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Indications of mesopelagic foraging by a small odontocete

Nynne H. Nielsen[1,2] · Jonas Teilmann[2] · Mads Peter Heide-Jørgensen[1]

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Abstract

The mesopelagic layer is represented in all oceans and is of crucial importance to the pelagic communities, and in this paper it is hypothesised that the Greenlandic harbour porpoise (*Phocoena phocoena*) is seasonally dependent on mesopelagic prey when abandoning the ice-covered continental shelf areas and remains in offshore areas. Data from 15 harbour porpoises instrumented with satellite-linked transmitters in West Greenland were analysed with regard to foraging that may target mesopelagic prey. Contact with the porpoises was maintained for an average of 404 days where they conducted extensive offshore movements and spent an average of 90% of their time over deep waters (> 1000 m) in the North Atlantic. When entering deep water, they increased their daily travel rate significantly from 22.5 to 36.7 km d^{-1}. Five of the 15 porpoises provided information on dive depth which suggested that dive depths > 100 m are important for these porpoises both day and night; however, the porpoises dove significantly more at nighttime compared to daytime. Harbour porpoises from West Greenland probably target vertically migrating species from the mesopelagic layer that are accessible at shallower depths at night and at lower energetic cost than during the day.

Introduction

The mesopelagic layer (200–2000 m) is found in all oceans and is of great importance to the global biological pump that transports dissolved organic carbon (DOC) material from the epipelagic layer (0–200 m) to the deep interior of the ocean (Volk and Hoffert 1985; Klevjer et al. 2016). Even though there is insufficient light in the mesopelagic layer to perform photosynthesis, the transportation of DOC sustains a high productivity that holds some of the oceans' largest fish biomasses (Radchenko 2007; Kaartvedt et al. 2012; Irigoien et al. 2014). The mesopelagic organisms are utilised by a variety of top predators, such as fish, cephalopods and marine mammals (Baird et al. 2001; Bertrand et al. 2002; Watwood et al. 2006; Doksæter et al. 2008). One of the most abundant groups of the mesopelagic layer, the lantern fish or Myctophidae, make extensive upward migration into the epipelagic zone during the night, followed by return migrations down to several hundred meters to reach their daytime depths (Pearcy and Laurs 1966; Gjøsaeter and Kawaguchi 1980; Sameoto 1988, 1989; Catul et al. 2011). Such vertical migrations are hypothesised to maximise feeding success while reducing the risk of predation by visual hunting predators that inhabit shallower waters such as birds, fish and marine mammals (Heywood 1996; Luo et al. 2000; Hays 2003).

In recent years, the importance of top predators in a healthy ecosystem has obtained more recognition (Block et al. 2011; Estes et al. 2011). In the ocean, the largest top predators are often cetaceans; however, they are challenging to study in offshore habitats. One way of gaining knowledge on these ocean dwellers is by instrumenting them with satellite-linked radio transmitters and data loggers that can provide information on movement and dive behaviour in relation to foraging (Sveegaard et al. 2011; 2012, Linnenschmidt et al. 2013; Heide-Jørgensen et al. 2015; Wisniewska et al. 2016; Nielsen et al. 2018).

Harbour porpoises are among the smallest odontocetes and are distributed widely in coastal areas around the

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✉ Nynne H. Nielsen
nel@ghsdk.dk

[1] Department of Birds and Mammals, Greenland Institute of Natural Resources, Box 570, 3900 Nuuk, Greenland

[2] Marine Mammal Research, Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark

Northern Hemisphere. They are primarily associated with the continental shelf (depth < 200 m) (Read and Westgate 1997; Read 1999), and data from tagged porpoises indicate that they dive to a mean depth < 30 m (Westgate et al. 1995; Otani et al. 1998, 2000; Teilmann et al. 2007). Harbour porpoises have also been detected in offshore areas outside the continental shelf (Read et al. 1996; Friday et al. 2013; Hansen and Heide-Jørgensen 2013; Stenson et al. 2011; Hammond et al. 2017) and a recent study of harbour porpoises from West Greenland documented long-term offshore movements during winter, followed by a return to the shelf area and site fidelity to the areas where they were tagged (Nielsen et al. 2018).

Porpoises have high metabolic rates (Lockyer 2007; Rojano-Doñate et al. 2018a, b) and are observed to forage almost continuously in the Danish waters (Wisniewska et al. 2016). However, it has been debated how general these findings may be for porpoises in other areas, but regardless, there is little doubt that porpoises can be categorised as high-intensity foragers (Wisniewska et al. 2016, 2018; Hoekendijk et al. 2018).

Information on porpoise diet from either stranded, bycaught or hunted animals show that porpoise prey on a wide variety of species with large geographical variation in prey preference; however, in most areas the prey is locally dominated by few species (Lockyer et al. 2003; Santos and Pierce 2003; Leopold 2015). Andreasen et al. (2017) identify more than 30 different prey species eaten by porpoises in the inner Danish water/western Baltic Sea. Their findings reflected a benthic or coastal diet with the three main prey items being gobies (*Gobiidae*), Atlantic herring (*Clupea harengus*) and Atlantic cod (*Gadus morhua*). Around Iceland, the main diet of porpoises is capelin (*Mallotus villosus*) and sandeel (*Ammodytidae*), but more than 40 other prey species have been identified (Víkingsson et al. 2003). On the continental shelf of West Greenland, the main diet is pelagic with three main species: capelin, Arctic cod (*Boreogadus saida*) and unidentified species of cephalopods; however, a total of 24 species have been found (Heide-Jørgensen et al. 2011). In the Bay of Fundy, Recchia and Read (1989) identified 11 prey species, but found Atlantic herring to be the most important species.

In this study, data from 15 harbour porpoises instrumented with satellite-linked transmitters in summer in West Greenland were used to gain insight into their offshore winter foraging. It is hypothesised that when leaving the continental shelf, harbour porpoises from West Greenland are capable of utilising prey species of the mesopelagic layer to fulfil their high energetic demand.

Materials and methods

Capture, handling and instrumentation of harbour porpoises

Harbour porpoises were live-captured on the continental shelf approximately 50 km south-west of Maniitsoq (Fig. 1), West Greenland, between 2012 and 2014. The porpoises were captured in a surface-set gill net following a short period (15–20 min) of herding by small boats into the net, where animals were quickly freed and lifted on board for measurements and tagging (about 5 min) (see Nielsen et al. 2018, for a detailed description of the capturing, handling and deployment).

The animals were instrumented with one of three types of Argos satellite-linked transmitters; SPLASH: 80 × 19 × 49 mm 76 g, Mk10: 108 × 41 × 21 mm 75 g, and SPOT5 tags: 81 × 19 × 51 mm 49 g [LxWxH]), all manufactured by Wildlife Computers (Redmond, WA, USA).

Data analysis

All 15 tags (Table 1) provided positions through the Argos Data Collection and Location System, and the quality of the locations was determined based on the number of uplinks and predicted accuracy by Argos. The data were decoded using Argos Message Decoder (DAP version 3.0, build 114, Wildlife Computers) and the positions were analysed using the freeware QGIS (version 10.2). The Argos positions were filtered using the package “argosfilter” (Freitas et al. 2008) by R (version 3.3.3., R Development Core Team 2008) and one daily average of location classes 1–3 was subsequently used for days of transmission when analysing movement and travel rate. Statistical analysis of travel rate was done in XLSTAT (version 2014.1.01).

Five tags (two SPLASH and three Mk10) transmitted additional information on dive depth (DD) and time at depth (TAD). This information was sampled at a default rate of once every second and stored in 6-h summary histograms (01:00–07:00, 07:00–13:00, 13:00–19:00 and 19:00–01:00 h), and relayed to the satellites during the following 24 h. In addition, the SPLASH tags also recorded the maximum dive depth during the past 24 h. The 6-h histograms of DD and TAD were binned according to 14 user-defined intervals. The first tags (SPLASH, deployed in 2012) were programmed following previous tag programming used on porpoises in Danish waters (Teilmann et al. 2007). Thus, the TAD intervals reflect their settings of 0 m, 2 m, 5 m, 10 m, 15 m, 20 m, 25, 30 m, 40 m, 50 m,

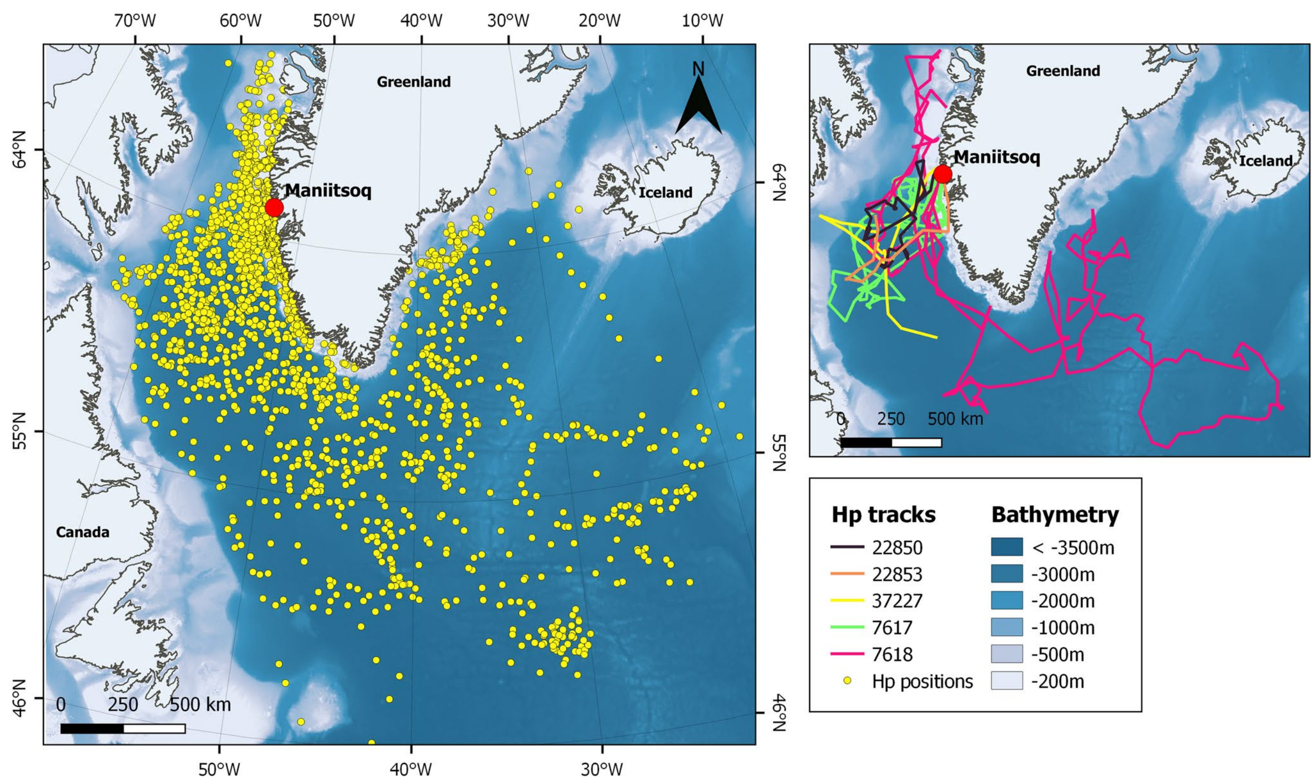

Fig. 1 Left: map of one daily filtered position for each of the 15 harbour porpoises (yellow dots) instrumented with satellite transmitters near Maniitsoq, West Greenland (red dot). Right: map of the filtered movement tracks of five porpoises which gave information on time at depth and dive depth. The five individual tracks are individually colour coded

60 m, 70 m, 80 m and > 80 m. The DD intervals were of 0 m, 5 m, 10 m, 15 m, 20 m, 25 m, 30 m, 40 m, 50 m, 60 m, 70 m, 80 m and > 80 m. Dives shallower than 4 m were ignored.

The Mk10 transmitters were deployed after the SPLASH tags and thus the intervals for the binned data were changed after it became obvious that the dives exceeded the maximum bin setting for the SPLASH tags. The intervals for TAD were 0 m, 2 m, 25 m, 50 m, 100 m, 150 m, 200, 250 m, 300 m, 350 m, 400 m, 450 m, 500 m and > 500 m, and for the DD the intervals were of 5 m, 10 m, 25 m, 50 m, 100 m, 150 m, 200 m, 250 m, 300 m, 350 m, 400 m, 450 m, 500 m and > 500 m. The statistical analysis of DD and TAD was done in XLSTAT and R (R development Team 2008). To compare the diurnal dive behaviour, information on sunrise and sunset (according to the almanac provided by the Danish Society of Astronomy, Table S1) was assigned for the area and the days with data from the tags. The daily 6-h binned time intervals for each month was fitted to the mean almanac time of the same month. Each time interval thus got assigned the event "night" or "day" according to the month of the year and the almanac data. Obviously, the binned time intervals did not match the almanac data throughout the year. Therefore, it was decided to assign the event according to the majority of time spent within the almanac hours, meaning that the dive behaviour in the interval 13:00–19:00 h, in January, was assigned the event "night", since the mean sunrise and sunset in January was between 08:30 and 15:22 h. This inaccurate assignment provides an approximation of the relationship between the dive behaviour and time of day.

Results

Fifteen harbour porpoises were tracked with satellite transmitter for a mean duration of 404 days (range 29–1047 days, SD = 323.9, Fig. 1, Table 1). All porpoises moved away from the coastal areas of West Greenland and into deeper water (> 1000 m) between 15 July and 20 January. Six of the 15 porpoises returned within 100 km of the shelf areas of Greenland, between 25 June and 9 August, after a mean duration of 360 days in areas with deep water > 1000 m (range 209–710 days, SD = 171.6). Here, they increased their mean travel rate significantly from a mean of 27.3 km d^{-1} (SD = 15.12) on the continental shelf to a mean of 38.2 km d^{-1} (SD = 7.83, paired t test, t 2.05, $P = 0.02$) in deep water areas.

Table 1 Data from 15 harbour porpoises tagged in West Greenland

							Porpoise behaviour in deep waters (> 1000 m)				Porpoise behaviour in waters < 1000 m			
PttID	Type	Deployment date	End of the transmission	Return to West Greenland	Tag longevity (days)	Sex	Arrival	Departure	Duration (days)	Mean travel rate (km d^{-1})	Maximum dive depth	Duration (days)	Mean travel rate (km d^{-1})	Maximum dive depth
7617	SPLASH	25-Jul-12	13-Nov-13	09-Aug-13	476	F	28-Jul-12	07-Aug-13	375	36.1 (±25.18)	390	101	15.6 (±14.78)	382
7618	SPLASH	25-Jul-12	20-Sep-13	24-Jul-13	422	F	30-Jul-12	22-Jul-13	357	40 7 (±24 64)	410	65	43.0 (±27.11)	410
22850	MK10	03-Oct-13	13-Dec-13		71	F	08-Oct-13	13-Dec-13[b]	66	29.4 (±25.18)	250[c]	5	49.0 (±20.81)	200[c]
22853	MK10	25-Sep-13	24-Oct-13		29	F	02-Oct-13	24-Oct-13[b]	22	40.0 (±19.95)	250[c]	7	52.4 (±27.09)	300[c]
37227	MK10	02-Oct-13	17-Nov-13		46	F	06-Oct-13	17-Nov-13[b]	42	38.7 (±25.11)	150[c]	4	57.0 (±21.82)	100[c]
20160	SPOT 5	07-Jul-13	07-Mar-14		243	M	25-Dec-13	07-Mar-14[b]	72	41.2 (±24.82)	NA	171	24.2 (±21.97)	NA
20164	SPOT 5	07-Jul-13	18-Jul-14	02-Jul-14	376	F	19-Nov-13	29-Jun-14	222	40.7 (±25.39)	NA	154	16.0 (±17.30)	NA
20165	SPOT 5	10-Jul-13	07-Aug-14	07-Aug-14[‡]	393	F	16-Jul-13	07-Aug-14	387	34.5 (±25.48)	NA	6	24.8 (±20.93)	NA
20166	SPOT 5	07-Jul-13	19-Feb-14		227	M	03-Aug-13	19-Feb-14[b]	200	50.0 (±21.01)	NA	27	21.7 (±16.59)	NA
20167	SPOT 5	10-Jul-13	03-Dec-13		146	F	15-Jul-13	03-Dec-13[b]	132	38.0 (±16.60)	NA	14	26.5 (±18.72)	NA
20169	SPOT 5	06-Jul-13	31-Mar-14		268	M	19-Dec-13	31-Mar-14[b]	102	57.6 (±24.82)	NA	166	17.1 (±17.11)	NA
21791	SPOT 5	16-Jul-14	25-Apr-16	25-Jun-15[d]	649	F	28-Nov-H	25-Apr-16[b]	514	33.1 (±23.12)	NA	135	16.7 (±15.46)	NA
21792	SPOT 5	30-Jul-14	11-Jun-17	05-Aug-16[a]	1047	M	26-Aug-14	11-Jun-17[b]	1020	33.0 (±25.31)	NA	27	16.1 (±13.91)	NA
372271	SPOT 5	11-Jul-14	29-Mar-16		627	M	20-Jan-15	20-Oct-15	273	26.0 (±20.97)	NA	354	12.8 (±14.32)	NA
372281	SPOTS	18-M-14	26-Mar-17		1043	M	26-Nov-H	26-May-17[b]	912	33.8 (±23.62)	NA	131	17.0 (±20.36)	NA

±SD is in parentheses

[a]A transmitter that ended > 100 km from the West Greenland shelf

[b]The end of transmissions

[c]The maximum dive depth from the binned dive depth

[d]Porpoises that returned to the shelf areas of West Greenland followed by a second return to the deep water areas. No dive information was obtained from the SPOT 5 tags

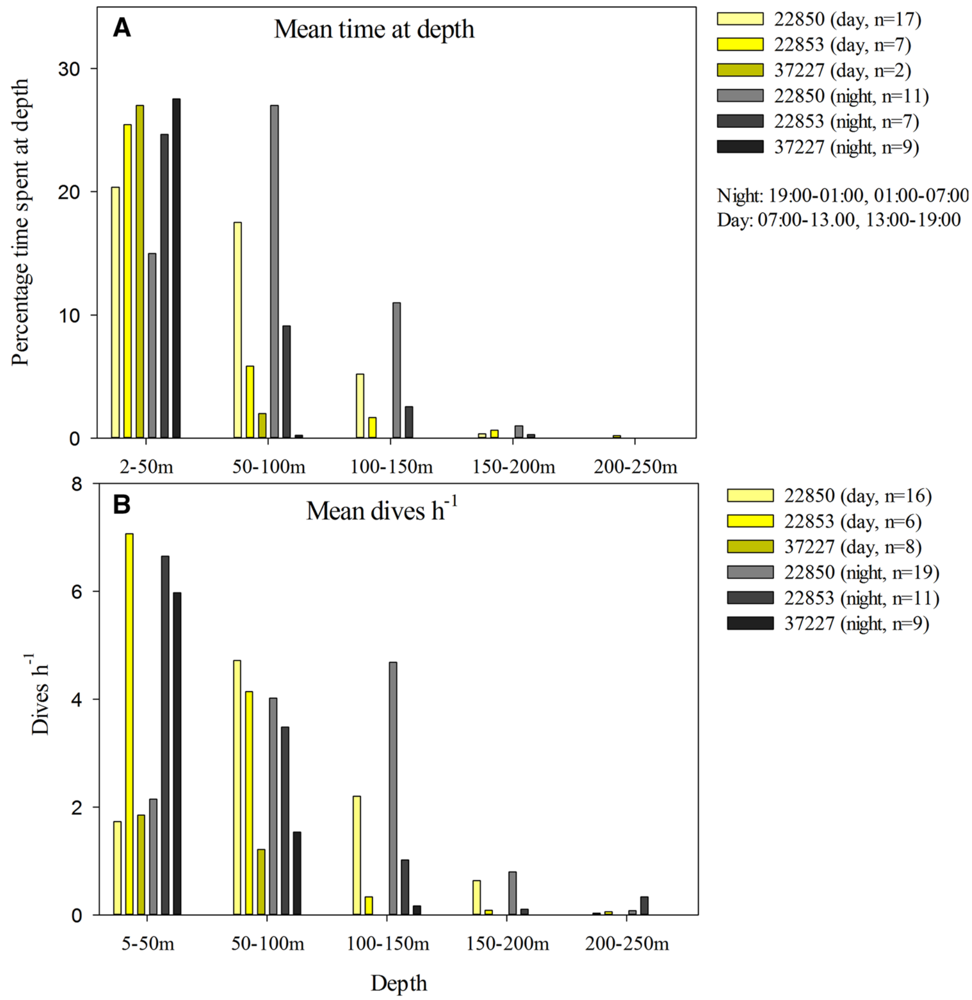

Fig. 2 **a** The mean time (%) each porpoise (PttID) spent at each binned depth during day (yellow scale) and night (grey scale). **b** The mean number of dives h^{-1} at each binned depth during day and night. Determination of night and day was done according to the local almanac data. *N* equals the number of data points (each data point represents 6 h of collected data)

Five of the 15 transmitters (Fig. 1, Table 1) provided information on diving behaviour, TAD (percentage time spend at pre-defined depth intervals) and DD (number of dives h^{-1} to pre-defined depth intervals). Three of these (Mk10: PttID 22,850, 22853 and 37227, Figs. 1, 2a, b, Table 1) were present in deep water areas for a mean of 49 days (range 29–71 days, SD = 21.1) before the transmissions ended.

When analysing each of the three porpoises, there was a significant difference in the time spent day and night by porpoise PttID 22850 (Kruskal–Wallis test, $H1 = 6.33/4.23$, $P < 0.05$). It spent significantly more time (mean 18.6%) at 50–100 m and 100–150 m, respectively, at nighttime compared to daytime (mean 11.3%) (two-sided Dunn's test $P < 0.0001$). When combining TAD data from all three porpoises, there were no overall significant differences in diurnal TAD (Kruskal–Wallis test, $H4$, $P > 0.5$), thus these data were merged prior to analysing the time spent at different depth bins. There was a significant difference in the TAD (Kruskal–Wallis test, $H4 = 97.7$, $P < 0.0001$) and they spent significantly more time (mean 17.6%) in the two lowest depth bins (2–50 m, 50–100 m) (two-sided Dunn´s test $P < 0.05$). The three porpoises spent a mean 2.3% of their time diving to the remaining three depth bins (100–150 m, 150–200 m, 200–225 m).

There was an overall significant difference in mean DD h^{-1} between day (1.6 dives h^{-1}) and night (2.1 dives h^{-1}) when combining DD data from all three animals (Kruskal–Wallis test, $H4 = 157.8$, $P < 0.0001$). At nighttime, the three porpoises dove significantly more frequently to the shallowest depth bin (5–50 m, mean 4.3 dives h^{-1}) and the third deepest depth bin (100–150 m, mean 2.6 dives h^{-1}, two-sided Dunn's test $P < 0.001$). The porpoises performed on average more dives to the two deepest depth bins (150–200 m, 200–250 m) at nighttime (0.23 dives h^{-1}) compared to daytime (0.19 dives h^{-1}), but this was not significant.

The two remaining porpoises transmitting dive data (SPLASH, PttID 7617 and 7618, Fig. 3) provided information on daily maximum dive depth (within the previous 24 h) for 375 and 357 days, respectively. Their mean daily maximum dive depth in deep water areas was on average 217 m (range 128–390 m, SD = 59.5) and 262 m (range 114–410 m, SD = 64.4), respectively. When present in deep water areas,

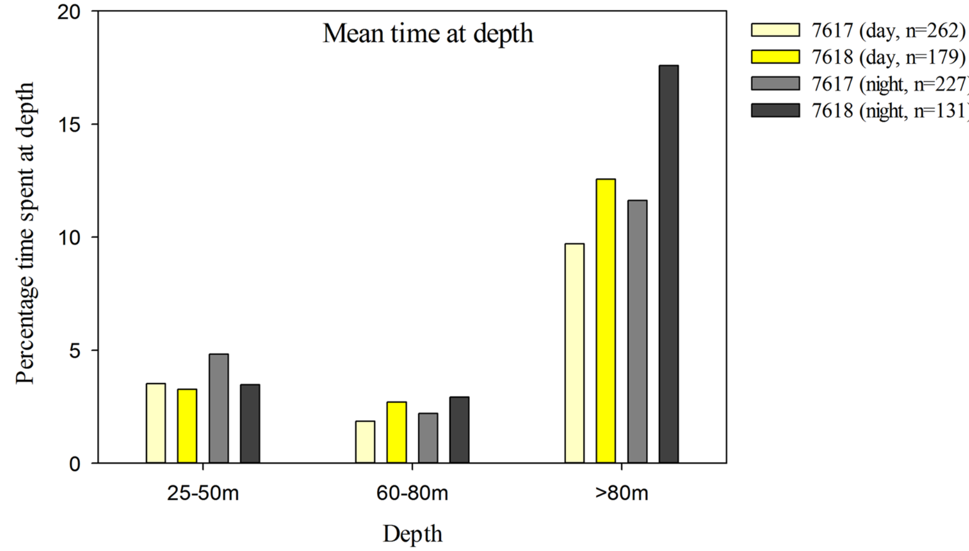

Fig. 3 The mean time tagged porpoises spent (%) in each depth bin during day and night. *N* equals the number of data points (each data point represents 6 h of collected data)

they made daily maximum dives ≥ 200 m during 61% and 88% of the time, respectively, and spent significantly more time in the greatest depth bin (> 80 m) compared to the shallower bins (Kruskal–Wallis test, $H_{13} = 22.36$, $P < 0.0001$).

During daytime, PttID 7618 dove significantly more in depth bins 25–50 m (ANOVA, F (1,1321) = 5.64 $P < 0.05$) and 50–80 m (F (1,1762) = 59.4 $P < 0.0001$, Fig. 3) compared to PttID 7617, but in depth bins > 80 m there was no difference ($P = 0.08$). At nighttime, PttID 7618 dove significantly more at depth bin > 80 m (ANOVA, F (1356) = 13.1 $P < 0.001$) compared to bin 25–50 m ($P = 0.082$) and 50–80 m ($P = 0.20$).

Discussion

Understanding the importance and biodiversity of the mesopelagic community has been the subject of numerous studies since its rather coincidental discovery nearly 70 years ago (Hersey et al. 1952). The billions of tons of biomass representing the vertically migrating species of the mesopelagic zone has been referred to as the "largest daily migration of animals on earth" (Hays 2003; van Haren and Compton 2013) and provide a major link in the food chain between microscopic plankton and top predators such as cetaceans and other mega fauna.

Instrumentation with satellite-linked transmitters is one approach for understanding this link, and has over the past two decades provided insight into how cetaceans utilise the environment (Laidre et al. 2003; Sveegaard et al. 2012; Heide-Jørgensen et al. 2014; Nielsen et al. 2015; Watt et al. 2017; Nielsen et al. 2018). This study provides new information on deep ocean diving behaviour of a small top predator, the harbour porpoise. Porpoises have high energetic demands which likely requires that they maintain an intensive pace of foraging behaviour (Wisniewska et al. 2016; Rojano-Doñate et al. 2018a). Moving to areas with predictable prey availability is a way of ensuring minimal energetic costs to maintain basic metabolism and blubber insulation. The porpoises in this study moved from subarctic cold water into temperate deep waters where they spent nearly 90% of the tag deployment period (average > 300 days), suggesting this is an important foraging area. Here, they likely locate high densities of prey from the mesopelagic layer at night, such as species of the Myctophidae family that are known to perform diel vertical migrations between the meso- and epipelagic regions (Catul et al. 2011). During daytimes, offshore harbour porpoises are dependent on locating prey that do not perform vertical migrations and live closer to the surface, or wait until the night to resume feeding. However, due to limited data on potentially epipelagic prey species within the area used by the tagged offshore harbour porpoises, it is not possible to identify the potential prey items utilised during the daytime.

When entering the deep water area, the porpoises more than doubled their travel rate compared to the coastal summering grounds. This may reflect more dispersed prey distribution or prey fields moving with the currents, which may require a larger search effort for the porpoises in the offshore areas. A less likely explanation, given the large biomass of mesopelagic prey, is that the increased travel rate is due to competition for food between harbour porpoises and other predators like dolphin (Spitz et al. 2006).

The three porpoises instrumented with Mk10 transmitters spent the majority of their time (%), day and night, between 2 and 100 m, but the number of dives per hour at night was higher. This suggests that depths > 100 m are important for the porpoises both day and night, but that they dive (and probably forage) more frequently at night. The ascent of species from the mesopelagic layer might increase the prey potential for the porpoises which they could utilise at night.

This agrees with Westgate et al. (1995) who found that porpoises from the Bay of Fundy dove more frequently at night than at day.

Due to the bin settings of the PttID 7617 and 7618, it is difficult to compare the data to the Mk10 transmitters. However, individuals PttID 7617 and 7618 spent large proportions of dives at depths > 80 m (the highest bin), and combined with the large proportion of maximum dive depths ≥ 200 m, these porpoises may have targeted the vertically migrating community of the mesopelagic layer. This means that porpoises could potentially target species of this family during night, which is also supported by observations of *Myctophidae* sp., in harbour porpoise stomachs from offshore bycaught animals (Read et al. 1996) and from porpoises on the continental shelf in West Greenland (Heide-Jørgensen et al. 2011). A trend towards more dive activity at dawn has been suggested for tagged porpoises by Teilmann et al. (2007). Data from the present study do not have sufficient resolution to reveal the relationship between dive behaviour and light pattern for offshore porpoises from West Greenland.

It is clear that harbour porpoises in West Greenland deviate from other harbour porpoise populations. Their dive activity most likely reflects a more fluctuating prey abundance compared to other porpoise populations that do not move into deep waters > 1000 m. During winter months, harbour porpoises tagged in West Greenland abandoned the ice-covered continental shelf areas and travelled to offshore areas (Nielsen et al. 2018) where prey probably is more scattered. When the porpoises move into offshore areas, they likely rely on a regular consumption of energy-rich prey, such as myctophid fishes, as also supported by the dive depth registered in this study.

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Data availability statement The datasets analysed during the current study are not publicly available due to continuous analyses on parts of the dataset, but are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no actual or potential conflicts of interest in relation to this work.

Ethical approval All work presented here complies with the current laws of the country in which they were performed (Greenland).

Research involving animals The tagging of harbour porpoises in this study was performed with permission from the Government of Greenland, permit no. 2012-069733, Doc. 1265044.

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