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Postweaning horizontal movements and diving behavior of a recovering grey seal (*Halichoerus grypus atlantica*) population in the western North Atlantic

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Abstract

Background Conserving marine predators is tantamount to maintaining functional marine ecosystems. Though intensively studied in other regions, little is known about at-sea movements and diving behaviors of a recovering population of grey seals (*Halichoerus grypus atlantica*) inhabiting northeastern United States continental shelf waters. Young-of-year grey seals may be particularly vulnerable to threats due to a lack of parental care postweaning. There is a need to establish baseline knowledge of at-sea behaviors in the face of large-scale ocean industrialization. We deployed 63 satellite relay data loggers on young-of-year grey seals to investigate postweaning at-sea movements and dive behaviors prior to the installation of offshore wind turbines.

Results Young-of-year grey seals dispersed widely across the continental shelf waters. Collective utilization distributions of seals overlapped with offshore wind planning areas in the winter and spring months, and overlap was lowest in the summer when the seals dispersed northeastward. Maximum diving depth and duration increased in the first two months of nutritional independence and stabilized by April. Dives were classified as being either benthic or pelagic depending on dive depth relative to bathymetry. Seals conducted more benthic diving in the spring and this coincided spatiotemporally with habitat and phenology of an important prey species. Following a diel trend, benthic diving peaked during daylight hours, while pelagic diving occurred more frequently at night. Benthic dives occurred more frequently than pelagic dives in sandy shoals and banks. Furthermore, seals conducted more benthic than pelagic dives in wind energy planning areas.

Conclusions Ours is the first comprehensive study on the horizontal movement and diving behaviors in the U.S. population of grey seals, contributing knowledge on the at-sea habits of a vulnerable demographic in relation to other anthropogenic uses of the marine environment. This information will serve as valuable input to conservation management and mitigation plans, and it contributes necessary regional context to the broader understanding of grey seal ontogeny across the North Atlantic. Furthermore, these results provide important baseline information for future comparative analyses of grey seal behavior as offshore wind development expands in scope in this region.

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Background

As marine mesopredators, pinnipeds (seals, sea lions, and walrus) play important functional roles in ecosystems through top-down predator–prey interactions including consumptive and non-consumptive risk effects, inter-specific behavioral facilitation, and bottom-up forcing such as translocation of nutrients [1]. For example, it is estimated that whales and seals in the Gulf of Maine may be responsible for supplying the euphotic zone with over 20,000 metric tons of nitrogen in a given year, amounting to more nitrogen input than the combined riverine systems in the region, and thus facilitating significant amount of primary production [2]. As such, the conservation of marine predators, including pinnipeds, is tantamount to maintaining functional ecosystems in the face of rapid environmental change induced by a myriad of anthropogenic activities.

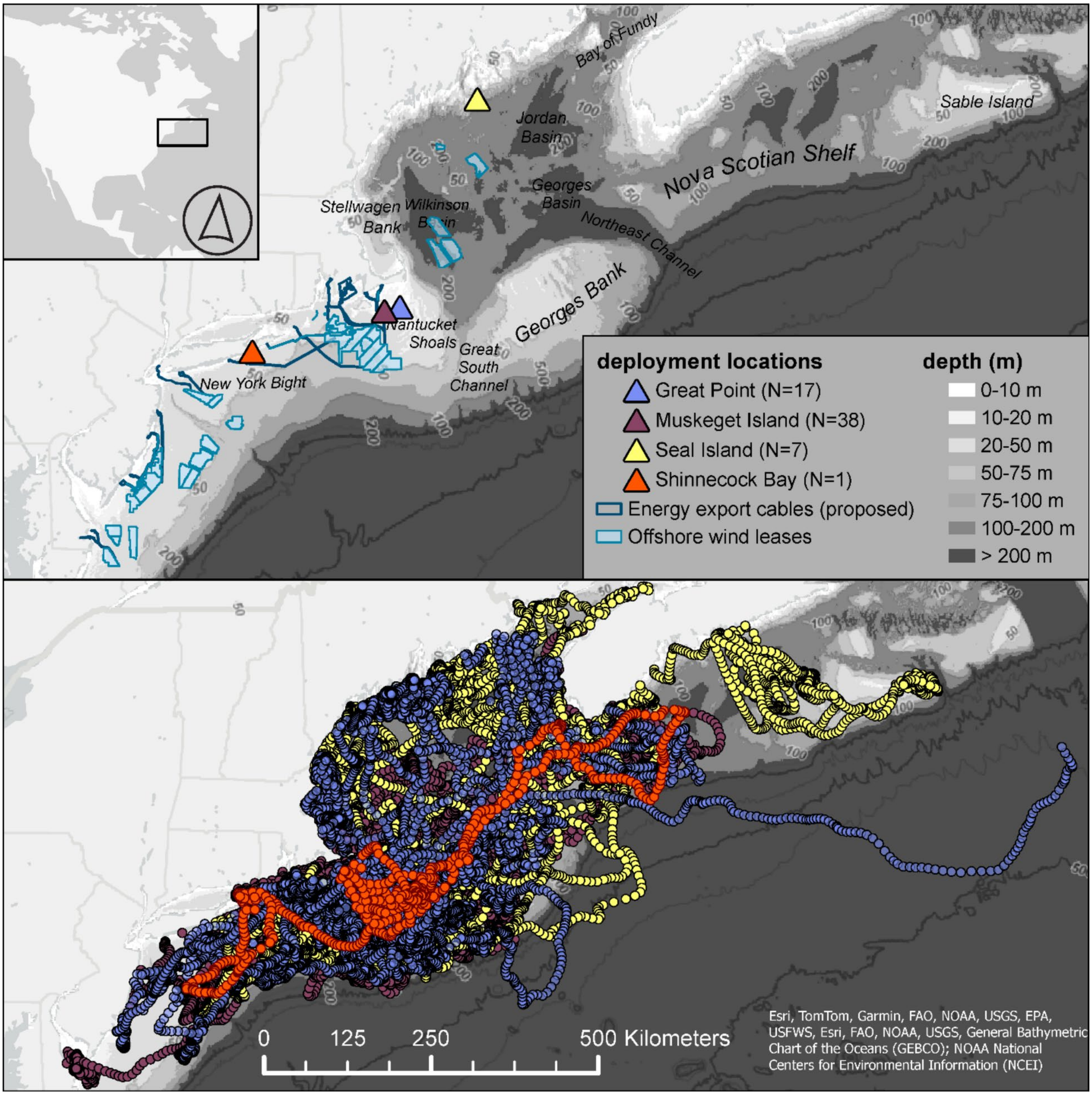
Rapid coastal urbanization and the expansion of built infrastructure into coastal and offshore zones [3] threatens semi-aquatic species such as pinnipeds [4]. Globally, the number of operational offshore wind structures has increased exponentially with infrastructure forecasted to be double that of oil and gas industry by 2040 [5]. Wind energy planning areas on the northwestern Atlantic continental shelf are located within or adjacent to marine and coastal habitats which are utilized by a variety of protected species and forage fish [6–8]. Pile driving noise is known to cause displacement or direct injury [9–11], yet offshore wind infrastructure is also known to alter the trophic structure of the benthos and water column [12–14], potentially providing habitat refugium or increased foraging opportunities for upper trophic predators [15, 16]. However, net impacts of offshore wind development to pinnipeds are not well understood.

The development of one of the first large-scale, offshore wind projects in the United States began June 1, 2023, with planned infrastructure adjacent to rookeries used for pupping and molting by a recovering population of western Atlantic grey seals [17] (*Halichoerus grypus atlantica*) [18]. One of the main offshore energy transport cables passes just west of the largest breeding colony in the U.S., which is located on Muskeget Island, Massachusetts (Fig. 1; Top frame). The proximity of the offshore wind footprint to this breeding population provides an opportunity to better understand the impacts of offshore wind construction and operation on western Atlantic grey seals, with implications for other pinniped species globally.

Extirpated due to bounty hunting in the 19th and early twentieth centuries [19], the western North Atlantic grey seal population underwent a genetic bottleneck [20] and was essentially absent from U.S. waters until legal protections led to re-establishment of pupping colonies in the late 1980s [21]. Portions of the population in Canada, particularly seals from Sable Island, are believed to be the source of the recolonized colonies in the United States [17]. Now, large congregations of grey seals use these pupping colonies from early December to late January for pupping and breeding and, at other times of year, to rest or to molt. The number of pups born at most sites has increased over the past several decades, and the number of breeding colonies in the U.S. has expanded as well [22].

Researching juveniles in wildlife populations is fundamental to understanding the key factors that influence population growth, survival, and fitness. For many aquatic mammals, immature individuals are likely more vulnerable to stressors than their adult counterparts due to underdeveloped dive physiology [23]. As long-lived, capital breeders female grey seals invest intensively in their pups during a brief lactation period (~ 17 days), losing a third of their body mass, while pups may more than triple their body mass [24]. After the lactation interval, females wean their pups and leave the colony. Pups remain for a postweaning fast of up to a month, the duration of which is affected by their body composition at weaning [25], before they return to sea for the first time [26, 27]. After the postweaning fast, grey seals must depart the natal colony to learn to forage and mitigate threats without parental guidance. Therefore, life history strategy and physiology may make young grey seals more vulnerable to disturbance [23, 28] as they learn necessary survival skills in areas, where anthropogenic sound and habitat disturbances are expected to increase markedly in the coming decades.

Grey seals are benthic feeders that are known to feed on demersal prey such as sand lances (*Ammodytes* spp.), gadoids, and flatfish such as winter flounder (*Pseudopleuronectes americanus*), yellowtail flounder (*Limanda ferruginea*), and fourspot flounder (*Hippoglossina oblonga*) [29–33]. Foraging also occurs in the pelagic zone [34], where grey seals are also known to feed on semi-pelagic species such as red hake (*Urophycis chuss*) and long-fin squid (*Doryteuthis pealeii*) [33]. The characteristics of their dives and the habitat exploited



Esri, TomTom, Garmin, FAO, NOAA, USGS, EPA, USFWS, Esri, FAO, NOAA, USGS, General Bathymetric Chart of the Oceans (GEBCO); NOAA National Centers for Environmental Information (NCEI)

Fig. 1 Top panel: study site and deployment locations at three pupping colonies and one haul-out location (Shinnecock Bay) along the United States northeast coast. Important submarine landforms in the study region are labeled in italics (e.g., Georges Bank, Nantucket Shoals). Current offshore wind lease areas are indicated with light blue polygons and proposed export cable routes are shown in dark teal. Bottom panel) State-space modeled tracks of young-of-year grey seals colored by deployment location Offshore wind lease areas and export cable data were obtained from the U.S. Bureau of Ocean Energy Management spatial data portal (accessed 2025-01-01): https://boem-metaport-boem.hub.arcgis.com/datasets/BOEM::offshore-wind-lease-outlines/about; https://boem-metaport-boem.hub.arcgis.com/datasets/BOEM::offshore-wind-export-cable-corridors-proposed/about

during foraging are likely mediated by the behavior and distribution of their prey [29, 34] and abiotic factors such as geomorphological features of the seabed [35]. Therefore, structures like wind turbines that alter both the benthic and pelagic habitats, and thus prey behavior and distribution, may have important consequences for the movement and foraging behavior of grey seals and other marine predators.

Extended-duration deployments of telemetry devices on aquatic species offer a key advantage in the collection of long-term time series of geolocation and depth data, allowing inferences to be made about physiology, behavior, and movements [36–38]. Telemetry studies of recently weaned grey seals have been conducted in the western North Atlantic on Sable Island, Nova Scotia [39, 40], as well as the eastern Atlantic [41–44] and Baltic Sea populations [45]. Like adults, pups are primarily restricted to continental shelf waters, at times utilizing the shelf break (≤ 200 m) [40, 41, 43, 44]. Dispersal strategies vary and pups may either stay close to natal colonies [44] or explore more widely immediately after departure [40, 41]. The post departure phase is characterized by an exploration-refinement foraging strategy starting with longer trip durations and distances, and more directed travel rather than area-restricted search patterns [40, 42, 44]. Similarly, dive duration, depth, bottom time, and benthic diving behavior typically increase rapidly over the initial months post departure [41]. Early life movement strategies vary region to region and are likely a result of intrinsic factors such as sex or body condition at departure [25, 28] and extrinsic factors such as prey availability, bathymetry, geomorphology, predation risk, and oceanographic conditions [40–42]. As such, it is important to fill the knowledge gap with respect to the at-sea movements and diving behaviors in recently weaned western Atlantic grey seals in U.S. waters.

Long-term, baseline knowledge of animal behavior and distribution is critical for understanding the causal relationships between responses and drivers in heterogeneous and dynamic environments [46]. In this paper, we describe the movements and dive behaviors of young-of-year grey seals for the first 8 months after leaving the rookery using telemetry data collected from January 2019 to May 2023. We chose this time series, because it represents a baseline period prior to the construction of the first major offshore wind project in the U.S. northwestern Atlantic, which began June 1, 2023 and is adjacent to grey seal pupping colonies in Nantucket Sound area. We hypothesized that young-of-year grey seals in this region would undergo an exploratory and learning phase similar to pups of the same Northwest Atlantic population originating from Sable Island, Nova Scotia. Correspondingly, we hypothesized that dive depth and duration would increase through time as pups continued to develop physiologically, and that pups would present spatiotemporal patterns (e.g., diel rhythms) in diving behavior as they responded to their environment and learned to forage. Finally, we hypothesized that their movements and foraging patterns would overlap with offshore wind lease areas given the proximity to the colonies.

Methods

Deployments

We deployed 63 (male = 31; female = 32) Argos satellite relay data loggers (hereafter SRDL or logger) on YOY grey seals between 2019 and 2023 at three U.S.-based grey seal colonies in the Northwest Atlantic: Great Point, Nantucket (*N* = 17), Muskeget Island (*N* = 38), Seal Island (*N* = 7), and one haul-out site: Shinnecock Inlet, Long Island NY (*N* = 1) (Table 1; Fig. 1). These loggers perform significant onboard processing, relaying summarized data via the Argos satellite system [47]. We deployed three different back-mounted logger

Table 1 Summary of grey seal satellite relay data logger deployments from 2019 to 2023

year	sex	N	mass (kg)[a]	length (cm)[a]	girth (cm)[a]	tag duration (d)[a]
2019	♀	5[b]	32.2 (3.5)	103.6 (7.4)	93.0 (8.9)	122.1 (62.5)
	♂	6	44.0 (7.8)	116.0 (12.2)	101.0 (9.8)	143.1 (53.9)
2020	♀	12	38.0 (6.7)	104.7 (7.4)	97.0 (6.2)	155.7 (82.1)
	♂	8	40.2 (7.3)	106.9 (5.5)	97.9 (6.0)	172.3 (90.8)
2021	♀	0	NA	NA	NA	NA
	♂	1	43.2	127.0	89.0	88.9
2022	♀	8	37.5 (9.2)	106.8 (6.6)	89.1 (10.3)	103.0 (56.0)
	♂	6	37.9 (7.1)	118.2 (9.2)	92.5 (9.5)	118.7 (73.8)
2023	♀	7	39.2 (5.4)	109.6 (4.9)	100.0 (6.7)	146.0 (37.8)
	♂	10[b]	37.7 (7.4)	106.4 (17.6)	104.8 (13.2)	102.0 (61.5)
Total	♀	32	37.2 (6.9)	106.1 (6.7)	95.0 (8.6)	135.6 (66.1)
	♂	31	39.8 (7.3)	111.3 (13.2)	99.4 (10.7)	131.9 (73.0)

N indicates the number of each respective sex tagged in a given year. Mass, total body length, and girth measurements are reported here as the mean and standard deviation for a given year, sex combination. Tag duration indicates number of days that an SRDL was on an animal and transmitting data

a: mean(± standard deviation), where $n > 1$

b: one logger failed to transmit and was removed for calculating mean tag duration (total = 1F, 1 M)

N = number of individuals tagged

configurations manufactured by Wildlife Computers: (1) Argos only positions (SPOT-293; $N=24$); (2) Argos positions and time–depth capability (SPLASH10; $N=15$); and (3) Argos, Fastloc GPS positions, and time–depth capability (SPLASH10-F; $N=24$) (Additional file 1: Table S1-1). Tagging campaigns occurred onshore in either January–February, which targeted newly weaned grey seals approximately 1 month, or in April, which targeted 4–5-month-old seals ($N=11$) (Additional file 1: Figure S1-1). After capture, the pups were weighed and then safely restrained without sedation to collect morphometric data (total length, weight, and girth) and affix loggers following best practices [48]. We secured each logger to the pelage of the dorsal cervical region with 5-min quick-set Devcon epoxy [49].

We programmed all SRDLs to begin transmitting once submerged in sea water. The loggers entered haul-out status when the conductivity sensor registered as dry for any 30-s period out of a minute for 5 consecutive minutes, and for those units equipped with Fastloc capabilities (Additional file 1: Table S1-1), a Fastloc position was recorded. A haul-out phase ended if the conductivity sensor read wet for any 45 s in a minute. The SRDLs attempted data transmission every 45 s at sea and every 90 s during the first 48 h of haul-out, resuming transmission at 45 s when the loggers exited the haul-out status. Depth and conductivity (wet/dry sensor) were archived at 10 s intervals, and summary data products were transmitted for each behavioral event (e.g., maximum dive depth and dive duration) or summarized at hourly intervals (e.g., percent dry timelines). The Fastloc-enabled loggers attempted to obtain a Fastloc position every 60 min, allowing four failed attempts in any 1 h period. Because seals were not recaptured to recover the full archived time series, our analysis relied on only summarized data successfully transmitted via the Argos satellite system. Data transmission failures occurred due to Argos bandwidth limitations and satellite availability, which vary in accordance with latitude, and despite optimizing transmission time periods for a given study site and temporal period, data gaps are inevitable. Data transmission failure is also caused by other conditions, including the geographical position of the study site, animal behavior, biofouling, prevailing environmental conditions, and the stability of the transmitters over time. Data gaps caused by intermittent transmission failures are a very important consideration for and limitation of studies relying on Argos technology in which tag recovery is not possible.

Data processing

Prefilter

We conducted all data processing and statistical analyses in R version 4.4.0 [50]. Argos location quality control procedures were implemented, including the removal of duplicate timestamps, location class Z, geographically impossible locations, and data occurring outside of each deployment time period. For Fastloc location data, we removed positions with both fewer than 6 satellites and residuals greater than 30 [51], resulting in 118,701 total positions for 61 YOY grey seals (Argos = 110355; Fastloc = 8346).

Identification of haul-out periods

Spatiotemporally precise haul-outs were indicated by the transmission of a Fastloc GPS position at the start and end of the haul-out bouts identified in situ by the wet/dry sensor. These records contained gaps for reasons discussed above. To mitigate these data gaps in the haul-out record and to identify haul-out events in the loggers that were not Fastloc capable, we utilized two additional sources: (1) hourly percent dry timelines, e.g., [52, 53], and (2) bathymetric depth and distance offshore, e.g., [40].

Hourly percent dry timelines represent the proportion of each hour that the SRDL registered as dry and each successfully transmitted record contains a summarized 24-h period. For each hour, the hour was assigned a hauled out status if the hourly bin was (1) $\geq 50\%$ dry or (2) adjacent to an hour $\geq 95\%$ dry [52]. This method excludes situations where the animal is likely at the surface breathing or resting ($< 50\%$), and includes instances where a multi-hour haul-out event likely started or ended in an adjacent bin [52]. If the timestamp of a location fell within an hour classified as hauled out, that location was classified as hauled out.

To obtain bathymetry and distance offshore estimates for each position, we fitted a continuous-time state–space model (SSM) with a correlated random walk movement process [54, 55] to account for Argos location error [56–58]. We applied a speed filter algorithm [59] with a maximum speed of 3.5 ms^{-1} [60] and fit the full tracks with the R package *aniMotum* [61]. Model fits were checked for convergence, and one-step-ahead residuals were calculated to check for independence, homoscedasticity, normality, and residual autocorrelation assumptions [62]. To account for location estimation error, we imputed 100 sample tracks for each tagged seal with a custom R function [63]. For each imputed position, we extracted bathymetry (ETOPO 2022) at 15 arc-second resolution using the R package *marmap* [64]. The distance offshore was calculated for each imputed position via *Rnaturalearth* [65] using a 10-m resolution coastline including major, and minor islands. Using all imputed estimates, the mean bathymetric depth and distance offshore were calculated for each location in a given track. A position was classified as hauled out if it was in waters ≤5 m depth [40]. If a position was identified as hauled out by either the percent dry timelines or the mean bathymetric depth threshold, but the mean distance offshore was greater than 7.5 km, it was assumed the true location was at sea.

Haul-out summary statistics, including duration and percentage of time spent hauled out, were calculated with all identified haul-out events. The percentage of time hauled out was computed as the sum of all haul-out durations divided by the number of location days (Additional file 1; Table S1-3). Tracks were later segmented into at-sea trips based on these identified haul-out events.

Trip definition

Once haul-out events were classified, we partitioned the data into distinct trips, defined here as continuous at-sea movements, lasting 24 or more hours, between identified haul-out events [39]. Where a trip did not end in a haul-out event due to tag attrition, or some other failure, we count this as an incomplete trip and did not include it in the utilization distribution analysis or descriptive trip metrics. To avoid modeling over large temporal gaps, we split trips into segments within which the time difference between consecutive locations did not exceed 24 h. Within the segmented tracks, locations were recorded on average every 1.35 (sd = 1.29) hour(s). State-space models were fitted and validated as described above for each trip or trip segment with sufficient positions for model convergence (≥ 50), and where necessary, tracks were routed around land [66] (Fig. 1; bottom panel). Only qualifying trips with complete, modeled segments were considered for spatial trip metrics and utilization distributions. Model fits were used to predict locations at regular 2-h intervals as well as the location of individual dive behavior given a set of dive times (described below). Overall, for the pre-construction period, we modeled 72,464 at-sea positions representing ~ 90% of the total possible at-sea positions for 384 complete trips across 59 individual seals. As such, we were not particularly concerned that our trip definitions or modeling criteria were resulting in the loss of much positional information. However, we do acknowledge that the biologging technologies used in this study are not ideally suited for assessing short duration (< 24 h), nearshore movements of pinnipeds.

Collective utilization distributions

Tracking data are often sparse, making population-level inferences about animal behavior or distribution challenging. Because the aim of this study was to characterize baseline spatiotemporal patterns in YOY grey seals, it was necessary to confirm that sample sizes were sufficient to represent the spatial distribution of this population and age demographic. To assess representativeness, the minimum required sample size was estimated via the overlap probability approach [67], the details of which are described in Additional file 2.

Trip kernel densities were produced using seasonally segmented tracks with the biased random bridge kernel density estimator [68, 69] available in the R package *adehabitatHR* [70]. A spatial bandwidth of 20 km was selected on the basis of the 99th percentile of the standard error estimates derived from state–space models, and the drift parameter 'D' was estimated via a maximum likelihood function [71], with a maximum time threshold for path segmentation of 2 h, based on the regularized time step of the SSM location estimates. If successive locations did not exceed 100 m horizontal distance, the algorithm assumed that the animal was stationary, although we expected little stationarity in the track segments because of the a priori removal of haul-out behavior.

Trip-based utilization distributions were created for each season with sufficient data and to align with the same seasons used to characterize juvenile grey seal diet in the region (winter = Jan–Feb; spring = Mar–May; summer = Jun–Aug) [33]. Collective seasonal utilization distributions were generated by taking the local mean of all trip raster utilization distributions within each season. Collective utilization distributions, summarized by sex at the 50% (core area) and 95% (home range) probability volume contours, provided spatiotemporal insights into the ontological and seasonal dispersal patterns of the YOY grey seals from weaning until approximately 8 months of age in the context of wind energy areas. The probability of trip overlap with wind energy areas was calculated as the sum of the kernel probabilities contained within wind energy areas over the total kernel probability density function.

Dive behavior

A subset of loggers ($N = 34$) also recorded time–depth dive data; although 39 were time–depth capable (Additional file 1: Table S1-1), 3 were programmed to collect only binned dive data, and 2 failed to collect any time–depth data and were thus excluded from analysis. The maximum dive depth was recorded on a per-dive basis, defined as submersion to 5 m or deeper for at least 1 min, and included details such as dive duration, dive depth, and inter-dive interval. Maximum dive depth was determined from onboard, archival depth data sampled every 10 s. Argos bandwidth limitations as described above also prevented the recovery of complete dive records. The SRDLs also recorded histograms of dive duration and depths for 4-h summary periods, and we compared the max depth and duration distributions for a subset of these complete records to those of the individual dive data to confirm that the successfully transmitted individual dive data were a nonbiased subsample.

The surface intervals were possibly aliased due to the 10-s depth sampling rate, which may have resulted in concatenated dive records and physiologically infeasible dive durations. To avoid reporting potentially erroneous dive records, we eliminated any dive with a duration of 15 min or greater, lacking a corresponding surface interval, or containing a maximum depth deeper than 455 m [34], resulting in the removal of ~3% of the transmitted dive records. Dive duration cutoffs were based on previously reported dive duration maxima for grey seals, which typically fall within 8 min [28, 72, 73], and a study reporting that 90% of dives in adult grey seals were less than 8 min, with recorded maximum durations of 20 and 22 min for males and females, respectively [74]. Our final dive data set for analysis consisted of 174,470 dive and interdive interval events for 34 YOY grey seals (females = 17, males = 17) (Additional file 4: Table S4-1).

Spatiotemporal patterns in dive behavior

To understand spatial patterns in diving behavior, we fitted SSM models as described above and predicted locations at the temporal midpoint of all qualifying dive events occurring within any trip or trip segment with 50 or more positions, inferring that these times were representative of the time when the seal was likely at maximum depth. We used the maximum recorded dive depth to narrow the distribution of plausible location estimates based on corresponding bathymetry. We implemented a rejection sampler, drawing realizations of each dive location estimate from the fitted SSM using a custom built function [63]. High resolution bathymetry was extracted to all imputed locations, and positions, where maximum dive depth exceeded bathymetry by more than 3 m were rejected. To account for some resolution error in the smoothed bathymetric data as well as the depth resolution of the loggers' pressure sensor, and to reduce computation time, we accepted positions where the maximum dive depth exceeded bathymetry by 3 m or less. This process was repeated until 100 plausible locations, and the corresponding bathymetry data were drawn for each dive. See Additional file 3 for an explanation of the sensitivity analysis we conducted to determine the optimal number of imputations (Figures S3-1, S3-2). To reduce the computation time further, positions that were rejected for 100 successive draws or where fewer than 50 plausible imputations were drawn were eliminated, representing ~4% of the records.

Using all imputed positions and corresponding bathymetry for each dive, we calculated the proportion of the water column reached at the maximum dive depth (PWC). An examination of the distribution of the PWC revealed bimodality in the diving behavior of YOY grey seals, and we developed a data-driven cutoff to delineate the two types of dives. A finite Weibull mixture model with two components was fitted [75] to the distribution, and we used the model-estimated parameters of the two distributions to calculate the intersection point and categorize the dive data as benthic/demersal (PWC $\geq$ 0.87), pelagic (PWC $<$ 0.87) or shallow-water dives occurring in waters shallower than 20 m [41]. We avoided classifying shallow-water dives as either benthic/demersal or pelagic due to the uncertainty relative to the water column depth. In addition, we calculated the empirical probability that a dive was benthic/demersal as the number of PWC values $\geq$0.87 over the total number of imputed values (Additional file 3: Figure S3-1). Overall, we classified 123,792 dive positions ($N = 33$: $M = 17$, $F = 16$) as either benthic/demersal, pelagic, or shallow-water in the pre-construction period (Additional file 4: Table S4-2).

The patterns of diving type, distance to shore and bathymetry, and dive depth, duration, and inter-dive interval were summarized at weekly intervals. Dives were also summarized hourly and seasonally as the proportion of total dives conducted in an hour for each dive type. The diel patterns were smoothed with a locally fitted polynomial curve or LOESS [76]. For each dive time and location, the sunset, sunrise, and nautical twilight times were calculated, and the seasonal average sunset and sunrise times and nautical twilight zones were visualized with the diel patterns. The spatial patterns of the dive types were summarized via hexagonal tessellation and mapped to examine diving behaviors in relation to wind energy areas and important habitat. Demersal prey species important for grey seals (e.g., sand lance) can have specific sediment grain size preferences [77–81]. As such, we extracted sediment grain size data [82] to the estimated dive locations and categorized values according to the Wentworth scale [83].

Results

Deployments

Between January 2019 and April 2023, 63 grey seal YOYs (male = 31, female = 32) were instrumented with satellite-linked transmitters, either shortly after weaning in January and February ($N = 51$) or when the YOYs were 3–4 months in April and March ($N = 12$) (Table 1). Only one animal was tagged in 2021 as a result of pandemic-related reductions in field efforts. Two SRDLs were excluded because of malfunction (SPOT = 1, SPLASH10-$F = 1$) (Additional file 1: Table S1-1). The remaining 61

SRDLs transmitted for an average of 134 days (sd = 69) and ranged from 4 to 287 days, although these measures varied slightly by year and by sex (Table 1; Additional file 1: Table S1-1). The resulting data set maintains good coverage of the postweaning dispersal until July, with tag attrition affecting representativeness during the late-summer and fall seasons (Additional file 1: Figure S1-1). Two SRDLs, both deployed on January 13, 2020, did not transmit beyond January 31 and thus did not contain at-sea trip segments long enough for SSM convergence (Additional file 1: Table S1-1). These SPOT deployments (female = 2) were excluded from any further results.

Movement and haul-out behavior

Male and female YOY animals dispersed broadly throughout the Gulf of Maine and Mid-Atlantic, with most (99.9% of modeled locations) distributed across the continental shelf to the 200 m isobath (Fig. 1 bottom panel; Additional file 1: Figure S1-2). Thirteen individuals traveled past the 200 m isobath, with one female traveling > 1100 km from the deployment location before the logger stopped transmitting (Fig. 1; bottom panel). Twenty-three individuals used Canadian waters, collectively representing 9% of all modeled locations. Median trip durations were approximately 8 and 7 days for females and males, respectively, but varied widely (Table 2). Trip duration, length, and distance offshore peaked during the spring season and decreased during summer and fall (Table 2). The majority of trips that were conducted in the winter and spring intersected with wind energy areas, and the probability of occurrence within a wind energy area was highest for females in spring. Conversely, the majority of trips in summer and fall did not overlap with wind energy areas, and the observed probabilities of occurrence within wind energy areas were nearly negligible (< 0.01) (Table 2). Haul-out behavior was also highly variable: seals hauled out on average 13.3% and 15.3% of the time for females and males, respectively (Table 2). The percentage of time spent hauled out also varied seasonally, with seals typically hauling out for a greater percentage of the time during the summer and fall. Haul-out durations averaged approximately 4–4.5 hours and were highly variable. Individual trip and haul-out statistics are available in Additional file 1: Tables S1-2 and S1-3, respectively.

Collective utilization distributions

Results of the minimum sample size analysis indicate that 12 individual seals represent a sufficient sample size for the utilization distribution analysis, and therefore, our results from 59 seals are robust enough to be used for population level inference (Additional file 2: Figure S2). Kernel density estimation revealed similar dispersal patterns between the sexes (Fig. 2). Despite making shorter trips in the summer and fall, there was little difference in the core and home range areas between the seasons, though UD areas were generally greater in the spring (Table 2). The collective core home ranges of the seals overlapped with the wind energy footprint in the winter and spring months and overlap was lowest in the summer, when seals appear to have dispersed farther north and east (Fig. 2; Additional file 1: Figure S1-2). Immediately after weaning, in the winter season, collective core home ranges (50% UD) for both males and females were concentrated in Nantucket Sound and nearshore waters of Nantucket Shoals (Fig. 2). By spring, when the YOY were approximately 3–5 months, the collective core ranges of males and females shifted into offshore waters, and by June, northeastward dispersal highways were evident along coastal Maine and across the Northeast Channel to the southern portion of the Scotian Shelf (Fig. 2).

Diving behavior

The distribution of PWC was bimodal, indicating that individual dives could be partitioned into two different behavioral modalities: (1) dives with maximum depths at or near the benthos (> 0.87PWC) or (2) dives with maximum depths remaining in the pelagic portion of the water column (PWC < 0.87) (Fig. 3a). Dives occurring in waters shallower than 20 m occurred mostly in the winter months following the postweaning fast (Fig. 3b). Benthic diving took place more frequently than pelagic diving through the spring season and then transitioned to more pelagic diving starting in June. A higher proportion of pelagic dives occurred in the summer, coincident with seals moving through deeper waters of the Gulf of Maine (Fig. 3c).

Diving ontogeny

After colony departure, maximum dive depth increased through February, stabilized between ~ 40 and 50 m by March, and was generally similar between the sexes in the first 8 month postweaning (Additional file 4: Figure S4-1a). The mean diving duration increased from ~ 90 s in January to 150–170 s in February and March before decreasing slightly in April–May (Additional file 4: Figure S4-1b). The interdive intervals remained relatively stable throughout the duration of postweaning dispersal decreasing slightly by mid-February (Additional file 4: Figure S4-1c). The initial rapid increases in depth and duration were driven primarily by benthic or demersal dives (Fig. 4a, and b). The mean weekly pelagic dive depth never exceeded 40 m, whereas the mean weekly benthic/demersal dive depth varied between ~ 40 and 100 m, regularly exceeding 50 m. Compared with benthic

Table 2 Summarized trip and haul-out metrics by season and sex for YOY grey seals

			Trips				**Utilization distributions**		**In WEA**		**Haul-out**	
Season	**Sex**	***N***	***n***	**Duration (d)[a]**	**Length (km)[a]**	**Dist. offshore (km)[a]**	**50% UD (km^2)[a]**	**95% UD (km^2)[a]**	***n* trips**	**Probability[a]**	**Duration (h)[a]**	**% time[b]**
Winter	♀	26	51	7.8 (9.9)	253.4 (336.4)	18.2 (18.8)	2760 (1432)	11,511 (5144)	49 (96%)	0.04 (0.15)	3.1 (9.9)	9.4 (6.5)
	♂	20	52	7.6 (7.9)	232.8 (341.7)	23.8 (37.8)	2693 (1876)	11,050 (8678)	51 (98%)	0.05 (0.20)	3.4 (14.1)	14.1 (9.1)
Spring	♀	24	102	11.0 (11.6)	431.0 (485.1)	56.6 (59.0)	3419 (2530)	15,916 (10,520)	99 (97%)	0.06 (0.25)	5.0 (13.0)	11.1 (5.7)
	♂	24	79	9.1 (8.7)	441.2 (374.8)	55.0 (43.6)	3186 (2708)	15,222 (11,990)	78 (99%)	0.02 (0.07)	6.1 (14.6)	14.0 (7.5)
Summer	♀	12	42	5.7 (7.2)	241.8 (395.3)	30.9 (39.5)	2824 (2378)	11,934 (16,190)	28 (67%)	< 0.01 (0.01)	4.4 (10.8)	23.9 (10.9)
	♂	13	41	5.3 (4.6)	289.6 (283.7)	35.1 (52.8)	3203 (5764)	14,292 (17,924)	24 (59%)	< 0.01	3.7 (6.6)	20.3 (7.1)
Fall	♀	2	4	5.3 (1.4)	241.9 (166.5)	40.8 (28.7)	3856 (3951)	14,390 (13,126)	2 (50%)	< 0.01	6.1 (11.5)	30.0 (17.6)
	♂	2	16	4.5 (2.2)	165.2 (97.3)	25.4 (20.2)	2176 (746)	9184 (2627)	4 (25%)	< 0.01	3.0 (5.6)	21.0 (3.9)
Total	♀	29	199	8.1 (9.7)	329.9 (438.6)	36.9 (54.1)	3034 (2389)	12,998 (10,381)	178 (89%)	0.02 (0.15)	4.5 (11.9)	13.3 (6.3)
	♂	30	188	7.0 (7.3)	327.0 (385.0)	39.2 (52.7)	2902 (2701)	13,347 (10,712)	157 (84%)	0.01 (0.07)	4.2 (8.5)	15.3 (5.5)

a: median(± interquartile range)

b: mean(± standard deviation)

Metrics include the number of tagged seals (*N*), total trips (*n*), trip duration, length, core (50%) and home range (95%) trip areas, distance to shore, number of trips within wind energy areas (wind energy area), and the probability of occurrence within wind energy areas. Median (IQR) are reported for metrics with heavily skewed distributions and mean (sd) are reported, where distributions were normally distributed

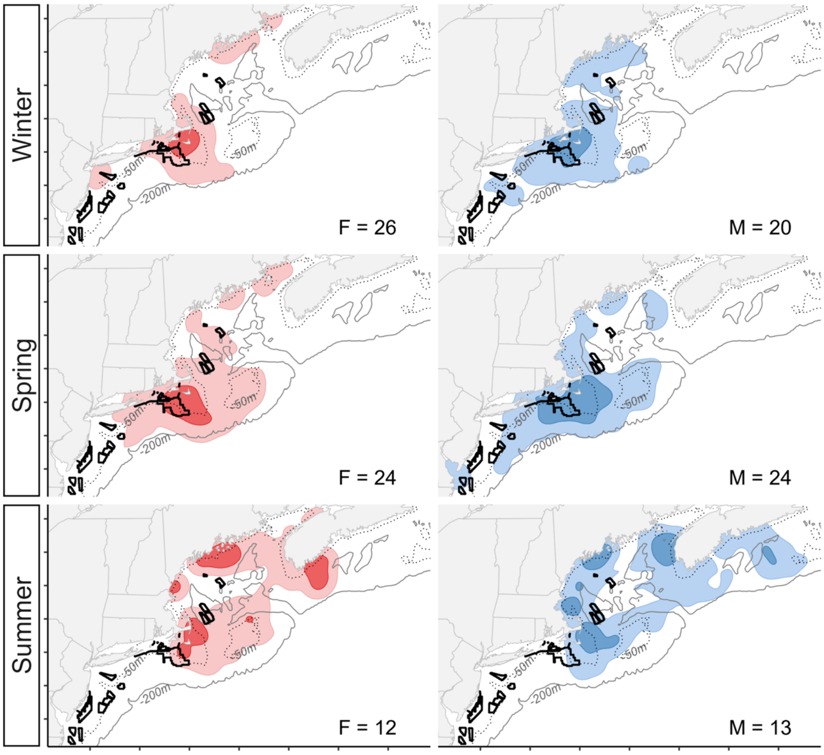


Fig. 2 Seasonal collective utilization distributions for female (left) and male (right) young-of-year grey seals. Darker colors (dark red; dark blue) represent the 50% utilization distribution and lighter colors (light red; light blue) represent the 95% utilization distribution. The number of individuals represented in each seasonal UD is in the lower right corner of each panel. Offshore wind energy lease areas are represented by black polygons

dives, pelagic dives tended to be shorter in duration, particularly during the spring season (Fig. 4b). Benthic diving duration also decreased after an initial peak in the spring. The proportion of benthic dives was highest in spring for both males and females and transitioned to relatively more pelagic dives during the summer (Additional file 4: Figure S4-2). The maximum dive depth recorded was 240 m for 6.8 min, and was conducted by a female. Owing to potential dive duration signal aliasing issues, maximum dive duration has not been reported.

Diel diving behavior

Clear diel patterns were observed in diving behavior across all seasons; pelagic dives took place more frequently during the night, and benthic or demersal diving peaked during daylight hours (Fig. 5). However, during the winter, i.e., in the weeks after the postweaning fast, seals undertook proportionally more shallow water dives and patterns were noisier (Fig. 5a). The twilight time periods appeared to serve as the transition point between the two diving types, particularly in the spring months (Fig. 5b). Absolute and relative number of benthic dives exceeded pelagic dives during the day only in winter and spring, whereas more pelagic diving was conducted in the summer (Fig. 5c). Overall, the absolute number of dives was highest during the spring, but this could be due to tag attrition and the number of data days in a seasonal partition rather than underlying biological or ecological mechanisms (Fig. 5d).

Geographical patterns in diving behavior

In the winter months following the postweaning fast, benthic or demersal diving behavior was mostly confined to areas within the 50 m isobath of Nantucket Shoals and Georges Bank, including inside wind energy areas slated for development (Fig. 6a). As the seals dispersed farther offshore in the spring, benthic diving was prevalent in waters shallower than 200 m, with high concentrations in and around Nantucket Shoals, Georges Bank, and west of the Great South Channel area (Fig. 6b). The YOY grey seals appear to have concentrated diving efforts in sandy, shoaling areas, particularly around the 50 m isobath of Georges Bank. Ledges and seamounts in the Gulf of Maine also appear to be of some importance, as they were frequently visited by some of the seals. As they dispersed into Canadian waters, seals undertook benthic dives around coastal Nova Scotia and the Scotian Shelf,

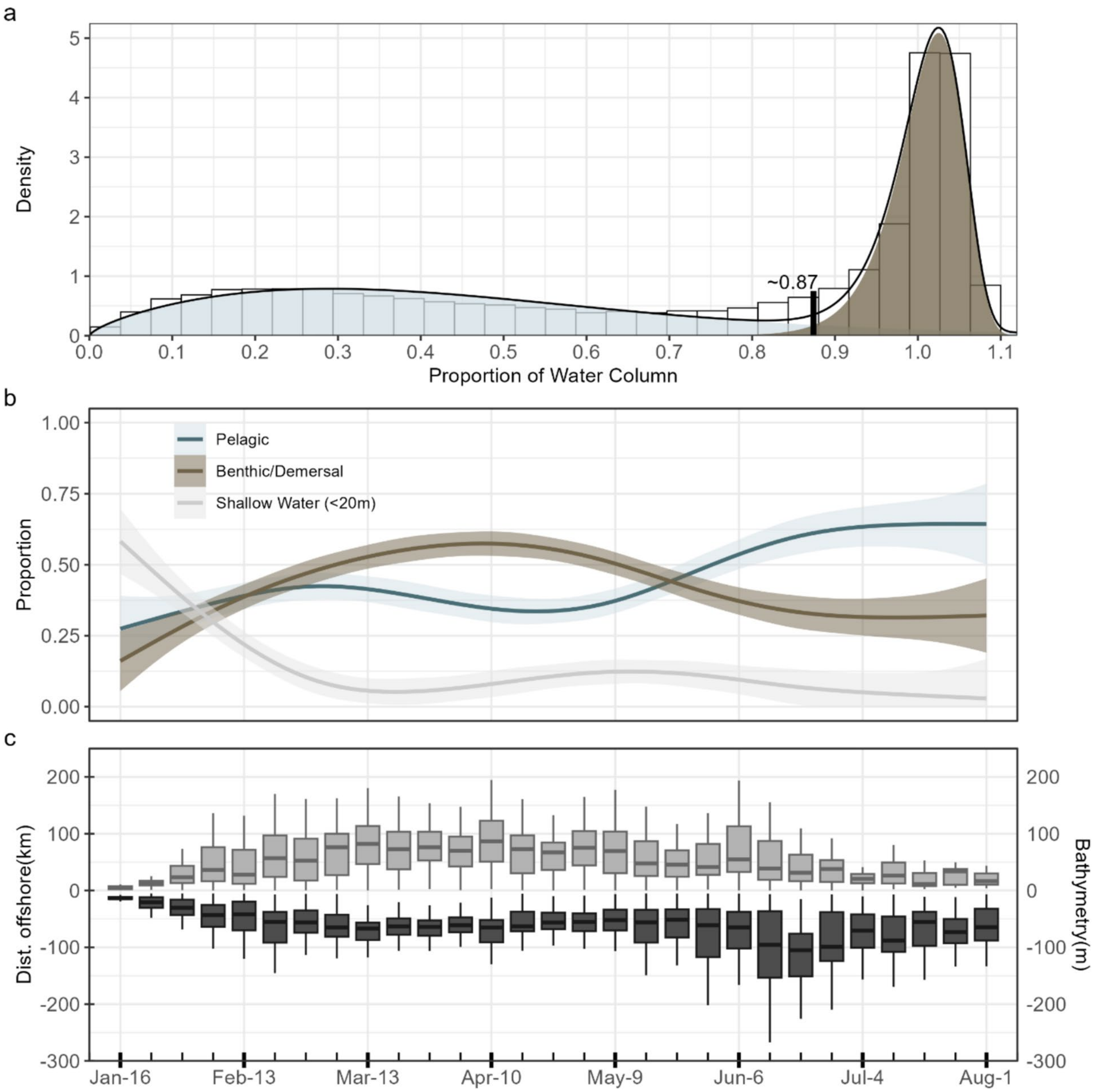


Fig. 3 **a** Bimodal distribution of the percentage of the bathymetric depth achieved at maximum diving depth and the estimated cutoff value between the two distributions (0.87), pelagic and benthic/demersal. **b** GAM smooth of weekly proportions of each dive type. Shallow dives were those dives that occurred in water column depths of less than 20 m. Weeks were subsetted such that each week represents a minimum of two individuals. **c** Corresponding weekly distributions of distance (km) offshore (top, light grey) and bathymetric depths (bottom, dark grey) of all dives performed in each week

although more pelagic diving was evident overall. By the summer months, the seals were dispersed northeastward and conducted proportionally more pelagic dives in coastal Maine and the Nova Scotian Shelf (Fig. 6c).

Important foraging areas, including Georges Bank and Nantucket Shoals contained primarily sediment grain sizes that could be categorized as medium sand or coarser (Fig. 6d). Seals conducted more benthic diving in fine, medium, and coarse sand, and gravel, while pelagic diving was greater in areas dominated by clay or silt and very fine sand (Fig. 6e).

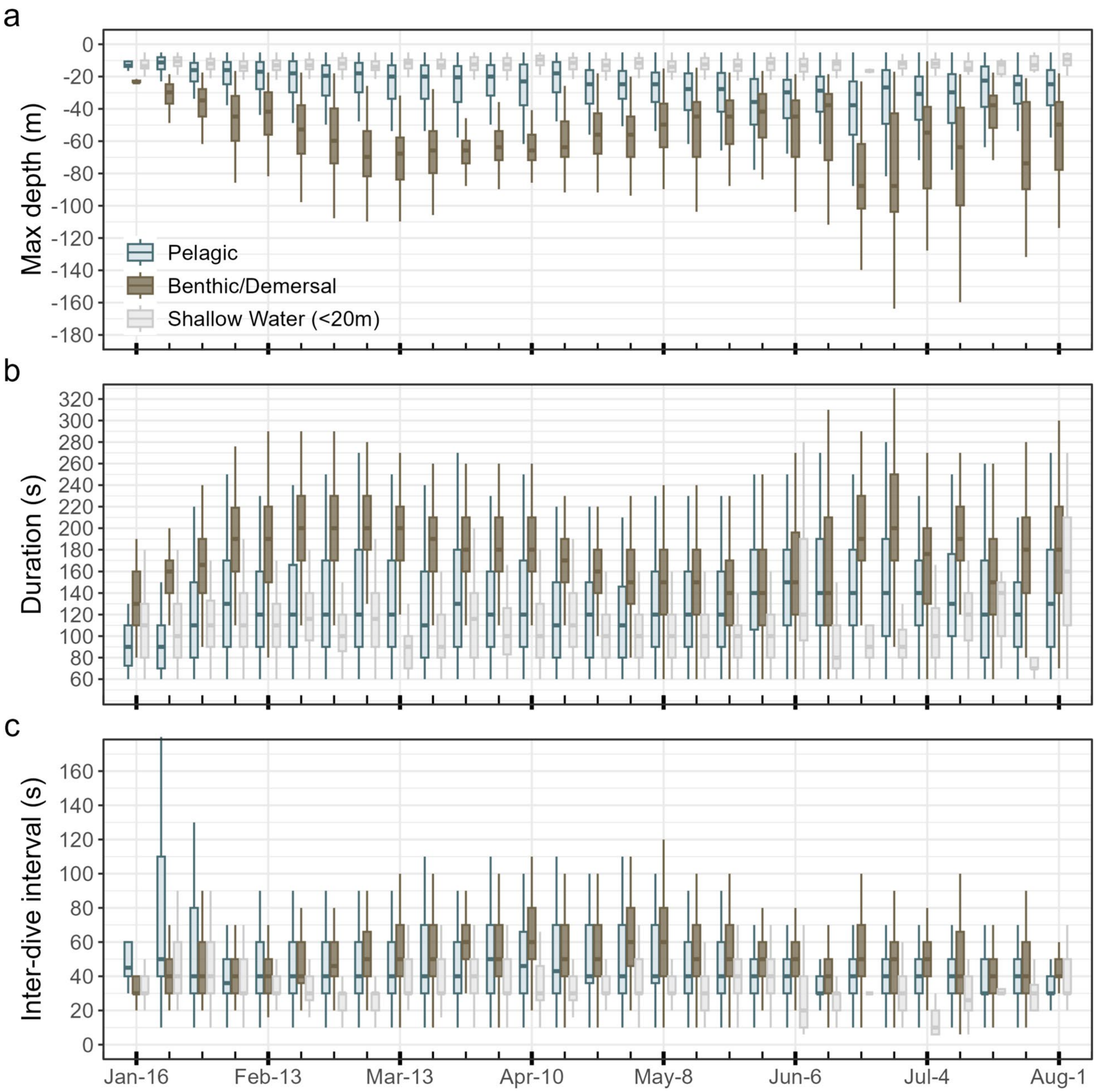


Fig. 4 Weekly boxplots of **a** maximum dive depth, **b** dive duration, and **c** inter-dive interval for pelagic, benthic, and shallow-water dives in young-of-year grey seals

Discussion

This is the first study to examine the horizontal movement and dive behaviors of young-of-year grey seals originating from U.S.-based colonies. Overall, young-of-year grey seals dispersed widely across the continental shelf, exhibited bimodal diving behavior with respect to bathymetry, and demonstrated increasing diving depth and duration consistent with the development of foraging skills. Seals displayed seasonal, diel, and spatial patterning in benthic or demersal dives as compared to pelagic dives. They also overlapped with offshore wind lease areas the most during their first 4 months of life.

Collective utilization distributions, trip distance, and duration indicate that the true ranging behaviors of the young-of-year grey seals (present study) are greater overall than those of their adult counterparts [84], particularly during the late spring and summer when white shark abundance peaks in nearshore waters [85–88]. Life-stage specific differences in at sea behaviors, whereby young-of-year range more widely than adults are observed

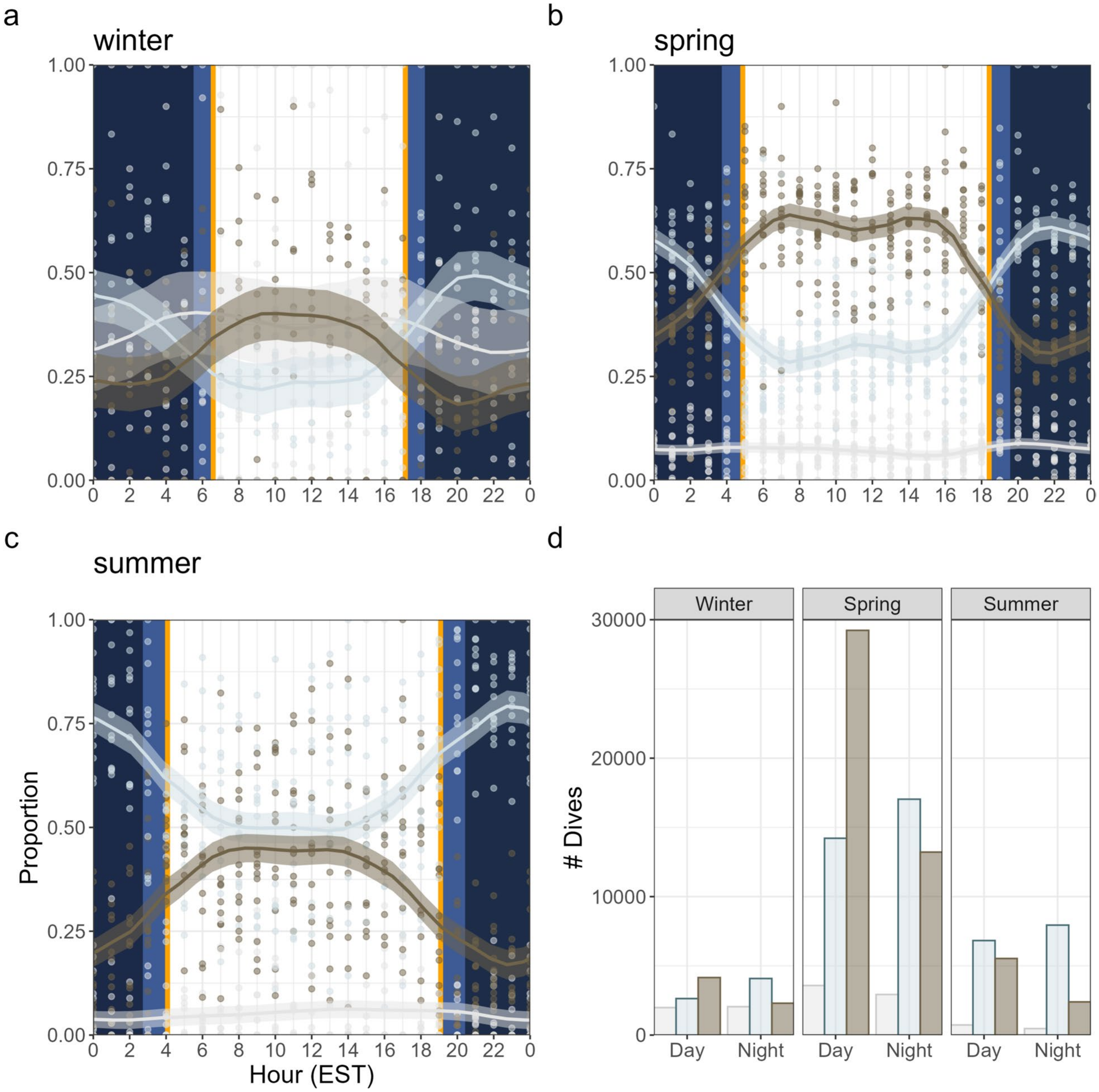


Fig. 5 Diel diving behavior in **a** winter, **b** spring and **c** summer. The relative proportion of dives completed in a given hour for pelagic (light blue) benthic (brown) and shallow water dives (bathymetry < 20 m, light grey). Average seasonal sunrise and sunset times are shown as orange bars, given the location and date of each dive in a season. Nautical twilight zones, defined as the period when the sun's center is between 6° and 12° below the horizon, are shown adjacent to sunset and sunrise times in medium blue, while night is shown in dark blue. Absolute number of dives conducted during the day and night across the three seasons (**d**). Seasonal, monthly sample sizes by sex are reported in Additional file 4: Table S4-2

among other grey seal colonies in the North Atlantic [39, 41]. Young-of-year grey seals may limit transit in nearshore waters during the warm season, instead opting for offshore foraging, away from coastal predation risk. For example, age-related habitat partitioning is known to occur in ringed seals (*Phoca hispida*), whereby subadults exhibit faster rates of travel and range farther offshore than adults, allowing subadults to exploit more optimal foraging grounds with reduced exposure to predation[89, 90]. Furthermore, habitat partitioning between age classes might also occur due to differences in prey species, size, or energetic density mediated by physiological differences in body size or diving ability [32, 91–93]. Alternatively, young-of-year grey seals may be forced to

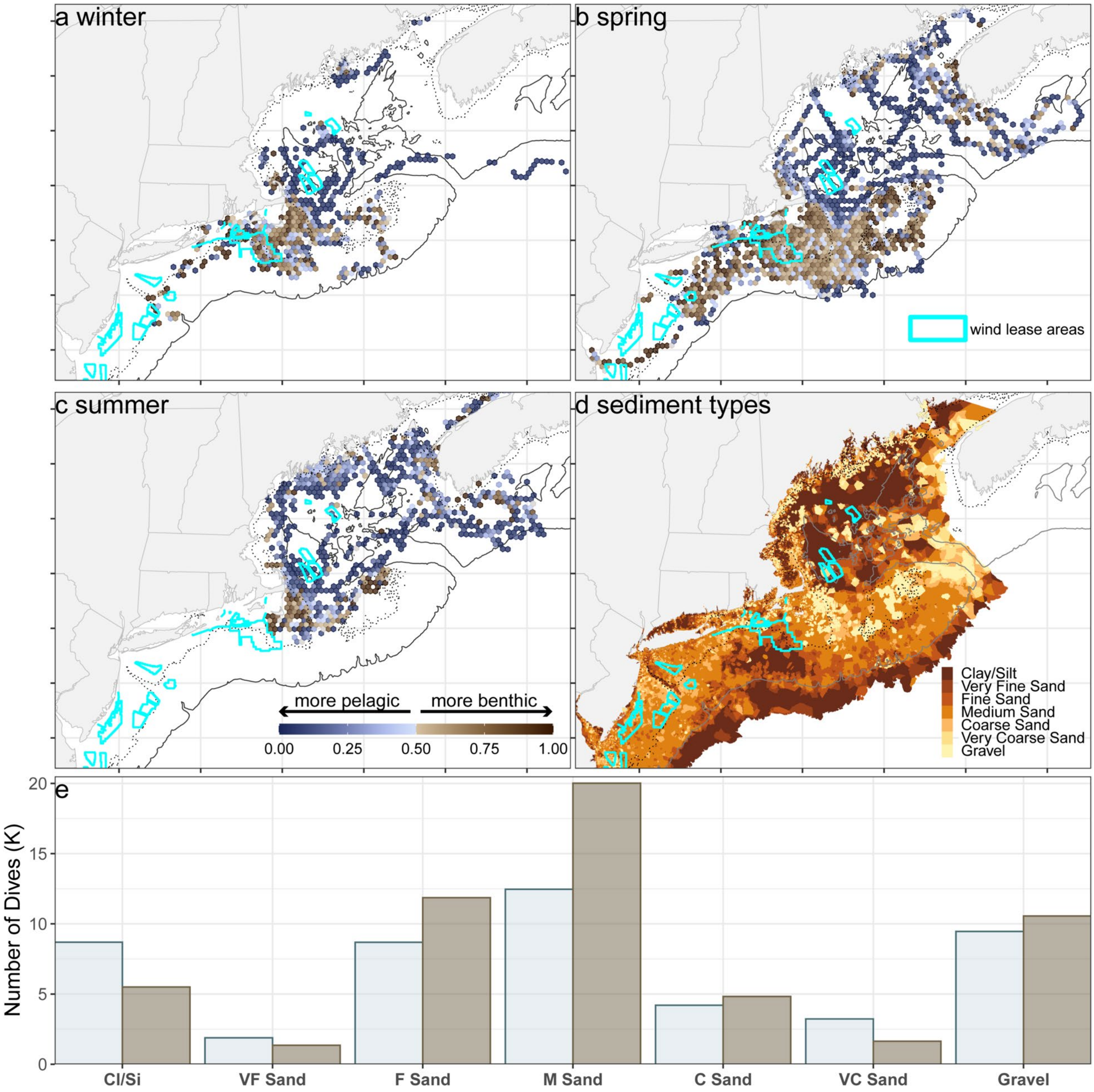


Fig. 6 Tessellated proportion of benthic/demersal diving in (**a**) winter, (**b**) spring and (**c**) summer. A tile tessellation is shown only if that tile aggregates 3 or more dives. Wind energy lease areas are outlined in cyan; (**d**) sediment grain size classification reproduced from the Northwest Atlantic Marine Ecoregional Assessment [82]. Grain sizes classified according to the Wentworth scale [83]: Cl/Si = clay/silt, VF = very fine; F = fine; M = medium; C = coarse; VC = very coarse. **e** Absolute number of dives, grouped by dive type (blue = pelagic; brown = benthic/demersal), conducted within each sediment category

utilize suboptimal foraging grounds farther offshore via intraspecific competition [40, 73] or to avoid increased risks of infanticide and cannibalism in nearshore waters [94–98]. Further studies of the U.S. portion of the western Atlantic population of grey seals are needed to explicitly assess demographic differences in habitat utilization in relation to predation pressures and prey quality, and more data are required to make population-level inferences regarding adult movements.

Consistent with our hypothesis, our results indicate that pups born in U.S. colonies undergo rapid behavioral development, exhibiting an early life exploratory phase following the postweaning fast similar to young-of-years from both western Atlantic [39, 40] and eastern

Atlantic grey seal populations [41, 42, 44]. However, we also observed an important difference: the < 5-month-old Sable Island pups initially moved farther offshore and then became more range restricted as they became more efficient foragers [40], whereas pups in the present study initially had shorter trip durations, smaller core ranges and were largely confined to the shallow-water areas surrounding the natal colonies in Nantucket Sound. This difference in strategy is potentially due to the different geographies of the pupping colonies. Whereas Sable Island is a long, sandy island, > 300 km offshore, the pupping colonies in the U.S. typically occur on islands close to continental land masses. The proximity to productive, nutrient rich coastal waters likely allow pups born in U.S. colonies to stay closer to their natal grounds following initial colony departure. Similarly, during this preliminary period, pups conducted proportionally more dives in near-shore waters that were typically shorter in duration and shallower in depth, possibly indicating that pups were still undergoing physiological and behavioral development [72]. We postulate that the shallow waters of Nantucket Sound and areas immediately surrounding the Muskeget, Great Point, and Monomoy breeding colonies are important nursery grounds and likely play a role in the learning and development of their foraging skills [43, 99–101]. This early development phase is critical, as naive young grey seals must learn how to forage effectively within a limited time window before energy reserves are depleted [28].

Diving and foraging behavior

As we hypothesized, diving depth and duration increased rapidly in the month following colony departure. The results of our dive type classification demonstrate that increases in depth and duration are driven primarily by benthic diving, a presumed indicator of foraging activity. Rapid increases in these dive parameters within the first several months of nutritional independence is fairly common among grey seals and other closely related Phocinae [41, 102–105].

Diving behavior became more patterned through time, particularly in the spring season following a period of exploratory shallow water diving near the natal colonies. We found that the habitats most utilized by pups in the spring and summer seasons primarily include the sandy shoals of the Great South Channel region (including Nantucket shoals), Georges Bank, Stellwagen Bank, and regions along coastal Maine. These regions encompass some of the most productive fisheries globally, and Georges Bank specifically represents one of the largest sand lance habitats in the Gulf of Maine and Mid-Atlantic Bight regions [106–108].

Spatiotemporal patterns in diving behavior of young-of-year grey seals suggest that seals may be targeting sand lance during their benthic or demersal dives. The springtime onset of increased benthic and demersal diving behavior in the present study coincides with the larval settlement and overwintering phenology of sand lance and may indicate that young-of-year grey seals respond to prey dynamics early in development. Larval sand lance have a defined settlement phase when larvae exit the pelagic larval stage and transition to demersal habitats [109, 110]. Sand lance caught in the Stellwagen Bank and Great South Channel areas in 2019 hatched between December and February, with larvae settling in early March through April in the Great South Channel region [108]. Some adult sand lance also burrow in an overwintering phase for 6–8 months [111–113] and emerge in the spring for a feeding season that lasts through the summer [114]. Our results demonstrate that much of the benthic or demersal diving activity occurred in two of the major habitats for sand lance in the Gulf of Maine and southern New England region: sandy shoaling regions west of the Great South Channel and Georges Bank. Together, these findings indicate that young-of-year grey seals originating from U.S.-based colonies may conduct proportionally more benthic or demersal dives in these habitats to forage on a concurrent pulse of a known prey species. In addition, we found that the spatial dive patterns of pups mirrored the habitat characteristics of smaller bodied sand lance. Sand lance modify their sediment preferences on the basis of their size class, with smaller bodied fish showing a preference for sediments composed of smaller grain sizes [77, 78, 115]. Smaller body sizes of pups likely force them to target smaller prey items compared to adults.

While our findings reflect the ontogeny of dive behavior in grey seals, we cannot easily distinguish between the effects of age or season in some of our results. For example, increases in depth and duration observed in the first 2 months after the postweaning fast are likely indicative of increased physiological capability or learning, as suggested by early post-departure decrease in interdive interval followed by stabilization throughout the remaining duration of the postweaning dispersal. If the post-dive recovery period (interdive interval) had increased during this time frame, we might expect increases in duration and depth to be a result of seals pushing their physiological limits rather than increasing their physiological capacity. Dive durations exceeded 8 min in only 0.4% of dive records, which is consistent with our expectations of reduced physiological dive capacity in comparison with adults [28, 39, 74]. However, after several months, decreases in benthic diving after an initial peak in the spring may be due to increased foraging efficiency for pelagic prey or to seasonal changes in demersal prey availability. We recognize that in some cases, our data do not allow us to clearly attribute variation in behavior to changes in the environment or to ontogenetic processes.

Diel behavior

Young-of-year grey seals displayed strong diel patterns in diving behavior, performing more benthic dives during daylight hours and more pelagic dives at night, with the crepuscular periods serving as a behavioral transition phase. Diel patterns such as this typically reflect foraging behaviors that track the vertical migration of prey items, such as smaller-bodied sand lance or long-fin squid [116]. Similar diel rhythms in diving frequency or depth are known to occur in other North Atlantic [32, 34] and Baltic sea [117] populations of grey seals as well as other closely related Phocinae species [118] such as harbor seals (*Phoca vitulina*) [119], ringed seals (*Pusa hispida)* [120], and Baikal seals (*Pusa sibirica*) [121]. Pinnipeds have also adapted to foraging under rapidly changing light conditions, often relying on visual cues for hunting at depth [122], and diel behavioral patterns likely reflect responses to the three-dimensional 'lightscape', balancing foraging and resting requirements, as well as predation risk [123, 124]. Diel rhythms of sand lance in the northwestern Atlantic were recently found to be size dependent: while larger size sand lance emerge from the seabed to feed during daylight hours [125], smaller bodied sand lance (< 150 mm) may often be burrowed in sediments during daylight hours [81]. Young-of-year grey seals increased benthic and demersal diving during daylight hours, particularly in the spring, indicating that seals may target smaller bodied sand lance and other demersal prey items that are at or near the benthos during daylight hours.

Implications for offshore wind

The initial months of post-independence are critical for seal physiological and behavioral development. Young-of-year grey seals had the highest probability of overlap with the wind energy planning areas in southern New England and New York Bight during this critical developmental window. Conversely, the probability of overlap with the wind energy planning area during the summer and fall months was negligible. Therefore, we speculate that grey seals born at U.S. natal colonies adjacent to wind areas may be more susceptible to pile driving or other stressors associated with offshore wind development during the first few months after departing the colony than they are in other months. Increased shipping traffic and noise in the marine environment during both the construction and maintenance phases of wind energy development can disrupt functional behavior (e.g., rest) at sea and alter normal behavioral progression even after the noise source has dissipated [126–130]. A recent baseline study of vessel presence in New England offshore wind energy areas revealed that 10–50% of a typical 24-h period contained vessel noise [7]. Construction of offshore wind energy turbines and associated nearshore and onshore infrastructure will further increase sound in the marine environment, the impacts of which are a serious consideration for pinnipeds and other marine species sensitive to anthropogenic noise.

Our dive behavior analysis shows that the benthic environment is important for apparent foraging activities in YOY grey seals. Offshore wind turbine structures have the capacity to alter the trophic structure of the entire water column by providing new habitats for biofiltering species from the splash zone to the seafloor [12–14]. These filter feeders enrich the pelagic and benthic zones via fecal waste, increasing macrofauna density and diversity [16, 131, 132]. Furthermore, metabolic waste deposition can alter sediment grain size and composition, with likely consequences for the behavior and distribution of demersal forage fish species and their predators [13, 16]. The tendency of offshore wind farms to alter benthic habitat and create a reef effect, attracting sedentary, substrate-dependent and mobile marine species, is a serious consideration for benthic forage fish and their predators. In U.S. waters of the northwestern Atlantic, forage fish serving critical ecosystem functions have preferences for habitats within wind energy areas, including sand lance, Atlantic mackerel and Atlantic menhaden [6], which are all important prey species for grey seals and other aquatic life. This could lead to an array of bottom-up impacts on larger predator communities, as sand lances are among the more abundant forage fish linking phytoplankton and zooplankton communities to upper trophic levels [133]. While the reef effect may increase foraging opportunities for marine predators, it might also concentrate foraging behaviors of all predators, increasing inter and intra specific competition. In addition, if offshore wind farms are designated as fishery exclusion zones, the spillover effect may also focus fishing efforts around the perimeter, potentially increasing spatiotemporal overlap with species vulnerable to bycatch, and thus increasing risk of lethal fisheries interactions.

Bycatch risk

The patterns we uncovered in the dive behavior of YOY grey seals can improve risk assessments of fisheries bycatch and inform potential mitigation measures. Among U.S. fisheries, bottom-tending sink gillnet fisheries have the highest numbers of bycaught grey seals [134], and in 2017, the bycatch constituted approximately

14% of the total U.S. pup production [135]. Previous assessments of the encounter risk of grey seals with the sink gillnet fishery considered the spatial and temporal overlap of seal movements with fishing effort but could not factor dive behavior into the assessment due to a lack of data [136]. Our results show that up to 75% of dives on average are at or near the benthos, especially in spring, when the estimated risk of encounter with the gillnet fishery is highest [136]. Knowledge about grey seal behaviors in the vertical dimension can help refine future estimates of risk probability by factoring in time spent on the bottom with estimates of co-occurrence with the fishery. Furthermore, we found that a greater proportion of benthic dives occur during the day than during the night in all seasons and that transitions between day and night dives occur at dusk and dawn. Thus, measures to mitigate bycatch might consider fishing short sets at night to reduce the probability of grey seal entanglement, though operational logistics such as soak time are a consideration for night sets. Short temporal gillnet sets are also used in the Coastal Bottlenose Take Reduction Plan to reduce the potential for dolphin bycatch [137].

Conclusions

Once young-of-year grey seals left sheltered waters adjacent to their natal U.S. rookeries, they dispersed broadly throughout the Northwest Atlantic, primarily within continental shelf waters, though sometimes traversing deep water basins within the Gulf of Maine. Similar to pups in other studies, they embarked on week- to month-long trips spanning thousands of square kilometers, demonstrating an initial exploratory phase followed by behaviors that indicated increased efficiency in foraging. Seals exhibited bimodal diving behavior, shifting their diving behavior according to the diel cycle. Overall, they conducted more benthic or demersal dives during the day and more pelagic dives at night, though this varied ontogenetically and seasonally. Seasonally, benthic diving peaked in mid-April, occurring primarily in foraging hotspots such as Georges Bank and sandy shoals west of the Great South Channel, and appeared to be a preferred diving modality in medium- to coarse-grained sediments. Interestingly, the seasonal spring peak in benthic foraging coincided with the phenology of sand lance, a known prey species. We used horizontal movements together with diving behavior to reveal important foraging habitats for young-of-year grey seals, and to demonstrate spatiotemporal overlap with wind energy planning areas during the critical developmental window, where they must become self-sufficient predators. Furthermore, we revealed spatial and temporal patterns in vertical water column use that might increase risk of bycatch; this in turn can help inform future studies of operational fishing practices designed to reduce seal interactions. This was the first comprehensive study on the horizontal movement and diving behaviors in the U.S. population of grey seals, producing invaluable knowledge on the at-sea movements of a vulnerable demographic in both the horizontal and vertical dimensions. This information will serve as valuable input to management and mitigation plans and contributes necessary regional context to the broader understanding of the ontogeny in grey seals across the North Atlantic.

Abbreviations

YOY	Young-of-year
SSM	State-space model
PWC	Proportion of the water column reached at the maximum diving depth
SRDL	Satellite relay data logger

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-025-00405-5.

Additional file 1.

Additional file 2.

Additional file 3.

Additional file 4.

Acknowledgements

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Author contributions

Conceptualization: E.I.H. and K.T.M. Methodology: E.I.H., K.T.M., and D.B.S. Formal analysis: E.I.H. Investigation and interpretation: E.I.H. and K.T.M. Resources: K.T.M., R.A.D., and L.D. Data curation: E.I.H. and K.T.M. Data collection: K.T.M., L.D., and R.A.D. Writing—original draft: E.I.H. and K.T.M. Writing—review and editing: E.I.H., K.T.M., D.B.S., R.A.D., and L.D. Supervision: K.T.M. Project administration: K.T.M., R.A.D., and L.D. Funding acquisition: K.T.M. and R.A.D.

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Availability of data and materials

The grey seal telemetry data set generated during the current study is available from the corresponding author on reasonable request. All

R code used to conduct the analysis is available at the public GitHub repository: https://github.com/NEFSC/PSD-CEB-EHeywood-MS1. Bathymetric data at 15-arcsecond resolution is available via query in R library marmap: bathy = marmap::getNOAA.bathy(lon1 = min(data$lon)-0.5, lon2 = max(data$lon) + 0.5, lat1 = min(data$lat)-0.5, lat2 = max(data$lat) + 0.5, resolution = 0.25) This queries the ETOPO 2022 database hosted on the NOAA website: https://www.ncei.noaa.gov/products/etopo-global-relief-model. High resolution land and minor island polygons used in the analysis are available at: https://www.naturalearthdata.com/downloads/10m-physical-vectors/. Bureau of Ocean Energy Management (BOEM) wind energy lease outlines and proposed cable routes are available at: https://boem-metaport-boem.hub.arcgis.com/datasets/BOEM::offshore-wind-lease-outlines/about. https://boem-metaport-boem.hub.arcgis.com/datasets/BOEM::offshore-wind-export-cable-corridors-proposed/about.

Declarations

Ethics approval and consent to participate

All animal capture and tagging procedures were authorized under the Marine Mammal Protection Act Research Permit #21719 issued to the Northeast Fisheries Science Center, Institutional Animal Care and Use Committee (IACUC) protocol #Atlantic IACUC-2018-004, and USFWS Special Use permits #53514-19-01, #53514-20-01, and #53510-FY2022-01.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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