criteria described in Section 2.4). Observations are pooled across years for analysis but are plotted here by year of release date to improve readability

Over the study period, a mere 3% of observations were classified as Exploratory, while 10% were classified as Sheltered. The remaining 87% of observations were assigned a 'known' Sheltered state based on the track segmentation rules (Fig. S4b).

The mean step length of both states increased across the range of temperatures measured over the study period. Sheltered state step lengths (measured over 15 min intervals) showed an increase from 2.02 m at −1.7°C to 2.48 m at 13.8°C (Δ 0.46 m) while Exploratory step lengths increased from 6.23 to 12.32 m (Δ 6.01 m) over the same temperature range (Table 2b, Fig. 5a). In contrast, angle concentration parameters decreased over the temperature range, with lobsters exhibiting much less directed movement at warmer temperatures compared to cooler temperatures, where the concentration parameters for both states were high, indicating higher directional persistence (Table 2b, Fig. 5b).

Covariates included in the long-term model revealed similar patterns to the short-term model results; however, time since release was not included in the model, whereas tide trend was included. There was a higher stationary state probability of being in a Sheltered state in females compared to males (Fig. 6a). This model provides state probabilities over a greater range of temperatures (Δ 15.5°C vs. Δ 8°C) but shows a similar relationship across temperature with an increased probability of individuals being in an Exploratory state at higher temperatures compared to lower temperatures (Fig. 6b). Like the short-term

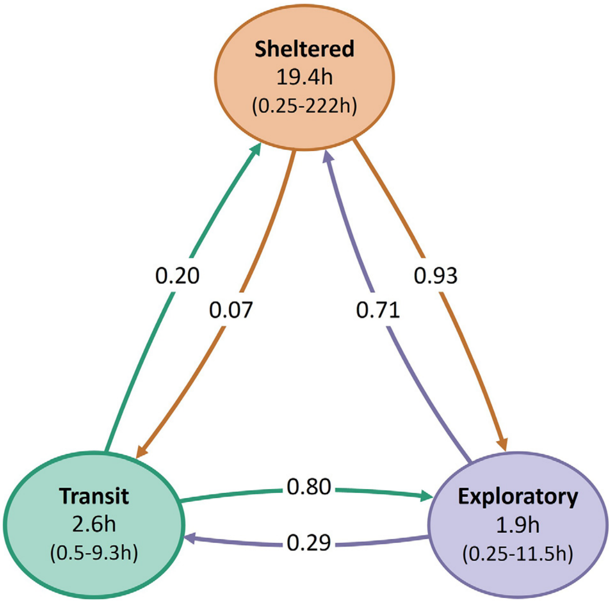

Fig. 4. State transitions for American lobsters immediately following release (short-term data set) calculated from predicted behavioural states over time. The average duration that lobsters spent in these states is indicated below the headings and the range for the time series is given in brackets. Long-term data are not shown, since only 2 behavioural states were modelled

model, individuals were more likely to shelter during the day compared to at night (Fig. 6c), and the probability of being in a Sheltered state increased with carapace length (Fig. 6d). Finally, there was a decreased probability of Sheltered behaviour and an increased probability of Exploratory behaviour with larger tide trend values (Fig. 6e). Like the short-term state predictions, there were strong associations between the inferred behaviour of observations and algal cover (Fig. 7). More observations were classified as Exploratory in areas with lower algal cover (⩽50% cover), although the behaviour was present across all habitats (Fig. S5b). Further, the highest proportion of 'known' state observation (Sheltered — no detection) was once again found in areas of higher algal cover (>50% cover). Behavior durations were longer, particularly for the Sheltered state, compared to the short-term data set. Lobsters spent an average of 3.31 h (range: 0.25–36 h) in an Exploratory state before sheltering, while they spent an average of 70 h (range: 0.25–1732 h) Sheltered before transitioning to an Exploratory state (Fig. S7).

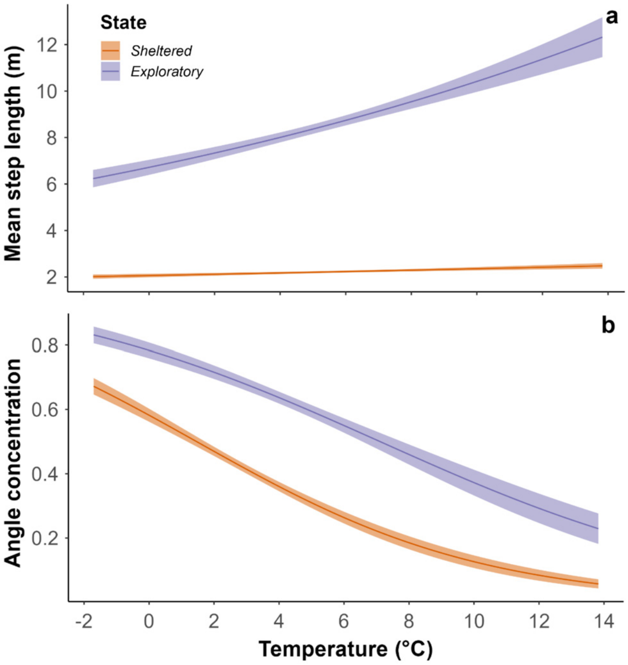

Fig. 5. Movement parameter estimates of (a) step length and (b) angle concentration across temperature for the long-term American lobster data set. Lines show the model estimates, and shading shows the 95% confidence intervals

4. DISCUSSION

This application of HMMs to tagged American lobsters provides a unique perspective on their movement, in that it identifies and parameterizes behaviour classes, establishes environmental co-variates that are associated with certain behavioural states, and furthers our understanding of their behavioural time budgets. These characteristics have important implications for understanding lobster ecology but also for improving lobster resource management. While other studies have drawn similar qualitative conclusions, the behavioural states described in this study provide movement parameters that can be used to improve catch per unit effort (CPUE) estimates of abundance. Moreover, the duration of the study and the natural environment added important realism (environmental conditions, predator fields, food availability, movement options) that has eluded many other fine-scale movement studies that were seeking more experimental control in laboratory or mesocosm environments (Golet et al. 2006, Watson et al. 2009, McMahan et al. 2013).

In our study, we identified 3 behavioural states; Sheltered, Exploratory, and Transit. We selected the number of states *a priori* based on previous work where similar states were identified (Karnofsky et al. 1989a, Watson et al. 1999). While these were all identified in this study, individuals spent the majority of their time Sheltered. The importance of shelters for American lobsters has been documented in other studies (Karnofsky et al. 1989a, Morse & Rochette 2016). Mean movement rates for the Sheltered state were 9.7 and 8.7 m h^{-1} for the short- and long-term study periods, respectively, which is within the range of values we observed for our fixed reference tag (median velocity 6.3 m h^{-1}). In addition, in the long-term study, few observations were classified in mobile states, and individuals spent notably longer on average in a Sheltered state before transitioning to a mobile state, which is consistent with the documented decline in activity with colder temperatures (Karnofsky et al. 1989b). The Exploratory state identified in our study likely captures what Watson et al. (1999) described as local meandering/foraging movements and medium-distance locomotion. This Exploratory state includes some local movements but also medium-distance movements and likely captures both foraging excursions and periodic excursions for lobsters to acquire situational awareness of their home ranges (Karnofsky et al. 1989a). It is possible that the step lengths and turn angles are similar between these movements, which would make them indistinguishable to the models. The Transit state was only characterized in the short-term data set, and while it is likely comparable to the rapid excursion

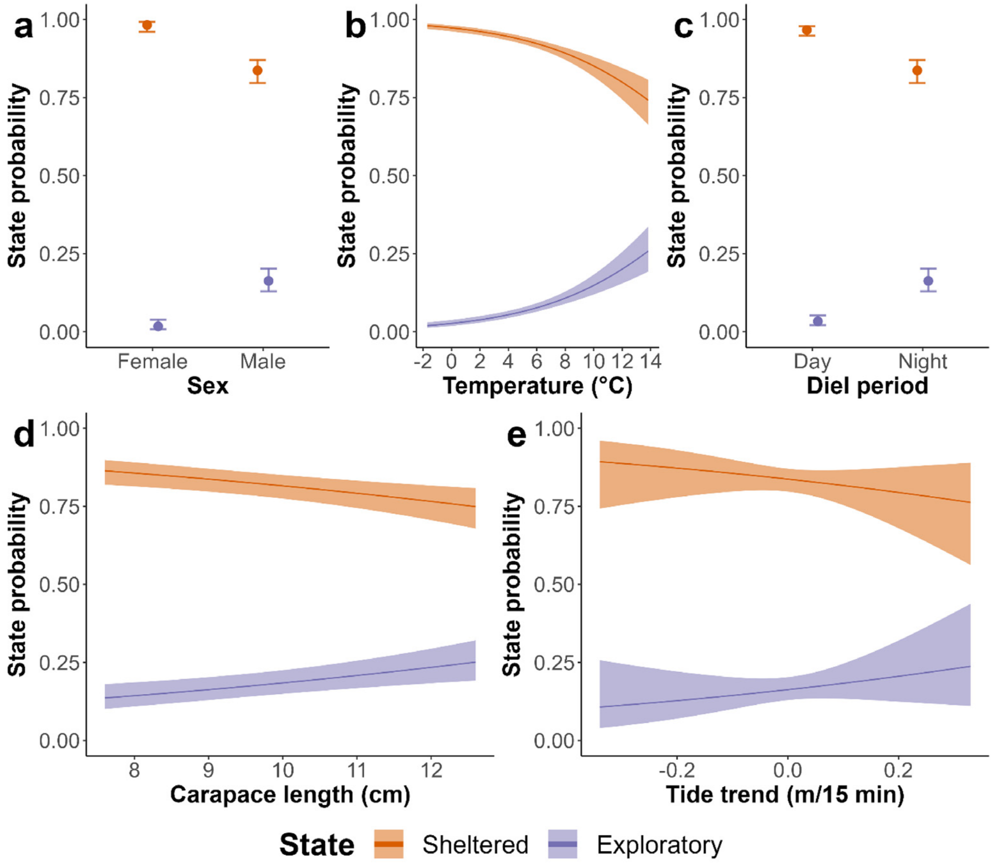

Fig. 6. Stationary state probabilities for the long-term American lobster data set with 2 behavioural states (Sheltered, Exploratory). Unless otherwise indicated, stationary state probabilities were calculated using covariate values of Male (sex), 10.6°C (temperature), night (diel period), 9 cm (carapace length), and 0 m per 15 min (tide trend). Lines show model estimates across these covariate values, and shading shows 95% confidence intervals

state described by Watson et al. (1999), this behaviour was most common in individuals immediately following release. This result suggests that it is likely a rare behaviour exhibited by resident lobsters under normal conditions, at least during the fall—winter season studied here. Directed, high-speed movements would be costly to lobsters from an energy expenditure perspective, so it is not surprising that they would avoid these behaviours when residing in a home range. The average rate of movement for lobsters reported by Watson et al. (1999) overall was 14 m h^{-1} after removing periods of inactivity, while the maximum straight-line speed was 75 m h^{-1}. This is less than the average Transit speeds observed in our study. However, since their straight-line distance measurements certainly underestimated distance travelled, it is possible that true movement velocities were much higher and possibly reached the ~148 m h^{-1} associated with Transit behaviour in our study.

Many quantitative aspects of lobster movement ecology that were observed in our study are in qualitative agreement with results documented elsewhere. For example, movement rate parameters for all states in the long-term model increased with temperature, as did the tendency to be in the more mobile Exploratory state. Other studies have detected similar positive relationships with temperature through laboratory studies (McLeese & Wilder 1958), direct observation (Ennis 1984, Karnofsky et al. 1989b), and telemetry studies (Bowlby et al. 2007, 2008), or inferred them through trapping rates (McLeese & Wilder 1958, Comeau & Savoie 2002, Drinkwater et al. 2006). Laboratory experiments showed that lobsters prefer temperatures near the upper end of the range measured in our study period (Crossin et al. 1998). Ectothermic animals have a broader metabolic scope at elevated temperatures (McGaw & Reiber 2015), but this comes at the cost of increasing energy demands (Klymasz-Swartz et al. 2019). Consequently, lobsters should compensate by spending more time foraging when water temperatures are higher. Interestingly, while average movement speeds were 71% higher during Exploratory phases in the short-term (warmer water) model period, the average duration of these events was

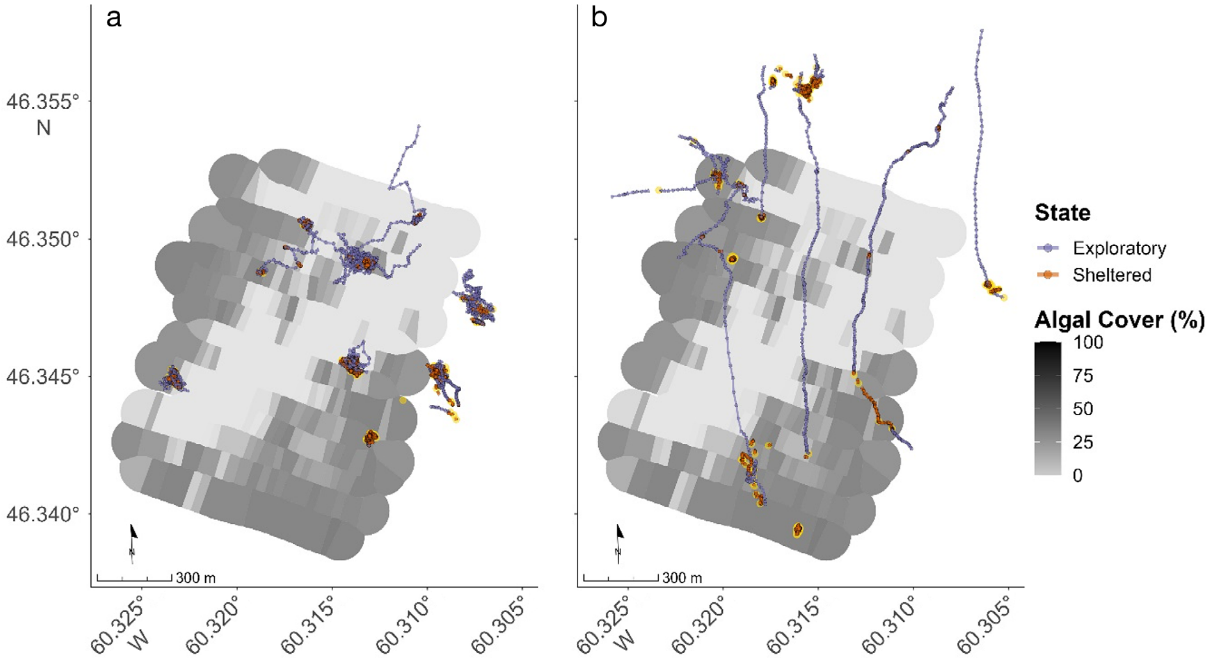

Fig. 7. Associations of inferred behavioural states (Exploratory, Sheltered) with algal cover classes for American lobsters in the long-term data set for (a) 2014 and (b) 2015. Specifically, note the larger-scale patterns of line colour (states) in relation to the algal cover. Yellow points show areas where lobsters were inferred to be in a Sheltered state (based on criteria described in Section 2.4). Observations are pooled across years for analysis but are plotted here by year of release date to improve readability

43% shorter. Even within the long-term model period, there was a trend for decreasing Exploratory event duration as water temperatures increased (Fig. S8). This suggests that during colder weather, lobsters may compensate for reduced movement capacity by extending foraging event duration. Our results also indicate that Exploratory movements became more directional as waters cooled. Other authors (Karnofsky et al. 1989a) have suggested that excursions from shelters may be used to gather information rather than searching for food. If this is true, more directional movements would allow lobsters to assess larger spatial scales, which may otherwise be challenging when movement velocities are metabolically constrained.

Diel responses of free-living, continuously monitored lobsters in our study also closely matched those reported by other authors who used laboratory environments (e.g. Jury et al. 2005), intermittent dive observations (Ennis 1984), and mesocosm studies (Golet et al. 2006), and studied other life history phases (Morse & Rochette 2016, Carloni et al. 2021). Like these previous studies, lobsters were much more likely to be in an Exploratory or Transit state at night relative to daytime periods. While Golet et al. (2006) noted considerable variation in diel activity patterns among individuals in a mesocosm, with some individuals exhibiting greater activity during the day, we observed very low levels of daytime activity in both our short- and long-term data sets. Nevertheless, our study shows that even at night, lobsters are still far more likely (>70%) to exhibit Sheltering behaviour than other more active behaviour states. Similar observations were presented by Morse & Rochette (2016), who found that juvenile lobsters spent most (~67–97%) of their time in shelters, and by Karnofsky et al. (1989a), who rarely observed lobsters feeding.

While lobsters exhibit clear tendencies for movement in response to the environmental drivers measured in this study, variation in lobster movement behaviour is well documented (e.g. Karnofsky et al. 1989b, Comeau & Savoie 2002, Golet et al. 2006). Some of this variation can be explained by individual characteristics such as size (Wahle 1992) and sex (Elner & Campbell 1981, Cromarty et al. 1998, Jury & Watson 2013, Carloni et al. 2021). Our data show that female lobsters tended to spend more time Sheltering than males. The dimorphic nature of this species and differing metabolic demands across life history stages (e.g. egg brooding; Carloni et al. 2021) likely influence movement patterns. For example, berried female lobsters have less effective escape responses than males (Cromarty et al. 1998), are less equipped to deal with intraspecific agonistic encounters (Elner & Campbell 1981), and may migrate to specific habitats to improve the survival of their eggs (Carloni et al. 2021). Certainly, we had difficulty capturing females to tag in 2014, consistent with local harvester knowledge that females typically leave coastal grounds earlier than males. This was supported in 2015, when females were more available during the earlier tagging season. Size was also an important model variable, with larger lobsters showing a slightly increased probability of movement as reported for other crustaceans (Florko et al. 2021). This is in contrast to Morse & Rochette (2016), who found no size differences in movements of juvenile lobster.

HMM construction and results differed for short- and long-term data sets. Notably, the best short-term model included 3 behavioural states and covariate effects of time since release, whereas the long-term model contained only 2 states, with tide trend as a covariate on state-transition probabilities. Further, the long-term model was improved by parameterizing behavioural states as a function of temperature. The Transit state was only identified in the short-term data set, and the addition of this third state did not improve the long-term model. In addition to this additional state, the short-term HMM identified time since release as an important covariate. A concern often raised in telemetry studies is the potential impact of tagging on animal behaviour (Florko et al. 2021, MacGregor et al. 2023). Some studies on crustaceans have reported undetectable effects of tags (e.g. Hewitt et al. 2023), while others have reported short-term behaviour changes, including elevated movement speeds that were presumed to be flight responses (Cote et al. 2019). Transit behaviour was characterized by the fastest, most linear movement tracks, which is consistent with a flight response. Lobsters were likely to be in a Transit state immediately following release, with the likelihood of being in that state declining rapidly within the first day of release. Tide trend was a covariate that improved the long-term model but was absent in the short-term HMM. We found a slight increase in the probability of Exploratory behaviour with positive tide trend values, which are representative of a rising tide. Tide height has been shown to influence juvenile lobster behaviour, with individuals being more active during high tide, and in particular during night-time high tides (Morse & Rochette 2016). In both studies, while the effects of tide are supported statistically, the effect size appears marginal and requires further investigation into when potential tidal effects are most important to consider. We chose to include temperature as a covariate on the HMM movement parameter estimates, since temperature has been reported as an important driver of lobster movement rates (Ennis 1984, Karnofsky et al. 1989b, Drinkwater et al. 2006). We were unable to include temperature as a covariate on the movement parameter estimates in the short-term model, as temperature was confounded with potential tagging effects on movement characteristics through time. While temperature may have improved the model, the short-term observations span a smaller range of temperatures and are therefore likely less influential compared to the long-term data set.

While not explicitly included in the HMMs, habitat also appeared to be linked to movement, with Sheltered behaviour being closely associated with areas of high macroalgal cover. In contrast, open sandy areas were frequently associated with Transit behaviour when it was used, and Exploratory behaviour was more equally distributed across habitats. Many studies highlight associations of lobsters with structurally complex habitats such as rocky areas (Geraldi et al. 2009), eelgrass (Karnofsky et al. 1989b), or kelp (Bologna & Steneck 1993). Despite this widely held habitat association, Tremblay & Smith (2001) and Geraldi et al. (2009) noted that trapping rates were higher in sandy habitats. The latter authors showed with coarse recapture data that lobsters trapped over sandy habitats move farther and faster and proposed that lobsters use open areas as movement corridors, which could result in increased encounter rates with traps. This is further supported by a study on European lobsters (Skerritt et al. 2015) that noted faster and more directional movement on soft substrates. Our data support these observations. While lobsters often occupy habitats of high complexity, they appear to spend most of their time in that habitat in a non-mobile state. Since predation risk is lessened as lobsters become adults (Wahle 1992), exposure moving through open, low-complexity habitats may be worthwhile for the sake of efficient movement, particularly if they have access to nearby cover. Individuals that remained in the array into the cold-water season were concentrated in habitats of cover and only sporadically exhibited periods of activity. These results mirrored those of others, who noted reduced activity at low water temperatures (Karnofsky et al. 1989b, Bowlby et al. 2007) and occupancy of shelters that were located principally in boulder habitat or under marine vegetation (eelgrass).

Other studies have suggested that lobsters appear to employ a form of central-place foraging (Wahle 1992), where they establish a central location (i.e. shelter) and conduct foraging excursions from this point. However, lobsters are not permanently fixed to a central location, as all individuals exhibited Sheltered behaviour at different locations (also observed by Ennis 1984, Karnofsky et al. 1989a, Scopel et al. 2009). Shifting locations may be motivated by several factors, including habitat patchiness, resources, conspecific density, and/or competition (Karnofsky et al. 1989a, Hovel & Wahle 2010). Males, in particular, may be more likely to move as a result of competition (Atema 1986), which may be why females more consistently exhibited Sheltered behaviour. Additionally, lobsters may move from their central location due to resource depletion in the area immediately surrounding the shelter (Ashmole's halo; Ashmole 1963). While these ideas are speculative, they provide potential explanations for the observed movement patterns and highlight areas for further research.

The introduction of high temporal and spatial resolution positioning systems further advanced our understanding of fine-scale movements in American lobsters, but our approach has some limitations. First, positioning-telemetry arrays are resource intensive, requiring high densities of receivers to position tagged animals. The consequence is a limited study area extent that reduced our ability to track dispersing lobsters to their winter habitats. Secondly, the natural behaviour of lobsters, which includes burying and sheltering in substrate or vegetation (Karnofsky et al. 1989a), can obstruct transmitter signals and affect detection frequencies (Weinz et al. 2021). We were able to overcome these issues by inferring behaviour during data gaps, particularly when animals reappeared at the same location. Last, while we were able to classify behavioural states, we are left to infer the activities associated with these states. This is particularly difficult for stationary states, which could include a combination of behaviours like resting, avoiding predators, and/or feeding. Complementary visual observations could overcome some of the latter issues, but their addition was unfortunately beyond the scope of this study.

Identifying and quantifying behaviours of lobsters and understanding how their habitat use changes with environmental conditions has practical applications. Importantly, many of the stock assessments for lobsters in Canadian waters are based on CPUE from either fisheries logbooks or trapping surveys (Watson & Jury 2013). While some environmental variables in our study (e.g. diel period and tide) are cyclical across time scales that may have a negligible impact on CPUE estimates (i.e. not detectable given temporal coverage of trap set times) others like temperature and habitat can greatly influence trap encounter rates. As waters warm over the season, higher temperatures will result in more lobster movement. For example, using Exploratory movement speeds and event durations, we estimate that at the coolest temperatures of the local fishery (1°C), lobsters can be expected to move on average about 54 m d^{-1}. This contrasts with the 384 m travelled per day that we might expect near the highest temperatures of the local fishery (14°C). Such differences will influence trap encounters and could mask the true degree of fishery-induced depletion as the fishing season (15 May to 15 July in Lobster Fishing Area 27) progresses from spring to summer. Our data also have implications at extended timescales, where climate change could influence interpretation of long-term trends of abundance.

While our study shows that lobsters are largely sedentary, their behaviours are influenced by individual characteristics (size and sex) and environmental conditions that can change rapidly in the natural nearshore environment studied. Characterizing movement behaviours and establishing time budgets over a range of environmental conditions will be useful for predicting the ecological implications of climate change and for refining stock assessment models for this species.

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