Acoustic evidence for seasonal migration by a cryptic top predator of the deep sea

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Data availability statement: Raw (256 kHz) and decimated (16 kHz) acoustic data from the MARS hydrophone are available at https://registry.opendata.aws/pacific-sound/. Code for processing acoustic data, analyzing sperm whale detections, and simulating individual-level movement strategies are available at https://doi.org/10.5281/zenodo.7860426.

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Abstract

In ecosystems influenced by strong seasonal variation in insolation, the fitness of diverse taxa depends on seasonal movements to track resources along latitudinal or elevational gradients. Deep pelagic ecosystems, where sunlight is extremely limited, represent Earth's largest habitable space and yet ecosystem phenology and effective animal movement strategies in these systems are little understood. Analyzing seven years of continuous population-level passive acoustic observations, we find evidence for seasonal, latitudinal movements by sperm whales (*Physeter macrocephalus*) in the Northeast Pacific. Integration of population-level empirical results with individual-level movement simulations provides evidence of seasonal migration in this cryptic top predator, likely to track deep-sea resources. We show that sperm whales track oceanographic seasonality in a manner similar to many surface ocean predators, but with dampened seasonal-latitudinal movement patterns. These findings shed light on the drivers of sperm whales' long-distance movements and the shrouded phenology of the deep-sea ecosystems in which they forage.

INTRODUCTION

The movement strategies that animals use to track resources in space and time drive many aspects of their ecology, mediate their ability to respond to environmental perturbations, and provide insight into the spatiotemporal dynamics of the ecosystems they inhabit[1]. These individual and group-level movement strategies typically result from spatiotemporal patterns of resource availability[2], and manifest in distinct patterns of population-level distribution in space and time[3]. For example, nomadic resource tracking has evolved in aseasonal and unpredictable environments, leading to irregular patterns of individual movement and population distribution[4]. Conversely, many species inhabiting seasonal ecosystems have evolved to undertake seasonal migrations between distinct ranges[4] or perform partial migrations, whereby a specific demographic of the population undertakes migration[5]. These seasonal migrations between distinct habitats (sometimes referred to as "to-and-fro" migrations), as in the migrations of many baleen whales, are distinguished by their persistent, relatively direct movements undistracted by proximate resources[6]. Other seasonal migrants (e.g., many ungulates) undertake seasonal movements to track the phenology of proximate resources (e.g., forage, favorable abiotic conditions, etc.) en route as resource availability propagates across spatiotemporal gradients such as latitudes or elevations[7,8]. These resource-tracking migrations have recently gained attention as an important connection between ecosystem dynamics and animal movement, closely linking ecosystem phenology with that of seasonal animal migrations[1,9]. Such resource tracking has been shown to provide a number of individual and population-level benefits, from enabling animals to have more prolonged access to food[10], to increasing fat gain[11] and allowing migratory populations to have higher growth rates than sedentary populations[12]. These linkages between resource dynamics and animal movement strategies are increasingly well-understood in seasonal terrestrial[2,7,9,13], freshwater[14], coastal marine[15], and epipelagic[16-21] ecosystems across the globe.

` Few studies have assessed these connections between ecosystem dynamics and animal movement in Earth's largest habitable space: deep pelagic ecosystems. These oceanic waters deeper than 200 meters, where little sunlight penetrates, have historically been characterized as stable and aseasonal, but poorly understood[22]. However, a growing body of evidence suggests elements of seasonality in the deep sea. For example, oceanographic studies have documented seasonal variation in the transport of biomass from the surface to the deep[23-25]. Further research has documented seasonality in sightings and biomass of low and mid-trophic level organisms in the mesopelagic[26-28]. Yet understanding of deep-sea phenology remains limited, particularly for highly mobile and high-trophic-level animals. This knowledge gap is underpinned by the challenge of making continuous and detailed observations in these ecosystems[22]. Given the global extent, high endemic biodiversity, and major role in global biogeochemical cycles of deep pelagic ecosystems, understanding the phenology of these ecosystems and the evolved movement strategies of their inhabitants is important to advance fundamental ecology and inform ecosystem management.

We address this gap by integrating long-term passive acoustic monitoring data and movement simulations for a deep pelagic top predator, the sperm whale (*Physeter macrocephalus*). Sperm whales are a deep-diving oceanic predator, diving to depths of hundreds to thousands of meters[29] to forage on diverse deep pelagic prey[30]. Thus, studying the movement patterns of these ocean giants can provide a rare window into the phenology of the deep-sea environment. In addition, sperm whales produce the loudest known biological sounds[31] which not only reveal the presence of this often-cryptic species over large ocean volumes, but also transmit rich behavioral and demographic information about detected individuals. Echolocation clicks are central to the foraging ecology of sperm whales in the low-light conditions of the deep sea, and further indicate individuals' behavioral state (foraging), size (both inter-click-interval[32] and inter-pulse-interval within individual clicks[33] correlate with size), and sex and age-class (sperm whales are sexually dimorphic[34], allowing for sex and age-class identification via inter-click-interval[32]). Sperm whales use echolocation in both the meso- and bathypelagic[35] to locate a variety of squid and fish prey species[30]. As a result, patterns of sperm whale echolocation click detection can provide insight into the phenology of both this top predator and the deep pelagic ecosystems in which they forage.

In the Northeast Pacific, foraging sperm whales have been detected acoustically year-round, specifically in the Gulf of Alaska (GoA)[36-38]. Individuals of this population have expansive home ranges, exhibiting wide-ranging movements which include travel between the GoA and the Central California Current System (CCCS; Figure 1A) among other lower-latitude habitats[39-41]. Yet the regularity, seasonality, and behavioral context of such movements have historically remained unclear. Previous studies based on individual-level sightings, genetic, and limited telemetry data have hypothesized that latitudinal movements are likely irregular, resulting from aseasonal nomadic movements[40] consistent with the canonical view of aseasonal deep-sea ecosystems. Yet recent acoustic studies in the GoA have suggested seasonality in foraging sperm whales' presence[36-38], challenging the hypothesis of aseasonal nomadic movements. Others have suggested that long-distance latitudinal movements represent migration between distinct high-latitude foraging and low-latitude breeding habitats[42], akin to the seasonal migrations of many baleen whales. Sex-specific partial seasonal migration (with only adult males undertaking migration to higher latitudes) has also been hypothesized based on individual-level sightings data[34,43], but both sexes have been observed in both the GoA[40] and CCCS[40,44]. Further, individuals with small body size (females and juveniles) are heard year-round in the GoA[38], refuting the hypothesis that only adult males undertake long-distance movements to high latitudes. While individual-level telemetry data can often provide sufficient sample sizes to understand population-level seasonal movement strategies[16], individual tracks of sufficient duration to assess seasonal movement are extremely limited for this sperm whale population[39]. As with most inhabitants of deep pelagic ecosystems, this murky understanding of sperm whales' movement strategies arises from the challenge of observing their behavior persistently at sufficient scale[45,46] and limited understanding of phenology in their foraging habitat.

Here, we investigate the strategies underlying movements of this deep pelagic top predator in the Northeast Pacific. We consider four hypothesized movement strategies. Three have previously been hypothesized: nomadic resource tracking[40], seasonal to-and-fro migration between distinct habitats[39,42], and sex-specific partial seasonal migration[34,42], The fourth, seasonal resource-tracking migration akin to that observed in many surface ocean and terrestrial predators[16,19], is hypothesized here based on growing evidence of seasonality in the deep sea at lower trophic levels[23-28]. We first characterize seasonal patterns of foraging sperm whale presence in the Central California Current System as compared to previously published results from the Gulf of Alaska by applying automated acoustic detection methods to more than seven years of passive acoustic recordings. Passive acoustic monitoring approaches provide a valuable Eulerian lens to assess population-level animal presence and behavior[47], particularly in largely inaccessible oceanic ecosystems when Lagrangian tracking data (e.g., telemetry) is scarce (as with sperm whales in the Northeast Pacific), and in cases where information beyond presence alone (e.g., behavioral state) can be discerned from the properties of detected acoustic signals[48]. We then test the alternative hypotheses by comparing these empirical patterns with emergent patterns derived from simulations of individual-level movement driven by each of the hypothesized movement strategies. Finally, we compare empirically observed seasonal-latitudinal patterns of foraging sperm whale presence to seasonal-latitudinal patterns in the location of the North Pacific Transition Zone, the dominant foraging habitat which numerous surface ocean predators track in the North Pacific[16,49]. Hypothesis-testing using this integrated approach allows us to *(i)* determine the unknown seasonality and regularity of foraging sperm whale presence in the Central California Current System and *(ii)* evaluate the individual-level strategies underlying sperm whales' wide-ranging movements by comparing simulated and observed patterns.

MATERIALS AND METHODS

Hydrophone recordings

To assess seasonal and interannual patterns of sperm whale presence in the CCCS, we analyzed passive acoustic recordings between 2015 and 2022 with nearly continuous (>95%) temporal coverage. Acoustic recordings were collected on the continental slope outside Monterey Bay, CA, via two icListen hydrophones sequentially deployed on the Monterey Accelerated Research System (MARS) cabled observatory (36° 42.75'N, 122° 11.21'W; depth 891 m; Figure 1A). These hydrophones recorded at 256 kHz; all recordings were decimated[50] to a sample rate of 16 kHz before analysis. While directional components of sperm whale echolocation clicks can have a peak frequency exceeding the Nyquist frequency of these 16 kHz audio files[31], this sample rate allows for reliable detection of the omnidirectional low-frequency component of these clicks. Previously, these clicks have been reliably detected in audio files with a sample rate as low as 1 kHz[36].

Passive acoustic analyses

Sperm whales produce a variety of click types associated with distinct behaviors. The present analysis focused only on "usual" clicks, which are used for echolocation[34] and are hereafter referred to as clicks. We used a two-step automated workflow (detection and filtration) to determine presence or absence of sperm whale clicks at daily resolution.

Candidate detections of individual clicks were generated using a band limited energy detection (BLED) approach implemented in Raven Pro v1.6[51]. We manually tuned the parameters of a BLED (Table S2) to maximize the chances of detecting sperm whale clicks under a range of background noise scenarios, but this first step in acoustic processing also generated many false positives. These false positives were filtered out in the second step of our automated workflow by searching BLED results for repetitive, evenly-spaced sequences of detections matching the known inter-click interval (ICI) range of sperm whale clicks (~0.5 – 2.0 seconds[52]). Because the intervals between clicks in sperm whale echolocation sequences are largely regular but not exactly constant (Figure 1C), we calculated the time difference between each BLED detection (inter-detection interval; IDI), then rounded to the nearest quarter second to enable a search for sequences of detections with a near-constant IDI. Each day of recording was automatically searched for IDI sequences matching three criteria: (1) rounded IDI must be between 0.5 and 2.0 seconds (inclusive); (2) rounded IDI must be constant; and (3) the number of consecutive IDI values meeting criteria (1) and (2) must meet a sufficient number of repetitions (r) to confidently determine sperm whale echolocation click presence. We considered any day with at least one sequence meeting these criteria to have sperm whale clicks present; all other days were considered to have such clicks absent. Setting the number of repetitions required to consider clicks present can significantly impact the accuracy of this automated workflow at daily resolution (Figure S1). The optimal value for this parameter was determined via comparison to manual identification of sperm whale search clicks. Manual assessments were completed for one randomly chosen day of each month in both 2016 and 2020, as well as two days of known sperm whale presence near our recording location in late 2022. These 26 days provided a representative range of soundscape conditions by covering the full seasonal cycle, including periods recorded by each of the two consecutively-deployed hydrophones, and including recording periods both affected (2020) and unaffected (2016, 2022) by the change in anthropogenic noise conditions associated with the COVID-19 pandemic[53]. We found optimal performance at r=6, yielding a daily balanced accuracy of 97% (precision=100%, recall=94%) and false positive rate of 0% (Figure S1).

Using this time series of daily-resolution presence and absence, we then calculated monthly percent of recording days with foraging sperm whales present over the time series. This metric is effective in the study context for multiple reasons: (1) it provides sufficient temporal resolution to assess seasonal trends, the primary timescale of focus in this study; (2) automated detector performance is very high at daily resolution (Figure S1), providing high confidence in this metric; and (3) this metric matches that used in previous studies of foraging sperm whale presence at Ocean Station PAPA in the Gulf of Alaska (GoA) over the years 1999-2001[36] and 2007-2012[37], allowing for comparison of seasonal presence of foraging whales across a large latitudinal range. Monthly percent presence values from the GoA were determined by digitizing the figures presenting this information in previous studies[36,37] and were later used in comparison to simulation results. The seasonal patterns from these earlier studies[36,37] match those recorded more recently in the GoA[38] (2011-2019), with all studies showing a summer maximum and winter minimum of foraging sperm whale presence in the GoA.

Seasonality in the detection of foraging sperm whales in the CCCS was assessed statistically via a generalized additive model of monthly percent presence as a function of month with year nested as a random effect, to test for the deviance in percent presence explained by the seasonal cycle alone. Finally, because inter-click-interval (ICI) correlates with body size and demographic group[32] and therefore can help assess the hypothesis of sex-specific partial migration, we calculated the ICI of all detected click sequences in the time series. We used ANOVA to test for seasonal effects on natural-log-transformed ICI distribution. To test for correlation between monthly mean ICI and monthly foraging sperm whale presence, we used linear regression.

Estimation of detection range

Because seasonality in foraging sperm whale detection could be influenced by seasonal differences in detection range, we assessed seasonality in both ambient noise levels and acoustic propagation loss between sound source and the acoustic receiver at MARS. From daily files of 16 kHz audio data spanning the full study period, daily mean noise levels (single-sided mean-square sound pressure spectral density) were computed for the frequency band targeted by the click detector (1.4-4 kHz). These daily ambient noise values were binned by month across years to examine seasonality.

Acoustic propagation loss was modeled for January and July to assess seasonality in click detection range (Figure 1B). This acoustic propagation loss modeling was conducted for a sound source matching the characteristics of sperm whale echolocation at the frequencies targeted by the automated detector. For a complete description of propagation loss modeling methods, see the Supporting Information.

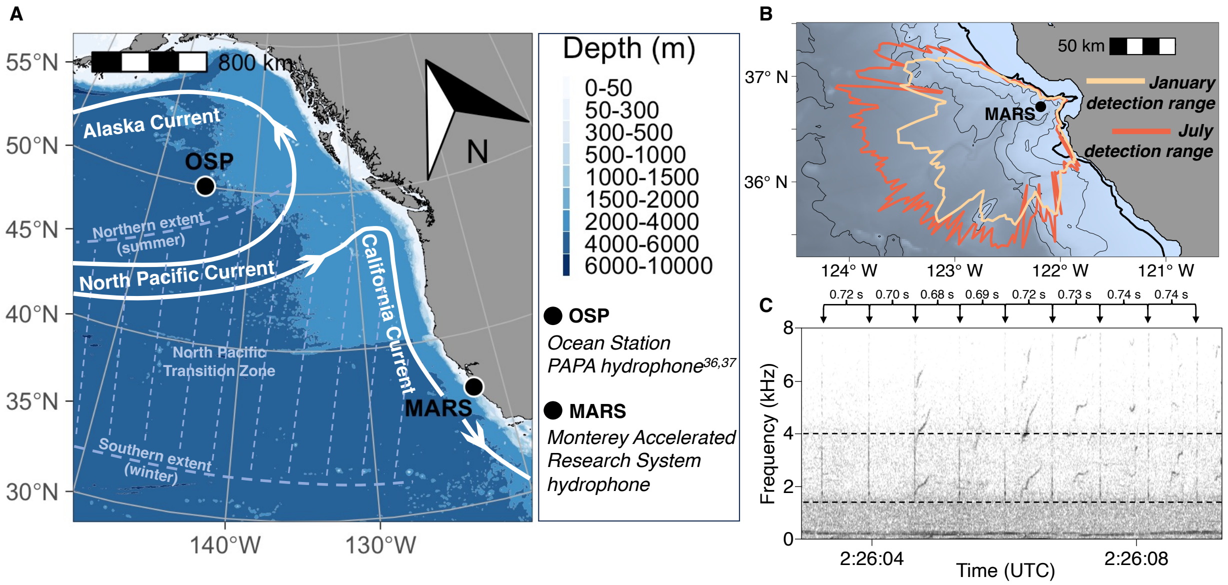

Figure 1. Study system and acoustic methods. (A) *The Northeast Pacific Ocean, showing the location of passive acoustic recordings from the present study (Monterey Accelerated Research System (MARS) in the Central California Current System) and previous studies[36,37] (Ocean Station PAPA (OSP) in the Gulf of Alaska). Some map elements adapted from [16,37].* ***(B)*** *The Central California Current System, indicating winter and summer detection ranges for sperm whale echolocation clicks produced at 500m depth (see Methods and SI for additional depths) based on average January and July oceanographic conditions over the period 2016-2022. The circle indicates MARS (891m depth), with contours representing the 200 m isobath (thicker line) and multiples of 1000m (thinner lines).* ***(C)*** *Example spectrogram of audio recorded at MARS on November 30, 2022, showing a period when a single foraging sperm whale's echolocation clicks (impulsive, broadband signals) were clearly visible and audible. Dashed horizontal lines indicate the minimum and maximum frequencies of the automated energy detector used to detect sperm whale echolocation clicks. Note the near-constant inter-click-interval used to discern echolocating sperm whales from other impulsive sound sources in this frequency range.*

Simulation of individual-level movement strategies

To test hypotheses regarding the individual-level movement strategies underlying empirically observed patterns of foraging sperm whale presence, we developed individual-based movement simulations which we compared to empirical patterns of whale detection. We employed simulations in which agents move through a spatial domain with two hydrophone "listening ranges" (one at higher latitude and one at lower latitude), analogous to passive acoustic monitoring of sperm whales in the GoA[36,37] and the CCCS (present study). In all simulations, 100 agents moved daily according to strategy-specific decisions over a ten-year period. The spatial domain in which these simulations occurred is not meant to specifically represent the spatial dimensions of the North Pacific or hydrophone listening ranges used in the present or previous studies.

Instead, this spatial domain (described in greater detail in the Supporting Information) provides a simplified arena for testing realistic individual movement strategies[54] and their influence on population-level spatiotemporal patterns of acoustic detection (Figure 2).

We used empirically determined information about step length and turn angle distributions, as well as seasonality of movement, for well documented movement strategies across diverse taxa and ecosystems[54] to formulate movement decision rules for agents representing the four hypothesized movement strategies (Table S2). We examined the population-level acoustic detection patterns resulting from each of these four movement strategies via four separate simulations with agents subject to these decision rules. At each daily timestep of each ten-year simulation, we recorded each agent's position and presence or absence in each of the simulated hydrophone listening ranges. The population-level patterns resulting from each simulation were compared to empirical observations of foraging sperm whale seasonality in the GoA[36,37] and the CCCS (present study) by calculating the root-mean-square deviation of simulated monthly mean acoustic detection results from both listening ranges relative to empirical results. For a complete description of simulation parameters (following methods established by [54]), see the Supporting Information and code[55] accompanying this manuscript.

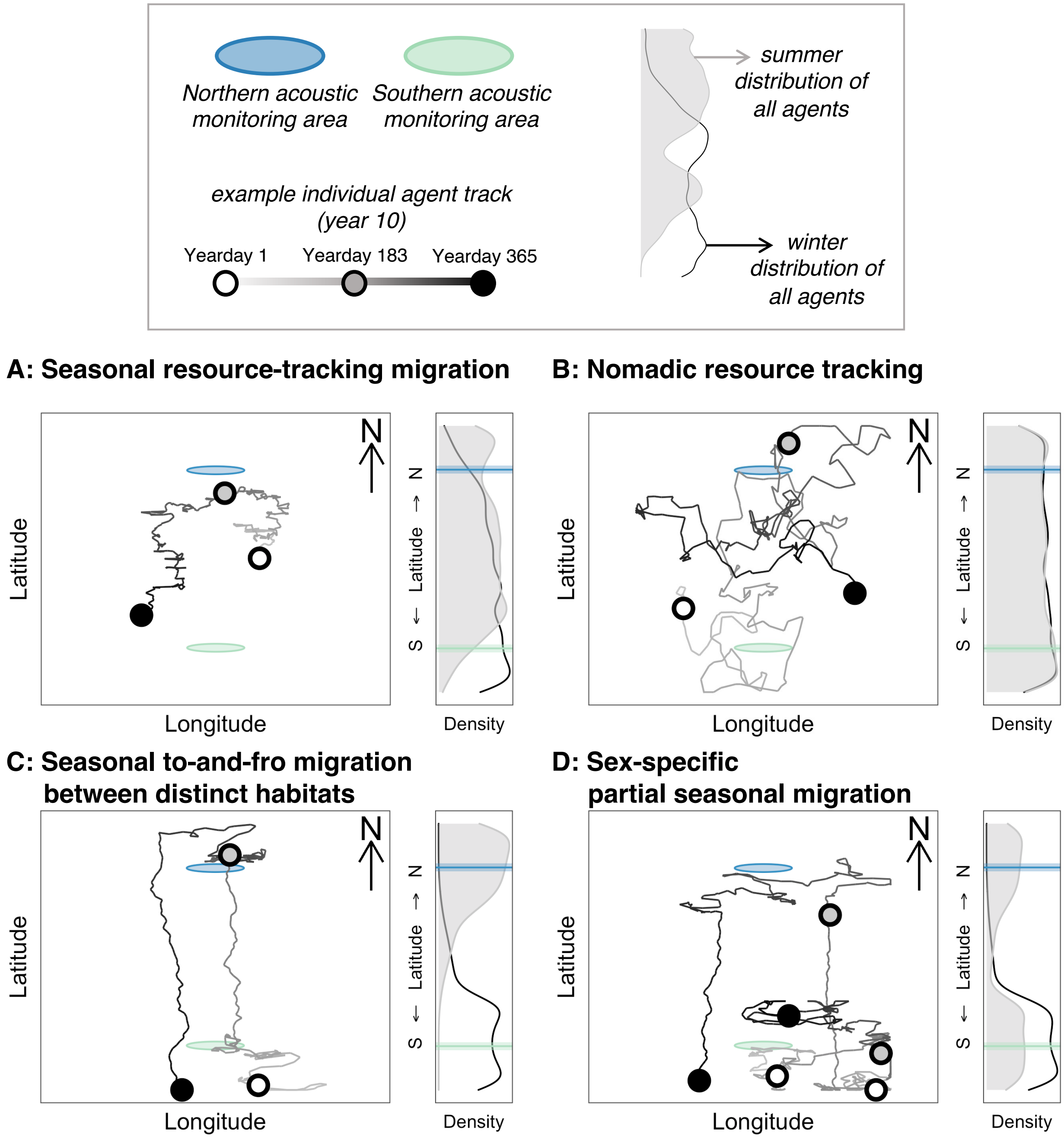

Figure 2. Simulated individual-level movement strategies. *Top panel provides a legend for the simulation domain. In each of the panels A-D, one individual's track (two individuals, one female and one male, in the case of sex-specific partial seasonal migration) is shown from year 10 of the simulation alongside the summer and winter distribution of all individuals over years 2-10. Circular acoustic monitoring areas appear elliptical due to distortion of the simulation domain in this visualization to highlight individual track details.*

Comparison to oceanographic seasonality

To consider whether presence of foraging sperm whales tracks seasonality in oceanographic habitat in a manner similar to many surface ocean predators[16], we compared seasonal patterns of foraging sperm whale presence to seasonal patterns in the location of the North Pacific Transition Zone (NPTZ; Figure 1A). The NPTZ is a major oceanographic feature in the North Pacific Ocean, representing a transition in surface primary productivity between the subpolar and subtropical gyre[56] and serving as important foraging habitat for a wide range of predators in the surface ocean[16,49]. The latitudinal position of the NPTZ varies seasonally, reaching its southern extent in the winter and northern extent in the summer (Figure 1A, [56]). We calculated the monthly latitude of the NPTZ for each month of the acoustic time series as in [56], identifying the mean latitude of the 18 °C sea surface temperature (SST) isotherm between 160-180 °W using monthly composite Aqua MODIS 0.025° daytime SST imagery (for comparison to 2015-2022 CCCS acoustic metrics) and Pathfinder v5.3 0.0417° daytime SST imagery (for comparison to pre-2006 GoA acoustic metrics and to fill Aqua MODIS data gaps). We then compared the monthly percent of days with foraging sperm whale present to the monthly NPTZ latitude via model II (ranged major axis) linear regression, given uncertainty in both the independent and response variables.

Software

All analyses of click detections and individual-level movement simulations were conducted in R v4.2.0[57]. The maps in Figure 1 were created using the packages “ggOceanMaps”[58], “geosphere”[59], and “marmap”[60]. Background noise, acoustic propagation, and satellite-based oceanographic analyses were conducted in Matlab[61]. Candidate click detections were generated using Raven Pro v1.6[50].

RESULTS

Seasonality in acoustic detection

Acoustic detection revealed year-round, seasonally varying presence of foraging sperm whales in the Central California Current System (CCCS; Figure 3). The frequency of foraging sperm whale presence in the average annual cycle reached a maximum in January (mean of 59.3% of days present) and a minimum in July (mean of 31.1% of days present). A generalized additive model revealed a significant relationship between monthly percent of days with presence and month, with year nested as a random effect ($p < 0.001$; 45.4% deviance explained; Figure S2), indicating seasonality in foraging sperm whale presence in the CCCS. Detection seasonality did not result from seasonal changes in ambient noise or maximum detection range. Maximum click detection range was slightly greater during the summer minimum in click detections relative to detection range during the winter detection maximum (Figures 1B, S3), indicating that the degree of seasonality shown here (Figure 3B) is a conservative estimate. Interannually, the percent of recording days on which foraging sperm whales were detected varied little, with the exception of 2016 (Figure 3A). Foraging sperm whales were detected on 63.4% of recording days in 2016, whereas the percentage in all other years varied between 38.6-49.9%.

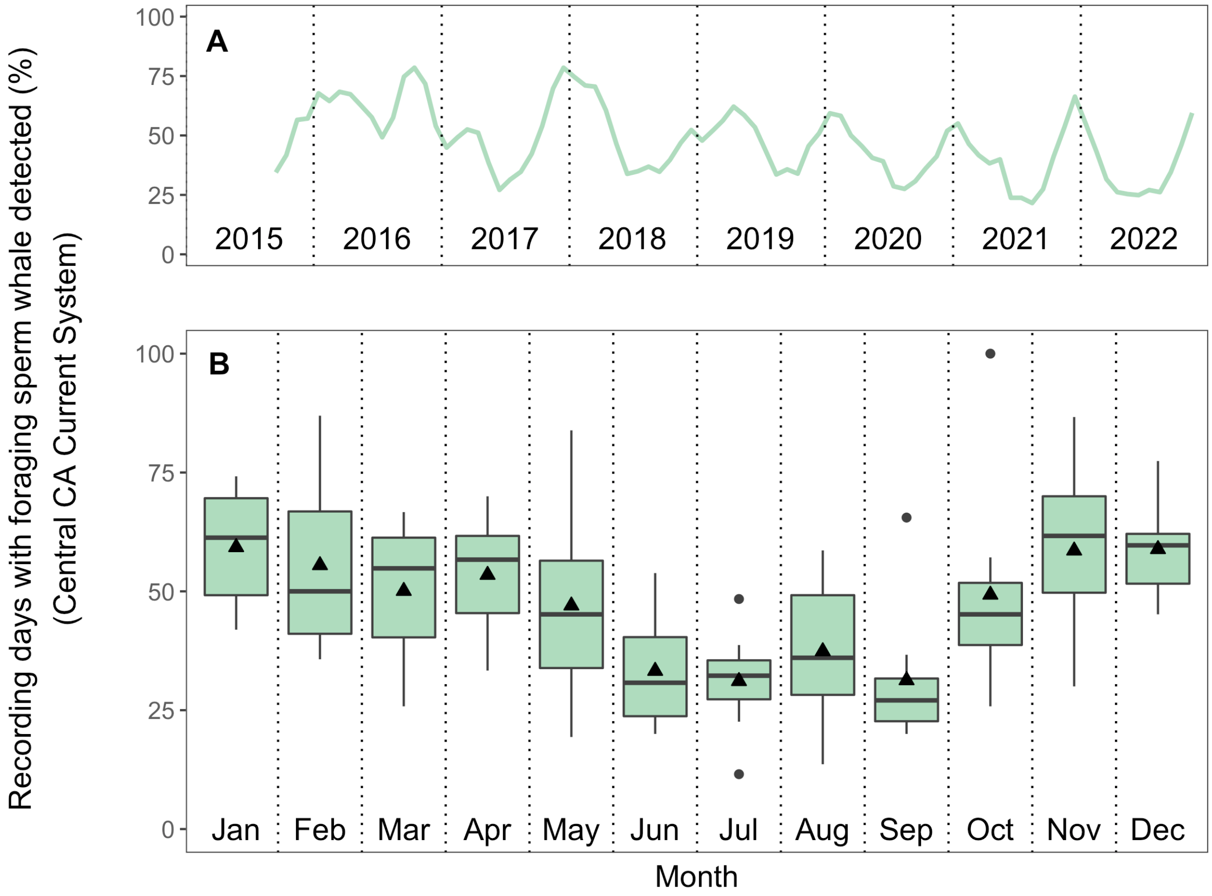

***Figure 3. Empirically observed foraging sperm whale presence in the Central California Current System. (A)** Monthly percent presence over the full study period (smoothed with a 3-month running mean). **(B)** Annual cycle of echolocating sperm whale presence over the full study period (Aug 2015 – Dec 2022). Boxplots show the median (center line), mean (triangle), 25th-75th percentile (box), ± 1.5*IQR (whiskers), and outlying points. A generalized additive model (GAM) revealed a significant relationship between monthly percent of days with presence and month, with year nested as a random effect ($p < 0.001$; 45.4% deviance explained; Figure S2),*

Seasonality of acoustically detected demographic groups

Inter-click-interval (ICI) can be used as a proxy for body-size and therefore demographics of acoustically detected individuals in this sexually dimorphic population[32]. Similar to acoustic results from the GoA[38], we detect three clear modes of ICI (Figure 4). We found no seasonality or interannual variation in the distribution of detected ICIs (and therefore, demographics): ANOVA on natural-log-transformed ICI data indicated no significant relationship between month ($F=1.52$, df = 11,70, $p > 0.14$) or year ($F = 1.70$, df = 7,70, $p > 0.12$) and ICI. We detected individuals with both large body size (adult males, ICI>0.8 s[32,38]) and small body size (females and juveniles, ICI<0.6 s[32.38]) in every individual month of the seven-plus year study period.

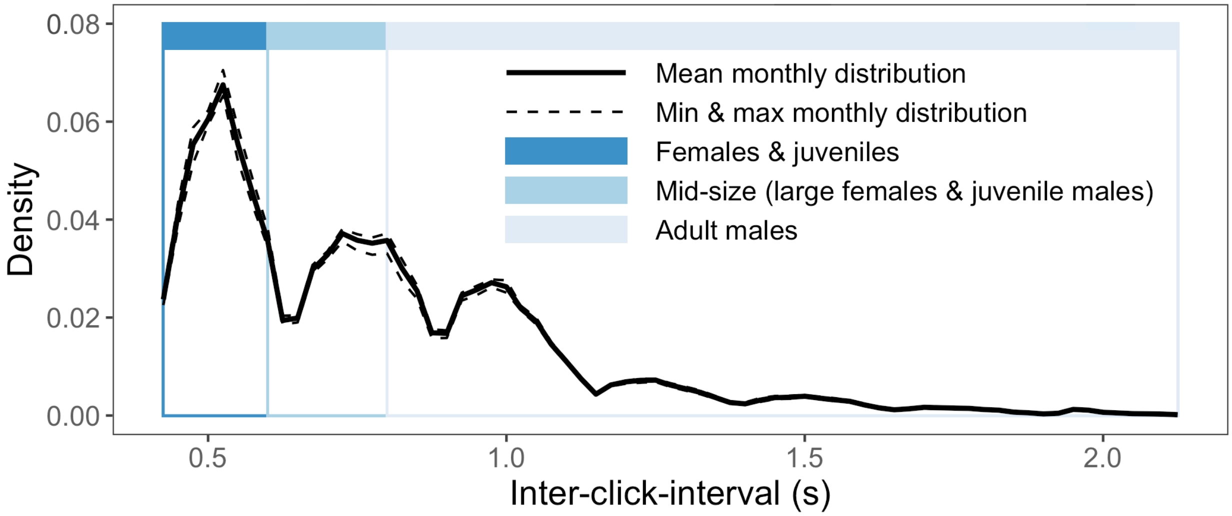

Figure 4. Inter-click-interval (ICI) monthly distributions (relative density). *Solid line represents the mean monthly distribution of ICI for detected sperm whale echolocation clicks over the full study period. Dashed lines represent the minimum and maximum monthly ICI distributions at each ICI value. Colors indicate the demographic groups associated with ICI values as per* [32,38].

Individual-level movement simulations

Simulations of individual-level movement yielded qualitatively and quantitatively distinct patterns in seasonal-latitudinal distribution (Figure 2) and seasonal acoustic detection (Figure 5), dependent on the movement strategy employed. The simulation of seasonal resource tracking individuals yielded year-round presence with moderate seasonality at both southern and northern listening ranges (Figure 2A), peaking in the winter and summer for the southern and northern listening ranges, respectively (Figure 5B). The seasonal patterns of acoustic detection arising from seasonal resource-tracking migration represented the only simulated results matching the defining qualities of empirically observed patterns: year-round presence with substantial and opposite seasonality at both higher and lower-latitude listening ranges (Figure 5). Agents following nomadic resource tracking decision rules showed no seasonality in detection at northern or southern listening ranges (Figure 5B), driven by similar winter and summer latitudinal distributions (Figure 2B). Agents undertaking seasonal to-and-fro migrations between distinct habitats showed strong and opposite seasonality in latitudinal distribution (Figure 2C). This simulation yielded a detection peak during winter and zero detections during summer at the southern listening range, while the northern listening range showed a summer peak in detections and zero detections during winter (Figure 5B). Simulation of sex-specific partial seasonal migration resulted in strong detection seasonality at the northern listening range (high levels of detection in summer, zero detections in winter) and year-round detection with moderate seasonality at the southern listening range (Figure 2D; Figure 5B). Simulated acoustic detection patterns for seasonal resource-tracking migration were also quantitatively most similar to empirical acoustic detection, yielding a root-mean-square deviation among monthly means of only 15.6% (Figure 5B). All other simulated movement strategies resulted in greater deviance from empirical observations (22.4% for nomadic resource tracking, 31.7% for seasonal to-and-fro migration between distinct habitats, 31.9% for sex-specific partial seasonal migration; Figure 5B).

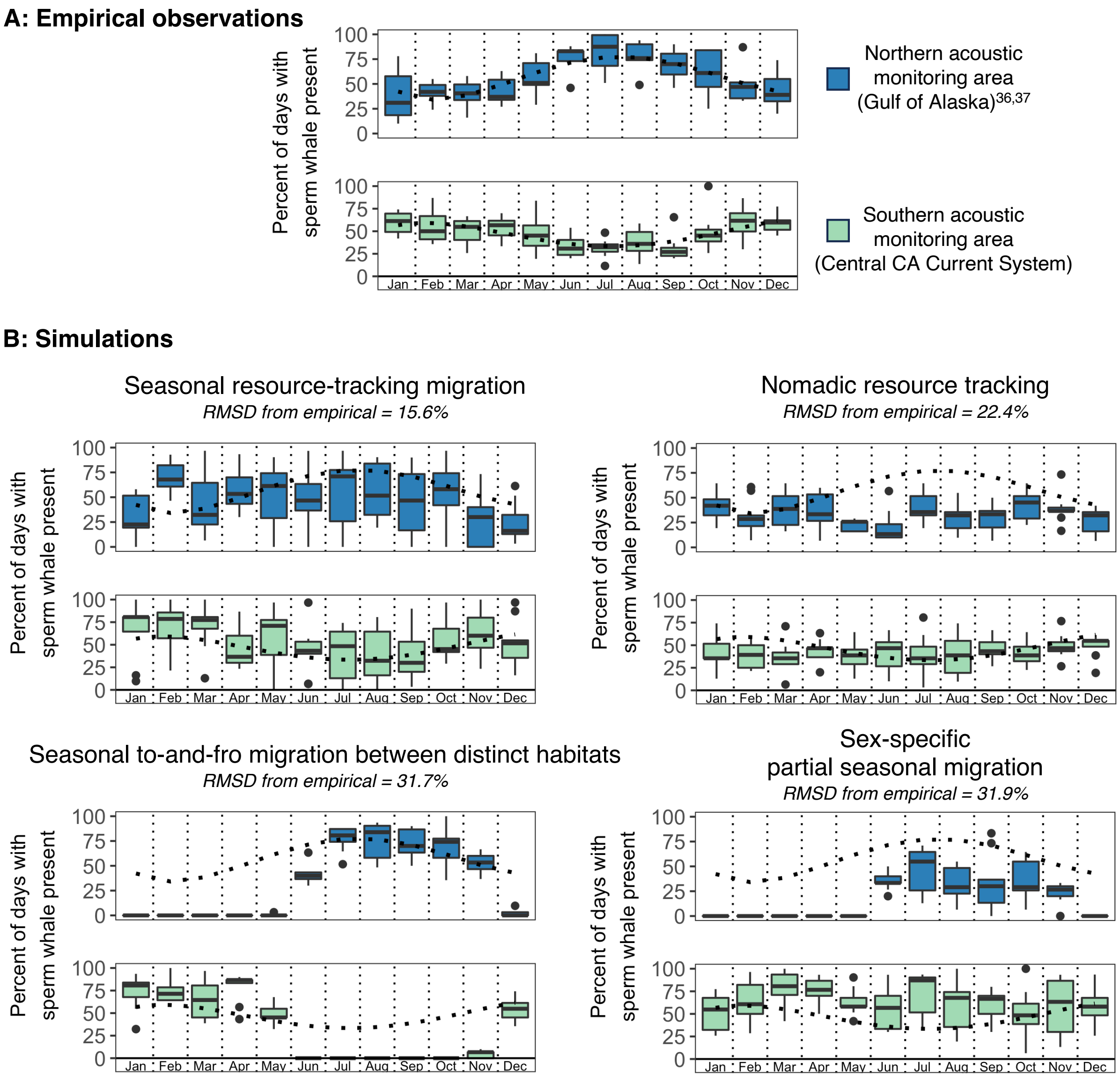

Figure 5. Comparison of empirical and simulated acoustic detection seasonality under hypothesized individual movement strategies. (A) *Empirical acoustic detections from the Central California Current System (green; present study) and the Gulf of Alaska (blue[36,37]). Dotted curves represent a fourth-order polynomial fit to empirical monthly data from each recording site.* ***(B)*** *Acoustic detection at northern (blue) and southern (green) listening ranges for simulated agents following each of the hypothesized movement strategies. Boxplots show the median (center line), 25th-75th percentile (box), ± 1.5*IQR (whiskers), and outlying points of monthly acoustic detection over years 2-10 of each simulation. RMSD refers to the root-mean-square deviation of each simulation's monthly mean acoustic detection results across both hydrophones relative to empirical observations. Empirical data fourth-order polynomial from (A) is overlaid on all simulated results.*

Comparison to seasonally shifting oceanographic habitat

Monthly percent presence of foraging sperm whales correlated with oceanographic seasonality in the Northeast Pacific Ocean (Figure 6). The latitude of the North Pacific Transition Zone (NPTZ) was inversely correlated with foraging sperm whale presence in the CCCS (highest detection rate with NPTZ at its southern extent) and positively correlated with foraging sperm whale presence in the GoA (highest detection rate with NPTZ at its northern extent).

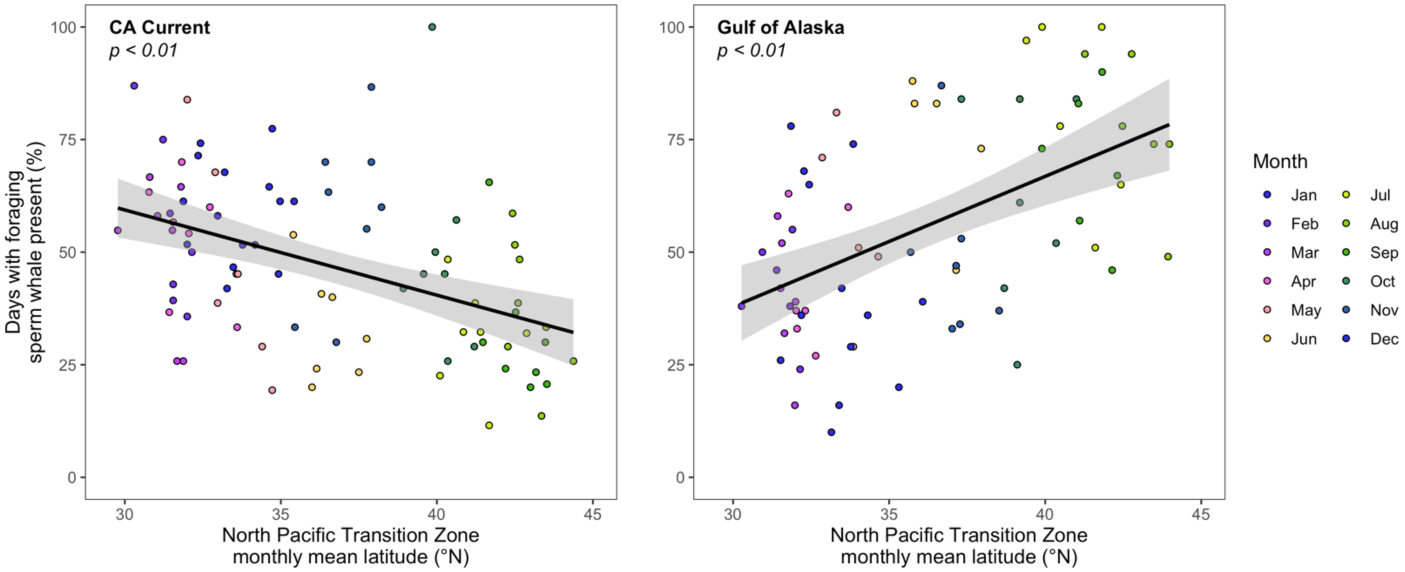

Figure 6. Foraging sperm whale presence follows oceanographic seasonality in the Northeast Pacific. *Monthly empirically observed acoustic detection of foraging sperm whales in the Central California Current System and the Gulf of Alaska*[36,37] *relative to the monthly mean latitude of the North Pacific Transition Zone. p-values reported for model II (ranged major axis; RMA) linear regression.*

DISCUSSION

Animals' movement strategies shape their ecology and their ability to respond to environmental perturbations. Moreover, these strategies offer a window into the spatiotemporal dynamics of the ecosystems they inhabit[1]. Our findings provide evidence for seasonal movements by a cryptic top predator in the deep ocean, the sperm whale, likely to track deep-sea resources. Below, we discuss several lines of evidence supporting this conclusion and consider how these findings advance understanding of seasonal movements in this population. More broadly, we discuss how these results advance knowledge of phenology in the poorly understood deep ocean ecosystems in which sperm whales forage.

The long-term acoustic detection results presented here indicate seasonality in the latitudinal movements of foraging sperm whales, with greater frequency of echolocation click detection in California during winter (Figure 3B; Figure S2), opposite the known summer peak of detection in the Gulf of Alaska[36-38] (Figure 5A). Despite this opposite seasonality, foraging sperm whales are detected year-round in both locations. Based on several lines of evidence, we posit that these patterns indicate a seasonal migration in this population, likely driven by proximate resource tracking in an ecosystem with dampened seasonality. Seasonal resource-tracking migration is the only hypothesized movement strategy allowing for both year-round presence and significant seasonality in presence across latitudes (Figure 2A; Figure 5B), matching empirical observations (Figure 5A). Other hypothesized strategies yield either year-round presence (as in nomadism) or seasonality in acoustic detection across latitudes (as in full and sex-specific partial migration between distinct habitats), but do not match both of these key attributes of the empirical observations (Figure 5). Additionally, if sex-specific partial seasonal migration were occurring, we would expect the migratory demographic (previously hypothesized to be adult males[34,43], with larger body sizes and higher inter-click-intervals (ICI)) to drive seasonal patterns in the distribution of detected ICIs. Yet we do not observe any significant seasonal shifts in the monthly distribution of detected ICIs in California, instead detecting clicks consistent with female, juvenile, and adult male body sizes year-round (Figure 4). We also find no relationship between monthly mean ICI and monthly percent presence (Figure S4), further indicating that the seasonal pattern observed in Figure 3 is not driven by adult males alone. These results are consistent with long-term acoustic results from the GoA which also show year-round use of high latitudes by females and juveniles[38]. This growing body of evidence from long-term, population-level observations via passive acoustics is inconsistent with the individual-sightings-based hypothesis of sex-specific latitudinal segregation, likely arising from differences in the scale and persistence of observation[45,46]. Even though significant uncertainty about the specific processes underlying these seasonal patterns remains, such continuous and detailed deep-sea acoustic observations provide useful insights toward enhancing our understanding of the phenology of sperm whale behavior and the vast and opaque ecosystem they inhabit.

Despite seasonality in the frequency of foraging sperm whale presence, whales are still detected year-round across latitudes (Figure 5A). This would be unexpected for a population migrating to track proximate resources in a strongly seasonal (e.g., terrestrial or surface ocean) ecosystem, but one might expect subtle population-level seasonality of this nature for predators tracking resources in an ecosystem with a dampened seasonal cycle. There is growing evidence that deep sea ecosystems exhibit such dampened seasonality[26-28], resulting from an indirect relationship with seasonal solar variation mediated by organic matter falling from the directly seasonal surface ocean[23-25]. Seasonal resource-tracking migration in such an ecosystem can be considered an intermediate strategy between the seasonal resource-tracking movements previously studied in strongly seasonal ecosystems and the nomadic resource-tracking movements found in aseasonal ecosystems. Given that our simulation of nomadic resource tracking yielded the second-closest match to empirical observations (Figure 5B), future work might test for individual-level variation along this continuum of nomadic to strongly seasonal resource tracking movements.

Our findings imply that sperm whales seasonally track a specific resource or resource-rich habitat in the Northeast Pacific. We tested whether sperm whales' acoustically inferred seasonal movements track seasonal-latitudinal patterns in the NPTZ, the dominant foraging habitat which numerous surface ocean predators track in this ocean basin[16,49]. We find support for this hypothesis, with higher detection of foraging sperm whales at lower latitudes when the NPTZ is at its southern extent (and vice versa; Figure 6). The considerable variation around this trend likely arises from the indirect link between surface biophysical processes (as measured via NPTZ latitude) and the behavior of a deep-sea top predator. Nevertheless, that this top predator of the deep ocean exhibits similar resource tracking behavior to that previously documented for surface ocean predators[16] suggests ecological links between surface and deep ocean processes and seasonality. Diel vertical migration of animals between the deep and surface ocean can vary seasonally in terms of depth distribution, total biomass, and carbon transport[27,62-64]. In Monterey Bay specifically, total biomass throughout the meso- and epipelagic is at a minimum in spring and summer, rises in the fall, and remains elevated through the winter[27], allowing for greater transport of biomass between surface and deep waters during the seasons when foraging sperm whale detections peak in this region (Figure 3B). It is important to note that we do not directly measure tracking of a forage resource here, and resource-tracking migrations can also include movements to track non-forage resources (e.g., predator-free habitat, favorable abiotic conditions, etc.[1,65]), Still, the intensive energetic demands of raptorial feeding at sperm whales' extreme body size[66] point to forage availability as a likely motivator of their movements in space and time. While our findings shed light on the likely resource-tracking seasonal-scale movements of sperm whales in the Northeast Pacific, future work might explore the habitat characteristics which sperm whales track at finer scale similar to previous studies on southern elephant seals (*Mirounga leonine*)[67,68], another highly mobile mesopelagic predator.

Seasonal resource-tracking migrations in terrestrial and epipelagic populations typically evolve as a strategy to maximize resource gain in dynamic, seasonal ecosystems[1,4,11]. Interannual variability around the average seasonal-latitudinal patterns exhibited by foraging sperm whales (Figure 3) suggests that the cues driving their latitudinal movements are not fixed seasonal cues (e.g., day length), thus affording flexibility to respond to environmental variation and change. Sperm whales were most often detected in the CCCS during 2016 (Figure 3A), a year in which a persistent marine heatwave combined with a strong El Niño to drive widespread biological impacts in both the CCCS[68] and GoA[69]. By exhibiting a movement strategy driven by resource tracking rather than fidelity to a fixed foraging area or migratory schedule, sperm whales appear to respond flexibly to interannual variability in oceanographic conditions (Figure 3A). Such flexibility is often characteristic of greater resilience to environmental perturbations[70] including marine heatwaves[71]. Understanding the individual and population-level outcomes of such flexibility in this sperm whale population remains an important and rich area for future study.

While the specific cues that enable these seasonal movements remain unclear, some combination of individual and social information is likely. As air-breathing predators, sperm whales spend significant time in surface waters subject to seasonal variability in solar irradiation, day length, and temperature. This provides a direct means of tracking progression of the seasons, perhaps enabling movements influenced by spatiotemporal memory similar to that observed in highly mobile epipelagic predators[19]. Because sperm whales echolocate to find prey, long-distance acoustic information on the foraging behavior of conspecifics might further direct this search, similar to the “mobile sensory networks” formed by echolocating bats[73]. Social learning of foraging and migration strategies could also play a role[74,75], as sperm whales are highly social animals[34].

Taken together, our findings suggest that growing evidence for seasonal processes in the deep ocean extend even to the seasonal movements of a top predator. This study underscores the need for additional research to understand phenology across trophic levels in light-limited deep pelagic ecosystems. A growing suite of technologies, including remotely operated vehicles, autonomous underwater vehicles, and continuous acoustic monitoring are providing an unprecedented opportunity to observe and understand deep ocean ecosystems[22,28,76]. Especially when integrated[28,77], these tools can shed light on our murky understanding of seasonal processes and animals’ resource-tracking strategies in the deep sea. In turn, we can provide more precise scientific insight in support of spatiotemporally dynamic ecosystem management efforts which have to-date been used on land and in the surface ocean[78], but which may be possible and valuable in open and deep ocean ecosystems[79].

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Supporting Information for:

Acoustic evidence for seasonal migration by a cryptic top predator of the deep sea

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Supporting information on simulation of individual movement strategies

The simulation methods used here follow methods introduced by Abrahms et al. (2017)[1]. Briefly, Abrahms et al. (2017)[1] generated “computer-simulated idealized movement syndromes representing suites of correlated movement traits observed across taxa”. Their paper compared these idealized syndromes and their corresponding step length and turn angle distributions to 130 individual tracks from 13 vertebrate species exhibiting a range of movement strategies (migration, nomadism, territoriality, and central place foraging) in both marine and terrestrial ecosystems. These tracks ranged in duration from several months to multiple years, and were processed to standardized, 1-hour position sampling intervals given the importance of fix rate to step length and turn angle distributions. These authors found strong statistical evidence that their simple suite of seasonal movement rules, turn angle, and step length distributions for distinct movement strategies robustly represent the movement strategies in the diverse tracking dataset to which they were compared. These suites of distributions and movement rules therefore provide a useful set of dimensionless distributions representative of distinct vertebrate movement “syndromes”.

We applied these suites of distributions and movement rules to a dimensionless simulation domain which provides a simplified arena in which to explore the patterns of detection in two geographically-distant monitoring areas under hypothesized movement strategies. This domain is not meant to specifically represent the spatial dimensions of the North Pacific, but instead provides an arena for simplified hypothesis-testing roughly analogous to the geometry of our empirical sensors in the North Pacific. Agent step lengths, hydrophone listening ranges, and domain dimensions were scaled proportionally to give agents limited probability of acoustic detection even if present at the latitude of a listening range (i.e., listening ranges covered only a proportion of both the latitudinal and longitudinal dimensions). This approach allowed for realistic probabilities of acoustic detection for a large number of individual position-days (365,000 per simulation) without the extreme computational expense of simulating a number of agents comparable to the estimated population size of sperm whales in the eastern North Pacific (~2000[2]).

All distributions for step lengths and turn angle, as well as seasonality and other elements of movement rules, are summarized in Table S1. These simulations were implemented in a domain with longitude ranging from -2000 to 2000 and latitude ranging from 0 to 30000 (dimensionless units). Hydrophone “listening ranges” were positioned at (0, 5000) and (0, 25000).

Nomadic resource tracking

We simulated nomadic individuals using decision rules previously documented for nomads[1]: low probability (P=0.1) of behavioral state switching between active foraging and searching, small step lengths and uniformly-distributed turn angles during active foraging, and longer step lengths during searching with normally-distributed turn angles (around the initial direction after switching from foraging to searching).

Seasonal resource-tracking migration

We simulated movements to track resources with a shifting seasonal-latitudinal distribution using decision rules similar to those for nomadic resource tracking as described above, but with differences in movement behavior between times and locations of active foraging. Rather than searching in a single direction with turn angles normally-distributed around a randomly-selected initial search direction (as in nomads), agents in this simulation moved between active foraging periods by tracking resources with headings normally-distributed around due north and due south. The probability of northward-centered or southward-centered heading distributions during resource tracking varied seasonally to mimic seasonal shifts in latitudinal resource availability.

Seasonal migration between distinct habitats

We simulated migration between distinct habitats again using the decision rules documented by[1]: four months of foraging in a southern range (steps defined by uniform step length and turn angle distributions), two months of northward migration (longer step lengths and normal turn angle distribution centered on north), four months of foraging in a northern range (steps again defined by uniform step length and turn angle distributions), and finally two months of southward migration (longer step lengths and normal turn angle distribution centered on south).

Sex-specific partial seasonal migration between distinct habitats

We simulated sex-specific partial seasonal migration by assigning 50% of agents to a migratory (male) group and 50% of agents to a resident (female and juvenile) group. Migrants followed the decision rules described above for migration between distinct habitats; residents followed the decisions rules described above for nomadic resource tracking, but only in the southern portion of the simulation domain.

Table S1. *Parameters for simulations of hypothesized individual-level movement strategies, derived from [1]. † Precise migration onset and duration varies slightly by individual (sd = 5 days).*

Simulated movement strategy	**Behavioral states**	**Step length**	**Turn angle (°)**	**Behavioral transition probability**	**Seasonality**	**Demographic elements**
Nomadic resource tracking	Active foraging	gamma distribution (shape=2, rate=2) *100	uniform distribution (min=0, max=360)	P = 0.1 (switch to searching)	N/A	N/A
	Searching	uniform distribution (min=0, max=300)	If transitioning from forage to search: uniform distribution (min=0, max=360) If continuing search: normal distribution (mean=preceding step angle, sd=60)	P = 0.1 (switch to active foraging)	N/A	N/A
Seasonal resource-tracking migration	Active foraging	gamma distribution (shape=2, rate=2) *100	uniform distribution (min=0, max=360)	P = 0.1 (switch to searching)	N/A	N/A
	Searching	uniform distribution (min=0, max=300)	normal distribution, either northward (mean=0, sd=10) or southward (mean=180, sd=10)	P = 0.1 (switch to active foraging)	probability of northward search varies seasonally (max of 0.8 in summer; min of 0.2 in winter)	N/A

Simulated movement strategy	Behavioral states	Step length	Turn angle (°)	Behavioral transition probability	Seasonality	Demographic elements
Seasonal migration between distinct habitats	Active foraging	gamma distribution (shape=2, rate=2) *100	uniform distribution (min=0, max=360)	P = 0.1 (switch to searching)	During ~4-month periods between northward & southward migrations	N/A
	Searching	uniform distribution (min=0, max=300)	If transitioning from forage to search: uniform distribution (min=0, max=360) If continuing search: normal distribution (mean=preceding step angle, sd=60)	P = 0.1 (switch to active foraging)	During ~4-month periods between northward & southward migrations	N/A
	Northward migration	constant (distance between habitats divided by ~2-month migration duration)	normal distribution (mean=0, sd=5)	N/A	~2-month period in spring-summer †	N/A
	Southward migration	constant (distance between habitats divided by ~2-month migration duration)	normal distribution (mean=180, sd=5)	N/A	~2-month period in fall-winter †	N/A

Simulated movement strategy	Behavioral states	Step length	Turn angle (°)	Behavioral transition probability	Seasonality	Demographic elements
Sex-specific partial seasonal migration	Active foraging	gamma distribution (shape=2, rate=2) *100	uniform distribution (min=0, max=360)	P = 0.1 (switch to searching)	During ~4-month periods between northward & southward migrations	N/A
	Searching	uniform distribution (min=0, max=300)	If transitioning from forage to search: uniform distribution (min=0, max=360) If continuing search: normal distribution (mean=preceding step angle, sd=60)	P = 0.1 (switch to active foraging)	During ~4-month periods between northward & southward migrations	N/A
	Northward migration	constant (distance between habitats divided by ~2-month migration duration)	normal distribution (mean=0, sd=5)	N/A	~2-month period in spring-summer †	Assigned 50% of population undertakes migration
	Southward migration	constant (distance between habitats divided by ~2-month migration duration)	normal distribution (mean=180, sd=5)	N/A	~2-month period in fall-winter †	Assigned 50% of population undertakes migration

Supporting information on acoustic propagation loss modeling

We modeled acoustic transmission loss for an impulsive sound source at 2.7kHz (the center frequency of the BLED), 185 dB re: 1μPa at 1m (peak level of the omnidirectional low-frequency component of sperm whale echolocation clicks[2]), and source depths of 100, 500 and 1000m (typical of echolocation in foraging sperm whales in many ecosystems[3-6]), received at the location of MARS. Propagation loss was modeled for January and July to assess seasonality in click detection range. Oceanographic water column properties for the January and July model runs were calculated as the climatological mean of oceanographic conditions over the period 2016-2022 as estimated by the HYCOM (HYbrid Coordinate Ocean Model) data assimilative system[7] with 4.8-minute spatial resolution. Acoustic propagation loss was then calculated for each of 360 1° bearings from MARS (Figure 1B) using a wave-theory parabolic equation model that accounts for absorption in both the water column and the bottom, scattering in the water column and at the surface and bottom, geometric spreading (spherical and cylindrical), refraction, and diffraction[8]. Finally, detection range for each source depth and season was estimated for each of these 360 bearings, requiring received level at MARS to exceed 5.0 dB (SNR of the click detector, Table S2) above monthly median ambient noise levels (Figure S3).

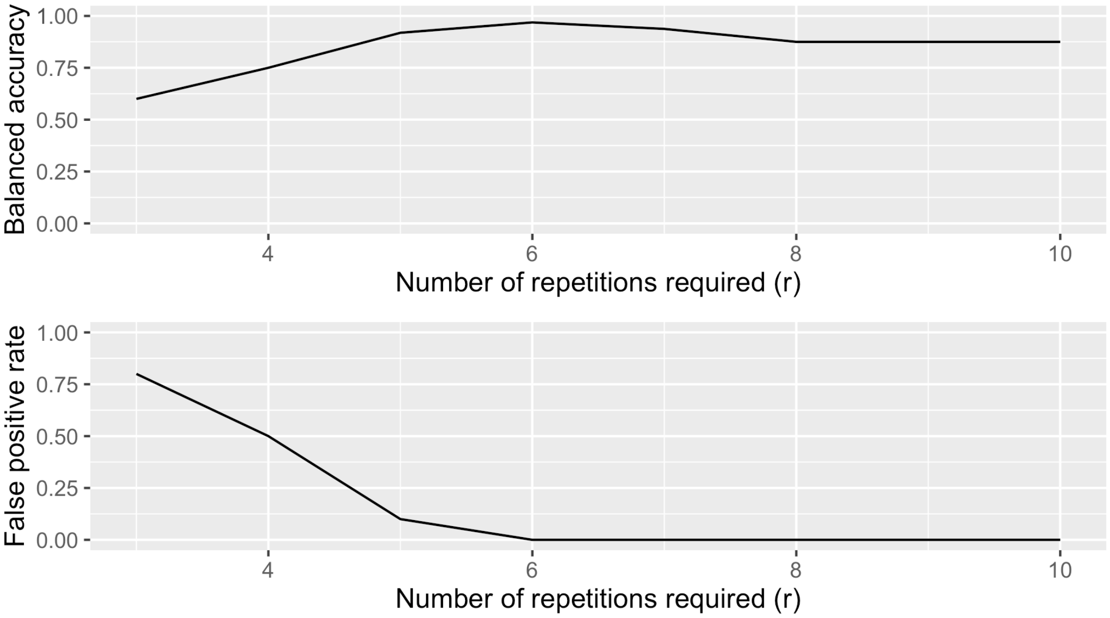

Figure S1. Performance of automated daily acoustic processing relative to manual assessment. Requiring six repetitions of click detection at near-constant inter-click interval (r = 6) yields a daily balanced accuracy of 97% and daily false positive rate of 0%.

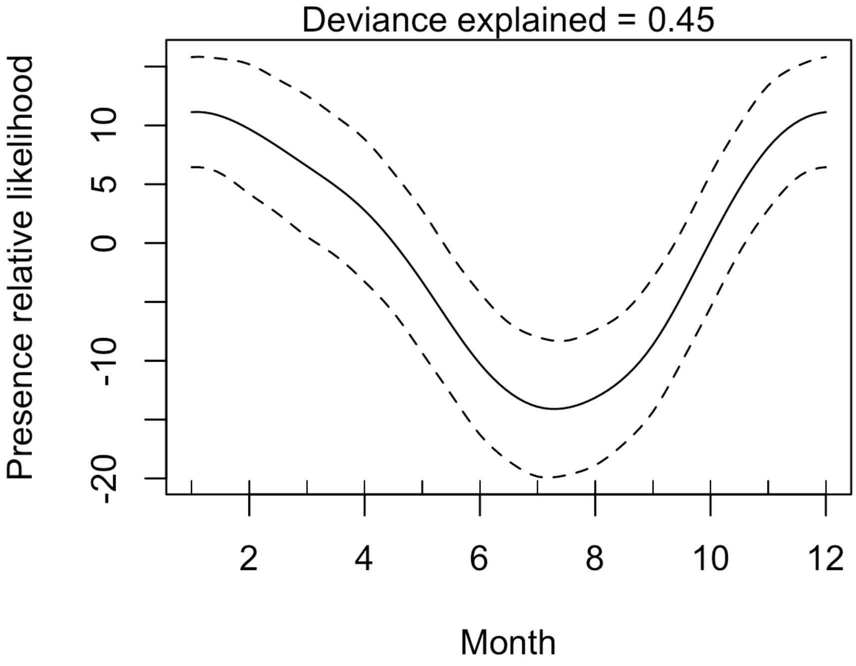

Figure S2. Generalized additive model fit relationship for monthly foraging sperm whale presence (% of days) and month, with year nested as a random effect.

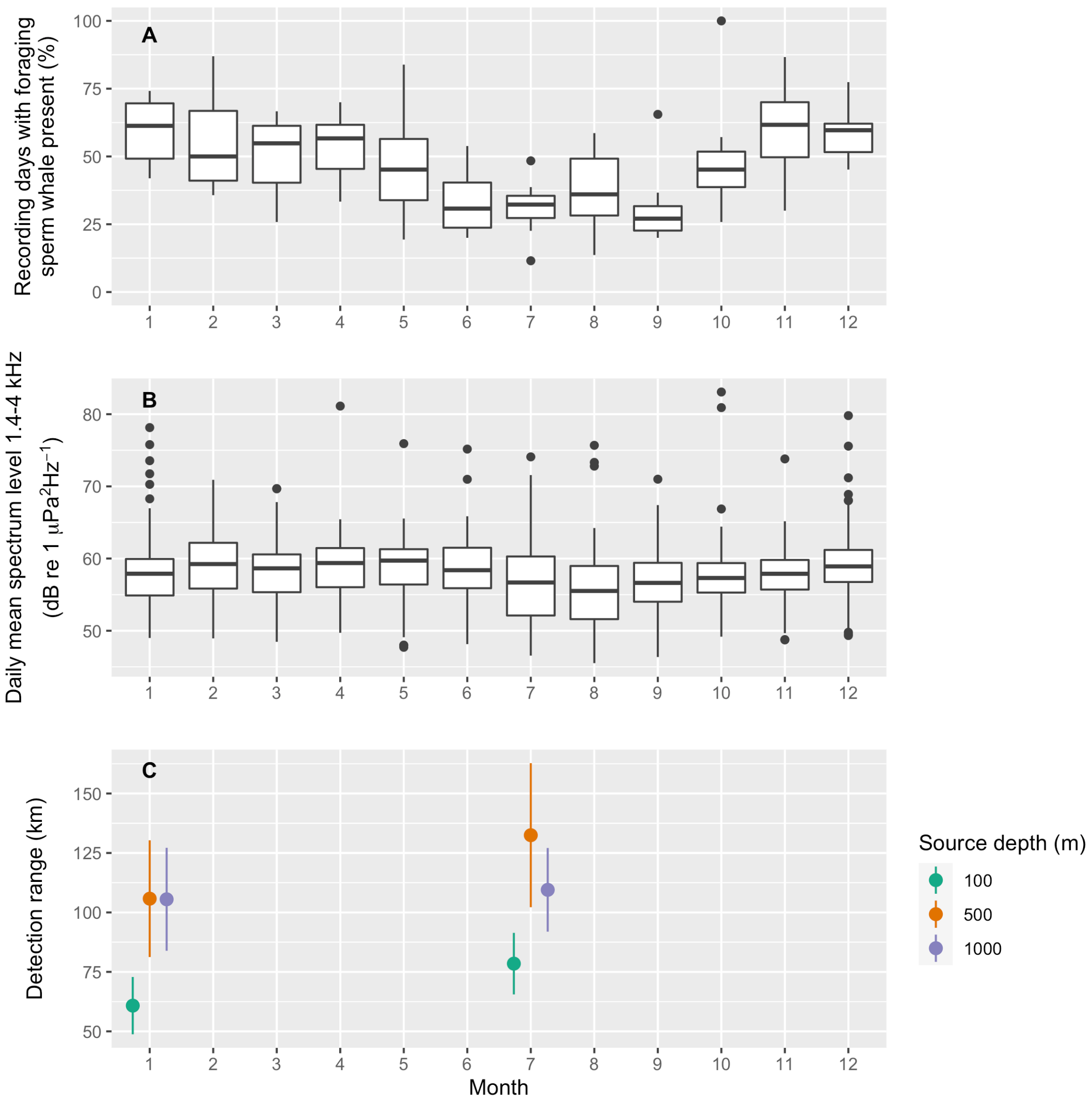

Figure S3. Seasonal variation in listening conditions at MARS. (A) Average annual cycle of echolocating sperm whale presence averaged over the full study period (Aug 2015 – Dec 2022), reproduced from Figure 3B in the main text. **(B)** Average annual cycle of ambient noise conditions at MARS in the frequency range (1.4-4kHz) targeted by the band limited energy detector employed to identify candidate sperm whale echolocation detections. **(C)** Estimated maximum detection range at MARS for sperm whale echolocation clicks produced at depths of 100, 500, and 1000m during the maximum (January) and minimum (July) months of foraging sperm whale presence. Points and lines represent the mean and standard deviation of 1-degree bearing ranges between 154-311° around MARS, representing the offshore area where 500m and 1000m source depth results are not limited by the shelf break (Figure 1B), and where sperm whales are most likely to be found. See Methods for information on modeling of acoustic propagation and detection range.

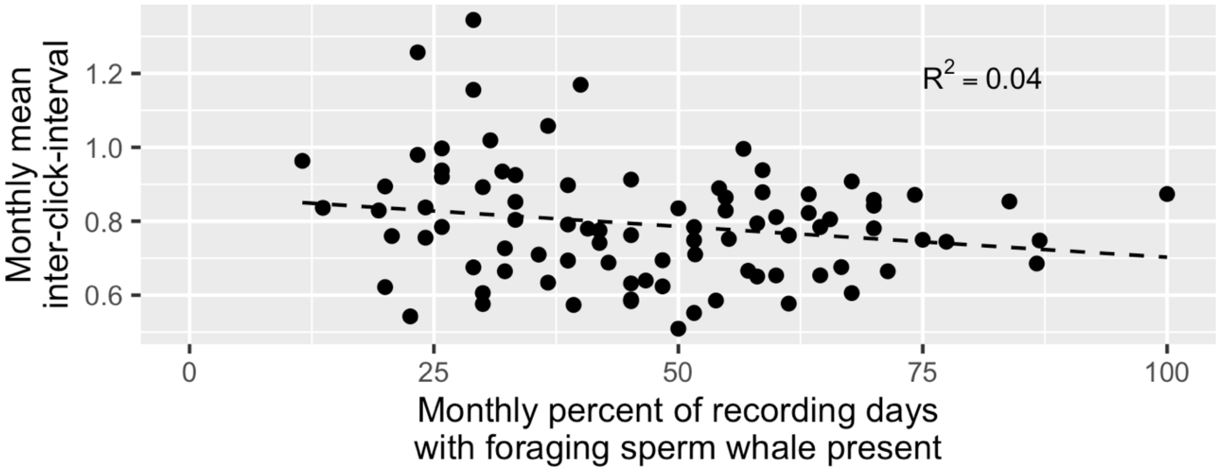

Figure S4. Additional inter-click-interval (ICI) comparison to monthly foraging sperm whale presence. Monthly mean ICI vs. monthly percent presence, indicating no significant relationship between these variables ($p > 0.05$).

Table S2. Band limited energy detector parameters.

BLED signal calculation	
Min. Frequency	1.4 kHz
Max. Frequency	4.0 kHz
Min. Duration	8.125 ms
Max. Duration	32.5 ms
Min. Separation	32.5 ms
BLED noise calculation	
Block size	2.0 s
Hop size	0.5 s
Percentile	20.0
Signal-to-noise parameters	
Min. Occupancy	70.0%
SNR Threshold	5.0 dB
Spectrogram calculation	
Window	Hann
Window Size	512 samples
Window Overlap	95%

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